Horticultural Reviews

VOLUME 41

WILEY Blackwell

HORTICULTURAL REVIEWS
Volume 41

Horticultural Reviews is sponsored by:

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HORTICULTURAL REVIEWS

Volume 41

edited by
Jules Janick
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WILEY Blackwell

A John Wiley & Sons, Inc., Publication

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Published by John Wiley & Sons, Inc., Hoboken, New Jersey

Published simultaneously in Canada

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***Library of Congress Cataloging-in-Publication Data*:**

ISBN 978-1-118-70737-1 (cloth)

ISSN 0163-7851

Printed in the United States of America

10 9 8 7 6 5 4 3 2 1

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Philipp W. Simon

Dedication: Philipp W. Simon

This volume is dedicated to Dr. Philipp Simon, plant breeder and geneticist, in recognition of his outstanding contributions to horticulture and vegetable crops. Dr. Simon, a leading world authority in carrot and garlic improvement, is a role model for what can be accomplished in vegetable breeding.

Philipp Simon was born and raised in Door County, Wisconsin, in 1950. He attended Carroll College in Waukesha, Wisconsin, where he graduated with a B.S. in Biology in 1972. While a college student, he read books on the subject of plant-based medicine and this influenced him to consider a career in biology and plant science. He enrolled at the University of Wisconsin-Madison and completed his M.S. in Genetics in 1975, working with Professor Stanley Peloquin. Simon's dissertation work focused on pollen vigor as a function of 2*n* gamete formation in that crop and the influence of the paternal parent on the origin of callus in anther culture of *Solanum* hybrids. Simon completed his Ph.D. in Genetics in 1977 and assumed the role of Research Geneticist and Adjunct Professor at Madison in 1978. He was promoted to Assistant Professor in 1980, Associate Professor in 1985, and Professor in 1990. Simon is presently the Research Leader for the Vegetable and Cranberry Research Unit of the U.S. Department of Agriculture-Agricultural Research Service and a breeder of carrot, garlic, and other vegetable crops. For more than 30 years, Simon has been a primary contributor to both national efforts in carrot and garlic improvement as well as local efforts at teaching, graduate student training, and mentoring in the fields of plant breeding and plant genetics. Simon's contributions in these areas have shaped the development of these crops globally and had many positive downstream effects on consumers. The genesis of Simon's interest in crop improvement for nutritional quality is a focus on consumer-driven traits in plants, though over the decades his work has served the seed industry as well as farmers and consumers.

I. CARROT

The U.S. carrot crop has a farm value of $530 million annually, making it one of the most valuable U.S. vegetable crops. To date, as with many important food crops in the United States, the great majority of carrot breeding activity is in the private sector. The carrot seed industry is represented by approximately two dozen seed companies, many of whom have a global reach. Throughout this period, the USDA program run by Simon has been a critical contributor to technologies for the inbred-hybrid industry programs, new sources of germplasm for carrot breeding, and analysis of important carrot quality traits. Carrot breeding programs exist in several European countries, as well as in China, Korea, and Brazil, and these have also benefited from germplasm resources and data developed by the USDA program. During a career spanning more than 30 years, Simon's primary foci in carrot have stressed determination of inheritance patterns of sugar, volatile terpenoid, carotene, and anthocyanin accumulation; development of genetic markers, maps, and genomic tools; description of transposable elements; and development of elite genetic stocks.

Knowledge of the flavor genetics of carrot is quite extensive and is attributable largely to the efforts of Philipp Simon and coworkers. Simon's first papers as a faculty member at UW-Madison included studies of the genetic and environmental components of carrot culinary and nutritive value and investigations of sensory and objective parameters of carrot flavor. His work has led to fairly routine procedures for sensory analysis and has helped breeders develop carrot germplasm with improved flavor. Among many discoveries, Simon determined that genetic variation exists for raw carrot flavor, that volatile flavor chemicals are quantitatively inherited, and that genetic variation for total volatile terpenoid levels and sugars account for most of the observed variation in sweetness and flavor preference of raw carrots. Many of the papers published from Simon's group during this period focused on the impact of the horticultural environment on carrot flavor. Research by Simon and students demonstrated patterns of inheritance for sugars stored in carrot roots. Together with student Roger Freeman, Simon found that the balance of reducing sugars to sucrose is controlled by the *Rs* (Reducing sugar) locus, which was discovered and characterized as a naturally occurring "knockout mutant" conditioned by a 2.5 kb insertion in the soluble invertase isozyme II gene.

These discoveries helped direct carrot breeders to focus on terpenoids for off-flavors and harsh flavors and on sugars for sweetness. Carrot germplasm released by Simon's program has improved sweet and

mild flavor and higher nutritional value than releases from prior decades. For example, inbred lines B9304 and B2566 are sweet, mild, and succulent (Simon et al. 1987). Germplasm developed by Simon is being widely used by commercial vegetable seed companies, and therefore it is a constituent component to fresh market carrots consumed in the U.S.

Simon and his collaborators and students have spent considerable effort developing a carrot genetic linkage map. To date, this map includes some 500 molecular markers and a number of phenotypic markers for nematode resistance, root pigments, and sugar type. Specific AFLP markers linked to important or interesting phenotypic genes have been converted to more easily evaluated codominant PCR-based markers. These maps have become fundamental tools for carrot geneticists and breeders. Seed companies use markers developed in the Simon laboratory to select for two difficult-to-score traits such as nematode resistance (*Mj-1*) and sugar type (*Rs*). Recently, Simon and colleague David Spooner have employed some of these markers to begin work clarifying the taxonomy of the genus *Daucus*.

Simon also developed molecular markers to identify and differentiate among male fertile carrots and the two major forms of male sterile cytoplasm conditioned by the mitochondrial genome. Molecular markers for the nuclear genome were then used to identify inbred parents and predict their hybrid patterns. A plastid marker was unexpectedly discovered by Simon within *Daucus carota* and used to confirm strict maternal inheritance of this organelle. A transposable element was also unexpectedly discovered, and has been used to develop molecular markers for general mapping and genome assessment. The molecular markers developed by Simon have accelerated the selection process of carrot breeding so that differentiation of male sterile and male fertile plants can be accomplished early in plant growth. This allows removal of undesired male fertile plants long before they flower.

Carrot contains high levels of certain carotenoids such as beta-carotene and alpha-carotene. These molecules are cleaved during digestion and turned into retinol, which is also known as vitamin A. The carotenoid molecules are also called provitamin A carotenoids for this reason. The situation for carrot root pigmentation is fortuitous, as higher levels of provitamin A carotenoids lead to both improved vitamin A delivery and deeper orange colors, which are also preferred by consumers. The appearance of orange carotenoids in carrot roots became widespread in the 17th century. Prior to this period, carrot roots were predominately purple and yellow, where the purple pigmentation

was due to anthocyanin and the yellow to xanthophylls, which are oxygenated carotenoids.

High carotene carrot germplasm released by Simon's program has been an important contributor to improved provitamin A levels of U.S. carrots over the past 40 years. Estimates suggest that these levels have increased by >40% since the 1970s. In addition, improved carotene levels in carrot have stimulated interest in carrot production as a source of provitamin A carotenoids in vitamin A-deficient areas of the world. Simon has worked in Haiti and other countries where vitamin A deficiencies are an important public health problem leading to childhood blindness. He and his colleagues developed the carrot cultivar 'BETA III' to help alleviate vitamin A deficiency, which was tested in 44 developing countries. Carrot trials have also been established in Philippines, India, Guatemala, Nepal, and Haiti. To date, the average carotene content of U.S. carrots is 130 ppm and per capita U.S. carrot consumption is 5.4 kg per annum.

Simon, working with nematologists, identified a major dominant gene, *Mj-1*, which conditions resistance to Javanese root-knot nematode, *Meloidogyne javanica*, a major pest in California carrot-producing regions. The *Mj-1* resistance gene also imparts resistance to *M. incognita*, another major nematode pest in carrot-producing regions. The nematode resistance revealed by this research may have significant impact in the major carrot-producing regions to reduce the need for nematicide application, which is expensive and poses significant environmental risks. Genetic resistance is being actively incorporated into new carrot breeding lines by seed companies using marker-facilitated selection and is appearing in advanced hybrids. Simon's work also demonstrated a genetic component to *Alternaria* leaf blight resistance and initiated germplasm development for carrot breeders. Simon and colleagues developed a method for screening bacterial soft rot resistance that has been used with some success in Europe, where it is a significant storage disease.

Simon's research has demonstrated relatively simple patterns of inheritance for certain aspects of carrot root carotene and anthocyanin accumulation. He has also shown a pattern of clustered quantitative trait loci conditioning the major provitamin A carotenes and lycopene. Knowledge of carrot pigment genetics is being used to improve commercial carrot germplasm for nutritional quality and to develop unique colors (including purple, red, yellow, and white) by several seed companies. Simon's program also released the first "new" carrot root color (purple) for modern use in 1992, with the release of a purple-rooted inbred line.

Interestingly, the first domesticated carrot roots were purple, and the crop remained purple-rooted for many centuries. Purple pigmentation of roots continued in parts of Asia and the Middle East but was largely lost in Europe and North America until very recently. To date, purple root pigmentation has made a comeback in carrot. Working with graduate student John Navazio, Simon also incorporated genes for orange fruit flesh color into U.S. pickling cucumbers and released the first U.S. orange cucumber.

II. GARLIC

Garlic is very important in the United States and worldwide. To date, global production of garlic exceeds 3 million tonnes with a value of $50 million to U.S. growers. Garlic production has been known for at least 5,000 years but, remarkably, routine seed production has never been reported for this crop. It is unclear if garlic has simply lost the ability to produce seed through genetic drift over millennia. Therefore, in spite of its long history, little is known about the genetic variation for this important world crop. No reports of true seed production in garlic can be found prior to 1950, and very little information has accumulated since that time. Working with a graduate student Margaret Pooler, Simon developed the first true seed production system for garlic in the United States and transferred this technology to the garlic industry so that garlic breeding and routine seed production is feasible for the first time. This work initially made use of controlled environment production in combination with certain garlic clones. To data, millions of garlic seed have been produced. Thus, for the first time in history garlic has been transformed from a strictly asexually propagated crop to one where classical plant breeding is now possible. A similar effort to develop garlic seed production was also independently undertaken in Japan. The availability of true garlic seed provided the basis for establishing the first genetic linkage map for garlic. Part of the successes of these projects resulted from the observation that bulbils in garlic inflorescences compete with developing seed, so routine bulbil removal was performed in early generations of garlic selected for seed production. The recognition and utilization of garlic's broad genetic base was an important component of the success of true seed production, since it was germplasm from close to the center of diversity for garlic in Central Asia, that contributed most significantly to the success in producing garlic seed.

III. TEACHING, TRAINING, AND MENTORING

For many years, Philipp Simon provided lectures on transposable elements in Stan Peloquin's legendary course on plant ctyogenetics. Simon's insight into the work of Barbara McClintock and the breakage–fusion–bridge cycle was a highlight of these lectures. One of the best aspects of Simon's formal teaching is his ability to help students understand the many levels of genetic organization from the most basic, fundamental cellular level to the organismal level. Being a plant breeder helps. Like his mentor Peloquin, Simon also has contributed to the teaching of fundamental genetics in Biocore 301, the first semester of the four-semester honors biology sequence at the University of Wisconsin-Madison. In a series of approximately 15 lectures, Simon takes the students from Mendelian heredity to population genetics and also runs some of the laboratories on cytogenetics. During the course of his career, Philipp Simon has trained 23 Ph.D. students, 2 M.S. students, 14 post-doctoral researchers, and 8 visiting scientists. He has also contributed significantly to the graduate research of 8 graduate students who received their degrees at other institutions but completed a portion of their research in his laboratory.

IV. GERMPLASM AND INTERNATIONAL ACTIVITIES

Simon's evaluation of molecular marker variation in germplasm collections of carrot and garlic demonstrated an unexpectedly high level of genetic diversity in carrot relative to other outcrossing diploid crop plants, and also higher diversity in garlic than expected for a strictly clonally propagated crop. These studies were the first evaluations of germplasm variation in these crops. This knowledge has been applied by carrot breeders in broadening the germplasm base of cultivated carrot breeding stocks and by garlic breeders in selecting all of the garlic stocks used for garlic seed production in the United States. For both crops, there was generally poor correlation between morphological traits, geographic origin, and molecular diversity. A wild relative of garlic, *A. longicuspis*, clustered together with no clear separation from garlic, suggesting these species are not genetically or specifically distinct. The molecular variation observed confirmed broad diversity in garlic.

Philipp Simon has provided leadership for the Vegetable and Cranberry Research Unit of the USDA-ARS at Madison, as well as for vegetable researchers and the vegetable industry. Since 1986, Simon has arranged germplasm and cultivar evaluation trials that are attended by

vegetable growers and seed industry representatives, including two popular annual trials in Bakersfield, California. He has been an active trainer of research apprentices, interns, graduate students, postdoctoral research associates, and visiting scientists from around the world. Simon has served as a cooperating scientist to Pakistan in a project focused on diseases of bulb vegetables, to India in a project focused on carrot breeding, to Brazil in a project on *in vitro* improvement of garlic, and to Bangladesh in a project on garlic and onion improvement. Simon's carrot and onion quality program at Madison serves as a model for establishment of similar vegetable quality laboratories in U.S. industry and other countries. Researchers from 36 U.S. companies and from India, Nepal, Bangladesh, Pakistan, China, Japan, Korea, Turkey, Syria, Poland, Germany, The Netherlands, France, Italy, Greece, England, Norway, Guatemala, Canada, Australia, Argentina, New Zealand, Brazil, Mexico, England, Denmark, and Nigeria were informally trained or otherwise assisted by Simon in their laboratory planning and programming. He has also initiated and codeveloped the RoBuST database to support Apiaceae and Alliaceae research and education.

Walking into the second floor entrance of the Plant Science building on the campus of the University of Wisconsin-Madison, one will encounter a hallway lined with tables that are heaped with carrots. Students, visiting scientists, and postdoctoral associates stand in front of the tables, wearing lab coats and wielding knives, trimming and cutting carrot roots, and making selections for breeding and seed production. Stacked next to the table are cardboard boxes bearing California postmarks and the unmistakable scent of carrot volatiles. Hanging from the ceiling are posters covering a wide range of research topics—from nematode resistance to Mediterranean germplasm collections to carrot gene-sequencing projects. Black and white photographs of plant chromosomes and unique cytogenetic features cover surfaces in the laboratory, and cabinets abound overflowing with theses, papers, articles, and notebooks. This is the Simon laboratory, one of the world's foremost destinations for the study of carrot and garlic genetics and breeding. Simon's contributions to improving these crops have been influential during the past 30 years, and his commitment to student and scientist training has improved the outlook for vegetable breeding globally.

V. HONORS AND AWARDS

Simon was named USDA, ARS Senior Scientist of the Year, Midwest Area in 2001 and was awarded the USDA Secretary's Honor Award for

Superior Service in 2002. He was elected Fellow of American Society for Horticultural Science in 2002 and named the American Society for Horticultural Science Outstanding Researcher in 2003. Simon was awarded an Honorary Doctorate from the Agricultural University of Krakow, Poland, 2003.

Philipp Simon is dedicated to both his career and his family. He and his wife Sandy have two grown children and have lived in Madison for many years. Through his work in germplasm collection and breeding, Philipp has had the opportunity to travel the world, and he considers traveling one of his hobbies. He is an avid follower of politics and reads broadly on a number of subjects. He is widely known as a kind and thoughtful person who has contributed much while remaining modest; a rare and highly desirable quality in a colleague.

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Circadian Regulation of Horticultural Traits: Integration of Environmental Signals

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ABSTRACT

Plants, animals, and fungi have evolved to contain an internal physiological clock that responds to external stimulus such as the light/dark cycles created by the rotation of the Earth. This pacer is known as the circadian clock. It is composed of a complex set of genes that is conserved in higher plants. Originally thought to be a mere coordinator of basic processes, research has shown that the clock plays a key role in aspects as important as flowering time, productivity, tuberization, and dormancy. Its functions are all related to the seasonal development in many crops. But the circadian clock intimately controls other biological processes such as adaptation to cold, pathogen resistance, stomatal movement, and scent production. Most of the knowledge about the plant circadian clock has been established by research on *Arabidopsis* but the apparent conservation of the circadian clock components in cereals, trees, and floriculture crops means that the circadian clock may influence many agriculturally relevant traits such as flowering, dormancy, productivity, or fruit and flower aromas.

KEYWORDS: cold acclimatization; dormancy; flowering time; gibberellins; plant growth; productivity; scent production; tuberization

Horticultural Reviews, Volume 41, First Edition. Edited by Jules Janick.
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I. INTRODUCTION

Plants are sessile organisms that have to cope with environmental fluctuations such as sharp changes in light and temperature on a daily basis. As a result, developmental programs in plants are partly controlled by environmental cues. How the main environmental signals are integrated into a default program of growth and development has been elucidated in many plants by a mixture of field experiments, breeding, genetics, and physiological studies. Today important evidence suggests that most if not all responses of phytoplankton (Prezelin 1992), cyanobacteria (Sandh et al. 2009), mosses (Imaizumi et al. 2002), and higher plants (Koornneef and Peeters 1997) to the environment are somewhat controlled by the circadian clock (de Montaigu et al. 2010). The circadian clock is formed by a set of genes whose main function appears to be the coordination of environmental cues and physiological responses (see below). Initial observations of rhythms in plants started with the rhythmic movement of leaves, reported already in 1726 (see McClung 2006 for a historical perspective of research on circadian rhythms in plants). Although early molecular experiments were performed in pea and wheat (Kloppstech 1985; Nagy et al. 1988), much of our knowledge has been accumulated in the plant

model *Arabidopsis thaliana*. Given the importance of the circadian clock as a general controller of plant growth, development, and response to stress, we expect to see an increase of knowledge transferred to horticultural crops. *Arabidopsis* might be used further to identify clock genes and how they function, but proof/application of the concept requires the identification of genes from the circadian clock causing modifications in horticultural traits such as flowering time, abiotic stress resistance, productivity, or volatile production. Furthermore, differences with *Arabidopsis* might explain crop singularities helping to improve cultural practices and breeding.

Circadian regulation is often considered plant specific, but rhythmic regulation of biological processes also occurs in cyanobacteria, fungi, and animals. It is extensively studied in the field of chronobiology. Two extensive reviews on the historical perspective of the circadian clock in plants have been published recently (McClung 2006, 2011). Harmer (2009) reviewed clock structure in *Arabidopsis*, while Yakir et al. (2007) and de Montaigu et al. (2010) reviewed the current view on circadian outputs controlling plant growth, flowering time, and cold response. The object of the current review is to provide an overview of the clock structure. We cover with some detail the environmental inputs that set the clock, a process called entrainment. We include examples of the knowledge of clock and related topics in plants of horticultural interest.

As many biological processes show rhythmic patterns, a detailed terminology describing a rhythm and its changes has developed over the years, which helps to identify changes in this phenomenon. An important component of the language used in chronobiology and data analysis tools originated in the field of signal processing in electrical engineering where wave-like signals are analyzed. Thus, it has remained a common language to a large extent, and new concepts related to biological aspects have enriched it, making it quite elaborate. Although not all the terminology has been used in the current review, we have compiled a table with a comprehensive list of terms used in chronobiology, for educational purposes and to ease reading further literature (Table 1.1). It is just good practice that data gathering, terminology, and measurements are standard as it allows proper data analysis, sharing of data, and classification of the different responses. Fig. 1.1 presents examples that indicate how changes in circadian regulation are observed.

II. GENERAL STRUCTURE OF THE PLANT CIRCADIAN CLOCK

A. *Arabidopsis*

Two physical signals, light and temperature, are constantly changing as a result of Earth axial rotation providing night and day as well as the

Table 1.1. Terminology used in chronobiology.

Term	Definition and/or description
Acclimation	Physiological changes occurring within the lifetime of an organism that reduce the strain caused by experimentally induced changes in particular climatic factors such as ambient temperature and/or photoperiod. The acclimation period is critical to obtaining reliable experimental data.
Acrophase	Peak of a mathematical curve fit to data. Refers to the time when a process has its maximum, starting from a point defined by the scientist, for example, dawn. It may be expressed in (negative) degrees as the lag from the acrophase reference (360°C = 1 period) or in calendar time units (hours, minutes, etc.).
Aliasing	Detection of a false period that is longer than the underlying true period as a result of sampling taken wide apart.
Amplitude	Distance from rhythmic mean to the peak or to the trough of a mathematical model (e.g., cosine) used to approximate a rhythm. A process without rhythm will have amplitude of zero.
CC	Constant environmental conditions. In chronobiology, CC indicates lack of environmental synchronizers, that is, constant light, constant temperature.
Circadian	Roughly 24 h, describing rhythms with about a 24 h cycle length whether they are synchronized with a 24 h periodic surrounding or not.
Circadian time	Time that spans the circadian period in relation to the light/dark regimen under synchronized conditions.
Circannual	A rhythm with a period of about 1 year (±2 months), synchronized with or desynchronized from the calendar year.
Circaseptan	A rhythm with a period of about 7 (±3) days, which may or may not be synchronized with the calendar week.
Circatrigintan	A rhythm with a period of about 30 (±5) days.
Cosinor procedure	A mathematical–statistical method of describing a rhythm by determining by least squares technique the cosine curve best fitting to the data and exploring the presence of a rhythm by examining the null hypothesis for amplitude in an *F*-test. If a rhythm can be described by this procedure, the cosinor yields a rhythm-adjusted mean (MESOR), an amplitude as measure of the extent of the rhythm, and an acrophase as indication of its timing with variance estimates for each of the three parameters.
Damping	Decrease in amplitude of a rhythm over time.
DD	Continuous dark conditions.
Endogenous rhythm	A biological rhythm that persists in the absence of external cues and is probably genetic.
Entrainment	Coupling of the period and phase of a biological rhythm (e.g., circadian) with another cycle (e.g., 24 h solar day). Entrainment signals (synchronizers) are light and temperature. Probably other components such as sugars play a role.
Free-running	Desynchronization of the period of a biological rhythm from the period of a known environmental synchronizer. Status of a rhythm under constant conditions (absence of synchronizers).

Table 1.1. (*Continued*)

Term	Definition and/or description
Frequency	Number of cycles for a given amount of time. It is the reciprocal of the period.
Gating	Pacing, or limiting a biological event to a certain period.
LD	Light period followed by dark period. Thus, 16 h light:8 h dark. LD might not always be 24 h periods as some experiments test effect of shorter or longer LDs.
Lighting regime	The light–dark cycle (LD), or constant light (LL), or constant dark (DD) conditions used for chronobiologic studies.
LL	Continuous illumination.
Masking	Change of rhythm characteristics (acrophase, amplitude, or Mesor) as a result of changes in environmental conditions.
Mesor	Midline estimating statistic of rhythm. The value midway between the highest and the lowest values of the (cosine) function best fitting to the data. The "M" is equal to the arithmetic mean only for equidistant data covering an integral number of cycles.
Pacemaker	A functional entity capable of self-sustaining oscillations that synchronize other rhythms. It is an internal component or set of components, not an external synchronizer.
Period (t)	Duration of one complete cycle in a rhythmic variation.
Photoperiod	In a light/dark regimen the duration of the light span (e.g., in light/dark = LD 12:12 h, the photoperiod L = 12 h).
Scotoperiod	In a light/dark regimen the duration of the dark span (e.g., light/dark = LD 12:12 h, the scotoperiod D = 12 h).
Synchronizer	Environmental signal or input that entrains a biological rhythm. In the literature several synonyms are used such as entraining agent, time giver, or Zeitgeber.
Trough	The lowest point in a series of measurements obtained as a function of time.
Ultradian rhythm	Peak of a mathematical curve fit to data. Refers to the time when a process has its maximum, starting from a point defined by the scientist, for example, dawn. It may be expressed in (negative) degrees as the lag from the acrophase reference (360° period) or in calendar time units (hours, minutes, etc.).
Zeitgeber	Time giver (German), it does not give time, but is a synchronizer.
Zeitnehmer	Time receiver (German); a molecule or mechanism that serves as input of environmental signals to the clock.

revolution of the tilted Earth around the sun that provides seasonal effects. It is a challenge for organisms to maintain a stable program of morphogenesis when important parameters regularly vary. The current hypothesis is that the circadian clock has evolved as a gene network that has a robust behavior, allowing daily adjustments to environmental changes such as photosynthetic apparatus maintenance or emission of

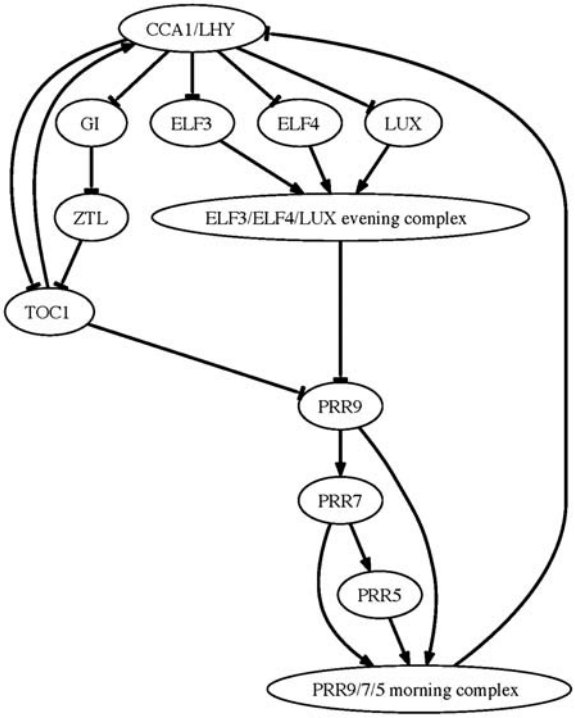

Fig. 1.1. A simplified structure of the current model of the circadian clock in *Arabidopsis*. The current model of the circadian clock comprises three groups of genes that are classified as the morning, midday, and evening loop. The morning loop is formed by three members of the same gene family *PRR9*, *PRR7*, and *PRR5*. These proteins form a complex that inhibits the midday loop formed by the genes *CCA1* and *LHY*. The evening loop is formed by *GI* and *ZTL*, two proteins that inhibit *TOC1* (another member of the *PRR* family), and a complex formed by *ELF3*, *ELF4*, and *LUX*. This evening complex inhibits the morning complex, thus closing the daily circle.

scent matching the time of pollinator activities (Locke et al. 2006; Akman et al. 2010; Thommen et al. 2010). A second task would be to consider long-term morphogenetic changes such as flowering, winter dormancy, and adaptation to cold or heat during the seasons. An endogenous clock should help maintain a constant flux of processes yet must be robust enough—for example, to prevent a short-day plant, would flower after being exposed to random shading on a dark day.

The current proposed structure of the plant circadian clock consists of three interrelated loops of genes that act by mutual activation and repression (Pokhilko et al. 2012) (Fig. 1.2). These feedback loops form an

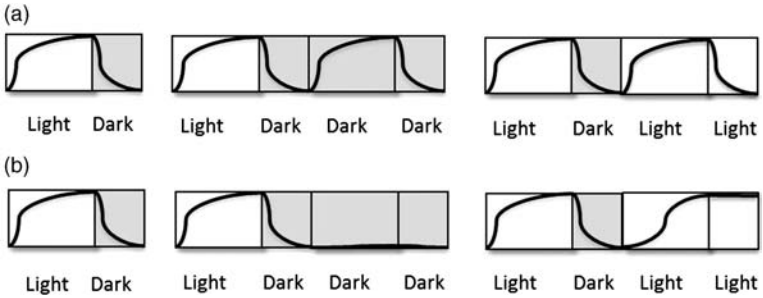

Fig. 1.2. Experimental design to identify processes that are circadian regulated in plants. As circadian experiments are timed usually, time zero is when light are turned on for a period and then off. This gives a pattern of light/dark, in most cases represented as LD. It follows that after a period of LD, the system is challenged with either a continuous light LL or an extended night (continuous dark) or DD. (a) Processes that are circadian regulated will maintain a rhythmic function in continuous dark (DD) and continuous light (LL). (b) A process that is light dependent will typically show a downregulation in continuous dark (DD) and constant high level in continuous light (LL).

oscillator that effectively cycles every day at a certain pace or amplitude (Table 1.1). As in many other biological regulatory processes, at least two levels of interaction occur inside the clock. One is at the transcriptional level, where activation and repression of gene expression play the main role. The second level of interaction is posttranslational changes where proteins form complexes and are selectively degraded or modified by phosphorylation. But the clock in plants also has an additional degree of complexity as several genes involved in clock function code for a photoreceptor that changes conformation and activity as a result of the light input (Jarillo and Pineiro 2006).

There are five *PSEUDORESPONSE REGULATOR* genes in the *Arabidopsis* genome, *PRR9*, *PRR7*, *PRR5*, *PRR3*, and *PRR1*, the latter known as *TIMING OF CAB EXPRESSION 1* (*TOC1*) (Uemura et al. 2010). All of them are components of the plant circadian clock. Assuming the morning as the beginning of a daily cycle, the first genes that show activity in the circadian clock are *PRR5*, *PRR7*, and *PRR9*. These genes act repressing the next loop of the clock in such a way that it causes a delay in its activation (Nakamichi et al. 2010). Two MYB transcription factor paralogs *LATE ELONGATED HYPOCOTYL* (*LHY*) and *CIRCADIAN CLOCK ASSOCIATED 1* (*CCA1*) form the middle loop, as they are expressed during the early part of the day. *CCA1* and *LHY* expression is repressed by *PRR5*, *PRR7*, and *PRR9*, from morning till midnight (Nakamichi et al. 2010), but *CCA1* and *LHY* activate *PRR5*, *PRR7*,

and *PRR9*. This interplay of repressing a function that then activates backwards creates a temporal pacer. A second component of the middle loop is *TOC1*. Recent work has shown that *TOC1* and the rest of the *PRR* family members are DNA-binding proteins (Gendron et al. 2012), indicating that their function in transcriptional control occurs via direct binding to regulatory sequences of target genes. The gene *REVEILLE8/LIKE CCA1 LHY 5* is a MYB transcription factor found recently to activate the *TOC1* gene, thus creating an additional connection between the morning and evening loops (Farinas and Mas 2011). The REV8 protein physically interacts with regulatory region of *TOC1* activating histone hyperacetylation. This causes a local loosening of the chromatin increasing the accessibility to the transcriptional machinery.

The evening loop comprises the genes *EARLY FLOWERING 3* and *4* (*ELF3* and *ELF4*), *LUX ARRHYTHMO* (*LUX*), *GIGANTEA* (*GI*), and the protein with photoreceptor capacity *ZEITLUPE* (*ZTL*). A recent work has shown that the ELF3, ELF4, and LUX proteins form a protein complex called the evening complex (Nusinow et al. 2011). The evening complex can bind DNA via LUX (Helfer et al. 2011), and represses its own expression and that of the morning gene *PRR9* (Dixon et al. 2011). This repression of the morning loop by the night loop closes the circle. Two recent papers have shown that *TOC1* is a general transcriptional repressor of the evening genes, that is, during the night, many genes have low transcriptional activity because of *TOC1* (Huang et al. 2012; Pokhilko et al. 2012). Again this mutual activation and repression of the clock genes creates waves of activation and repression that effectively pace the plant cell. The evening part of the clock is not completely understood. A number of components are missing and the way known components interact with each other remains incompletely defined. As a summary, the plant circadian clock has the architecture of several negative feedback loops interconnected with each other. These loops have been defined as morning, midday, and evening loop based on the time of the day when these genes display a maximum peak of expression.

B. Clock Genes in Crops

If we consider circadian regulation, we identify three layers where evolution might show conservation and divergence. One is the presence of conserved genes, orthologous to those found in *Arabidopsis* and other plants. A second more subtle but in this case as important is the conservation of the gene interactions found in other clocks, that is, the network motifs (Alon 2007). Yet a third level is the

conservation of input signals and output reactions. We will cover the conservation of these three levels, considering the fact that our depth of knowledge varies greatly for each of the layers depending on the trait described.

The actual knowledge of both the structure of the circadian clock and its functions is in its infancy in plants beyond *Arabidopsis*. The first layer of comparison, that is, identification of orthologs and paralogs, is the stage where most of our knowledge in crops is right now. Orthologs of *CCA1* or *LHY* are not always found as gene pairs in plants with complete genome sequence, which would allow comprehensive identification of coding sequences without missing one of the genes. Indeed, in the monocots, rice, and sorghum, there is a single-copy gene with higher homology to *CCA1*. Genes in core eudicots (Bremer et al. 1998) such as *Mesembryanthemum crystallinum* and the cactus pear (*Opuntia ficus-indica*) show higher degree of phylogenetic similarity to *CCA1* (Takata et al. 2009; Mallona et al. 2011), whereas in eudicots such as *Poplar*, *Castanea*, *Vitis*, or *Phaseolus*, the genes found tend to be *LHY*-like genes either as single or as double copies (Takata et al. 2009). The synteny analysis suggests *LHY* might be ancestral (Lou et al. 2012). Experiments in soybean show that there are *LHY* and *CCA1* orthologs in this crop with circadian expression patterns resembling *Arabidopsis* in the leaf tissues (Hudson 2010). In *Poplar*, two *LHY* paralogs, *LHY1* and *LHY2*, show differing expression patterns, indicating that they might have divergent functions (Takata et al. 2009). It remains to be determined whether the function of *CCA1* and *LHY* is conserved in other plants or if there are functional differences.

The five *PRR* genes in *Arabidopsis* are conserved in rice (Murakami et al. 2003). Sequencing of other eudicots has shown that there are 5 *PRR* genes in papaya (*Carica papaya*) (Ming et al. 2008; Uemura et al. 2010) while *Populus* has 11 *PRR* genes (Ramirez-Carvajal et al. 2008). *Brassica* comprises a large number of crops including Chinese cabbage, bok choy, turnip, broccoletto, or rapeseed. Recent work has shown that in the rapeseed (*Brassica rapa*), an amphidiploid, there are at least eight *PRR* genes and they show differences at the gene structure level indicating possible divergence in function with *Arabidopsis* (Kim et al. 2012). This emerging hypothesis awaits support of functional studies in this important group of plants.

There is a single copy of *GIGANTEA* in the *Arabidopsis* genome. The structure of the *GIGANTEA* locus has been studied in the yellow poplar (*Liriodendron tulipifera*). The *GI* locus is conserved in eudicots but is more divergent from rice or sorghum, indicating a possible departure at

the genome level (Liang et al. 2010). A recent analysis of the only *GI* ortholog found in the rice genome, Os-*GI*, has shown a somewhat different picture of what one would predict from the *Arabidopsis* data (Izawa et al. 2011). Rice plants carrying a null allele of Os-*GI* do not show extreme flowering time phenotypes or yield changes. Furthermore, although 75% of the 27,201 genes analyzed by microarray were significantly affected in the loss of function allele Os-*GI*, only the phenylpropanoid pathway showed changes at the metabolic level, indicating an extreme robustness of the clock under field conditions. These experiments also suggest that the two additional layers of conservation, that is, gene networks and clock input and outputs, might be different for *GI* between rice and *Arabidopsis*.

Based on studies in several plants, the genetic functions of many of these genes seem to be highly conserved. The gene *ELF3* seems to be conserved in most plants. Work performed in rice and barley shows that it plays a crucial role in adaptation to different environments (see below on flowering time). A recent genomic comparison between *B. rapa* and *Arabidopsis* has shown that except for *ZTL*, circadian clock genes tend to maintain gene copy number after genome-wide duplication events, indicating that there is selection against losing one gene out of a complex network (Kim et al. 2012).

Overall circadian clock genes are extremely well conserved, not only in terms of specific genes but also in terms of the number of genes present in the genome. This indicates that orthologs and paralogs of the core clock genes are probably found in all higher plants. However, detailed work is required to understand the structure of the clock in crops, and maybe more important is to test their effect in controlling certain important traits for horticulture. The knowledge about outputs is expanding rapidly and it shows great promise in this group of genes (see below).

III. ENVIRONMENTAL INPUTS

A. Light

Light plays two distinct roles for plants: one is the source of energy for photosynthesis and the second is as a signal for development. Most plant processes are controlled by light, and comprehensive reviews on photoperiod, photoreceptors, and plant development in all its aspects have been published in recent years (Fankhauser and Staiger 2002; Jarillo and Pineiro 2006; Jiao et al. 2007; Franklin and Quail 2010). Like

in other parts of this review, most of our detailed molecular knowledge on light has been obtained in *Arabidopsis* and only recently has this knowledge spread into other plants of horticultural importance.

Light is perceived in plants by at least four types of receptors: phototropins, phytochromes, cryptochromes, and members of the *ZTL/LOV KELCH PROTEIN 2* (*LKP2*)/*FLAVIN-BINDING KELCH REPEAT F-BOX 1* (*FKF1*) gene family (Fankhauser and Staiger 2002). Some of the clock proteins (ZTL and FKF1) are photoreceptors, and others, such as ELF3, can form complexes with ZTL. The distinction between light signaling and circadian clock is not always possible and could be somewhat artificial. First, red light activates the transcription of the morning loop genes *CCA1* and *LHY* (Alabadi et al. 2001) but this activation requires, to some extent, the proper function of the evening loop gene *TOC1* (Mas et al. 2003a). *CCA1* activated by light signals directly binds to promoters of *CHLOROPHYLL A/B BINDING PROTEIN* (*CAB*) genes, thus anticipating the morning (Wang et al. 1997).

The first gene found to act as a zeitnehmer or time taker (Table 1.1) is *ELF3* (McWatters et al. 2000). Indeed *elf3* mutants do not have detectable circadian rhythms in continuous light, but display circadian rhythms in the dark (Hicks et al. 1996). The protein ELF3 interacts with PHYTOCHROME B protein (Liu et al. 2001) and apparently gates red and blue light receptor signals (Covington et al. 2001). The null allele *elf3-1* displays gating defects in repressing light-dependent gene expression during the dark. For example, *CAB* is activated by light during the subjective night in *elf3* but not in wild-type plants (McWatters et al. 2000; Covington et al. 2001). The important concept is that light-induced genes and the corresponding processes do not maintain similar levels throughout the day and night because there is a rhythmic repression of the light-signaling pathway during dark periods, partly controlled by *ELF3*.

Two proteins, ZTL and LKP2, regulate TOC1 via degradation (Mas et al. 2003b). As the protein LKP2 has light sensing properties (Imaizumi et al. 2003), the complex picture becomes somewhat easier to interpret. Light entrains the clock by activation and degradation of several components, thus achieving a sort of rhythmic input partly caused by the fact that the morning and evening components are differentially affected, that is, morning elements *CCA1* and *LHY* mRNA synthesis is activated by light, whereas the evening element TOC1 protein is targeted for degradation.

It turns out that ZTL itself is a blue light receptor as the LOV (light, oxygen, voltage) domain present in the ZTL protein is a flavin-binding domain. When light is present, the ZTL protein binds to GI and is

stabilized, but is selectively degraded in the dark. Mutations in the LOV domain result in poor binding of ZTL to GI (Kim et al. 2007). The stability of ZTL is important as ZTL directly controls the protein levels of TOC1 (Fujiwara et al. 2008).

The conclusions are that there are at least three places where the clock directly interacts with the light signaling, one via CCA1/PHYB interaction, the second one also dependent of PHYB, that is, ELF3/PHYB, and the third one via ZTL and FKF1 as photoreceptors and clock genes. Morning light signals enhance transcription of other genes, whereas evening light is interpreted in terms of protein degradation of clock components.

B. Temperature

As plants cannot actively control the temperature of their organs, changes in environmental temperature have several parallel effects on plants. First, many biochemical reactions have a linear dependency on temperature. The so-called Q10 or temperature coefficient measures the rate of change in chemical reactions as a result of increasing the temperature by 10°C. Indeed biochemical reactions have certain temperature optima, that area seldom maintained for long periods in plants, as day temperature fluctuates, and on a given day, temperatures will not stay the same for more than 3 or 4 h. Second, extreme temperatures cause damages, and adaptation to cold and hot weathers involves genetic activation of the so-called acclimation processes (Browse and Xin 2001). Finally, temperature plays a role as a signal for important developmental processes that include seed germination (Bewley 1997), growth, winter dormancy, and flowering (Henderson et al. 2003). Thus, the three aspects described could be seen as short-term (hours), middle-term (days to weeks), and long-term (weeks to season) responses elicited by temperature.

Studies performed in *Drosophila* and *Neurospora*, two organisms that, like plants, are poikilothermic, that is, they do not control body temperature, indicate that an intrinsic aspect of biological circadian clocks is the temperature compensation that allows biological processes to maintain a rhythm as autonomous as possible (Hogenesch and Ueda 2011). The identification of temperature compensation mutants in *Arabidopsis* was performed by analysis of accession-specific variations in the pattern of temperature compensation for rhythms of leaf movement between the ecotypes Columbia (Col) and Landsberg erecta (Ler) and between Ler and Cape Verde Islands (Cvi). This experimental approach identified several quantitative trait loci

(QTL) and some of them corresponded to known clock genes (Edwards et al. 2005). One QTL matched to the gene Flowering Locus C (FLC) (Edwards et al. 2006). Indeed at 27°C, a fairly high temperature for *Arabidopsis*, *FLC* lengthens the circadian period, thus compensating for otherwise excessive speed of metabolic processes. In contrast, the gene *GIGANTEA* is required to maintain rhythmicity at 12 and 27°C (Gould et al. 2006), indicating that several genes in the clock are involved in temperature compensation. The genes *PRR3*, *PRR5*, and *PRR9* form the morning loop, and PRR7 and PRR9 are involved in compensation at high temperatures, as the double mutant *prr7,prr9* overcompensates at 30°C, indicating that they are involved in repression of an otherwise fast-paced clock under these conditions (Salome et al. 2010).

One molecular mechanism of part of the temperature compensation was recently found for *CCA1*, which tends to bind to its target genes with higher affinity at higher temperatures. This increased affinity is counterbalanced by a protein kinase 2 (CK2) that phosphorylates CCA1 at higher temperatures, lowering its DNA-binding affinity. This effectively compensates the tendency of part of the clock reactions, like any other reaction in the cell, to run faster as temperature increases (Portoles and Mas 2010).

In conclusion, temperature changes have a lower effect on plant basic processes in plants because the circadian clock compensates daily differences. Nevertheless, temperature entrains the system in a way that is not fully understood. Adaptation to temperatures and their effect on development are discussed below.

IV. CONTROL OF PLANT GROWTH AND MORPHOGENESIS

Plant growth and morphogenesis is a complex process comprising shoot and root apical meristem maintenance, lateral organ formation, flowering, tuber formation, or seed development. Some of these processes are controlled in a number of plants by environmental cues. As a result, evidence has accumulated that some of the major decisions during plant morphogenesis are somehow related to clock function. There is clear evidence about the effect of plant growth regulators on morphogenesis, and there is very strong evidence showing that at least gibberellins (GAs) are directly under the control of the clock. We present an overview of what is known about plant hormones and several developmental processes found to be directly controlled by the clock machinery.

A. Plant Hormones and Circadian Clock

Endogenous plant hormones regulate an extensive array of physiological processes over the whole plant life cycle from seed germination to flowering. The phytohormones include cytokinin, auxin, brassinosteroid (BR), abscisic acid (ABA), GA, ethylene, and salicylic acid (SA). They function like partially interacting mediators allowing plants to sense their exogenous and endogenous conditions in order to assure maximal fitness under the varying environment (Hanano et al. 2006).

Among the exogenous growth conditions that affect the endogenous plant hormones are light, temperature, abiotic stress, and disease. But the biological oscillations in the form of the circadian rhythm also affect phytohormones. Comprehensive transcriptome data set analysis clearly demonstrated a circadian periodicity in genes responsible for synthesis of plant hormones and responses (Covington and Harmer 2007; Covington et al. 2008; Mizuno and Yamashino 2008; Maloof et al. 2011) and transgenic plants carrying promoter-luciferase reporter gene fusions (Bancos et al. 2006; Hanano et al. 2006) further confirmed that the circadian system modulates plant responses to most hormones.

The phytohormone GA controls important aspects of plant growth such as seed germination, elongation growth, and flowering. A key role in GA signaling lies in its interaction with the DELLA repressor protein in a GA-dependent manner. DELLA proteins restrain GA-dependent growth responses, and their repressor activity is relieved by their GA-dependent degradation (Schwechheimer and Willige 2009). Several pathways have been shown to cross talk with GA signaling, including the circadian clock, and it was proposed that GA pathways contribute to the diurnal growth pattern (Maloof et al. 2011). Rhythmic plant growth, characterized by maximum rates during the second half of the night, is controlled by a concerted action of both the light signaling, which represses growth during the day, and the circadian clock that gates growth toward the end of the night. The transcription factors *PHYTOCHROME-INTERACTING FACTOR4* (*PIF4*) and *PIF5* are key elements in the hormone gating through the circadian clock (Nozue et al. 2007). The PIF proteins physically interact with members of the phytochrome family and transduce environmental light signals to responsive nuclear genes (Quail 2000). According to a model proposed by Nozue et al. (2007), during the day, light inactivation of PIF as well as an inhibitory interaction between DELLA and PIF proteins prevents growth (Nozue et al. 2007). DELLA interacts with PIF4/5 and inhibits their DNA-binding abilities. Early during the night, circadian clock genes prevent PIF transcription, leaving growth-promoting PIF action to

a short period before dawn, when DELLA protein levels are reduced (Alabadi 2009; Yamashino et al. 2010). Suppression of growth during light periods might be further related to maximum expression of genes for GA catabolic enzymes, as observed in *Arabidopsis* (Zhao 2007).

Auxin is an additional phytohormone whose action is found to be circadian clock gated as auxin-related genes, including production and response, show clock-regulated expression (Covington and Harmer 2007; Thines and Harmon 2011). Auxin is a central controller of plant growth, development, and cellular physiology including embryogenesis, vascular patterning, formation of lateral and adventitious roots, control of apical dominance, phototropism, gravitropism, cell turgor, elongation, division, and cell differentiation. The subset of auxin-related transcripts in *Arabidopsis* exhibiting circadian cycling includes those of *de novo* auxin biosynthesis genes, auxin responsive genes, genes involved in auxin signaling, and negative regulators of auxin responses (Thines and Harmon 2011). The above-mentioned *PIF4* and *PIF5*, which integrate light and circadian clock signaling to generate rhythmic plant growth, were proposed to directly modulate auxin pathway and response genes (Kunihiro et al. 2011; Maloof et al. 2011). PIFs therefore play a fundamental role in the circadian clock gating of both GA and auxin responses. Still, other PIF-independent pathways might also contribute to the circadian regulation of growth via auxin gating, such as the transcription factor *REVEILLE1* (*RVE1*) from *Arabidopsis*, homologous to the central clock genes *CCA1* and *LHY*. *RVE1* controls free auxin levels by positively regulating the expression of the auxin biosynthetic gene *YUCCA8* (*YUC8*) during the day (Rawat et al. 2009).

A third group of phytohormones regulated by the circadian clock includes BRs, one of the most recently characterized groups of plant hormones. BRs are involved in seed germination, stem and root elongation, vascular differentiation, leaf expansion, and apical dominance, responses that are also controlled by auxins (Halliday 2004). It was shown that brassinosteroid and auxin signaling pathways converge at the level of the transcriptional regulation of common target genes (Nemhauser et al. 2004). In *Arabidopsis*, two BR-biosynthetic genes, *CPD* and *CYP85A2*, are under diurnal regulation (Bancos et al. 2006), and similar to the circadian regulation of auxin action, light regulation of *CPD* is primarily mediated by phytochrome signaling (Bancos et al. 2006). Interestingly, under light, but not in the dark, transcriptional control is independent of hormonal BR feedback regulation, showing that rhythmicity also involves changes in plant sensitivity to a hormone via feedback loops.

Circadian regulation has also been described for genes contributing to the signaling of ABA. The core clock protein TOC1 is linked to ABA signaling-related growth processes by a feedback loop. TOC1 binds to the promoter of the ABA-receptor ABAR/CHLH/GUN5 (Legnaioli et al. 2009), repressing *ABAR* expression, and *TOC1* is in turn induced by ABA. The reciprocal regulation allows fine-tuning of circadian responses to ABA (Thines and Harmon 2011). ABA plays a major role in seed maturation and germination, as well as in adaptation to abiotic environmental stresses. It further promotes stomatal closure by rapidly altering ion fluxes in guard cells (Leung and Giraudat 1998). It was proposed that some aspects of plant stress responses are mediated by ABA through the circadian clock. Thus, plants prepare properly for action against common ambient stresses that keep changing in response to the light/dark and hot/cold daily cycling by anticipating the diurnal day/night cycle (Mizuno and Yamashino 2008; Legnaioli et al. 2009).

In summary, phytohormonal control of processes that fluctuate on a daily basis, such as plant growth or stress due to hot/cold cycling, is gated by the circadian clock, allowing anticipation of the diurnal day/night period and a fine-tuning of daily plant responses. The largest body of evidence has been found so far for the GA signaling involved in germination, growth, and flowering. But other plant hormones such as BR and ABA are also circadian regulated.

B. Seed Development and Germination

From a horticultural perspective seeds are important both as plant material for propagation and as a product. The involvement of circadian regulation on seed development before maturation is not understood with detail. Evidence comes from the fact that transient starch synthesis is circadian regulated and sugars are used in developing seeds as sources to accumulate important metabolites, that is, carbohydrates, fats, and proteins. Recent work has shown that in soybean there is a circadian regulation of genes involved in carbohydrate metabolism related to photosynthesis and lipid synthesis, whereas carbohydrate metabolism unrelated to photosynthesis did not follow a circadian trend (Hudson 2010). The flag leaf of rice is thought to be the source of carbohydrates for rice grain formation, and a strong diurnal cycling was found in this leaf and seedling leaf whereas additional genes showed a diurnal pattern only in flag leaves, suggesting their importance in the grain filling process (Xu et al. 2011). These data indicate a role for circadian regulation on grain productivity (see below).

Seed germination is an important aspect in the plant nursery, and proper expertise and practices make a difference in terms of percentages of germination and seedling quality. Plants assess the environmental situation to avoid germination when environmental conditions are not conducive to seedling establishment. Studies in different plants have shown that seeds have some degree of dormancy. In principle, seed dormancy is not a wanted horticultural trait as high-speed germination and growth are an asset in most crops. However, a complete lack of dormancy may cause the so-called preharvest sprouting, an unwanted trait selected against in cereals such as rice, sorghum, and wheat (Iusem et al. 2001; Humphreys et al. 2009; Sugimoto et al. 2010). Thus, a balance between both processes is required. Indeed seed dormancy and germination are thought to be one and the same process where levels of abscisic acid and gibberellins counteract each other in equilibrium (Bewley 1997). Recent reviews cover this issue in depth (Finch-Savage and Leubner-Metzger 2006; Penfield and King 2009). But the involvement of the circadian clock on seed germination and dormancy is a relatively new concept. Light plays a role in seed germination and hundreds of experiments have shown the importance of light of different qualities to promote germination in uncountable species. As these three parameters, that is, light, ABA, and GAs, are known to be entraining signals and output pathways of the clock, it was not surprising that a direct link was found.

Under natural conditions, once seed development occurs, seed dormancy is established, and a period called afterripening takes place where time and environment determine germination potential of dry seeds (Carrera et al. 2008; Holdsworth et al. 2008). The clock genes *CCA1* and *LHY* show partially redundant function in germination. The *cca1*,*lhy* double mutants show enhanced germination under continuous cold treatment (Penfield and Hall 2009). Both *lhy* and *cca1*,*lhy* double mutants show better germination than wild types under cycling temperature regimes (27°C at day and 17°C at night), indicating that clock genes play a direct role in the control of seed dormancy and signaling to germinate, in this case by temperature. The mutant *gi* has opposite effects to those observed in *cca1*,*lhy* double mutants, as it displays poor germination after storage. This means that the GI protein is required for afterripening, an important process in cereals and any seed that will be maintained for more than just a few days before germination.

C. Flowering Time

Flowering time in plants is among the most important traits in horticulture. Work in *Arabidopsis* showed that several pathways can

promote flowering including gibberellins, photoperiod, temperature, or even vegetative growth (Simpson et al. 1999). As a result, today flowering time is dissected into the so-called GA-dependent, light-dependent, temperature-dependent, and autonomous pathway. One current hypothesis is that differences between plants relate to the degree of importance of these pathways involved in flowering time. This hypothesis is supported by studies in several crops such as tomato, a neutral-day plant that follows the autonomous pathway (Lifschitz and Eshed 2006; Lifschitz et al. 2006). Rice, on the contrary, is a short-day plant and it flowers in a manner opposite to *Arabidopsis* (Tsuji et al. 2011).

As some of the *Arabidopsis* mutants affected in the photoperiodic flowering pathway turned out to be clock genes, it became clear that at least this pathway is circadian regulated (Hayama and Coupland 2003). Among the clock genes that show a flowering time phenotype in *Arabidopsis* are *ELF3*, *ELF4*, *CCA1*, *LHY*, and *GI*. Strong evidence of a role of clock genes in flowering in crops has started to accumulate. The identification of *PDD-H1*, the ortholog of *PRR7* from barley, as major determinant of flowering, and partly responsible for the winter or summer genotypes, indicated that the clock genes play a role in flowering in monocots. Variations in orthologs of *GIGANTEA* from the evening loop with a function in flowering have been found in pea and soybean (Hecht et al. 2007; Watanabe et al. 2011), indicating that this part of the loop might have conserved functions in flowering time in *Arabidopsis* and legumes. The evening loop gene *ELF3* also shows conserved functions in *Arabidopsis*, barley, and rice where it shares a function on responses to photoperiod (Fu et al. 2009; Saito et al. 2012). Finally, *GHD7*, a gene with sequence homology to the PRR family, has been found in rice that increases yield and has additional heading phenotypes (Xue et al. 2008). The data show that a number of clock genes play a role in flowering time, and in some cases, they also have additional functions in growth and productivity. A list of genes with phenotypes relevant to flowering in *Arabidopsis*, which show modified phenotypes in other plants, can be seen in Table 1.2.

One of the clock outputs that is better understood is the activation of flowering through the gene *CONSTANS* (*CO*). During the evening of long days, there is an increase in the level of mRNA of *CO* resulting from the inhibition of *CYCLING DOF FACTOR* by *GIGANTEA*. This allows the formation of CO protein that activates the gene *FLOWERING TIME* (*FT*).

The *CO* gene activates the transcription of *FT*, currently thought to be the flowering signal (Samach et al. 2000; Suarez-Lopez et al. 2001). The

Table 1.2. Flowering and growth-related phenotypes of clock genes in *Arabidopsis* and in crop plants.

Clock position	Species	Gene	Phenotype
Morning loop	*Arabidopsis*	*PRR7*	Light insensitive (Kaczorowski and Quail 2003)
	Barley	*Pdd-H1* ortholog of *PRR7*	Major determinant of photoperiod (winter vs. spring) (Turner et al. 2005)
Midday loop	*Arabidopsis*	*cca,lhy* double mutant	Semidwarf, early flowering in short days, pale green in short days, accelerated germination (Mizoguchi et al. 2002; Penfield and Hall 2009)
		cca1 loss of function	Early flowering in short days (Mizoguchi et al. 2002)
		lhy loss of function	Delayed flowering and elongated hypocotyls (Schaffer et al. 1998)
Evening loop	*Arabidopsis*	*Early flowering 3*,	Early flowering, photoperiod independent (Zagotta et al. 1992)
		ELF3	Defective inhibition of hypocotyl elongation (Zagotta et al. 1996)
		Gigantea; *gi*	Late flowering (Araki and Komeda 1993)
	Barley	HV Elf3; *Praematurum a* (*mat-a*); *early maturity 8*, *eam8*	Adaptation of barley to lower latitudes, early flowering irrespective of photoperiod (Faure et al. 2012; Zakhrabekova et al. 2012)
	Pea	*PsELF4/DNE*	Early flowering (Liew et al. 2009)
		PsGi/Latebloomer1	Allele specific response to photoperiod. Late flowering (Hecht et al. 2007; Liew et al. 2009)
	Rice	*OsELF3*	Later flowering irrespective of photoperiod (Fu et al. 2009; Saito et al. 2012)
		OsGi overexpression	Photoperiod-independent late flowering (Hayama et al. 2003)
	Soybean	*GmGia*	Early flowering (Watanabe et al. 2011)
Unknown	Rice	*Ghd7*	Increased yield and delayed heading time under long days (Xue et al. 2008)

gene *FT* from *Arabidopsis* is expressed in the vascular tissue but the protein is exported to and travels to the SAM where it activates the flowering program. This has been empirically demonstrated as FT signal can be transmitted from stock to scion in tomato, a neutral-day plant (Lifschitz et al. 2006), and in *Arabidopsis*, a long-day plant (Corbesier et al. 2007). Although rice is a short-day plant, FT is the conserved flowering signal (Tamaki et al. 2007). Furthermore, overexpression of the FT (*MdFT1*) in *Poplar* and apple causes extreme early flowering, as apples flower directly in *in vitro* culture (Trankner et al. 2010). The FT protein activates among other genes the gene *SUPPRESSOR OF OVER-EXPRESSION OF CONSTANS* (*SOC1*) that is involved together with other genes in triggering the flowering process (Samach et al. 2000; Lee and Lee 2010).

Experiments around this process are bringing mechanistic ways to understand some phenomena such as alternate bearing in fruit trees (Monselise and Goldschmidt 1982). Recent work performed in mandarins with the alternate bearing variety 'Moncada' has shown that both timing of fruit harvest and load directly affect expression of *SOC1* (Munoz-Fambuena et al. 2011). This gives for the first time a mechanistic explanation to this important fruit tree behavior opening a new approach to improve and homogenize yields. The accumulated evidence for a key role of circadian regulators on flowering and related processes in crops, especially in trees, has significant horticultural implications.

The effect of gain and loss of function of core clock genes and their orthologs on flowering time in plants of agricultural importance is emerging at high speed in cereals, legumes, and trees. Clearly, there is a huge gap between what we know in *Arabidopsis* and what is known in other plants, but the evidence of a role of the clock in flowering time seems to be universal.

D. Winter Dormancy

Woody plants go through the so-called dormancy period. The process of dormancy in plants refers to the cessation of growth and development during its life cycle. Temperate woody plants show a dormancy period in the winter and some tropical trees go dormant during the dry season. It is considered an adaptive trait of woody plants that allows survival during especially hard periods. Dormancy is induced by environmental cues. Indeed, in most woody plants, short days lead to growth cessation. Additional dormancy features include leaf fall and cold tolerance (Allona et al. 2008). When spring conditions appear and dormancy is

broken, growth rates increase, and floral buds appear. Thus, it is important to consider that during the juvenile period, dormancy leads to seasonal growth cessation during winter period, followed by growth periods. Only when the juvenile period is over, dormancy break is accompanied by seasonal flowering (Egea-Cortines and Weiss 2001). The juvenile period can last several years in many trees, for instance oranges (Peña et al. 2001). Breakthrough experiments performed in hybrid aspen showed that the constitutive expression of the *FT* gene from poplar induces flowering within 4 weeks compared to the 8–20 years required for wild-type trees (Bohlenius et al. 2006). This indicates that FT or downstream genes can overcome the juvenile phase. Short-day-induced growth cessation is also disrupted in these plants, indicating that flowering and dormancy are part of the same process. Furthermore, natural variation in day length for growth cessation of accessions of European aspen (*Populus tremula*) ranging between 51° and 63° latitude can be explained by changes in the *PtCO* gene, indicating that the time to flower and seasonal growth cessation are controlled by a common mechanism.

Work performed in dormant chestnut (*Castanea sativa*) showed that winter dormancy disrupts cycling of *CsTOC1* and *CsLHY* (Ramos et al. 2005). Further work has shown that *CsPRR5*, *CsPRR7*, and *CsPRR9* are also disrupted in their expression pattern during the winter (Ibañez et al. 2008). This disturbance in cycling was also achieved by cold temperatures of 4°C. Artificial transfer of plants that have not fulfilled the chilling requirements during the winter, to temperatures of 22°C, causes a reactivation of the endogenous clock (Ramos et al. 2005; Ibañez et al. 2008). Studies in hybrid aspen have also shown that downregulation of *PttLHY1* and *PttLHY2* using RNA-i interference caused a delay in bud burst (Ibañez et al. 2010), indicating again that dormancy in trees is under direct control of the circadian clock.

Altogether, it is clear that juvenility and winter dormancy are processes related to flowering time and as such, the circadian clock probably plays a role. The data obtained in hybrid aspen indeed indicate that future studies could find additional connections in trees, not only helping to solve growth and seasonality problems but also increasing the efficiency of fruit tree breeding programs.

E. Tuberization

The process of tuberization in potato is controlled by day length as commercial cultivars undergo tuber formation under short days (Rodriguez-Falcon et al. 2006). Although flowering time and tuberization

are affected by day length, genetic experiments show that flowering time in *S. tuberosum* ssp. *andigena* is not responsive to photoperiod whereas tuberization remains short-day dependent (Gonzalez-Schain and Suarez-Lopez 2008). It has long been known that application of GA3 inhibits this process (Rodriguez-Falcon et al. 2006). This indicates that two independent pathways can promote tuberization, one dependent on GA signals and the second dependent on short days.

The day-length-dependent pathway involved in flowering in *Arabidopsis* has as a major output the activation of *CO* (see above). The first evidence of a role of *CO* in tuberization was obtained in transgenic potatoes expressing the *AtCO* gene. These plants are smaller than control plants and tuberization is inhibited under short-day conditions (Martinez-Garcia et al. 2002). These results demonstrate a negative effect of *CO* on the photoperiodic control on tuberization. The activation of the gene *FT* by *CO* in tomato, rice, and *Arabidopsis* indicates that *FT* is the active signal that causes flowering (Suarez-Lopez et al. 2001; Yanovsky and Kay 2002; Hayama et al. 2003; Lifschitz et al. 2006). A recent study has shown that expression of the *Hd3a* gene from rice, ortholog of *FT*, can induce strict short-day tubering types to tuberize under long-day conditions (Navarro et al. 2011). As the *FT* signal is graft transmissible, the authors demonstrated that the *Hd3a* signal could travel from stock to scion. Furthermore, it appears that in potato two *FT* paralogs, *StSP3D* and *StSP6A*, respond to independent environmental cues. The gene *StSP3D* seems to be involved in flowering, whereas *StSP6A* is responsible for tuberization (Navarro et al. 2011).

F. Productivity

Productivity, understood as the amount of useful yield of a crop, is a loose term, as it might refer to fruits, grain, leaves, or number of flowers. However, all of these horticultural products are the result of plant growth. As the circadian clock controls growth, we present the evidence of direct relations between clock genes and this important trait.

One large family of genes in plants is the *CYCLING DNA BINDING WITH ONE FINGER FACTORS* (*CDF*). One of them, *CDF*, represses *CO* involved in flowering (Fornara et al. 2009). However, there are *CO* genes in nonflowering single cell algae such as *Chlamydomonas reinhardtii*. In this unicellular alga, *CrCO* plays a completely different role: it controls starch accumulation and the circadian control of cell cycle progression (Serrano et al. 2009). There are at least 30 *CDF* genes in rice and 36 in *Arabidopsis* (Lijavetzky et al. 2003). Recent work found that in rice, reduced expression of *RICE DOF DAILY FLUCTUATION 1* (*RDD1*)

by means of antisense RNA caused significant decrease in plant size, late flowering, and significant reduction in grain yield (Iwamoto et al. 2009). As *RDD1* maintains circadian gene expression under continuous light and continuous dark conditions, the authors concluded that *RDD1* is circadian regulated and plays a role in rice productivity by a mechanism that is not determined.

Recent work has shown that expression of the gene *BBX32* from *Arabidopsis* in soybean increases yield in grain in a multiyear in experiments performed in the United States and Argentina (Preuss et al. 2012). This gene was found to increase the period of pod and seed development while inhibiting leaf senescence. As *GmBBX32* shows circadian expression and its overexpression affects *GmTOC1* and *GmCCA1* expression, the authors conclude that genes related to the circadian clock are of major importance for productivity.

It remains to be determined the extent and tightness of the connection. Independent works linking GA to heterosis in cereals (Auger et al. 2005; Su et al. 2005; Zhang et al. 2007; Wang et al. 2009) might increase this emerging evidence.

G. Primary Metabolism

Primary metabolism comprises synthesis and degradation of macromolecules including RNA, protein, and carbohydrates. Early experiments using large-scale transcriptomics showed that the number of total genes from the *Arabidopsis* genome that showed daily cyclic expression was much larger than expected. Indeed, two independent experiments showed that between 6% and 8% of all the open reading frames could be circadian regulated (Harmer et al. 2000; Schaffer et al. 2001). These experiments were later replicated in other plants and the hypothesis does hold tight. Circadian regulation under light cycling involves 23% of the annotated genes in maize (Hayes et al. 2010), and 30–40% in rice and poplar (Filichkin et al. 2011). Experiments in *Arabidopsis* with a golden-standard annotated genome have shown that from 20,000 transcripts, 89% cycle and show a peak level at a certain time of the day when tested for photocycle, thermocycle, or circadian cycle. From these genes, 34–53% are diurnally regulated, and 6–31% are circadian regulated (Michael et al. 2008). Furthermore, thermocycles can drive half of the transcripts. Genes involved in large-scale processes show distinct patterns of phasing. For instance, expression of genes involved in DNA processing, energy metabolism, cell cycle, and protein synthesis is phased between midnight and dawn under the thermocycle conditions. In

contrast, the expression of those related to the energy metabolism is phased after dawn under photocycle conditions (Michael et al. 2008).

Rhythmic changes in mRNA do not always translate into circadian enzymatic activities as different isoforms can mask each other's activities when measured in bulk. Furthermore, accurate determination of individual protein levels is technically challenging compared to transcriptomic analyses. Work performed in rice has shown that proteins involved in carbohydrate metabolism, redox regulation, protein binding and folding, nitrogen and protein metabolism, energy conversion, and secondary metabolism display a light/dark cycling (Wang and Wang 2011).

At the metabolic level a number of works show effects of circadian clock mutants. The coordination of several apparently independent metabolic pathways has been found as a result of metabolomic characterization of *prr9*,*prr7*,*prr5* triple mutants that show regulation of chlorophyll, carotenoid, ABA, and alfa tocopherol synthesis modifications (Fukushima et al. 2009). The circadian clock seems to control nitrogen assimilation rates and free amino acid levels. The enzymes nitrate reductase, glutamine synthase, and glutamine dehydrogenase show circadian oscillation (Lillo and Meyer 2001; Lillo et al. 2001). Although the enzyme activities may fluctuate as a result of circadian clock control, only few amino acids show quantitative changes in constant light (Fukushima et al. 2009), indicating that nitrogen levels might be more stable than carbohydrate levels.

Altogether primary metabolism seems to be extensively controlled by the circadian clock (Farre 2012). The best evidence is at the large-scale transcriptional level. Changes in protein levels or in certain metabolic pathways seem to be a case-by-case situation. As carbohydrate metabolism plays such an important role in plants and it has been studied with more detail, we have reviewed it separately.

H. Starch Metabolism

Plant productivity is not a simple equation of carbon uptake. Plant photosynthate is converted into raw biomass for growth, stored, or lost as a result of photorespiration, emission of volatiles, or root exudates. Partitioning of photosynthate between storage (starch, fructan, and lipids) or growth is currently not understood. The so-called transient starch that is produced during the light period of the day, and consumed during the night to foster growth and inner metabolism, is the key to plant productivity (Smith and Stitt 2007; Sulpice et al. 2009). A series of *Arabidopsis* mutants that cannot degrade

starch at the proper speed or cannot accumulate starch show decreased growth rates (Graf and Smith 2011).

Starch granules are in equilibrium of synthesis during the day and degradation during the night. In snapdragon, the *GRANULE BOUND STARCH SYNTHASE*, an ortholog of the *waxy* gene in maize, is circadian regulated (Merida et al. 1999). Further work in *Arabidopsis* has shown that *GBSS1* oscillation is abolished by overexpression of *CCA1* (Tenorio et al. 2003). This indicates that starch granule synthesis is directly controlled by the circadian clock.

Plants can measure day and night length with a great deal of accuracy, and starch degradation is adjusted to night length, thus ensuring a proper carbohydrate balance until dawn. This balance or speed of degradation becomes adjusted every day by the circadian clock. Elegant experiments performed in *Arabidopsis* have shown that when plants are grown for a period of time at a certain light regime such as 12 h light/12 h dark, a single elongated night causes a situation of carbon starvation during the period of the first extended night. This is immediately corrected to accommodate a new speed of starch degradation according to the new expected night lengths (Graf et al. 2010). Giving an early night, that is, starting the dark period before the schedule, causes an immediate rearrangement of starch metabolism to decrease degradation speed and maintain levels until dawn.

Studies performed in maize, a C4 plant, show that key enzymes involved in starch synthesis display circadian regulation. Expression of *AGPL*, a subunit of AGPase that is the major regulatory enzyme in starch biosynthesis, converting glucose 6-phosphate to ADP-glucose, the substrate for starch synthase, peaks at dawn. Two STARCH SYNTHASE transcripts peak early in the morning (Khan et al. 2010), showing that, like in *Arabidopsis*, maize anticipates carbon requirements and launches the starch synthesis machinery to be ready for action when photosynthesis starts.

I. Photosynthesis

The light-harvesting CHLOROPHYLL a/b protein, small subunit of RIBULOSE-1,5-BISPHOSPHATE CARBOXYLASE, and early light-induced protein were the first genes found to cycle in a circadian fashion in peas (Kloppstech 1985). The expression of the photosynthesis apparatus genes shows daily maxima at the end of the night. In contrast, those with tasks in electron transport photosystems show their maximum transcriptional activity during the day. This is true in

maize (Khan et al. 2010), rice, poplar (Filichkin et al. 2011), or *Arabidopsis* (Harmer et al. 2000).

Circadian assimilation of CO_2 has been demonstrated in *Phaseolus* leaves (Hennessey and Field 1991). Circadian regulation of stomatal opening, electron transport, and light-induced electron flow also occurs in legumes (Fredeen et al. 1991; Hennessey et al. 1993), indicating that the photosynthetic process as a whole is strictly coordinated. Studies using *Arabidopsis* mutants have shown that photosynthesis is affected in clock mutants causing reduced growth and fitness (Dodd et al. 2005). In spite of a cause–effect of circadian regulation on photosynthesis, our mechanistic understanding of how it happens is shallow, suggesting that new discoveries in this field could uncover important advances in terms of productivity.

Plants with CAM photosynthesis behave opposite to C3 and C4 metabolic-based plants as they absorb CO_2 during the night (Mizrahi et al. 1997). Studies performed in cactus pear, an obligate CAM, show that the circadian clock oscillator is different from that in *Arabidopsis* (Mallona et al. 2011). Two clock genes *OfiPRR9* and *OfiCCA1* display two significant expression peaks, one in the morning, and the second in the evening. This would indicate that the evolution of photosynthesis could be the result of changes in a few circadian clock genes that control it, rather than the modification of hundreds of genes at their regulatory regions.

J. Scent Production

Plant scent production is among the most complex and least well-understood traits. Although a great deal of information is available about the biochemical pathways of volatile biosynthesis, there are gaps in our understanding on how these pathways are controlled during development and modulated by the environment. It is known, however, that fragrance is involved in pest repellence, and pollinator and seed-dispersing animal attraction. From an economic perspective, scent is probably one of the most important traits as it is directly responsible of the flavor and aroma of edible crops and their products. Furthermore, changes in composition of plant volatiles can give resistance to pests (Gatehouse 2002; Kessler and Baldwin 2002). Most flowers emit scent during certain day periods in order to attract specific pollinators. Rhythmic emission of floral scent has been found in many plants including rose (Helsper et al. 1998), orchids (*Odontoglossum constrictum*), citron (*Citrus medica*), *Hoya carnosa*, and *Stephanotis floribunda* (Matile and Altenburger 1988). Circadian

regulation of these rhythmic emissions was demonstrated using extended periods of light and dark. Snapdragon and petunia show opposite volatile emission patterns. Snapdragon produces volatiles in the morning, whereas petunia does it in the evening, but both emit in a rhythmic fashion (Kolosova et al. 2001).

Volatile compounds identified in plants include fatty acid derivatives, benzenoids, phenylpropanoids, isoprenoids, and nitrogen- and sulfur-containing compounds with over 1,700 independent compounds identified in different plants (Knudsen et al. 1993). Many of these are produced in vegetative parts as a result of response to insect attacks but the biochemical pathways and many of the genes involved in their synthesis are either the same or paralogs with a specific function in floral scent production (Dudareva et al. 2004; Pichersky et al. 2006).

Methyl benzoate is one of the major volatile compounds produced from the phenylpropanoid pathway. This compound is produced by methylation of benzoic acid in a reaction catalyzed by benzoic acid carboxyl methyltransferase (BAMT) and follows a rhythmic oscillation. Analysis of BAMT activity in snapdragon petals shows slight variations in enzyme activity during day/night cycles, following a rhythmic pattern. The coincidence of high levels of BAMT enzymatic activity with low levels of methyl benzoate emission during the night period, as well as during continuous night conditions, suggests that BAMT activity is not the factor controlling oscillations. Therefore, it is thought that the amount of benzoic acid available in petal cells is the limiting/driving factor (Kolosova 2001). Indeed, measuring endogenous benzoic acid at different times of day/night cycle in snapdragon demonstrated that BA follows a circadian rhythm, reaching maximum levels during the day and minimum levels during the night. Moreover, the rhythmic fluctuation of benzoic acid levels may be caused by the rhythmic regulation of phenylalanine ammonia-lyase (PAL) and/or other enzymes upstream in the biosynthesis pathway. Analysis of PAL activity shows a difference in oscillations by almost 12 h, compared to BAMT activity, at the transcriptional level (Kolosova et al. 2001). The mRNA levels are constant under constant night conditions, a result consistent with the theory that light signalling regulates the amounts of BAMTand PAL mRNA (Fig. 1.2).

Methyl benzoate is also one of the major volatile compounds emitted by *Nicotiana silvestris*, *Nicotiana. suaveolens* (Loughrin et al. 1991), and Petunia (Kolosova et al. 2001). Unlike snapdragon, these plants reach maximum levels of emission during the night, indicating that it is not the biochemical pathway but rather the regulation of emission the

one important factor in terms of harvesting tissue for extraction of chemicals. Additionally, other phenylpropanoids, such as phenethyl alcohol and phenethyl acetate, have been found in the floret tissue of *Trifolium repens*. These compounds are released from their glucoside conjugates by a β-glucosidase. Analysis in *T. repens* shows that the concentration of volatiles is highest both in the tissue and in the headspace just prior to flowering (Jakobsen and Christensen 2002). As the relationship between volatiles in the tissue and emitted volatiles is not linear, the authors interpret that a second factor is responsible for the rhythmic emission, a hypothesis formulated earlier as a result of similar data observed in other plants (Altenburger and Matile 1990).

Terpenoids are derived from two different pathways, the methylerythritol phosphate (MEP) pathway that provides isopentenyl diphosphate IPP and dimethylallyl diphosphate for hemiterpene, monoterpene, and diterpene biosynthesis, and the mevalonate pathway that takes part in sesquiterpene biosynthesis. Nevertheless, floral volatile terpenes are only derived from the MEP pathway (Dudareva et al. 2005). Experiments about volatile composition in *Antirrhinum* confirm that the mayor terpenoids emitted are three monoterpenes, myrcene, (*E*)-β-ocimene and linalool, and the sesquiterpene nerolidol (Dudareva et al. 2003). Furthermore, all of these compounds are mainly emitted during the day following a rhythmic pattern that coincides with MEP activity. This oscillation is strongly correlated with the pattern of 1-desoxy-D-xylulose phosphate synthase (DXPS) gene expression, which is one of the first steps of the MEB pathway (Dudareva et al. 2003). This information, together with data that confirm that during DD continuous dark periods oscillations of myrcene and nerolidol continue under free-running conditions, indicates that circadian clock is responsible for volatile terpene rhythmic emission.

Another example of terpenoids rhythmic emission is found in rose flowers. The main terpenes emitted are germacrene D and geranyl acetate. Both compounds oscillate in the same way during the daily cycle with a peak early in the light period. However, expressions of their biosynthetic genes are dramatically different. On the one hand, ALCOHOL ACETYL TRANSFERASE (*RhAAT*), the geranyl acetate biosynthetic gene, maintains rhythmic expression under continuous illumination and/or continuous darkness and the endogenous level of this compound also cycles. This information indicates that the circadian clock regulates geranyl acetate emission. On the other hand, the endogenous level of germacrene D and the expression of its biosynthetic gene, *GERMACRENE D SYNTHASE* (*RhGDS*), are constant throughout the day and oscillations of germacrene D emission stop

under LL. This suggests that the mechanism of germacrene D production is light dependent (Hendel-Rahmanim et al. 2007).

Some terpenoids are produced from carotenoid degradation. These compounds are important in floral scent and fruit aroma (Simkin et al. 2004a). Indeed, they are correlated with taste ratings (Vogel et al. 2010). The volatiles, β-ionone, pseudoionone, and geranylacetone, are produced by the *CAROTENOID CLEAVAGE DIOXIGENASE 1* (*CCD1*) in tomato (Simkin et al. 2004a) as well as in Petunia (Simkin et al. 2004b). In Petunia, this gene shows oscillations in normal conditions of day/night cycle. Under DD and LL conditions, transcript levels maintain this rhythm but the decrease in transcript levels and the residual oscillations observed in constant darkness suggest that *PhCCD1* is regulated by both light and circadian mechanisms (Simkin et al. 2004a).

Osmanthus fragrans var. *aurantiacus* is one of the plants emitting the highest diversity of carotenoid-derived scent compounds. In this plant, carotenoid content, volatile emissions, and *Of*CCD1 transcript levels are subjected to rhythmic changes increasing during daylight hours. The two primary carotene products of *Osmanthus* flowers are α- and β-ionone. As in petunia, the β-ionone emission is still increasing when transcript levels begin decreasing during the afternoon. It suggests that there may be some limitation due to the substrate availability. In addition, analysis in *Osmanthus* suggests that volatile emission is light inducible and is controlled by the circadian clock (Baldermann et al. 2010).

Altogether, scent production is controlled in one way or another by the circadian clock. This is true for scent compounds produced from the phenylpropanoid pathway, the nonmevalonate pathway, terpenoids produced from both synthesis and fatty acid degradation. The complexity of scent and the possible points of control at the RNA, protein, and metabolite level make it a challenge worth taking for future studies.

V. ADAPTATION TO BIOTIC AND ABIOTIC STRESS

In spite of our improvements in cultural practices and breeding material, abiotic and biotic stresses represent the major challenge for productivity and in postharvest loss of crops. These two types of stresses have been linked to circadian regulation at different paces and for different reasons. While the evidence of circadian clock relations to pathogen resistance is only recent and is the result of transcriptomic studies, the connection with abiotic stress has been known for a longer

period of time and some details are known about how they connect. We describe the work in *Arabidopsis* that has as special feature its natural resistance to cold compared to many horticultural crops such as tomato, cucumber, or cut flowers, just to name a few. Current evidence in horticultural crops is lacking and this is probably one of the fields of work where more profit could be obtained, as some of the pathways are understood with good detail.

A. Pathogen Resistance

Pathogen resistance was thought to be a process dependent on resistance genes but evidence has shown that time of the day and environmental signals also play a role in the way plants react to pathogens. First evidence about a connection between circadian clock and pathogen resistance was obtained in *Arabidopsis* exposed to *Pseudomonas syringae*. These plants showed an upregulation of a transcript, *PCC1*, that displayed a circadian expression pattern in plants treated with $MgCl_2$, suggesting that the upregulation was not totally related to the presence of the bacteria (Sauerbrunn and Schlaich 2004). Furthermore, plants overexpressing *PCC1* are resistant to virulent oomycetes, indicating a potential circadian component in pathogen resistance. A phosphate transporter *PHT4* has been shown to be important for the defense against *P. syringae*, and again this gene is circadian regulated indicating that at least part of the components involved in plant defense are under control of the circadian clock (Wang et al. 2011a).

Among the day signals involved in plant defense light stands as an important cue. Experiments performed in *Arabidopsis* have shown that launching of systemic acquired resistance requires signal transduction of PHYA and PHYB (Griebel and Zeier 2008). Biotrophic pathogens depend, to a large extent, on the plant metabolic status. The main defense strategy against biotrophic pathogens is based on resistance genes or R genes that launch programmed cell death (PCD). Recent analysis of 22 new mutants compromised in resistance against *Hyaloperonospora arabidopsidis* (*Hpa*), an obligate biotrophic oomycete pathogen that causes downy mildew disease, was carried out in *Arabidopsis* (Wang et al. 2011b). Bioinformatic analysis showed that the regulatory region of 14 genes had an enrichment of night elements or CCA1/binding sites, and showed circadian gene expression. This led to the direct testing of resistance in circadian clock gene mutants. Mutants in *CCA1* and *ZTL* had compromised resistance to pathogens whereas overexpressors of *CCA1* showed increased resistance. These results suggest that the circadian clock launches a preventive basal resistance

in the absence of pathogens, "anticipating" attack according to a circadian schedule.

Recent work in wheat has shown that effector-triggered susceptibility to necrotic pathogens is under control of a gene *TSN1* with features typical of plant resistance genes (Faris et al. 2010). Attempts to identify changes in gene expression levels failed to give a clear pattern, leading the authors to perform samplings with 3 h intervals. This allowed uncovering a circadian regulation of *TSN1*, indicating that circadian control of at least part of the pathogenesis response is a common feature to higher plants.

The accumulation of evidence suggesting a role of the circadian clock apparatus in controlling plant pathogen resistance data supports a connection between both processes. As a result, experiments in growth chambers should take into account time of the day, light, and temperature as variables that profoundly affect experimental outcomes. Experiments done in naturally illuminated greenhouses or in the field will be under truly natural conditions but timing of infections might also play a role.

The circadian behavior of insects seems to be matched by plants. Recent work has shown that cabbage loopers (*Trichoplusia ni*) have a circadian feeding behavior. When plants are entrained with the rhythm of the insects, they suffer moderate leaf loss compared to those entrained out of phase (Goodspeed et al. 2012). The accumulation of jasmonic acid and salicilate that act in opposite ways also shows opposite phase accumulations, indicating that these two compounds are under circadian regulation. A proper circadian clock seems to be required to launch a proper defense against insect attacks.

B. Cold Sensing and Cold Tolerance

Adaptation of plants to cold or cold acclimation occurs when plants gain tolerance to cold while exposed to chilling (nonfreezing temperatures) for a short period of time. Cold acclimation is thought to occur via orchestrated activation of several parallel transcriptional pathways (Chinnusamy et al. 2006). Although low-temperature receptors are not well understood in plants, there is ample evidence that cold causes changes in gene expression that results in increased cold tolerance.

One conserved mode of cold response is via the activation of the C-*REPEAT BINDING FACTOR* genes or CBFs, also known as *DEHYDRATION* RESPONSIVE ELEMENT *BINDING PROTEINS* or DREBs. The CBF/DREB family of transcription factors contains AP2 DNA-binding domains, a protein domain specific to plants (Okamuro et al. 1997;

Gilmour et al. 1998). Misexpression of *CBFs* in different plants, such as tomato (Hsieh et al. 2004), *Arabidopsis* (Jaglo-Ottosen et al. 1998; Gilmour et al. 2000), *Brassica* (Savitch et al. 2005), tobacco (Gutha and Reddy 2008), grapevine (Tillett et al. 2011), or apples (Wisniewski et al. 2011), causes important increases in cold resistance. Pleiotropic effects accompany this increased resistance, and in the case of apples, it causes modification of flowering time. The decreased growth observed under cold conditions can be mechanistically explained, at least in part, because *CBF* activates GA2 oxidase synthesis that causes a decrease in the levels of active GAs (Achard et al. 2008). The data available show that the CBF transcription factors can activate a cold response in different plants improving cold tolerance.

Daily fluctuations in temperature can be larger than 20°C in many climates and pioneering work showed that activation of cold adaptation occurs when plants sense low temperatures during day but not during the night. The interpretation is that decreases in day temperatures are indicative of seasonal changes, whereas low night temperatures may not. Several independent experiments have shown that the circadian clock gates activation of the CBF pathway. Expression of *CBF* genes is increased if the cold treatment occurs 4 h after dawn compared to 4 h after dusk (Fowler et al. 2005). Experiments performed in *cca1 lhy* double mutants show that *CBF1*, *CBF2*, and *CBF3* are not properly activated by cold, demonstrating a connection of the circadian clock machinery with cold response. Importantly CCA1 and LHY bind directly to the *CBF* locus that comprises three genes, the aforementioned *CBF1*, *CBF2*, and *CBF3*, thus showing that the control is direct (Dong et al. 2011). Thus, the circadian clock would be involved in activation of the CBF regulon. Notably, *cca1*,*lhy* double mutants are compromised in cold acclimation and show higher death rates than wild type when temperatures drop (Dong et al. 2011).

Expression of *CBF* without activation by cold has been reported also in triple mutants for the morning loop genes *PRR9*, *PRR7*, and *PRR5* (Nakamichi et al. 2009). This line called *d975* (Nakamichi et al. 2005) by the authors displays an extreme late flowering phenotype and can survive at −5°C whereas wild-type plants display complete mortality under the experimental setup of the authors (Nakamichi et al. 2009). The *d975* line displays constitutive expression of *CBF1*, *CBF2*, and *CBF3*, thus explaining the observed resistance to cold, and also to other abiotic stresses including drought and salinity. The interaction between salinity, cold, and drought stress is a general response as abiotic stresses share some components in the signaling process (Seki et al. 2002), and CBF1/DREB1 is one of them (Kasuga et al. 1999).

From a practical perspective, the importance of the current data on circadian regulation stems from two aspects. First, identification of cold resistance cultivars could be the result of loss of function alleles that show recessive or additive segregation. But perhaps, more relevant is the way experiments are performed, for example, in growth chambers rather than in the field. Indeed, the number of genes found to change by cold varied depending on when the cold treatment was given to the plants, showing a higher level when cold was applied during the day (Bieniawska et al. 2008). The fact that cold temperature disrupts the clock in *Arabidopsis* and chestnut (Ramos et al. 2005; Bieniawska et al. 2008; Ibañez et al. 2008) underscores the point and understanding of clock outputs could help us improve crops for this difficult trait.

Although the *CBF*/*DREB* pathway is understood to some extent, other pathways are responsible for cold acclimation. It was found that mutations in *GI* cause hypersensitivity to cold (Cao et al. 2005), but this resistance did not cause increased levels of *CBF*/*DREB* expression. This suggests that the circadian clock machinery has several points of interaction with the cold response.

Postharvest management of fruits, vegetables, and flowers is performed under conditions matching the industrial chain (Fernandez-Trujillo et al. 1998; Malacrida et al. 2006; Gomez di Marco et al. 2009). In most cases, fresh fruits, vegetables, and flowers are stored in cold chambers in the dark with temperatures ranging between 2 and 10°C, depending on the availability of the facility. It is interesting to note that experiments performed mimicking industrial conditions failed to find *CBF* activation by cold in tomato fruits (Weiss and Egea-Cortines 2009). These results suggest that under certain circumstances experimental designs geared toward established industrial processes might hamper identification of circadian processes.

VI. SUMMARY AND CONCLUSIONS

The involvement of the circadian clock in so many traits that span development, productivity, and resistance to both biotic and abiotic stresses indicates that it should be taken into account when scientists design experiments. Physiological parameters and genetic studies should be carefully controlled with the following aspects in mind:

1. In terms of horticultural research, proper experimental design should take into account the circadian clock scheme if any of the traits being studied are known to be circadian clock regulated.

Many studies take into account the time of the day during sampling, although, in most cases, the sampling times are too far apart to detect a circadian effect due to the aliasing problem (Table 1.1).

2. We have not covered the mathematical analysis of circadian clock data to be able to uncover differences between samples. This is by no means a trivial aspect that would require a complete review about the topic. Mathematical methods include fast Fourier-transform analysis (Bitter et al. 1973), hierarchical segmentation (Fushing et al. 2009), maximum entropy (Langmead et al. 2002), or nonparametric methods (Hughes et al. 2010); see Refinetti et al. (2007) for a review on procedures. Data handling can become cumbersome if we take samples every 2 h as compared to a sample per day, making imperative an experimental design tailored to pattern identification based on time series analysis.
3. The number of candidate genes influencing a trait should include clock or related genes. This is especially true for flowering time where most natural variation found in trees and cereals seems to fall in this group and not into pure flowering time genes. However, in those cases where candidate gene approaches are carried out, clock genes should be included as part of the analysis.

ACKNOWLEDGMENTS

Work in the lab of MEC and JW was supported by Ministerio de Ciencia e Innovación-FEDER (project BFU-2010-15843) and Fundación Séneca (project 11895/PI/09). We would like to thank Rob Mcclung and Isabel Allona for critics and comments in the manuscript.

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Response of Perennial Horticultural Crops to Climate Change

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Horticultural Reviews, Volume 41, First Edition. Edited by Jules Janick.
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ABSTRACT

Perennial horticultural crop production is sensitive to temperature, water availability, solar radiation, air pollution, and CO_2. The value of perennial horticultural crops is derived from not only the quantity but also the quality of the harvested product. Perennial crop production is not easily moved as the climatic nature of a region changes due to many socio-economic factors including long reestablishment periods, nearness to processing plants, availability of labor, and accessible markets. Two deciduous temperate fruit crops (apple and grape), two evergreen subtropical crops (citrus and coffee), and two tropical crops (banana/plantain and cacao) were selected as representative case studies. We evaluated the literature affecting the production of these crops to provide an overview of the potential impacts of climate change. The literature survey identified limiting factors and provide information in assessing future climate change impacts. Although lack of data precludes a comprehensive assessment of CO_2 responses and interactions with other abiotic (and biotic) factors for most of the crops analyzed, the response of these crops to a doubling of atmospheric CO_2 is evaluated. The CO_2 fertilization effect may be amplified and sustained longer for perennial horticultural crops if other resources (e.g., nutrients and water availability) are amply supplied, and if proper management options (e.g., spacing, pruning, thinning) are practiced to facilitate the prolonged CO_2 effects. This will likely require maintaining intensive and environmentally sustainable cropping systems. In addition, the positive CO_2 effect may be negated by the detrimental effects of extreme temperatures on phenology, carbon sinks, reproductive physiology, and changes in the disease/pest complex in the agroecosystem. There is a lack of information on the yield and quality responses of perennial horticultural crops to elevated CO_2 and the interaction with warming temperatures. Innovative research, modeling, and field trials for low-input cropping systems that integrate existing knowledge to capitalize on the benefits of elevated CO_2, while minimizing the input and costs, and temperature stresses are required to improve understanding in these crop species' responses to climate change and will better address adaptation and mitigation needs in these highly important and complex cropping systems.

KEYWORDS: apple; banana; cacao; carbon dioxide; coffee; citrus; disease; grape; insect; ozone; solar radiation; water use

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ABBREVIATIONS

BBTD	Banana bunchy top disease
BBTV	Banana bunchy top virus
BLS	Black leaf streak
CCCMA	Canadian Center for Climate Modelling and Analysis
CCSM	NCAR's Community Climate System Model
CCSM3	NCAR's Community Climate System Model version 3
CGCM3	CCCMA's Coupled Global Climate Model version 3
CV	Coefficient of variance
CVC	Citrus variegated chlorosis

ETP	Evapotranspiration
EU	European Union
FACE	Free-air CO_2 enrichment
FTA	Free Trade Agreement
GCM	Global Climate Model, also referred to as Global Circulation Model
IPCC	Intergovernmental Panel on Climate Change
LAI	Leaf area index
NCAR	National Center for Atmospheric Research, United States
PES	Payments for Environmental Services
RCP	Representative Concentrations Pathways (Moss et al. 2010)
RCP4.5	One of the RCP scenarios used for the Coupled Model Intercomparison Project phase 5 (CMIP5) used for the IPCC Fifth Assessment Report (AR5). RCP4.5 describes an stabilization scenario where the total radiative forcing is stabilized at 4.5 W/m^2 before 2100 by the employment of a range of technologies for reducing greenhouse gas emissions (see Clarke et al. 2007 for details).
RCP6.0	One of the RCP scenarios. An scenario in which the radiative forcing is stabilized at 6.0 W/m^2 before 2100 (see Fujino et al. 2006; Hijioka et al. 2008 for full details).
RH	Relative humidity
SRES	Special Report on Emissions Scenarios
SRES-A1B	One of the SRES scenarios used in the IPCC fourth assessment report. This scenario describes a future world of very rapid economic growth, global population that peaks in the mid-century and declines thereafter, and rapid introduction of new and more efficient technologies
SRES-A2	One of the SRES scenarios used in the IPCC fourth assessment report. This scenario describes a very heterogeneous world with continuously increasing global population and regionally oriented economic growth that is more fragmented and slower than in other storylines
SRES-B1	One of the SRES scenarios used in the IPCC fourth assessment report. This scenario describes a mitigation-oriented world, with lower population growth and globalized adoption of energy- and carbon-efficient technologies. In this scenario, emissions increase at a far lower rate than SRES-A2, and peak in 2050s
SWE	Snow water equivalent
VPD	Vapor pressure deficit
WUE	Water use efficiency

I. INTRODUCTION

Climate change brings both challenges and opportunities to agriculture for sustaining food and energy supplies while protecting and maintaining the environment and natural resources essential for global food production. Perennial fruit crops such as apple, banana, grape, and citrus are important components of human diet providing fiber, vitamins, antioxidants, and nutrients such as manganese and calcium that can improve human health but are often limited in cereals and other major food crops. Perennial horticultural crops are also high value agricultural commodities that are important for the local as well as the global economy. For example, coffee, grape, banana, and apple were ranked among the top 20 agricultural value commodities that included row crops and animal products in terms of their production value worldwide in 2010 (FAOSTAT 2012). Perennial horticultural crops occupy a unique and important agricultural niche as they provide important health benefits, serve as income sources, especially in subsistence and smallholder farms (e.g., banana and plantain in Sub-Saharan Africa), and deliver additional benefits in agroecosystems such as carbon sequestration, erosion protection, biodiversity, and water retention. In addition, perennial crops have a long lead-time for adaptation. Thus, adaptation strategies, particularly those involving substantial transformation, must be planned and implemented in a rational manner. For these reasons, it is imperative to understand the responses of these crops to changes in climates and the implications of these responses to overall agroecosystem responses.

Like all other crops, perennial horticultural crops are sensitive to temperature, water availability, solar radiation, air pollution, and CO_2. Increased atmospheric CO_2 generally increases growth rate and yield, resulting in a higher accumulation of biomass, fruit production and quality in both temperate and tropical fruit trees (Idso and Kimball 1997; Centritto et al. 1999a,b; Kimball et al. 2007). Nevertheless, two main characteristics make perennial systems unique in nature: (1) the value of perennial horticultural crops is derived from not only the quantity but also the quality of the harvested product (e.g., the size of a peach, the red blush on an apple, the color of banana, and the oils and aromatics in grapes, coffee, and cocoa); and (2) in contrast to annual agronomic crops, perennial crop production is not easily moved as the climatic nature of a region changes due to many socio-economic factors including long reestablishment periods, nearness to processing plants, availability of labor, and accessible markets. Climate change further complicates perennial crop production.

Rising atmospheric concentrations of CO_2 and other greenhouse gases have proven to substantially impact the dynamics of the earth system by increasing radiative forcing (IPCC 2007a). According to the Intergovernmental Panel on Climate Change (IPCC), these changes will cause increasing temperatures, thus causing alterations to the whole hydrological cycle (IPCC 2007a; Gosling and Arnell 2011; Joshi et al. 2011) and also altering seasonal and inter-annual rainfall patterns (Meehl et al. 2007; Foster and Rahmstorf 2011; Stevenson et al. 2011. Although the exact response of the climate system is highly uncertain (Meehl et al. 2007; Hawkins and Sutton 2009), global mean temperatures are expected to rise in the range 1.5–4.0°C, depending on the emissions scenario (Nakícenovíc and Swart 2000; Moss et al. 2010), with the northern hemisphere warming at higher rates than the tropics, with varying (and uncertain) changes in precipitation patterns (Hawkins and Sutton 2011; Joshi et al. 2011). Changes in climates are expected to lead to challenges and opportunities in present-day agricultural systems. State-of-the-art climate change models indicate that the +2°C threshold (beyond which effects of climate change are predicted to be irreversible) is predicted to be crossed around 2050s globally (SRES-A1B), and between 2030s and 2040s across most of the southern hemisphere. In most of Asia (primarily China and India), +2°C could be reached in the early 2030s, whereas this threshold is predicted to be crossed by 2050s in the United States and most of central America (SRES-A1B emissions scenario, Joshi et al. 2011). Recent analyses with the new state-of-the-art climate model ensemble (i.e., CMIP5) indicate similar figures under some of the RCP scenarios, particularly RCP 4.5 and RCP 6.0 (see Meinshausen et al. 2011; Knutti and Sedlácek 2012). Under a more mitigation-oriented scenario (SRES-B1), the same threshold is likely to be reached globally about 25 years later (Joshi et al. 2011), depicting the importance of climate change mitigation in "buying" time for adaptation, here broadly defined as the incorporation of new technology and germplasm into existing cropping systems as well as relocation of cropping systems to regions with environmental conditions more favorable to the current cropping system technology. Despite uncertainties, some extreme events have also been predicted to increase in frequency and severity as a result of the shift in mean conditions and/or changes in climate variability (McCarthy et al. 2001; Easterling 2002). These extreme events and climatic variation will also pose additional challenges to perennial horticultural cropping systems. These changes have a number of implications for agricultural systems including the trade-off between adaptation and mitigation and the importance of eco-efficient adaptation strategies in which time is a critical constraint for adaptation, particularly for perennial crops (Wolfe et al. 2005; Lobell

et al. 2006; Mathur et al. 2012). Changes in climates are expected to shift the highly specified niches of coffee (Schroth et al. 2009), cacao (Läderach et al. 2013), and Musa crops (Ramirez et al. 2011; Van den Bergh et al. 2012). Although similar analyses do not exist for other perennial crops, it is highly likely that similar changes would occur in other perennial systems (Wolfe et al. 2005). A variety of phenological changes have also been predicted for apple (Eccel et al. 2009) and grapevine (Jones et al. 2005; Petrie and Sadras 2008; Duchene et al. 2010), as two of the most important perennial crop systems in temperate regions.

The value of a horticultural crop is determined and limited at many points before and during the growing season because the value is based on not only production quantities (i.e., biomass, yield) but also size, color, chemical composition, firmness, and other measurable criteria. Several examples exist that illustrate the sensitivities and the complexity of responses of perennial crop systems to climate change and climate variability (Lobell et al. 2006). For instance, in the year prior to harvest in apple production systems, floral initiation occurs in late spring/early summer (Abbott 1970) and high temperatures reduce the number and vigor of the potential floral buds (Tromp 1976, 1980). During the dormant winter months, extreme cold can kill plant tissues and warming periods can deacclimate buds making them susceptible to later winter damage (Burke et al. 1976). In the spring, frost periods can kill flowers (Burke et al. 1976). As the fruits are growing in the spring, high temperature can reduce cell division resulting in small fruits (Caprio and Quamme 1999). During the summer months, high temperature can cause sunburn damage, which reduces production efficiency, that is, pack-out at harvest (Caprio and Quamme 1999). High temperatures can also alter maturity, fruit firmness, color development, and decrease the suitability of fruit for short- or long-term storage (Woolf and Ferguson 2000).

Adaptation strategies are thus needed for perennial crops, but these need to be carefully planned. Perennial cropping systems are commonly in place as long as 30 years and this poses a challenge with a changing climate since rapid changes in climates could imply that a cultivar planted today would not be adapted sometime in the near future. In addition, the development of new cultivars for perennial horticultural crops commonly requires 15–30+ years and is highly driven by market demands, further limiting the opportunity to shift cultivars and the overall cultivar variation. A clear example of this is commercial dessert banana production systems, which rely on one single cultivar ('Cavendish' banana) due to the lack of others with enough market acceptability (Heslop-Harrison and Schwarzacher 2007). Nevertheless, the socio-economic factors, market demand for specific cultivar characteristics, and inability to rapidly identify adapted cultivars do not necessarily make the perennial horticultural cropping

systems more vulnerable to climate change, but they do call attention to the needs of the industry for new cultural and genetic tools and research to adapt in a timely and economic manner.

Past climate changes have already affected perennial cropping systems, and modeling suggests that future warming will continue to impact cropping systems throughout the world. With the aim of identifying horticultural crop sensitivities to climate change and providing information for use by crop/climate modelers and policy makers in assessing future climate change impacts, a literature review was carried out to provide an overview of the impacts of climate change on horticultural crops and six were selected: two deciduous fruit crops (apple and grape), two evergreen subtropical crops (citrus and coffee), and two tropical crops (banana/plantain and cacao). Sufficient peer-reviewed literature has been generated to provide a perspective of past and future climate change effects on these key crops. Without being excessively comprehensive (as each case study was drawn from a number of highly detailed studies), the response and interactions of perennial horticultural crops with abiotic factors associated with climate change are documented and for the first time put together into a review. Crop responses to environmental variables are documented and where needed, specific thresholds related to these responses are also provided. Finally, general cross-cutting and crop-specific future research priorities, as well as adaptation strategies, are identified and discussed.

II. RESPONSE OF PERENNIAL HORTICULTURAL CROPS WITH ABIOTIC FACTORS ASSOCIATED WITH CLIMATE CHANGE

A. Elevated CO_2

In general, woody plants have shown sustained stimulation of photosynthesis and growth under elevated CO_2 (Curtis and Wang 1998) with little down-regulatory acclimation in the field studies using open-top chambers (Norby et al. 1999) or free-air CO_2 enrichment (FACE) (Ainsworth and Long 2005). Experimental studies on perennial horticultural crops have reported similar results and patterns in photosynthesis and growth in response to elevated CO_2. Note that studies reviewed here examined crop responses to roughly doubled CO_2 relative to a base ambient CO_2 ranging from 330 to 400 ppm with most studies using 350 ppm as the base level. For example, leaf-area based net CO_2 assimilation at saturating light and growth CO_2 (A_{max}) was enhanced by an average of 44% in the selected fruit crops in response to roughly doubled CO_2 (NCA 2012). Some of these crops have exhibited detectable photosynthetic down-regulations (e.g., apple, Chen

et al. 2002a,b; citrus, Adam et al. 2004) while others showed mixed (cherry, Druta 2001; Centritto 2005) or little acclamatory responses (e.g., grape, Moutinho-Pereira et al. 2009; peach, Centritto et al. 2002) (also see NCA 2012). Stomatal conductance to water vapor (g_s) in general was reduced in these crops grown at elevated CO_2 by an average of 23%, which is similar to reported tree response in forest ecosystems (Medlyn et al. 2001). This increased A with reduced g_s under elevated CO_2 resulted in a considerable increase in leaf water use efficiency (58%). A similar response was reported at the crop-level water use efficiency (WUE) in several crops (i.e., cherry, citrus, and peach) (NCA 2012). However, despite a considerable increase in water use efficiency at both leaf and crop levels, the actual amount of crop water use remained similar. This is likely because of an increase in tree leaf area offsetting the increase in WUE per leaf area under elevated CO_2.

On average, aboveground biomass increased by 60% in elevated CO_2 across the crops reviewed (NCA 2012); however, root:shoot ratio remained similar in apple (Chen et al. 2002a,b) and citrus (Kimball et al. 2007) while it slightly increased in cherry (Druta 2001). A rapid increase in tree leaf area during the early season accelerates early growth and biomass accumulation especially in open canopies (referred to as "compound interest effect" by some) (Norby et al. 1999; Korner 2006). However, this accelerated growth response such as shown in apple (Chen et al. 2001) and cherry (Centritto et al. 1999a,b) is likely to be less pronounced in a full canopy in which the leaf area index (LAI) is more or less stable so that competition for light and other resource is high (Norby et al. 1999). This is particularly true for natural systems where below-ground resources such as nutrients, soil moisture, and space are major limiting factors. It has been suggested that long-term, natural responses to increasing CO_2 are likely to be less drastic than what has been reported in short-term experiments where plant–soil and/or plant–atmosphere connection have been decoupled (Korner 2006). However, many orchard and other perennial horticultural cropping systems are highly managed with optimal fertilization, irrigation, spacing, canopy management, thinning and pruning, and other cultural practices to realize high yield and produce quality. With these management practices that minimize resource limitations, it is conceivable that initial stimulation of high CO_2 is sustained and in some cases amplified in perennial horticultural crops. One such case study is a long-term CO_2 enrichment experiment comparing responses at ~350 and ~650 ppm of growth CO_2 on citrus that ran for 17 years in Phoenix, AZ (Kimball et al. 2007). In this experiment, the enhancement in biomass accumulation under elevated CO_2 was sustained at 70% after a peak stimulation occurred 2–4 years since the start of the experiment (Kimball

et al. 2007). A less dramatic but still consistent and considerable CO_2 stimulation has been also observed in citrus grown using open-top chambers in humid Florida (Allen and Vu 2009).

While multiple studies examined biomass and allocation responses to elevated CO_2, only a limited number of studies reported fruit yield responses (Idso and Kimball 1997; Bindi et al. 2001; Ito et al. 2002). Even fewer studies have addressed the effects of elevated CO_2 on produce and product quality with an exception of wine grapes (Bindi et al. 2001; Goncalves et al. 2009; de Orduna 2010; Moretti et al. 2010). Produce and product quality measures are likely to reflect different biochemical and physiological pathways of interactions between CO_2, nutrients (N in particular), temperature, and pest damage. Several studies have examined leaf chemistry of fruit trees grown in elevated CO_2 (e.g., Centritto et al. 1999a,b, 2002; Adam et al. 2004; Moutinho-Pereira et al. 2009). In these studies, leaves grown under elevated CO_2 had about 15% lower nitrogen concentration across commodities on average. Similarly, significant increases in leaf sucrose, starch, and overall C/N ratio have also been found in several studies (e.g., Pan et al. 1998; Chen et al. 2002b; Vu et al. 2002; McElrone et al. 2005).

In summary, perennial horticultural crops exhibit physiological and growth responses that are similar to trees in forest and other unmanaged ecosystems. The CO_2 fertilization effect may be amplified and sustained longer for perennial horticultural crops if (1) other resources (e.g., nutrients and water availability) are amply supplied, and (2) proper management options (e.g., spacing, pruning, thinning) are practiced to facilitate the prolonged CO_2 effects. This will likely require maintaining intensive cropping systems. In addition, the positive CO_2 effect may be negated by the detrimental effects of extreme temperatures on phenology, carbon sinks, and reproductive physiology. Thus, innovative research for low-input cropping systems that integrates our current knowledge to capitalize on the benefits of elevated CO_2 while minimizing the input and costs, and temperature stresses, is highly needed.

B. Ozone

At seven out of nine rural and remote sites in the western United States, there were significant increases in ozone with a mean trend of 0.26 ppb year^{-1}, corresponding to an average increase of 5 ppb between 1987 and 2004 (Jaffe and Ray 2007). Current levels at background sites range between 20 and 45 ppb, depending on location, elevation, and distance to emission sources (Vingarzan 2004). According to Fuhrer (2009), there is likely an increase in worldwide ozone in the next century.

While Mills et al. (2007) generally classifies horticultural crops as ozone tolerant, other literature indicates threshold levels reducing photosynthesis between 25 and 40 ppb (Reich et al. 1986; Olszyk et al. 1990; Retzlaif et al. 1991; Howitt and Mutters 1994; Sullivan et al. 1994; Walton et al. 1997; Gauchera et al. 2003; Fares et al. 2010) for the representative perennial horticultural crops of this assessment.

As reviewed by Fuhrer (2009), when elevated ozone is combined with elevated CO_2, yield loss is typically considerably less than with ozone alone. The protective effect of CO_2 is primarily due to reduced stomatal conductance reducing ozone flux into the leaf and this mechanism is associated with elevated CO_2. Consequently, elevated ozone can also diminish the stimulating effect on yield of elevated CO_2 and the CO_2 protection from ozone effects also becomes less effective with increasing temperature.

C. Solar Radiation

Perennial horticultural cropping systems require high light intensity and proper light quality for both biomass production and fruit quality (Jackson 1980; Dokoozlian and Kliewer 1996). Pruning and training systems optimize light interception and distribution within the canopy to increase fruit quality. Excessive light can result in solar damage/sunburn while insufficient light can reduce fruit bud formation, color development, soluble solids development, and fruit size (NCA 2012).

III. CASE STUDIES

A. Apples

1. Europe, South Africa, and Japan. World apple production for 2011/2012 is estimated to be a record of 65 million tonnes (t) and 81% is used for the fresh market. Approximately 5 million t are exported worldwide and Russia is the primary buyer. China produces more than half of the world's apples and China is expected to produce 35 million t in 2012. The European Union (EU) will produce approximately 11.8 million t in 2012, and the primary producing countries, in order of production, are Poland, Italy, France, and Germany. The EU consumes 70% of the fresh market apples and exports 1.2 million t. South Africa produces approximately 0.8 million t, consumes 31% of the fresh market apples, and exports 0.31 million t. Japan produces approximately 0.8 million t but consumes 81% of the fresh market apples and exports 0.02 million t. China and the EU produce 600K and 474 thousand t of concentrated apple juice, respectively (U.S. Apple Association 2011).

Production. Europe experienced an average increase of 0.6°C, during the 20th century; the 1946–1975 temperature levels increased in Scandinavia and central Europe but decreased in western and north eastern Europe (IPCC 2001a). There was an intensive warming over most of Europe from 1976 to 1999, with increases in yearly means of 0.25–0.5°C (IPCC 2001a). According to Ahas et al. (2002) for the period of 1951–1998, the onset of spring has advanced 4 weeks in western and central Europe. Western European spring begins earlier due to the influence of the intensifying flow of Atlantic air during early spring and summer periods, which is a result of recent changes in the North Atlantic Oscillation (Hurrell 1995). Eastern Europe has a different phenological pattern that is driven by a delayed Siberian high. In this time period, the highest rate of phenological change (−0.3 to −0.4 days per year) occurred in the western Europe and Baltic Sea regions. The highest rate of change observed in the Baltic Sea region (−0.46 days per year) and the eastern European Plain (−0.57 days per year) can be directly linked to an earlier disappearance of snow cover (Jaagus 1997). Phenological studies from the International Phenological Gardens network show that spring phases in Europe begin 10–20 days earlier than 50 years ago except in eastern Europe where the beginning of spring had smaller changes, with values of 5–15 days earlier over the study period (Ahas et al. 2002).

Apple bloom dates have advanced 2.3 to 7 days per decade across Europe (Table 2.1). Urban areas have apple bloom 2 days earlier than rural areas for 1951–1995 on average (Roetzer et al. 2000). In Germany, apple bloom was highly correlated to the February and April temperature and the regression coefficients indicated that a 1°C increase advanced apple bloom 5 days (Chmielewski et al. 2004, 2011). From February to April the average increase of air temperature was +0.41°C per decade, and the strongest trend was found for March (+0.58°C per decade). The threat of

Table 2.1. Advance of apple and lilac bloom in Europe, South Africa, Japan, and the United States.

Country	Time period	Advance (days year^{-1})	Source
Germany	Feb–April	0.23	Chmielewski et al. (2004)
Italy	Mid-March–May	0.3	Eccel et al. (2009)
Germany	March–April	0.2	Menzel et al. (2006)
Japan	March–April	0.2–0.3	Fujisawa and Kobayashi (2010)
South Africa	Aug–Sept	0.1–0.2	Grab and Craparo (2011)
France	March–May	0.7	Guedon and Legave (2008)
Northeast U.S.	March–May	0.2	Wolfe et al. (2005)
Western U.S.	March–May (lilac)	0.2	Cayan et al. (2001)

late spring frosts, combined with more frequent mild winters, increases the probability of killing frosts in the spring (Burroughs 2002). Eccel et al. (2009) document that apple bloom in the Trentino region of Italy has advanced 2.7 days per decade in the last 25 years. Unlike in Germany, they found a general reduction in the risk of spring frost for apples in recent decades, based on the phenological simulation of flowering dates. The authors project that for the period 1991–2051, the daily maximum temperature will increase 0.021–0.025°C per year and plants would benefit from higher daytime temperatures, fostering faster development, while minimum temperatures would be only slightly higher than present ones; increasing 0.016°C per year. Their models predicted a reduction in the incidence of frost episodes in the area and their predicted temperatures were in agreement with the IPPC prediction (IPCC 2007b,c). Overall they project a decreasing trend of frost injury for the next few decades.

According to Grab and Craparo (2011) in the southwestern apple-growing regions of the South African cape, for the period 1973–2009, mean annual temperature increased +0.55°C per decade, the maximum increased +0.37°C per decade while the minimum increased +0.74°C per decade. Thus, for the 37-year period, the observed warming is +2.0°C, which was driven primarily by substantial increases in daily minima. The mean warming trend in June/July (winter) was +0.34°C per decade and was +0.45°C per decade in August/September (spring). Most noteworthy is the pronounced daily minimum increase of +0.68°C per decade as opposed to the daily maximum of +0.23°C per decade during early spring. 'Golden Delicious' and 'Granny Smith' had earlier bloom dates at a rate of 1.9 and 1.1 days per decade, respectively. Such trends are associated with a mean early spring temperature increase of +0.45°C per decade. Bloom of 'Golden Delicious' apples was advanced (+4.2 days per °C) and 'Granny Smith' apples (+2.4 days per °C). There were no significant correlations between winter temperatures and spring bloom in apple and pear, suggesting that chill accumulation was not significantly affected; however, the late winter/early spring temperatures 5 weeks before bloom most significantly determined bloom date.

In Finland, the areas of successful apple production have expanded northwards from the 1970s to the present day (Kaukoranta et al. 2010). It is predicted that in 2011–2040, climate warming will allow expansion of commercial production into the southeastern lake area, and a wider selection of cultivars for home gardens up to latitudes 65–66°N. Risk of extremely low temperatures (−26°C) has decreased from the 1980s to the present but may not reduce much more in 2011–2040. Risk to shoots from fluctuating temperatures in winter and spring is likely to increase

under the high warming scenario, with more risk in the southwest than in the southeast. Risk to trees from winter injury (<15°C) with a concurrent thin snow cover is not predicted to increase. In western inland Finland and in the southwestern coastal areas, the frost risk during flowering may increase, especially in the early flowering cultivars (Kaukoranta et al. 2010).

Kiritani (2006) has reported an increase in mean annual temperatures of about 1.0°C over the past 40 years in Japan. According to Sugiura and Yokozawa (2004), the favorable regions to cultivate apples will gradually move northward in Japan. In 2060s, the plains of central Tohoku will be unfavorable for apple cultivation, while most of Hokkaido will be suitable because the plains of northern Tohoku are predicted to attain annual mean temperatures higher than those of the current apple-producing areas.

Disease. Climate change could alter stages and rates of development of the pathogen, modify host resistance, and result in changes in the physiology of host–pathogen interactions (Coakley et al. 1999). The most likely consequences are shifts in the geographical distribution of host and pathogen and altered crop losses, caused in part by changes in the efficacy of control strategies. In tree fruit production, increases in summer temperature and the frequency of precipitation would favor apple powdery mildew but reduce peach leaf curl.

Garrett et al. (2009) have pointed out that with increasing air temperature, some pathogen species may be able to maintain their synchrony with target host tissue, and others may be asynchronous. Disease prediction models will need to accommodate potential impacts from climate change. For example, in efforts to predict the risk of apple scab (*Venturia inaequalis*), the concept of ontogenic resistance was utilized along with inoculum production because tissue susceptibility is affected by the maturity of the host tissue.

The appearance of the black rot fungus *Diplodia seriata* in northwestern Europe can be explained by the rising temperatures during the vegetative period (Weber 2009). An increase in fruit rot caused by *Nectria galligena* is anticipated because milder and more humid winter months favor canker formation on twigs and branches that increases inoculum for fruit infections. The increasing incidence of *Neofabraea alba* and *Glomerella cingulata* and/or *G. acutata* as storage rots of apples in northern Germany cannot be correlated with the climate change at present. The infection conditions of *Phacidiopycnis washingtonensis* are currently being examined to evaluate whether climate change might be correlated to the spread of rubbery rot in Europe (Weber 2011).

According to Beresford and Kim (2011) a threshold for European canker (*Neonectria galligena*) was when it both rained on >30% of days month^{-1} and there was an average of >8 h day^{-1} with temperature of 11–16°C. Increasing temperature and rainfall would lead to increased infection and damage.

Insect Pests. The prediction of an increase in the frequency and intensity of insect pest outbreaks through disruption of parasitoid-herbivore dynamics as climate becomes more variable is documented in 15 databases from previously published reports (Stireman et al. 2005; Thomson et al. 2010). Climate change may result in changes to geographical distribution, increased overwintering, changes in population growth rates, increases in the number of generations, extension of the development season, changes in crop–pest synchrony of phenology, changes in interspecific interactions, and increased risk of invasion by migrant pests (Porter et al. 1991; Memmott et al. 2007; Parmesan 2007; Ladányi and Horváth 2010).

According to Harrington et al. (2007) aphids generally have a low developmental temperature threshold (~4°C) and a short generation time (120 day degrees above ~25°C). With a warming of 2°C an extra five generations a year might be expected (Yamamura and Kiritani 1998). Higher rainfall was associated with later aphid flight and higher temperature was associated with earlier flight. Harrington et al. (1995), modeled winter temperature and first flight record of *Myzus persicae* (green peach aphid) at Rothamsted, and predicted that first flight record would be advanced approximately 14 days °C^{-1}. Zhou et al. (1995) using a different index of phenology predicted an average advance of 9 days in the United Kingdom for the same species and temperature increase.

Kiritani (2006) reported an increase in mean annual temperatures of about 1.0°C over the past 40 years in Japan. Differences in the pattern of response to temperature changes would disrupt synchronization in phenology between insects and host plants or natural enemies. Spider generations and numbers are not expected to rise with increasing temperature due to their wide prey range. However, if insect pests such as *Halyomorpha halys* (Pentatomidae), which is prevalent in northern Japan and an emerging U.S. pest, experience warmer winters, their winter mortality will decline. For every 1°C rise in temperature there would be a 15% reduction in the winter mortality of *H. halys*.

Water Use. According to Lavalle et al. (2009), on average, the annual rate of increase in water demand in Europe is around 50 m^3 ha^{-1}, but

in Italy, Greece, Maghreb, central Spain, southern France, and Germany it was more than 150–200 m^3 ha^{-1} resulting in a significant increase in water demand (50–70%). Areas with an increase in rainfall have been observed in the Balkan Peninsula, the Alpine region, Scandinavia, Scotland, Benelux, the Czech Republic, Slovakia, Poland, Hungary, and many Turkish areas. These historic trends are predicted to continue in the climatic projections for Europe (IPCC 2007b,c) in which precipitation increases in the north but decreases in the south, especially during the summer. Also the extremes of daily precipitation are projected to increase in the north and the annual number of rainy days to decrease in the Mediterranean. The risk of summer drought is therefore likely to increase in central Europe and in the Mediterranean area.

According to Grab and Craparo (2011), in the southwestern apple-growing regions of the South African Cape, the annual total precipitation has declined 83.4 mm per decade over the 37-year period, and 66.5 mm per decade for the May to October rainfall period for the period 1973–2009. February was the only single month with a statistically significant monthly decrease over the past 37 years (6.2 mm per decade). Thus, temperature increases are more significant than precipitation decreases over recent decades in this horticultural region.

2. United States. Apples are grown in every state in the continental United States, with the greatest production in Washington, New York, Michigan, Pennsylvania, California, and Virginia (in declining order). The U.S. apple crop is approximately 3.9 million t. Approximately 7,500 apple growers manage orchards covering 153,000 ha. Approximately 68% of the apple crop is produced for the fresh fruit market, 47% is domestically consumed as fresh fruit, and 18% of the fresh fruit is exported (US Apple 2011).

Northeastern (NE) Region. In terms of production, an extended frost-free period as projected for the northeast United States (Frumhoff et al. 2006; Hayhoe et al. 2007; Wolfe et al. 2008) will tend to benefit perennial horticultural cropping systems requiring a relatively long growing season such as apples, peach, and grape. However, projections for an increase in summer heat stress and drought can reduce yield and crop quality. Wolfe et al. (2008) found that apple yields for western New York (1971–1982) were lower in years when winters were warmer than average (based on accumulated degree days $>5°C$ from January 1 to bud break). This was likely related to more variable fruit set following warmer winters. Wolfe et al. (2008) compared projections of summer

heat stress frequency (increase in number of days with maximum temperature exceeding 32°C) with the increase in number of heat stress days in the month of July in early-, mid-, and late-21st century. At the higher emissions scenario, within just the next few decades (2010–2039), a 5–10-day increase in the number of July heat stress days is projected for the southern half of the region, that is, much of Pennsylvania, New Jersey, Delaware, Connecticut, and southern New York. With a lower emissions scenario, the climate change impact does not become substantial until mid-century (2040–2069). By the end of century (2070–2099), with higher emissions, most days in July are projected to exceed the 32°C heat stress threshold for most of the U.S. northeast. Even assuming relatively lower emissions, much of the northeast is projected to have 10–15 more days of heat stress in July by end of the century, except for some northern areas, for example, northern Maine and Vermont, where the increase is in the range of 5–15 days. The projected increase in summer heat stress will be particularly detrimental to many cool temperature-adapted crops (e.g., apple) that currently dominate the northeast agricultural economy. For many high value horticultural crops, very short-term (hours or a few days) and moderate heat stress at critical growth stages can reduce fruit quality by negatively affecting visual or flavor quality even when total tonnage is not reduced.

An increase in winter temperatures will affect the northeast perennial horticultural cropping systems. Mid-winter warming can lead to early bud-burst or bloom of some perennial plants, resulting in frost damage when cold winter temperatures return. An extreme example occurred in 2012 in the U.S. Midwest for apple when bloom occurred fully 4 weeks early with disastrous consequences from an early frost. Yields will be negatively affected if the chilling requirement (i.e., hourly cumulative thermal units below a threshold temperature) is not completely satisfied because flower emergence and viability will be low. All temperate perennial horticultural crops have a chilling requirement ranging from 200 to 2,000 cumulative hours. Wolfe et al. (2008) analyzed the future chill requirements of the NE and found that a 400 h chilling requirement will continue to be met for most of the NE during this century regardless of emissions scenario. However, crops with prolonged cold requirements (1,000 or more hours) could be negatively affected, particularly in southern sections of the NE and at the higher emissions scenario, where less than 50% of years satisfy the chill requirement by mid-21st century. The impact on crops will vary with species and cultivar since each species has a range of cultivars with widely varying chill requirement.

There is a historical trend for increased frequency of high-precipitation events (>5 cm in 48 h) (Wake 2005) in the NE, and this trend is expected to continue with a further increase in number of high precipitation events of 8% by mid-century and 12–13% by the end of the century (Frumhoff et al. 2006). More rainfall concentrated into high precipitation events, combined with stable to modest reductions in summer and fall rainfall and increased temperatures, leads to a projection for more short- (1–3 months) and medium-term (3–6 months) droughts for the region, particularly in the north and eastern parts of the NE (Frumhoff et al. 2006; Hayhoe et al. 2007). Drought frequency is projected to be much greater at the higher (A1F1) compared to lower (SRES-B1) emissions scenario, according to Wolfe et al. (2008). By the end of the century and with higher emissions, short-term droughts are projected to occur as frequently as once per year for much of the NE, and occasional long-term droughts (>6 months) are projected for western upstate NY where perennial horticultural crops are a major industry (Wolfe et al. 2008).

In the NE, the projected increase in short- to medium-term drought (Hayhoe et al. 2007) will tend to decrease the duration of leaf wetness and reduce some forms of pathogen attack on leaves. However, an increase in humidity and frequency of heavy rainfall events projected for the NE (Frumhoff et al. 2006) will tend to favor some leaf and root pathogens (Coakley et al. 1999) and the projected increased rainfall frequency (Frumhoff et al. 2006) may reduce the efficacy of contact fungicides requiring more frequent applications.

A warming trend is likely to lead to increased pesticide use in the NE due to earlier arrival of migratory insects, more winter survival of insects that currently are only marginally adapted to the region, and more generations of insects within a single season (Wolfe et al. 2008). In addition, some classes of pesticides (pyrethroids and spinosad), key to perennial horticultural cropping systems, have been shown to be less effective in controlling insects at higher temperatures (Musser and Shelton 2005).

Increased drought frequency in the NE together with warmer growing season temperatures will result in greater crop water requirements (Wolfe et al. 2008). Perennial horticultural crops have reduced yield and quality in association with water deficits and reduced profits as a result. While many producers of perennial horticultural crops in the NE have some irrigation equipment, most have not invested in enough equipment to optimize irrigation scheduling and fully meet evapotranspiration (ETP) requirements of all of their crop area (Wilks and Wolfe 1998).

Pacific Northwest. Stöckle et al. (2010) predicted that climate change would slightly decrease the production of apples by 1%, 3%, and 4% for the 2020, 2040, and 2080 scenarios with no elevated CO_2 effect. Under a warmer climate, crop development will proceed at a faster rate, reducing the opportunity for biomass gain. However, when the effect of elevated CO_2 and warming is modeled, yields are projected to increase by 6%, 9%, and 16% for 2020, 2040, and 2080 scenarios compared to current levels, assuming the availability of cultivars able to use the extended season or other adaptive technologies. Although average temperatures are projected to increase for all climate scenarios, the frequency of frost events may limit cropping due to earlier flowering. Under the projected climate change, flowering will occur about 3 days earlier in the 2020 scenario, which will slightly increase the frequency of frost events, increasing yield loss from frost damage, or increase the need and expense for frost protection. Limited chill accumulation is not projected to limit apple production in eastern WA. Water supply was assumed sufficient for irrigated crops, but other studies suggest that it may decrease in many locations due to climate change.

In eastern WA, cherry powdery mildew is predicted to increase under the NCAR's Community Climate System Model version 3 (CCSM3) (2020 only) and the CCCMA's Coupled Global Climate Model version 3 (CGCM3) projected climate. There will be small increases or no change in the risk from grapevine powdery mildew for all climate projections. Overall, a warmer climate but with small changes in precipitation during the growing season would tend to maintain and eventually reduce the incidence of these diseases, unless there is an increase in precipitation early in the growing season (Stöckle et al. 2010).

Stöckle et al. (2010) simulated codling moth development using baseline climate and projections from four Global Climate Models (GCMs). These simulation indicated first adult flights occurring 6, 9, and 14 days earlier on average than the baseline for the 2020, 2040, and 2080 scenarios. The beginning of the first-generation egg hatch was advanced by 6, 8, and 13 days, and the beginning of the second-generation egg hatch was advanced by 10, 14, and 21 days for the 2020, 2040, and 2080 scenarios. Earlier emergence of adults in the spring coupled with warmer summer temperatures increased the likelihood that most apple-growing locations in the state would have a complete third-generation egg hatch. Current pheromone technology would not last an entire season unless more pheromone was added to dispensers, increasing grower costs. In order to protect later maturing cultivars, one to two additional sprays per season would most likely be

needed. Warmer winter temperatures could result in an extended emergence pattern for codling moth making it more difficult to precisely time control applications, further increasing control costs for growers.

Elsner et al. (2010) simulated the hydrology of Washington State and the Yakima River Basin, and projected April 1 snow water equivalents (SWEs) to decrease by 28–30% across the State by the 2020s, 38–46% by the 2040s, and 56–70% by the 2080s. In the Yakima Basin, April 1 SWE will decrease by 35–37% by the 2020s, 47–57% by the 2040s, and 68–82% by the 2080s. The peak weekly SWE historically occurs near mid-March. Projections of weekly SWE for the 2020s indicate that SWE will be reduced by an average of 39–41%. The peak week is projected to shift to early or mid-March. By the 2040s, SWE will be reduced by 50–58% with a peak projected to occur near early March, and by 67–80% by the 2080s with a peak projected to occur near mid-February. Competition for water will increase between urban, agricultural, and watershed interests.

B. Grapes

1. Europe and Australia. Grape production is increasing worldwide. Global grape production is expected to be 16.5 million t in 2012 with a trend for increasing production into the future (USDA, NASS 2012). The top 10 grape producers are China, Italy, United States, Spain, France, Turkey, Chile, Argentina, Iran, and Australia with China producing 8.7 million t in 2011. Grapes are marketed as fresh table grapes, processed for wine and dried for raisins. China produced 6.7 million t of table grapes in 2011. Turkey and the EU produced 2.2 and 1.9 million t, respectively, while Brazil, Chile, India, and the United States produced 1.3, 1.2, 1.0, and 0.9 million t, respectively (USDA, NASS 2012). Global wine production in 2010 was 25.6 million t. The top seven wine-producing countries, in million tonnes (Mt) per year, were Italy (4.6), France (4.5), Spain (3.6), United States (2.2), China (1.7), Argentina (1.6), and Australia (1.1) (FAOSTAT 2012). Global raisin production was 1.1 Mt with Turkey and the United States leading the production. Raisins are the most popular dried fruit in the United States, accounting for about two-thirds of total U.S. dried fruit consumption. Global raisin exports were about 0.7 Mt in 2010 and are generally stable from year to year (USDA, FAS 2012).

In the current climate, major production areas are represented by locations in China, Europe, United States, Australia, Chile, and South Africa (Jones et al. 2005). Reflecting the importance and influence of viticulture and wine to global economy and culture, a high volume of

published research has addressed the impacts of recent and future climate change on viticulture and wine quality throughout the world. Many of these studies focused on the regions in Europe, United States, and Australia while fewer studies covered China, South America, and South Africa (Jorquera-Fontena and Orrego-Verdugo 2010; Agosta and Canziani 2012; Bonnardot et al. 2012).

Production. In Europe, numerous long-term phenological data sets exist for grapevines and these data have been utilized for studying climate impacts on wine production and quality. For example, records of grape harvest dates in Burgundy, France have been used to reconstruct historical temperature data from 1370 to 2003 (Chuine et al. 2004). Likewise, recent climatology data (1952–1997) revealed that the phenology of grapevines in Bordeaux in the last two decades of the period was characterized with earlier phenological events, shorter phenological intervals, and longer growing seasons (Jones and Davis 2000). The same study found that 'Merlot' is more phenologically and climatologically sensitive than 'Cabernet Sauvignon' in Bordeaux. In the Parisian and Burgundy regions of France, yearly minimum temperature increased approximately 1.0°C in the 20th century (Tourre et al. 2011). It is speculated that 'Pinot Noir' grape, which has a narrow climatic niche, may be partly eliminated and replaced by other cultivars in Cote de Beaune region of Burgundy in response to climate change (Tourre et al. 2011). Similar warming trends have also been observed in Spain and Italy (Dalla Marta et al. 2010; Garcia-Mozo et al. 2010; Tomasi et al. 2011). In the Veneto region of Italy, the average growing season temperature increased by 2.3°C from 1964 to 2009. This warming resulted in 13–19 days acceleration in bloom, veraison, and harvest dates across early-, middle-, and late-maturing cultivars (Tomasi et al. 2011). This change over time approximately translates to an average advancement of 8 days per 1.0°C warming during this period (Tomasi et al. 2011). Similar results were observed in Spain with an average of 10 days advancement in leaf unfolding over the 1989–2000 period (Garcia-Mozo et al. 2010).

Using bioclimatic envelope modeling, detrimental impacts on production and quality have been predicted in southern Europe, mainly due to increased dryness and cumulative thermal effects during the growing season (Malheiro et al. 2010). However, projected climate conditions are predicted to benefit not only wine quality, but might also expand the potential production areas for viticulture in western, central, and eastern Europe (Malheiro et al. 2010; Ruml et al. 2012). In the Alsace region of France, veraison is projected to advance up to

23 days for 'Riesling' and 'Gewurztraminer' by 2100 (Duchene et al. 2010). A similar advancement of up to 17 days from bud-burst to flowering and 46 days from sprouting to harvest by 2100 has also been projected for the 'Gewurtztraminer' in southern Chile (Jorquera-Fontena and Orrego-Verdugo 2010). In the Douro region of Portugal, yield is projected to increase by 2100 using a statistical grape yield model based on ensemble simulations under the SRES-A1B emission scenario (Santos et al. 2011). High elevation areas have been projected to show more pronounced phenological and growth responses suggesting that some mountainous areas such as the Italian Alps may become suitable for viticulture (Caffarra and Eccel 2011). This may be an adaptation strategy to increase profitability in mountain viticulture of the region. However, northward range shifts of grape production areas may be less than expected if winter freeze events increase in frequency during the early stages of cold acclimation (i.e., November to mid-January in northern Europe or Pacific Northwest) (Quamme et al. 2010). When combined with elevated CO_2 effects, global climate projections produced increased mean biomass and increased variability in fruit and total biomass in a study that used a process-based crop growth model (Bindi et al. 1996).

In Australia, an average advance of 1.7 days per year in wine grape maturity was observed during the 1993–2009 period (Webb et al. 2011). Earlier ripening trends in the past 64 years have been attributed to climate warming and declines in soil water. Yield reduction and management practices have also contributed to the observed advances in maturity (Webb et al. 2012). Specifically, early maturity in southeastern Australia due to high temperatures has been attributed to the early onset of ripening (veraison) rather than faster ripening (Sadras and Petrie 2011). Advanced maturity of between 0.5 and 3 days per year has been observed in 'Chardonnay', 'Cabernet Sauvignon', and 'Shiraz' grown in Australia between 1993 and 2006 (Petrie and Sadras 2008); this is somewhat greater than the reported phenological advancements observed in the northern hemisphere (Jones and Davis 2000; Jones et al. 2005; Wolfe et al. 2005).

Based on multiple regional climate projections, a continued advancement in wine grape phenology is projected to occur in Australia (Webb et al. 2007). When a median growing season temperature $>21°C$ was used as an indicator of the climate conditions limiting wine quality and wine grape production, only 3 regions out of 61 regions that are currently recognized for wine grape growing in Australia were delineated to sit outside the threshold in the current climate. However, this number increased to 21 regions by 2070 based on a Mk3.0 GCM

scenario (Hall and Jones 2009). In Australia, the greatest change in grapevine-growing season temperature is projected to occur in the Perth Hills region with a projected increase of 2.7°C by 2070 while the least change was modeled to occur in the Kangaroo Island region, which will increase as much as 1.3°C by 2070 (Hall and Jones 2009). Budburst of 'Cabernet Sauvignon' in Coonawarra is projected to occur 6–11 days earlier and harvest will be accelerated up to 45 days in 2050 (Webb et al. 2007). Warming in some regions may adversely delay budburst because chilling requirements are unmet in a warmer climate (Webb et al. 2007).

Physiologically, impacts of high temperature on reproductive growth and the grape ripening process are closely linked to carbon assimilation (Greer and Weston 2010) as well as other limiting factors such as soil water and nitrogen (Van Leeuwen et al. 2004). In 'Semillion' grape, light-saturated photosynthesis exhibited an optimal at 30°C in ambient CO_2 (389 ppm) and was inhibited by 60% at 45°C compared with 25°C (Greer and Weedon 2012). However, heat stress in various phenological stages did not affect gas-exchange and yield of irrigated 'Shiraz' suggesting varietal differences in their photosynthetic response to temperature (Sadras and Soar 2009; Soar et al. 2009). A detailed review of climate impacts on grape reproductive growth, yield, and fruit chemical composition is provided by Keller (2010).

Quality. Wine grapes are sensitive to climate change because of the intrinsic link between the climate, plant stress, grape characteristics, and the resulting wine quality. Growing season temperature has considerable impacts on grape quality and viability throughout the phenological stages from spring vegetative growth, berry growth and ripening, and maturation (Jones et al. 2005). High-quality wine production areas in western and central Europe have experienced increased quality ratings associated with recent warming trends (Jones et al. 2005; Duchene et al. 2010; Malheiro et al. 2010; Bock et al. 2011). However, the presumed rule of thumb "the warmer the better" in viticulture may not be true globally in the future as numerous wine-producing regions appear to have optimum temperatures for the current cultivars regardless of climate maturity groups (Jones et al. 2005). Furthermore, many regions and cultivars are currently at or near the optimal growing season temperature, suggesting that further warming will likely negatively impact viticulture and wine quality of many regions (Jones et al. 2005). The amount and concentrations of sugars, amino acids, phenolic compounds, soluble solids, and pH during grape ripening are tightly associated with wine quality (Keller 2010). The phenolic

compounds are closely related to the status of plant stress; grapevines with moderate vigor experiencing mild-to-moderate stress (e.g., water deficit, nitrogen stress) are known to produce grapes for high-quality wines (Van Leeuwen and Seguin 2006). Concentrations of key phenolic compounds (i.e., anthocyanins, tannins, and total phenolics) have been positively correlated with cool temperatures following harvest in the previous year, warm temperatures from budburst to bloom, and cool temperatures from bloom to veraison in California (Nicholas et al. 2011) whereas anthocyanin concentration at 35°C was reduced to less than 50% of that at 25°C in Cabernet Sauvignon in a controlled environment study (Mori et al. 2007).

In general, climate change (i.e., warming) is expected to influence wine quality by increasing grape sugar concentration leading to high alcohol levels and lower acidities (de Orduna 2010). Sugar:acid ratio, berry weights, and potential wine quality have increased for 'Merlot' and 'Cabernet Sauvignon' grown in Bordeaux, France in the past 50 years (Jones and Davis 2000). Similar results showing increased sugar content with decreased acid components were found in the northerly Lower Franconia region growing white grape cultivars such as 'Muller-Thurgau', 'Riesling', and 'Silvaner' (Bock et al. 2011). Higher pH in wines can change microbial ecology associated with musts and wines increasing the risk of spoilage and degradation (de Orduna 2010).

In Australia, the reduction in grape quality was predicted to vary regionally, with greater quality reductions calculated for the inland regions (Webb et al. 2008). Webb et al. (2008) predicted that wine grape quality may be reduced from 7% with lower warming to 39% with higher future warming by the year 2030, and from 9% with lower warming to 76% with higher warming by the year 2050.

2. United States

Production. White et al. (2006) calculated that U.S. premium wine grape production area could decline by up to 81% by the late 21st century. They found that increases in heat accumulation will likely shift wine production to cultivars adapted to warmer temperatures, which may be lower quality, and that while frost constraints will be reduced, increases in the frequency of extreme hot days (>35°C) in the growing season are projected to completely eliminate wine grape production in many areas of the United States. Grape and wine production will likely be restricted to a narrow West Coast region and to the northwest and northeast, where excess moisture is already problematic. Jones et al. (2010) examined suitability for viticulture in the western

United States. They contrived five regions (I–V) with broad suitability for viticulture across cool to hot climates, and they also listed cultivars that grow best in those regions. Regions I, II, III, IV, and V had GDD = 850–1,389, 1,389–1,667, 1,667–1,944, 1,944–2,222, and 2,222–2,700, respectively. The coolest region (I) occurs highest in elevation, most coastal, and most northerly (e.g., the Willamette Valley), while the warmest region (V) areas are mostly confined to the Central Valley and further south in California (e.g., the San Joaquin Valley). Based on the historical record, 34% of the western United States falls into regions I–V with 59% being too cold and 7% too hot. Of the area suitable for viticulture, Region I encompasses 34.2%, region II 20.8%, region III 11.1%, region IV 8.7%, and region V 25.2%. According to Jones et al. (2010), projections for average growing season temperatures from the Community Climate System Model (CCSM) of 1.0–3.0°C for 2049 result in a range of increases in growing degree-days of 15–30%. For a 15% increase in growing degree days by 2049, the area of the western United States in regions I–V increase 5% from 34% to 39% and at the higher range of a 25% increase in growing degree days, increases by 9–43%. Overall the changes show a reduction in the areas that are too cold from 59% to 41% while the areas that are too hot increase from 7% to 16% in the greater warming scenario. Within the individual regions there are shifts to predominately more land in region I (34.2– 40.6%), smaller changes to region II (20.8–23.4%), region III (11.1–14.2%), and region IV (8.7–10.1%), and a reduction of region V area from 25.2% to 11.6% which is shifting the regions toward the coast, especially in California, and upwards in elevation (most notably in the Sierra Nevada Mountains).

In another regional analysis for the west coast of the United States, Lobell et al. (2006) examined the impacts of climate change on yields of perennial crops in California. The research combined the output from numerous climate models with statistical crops models for almond, walnut, avocado, and wine, and table grape. The results show a range of warming across climate models of ~1.0–3.0°C for 2050 and 2.0–6.0°C for 2100 and a range of changes in precipitation from −40% to +40% for both 2050 and 2100. Wine grapes showed the smallest yield declines compared to the other crops, but showed substantial spatial shifts in suitability to more coastal and northern counties. For oranges, walnuts, and avocados, not only are the areas with the potential for high yields dramatically reduced but the areas with appropriate climate tend to be in dry or mountainous regions with limited opportunities for agriculture. Less than 5% of simulations for almonds, table grapes, walnuts, and avocados indicated a zero or positive response to climate change by

mid-century. Two main factors contribute to this result: (1) all of these crops are either at or above their optimum temperatures in current climate and all climate models project at least some climate warming, and (2) all of these crops are irrigated, so that the precipitation projections have a relatively minor effect. The authors also note that historical increases in yield have low attribution to climate trends and were due more to changes in cultural and genetic technology. Hayhoe et al. (2004) predicted by the end of the century that snowpack declines 73–90%, with cascading impacts on runoff and stream flow that, combined with projected modest declines in winter precipitation, could fundamentally disrupt California's water rights system.

Insects. The vine mealybug (VMB, *Planococcus ficus*) is a major pest of grape production in California (Gutierrez et al. 2006). Extensive biological control efforts are under way to control VMB, but to date, success has been elusive (Gutierrez and Daane 2005). High VMB densities occur in more northern regions and in coastal regions of southern California. VMB is less abundant in dryer warmer regions. The distribution and abundance of the natural enemies are patchy across the different grape-growing regions. If biological control of VMB is finally established, climate change could adversely affect it.

Water Use. Increased drought frequency in the NE together with warmer growing season temperatures will result in greater crop water requirements (Wolfe et al. 2008); however, most growers have not invested sufficient capital to optimize irrigation scheduling and fully meet ET requirements of all of their acreage (Wilks and Wolfe 1998).

As discussed previously with apple, the hydrology of Washington State is projected to be altered so that April 1 SWE will decrease by 28–30% across the state by the 2020s, 38–46% by the 2040s, and 56–70% by the 2080s (Elsner et al. 2010). The peak weekly SWE historically occurs near mid-March in Yakima River Basin. The peak week is projected to shift to early or mid-March by the 2040s and to near mid-February by the 2080s. Similarly in California, Miller et al. (2003) simulated the hydrology for Sacramento, American, and Merced Basins. The SWE decreases for most basins, and the peak is earlier for all basins by 2080–2099. There is an early season increase in snowmelt water from 2010 to 2099 with earlier snowmelt seasons with a slower river flow rate later in the season. These reductions in growing season irrigation water will greatly limit perennial horticultural crop production in the arid and semiarid crop production regions unless sufficient water is stored in reservoirs. The impact will be most on late season crops. Impact on crop

water use efficiency of elevated CO_2 on the selected crops is reviewed (NCA 2012). In general, water use efficiency (i.e., biomass or yield per water use) in perennial horticultural crops is likely to increase because of reduced stomatal conductance and growth stimulation in high CO_2. However, overall water use in many crops is likely to remain similar or even increase as a result of corresponding increases in leaf area (NCA 2012) and especially as a result of rising temperatures (e.g., Kimball and Bernacchi 2006; Kimball 2007).

C. Banana/Plantain

1. Production. Bananas (*Musa* sp.) are mostly grown throughout the tropical developing world (Plate 2.1, Table 2.2), particularly in sub-Saharan Africa, where they provide a critical part of the dietary basis and often the sole source of income for rural populations (Lemchi et al. 2005; van Asten et al. 2011). Although Musa crops are highly sensitive to excessively high or low temperatures, they are also grown in subtropical environments in India, China, and Brazil (Delvaux 1999; FAO 2010). Originating in Asia (Heslop-Harrison and Schwarzacher 2007;

Table 2.2. Production, harvested area, and yield of banana and plantain in the top 15 producing countries (ranked according to total production).

Country	Production (million t)[a]	Production (%)	Harvested area (1,000 ha)[a]	Harvested area (%)	Yield (t ha^{-1})[a]
India	31.90	24.1	844.0	9.0	37.8
Uganda	10.15	7.7	1,843.0	19.6	5.5
China	9.85	7.4	413.9	4.4	23.8
Philippines	9.10	6.9	449.6	4.8	20.2
Ecuador	8.48	6.4	328.8	3.5	25.8
Brazil	6.98	5.3	487.0	5.2	14.3
Indonesia	5.81	4.4	98.0	1.0	59.3
Colombia	4.85	3.7	425.6	4.5	11.4
Ghana	3.60	2.7	335.2	3.6	10.7
Tanzania	3.58	2.7	690.0	7.3	5.2
Cameroon	3.55	2.7	275.0	2.9	12.9
Guatemala	2.82	2.1	72.7	0.8	38.8
Rwanda	2.75	2.1	333.8	3.6	8.2
Mexico	2.10	1.6	76.9	0.8	27.3
Costa Rica	1.89	1.4	52.9	0.6	35.8

Source: Data from FAOSTAT (FAO 2010).

[a]Totals of production and harvested area of banana and plantain were used as opposed to individual quantities because the FAO labeling is not totally reliable.

De Langhe et al. 2010) bananas have spread throughout all the tropics and subtropics, where they are now grown as either cash or food security crops in 126 countries (Delvaux 1999; Heslop-Harrison and Schwarzacher 2007; FAO 2010); moreover, bananas and plantains contribute to the food supply by weight in more than half the countries in the world (FAO 2010), including many developed countries, where they are consumed as dessert fruits (De Langhe et al. 2010).

Changes in climates in banana-growing regions have been examined elsewhere (Ramirez et al. 2011; Van den Bergh et al. 2012) using state-of-the-art GCMs. These studies have found that by 2020s, precipitation changes in banana-growing regions are highly geographically variable (changes between −200 mm to +240 mm per year), with sub-Saharan Africa and Australasia predicted to experience increases in annual precipitation, while northern Africa, central America, and the Caribbean are predicted to experience reductions of up to 100 mm per year. About 9% of the total global harvested area could experience important decreases in annual rainfall (>50 mm), while 10% is predicted to have increases in annual mean temperature in the range 1–1.5°C (Jarvis et al. 2008; Ramirez et al. 2011).

Although a large number of studies have focused on the responses of banana to environmental conditions (Turner and Lahav 1983; Turner 1998a; Gaidashova et al. 2009; Nyombi 2010), the literature on the responses of bananas to climate change is sparse (Ramirez et al. 2011), primarily because there is no reputable process-based crop growth model with which such responses can be assessed for banana cultivars of different genomic constitution (Nyombi 2010; Ramirez et al. 2011; Youssef et al. 2011). Two studies were identified in the literature as the only ones using models to assess the possible responses of banana cropping systems under future climate scenarios (see Ramirez et al. 2011; Van den Bergh et al. 2012). These two studies assess the impact of climate change on the crop using a climatic suitability model named EcoCrop (fully described by Ramirez-Villegas et al. 2013). Briefly, EcoCrop calculates the potential suitability of a climate using the ranges of temperature and precipitation in which the crop can grow and spatially explicit databases of mean climatology (such as those of Hijmans et al. 2005). Any further references to banana suitability as well as Plate 2.2 have been derived either directly or indirectly from the EcoCrop model results in the studies of Ramirez et al. (2011) and Van den Bergh et al. (2012). Changes in climates are expected to impact Musa productivity and any associated climate-constrained pests or diseases (Jarvis et al. 2008; Ramirez et al. 2011; Van den Bergh et al. 2012). Future climates (2020s) are expected to be less suitable

in more than 70% of the global land areas (mainly tropical areas), although there could be gains toward the subtropics that could both increase yields and expand areas suitable for Musa (Mathur et al. 2012; Van den Bergh et al. 2012).

Bananas grow optimally with abundant water and temperatures in the range 20–30°C (Simmonds 1962), although they are also grown successfully in subtropical monsoonal environments where conditions are outside the optimal range. For example, India, being mostly a subtropical country, is the major producer of banana (Table 2.2). Of the various environmental controls on banana growth and development, the combined environmental effects on fruit quality, yield, and crop cycle length are probably among the most critical, as these are critical traits for timely market supply and fruit consumption (Turner and Lahav 1983; Robinson 1996; Turner 1998b; Turner et al. 2007).

The main factors that operate against banana production, apart from pests and diseases, are prolonged dry seasons (1–3 consecutive dry months) (Grimm 2008; van Asten et al. 2011), cold spells and frost events, and extremely hot and cyclonic winds (Sastry 1988). Temperatures outside the range 26–28°C decrease foliar development (Ganry 1980; Turner and Lahav 1983; Turner 1998a) and outside the range 29–30°C decrease the rate of fruit maturation (Turner et al. 2007). Furthermore, in most cultivars temperatures below 16°C significantly slow growth rates and below 10°C stop growth (Aubert 1971) as do temperatures of 38–40°C (Turner and Lahav 1983; Van den Bergh et al. 2012). Fruits suffer distortion with temperatures below 16°C (Stover and Simmonds 1987).

Bananas require around 1,300–2,600 mm water/year for adequate growth, although they can grow in far more humid environments (in the range of 5,000 mm/year) in well-drained soils (Nyombi 2010; Ramirez et al. 2011). Biomass accumulation, bunch weight, and fruit quality substantially benefit from both adequate rainfall amounts and distribution or from supplementary irrigation (Stover 1972; Sastry 1988).

The impacts of climate change are expected to vary on a regional basis (Ramirez et al. 2011; Van den Bergh et al. 2012). Where banana is grown in subtropical environments, increases in minimum temperatures and in degree days above 14°C can accelerate fruit development (Ganry and Meyer 1975; Turner and Barkus 1982) and shorten the crop cycle length, thus increasing the capacity of such regions to produce an increasing market supply (Van den Bergh et al. 2012). Nevertheless, this could be offset if substantial changes in extremes occur (Meehl et al. 2007). Changes in the distribution and decreases in the amount of rainfall in East Africa (i.e., Uganda, Kenya, Tanzania, and Malawi) could pose a severe additional constraint for highland bananas, which already suffer

from drought (Ramirez et al. 2011; van Asten et al. 2011). In contrast, in the growing areas of Costa Rica and Colombia, where rainfall amount is considerably high, decreases in rainfall are expected to either cause beneficial effects from the decrease in black leaf streak (BLS) disease prevalence or not significantly affect the cropping system. Although conclusions regarding impacts are contingent on climate model skill and uncertainty, which is inevitably high, particularly for rainfall (Hawkins and Sutton 2009, 2011), precipitation amounts are predicted to increase in eastern Africa and decrease in central America (Ramirez et al. 2011).

Future climatic suitability is predicted to be significantly reduced in several lowlands (Plate 2.2) and benefits have been reported in highlands (Ramirez et al. 2011). Many lowland areas in Latin America, coastal western Africa, and large parts of Asia and the Pacific are likely to experience short periods of excessively high temperatures, thus affecting flowering and fruit filling, particularly toward the end of the 21st century (Brat et al. 2004; Joshi et al. 2011; Ramirez et al. 2011; Van den Bergh et al. 2012). Additionally, particularly high decreases in banana climatic suitability are predicted for the Amazon, northern Colombia, large areas of central America, and western Africa. Overall, sub-Saharan Africa is predicted to experience increases in suitability (Plate 2.2d). However, it must be noted that the model used to produce these predictions does not take into account specific abiotic stresses arising from short periods of high or low temperatures or rainfall (Ramirez et al. 2011).

Poor fruit development is likely to be experienced across West Africa and the lowlands of Latin America, primarily due to drought. Many positive impacts are predicted in subtropical areas arising from increases in temperatures; however, these could be offset by changes in rainfall distribution (IPCC 2007a). Such changes (not studied for banana to date) could lead to significant decreases in rates of leaf emergence (Turner and Lahav 1983; Turner 1998a). Overall, crop climatic suitability changes indicate that both benefits and challenges are expected for banana production. Major producing areas are predicted to shift geographically due to the increases in baseline temperatures, although for some regions this could bring substantial benefits; thus, East Africa is predicted to experience increases in suitability between 5% and 30% in 80% of its areas. Although much more detailed modeling is required to reach more accurate conclusions, future abiotic constraints can result in increased market supply for some regions such as the subtropics, but can pose a constraint for tropical areas in Latin America with high present-day temperatures, including Costa Rica,

where banana production has a large contribution to the national agricultural GDP (Ramirez et al. 2011).

The specificity of the export banana market, which is restricted largely to the Cavendish subgroup, AAA, and the difficulty in conventional breeding (J. Aguilar, pers. commun.), makes cultivar development and substitution a hard task for any market-oriented production system such as most of the production areas of Latin America. Adapting to challenges for the banana sector will require improved agronomic practices that preserve soil quality and avoid high canopy temperatures, as well as the development of more resilient cultivars with increased tolerance of drought and temperature extremes, and with fruit quality that is acceptable to markets.

2. Disease. Banana production has been historically hampered by biotic stress, and to date, about 50% of total investment on banana production per year in the major humid production areas of Latin America is solely dedicated to controlling pests and diseases (Kema 2009; Garcia et al. 2010). Commercial banana plantations are all clones of AAA Cavendish subgroup and hybrids and/or landraces that show both resistance to pests and diseases and fruit quality that is acceptable to the market are lacking (Heslop-Harrison and Schwarzacher 2007; Grimm 2008). This makes banana production particularly vulnerable to diseases (Ploetz 2006; Grimm 2008). A clear example of this is the crisis in the second half of the 20th century, when race 1 of *Fusarium* wilt (FOC, *Fusarium oxysporum* f. sp. *cubense*) almost caused the collapse of the banana sector worldwide, with an estimated loss of U.S. $400 million (Ploetz 2006).

The most economically important banana disease is (BLS, *Mycosphaerella fijiensis* M.) (Vuylsteke 2001; Marín et al. 2003; Lemchi et al. 2005), although many other important diseases are spread throughout the world: FOC, particularly tropical race 4 (TR4) in Asia (Molina et al. 2009); banana bunchy top disease (BBTD, caused by banana bunchy top virus (BBTV) in Asia and Africa (Thomas and Caruana 2000); and various bacterial wilts and nematode species (Gaidashova et al. 2009). Nonchemical alternatives to control banana diseases are limited or nonexistent. Furthermore, recent research at the *Corporacion Bananera Nacional* (CORBANA) in Costa Rica has shown that there is no single hybrid that can tolerate FOC TR4 (J. Sandoval, pers. commun.).

In spite of the importance of bananas worldwide, the economic importance of pests and diseases for the banana sector and the forthcoming threat of climate change, limited research has been carried out

on the impacts of climate change on banana pests and diseases (Jarvis et al. 2008; Alves et al. 2011; Ramirez et al. 2011). Such studies have focused on the prevalence of BLS using empirical and/or statistical approaches rather than process-based models [see Forbes et al. (2008) for an example of a disease process-based model] whose applicability outside calibration ranges is limited; therefore, existing projections have not been done for novel climatic conditions (Williams et al. 2007). In addition, the responses of the various nematode species that affect banana production, and the future status of other nonclimatic dependent pests or diseases have only been barely, if at all, explored (Ploetz 2006; Molina et al. 2009; Ramirez et al. 2011). For these reasons, we focus primarily on the expected response of BLS, yet briefly summarize some preliminary-expected trends in other pests and diseases.

BLS is a fungal disease that causes necrosis to the leaf tissues, thus reducing photosynthesis and leaf appearance rates. In susceptible cultivars, it can cause either plant death or early bunch ripening (Stover 1972; Fouré 1994; Craenen and Ortiz 2003). Commercial bananas are all highly susceptible to BLS (Fouré 1994; Vuylsteke 2001; Ramirez et al. 2008, 2011) and hence the disease in such systems has to be managed primarily by means of fungicide applications. In humid areas of Costa Rica, Colombia, and Ecuador, fungicide applications are done on a weekly basis, or even more often (Marín et al. 2003; Orozco-Santos et al. 2008). Plantains, in contrast, often show more resistant responses (Fouré 1994).

The climatic niche to which BLS is suited is almost perfectly matched with the climatically suitable environments of bananas: both banana and BLS optimum development occur in the range 20–30°C (Simmonds 1962; Stover 1972; Stover and Simmonds 1987; Porras and Perez 1997). Development of *M. fijiensis* occurs in the range 12–36°C, with an optimum temperature of 27°C (Stover 1983; Jacome et al. 1991; Porras and Perez 1997). High relative humidity (RH), leaf wetness, and winds increasingly favor the reproduction and spread of the pathogen (Stover 1972, 1983; Jacome and Schuh 1992). On the other hand, areas with strong monsoonal influence and drought periods accompanied by temperatures above 30°C will severely limit the prevalence and development of the disease (Marín et al. 2003; Alves et al. 2011).

Previous studies have shown that subtropical regions currently lacking BLS could become suitable for the pathogen as low temperature thresholds are exceeded (Jarvis et al. 2008). In Brazil, disease prevalence is expected to shift downward (Alves et al. 2011). Overall, however, by

2050s, increases in temperature will likely cause some 90% of the areas currently suitable for BLS in the tropics to have predicted decreases in disease prevalence (Ramirez et al. 2011). Nevertheless, in areas where rainfall increases are expected, such as East Africa, the disease could be triggered, particularly in highlands, where minimum temperatures would not be expected to remain a constraint for the fungi to develop (Jacome and Schuh 1992; Porras and Perez 1997; Ramirez et al. 2011). Predicted drier climates in central America and the Caribbean are expected to reduce disease prevalence (Ramirez et al. 2011).

3. Nematodes. The severity of nematodes of the species *Radopholus similis* would increase in humid highlands if rainfall amount is to decrease, whereas those of the species *Pratylenchus goodyei* would be expected to be negatively impacted by such drier climates (I. van den Bergh, pers. commun.). FOC TR4 severity would also be expected to decrease with increasing temperatures, as these are likely to promote plant growth (Brake et al. 1995; Mak et al. 2004). Although not climatically driven, the severity of BBTV is also expected to increase with time (P. van Asten, pers. commun.).

D. Citrus

1. Tropical Regions

Production. Citrus of various species (*Citrus* sp.) is produced in 140 countries. Approximately 47 million t of citrus is produced in non-U.S. tropical and subtropical regions. Brazil and China are the top non-U.S. citrus producers. Brazil exports the majority of juice, approximately 12.7 million t, with in-country production of 18.2 million t. China produces approximately 10 million t with minimal exports (USDA, NASS 2012). In the northern hemisphere, citrus production will expand into more northern latitudes due to both reduced winter damage risk and higher growing season temperatures in the current production areas that affect both plant physiology, disease, and insects populations. According to Duan et al. (2010), in the northern and western subtropics of China, freeze injuries in the winter are expected to decline resulting in more stable production. In the southern subtropics high temperature extremes and gradual temperature increases result in yield and quality reduction, due to heat stress and high temperature-related disorders. Because of changes of precipitation caused by temperature changes, the winter and June precipitation in the subtropics is predicted to

decline in the future but rainfall in other months will increase to various degrees (Tang et al. 2008). The predicted precipitation variation will mitigate, to some degree, the arid regions' water shortage but increase precipitation in the pluvial areas of South China and Sichuan Basin resulting in waterlogged soils and reduced citrus pollination. Sugiura and Yokozawa (2004) simulated climate change impacts on 'Satsuma' mandarin (*Citrus unshiu* Marc.) in Japan and predicted that the favorable production regions will gradually move northward. By 2060s, the favorable areas for production will possibly move from the southern coastal sites to inland areas of western and southern Japan, the plains of Kanto, and the littoral zones of the Japan Sea in the central and western Japan and in southern Tohoku.

By 2030, annual precipitation in Australia is expected to remain stable in the far north and decrease by 2–5% over most of southern and eastern Australia, particularly in winter and spring (Aurambout et al. 2009). By 2070, precipitation ranges are projected to be larger and more variable. The range of annual precipitation change for low to high emission scenarios, respectively, is projected to be from −20% or −30% up to +10% or +20% in central, eastern, and northern areas. In the south, the projected change varies between −30% and +5% with a best estimate of −10%. Projected rainfall decreases in the southwest in winter and spring could be as low as −30% or −40%, adversely affecting production. In Spain, simulation of citrus yield in the arid and semiarid Cordoba and Murcia regions indicated increasing yield with increasing temperature change up to 5°C for the period of 2071–2100 (Iglesias et al. 2010) and substantial increase in the amount of water needed for irrigation due to increased air temperature. In areas where citrus crops are grown, the competition for water is already an acute problem in Spain. In Italy, the water deficit of the entire Apulia territory in southern Italy is projected to increase by 30% by the end of century (Kapur et al. 2010). The net irrigation requirement for citrus production is expected to increase 48% during this period. Separate from increased temperature, elevated CO_2 will increase citrus yield. Sour orange trees responded to elevated CO_2 of 300 ppm above ambient with a 70% increase in fruit number and yield but size was not affected (Kimball et al. 2007).

Insects. The Asiatic citrus psyllid (*Diaphorina citri*, Hemiptera: Psyllidae) does not occur in Australia, but if introduced would pose a major threat to the viability of the Australian citrus industry and to native *Citrus* species. The Australian climate has been assessed as suitable for establishment and spread of the psyllid. Historical temperatures

confirm that *D. citri* could survive in more than 50% of Australia's citrus-growing regions where it becomes established (Beattie 2002). Annual average temperature increases of approximately 1°C (0.7–0.9°C in coastal areas and 1.0–1.2°C inland) are projected by 2030 for a mid-range (SRES-A1B) emission scenario (Nakícenovíc and Swart 2000). The effect of warming is projected to be lower in winter than in other seasons, and on the coasts as opposed to inland, with the exception of northwest western Australia. Aurambout et al. (2009) modeled the impact of climate change on the behavior, distribution, and breeding potential of Asiatic citrus psyllid, one of two known vectors of huanglongbing (citrus greening) caused by a phloem-limited bacterium, *Candidatus liberibacter asiaticus*. They modeled three time frames (1990, 2030, and 2070) and demonstrated that the increasing temperatures projected under climate change will affect the timing and flush duration of new citrus growth necessary for psyllid development throughout Australia. Flushing will start progressively earlier as the temperature increases and be of shorter duration. There will also be a gradual southward expansion of shorter flush durations. Increasing temperatures will impact *D. citri* directly through alteration of its temperature-dependent development cycle and indirectly by altering the host flushing cycle. Under 1970–2000 average climatic conditions for the location of Narrandera, New South Wales, the first flush starts on the 62nd day of simulation and lasts 94 days, the second flush starts on day 213 and lasts 26 days, and the third flush starts on day 250 and lasts 27 days. If the daily temperatures for the same location are increased by the worst case scenario of 6°C, the first flush would start 58 days earlier and last 92 days (shortened by 2 days), the second flush would start 57 days earlier and last 17 days (shortened by 9 days), and the third flush would start 71 days earlier and last only 13 days (shortened by 14 days). Results averaged for Australia indicated that *D. citri* adults will emerge 6.1 days earlier in 2030 (18 Sept.) than in 1990 (24 Sept.) and 18 days earlier in 2070 (6 Sept.). This advancement in adult emergence is consistent with the predicted advancement in spring flush emergence. The occurrence of warmer temperatures during the growing season will shorten the time taken for the psyllid to complete its life cycle, potentially leading to more generations being produced. However, warmer temperatures during the growing season will shorten the time necessary for soft tissues to harden, thereby decreasing the amount of time available for the *D. citri* to reproduce and multiply. Aurambout et al. (2009) demonstrated that reduced availability of young citrus growth will negatively affect the capacity of *D. citri* to reproduce, leading to the production of fewer egg clutches.

The trend could be different if more than three flushes per year were produced. For example, in Darwin, Northern Territory, natural flushing cycles are relatively continuous from the beginning of the wet season in October until the end of the wet season in April providing more breeding surfaces and time for *D. citri* to reproduce. The risk of establishment by *D. citri* is projected to decrease under increasing temperatures, due to shortened intervals when it can feed on new leaf flushes. However, the southern coastline of Australia could become more suitable for *D. citri* than projected under current temperatures.

Climate has a major influence not only on the parasite–host association, but also on interspecific competition between scale parasitoids in citrus production (Benassy 1961). Direct or indirect climatic influences on the host scale insects or the parasites are important factors in the natural enemy's effectiveness because the dynamics of the same species may vary considerably under different weather regimes (Huffaker et al. 1971; Huffaker and Gutierrez 1990; Rochat and Gutierrez 2001). Climate change will alter the parasite composition in citriculture. *Aphytis melinus* is considered a superior competitor in the field because it is better adapted to dry and hot climates (Rosen and DeBach 1979). The displacement of *Aphytis* species by *A. melinus* has been related to climate adaptability and other biological differences between species (Kfir and Luck 1979; Huffaker and Gutierrez 1990). There is a direct relationship between temperature and humidity of one area and the dominant *Aphytis* species. Cooler winter temperatures and mild summers are the main differences between Valencia citriculture and other citrus areas where *A. melinus* has totally displaced *A. chrysomphali*. Kfir and Luck (1984) suggested that susceptibility of *A. chrysomphali* to high temperatures and low RH was probably the main reason it was replaced by *A. melinus* in California. Sorribas et al. (2010) found that dry areas with hot summer temperatures are preferred by *A. melinus*, which is able to complete the displacement of *A. chrysomphali*, but areas with mild summer temperatures have a significant abundance of *A. chrysomphali*. In addition, this parasitoid usually appears near coastal or humid zones in Florida, Cyprus, Australia, or Uruguay (Muma 1959; Orphanides 1984; Dahms and Smith 1994; Asplanato and Garcia-Marí 2002) where summer temperatures are milder and humidity higher than in inland areas. Climate change may alter the composition and distribution of these key scale predators in all citriculture areas.

Disease. As reviewed by Ghini et al. (2011), Jesus Júnior et al. (2008) analyzed the impact of climate change on citrus diseases in São Paulo

State and predicted that citrus variegated chlorosis (CVC) (*Xylella fastidiosa*) would increase in the central and southern regions of Brazil because the production of shoots in spring and summer would increase with increased temperature, stimulating the population of leafhoppers (*Dilobopterus costalimai*, *Oncometopia facialis*, and *Acrogonia* sp.), the primary vectors of the bacterium. The abundance of leafhoppers will also increase with rising temperatures. There is a projected reduction in precipitation in these citrus production areas and CVC symptoms will be aggravated by increased temperature and more frequent periods of water deficit. The projected reduction in precipitation could also stimulate the early development of the mite populations (*Brevipalpus phoenicis*) and consequently increase the viral disease, citrus leprosis. Damage from citrus black spot (*Guignardia citricarpa*) and floral rot (*Colletotrichum acutatum*) is expected to increase with rising temperatures (Jesus Júnior et al. 2008). Unfortunately, the efficacy and stability of biocontrol agents will likely diminish with climate change, since high temperature is one of the problems with applying antagonists (Garrett et al. 2006).

2. United States

Production. The United States is expected to produce 11.7 million t of citrus in 2012 with California producing 3.9 million t primarily for the fresh market, Florida producing 7.4 million t for the juice market and 0.7 million t will be exported (USDA, NASS 2012). Tubiello et al. (2002) simulated U.S. citrus production in future climate change scenarios. Overall, yields increased 20–50%, while irrigation water use decreased in many locations due to reduced freeze prevention irrigation. Crop loss due to freezing was 65% lower on average in 2030 and 80% lower in 2090, at all sites. In the primary citrus production areas, Miami, FL, experienced the smallest increases, 6–15%, and in the other major production sites in AZ, TX, and CA, increases were 20–30% in 2030 and 50–70% in 2090. All sites experienced a decrease in crop loss from freezing. Potential for northward expansion of U.S. citrus production was small because results indicated that in 2030 and 2090 northern sites of current marginal production would continue to have lower fruit yield, higher risk of crop loss due to freezing, and lower water availability than the southern sites.

Insect Pests. The geographic range of the Mediterranean fruit fly (medfly, *Ceratitis capitata*) is currently restricted to more southern regions of California (Messenger and Flitters 1954), but there are

incipient medfly populations in southern California (Carey 1996) with occasional infestations and winter dieback in more northern areas. The medfly would likely expand northward into current fruit-growing regions (Gutierrez et al. 2006).

In California, DeBach and Sundby (1963) introduced a series of parasitoid species to control California red scale on citrus. These releases resulted in a sequence of climatically adapted parasitoids displacing each other in some areas. This displacement occurred until each species established itself in the subset of Californian environments most favorable for its development. These and other biological control successes could be jeopardized by climate change.

Water Use. In California, Miller et al. (2003) simulated the hydrology for Sacramento, American, and Merced Basins and predict an early season increase in snowmelt from 2010 to 2099 with earlier snowmelt seasons with a slower river flow rate later in the season. These reductions in growing season irrigation water will greatly limit perennial horticultural crop production in the arid and semiarid crop production regions unless sufficient water is stored in reservoirs. The impact will be most on late season crops.

E. Cacao

The cocoa tree (*Theobroma cacao*) is cultivated in the humid tropics, the vast majority of which is used in the food industry for the production of chocolate and cocoa powder. A small proportion is also sold as cocoa butter, which is used in the pharmaceutical and cosmetic industries. Cacao is of international importance as a smallholder crop (5–6 million farmers) with only about 5% of the world crop (annual total = 3.6 million t) produced on plantations (Carr and Lockwood 2011). Like coffee, cocoa is a crop of major importance for smallholder livelihoods and ecosystems in many tropical countries; as an internationally traded commodity, cocoa contributes to the livelihoods of an estimated 40–50 million people (World-Cocoa-Foundation 2010). In the year 2008/2009, world production was worth approximately 9 billion USD (ICCO 2008). Ghana and Côte d'Ivoire were the largest producer countries accounting for 53% of world production (ICCO 2008). Cocoa contributed 7.5% to the Gross Domestic Product of Côte d'Ivoire and 3.4% to that of Ghana (FAO 2008). Cacao occupies 2.4 million ha in Côte d'Ivoire and 1.5 million ha in Ghana, more than in any other country in the world (Franzen and Borgerhoff Mulder 2007). Cacao is an understory rain forest tree and is known to be sensitive to drought, although quantitative

information on crop–water relations from mature, field-grown plants is scarce (Carr and Lockwood 2011).

Until recently, climatic forecasts for the West African rain forest belt have been highly uncertain. Brown and Crawford (2009) showed that West Africa in general and the Sahelian region in particular are characterized by some of the most variable climates on the planet. Climate variability seems to have become particularly pronounced in the 20th century. A period of unusually high rainfall from the 1930s to the 1950s was followed by extended drought for the next three decades (Brown and Crawford 2009). This decrease in average rainfall and the high variability have negatively impacted the region's climatic suitability for cocoa especially during the 1970s and 1980s (Leonard and Oswald 1996). However, the drying pattern has not been homogeneous throughout the region and data from Nigeria suggest that it was relatively more pronounced in the savannah than in the rain forest region where cocoa is grown (Oguntunde et al. 2011). Carr and Lockwood (2011) point out that since cocoa is a drought-sensitive crop, and a large proportion of the world's cocoa is grown in parts of the tropics having a distinct alternation between wet and dry seasons, it is to be expected that the water relations of cocoa would have been the subject of research, which however is not the case.

Flower production is primarily controlled, either directly or indirectly by climatic factors (Alvim 1966; Mohr and Schopfer 1994). Omolaja et al. (2009) showed that flowering intensity was regulated by temperature and rainfall and varied across different *T. cacao* clones. Flowering is inhibited by water stress but synchronous flowering occurs soon after the dry season ends (Carr and Lockwood 2011). Genotypes differ in the sensitivity of fruit growth to changes in air temperature, which can affect time to fruit ripening, fruit losses from cherelle wilt, final pod size, bean size, and lipid content (Daymond and Hadley 2008). Leaf and shoot growth occurs in a series of flushes, which are synchronized by the start of the rains following a dry season (or an increase in temperature), alternating with periods of "rest" (Carr and Lockwood 2011). Under progressive climate change flowering, fruiting, and leaf and shoot growth are likely to be altered significantly.

Läderach et al. (2013) show that under the IPCC's (2007) SRES-A2 (business as usual) scenario, the average rainfall in the cocoa belt of Ghana and Côte d'Ivoire is predicted to decrease only insignificantly from 1,467 mm now to 1,455 mm in 2050, with most of the change occurring after 2030 (Plate 2.3). In 2030 (data not shown), the precipitation is predicted to decrease by a range of 7–20 mm in most parts of Côte d'Ivoire and to increase by a range of 5–21 mm in southern Ghana

(coastal regions). Thus, southern Ghana will initially become slightly wetter, before a weak drying tendency prevails throughout most of the cocoa region (Plate 2.3). In 2050, the earliest and strongest decrease in precipitation will be seen in the west of the region, with decreases ranging from 20 mm to 39 mm in Bafing, Worodougou, Valle du Bandama, and Zanzan in Côte d'Ivoire, then gradually expanding to Brong Ahafo in Ghana. In Ghana, the coastal region, outside of the core area of cocoa production, is predicted to experience an increase in precipitation by 20–30 mm. The maximum number of cumulative dry months, defined as the maximum number of months with less than 100 mm precipitation, is predicted to decrease from 4 months now to 3 months in 2050.

Mean annual temperature is predicted to increase by 2.1°C on average by 2050 passing through a 1.2°C increase in 2030 (Plate 2.4). The predicted increase in temperature by 2050 is between 1.7 and 2.1°C for the southern (forest) regions and up to 2.5°C for the northern (savanna) regions in both countries. The mean daily temperature range is predicted to remain almost constant with 9.1°C now and 9°C in 2050.

Läderach et al. (2013) further showed using Maxent, a crop suitability model, that under the predicted climate changes the climatically most suitable cocoa areas in Ghana are mainly in the eastern, central, Ashanti, western, and southern Brong Ahafo regions, while in Côte d'Ivoire they are mainly in Sud-Comoe, Agneby, Moyen Comoe, Sud-Bandama, and Fromager regions (Plate 2.5). For 2050 the model predicts an overall decrease in the climatic suitability of the current growing regions (Plate 2.6). This would be expected since the temperature mediated increase in ETP is not compensated by increasing rainfall, increasing the risk of drought to which cacao is very susceptible (Anim-Kwapong and Frimpong 2006). The coefficient of variance (CV) for the 2050 bioclimatic variables ranged from 0% to 25% suggesting reasonable agreement among climate models (Plate 2.7). Most affected by the suitability decrease are the southern Brong Ahafo and Volta Regions in Ghana, and Lagunes, Moyen Cavally, Marahoue, and Haut Sassandra in Côte d'Ivoire. Parts of these areas will become marginal or even unsuitable for cocoa, while other parts will remain suitable though less so than they are today. Apart from the southern parts of Bas Sassandra in Côte d́Ivoire and some marginal areas in the southern part of the western region in Ghana, there are only a few areas where the model predicts improving climatic conditions for growing cocoa. These are generally in hilly terrain, such as the Mampongtin Range and Atewa Hills (also called the Kwahu Plateau) in Ghana, and hilly parts of western Côte d́Ivoire and reflect the increase in average temperature

by up to 2°C (Plate 2.5). Läderach et al. (2013) also showed that negative suitability changes were mostly driven by the increase in potential ETP, especially during July to September (the coldest quarter, which includes the short dry season), possibly because of the sensitivity of pod growth during this phase to drought. This was followed in statistical significance by a variable related to temperature increase, which is also the driver of increased ETP. For the relatively few data points that showed increasing climatic suitability, this increase was most highly correlated with an increase in the seasonality of the climate (measured as the CV of monthly rainfall within a given year). These areas are mostly in the wettest, southwestern corners of the two countries where an increase in seasonality of rainfall may be beneficial for the cocoa crop (Plate 2.6).

F. Coffee

1. Production. The genus *Coffea* includes more than 90 species (Davis et al. 2006) but only two species are commercially viable: Arabica coffee (*Coffea arabica*) and Robusta coffee (*C. canephora*). Arabica grows in mid-elevation (600–1,500 m depending on the latitude) regions in the tropics and yields a smooth, slightly acidic beverage after roasting, whereas at lower elevation (0–800 m) Robusta is more tolerant to growth in full sun and produces a relatively harsher cup of coffee with higher caffeine content (Charrier et al. 2009). Because the Arabica species produces higher quality coffee, it generates more economic value; in contrast, Robusta generates higher yields per plant than Arabica, but produces beans that horticultural markets generally consider of lower quality and economic value. In this chapter we are focusing mainly on Arabica coffee.

The coffee trade generates approximately 15 billion USD worth of exports and employs approximately 25 million farmers; it is therefore an important revenue generator for developing countries (ICO 2011). Furthermore, coffee production provides a variety of environmental benefits such as water storage, carbon sequestration, biodiversity, and soil conservation to downstream populations (Läderach et al. 2010a).

Coffee growth, photosynthesis, and production require specific ecological and physical environmental characteristics, limiting the specific regions in which coffee is grown. For example, coffee is dependent on seasonal rainfall in the tropics for both production of flower buds (following a drought) and flowering (following a dry-season rain) (Cannell 1976; Magalhaes and Angelocci 1976; Carr 2001). Water availability, as well as small changes in temperatures, can affect coffee

photosynthesis (Nunes et al. 1968; Cannell 1976). Because coffee is not frost resistant (DaMatta 2004), the upper elevations and latitudes at which coffee can be cultivated are limited. Likely due to its evolution in the understory of tropical forests, the maximum photosynthetic rate of Arabica plants is at moderate temperatures and under moderate levels of shade (Nutman 1937; Lin et al. 2008) and thus it has traditionally been cultivated as an understory crop. Understory crops are trees, shrubs, vines, or other plants that thrive in the environment under the canopy of taller trees, are often grown within orchards, and may also be cultivated in natural forests or conservation areas (Davis et al. 2006).

Flowering is a complex sequence of biochemical, physiological, and morphological events that are affected by several factors such as temperature, light, soil, air, water availability, carbon-to-nitrogen ratio, crop load, and genotype (Rena et al. 1994). Under natural conditions, the rest of the flower buds are often broken by the first rains in the season following a dry period (Barros et al. 1999). The development of all coffee fruits within a single tree is separated temporally over several sequential periods of growth periods (2–4). Coffee flowering and fruit development are phased to maximize the likelihood that the fruits will expand during the rainy period and after a flush of new leaves (Cannell 1976). Rapid vegetative growth and fruit development appear to occur at different times. Farmers and meteorological stations report shifts in dry and rainy seasons, which significantly affect flowering, fruiting, and plant growth.

Climate models predict that the mean annual temperature in Mesoamerica will rise 2–2.5°C. Honduras, Mexico, and Nicaragua will likely experience the greatest increases whereas the increase in Costa Rica, El Salvador, and Guatemala is predicted to be less (see Table 2.3 and Plate 2.8). With increasing temperatures, areas at higher altitudes become suitable for producing coffee and currently marginal areas will become unsuitable. For example, the optimum coffee-producing areas in Nicaragua are currently at an altitude of 1,200 m; by 2050 the optimum increases to 1,600 m. Consequently, for an increase of 2.5°C, coffee-growing areas have to move 300–400 m up in altitude. At the national scale, Costa Rica, El Salvador, and Nicaragua have the highest percentage of land affected most drastically, with drops in suitability of 40% or greater.

Models predict lower annual rainfall in most of Mesoamerica. Honduras and Nicaragua will experience the most drastic changes, decreases on the order of −5% to −10%. Reduced water supply could constrain coffee cultivation and some methods of processing. Farmers already confirm that rainfall is becoming erratic and exhibits greater

Table 2.3. Projected changes in temperature, precipitation, and coffee yield by 2050 in Mesoamerica (Läderach et al. 2010a).

		Distribution in (%) of area									
		Temperature change (°C)		Precipitation change (%)				Coffee suitability change			
Country	Coffee contribution to GDP (%)	2.00–2.25	2.25–2.50	>−10	−5 to −10	−5 to 0	0 to 5	≥40% reduction	40–20% reduction	20–0% reduction	≥0% increase
Costa Rica	1.3	100.0	–	–	–	100.0	–	55.4	40.5	2.7	+1.4
El Salvador	2.5	78.3	21.7	–	1.1	98.9	–	45.5	43.7	10.9	–
Guatemala	4.2	60.8	39.2	–	17.4	82.6	–	12.9	25.5	54.2	+7.4
Honduras	8.2	5.4	94.6	5.8	94.2	–	–	38.2	49.8	11.0	+1.0
Mexico	5.0	20.6	79.4	–	49.0	50.5	0.4	18.2	34.6	46.9	+0.3
Nicaragua	7.2	7.9	92.1	1.2	98.0	0.8		35.3	32.1	32.5	+0.1

extremes, which is significantly impacting coffee, whose production cycle is highly dependent on rainfall patterns. Coffee flowering is triggered by the first rainfalls at the onset of the rainy season, but if precipitation drops off or becomes too heavy, both coffee flowers and fruits may drop from the tree. This stunted fruit growth would result in fewer, smaller beans of lower quality, which in turn fetch lower prices. Harvesting often represents the majority of production costs; therefore, erratic flowering and ripening cycles require additional harvesting cycles, which raises costs.

2. Quality. The climatic factors most often quoted in literature to influence coffee quality are average annual rainfall, rainfall distribution, humidity, and temperature. Temperature is the most decisive factor; this is also expressed in the fact that in many countries, altitude, as a proxy for temperature, is used to distinguish quality grades. An optimum annual average temperature of 18–22°C is generally quoted (Sylvain 1965; Guharay et al. 2000; COFENAC 2003b). Above or below these temperatures, the yield and quality of *C. arabica* are greatly reduced (DaMatta 2004). Diurnal temperature range is known to have strong influence on coffee quality (Illy 2001). Griffin (2001) states that a greater diurnal range promotes the production of sugars in fruits in general. Consequently, large diurnal ranges in temperature may increase the sweetness of a coffee. Njoka and Mochoge (1997) state that Arabica coffee requires temperatures ranging from a daily maximum of 32°C to a minimum of 7°C. The minimum diurnal range should be about 19°C. Annual rainfall where coffee is grown varies according to the region, ranging from 600 mm in Zimbabwe (Naylor 1990) to 4,000 mm in Ecuador (Cofenac 2003a). Rainfall where high quality is grown varies less, ranging from 1,000 mm (Njoka and Mochoge 1997) to a little over 1,700 mm (Avelino 2006). Apart from total annual rainfall, its distribution is also important. Ibarra (1986) states that in Honduras, the best coffee is produced where the wet seasons are as long as 9 months. Other authors recommend a dry season of no more than 3 or 4 months. Also rainfall distribution during berry development is crucial, since it directly influences harvest quality (Suarez 1979). Venkataramanan (2003) states that inadequate rainfall during berry development causes water stress in the plants and results in physical defects of the beans. In particular, inadequate rainfall during the stage of rapid swelling of the berries (42–102 days after flowering) and first endosperm filling stage (117–152 days) can affect normal berry development and may result in small beans and a lower percentage of best quality beans (Venkataramanan 2003). High-quality coffee beans develop when the

RH is 70–95% (Enríquez 1993; Fischersworring and Robkamp 2001); consequently periods of hot dry weather will decrease bean quality.

Higher ambient temperatures speed up the ripening of coffee berries, leading to poorer cup quality. This is because important components of coffee quality such as sugars, amino acids, and fats do not have sufficient time to accumulate, which results in poorer quality (Vaast et al. 2006). High value Arabica coffee, especially the type that meets the qualifications of more lucrative horticultural markets, requires lower temperatures. Areas currently growing Arabica may therefore need to be replaced by (lower value) Robusta coffee, cattle pasture, and food crops. Higher quality beans fetch higher prices, but there are also other methods to secure better returns, including "Denomination of Origin" (DO) status. As coffee in current DO zones becomes less suitable for producing high-quality coffee, producers in such regions may lose DO certification (Läderach et al. 2010b).

3. Insects. There is very little research published on the effect of climate change on coffee pest and disease except for the coffee berry borer (*Hypothenemus hampei*). Data from Jimma (Ethiopia) revealed that before 1984 it was too cold for *H. hampei* to complete even one generation per year, but thereafter, because of rising temperatures in the area, 1–2 generations per year/coffee season could be completed (Jaramillo et al. 2009). Jaramillo et al. (2011) also predicted the impact of progressive climate change on *H. hampei* in East Africa. *H. hampei* is forecasted to worsen in the current *C. arabica* producing areas of Ethiopia, the Ugandan part of the Lake Victoria, and Mt. Elgon regions, Mt. Kenya and the Kenyan side of Mt. Elgon, and most of Rwanda and Burundi. The calculated hypothetical number of generations per year of *H. hampei* is predicted to increase in all *C. arabica*-producing areas from 5 to 10 (Jaramillo et al. 2011).

IV. ADAPATION

Climate change presents new environmental challenges to the adaptive and coping capacity of both large and small perennial crop growers, and processors, while raising new issues for researchers, consumers, and policy makers. Growers and processors are always adapting management practices to reduce risks associated with weather variability but further transformational type changes will be required to meet the new demands of climate change in the coming decades (Howden et al. 2007). The background information and case studies of selected perennial

crops presented here (see Section III) clearly indicate that many production systems will require profound changes in the next century, particularly those located in marginal climate ranges. Effective science-based adaptation of the direct and indirect effects of climate change will require capitalizing on any opportunities while minimizing or avoiding any negative impacts. Adaptation can, however, happen in different ways, largely depending on the magnitude of the impact and the spatio-temporal scale at which the adaptation measures are being developed and/or implemented. Adaptation can either anticipate the production system needs or react to the change.

A. General Concepts of Climate Change Adaptation

Adaptation to climate change is, undoubtedly, the final target of any impact prediction (Moser and Ekstrom 2010; Challinor et al. 2012). The IPCC (2001b) has defined adaptation as

> Adjustment in natural or human systems in response to actual or expected climatic stimuli or their effects, which moderates harm or exploits beneficial opportunities. Various types of adaptation can be distinguished, including anticipatory and reactive adaptation, private and public adaptation, and autonomous and planned adaptation.
>
> (IPCC 2001b)

Implicit in the IPCC definition of adaptation is the scale at which the *adjustment* can happen. To this aim, a more comprehensive definition has been attempted by Moser and Ekstrom (2010). This view considers the fact that not only *adjustments*, but also longer term *transformations* to systems may be required:

> Adaptation involves changes in social-ecological systems in response to actual and expected impacts of climate change in the context of interacting nonclimatic changes. Adaptation strategies and actions can range from short-term coping to longer-term, deeper transformations, aims to meet more than climate change goals alone, and may or may not succeed in moderating harm or exploiting beneficial opportunities.
>
> (Moser and Ekstrom 2010)

Adaptation can be seen as an iterative process that starts from the development of knowledge about a system and its problems (i.e., quantifying impacts). This knowledge is then used to develop and select options, which are finally implemented and evaluated

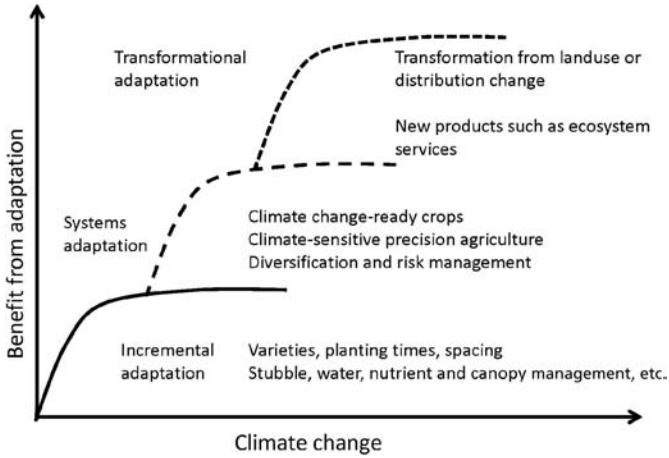

Fig. 2.1. Levels of adaptation in relation to benefits from adaptation actions and degree of climate change, with illustrative examples. *Source*: Howden et al. (2010).

(Fig. 2.1). Such iterative process can happen at a variety of scales, ranging from seasonal to multidecadal (Howden et al. 2007; Moser and Ekstrom 2010; Park et al. 2012).

Fig. 2.1 illustrates the different types of adaptive responses in agriculture as the degree of climate change increases. In agricultural systems, farmers constantly change their management practices in response to climate and climate-related stresses (i.e., pests and diseases). These adjustments can be considered as short-term coping strategies and are typically incremental and messy (Moser and Ekstrom 2010). Such adjustments may include changes in the amount and timing of fertilizer, irrigation and fungicide applications, changes in sowing dates, and changes in varieties.

The degree of climate change is expected to be higher in the future (Joshi et al. 2011). Adaptation planning at larger time scales needs to consider further and more substantial changes to the system (Moser and Ekstrom 2010; Park et al. 2012). Therefore, the approach of relying solely on incremental short-term adjustments may not be successful with long lead times. This is because there is a degree of change in climate beyond which the available short-term options for a farmer may all not work or because the negative impacts of climate change may arise at rates and in a multidimensional fashion that would make it difficult for farmers to respond. For example, both the genetic variation within a given crop's gene pool and the speed at which climate-adaptation

beneficial genes can be incorporated in existing varieties have limits (Reynolds et al. 2011).

Systems adaptation (Fig. 2.1) involves changes in the whole cropping system such as changing the crops in the rotation, diversifying the system to include a wider range of species with diverse uses (i.e., agroforestry), or optimizing production at the maximum extent possible through precision agriculture (Rickards and Howden 2012). The last type of adaptation would be needed when a given farming system becomes completely economically or environmentally unsustainable. Transformational adaptation planning is required when the degree of climate change is expected to cause an irreversible loss to the system object of analysis (Moser and Ekstrom 2010; Rickards and Howden 2012). In that sense, it is designed to avoid severe impacts of climate change and/or capitalize increasingly positive effects that can arise from a system shift (Park et al. 2012). Transformational changes in a cropping system can occur in different dimensions and often overlap with system-level adjustments. Transformational adaptation may include livelihood changes such as changes from cropping to livestock systems (Jones and Thornton 2009), community migration, or a complete change in the focus of the system (e.g., from an agricultural system to a national natural park) (Rickards and Howden 2012).

The time at which each type of change is required in a given farming system largely depends upon the type of system. Perennial systems are expected to substantially benefit from longer term transformational planning, given the high costs associated with establishing these cropping systems. Annual rotations are somewhat more flexible because crops can be changed in a yearly basis. However, socio-economic and market-related barriers would be expected in both cases (Moser and Ekstrom 2010). For more comprehensive reviews on adaptation the reader is referred to Howden et al. (2007), Moser and Ekstrom (2010), and Park et al. (2012). Of particular relevance to transformational adaptation is the review of Rickards and Howden (2012).

B. System-Level Adaptation Strategies in Perennial Cropping Systems

1. Genotypic Adaptation. We focus primarily on genotypic adaptation as it is among the most promising adaptation strategies (Butler and Huybers 2012). Genetic variation within a crop's gene pool can, to a large extent, allow the adaptation of agricultural systems. On one hand, promising but already existing varieties can be used to replace currently growing ones. On the other hand, specific traits and/or genes can be

incorporated into existing varieties by means of crosses or genetic engineering (Hajjar and Hodgkin 2007). Genes to tolerate drought, excessive heat, and to resist pests and diseases can be found in both existing landraces (Beaver et al. 2003; Reynolds et al. 2011), and in wild progenitors of crops (Hajjar and Hodgkin 2007; Jansky et al. 2009; Guarino and Lobell 2011). Crop improvement networks have historically focused on incorporating stress-tolerance and/or disease-resistance genes into high-yielding cultivars (Reynolds et al. 2011; Stamp and Visser 2012) as a way to decrease production costs and close yield gaps (Reynolds et al. 2011).

Genotypic adaptation involves both the replacement of currently used cultivars by those existing within a given neighborhood (i.e., varietal shifts) and the development of new cultivars through the incorporation of traits that may become beneficial under certain degrees of climate change (i.e., developing climate-smart crops). Thus, genotypic adaptation is relevant in the context of both short-term adjustments and systems adaptation (Jarvis et al. 2011). Breeding programs are currently challenged with having to set priorities based on climate change impacts predictions. Decisions of *which* traits to breed and by *when* would cultivars need to hold such traits are expected to be largely influenced by the type (e.g., increase in mean, increase in extreme events), direction (e.g., drier and warmer, wetter and warmer), and extent (how warmer, how drier) of the predicted climatic changes in a given area (Stamp and Visser 2012).

Modeling studies have attempted to quantify the benefits of genotypic adaptation. Water–stress adaptation, in particular, can account for the majority of negative climate change effects (Bryan et al. 2009; Hawkins et al. 2012). Challinor et al. (2010) found that adapting Chinese wheat varieties to high temperature and water stress thresholds during anthesis can reduce the percent of failed seasons under future scenarios by 30% and 50%, respectively. Jarvis et al. (2012) report that in addition to cassava's great potential for adaptation, capitalizing benefits from further improving its drought and cold tolerance may bring substantial benefits under future climate scenarios. Studies of these types are scarce or nonexistent for perennial systems, but they provide examples and models for adaptation studies and breeding programs in horticultural crops.

2. Other Adaptation Strategies. A review of European (Iglesias et al. 2012), United States (NCA 2012), and global (Howden et al. 2007; Foley et al. 2011) adaptation options at the local farm level included changes in crop management (e.g., cultivar selection, timing of

field operations, management of landscape biodiversity, and integrated pest management), improved water management (e.g., floodplain and wetlands restoration, efficient irrigation, and water harvesting), and a sustainable use of plant genetic resources (Dusen et al. 2007; Burke et al. 2009). These adaptation strategies address the needs for perennial fruit crops in both temperate and tropical climates.

Under future scenarios, increases in extremes of temperatures (i.e., warm day occurrence and heat wave length) are expected (Thibeault et al. 2010; Orlowsky and Seneviratne 2012). Technologies to reduce the impact of stresses that occur during specific times of the year will thus be needed under global warming. High temperatures reduce plant productivity even in the current environment. Perennial horticultural crop growers have a wide assortment of established management tools to adjust for climate change and increasing growing season temperatures including: crop load adjustment, canopy pruning/training/spacing, and irrigation. While very water use inefficient, overhead irrigation effectively buffers canopy temperature and is effective in frost mitigation. Shade in coffee has been shown to be beneficial in offsetting the effects of high temperatures (Schroth et al. 2009). Technology is being developed that reduces canopy and fruit temperature through reflective particle films (Glenn 2009) and provides increased yield and quality with increasing growing season temperatures without the use of additional irrigation. Other approaches such as the use of endophytic symbionts that reduce crop environmental stresses in conjunction with genetic or technological adaptations are also being developed (Bae et al. 2009; Redman et al. 2011; Kim and Cregg 2012; Knoth et al. 2012).

Adaptation options for managing crop pests and diseases in the absence of resistant genotypes will likely require increased use of pesticides. This will need to be done in a sustainable way. First, it will require increasing the resilience of agricultural systems to changes in pest pressures by varietal diversification and management of biodiversity at both field and landscape scale. Second, a better pest and disease management will be required to prevent pest and disease resistance to chemical control agents. These may include the development of new pesticide products and the implementation of pest and/or disease forecasting tools for better targeting applications to reduce environmental impacts.

3. Constraints and Trade-offs Related to Adaptation in Perennial Systems. Modeling outcomes need to be appropriately scaled (either up- or down-scaled) in order to provide information that allows

growers, processors, researchers, and policy makers to develop assessment tools that can help in targeting adaptation responses. Models ought to be treated as tools from which information can be extracted (Challinor et al. 2012). Such information, along with any relevant uncertainties needs to be appropriately communicated to the relevant stakeholders. Communicating uncertain (and potentially risky) outcomes has been identified as one of the main barriers to adaptation (Mearns 2010).

The process of adaptation may not be straightforward, as a given adaptation strategy may present trade-offs. More specifically, it is difficult to develop and/or implement adaptation strategies to increase production and or sustain crop productivity while at the same time reducing the environmental footprint or mitigating climate change (Foley et al. 2011). A clear example of this is provided by the wine producers in British Columbia, Canada. This example illustrates the unintended consequences of public policy interacting with local climatic conditions and the consequent environmental and climate-risk related cost (trade-off) (Belliveau et al. 2006). The Canada–United States Free Trade Agreement (FTA) in 1989 changed the market of Canadian wine produced in the Okanagan valley. Prior to the FTA, importation of foreign wines was prohibited and Canadian growers provided sweet red wines to the national market. Following the FTA, the flood of premium foreign wines greatly reduced this market. In response to this market shift, grape producers replaced existing low-quality, but winter-hardy, grape cultivars with more cold-sensitive but higher-quality cultivars, with significant sponsorship and subsidies from the government. This change enhanced the wine industry's domestic and international competitiveness, thereby reducing market risks (wine is now the second highest commodity in the Okanagan valley following apples). This market expansion came at an environmental cost, however, because the premium European cultivars had increased susceptibility to winter injury and high summer temperatures. Producers must irrigate to prevent frost damage in winter, which decreases market competitiveness because it reduces the quality of the grapes in years when it is used. Winter irrigation also increases production costs, the water footprint, disease risks, and producers' vulnerability to water shortages. High summer temperatures (>35°C) can delay maturity in an already short-growing season as well as reduce wine quality. The strategy of switching cultivars changed the nature of the system to make it better adapted to the market but simultaneously made it more vulnerable to climatic stresses to which it was previously less sensitive. Whether the strategy of irrigating is viable under future climatic change scenarios will be a

matter of serious concern at the local and national level in the coming years.

In the following sections, crop-specific climate change–related constraints are identified and, where possible, adaptation strategies to address such constraints are reported.

4. Crop-Specific Adaptation Options

Apples. Apple production will be limited by climate change and require adaptation to a number of factors as follows.

Advanced Bloom Dates Increase Frequency of Frost Damage Apple bloom dates have been observed to advance significantly in the major growing areas of Europe (Table 2.1), the United States, and South Africa, thus increasing the risk of late spring frosts (see Section III.A). Technology to protect flowers from freezing temperatures (Wisniewski et al. 2002) and to limit the dependence of spring flowering on winter temperatures (Wisniewski et al. 2011) could mitigate the more variable spring conditions expected in the future.

Warmer Winters Decrease Chill Accumulation Limited chill accumulation is not projected to limit apple production in eastern Washington State (Stöckle et al. 2010). In northeastern United States, Wolfe et al. (2008) found that a 400 h chilling requirement will continue to be met for most of the NE during this century regardless of emissions scenario. However, cultivars with prolonged cold requirements (1,000 or more hours) could be negatively affected, particularly in southern sections of the NE, where less than 50% of years satisfy the chill requirement by the 2050s (high emissions). The adoption and development of lower chill requirement cultivars together with dormancy-breaking chemicals and technology are expected to mitigate the effect of warmer winters.

Increased Temperature and/or Reduced Precipitation Increase Water Demand By 2060s the plains of central Tohoku's plains in Japan are predicted to be unfavorable for apple cultivation due to increased temperature (see Section III.A). Water demand is expected to increase in Europe ($\sim$50 m^3 ha^{-1} on average) as well as in the South African Cape (Grab and Craparo 2011, also see Section III.A). Water shortages have been predicted across Washington State in the United States (Stöckle et al. 2010). In Washington State water supply was assumed sufficient for irrigated crops, but other studies suggest that it may decrease in many locations due to climate change (Stöckle et al. 2010). Miles

et al. (2010) evaluated climate change impacts on the apple industry of Washington State using the IPCC AR4 scenarios downscaled to the state. They projected that the Yakima basin water supply will have shortages 36% of the years compared to the historical shortfall of 14% in the future 50 years. The effect on apple productivity will be minor with a 3% productivity decrease in the absence of a CO_2 response (Stöckle et al. 2010). A CO_2 response in apple may negate any adverse temperature effect. Water short years will increase from 14% historically to 36%. They propose that productivity can be maintained over the short term (i.e., 10–20 years) by adjusting production practices, adopting new technologies, improving agricultural water management, and statewide monitoring to gather and interpret data on climate change impacts to further aid policy and farm-level decisions. In the northeastern United States, Wolfe et al. (2008) evaluated projections of summer heat stress frequency and determined that summer heat stress will be particularly detrimental to apple production. By the end of the century and with higher emissions, short-term droughts are projected to occur as frequently as once per year for much of the NE, and occasional long-term droughts (>6 month) are projected for western upstate New York where perennial horticultural crops are a major industry. New water management and cultural technologies to reduce water needs will be needed together with more drought/heat tolerant and water use efficient cultivars. Productive apple systems currently optimize the desired crop load to the leaf area in order to optimize fruit size. However, future adaptation may require matching leaf area to available water resources and the growing season potential ETP. New cultural management tools needed to protect fruit from excessive heat and light may include pruning strategies that increase fruit shading, reflective sprays, and shade netting to reduce the heat load, and orchard location strategies that avoid southern exposure (N hemisphere).

Earlier Pest Development Associated with Increasing Temperatures Increased pest prevalence and less effective pesticides are expected in the NE of the United States (Wolfe et al. 2008), as well as across the Pacific Northwest (Stöckle et al. 2010) (see Section III.A). An increase in humidity and frequency of heavy rainfall events is projected for the NE (Frumhoff et al. 2006), which will favor some leaf and root pathogens (Coakley et al. 1999), and the projected increased rainfall frequency (Frumhoff et al. 2006) may reduce the efficacy of contact fungicides requiring more frequent applications. Pest management monitoring systems and targeted pest control methods are needed to mitigate the changing biotic complex of pests. Effective monitoring for

new and exotic pests together with targeted pest control and ecologically based pest management will be needed as production areas move or adjust to the changing complex of biotic pests.

In summary, Wolfe et al. (2008) determined that farmers most vulnerable to climate change impacts will be those without the financial resources to adapt, those unwilling or unable to change their current production system, and those who make poor decisions regarding the type and/or timing of appropriate adaptations. Conversely, the potential beneficiaries will be the growers currently growing or willing to shift to better-adapted crops, those with multiregional production options such as moving or expanding their operation into more appropriate climates, those who guess correctly about climate and market trends, and those who have the financial resources to implement adaptation strategies in a timely manner.

Grape. Grape production and quality will be limited by climate change and require adaptation to the following vulnerability factors.

Yield and Fruit Quality Reduction due to Warming and Extreme Heat Events Wine grape production is particularly sensitive to excessive heat stress, which can reduce fruit yield and quality. While slightly stressed grapes are known to increase the wine quality, frequent extreme heat stresses reduce acid levels and alter secondary compounds that determine the flavor of wine (White et al. 2009). Furthermore, grape production worldwide has experienced and will continue to experience earlier phenological events, shorter phenological intervals, and longer growing seasons due to increasing overall growing season temperatures. Together with increases in the frequency of extreme heat events, overall warming during the growing season leads to early maturity and could further reduce fruit yield and quality. In particular, U.S. premium wine grape production could be replaced (in roughly 80% of the areas) by cultivars adapted to warmer temperatures, but of lower quality. In Australia when a median growing season temperature $>21°C$ was used as an indicator of the climate conditions limiting wine quality and wine grape production, 21 of 61 regions were found to exceed the threshold by 2070 (Webb et al. 2007; Hall and Jones 2009).

Increasing the ability to cope with heat stress is identified as the most critical adaptation "wedge" for wine grape production in the western United States (Diffenbaugh et al. 2011). The growers have been and are likely to continue using various autonomous farm-level adaptation options such as irrigation, canopy management (e.g., particle films as sun screen, evaporative cooling, canopy architecture), switching

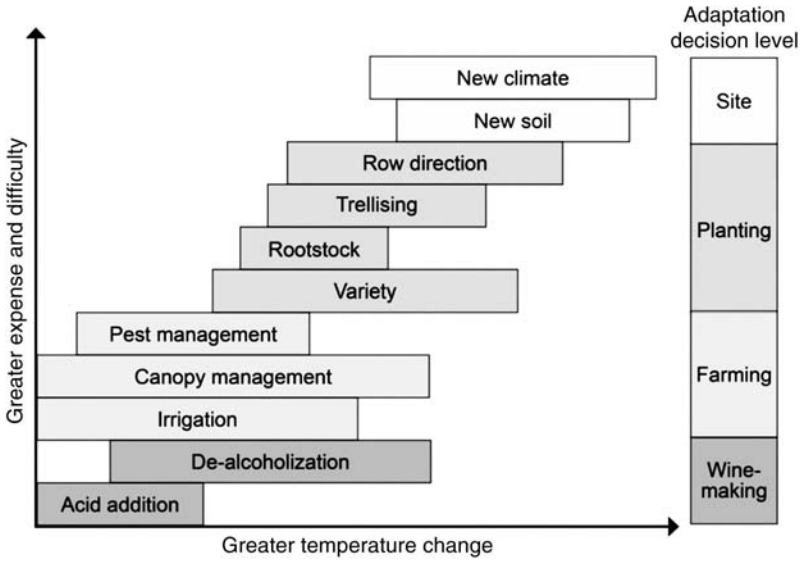

Fig. 2.2. Vineyard-scale adaptation options to stresses associated with climate change. *Source*: Adapted from Nicholas and Durham (2012).

rootstocks and cultivar, adaptive pest management, and changing row directions (see Fig. 2.2; Nicholas and Durham 2012). In addition to these autonomous farm-level adaptations, more "planned" adaptation strategies based on informed economic policies will be critical to sustain the agroeconomy associated with viticulture and wine throughout the world in a rapidly changing climate (Metzger and Rounsevell 2011).

Climate, Soils, and Cultivar Mismatch Climate change is likely to shift the regions in which the climate is favorable for growing specific wine grapes. Since climate is the most important factor determining the wine quality and the link between climate, soils, and cultivar selection is critical for wine ratings, a rapidly changing climate is likely to break the tight union known as "terroir" between the regions of specific climate and soils, grape cultivar, and wine quality especially in the "Old World" wine-growing regions of Europe (White et al. 2009). Terroir is a viticultural concept relating the sensory attributes of wine with a combination of climate, soil, cultivar, and cultural practices (Van Leeuwen and Seguin 2006). Changes in the system can alter the terroir and subsequently lead to narrow-niche cultivars no longer being suitable (see Section III.B). Detrimental impacts on production and quality have been predicted in several regions of southern Europe, mainly due to

increased dryness and cumulative thermal effects during the growing season (Malheiro et al. 2010). However, other regions (e.g., northern and high altitude sites in western and central Europe, southern Chile, and the Douro region of Portugal) may benefit from the changing climate (Jorquera-Fontena and Orrego-Verdugo 2010; Malheiro et al. 2010; Ruml et al. 2012; also see Section III.B). However, many regions and cultivars are currently at or near the upper bound of their optimal growing season temperature, suggesting that further warming will cause mismatches between the site climate, grape cultivar, and wine quality of many well-known wine-growing regions (Jones et al. 2005; White et al. 2009). Thus, climate change could potentially aggravate already contentious trade conflicts surrounding terroir (Josling 2006).

Farm-level adaptations such as introducing water supply by irrigation and cooling technologies may provide short-term solutions for maintaining the "terroir." Similarly, selection of late ripening genotypes or genotypes that can produce high-quality wines under high temperatures within the existing gene pool and cultivars will also be critical mid-term adaptation options (Duchene et al. 2010). Eventually, changing cultivars and shifting production areas (see Fig. 2.3) may become inevitable in some regions, although a majority of winegrowers in the traditional European premium wine-producing regions appear to be not

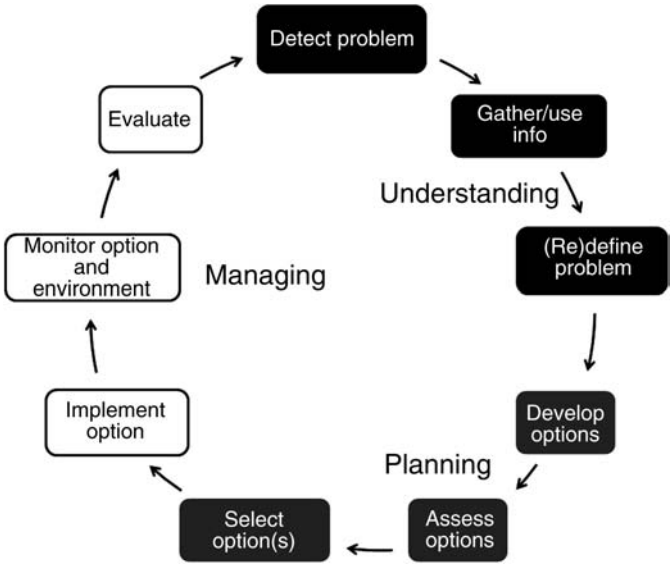

Fig. 2.3. Steps in the adaptation process. *Source*: Moser and Ekstrom (2010).

amicable to this particular adaptation option (Battaglini et al. 2009). The notion of terroir along with the AOC system (*appellation d'origine contrôlée*—a French system legally delineating geographical regions with their agricultural products) may have to be reconsidered in a changing climate (White et al. 2009; Metzger and Rounsevell 2011). Wine industry as a whole will likely have to develop novel marketing strategies to promote the concept of novel terroir that bridge the traditional notions of history and culture with new wine products produced from alternative regions and technologies in a rapidly changing climate (White et al. 2009). This type of entrepreneurial and cultural adaption strategy could help mitigating the cascading impacts of climate change on grape production and quality that could evolve into economic, social, and cultural issues and conflicts between wine-producing countries around the world (Belliveau et al. 2006). Development of economic and social solutions will be critical for adapting global wine industry to the challenges and for capitalizing on the potential benefits presented by climate change.

Bananas and Plantains. Musa production and quality will likely be limited by climate change and require adaptation to the following factors.

Prolonged Dry Seasons As mentioned earlier in the chapter (see Section III.C), changes in the distribution and decreases in the amount of rainfall in East Africa could pose a severe and additional constraint for highland bananas, which already suffer from drought (Ramirez et al. 2011; van Asten et al. 2011). Poor fruit development is likely to be experienced across West Africa and the lowlands of Latin America, primarily due to drought.

Bananas (*Musa acuminata*) are highly sensitive to drought (Stover and Simmonds 1987; Turner et al. 2007) in contrast to plantains (*Musa balbisiana*), which have greater drought tolerance (Robinson and Saúco 2010). The most effective way to manage drought would be through incorporation of drought-tolerant genes from the B genome of plantains (Nyombi 2010; van Asten et al. 2011). However, breeding bananas has proven to be a formidable task due to the seedlessness of banana and the infertile characteristics of the widely grown Cavendish clones (Grimm 2008; D'Hont et al. 2012).

Water conservation strategies have been implemented in Costa Rica. These include integrated weed management to improve soil cover, use of pits in between plants to store and preserve water, and incorporation of organic matter into the soil profile. The use of drip irrigation has proven a successful strategy in bananas in Colombia, but the cost of

establishing the system remains a constraint for its implementation where banana is not grown for commercial purposes.

Temperature Extremes Limiting Productivity Future climatic suitability is predicted to be significantly reduced in several lowlands, the Amazon, northern Colombia, large areas of central America, and western Africa, and benefits have been reported in highlands and Sub-Saharan Africa (Plate 2.2, also see Section III.C). Adaptation strategies in the cropping system to reduce high temperature damage remain unexplored. Under high temperatures, banana leaves fold downward across the petiole. This reduces leaf temperatures by 7–8°C, and the amount of water transpired (Turner 1998a; Turner et al. 2007). Previous research reports that fruit damage due to high temperatures can be avoided through the use of paper layers in between the bunch and the bunch cover (Turner 1998b; Turner et al. 2007).

Pest Damage BLS will continue to be an important constraint for banana systems, and particularly for commercial ones (Kema 2009). Currently, roughly one fungicide application per week is done in the banana cropping systems of the humid lands of Latin America. Due to the reproductive characteristics of BLS, it has developed resistance to a large number of fungicides.

Particular attention must be paid to the management of BLS, as it constitutes a major production cost. Cropping systems in southern Brazil and Africa where BLS is not a major constraint need to look forward and learn from experiences of other countries where the current disease prevalence levels are high (e.g., Costa Rica, Colombia, and Ecuador) (Ramirez et al. 2008). Currently, the only existing method to control the levels of BLS experienced in the humid lands of Latin America is the application of fungicides (Kema 2009). However, additional practices such as the removal of infected leaves at early stages may be useful when attempting to reduce the number of pesticide applications in areas where prevalence levels are not extremely high.

In managing BLS, it is critical that disease forecasting systems are put in place. It has been observed that BLS outbreaks are largely related to rainfall, temperature, and humidity of previous weeks or days (Stover 1972; Perez-Vicente et al. 2000). Moreover, the dispersion of the disease is highly dependent on prevalent wind conditions (Stover 1972). Using disease and weather observations it is possible to develop statistical models to predict the evolution and spread of the disease. Bioclimatic predictions can be done using these models and fungicide applications can be applied during early development stages of the pathogen. In this way, further spread and infection would be avoided.

Additional options to adapt banana production systems may include changes in crop management, changes in cultivars, genetic improvement, and migration to more suitable zones (Ramirez et al. 2011). The future "vision" of more robust Musa systems should be pursued by widening the genetic base by exploring additional sources of genes within the gene pool, while also implementing improved management practices such as more targeted irrigation, shifts to annual or perennial systems with optimized planting dates, and the spread of resilient mixed cropping systems (van Asten et al. 2011).

Citrus. Citriculture will benefit from increased temperature by reduced freeze damage and crop loss. U.S. citrus production areas are projected to have yield increases in the range 20–50% through 2090 (Tubiello et al. 2002) and citrus production in the northern and western subtropics of China are expected to have more stable production (Duan et al. 2010). In contrast, citriculture will be limited by climate change and require adaptation to the following factors.

Increased Temperature and/or Reduced Precipitation Increase Water Demand and Reduce Quality Higher growing season temperatures will likely reduce crop quality. Japanese citrus production will likely move northward due to higher temperatures (Sugiura and Yokozawa 2004). By 2060s, the favorable areas for 'Satsuma' mandarin production will possibly move from the southern coastal sites to inland areas of western and southern Japan, the plains of Kanto, and the littoral zones of the Japan Sea in the central and western Japan and in southern Tohoku. Potential for northward expansion of U.S. citrus production was small because results indicated that in 2030 and 2090 northern sites of current marginal production would continue to have lower fruit yield, higher risk of crop loss due to freezing, and lower water availability than the southern sites.

In California, Miller et al. (2003) predicted an early season increase in runoff from 2010 to 2099 with earlier snowmelt seasons but with a slower river flow rate later in the season resulting in reduced availability of growing season irrigation water. Fortunately, irrigation needs for frost protection will likely decrease (Tubiello et al. 2002). Decreases in mean rainfall and increases in rainfall volatility are predicted in southern and eastern Australia (Aurambout et al. 2009). In Spain and Italy, net irrigation requirements will likely increase as a result of increased temperatures (Iglesias et al. 2010; Kapur et al. 2010; also see Section III.D). The effects of CO_2 are expected to increase citrus yields with little effect on water use (Section III.D). The principal adaptation will be the movement of the production regions to capitalize on the changing

growing season conditions and development of water resources in new production areas as well as more efficient use of current water resources. New rootstocks adapted to local soils may also be needed.

Earlier Pest Development and New Pests Associated with Increasing Temperatures In Australia, the risk of establishment by *D. citri* is projected to decrease under increasing temperatures due to shortened intervals when it can feed on new leaf flushes. However, the southern coastline of Australia could become more suitable for *D. citri* than projected under current temperatures (Aurambout et al. 2009). The medfly would likely expand northward into current fruit-growing regions in California (Gutierrez et al. 2006). Climate change will alter the parasite composition in citriculture because *A. melinus* will become a superior competitor in the field because it is better adapted to dry and hot climates (Rosen and DeBach 1979). In Brazil, CVC (*X. fastidiosa*), is predicted to increase in the central and southern regions of Brazil because the production of shoots in spring and summer would increase with increased temperature, stimulating the population of leafhoppers (Jesus Júnior et al. 2008; Ghini et al. 2011). CVC symptoms will be aggravated by increased temperature and more frequent periods of water deficit. The projected reduction in precipitation could also increase citrus leprosis, whereas higher temperatures could increase damage from citrus black spot and floral rot (Jesus Júnior et al. 2008), with little hope that antagonist biocontrol agents will be a feasible solution (Garrett et al. 2006; also see Section III.D). As with other perennial systems where diseases are limiting (e.g., apple, Musa), pest and disease monitoring together with effective and ecologically based pest management will be needed throughout the 21st century.

Cocoa. Cocoa production will be limited by climate change and require adaptation policies. Changes in the climatic suitability for growing cacao will be a gradual process and it will not affect all parts of the growing areas equally. It is, however, important to start working on adaptation measures and strategies today in order to have solutions ready when needed. There is no reason for farmers, governments, and supply chain components to panic but the industry needs to plan ahead. We have identified the following factors as the main constraints to future cocoa production.

Increased Temperature and Increasing Drought Future climate scenarios in cocoa-growing areas will likely feature increases in transpiration demand and increased drought. Given the susceptibility of the cocoa

plants to drought (Anim-Kwapong and Frimpong 2006; Läderach et al. 2013), new cultivars with drought tolerance and heat resistance will be the most successful adaptation. The use of endophytic symbionts is also a promising approach that can accompany crop improvement efforts to reduce drought and heat stresses in cacao plants (Bae et al. 2009).

Decreased Yield and Quality Compounded by Increased or Changed Insect and Disease Pressure There is little information regarding the impacts of climate change on yield, quality, and pest and disease pressure available. However, it is very likely that climate change may have a negative effect on these factors across many regions. Therefore, more research is needed to understand the impacts of climate change in order to develop adequate adaptation strategies.

Coffee. Coffee production will be limited by climate change and require adaptation to the following factors.

Increased Temperature, Increasing Drought, and Reduced Crop Quality An optimum annual average temperature for coffee production is 18–22°C (Sylvain 1965; Guharay et al. 2000; COFENAC 2003b). Above or below these temperatures the yield and quality of *C. arabica* are greatly reduced (DaMatta 2004). Climate models predict that the mean annual temperature in Mesoamerica will rise 2–2.5°C. With increasing temperatures, areas at higher altitudes become suitable for producing coffee, and currently marginal areas will become unsuitable. At the national scale, Costa Rica, El Salvador, and Nicaragua have the highest percentage of land affected most drastically, with drops in suitability of 40% or greater. High value Arabica coffee, especially the type that meets the qualifications of more lucrative horticultural markets, requires lower temperatures. Areas currently growing Arabica may therefore need to be replaced by (lower value) Robusta coffee, cattle pasture, and food crops. Higher quality beans fetch higher prices, but there are also other methods to secure better returns, including DO status. As coffee in current DO zones become less suitable for producing high-quality coffee producers in such regions may lose DO certification (Läderach et al. 2010b). Models predict lower annual rainfall in most of Mesoamerica. Reduced water supply could constrain coffee cultivation and some methods of processing.

Pest Damage Coffee berry borer damage is forecast to increase in the *C. arabica* producing areas of Ethiopia; the Ugandan part of the Lake

Victoria and Mt. Elgon regions; Mt. Kenya and the Kenyan side of Mt. Elgon; and most of Rwanda and Burundi (Jaramillo et al. 2011).

The climate impacts on coffee production are predicted to be very site-specific, which will require site-specific adaptation strategies. However, there are three different categories of exposure profiles that can be distinguished: (1) areas that are highly exposed to progressive climate change, (2) areas that are moderately exposed, and (3) areas that will be more suitable in the future to produce coffee. Table 2.4 gives an overview of the adaptation options for central America.

Table 2.4. Overview of climate change adaptation options in central America.

Activity	Stressor to be addressed	Caveats
Highly exposed		
Crop insurance for smallholder farmers	Increased risk of extreme events	Could in certain cases delay adoption of necessary adaptation measures
Promote diversification of land use systems and income sources including payments for environmental services (PES)	Increased variability of coffee production and quality and increased risk of crop failure, interacting with market risks	Need to avoid prescriptive, top-down approaches, requires careful market analysis for new options, sustainable funding for PES
Breed coffee varieties with greater tolerance of high temperatures, low precipitation, and altered pest/disease pressure	Temperature increase and its effects on coffee production and quality	Varieties are still in development and not readily available to producers
Moderately exposed		
Improved shade structure and management	Greater maximum temperatures, increasing risk of rainstorms and landslides	Complex relationships between shade and coffee under drought conditions, labor requirements for shade management
Implement irrigation where feasible	Changing precipitation patterns and droughts	Costly infrastructure
Increase water efficiency in coffee production and processing	Lower average rainfall, increased drought risk	Requires low-cost credit especially for small farmers
Promising new areas		
Evaluate potential agroecological, social, economic, and infrastructural potential of promising areas	Suitable areas are decreasing under progressive climate change and areas at higher altitudes become more suitable	Areas at high altitudes are usually protected forest areas providing environmental services to downstream population

Source: Adapted from Schroth et al. (2009).

V. FUTURE RESEARCH NEEDS

We have identified (1) the exposure potential of key perennial crops to the varied effects of climate change and how it could affect production, (2) the sensitivity of the crops to measured and modeled changes in the biotic and abiotic factors related to climate change, and (3) the adaptive changes needed to minimize the vulnerability of these crops to climate change. Perennial cropping systems have developed under a generally stable climate, which has allowed management and policy decisions to use a well-developed database of information to solve problems as they develop. The expected increase in weather variability and climate change presents unprecedented challenges to this paradigm of sustainable production. Producers and processors are already or will be faced with climate-driven problems with little or no knowledge or experience to develop effective management strategies. Consequently, future management decisions will be based on a higher level of uncertainty, which is inherent in future climate impacts predictions. Managing and communicating this uncertainty will be a challenge for researchers. Additional research will be needed to provide data-driven information for growers, processors, governments, and policy decision makers.

A. Cultivar Development

Foremost among the adaptation strategies is cultivar development (see Section IV.B.1). Chloupek and Hrstkova (2005) compared yield increases of 26 crop species between Europe and the United States between 1961 and 2003. Adaptability to climate change was closely related to the annual yield increases of the crops studied both in the EU and in the United States. Crops that are more intensively bred (which have more registered cultivars) and/or have been in cultivation longer and/or are generatively propagated have higher adaptability in Europe. In order to adapt to and gain from climate change, breeding and testing targets should be modified within 5 years and they should include reduced sensitivity to temperature fluctuation in winter, late flowering, and frost tolerance of flowers.

There are a wide variety of adapted cultivars that can be evaluated for new regions. For most perennial crops, however, perennial breeding programs require 10–30 years to confirm and improve a cultivar for disease, insect, stress resistance, as well fruit quality. In bananas, for instance, years of breeding have not yielded the first single cultivar with both market acceptance and BLS disease resistance (Kema 2009). This breeding hurdle could be overcome using molecular approaches

(Kean 2010; Srinivasan et al. 2010) to reduce perennial cultivar generation time to months instead of years while also helping incorporate traits that are present in different but closely related wild species (D'Hont et al. 2012). Priority breeding traits vary on a crop basis. For example, in temperate perennial horticultural crops, the timing of dormancy is fundamental to minimize killing frosts both in spring and in fall. This would require that the plant react to day length instead of temperature patterns and would provide flexibility in growing season length and initiation and time of fruit maturity. Wisniewski et al. (2011) have transformed apple from temperature-induced dormancy to photoperiod-induced dormancy using a technology that is adaptable for other perennial horticultural crops. In banana production, photoperiod sensitivity and frost damage are practically irrelevant, but dwarfism is relevant in several cyclone-prone areas of Africa (Van den Bergh et al. 2012). Currently, molecular techniques are being used to identify genes associated with climate change (Hancock et al. 2011) in addition to disease, insect, stress, and quality traits that will benefit perennial horticultural crops in the future. Molecular tools will be needed to meet the rapidly changing climate of the current production areas as well as the needs of geographically shifted production systems.

B. Yield and Quality Responses to Climatic Changes

Crop responses to combinations of environmental factors remain poorly or only partially understood. During the course of the present review, it was found that knowledge gaps were somewhat complementary in temperate and tropical systems. On one hand, physiology-level knowledge on the responses to CO_2, temperatures, and water was more abundant in temperate crops (Sections II.A and II.B). By contrast, in tropical crops (coffee, bananas, cocoa), global and regional assessments and scientific priority setting studies were much more frequent (Sections III.C and III.F). For instance, no single FACE experiment has been carried out for bananas, and the CO_2 responses in coffee are only starting to be investigated (E. Assad, pers. commun.).

Increased CO_2 concentrations are expected to increase crop biomass, but this largely depends on the photosynthetic mechanism of the plant as well as on the prevailing climate conditions, particularly temperature and vapor pressure deficit (VPD) (Leakey et al. 2009). In addition, CO_2 fertilization effects can be negated or can even enhance the negative response of crops to high temperatures (Vara Prasad et al. 2006). In addition, intermittent drought is a significant limiting factor in most rainfed perennial systems (van Asten et al. 2011), but little is known

(particularly in tropical species) about the interactions between different types of drought, changes in VPD, and high temperatures. Ozone is expected to be detrimental for crop growth (Hollaway et al. 2011), but responses have been barely if at all assessed in experimental or farmers fields (Fuhrer 2003). Moreover, the effects of all these factors and their interactions on fruit development and quality remain a topic for further research.

C. Ecological Interactions in Cropping Systems

In combination with genetic improvements of crops, other methods (e.g., physiological, cultural, and ecological) for alleviating environmental stresses in horticultural crops need to be explored simultaneously. For example, utilization of existing and novel symbiotic relationships between endophytes and crops can be an ecological approach as a short- to mid-term adaptation option to climate change to reduce heat, nutrient, and water stress (Redman et al. 2011). Furthermore, selection and improvements of beneficial microbes that confer stress mitigation and growth promotion in crops may provide a more rapid, timely tool for adapting perennial horticultural crops to climate change.

D. Disease and Insect Response to Climate Change

Insect pests and pathogens are expected to expand or shift ranges as well as move with global trade. It is not well understood how naturally occurring biological control of pathogens and insect pest by other organisms could change under changed temperature, CO_2, and moisture regimes (Fuhrer 2003). Effective and environmentally friendly approaches for controlling more aggressive and new insects and weeds will be needed. Research in pheromone-based monitoring systems, attract-and-kill technologies, and introduction of effective biocontrol agents are some of the emerging technologies.

E. Reducing Production Costs

The costs of production will likely increase due to the input costs for the management of insects, weeds, and pathogens in addition to energy and water costs associated with irrigation. Research in automation, sensors, information technologies, and overall improvement of agricultural management will be required to reduce costs (Jiménez et al. 2011).

F. Chilling Requirements and Frost Damage in Temperate Crops

Weather variability in the spring will affect flowering and the potential for frost damage. Areas with reduced winter chilling will require either adapted cultivars with less chilling requirement or chemical methods to mimic chilling hours. Research on technology to protect flowers from freezing could stabilize production. Chemical agents to break dormancy have not been developed beyond the use of hydrogen cyanamide, and further improvements will be needed for all the deciduous crops. Mitigating freeze damage is approached in two nonexclusive areas of research: freeze avoidance and freeze tolerance. Many physical mechanisms of freeze avoidance have been identified and include ice nucleators, anti-nucleators, preferential ice accumulation sites, supercooling, and ice barriers (Gusta and Wisniewski 2012). However, no commercial product has been developed that consistently avoids freeze damage. Mechanisms associated with freeze tolerance are associated with biochemical adaptations under genetic control. Effective biochemical changes associated with freeze tolerance include compositional changes in cell membranes, increased osmotic adjustment, cryoprotective compounds, antioxidant defense systems, and cold-induced proteins (Gusta and Wisniewski 2012). Modern molecular biology, genomics, proteomics, and metabolomics will provide markers and genes for adapted cultivars with freeze tolerance and perhaps avoidance.

ACKNOWLEDGMENTS

A portion of this work is part of the United States Department of Agriculture's National Climate Assessment for 2012 and portions of the research were conducted under the global CGIAR Research Program on Climate Change, Agriculture and Food Security (CCAFS, http://ccafs.cgiar.org). The authors greatly acknowledge the valuable contributions of Charles Staver, Inge Van den Bergh, and David Turner on the section about bananas. Authors thank three reviewers and the editor for the valuable inputs aimed at improving the manuscript. Remaining errors and omissions are the authors' responsibility.

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3

Nonchilling Physiological Rind Disorders in Citrus Fruit

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ABSTRACT

Appearance is the primary parameter used to evaluate the quality of citrus fruit for the fresh market; so the condition of fruit rind is an important quality attribute. Preventing the development of nonchilling physiological

Horticultural Reviews, Volume 41, First Edition. Edited by Jules Janick.
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rind disorders such as rind breakdown, rind pitting, rind staining, puffiness, and peteca spots is one of the key challenges in postharvest handling of citrus fruit. Intensive research has been conducted toward better understanding of the factors contributing to the incidence of these disorders. This chapter examines the preharvest and postharvest factors contributing to the incidence and severity of nonchilling physiological rind disorders in citrus fruit, and presents a physical characterization of these disorders. It also describes the molecular, biochemical, and physiological basis of rind disorders and highlights the techniques for inducing rind disorders for research investigations. To date, the mechanism of citrus rind pitting disorder and the relationship with other physiological rind disorders is not well understood. However, it has been established that fruit susceptibility to these disorders is influenced by the microclimate inside the fruit canopy. The prospects for biochemical markers to predict the development of rind disorders and the use of nondestructive technologies to sort affected fruit are discussed in the chapter.

KEYWORDS: citrus fruit; chilling injury; physiological rind disorder; rind breakdown; rind disorder; rind pitting; rind staining

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I. INTRODUCTION

Citrus fruit are the highest value fruit crop in international trade. Current annual worldwide citrus production is estimated at over 122 million tonnes, worth over 20 billion US dollars (FAO 2010). However, citrus fruit are prone to develop various types of physiological rind disorders, manifested by a multitude of symptoms during handling and storage (Kader and Arpaia 2002; Alquezar et al. 2010). The incidence of fruit affected by these disorders can reach up to 60% of the total production (Agustí et al. 2001). Physiological rind disorders include chilling injury, peteca spot, rind breakdown, nonchilling rind/peel pitting and rind staining, puffiness, creasing, oleocellosis, stem end rind breakdown (SERB), and stylar end breakdown (Cronje 2007).

Although these physiological disorders affect the rind and do not compromise the edible internal portion of the fruit, they do however decrease postharvest fruit market value since external appearance is the primary specification used to evaluate quality of citrus fruit and a major consumer complaint (Alquezar et al. 2010). Limited knowledge of the physiological mechanism underlying these disorders affects supply, profits, and loss. The challenge is significant regarding citrus physiological rind disorders such as rind breakdown of 'Nules Clementine' mandarins (*Citrus reticulate* Blanco) (Cronje et al. 2011a,b), rind breakdown of 'Navel' orange [*C. sinensis* L. (Osb.)] (Agustí et al. 2001), and nonchilling postharvest rind pitting of 'Marsh' grapefruit (*C. paradisi* Macf.) (Alférez and Burns 2004; Alférez et al. 2005), which characteristically do not manifest during harvest grading but develop about 1–5 weeks after harvest (Cronje et al. 2011a). If fruit are shipped over long distances, symptom development usually coincides with the commercial shipping period and is visible at the point of sale. This is therefore extremely problematic as rind disorders can lead to tremendous financial losses at this stage of the logistical supply chain.

This chapter examines citrus fruit rind quality with particular emphasis on the current knowledge of morphological and physiological aspects of nonchilling physiological rind disorders of citrus fruit. The authors will first emphasize the magnitude of the problem, followed by characterizing each of these disorders by encompassing their visual symptomology, microstructural periphery of the fruit affected by these disorders. This section will include a summarized tabular quick reference version for different physiological rind disorders. Section IV includes causal factors, both preharvest and postharvest, while Section V discusses the physiology and molecular biology of these disorders. Finally, we will discuss possible preventative or control measures and

list future research avenues including the potential of nondestructive technologies to predict and determine fruit susceptibility to physiological rind disorders.

II. CITRUS RIND DISORDERS

A. Terminology

Numerous rind disorders that are discussed in the literature can be classified as nonchilling physiological rind disorders of citrus fruit. The terminology used to refer to these physiological rind disorders depends mostly on symptomology, species, cultivar, region in which the research was conducted, and so on. It is not well understood how the different rind disorders described in the literature in different citrus cultivars are related to each other (Lafuente and Sala 2002).

In the literature, the collective term referring to the rind nonchilling physiological disorder is "nonchilling rind (or peel) pitting" and is sometimes used interchangeably with "peel pitting," although some authors distinguish between "rind pitting" and "rind breakdown" or necrosis (Petracek et al. 1998a,b; Ben-Yehoshua et al. 2001). For the reason that the different terminology relating to specific symptoms observed on a specific cultivar has been established in literature, this chapter will stick to this common terminology and its definition as much as possible. "Rind" or "peel" both describe the same structure (flavedo and albedo). The use of either one follows the general use in the country a specific disorder is seen in, namely, peel pitting is used in Spain (Cajuste and Lafuente 2007) and USA (Alférez et al. 2005), whereas rind breakdown is used in South Africa (van Rensburg et al. 2004) and Australia (Treeby et al. 1995). In general, the common name of a disorder is always associated with a cultivar, and this combination, as for example, noxan of 'Shamouti' (Peretz et al. 2001), rind breakdown 'Nules Clementine' mandarin (Plate 3.1b) (Cronje et al. 2011a), or rind staining of navel (Plates 3.2a and b and 3.3a) (Alférez et al. 2003), separates the disorder from similar ones and helps to identify the associated causal factors.

B. Symptomology

Externally, symptoms of nonchilling physiological rind disorder may resemble the symptoms of postharvest chilling injury (Plate 3.4a and b) (Freeman 1976; Arpaia et al. 1991). Chilling injury is defined as "the permanent or irreversible physiological damage to plant tissues, cells,

or organs, which results from exposure of plants to temperatures below some critical threshold but nonfreezing temperature that causes injury" (Lyons and Breidenbach 1987). Nonchilling rind disorders are distinguished from chilling injury in that the symptoms develop at nonchilling cold storage temperatures (Petracek et al. 1995; Cronje 2007). Nonchilling rind disorders are distinguished from chilling injury because most of them affect both the albedo (the inner, white part of the peel) and the flavedo (the pigmented part) tissues (Petracek et al. 1995; Alférez and Burns 2004; Cronje 2007) and that fruit may be predisposed to the disorder while still attached to the tree (Sala et al. 1992).

An overview of symptomology, time of occurrence, and causal factors of different nonchilling physiological rind disorders in oranges (Table 3.1), grapefruit (Table 3.2), and mandarin fruit (Table 3.3) is reported with selected recent review publications in Table 3.4. The time of symptom development is thought to offer some suggestion as to the cause of a rind disorder. Therefore, it is highly possible that "peel pitting," "rind pitting," and "rind staining" on 'Navel' oranges; "rind breakdown," "nonchilling peel pitting," and "rind staining" of 'Navelate', 'Pinalate', 'Navelina' oranges; and "peel pitting" of 'Fallglo' and 'Fortune' mandarins, all of which can develop within 1 week after harvest, refer to the same disorder. However, "noxan" of 'Shamouti' orange differs from rind pitting because of its superficial nature. Although the symptoms and the terminology are the same, "peel pitting" of 'Marsh' grapefruit differs from the rest of the listed disorders in that it develops within 2 days after harvest. In addition, there have been several reports of fruit developing nonchilling "rind pitting," "peel pitting," "rind staining," and "noxan" while still on the tree at nonchilling temperatures (Almela et al. 1992; Duarte and Guardiola 1995; Vitor et al. 2000; Agustí et al. 2001, 2003; Tamim et al. 2001; Assimakopoulou et al. 2009). Rind breakdown of 'Nules Clementine' mandarin and SERB are differentiated appreciably from all these disorders by the fact that no preharvest symptoms have been reported (Cronje 2009).

In general, rind postharvest physiological postharvest disorders, with the exception of stem end rind breakdown, are initially manifested on the equatorial plane as small, irregular, slightly sunken, and colorless patches of about 3–6 mm in diameter scattered about the flavedo (the outermost, pigmented part of citrus peel) of the fruit. Typical visual symptoms of nonchilling postharvest pitting of 'Nova' mandarin (Plate 3.1a) (Duarte and Guardiola 1995), rind breakdown of 'Nules Clementine' mandarin (Plate 3.1b) (Cronje et al. 2011a), rind breakdown (Plate 3.5a) and preharvest rind pitting of 'Navelate' sweet orange

Table 3.1. An overview of symptomology, time of occurrence, and causal factors of different physiological rind disorders on oranges.

Cultivar	Name of disorder	Symptoms	Causal factors	Time of occurrence	Pre/postharvest	Country	References
Navel	Peel pitting	Collapsed areas of flavedo and part of albedo that becomes brown with time	Wide array of preharvest, postharvest factors	ND	Pre- and postharvest	China	Gao et al. (2006)
Navel	Postharvest rind pitting or rind staining	Scattered clusters of pits over the fruit surface that turn dark brown after several weeks	Water loss, sudden changes from low to high RH, waxing	1–2 weeks	Postharvest	Spain	Alférez and Zacarìas (2001)
Navel	Peel pitting	Collapsed areas of the flavedo and part of the albedo that becomes brown with time	Wide array of preharvest, postharvest factors	1 week	Postharvest	China	Li et al. (2009)
Navel	SERB	Collapse and browning of the peel at the stem end of the fruit	Water loss, sudden changes from low to high RH	–	Postharvest	USA	McCornack (1970)
Navel and Valencia	SERB	Collapse and browning of the peel at the stem end of the fruit	Rootstock and storage temperature	9 days	Postharvest	USA	Ritenour et al. (2004)
Navelate	Peel pitting/rind breakdown/ rind staining	Collapse, drying, and browning of the flavedo	Water loss and sudden changes from low to high RH	7–28 days	Postharvest	Spain	Alquezar et al. (2010)

Navelate	Nonchilling peel pitting	ND	Ethylene inhibition by 1-MCP (reduced by external ethylene application)	2–14 days	Pre- and postharvest	Spain	Estables-Ortiz et al. (2009)
Navelate	Nonchilling peel pitting	Irregular depressed areas on the flavedo that may turn brown with time	Lack of epicular wax and dehydration	7–22 days	Postharvest	Spain	Cajuste and Lafuente (2007), Cajuste et al. (2010)
Navelate	Nonchilling peel pitting		Dehydration	14–56 days	Postharvest	Spain and Italy	Alférez et al. (2005)
Navelate and Pinalate	Rind breakdown	Sunken areas of the peel that develop into reddish-brown, dry areas on the flavedo	Water loss and sudden changes from low to high RH	–	Pre- and postharvest	Spain	Agustí et al. (2001)
Navelate	Nonchilling peel pitting	ND	Lack of epicular wax and dehydration and increased internal ethylene production	14 days	Postharvest	Spain and Italy	Sala et al. (2005)
Navelate and Pinalate	Rind staining	Collapsed and dry areas of the flavedo and part of the albedo that becomes dark with time	Abscisic acid, ethylene, RH, and storage temperature	6–24 days	Postharvest	Spain	Lafuente and Sala (2002)
Navelina	Nonchilling peel pitting	ND	Water loss and sudden changes from low to high RH and increase in ethylene	7–28 days	Postharvest	Spain	Sanchez-Ballesta et al. (2008)

(*continued*)

Table 3.1. (*Continued*)

Cultivar	Name of disorder	Symptoms	Causal factors	Time of occurrence	Pre/postharvest	Country	References
Pinalate	Rind breakdown	ND	Increased water loss	5 days	Postharvest	Israel	Porat et al. (2004)
	Superficial rind pitting	Collapse and necrosis of flavedo	Water loss	3–5 weeks	Pre- and postharvest	Israel	Tamim et al. (2001)
Shamouti	Noxan	Superficial necrosis and pits on flavedo	Low RH, increased water loss	7–28 days	Postharvest	Israel	Peretz et al. (2001)
Shamouti	Noxan	Collapsed hypodermis cells in the flavedo	Low RH, increased water loss	10–60 days	Postharvest	Israel and South Korea	Ben-Yehoshua et al. (2001)
Navel	SERB	Collapse and browning of the peel at the stem end of the fruit	Holding fruit at low RH after picking	2 weeks	Postharvest	USA	McCornack (1970)
Valencia	Pitting	Sunken necrotic areas on the stylar end of the fruit	Tree water stress at maturity	ND	Pre- and postharvest	USA	Albrigo et al. (1970)
Valencia	SERB[z]	Collapse and browning of the peel at the stem end of the fruit	Lack of epicular wax and dehydration	ND	Postharvest	USA	Albrigo (1972a)

[z]SERB, stem end rind breakdown.
[ND]No data.

Table 3.2. An overview symptomology, time of occurrence, and causal factors of different nonchilling physiological rind disorders on grapefruit.

Cultivar	Name of disorder	Symptoms	Causal factors	Time of occurrence	Pre/postharvest	Country	Reference
Marsh	Peel pitting	Depressions in the flavedo that ultimately affect oil gland	Low RH during harvest before storage at high RH	2–6 days	Postharvest	USA and Spain	Alférez et al. (2005)
Marsh	Pitting	Clusters of collapsed oil glands over the surface of the fruit	Waxing		Postharvest	USA	Sun and Petracek (1999)
Marsh	Peel pitting	Sunken areas on the flavedo followed by browning and dryness	Waxing, warm-temperature storage, and sudden changes from low to high RH	2–20 days	Postharvest	USA	Alférez and Burns (2004)
Marsh	Peel pitting	Sunken areas on the flavedo followed by browning and dryness	Variation in water, osmotic, and turgor potentials	2–20 days	Postharvest	USA and Spain	Alférez et al. (2010)
Marsh	Pitting	Clusters of collapsed oil glands over the surface of the fruit	Waxing coupled with warm-temperature storage	10 days	Postharvest	USA	Petracek et al. (1995, 1998b)
Ray ruby	SERB	Collapse and browning of the peel at the stem end of the fruit	Rootstock and storage temperature	9 days	Postharvest	USA	Ritenour et al. (2004)

Table 3.3. An overview of symptomology, time of occurrence, and causal factors of nonchilling physiological rind disorders reported on mandarin fruit.

Cultivar	Name of disorder	Symptoms	Causal factors	Time of occurrence	Pre/postharvest	Country	Reference
Clementine	Preharvest rind spotting	Irregular-shaped necrotic spots on the rinds	Sudden changes in climatic conditions	ND	Preharvest	Greece	Assimakopoulou et al. (2009)
Encore	Preharvest rind staining	Chlorotic spots	Exposure to solar radiation	ND	Postharvest	Portugal	Maia et al. (2004)
Encore	Peel pitting	Chlorotic spots on the epicarp	Exposure to direct sunlight	ND	Preharvest	Portugal	Vitor et al. (2000)
Encore	Peel pitting	Chlorotic spots on the epicarp	Exposure to direct sunlight	ND	Preharvest	Portugal	Medeira et al. (1999)
Fallglo	Postharvest pitting	Necrosis and scattered collapse of the flavedo	Waxing	2–20 days	Postharvest	USA	Petracek et al. (1998a)
Fallglo	Peel pitting	Depressions in the flavedo that ultimately affect oil gland	Low RH during harvest before storage at high RH	2–6 days	Postharvest	USA and Spain	Alférez et al. (2005)
Fortune	Pitting, necrosis, staining	ND	ND	ND	Postharvest	Spain	Sanchez-Ballesta et al. (2001)
Fortune	Peel pitting	Sunken lesions and darkening of oil glands	Prolonged storage and dehydration	15 days	Postharvest	Morroco	El-Hilali et al. (2004)

Fortune	Rind pitting	ND	Exposure to direct sunlight and high maturity	14–28 days	Pre- and postharvest	Spain	Duarte and Guardiola (1995)
Nova	Rind pitting	ND	Exposure to direct sunlight and high maturity	14–28 days	Pre- and postharvest	Spain	Duarte and Guardiola (1995)
Nules Clementine	Rind breakdown	Collapse of the oil gland cells leaking into the flavedo, causing oxidation and browning of rind	Higher shipping temperature and fruit from inside of the tree	42–84 days	Postharvest	South Africa	van Rensburg and Bruwer (2000)
Nules Clementine	Rind breakdown	Collapse of the oil gland cells leaking into the flavedo, causing oxidation and browning of rind	Direct sunlight, higher shipping temperatures	42–84 days	Postharvest	South Africa	van Rensburg et al. (2004)
Nule Clementine	Rind breakdown	Dark/brown spots associated with the collapse of oil glands	Shading and low sunlight	3–5 weeks	Postharvest	South Africa	Cronje et al. (2011a)

[ND]No data.

Table 3.4. Review publications on citrus postharvest physiological disorders since 2000.

References[z]	Scope of the review
Agustí et al. (2002)	Citrus fruit quality, physiological basis, and techniques of improvement
Agustí et al. (2004)	Causes, characteristics, water relationships, and control measures of the most important postharvest physiological disorders occurring in citrus fruit
Lafuente and Zacarias (2006)	An overview of the most important postharvest physiological disorders occurring in citrus fruit
Ladaniya (2008)	Causal factors of major physiological disorders in citrus and their management
Rodov et al. (2010)	Discussion of the effect of modified humidity packaging on fresh produce including physiological disorders of citrus fruit
El-Otmani et al. (2011)	Citrus fruit development, maturation in relation to quality, and physiological disorders during postharvest

[z]These reviews did not cover rind anatomy, histological characteristics, and molecular biology of fruit affected by the disorders versus unaffected fruit as well as potential aspects of using nondestructive technology to predict fruit susceptibility to these disorders.

(Plate 3.5b) (Agustí et al. 2001), and rind staining of 'Navelate' (Plate 3.2a), 'Navelina' (Plate 3.2b), and 'Navel' oranges (Alférez et al. 2003) are portrayed. Chilling injuries in 'Navel' orange and 'Satsuma' mandarin are displayed in Plate 3.4a and b, respectively, for comparisons.

The sunken areas associated with nonchilling rind disorders are 0.1–0.7 mm in depth (Petracek et al. 1995), occurring directly above and among the oil glands of the affected flavedo. The affected areas coalesce, producing larger affected areas, turning reddish-brown to dark brown, becoming dry and necrotic in the severe stages of the disorder with extended storage (Alférez et al. 2003; Alférez and Burns 2004; Cronje 2005, 2009; Assimakopoulou et al. 2009). Browning of affected rind surface of 'Navelate' oranges (Plate 3.5b) appears to be the result of oxidative processes (Agustí et al. 2001). In contrast, stem end rind breakdown (Plate 3.6) involves the collapse and darkening of the epidermal tissues around the stem end of the fruit and does not target oil glands as postharvest rind pitting (Grierson 1986; Porat et al. 2004).

III. RIND ANATOMY AND HISTOLOGICAL CHARACTERISTICS

A healthy citrus flavedo is characterized by an epidermis with an apolyhedral arrangement of cells, covered by a cuticle (Fig. 3.1a) (Albrigo 1972a,b; Medeira et al. 1999). The flavedo consists of an external layer of epidermal cells and inner tightly packed parenchyma/collenchyma cells with no intercellular air spaces. Under cryo scanning electron microscopy, flavedo cells gradually increase in size toward the inner parts of the rind (Alquezar et al. 2010). The albedo of the rind is a complex mesh of meristematic cells in which each single cell has direct plasmodesmata connections with eight other adjacent cells (Storey and Treeby 1994; Alquezar et al. 2010). This structure results in large intercellular air spaces between the cells and provides the typical spongy morphology of albedo tissue. Intercellular spaces are bigger at the inner layers of the albedo near the pulp (Agustí et al. 2001).

In 'Fortune' mandarin, the damage caused by nonchilling rind pitting disorders is manifested by flattened and collapsed parenchyma cells immediately above the oil glands (Fig. 3.1b) (Vercher et al. 1994). Similarly, subepidermal cell orientation in affected areas of 'Encore' mandarin resembles the damage described in 'Fortune' mandarin as well as the postharvest chilling injury symptoms of lemons (Obenland et al. 1997; Medeira et al. 1999). Damaged cell layers were found to be orientated parallel to the rind surface, extending all along the flavedo (Vercher et al. 1994; Medeira et al. 1999). The deterioration processes were found to begin in epidermal cells, later extending to hypodermal

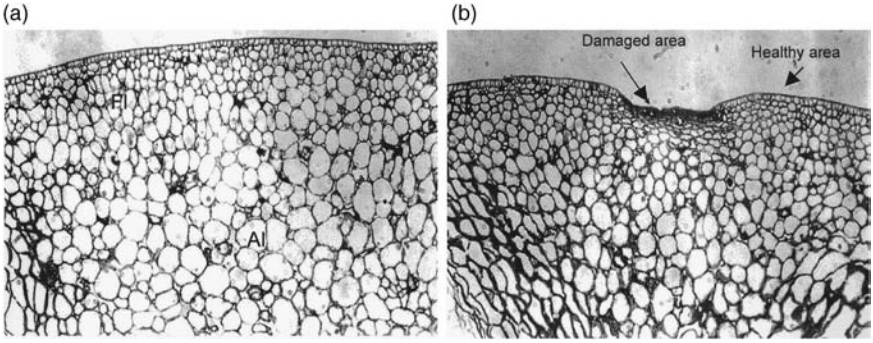

Fig. 3.1. Crosssections of rind of 'Navelate' sweet orange. Healthy fruits (a) and fruit with well-developed (b) symptoms of rind breakdown. Note that in (b), the epidermal and hypodermal cells are crushed; the surface of the fruit is sunken. *Source*: Agustí et al. (2001).

cells. The first signs of cellular damage are associated with internal membrane disorganization of the plastids, followed by vesiculation and degradation of the cytoplasm (Medeira et al. 1999).

Rind breakdown of 'Navelate' sweet orange fruit begins at the transitional zone of the flavedo–albedo and subsequently advances across the flavedo reaching the epidermis (Agustí et al. 2001). It was further substantiated that cells from fruit affected by the disorder have reduced amount of cytoplasm located in a central position and have twisted and squashed walls, forming areas of collapsed cells among healthy cells of the flavedo and albedo. Collectively, these observations suggest that although citrus nonchilling rind pitting is superficial, it begins in the cell membrane structure and progresses to epidermal and subepidermal tissues, flattening several layers of surrounding cells and causing cells and oil glands to collapse.

Obenland et al. (1997) and Petracek et al. (1998b) were of the opinion that oil glands are the primary sites of damage and that rupture of oil bodies could, in turn, release oil into the surrounding cells, causing rind pitting injury to citrus fruit. However, the oil glands of 'Fortune' (Almela et al. 1992) and 'Clementine' (Assimakopoulou et al. 2009) mandarins affected by rind spotting remained intact and unaffected (Medeira et al. 1999). Similarly, no relationship has been shown between the oil gland and peel pitting disorder in 'Encore' mandarins (Medeira et al. 1999; Vitor et al. 1999, 2000). These observations suggest that rind spotting in 'Fortune' and 'Clementine' mandarins as well as peel pitting injury in 'Encore' mandarin might not be originating from the oil gland disruption. In contrast, the collapse of oil glands was the initial symptom of postharvest peel pitting in grapefruit (Alférez and Burns 2004). At advanced stages of the disorder, the collapsed oil glands became deformed with layers of flavedo cells below oil glands and adjacent deeper areas appearing twisted and wrinkled (Fig. 3.2), concomitant with browning of the flavedo. Epidermal and subepidermal cells appeared strongly stained and crushed, indicating a collapse in these tissues and flattening of some layers of enveloping cells of the oil glands.

Vitor et al. (1999, 2000) investigated the interactions between hydroxyl radical production and the composition of the epicarp cells associated with pitted tissues and observed that the phosphatidylinositol content of dark-stained cells was lower in unpitted than in pitted tissues. The significant change of the membrane composition in pitted tissues is closely associated with acyl lipid peroxidation, mediated by hydroxyl radical production (Vitor et al. 2000). It was concluded that degradation of fatty acids in pitted tissues was incomplete. In addition,

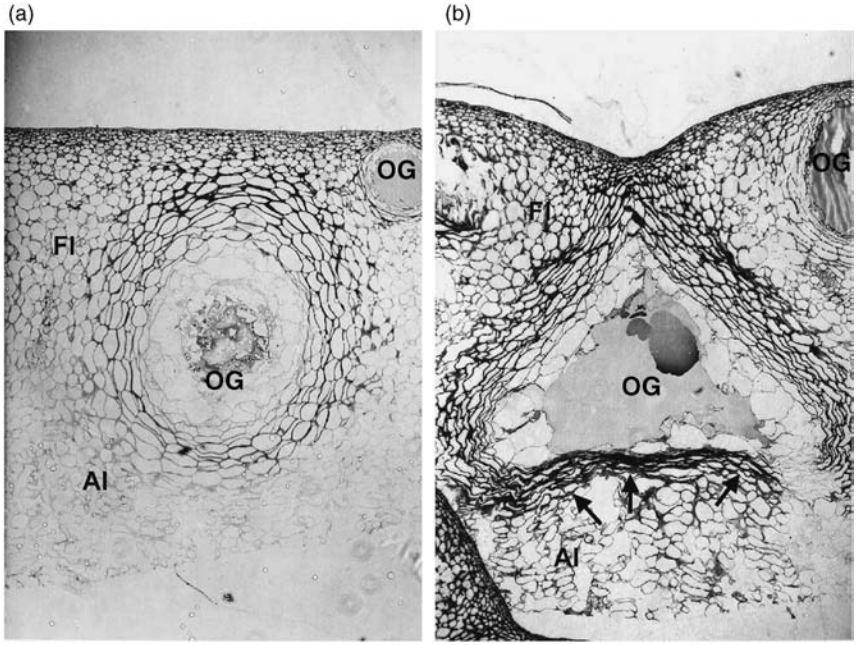

Fig. 3.2. Light micrographs of crosssections of 'Marsh' grapefruit peel from healthy (a) and pitted (b) fruit. Al: albedo; Fl: flavedo; OG: oil gland. *Source*: Alférez and Burns (2004).

the disorder has been shown to be related to tonoplast disruption and unrepaired damage to cell membranes in the flavedo (Sawamura et al. 1984; Vitor et al. 2000). Tonoplast disruption in injured cells accelerated the propagation of disorder to adjacent cells through oxidative product release preventing the normal function of organelles and membranes (Vitor et al. 2000).

IV. CAUSES OF PHYSIOLOGICAL RIND DISORDERS OF CITRUS FRUIT

Physiological rind disorders of citrus fruit are believed to be affected by various preharvest, harvest, and postharvest conditions to which the fruit is exposed. Most fruit physiological disorders are theoretically associated with preharvest, ecophysiological, and postharvest factors (Witney et al. 1990; Peiris et al. 1998a). Similar to most physiological disorders, some of the causes of nonchilling rind pitting disorders are

inherent to the fruit and cannot be changed (Davies and Albrigo 1994; Agustí et al. 2003), while others are external and can be altered (Agustí et al. 2004; Alférez and Burns 2004). Intensive research has been conducted in the past toward determining the factors triggering rind pitting. For example, there was a correlation of preharvest and postharvest factors to nonchilling rind pitting physiological disorders (Agustí et al. 2001; Alférez et al. 2003). However, the mechanism(s) governing the occurrence of these disorders and the manner it is related to other physiological rind disorders is still not well understood (Agustí et al. 2004). Since little is known about the exact causative factors, the occurrence of various citrus nonchilling pitting disorders is erratic and unpredictable, showing high variability from year to year, among orchards, cultivar, harvest dates, canopy microclimate, postharvest handling, length of storage, and even among fruit of a given tree (Alquezar et al. 2010; Cronje et al. 2011a).

A. Preharvest Factors

Most of the earlier experiments on rind disorders focused on the effect of postharvest factors, such as ethylene and wax application (Alférez and Zacarìas 2001; Cronje 2005). Recently, preharvest aspects influencing rind condition have received attention due to the fact that a number of fruit disorders do not always require specific conditions to be expressed but are closely related with later stages of fruit ripening (Ferguson et al. 1999). The great number of references that relate fruit physiological disorders with climatic conditions indicate that variations in environmental conditions during the growing season and within particular orchards including canopy microclimate may influence the susceptibility of fruit to physiological disorders (Ferguson and Watkins 1989; Assimakopoulou et al. 2009).

1. Scion Cultivar and Rootstock. The sensitivity of a fruit to develop a physiological rind disorder varies among different cultivars. Although these disorders occur in most citrus fruit, certain cultivars are more susceptible to these disorders than others. For instance, 'Navelate', 'Navelina', 'Washington' navel, 'Shamouti' orange, and 'Lane late' are among orange cultivars that have been listed to be highly sensitive to nonchilling rind pitting disorders (Table 3.1) (Agustí et al. 2003, 2004; Alférez et al. 2003; Estables-Ortiz et al. 2009). Fruit of 'Navelate' oranges are sensitive to peel pitting on the tree as well as under postharvest storage. 'Navelina' oranges on the other hand, develop the disorder only during postharvest storage (Lafuente and Sala 2002). 'Marsh' grapefruit

(Table 3.2) and 'Fallglo' tangerine are also among citrus fruit liable to suffer from nonchilling rind pitting (Petracek et al. 1995, 1998a,b) while 'Shamouti' orange and 'Nules Clementine' mandarin are sensitive to superficial flavedo necrosis "noxan" and rind breakdown, respectively (Ben-Yehoshua et al. 2001; Cronje et al. 2011a). It is of interest to note that some mutants of cultivars that are prone to one rind physiological disorder are tolerant to another. For instance, 'Nules Clementine' mandarin is susceptible to the progressive postharvest rind breakdown, whereas the 'Oroval Clementine' mandarin produced in the same production unit is not susceptible to rind breakdown (Table 3.3) (van Rensburg and Bruwer 2000; van Rensburg et al. 2004; Khumalo 2006). Furthermore, it has been shown that 'Pinalate' orange fruit are tolerant to chilling injury but very prone to develop nonchilling peel pitting in contrast to 'Navelate' orange fruit that are prone to chilling injury. This suggests that the sensitivity of fruit to a particular type of physiological rind disorder is genetically inherited and 'Navelate' orange fruit might have an additional defense mechanism that assists in reducing nonchilling peel pitting. Furthermore, this mutant may be used as a model to understand the mechanisms underlying chilling-induced superficial scald and nonchilling peel pitting disorders.

In addition to cultivar effect, rootstock has been reported to play a role in fruit sensitivity to disorders (Zacarìas et al. 2000). Rootstocks may influence water balance, water circulation, mineral nutrition, plant growth regulators, and growth rate of the fruit and the whole plant (Alférez et al. 2010), thus affecting water and osmotic potentials in the fruit rind (Albrigo 1977). Rootstocks may also modulate susceptibility to develop nonchilling peel pitting on the tree and during postharvest storage (Treeby et al. 1995; Alférez et al. 2010). In cultivars such as 'Navelate' orange, rootstock has been shown to influence both incidence and severity of fruit peel pitting. Fruit harvested from trees grafted in 'Citrange carrizo' are more susceptible to postharvest rind pitting (Zacarìas et al. 2000). This phenomenon is not unique to orange fruit as 'Marsh' grapefruit grafted on 'Carrizo' citrange rootstock has higher susceptibility to develop rind disorders compared with those grafted on 'Cleopatra' mandarin or sour orange (Agustí et al. 2003, 2004; Ritenour et al. 2004). Flavedo and albedo of 'Carrizo' rootstock have been shown to undergo more pronounced decreases in water potential under water stress conditions and have better ability to recover when transferred to a high relative humidity (RH) environment (Zacarìas et al. 2000), suggesting that more rapid water movement through peel tissues may be linked to peel pitting (Alférez et al. 2010).

2. Canopy Position. Different research groups have established that different microclimates can influence the sensitivity of fruit to manifest physiological rind disorders (El-Otmani et al. 1989; Arpaia et al. 1991; Wild 1991; Almela et al. 1992; Duarte and Guardiola 1995). They demonstrated that fruit susceptibility to different disorders varies depending on seasonal climatic and orchard environmental conditions. In a study conducted in Spain (northern hemisphere), Almela et al. (1992) showed that these fluctuations could also be observed among fruits from the same tree, the incidence of rind spots in 'Fortune' mandarins being higher in fruit exposed to the sun than nonexposed fruits, and higher on sun-exposed than the nonexposed side of individual fruits. These investigators further showed that fruit oriented to the northwest (NW) in canopy were most affected by the disorder. In a later study conducted in the same country, Agustí et al. (2001) corroborated 'Navel' fruit exposed to the NW face of the tree to be more prone to developing rind breakdown disorder and this was reported to be consistent over five seasons. Similar observations were previously observed in 'Fortune' (Duarte and Guardiola 1995) mandarin fruit, where it was maintained that the rind pitting disorder affects mainly the exposed fruit from the NW quadrant of the tree and was higher on fruit exposed to the sun than nonexposed (covered by foliage) fruit. Similarly, Vitor et al. (2000) showed that shaded 'Encore' mandarin fruit had significantly lower peel pitting compared with sun-exposed fruit. Chikaizumi (2000) further substantiated that sun-exposed sides have more pitting disorder than shaded sides of the same individual fruit. The mechanism defining the trend of lower rind physiological disorder on fruit borne on different canopy position is related to temperature, water potential, and irradiation as discussed in the next two sections.

In a study conducted in Australia (southern hemisphere), Wild (1991) reported similar observations with peteca of lemon (Plate 3.3b) (*Citrus limon* Burn), a disorder similar to rind pitting, where fruit hanging on the eastern side of trees were found to be more susceptible than those on the western side. Moreover, the disorder has been reported to be more prevalent at the exposed face of the individual fruit, irrespective of its location on the tree. A study conducted in Portugal (northern hemisphere) showed mandarin fruit from the south and southwestern areas of the canopy to be severely affected by nonchilling rind pitting disorder (Medeira et al. 1999). The authors speculated that solar radiation may be involved in the structural alteration of the cuticle, and a high rind temperature over a long period may induce localized dehydration in the epidermal and subepidermal cells leading to plasmolysis and membrane collapse.

The positional effect on development of rind disorder is not unique to nonchilling rind pitting. It has also been demonstrated in the chilling injury disorder by McDonald et al. (2000). These investigators conducted a study to determine the effect of canopy position on sensitivity of grapefruit to gamma irradiation and if a short-term heat treatment before irradiation would reduce the severity and incidence of rind pitting and chilling injury. They reported more rind pitting in exterior canopy fruit than in interior canopy fruit. These results agree with earlier observations reported by McDonald et al. (1993) whereby grapefruit from the sun-exposed exterior canopy were more susceptible to chilling injury than those from the shaded interior canopy. These studies further showed that the development of chilling injury symptoms on exterior canopy grapefruit was related to epicuticular wax morphology and composition. Exposed sides of the fruit reached higher temperatures than shaded sides (Syvertsen and Albrigo 1980) and have been reported to age faster than shaded sides (El-Otmani et al. 1989). Therefore, the higher susceptibility of the exposed side to nonchilling injury may be the consequence of accelerated senescence.

Direct Solar Radiation Effect. The great number of references that relate nonchilling rind physiological disorders indicate that visual symptoms of nonchilling physiological rind disorders mostly appear in the portions of the rind most exposed to solar radiation (Wild 1991; Medeira et al. 1999; Chikaizumi 2000). From the listed observations, it would seem logical to assume that preharvest conditions such as high temperature and irradiation may induce localized flavedo dehydration, plasmolysis, and cell collapse, resulting in rind pitting of citrus fruit (Medeira et al. 1999). Direct radiation could result in temperatures exceeding 38°C on exposed fruit (Chikaizumi 2000). High light intensities induce oxidative stress in the epicarp that is characterized by an increased peroxidation and degradation of cell membranes (Vitor et al. 2000). A major accumulation of high levels of H_2O_2 radicals was demonstrated and the peroxidase system that shields the epicarp against photooxidative stress had an inhibited catalase activity and increased superoxide dismutase functioning. McDonald et al. (2000) demonstrated that radiation induced a transient increase in phenylalanine ammonia lyase (PAL; EC 4.3.1.5) activity and was correlated with fruit peel pitting.

Maia et al. (2004) showed that rind stain of 'Encore' mandarin started after summer at high temperature and when the relative humidity increased. With regard to the effect of high temperature on rind pitting, results by McDonald et al. (2000) showed that pitting was reduced by

heat treatment. This is difficult to explain as fruit exposed to higher preharvest temperatures had higher incidence of the disorder and those exposed to postharvest heat treatment at the same temperature had lower incidence of rind pitting. Considering this, one would expect fruit treated with postharvest heat treatment to have higher incidence of the disorder. Although there are limited reports of compositional differences between exterior and interior canopy of citrus fruit (McDonald et al. 1993, 2000), it is apparent that canopy position exerts a very strong influence on the biochemical makeup of flavedo and the whole fruit. These observations suggest that variations in microclimatic conditions during the growing season and within an orchard may influence fruit biochemical profile of the rind and subsequently play a significant role in the development of rind nonchilling physiological disorders by postharvest factors.

Effect of Canopy Position on Carbohydrates Content in the Flavedo. Fruit position, and therefore exposure to high (outside) or low (inside) light levels in the canopy, affects the flavedo content of sugars during fruit development (Cronje et al. 2011a). The flavedo from fruit borne on the outside of the canopy had significantly higher sucrose, glucose, and fructose content than the fruit borne inside the canopy. Lower osmotic potential due to higher sucrose, an osmoregulatory compound in plant cells, was also observed, demonstrating a possible link between fruit position, rind sugar content, and ultimately development of the disorder (Cronje et al. 2011a). The incidence of rind breakdown in 'Nules Clementine' mandarin was higher on inside fruit compared with the outside fruit and this was consistent from season to season and could be attributed to their exclusion from adequate sunlight during development (Cronje 2009). In addition, fruit borne inside the canopy had lower chlorophyll and carotenoid contents, and therefore poorer rind color (Khumalo 2006) and lower carbohydrates that were correlated to their susceptible to the disorder (Cronje 2009). Although fruit canopy positions have been consistently reported to significantly affect rind pigment and antioxidant capacity at harvest, earlier results by Khumalo (2006) showed that the development of rind breakdown after storage was not affected by fruit canopy position. To the knowledge of the authors, the cited research work is the only work conducted thus far that has successfully attempted to relate the effect of fruit position on rind biochemical composition. It was hypothesized that rind photosynthesis contributes significantly to rind condition. Reduction in photosynthetically active radiation on shaded portions of the canopy reduced fruit photosynthesis rate and osmotic potential that are thought to have

contributed to rind breakdown disorder. Although very limited research has been conducted to study the effect of canopy position on rind biochemical profile, the effect on fruit internal quality is well documented in the literature (Genizi and Cohen 1988; Barry 2000; Morales et al. 2000; Vitor et al. 2000; Barry et al. 2003, 2004).

3. Fruit Maturity. Fruit maturity is believed to play a critical role in the development of citrus postharvest rind disorders (Wild 1991). Fruit susceptibility to rind pitting is mostly at the beginning of color break and develops with pigmentation until harvest (Assimakopoulou et al. 2009). Green fruit are not susceptible to rind pitting disorder (Duarte and Guardiola 1995). Almela et al. (1992) studied the occurrence of rind breakdown in 'Fortune' mandarins and noted that fruit were highly sensitive to this disorder during maturation. On hanging fruit, the occurrence of rind pitting in citrus fruit is reported to extend from the onset of color break and continue for several weeks thereafter, depending on climatic conditions (Agustí et al. 2001). During postharvest storage, the incidence of the disorder takes place irrespective of harvesttime but increases quantitatively with fruit maturity (Alférez and Zacarìas 2001). Furthermore, a positive correlation between maturity and peteca spot on lemons has been reported, with fruit harvested with yellow rinds developing more rind pitting than green fruit (Duarte and Guardiola 1995; Undurraga et al. 2006).

Application of GA_3 at color break delayed chlorophyll loss and the accumulation of carotenoid pigments in rind tissue, and retarded the development of rind pitting (Agustí et al. 1981; Coggins 1981; Duarte and Guardiola 1995). The primary quality benefit of using GA_3 is a reduction in preharvest and postharvest rind disorders due to delayed rind senescence (Duarte and Guardiola 1995). In considering these observations, it could be possible that the disorder is dependent upon fruit maturity and/or an increase in flavedo pigments such as carotenoids. The above observations consistently support the hypothesis that sun-exposed warmer fruit mature faster than shaded fruit (Barry et al. 2003) and pitting susceptibility develops with maturity and rind pigmentation (Cronje 2009). As antioxidants, carotenoids may play an essential role in scavenging reactive oxygen species and protecting membrane lipids from oxidation (Larson 1988; Allan and Fluhr 2007).

4. Fruit Mineral Nutrition. Mineral elements fill a vital role in plant growth and development. They are involved in synthesis, heredity, and energy processes, and are essential components of plant constituents, taking part in enzyme activation, osmotic regulation, and membrane

permeability (Clarkson and Hanson 1980; Mengel and Kirby 1982; Devlin and Witham 1983; Tisdale et al. 1985). Similar to other plants, citrus fruit trees require at least 13 mineral elements, the so-called "essential elements," for normal growth and reproduction, which include major and minor plant nutrients (Joiner et al. 1983; Marschner 1995). Resnizky and Sive (1993) verified that various physiological disorders arising from the extension of the storage life of a fruit are related to the mineral content present before harvest. For the purposes of this chapter, only the nutrients known to play a key role in fruit quality such as nitrogen, calcium, potassium, phosphorus, magnesium, and boron and some other microelements will be discussed.

The best documented relationship between the fruit mineral content and fruit disorders concerns Ca. Interelemental relationships also exist between minerals such as Mg, K, B, Ca, and N. Ca is known to have a considerable influence on fruit physiology, and the effect that this element has on important aspects of fruit quality has been of particular interest for many years. Due to its role in cell wall structure and membrane function, calcium has been implicated in physiological disorders of many fruits (Poovaiah et al. 1988). Low Ca levels have been directly coupled with physiological disorders such as bitter pit, internal breakdown, and lenticel discoloration in apples (Snay and Bramlage 1973; Wills et al. 2004), blossom-end rot in pepper (Ehert and Ho 1986; Morley et al. 1993; Li et al. 2004) and tomatoes (Bangerth 1976), cuticle cracking in cherries (Seske 1995) and sweet pepper (Opara et al. 1997; Aloni et al. 1998), as well as vascular and pulp browning in avocado (Bower and Cutting 1988; Thorp et al. 1997).

In lemons, calcium and boron were identified by Khalidy et al. (1969) to play a role in the development of the peteca disorder. Cronje et al. (2011b) studied the possible relationship between the incidence of citrus rind disorders and the mineral composition of citrus fruit. Fruit mineral composition was one of the important factors playing a role in postharvest rind pitting. The mineral composition of citrus fruit was found to vary with position in the tree canopy. Inside fruit were found to have a significantly higher concentration of potassium, a mobile element, than outside fruit. Outside fruit were found to contain higher levels of calcium and magnesium. It was interesting to note that visual symptoms of rind breakdown disorder appeared on the fruit from the shaded position of the canopy. Similar observations were reported in an industry experimental report by Kruger et al. (2005). Compared with disorders such as rind staining in 'Fortune' mandarins and rind breakdown in 'Navel' oranges where peel disorders were associated with sun/heat exposure, rind breakdown disorder in 'Nules Clementine' occurs on

inside fruit because it is associated with low mineral and carbohydrate allocation and therefore premature senescence. Cronje et al. (2011b) concluded that the reduction of transpiration potential by lower temperatures and higher humidity inside the canopy could be responsible for the reduced accumulation of Ca and Mg. The high K concentration of inside fruit flavedo is suggested to be a stress response, due to the low light levels, to maintain osmotic potential in the shaded rind tissue, and this imbalance could possibly lead to a reduction in rind condition, which manifests through rind breakdown symptom development.

It is well known that calcium plays an important role in the healthy development of citrus fruit because of its role in plant cell wall. Storey et al. (2002) revealed that concentration of Ca in the flavedo and albedo was negatively related with the incidence of creasing. Similarly, Storey and Treeby (2002) as well as Treeby and Storey (2002) reported the effectiveness of different Ca sprays as a control measure for rind breakdown disorder of navel orange fruit. These observations were also reported by Li et al. (2009) in 'Navel' oranges, where fruits sprayed with 0.5% $Ca(NO_3)_2$, preharvest, developed significantly lower (50% less) rind pitting compared with untreated fruit. Treating fruit with 1% $CaCl_2$ effectively decreased the development of the disorder. The ability of Ca treatment in reducing the disorder was related to its ability to reduce electrical conductivity of the cells and reducing activities of enzymes such as polyphenol oxidase (PPO) and peroxidase (POD; EC 1.11.1.7) (Cajuste and Lafuente 2007). On the other hand, no significant differences in the rind concentrations of nutrient elements between rind pitting-affected and nonaffected 'Clementine' mandarin fruit were observed (Assimakopoulou et al. 2009). Considering that results by the later authors and the fact that the cracks appearing on the cuticle and strata and oil glands remained intact, the physiological disorder should be attributed to sudden changes of climatic conditions and not to nutritional imbalance.

5. Rainfall and Fruit Water Potential. The amount and distribution of rain over a season has been reported to play a role in the development of physiological rind disorders. In lemons, Undurraga et al. (2006) reported that extending the days of harvest after rainfall reduces the intensity of peteca spot. Similarly, preharvest water stress induced by blocking irrigation and rainfall for 49 days before harvest increased peel breakdown (Ritenour et al. 2008). The effect of water potential on postharvest nonchilling rind pitting disorders has been confirmed in citrus fruit by showing that alteration of rind water potential, particularly water stress, of citrus may be a triggering factor related to rind

pitting. Water potential and its components (osmotic and turgor potentials) of citrus fruit provide information on water status of fruit tissues during postharvest storage and in response to variation in storage conditions (Alférez et al. 2010). In 'Navelate' and 'Navelina' oranges in Spain, sudden changes from low to high relative humidity during postharvest storage induced peel pitting disorder by lowering flavedo water potential (Alférez et al. 2003). Peel water potential of 'Marsh' grapefruit stored at 45% RH for 4 weeks was lower, leading to cell collapse and peel damage, but transferring dehydrated fruit to 95% RH after 12 days increased the water potential of flavedo and albedo (Alférez et al. 2010; Alquezar et al. 2010). These observations link the alteration in water, osmotic, and turgor potentials with the induction of peel pitting in citrus fruit. Therefore, the inability to carry out proper adjustments lead to postharvest peel pitting in 'Marsh' grapefruit and possibly other citrus fruit.

B. Postharvest Factors

1. Water Loss. Citrus fruit are characterized by high postharvest weight loss, and this is essentially due to water loss by transpiration, as it accounts for 90% of total weight loss (Ben-Yehoshua et al. 2001). A percentage water loss rate of 1% per day, during the first 6 days after harvest, and 0.6% thereafter, was reported on 'Marsh' grapefruit stored at 21°C and 30% RH (Alférez and Burns 2004). Similarly, Alférez et al. (2010) reported water loss between 9% and 15% on fruit stored at 45% RH. Water loss from the fruit occurs by means of a passive process, resulting from a vapor pressure gradient prevailing between the fruit peel, which is close to saturation with water, and the less-saturated outside atmosphere (Kader et al. 1989; Ben-Yehoshua et al. 1994, Macnish et al. 1997). Postharvest water loss has negative implications on the fruit as it is a finite resource (Turner 1997). Initial symptoms of excessive water loss in fruit are shriveling, which is immediately visible on the peel, loss of shine, softening, and senescence of the affected fruit. For instance, in lemon fruit, a 5% weight loss results in severe shrinkage rate followed by development of SERB (McCornack 1975). Moisture loss is also important in the postharvest softening of fruit such as lemon (Ben-Yehoshua et al. 1983) and oranges (Ben-Yehoshua 1969). Minimizing water loss helps to maintain turgidity and prevents collapse of hypodermal cells and formation of noxan disorder in 'Shamouti' oranges (Peretz et al. 2001). In 'Valencia' oranges, Albrigo (1972a,b) reported the total concentration of wax on the surface of fruit to be inversely correlated to postharvest weight loss.

Several theories have been developed to suggest the potential postharvest causes of the rind pitting disorders (e.g., Arpaia 1994; Petracek et al. 1995, 1998a,b). Change in water status of flavedo and albedo is a primary postharvest factor in the susceptibility of citrus to rind pitting at nonchilling temperatures (Alférez et al. 2010). Evidence in the literature indicates that fruit exposed to dehydration are prone to develop rind pitting after storage at high RH (Agustí et al. 2001; Alférez et al. 2003, 2005). Cohen et al. (1994) suggested that low humidity storage might be responsible for citrus rind pitting.

Alquezar et al. (2010) examined morphological and structural changes, and their relationship to water potential, in flavedo and albedo of 'Navelate' fruit exposed to postharvest storage conditions inducing rind breakdown. After 1 month, fruit stored at high (95%) relative humidity had no signs of cell disruption or collapse of epidermal or flavedo cells. However, albedo cells of fruit stored for the same period at lower (45%) relative humidity were dehydrated and compacted, forming clusters of amorphous and flattened cells in which the typical spongy structure of the albedo was lost, showing typical symptoms of peel pitting.

It was further noted that transfer of fruit to high RH after a week of storage at lower RH produces a marked increase in the incidence of rind pitting in 'Navelate' oranges (Alquezar et al. 2010). These observations were in accord with those previously reported by Alférez et al. (2003) and Alférez and Burns (2004) and further confirmed that changes in postharvest RH and consequent rind water potential are important factors inducing rind pitting in citrus fruit. Higher incidence of rind pitting in fruit stored at high relative humidity compared with those stored at lower RH have been previously reported by Lafuente and Sala (2002). Subsequently, this phenomenon was also reported by Alférez et al. (2003) in 'Navelina' and 'Navelate' oranges, Alférez and Burns (2004) in 'Marsh' grapefruit, Alférez et al. (2005) in 'Fallglo' tangerines, Henriod (2006) in 'Navel' oranges, and Alférez et al. (2010) in 'Marsh' grapefruit.

All the above evidence suggests that alterations of postharvest RH and, in particular, the shift of water-stressed fruit to high RH improves water potential within rind tissues under less water vapor pressure deficit (VPD), which is somehow detrimental to cell integrity (Syvertsen and Albrigo 1980). Treating fruit in the reverse order, from high to low RH, or at low or high RH alone, did not result in the same incidence of the disorder (Burns et al. 2007). Alférez et al. (2005) conducted a study to determine the minimum time of dehydration prior to storage at high RH sufficient to induce rind pitting in 'Marsh' grapefruit and 'Fallglo' tangerines. Alférez et al. (2004) demonstrated that 3 h of low-RH storage

were sufficient to induce rind pitting after transfer to high RH. This implies that fruit harvested during or after being exposed to weather conditions promoting rind dehydration are very susceptible to develop the disorder when they undergo the industry's degreening practice that requires fruit to be held at 90–95% RH. However, it is worth noting that while on the tree, the fruit has a soil water supply and may not undergo sufficient peel drying to lead to this problem. Earlier work in Florida on SERB clearly showed that hot, drying conditions in the field could lead to breakdown (McCornack 1970). Long adverse water and temperature conditions in Florida could lead to a peel breakdown in the field (Albrigo 1972b).

Alquezar et al. (2010) investigated the water potentials of albedo and flavedo before and after storage and reported a 30% decrease in water potential of flavedo, while that of albedo remained almost unaltered. Vascular system lies at the bottom of albedo, with no connection to pulp or flavedo; thus, postharvest water loss is mainly from the rind (Bain 1958; Ben-Yehoshua 1987). Therefore, Alquezar et al. (2010) suggested that flavedo is more sensitive to water stress than albedo. This suggestion concurs with statement by Ben-Yehoshua (1969) that most water lost to the atmosphere in the initial period of storage originates from the flavedo. However, the results by Agustí et al. (2001, 2004) suggested that excessive water loss from hypodermal, flavedo, and albedo cells is responsible for the disorder. Water loss is probably from both the flavedo and albedo, but greatest stress may be on flavedo since most of the anatomical research shows that most of the tissue damage is near the surface (Agustí et al. 2001; Alquezar et al. 2010).

A study on 'Marsh' grapefruit showed a significantly positive correlation between rind pitting index and percent cumulative weight loss prior to postharvest storage at high relative humidity, although very low correlation coefficient was obtained (Alférez and Burns 2004). Estables-Ortiz et al. (2009) also argued that although the severity of the disorder may be enhanced by dehydration–rehydration, the disorder also occurs naturally in nonstressed fruit held continuously at 22°C and high RH (90–95%). This observation and low correlation coefficient between the rind pitting index (RPI) and weight loss obtained by Alférez and Burns (2004) suggested that development of the disorder might be attributed to other factors in addition to change in RH during postharvest storage. It might also be argued that these fruit might have been held for an extended period under low RH conditions before they were moved to high RH. However, VPD is more important to water loss than relative humidity (El-Otmani et al. 2011).

2. Postharvest Wax Application. Citrus fruit, with the exception of organic fruit, are usually waxed to improve appearance and to reduce water loss. It also serves as a medium to apply 2,4-dichlorophenoxyacetic acid (2,4-D) and fungicides such as tiabendazole (TBZ) and sodium *o*-phenyl phenate (SOPP), thus extending shelf life (Alférez et al. 2010). Although beneficial, coating fruit with commercial waxes coupled with warm-temperature storage has been reported to promote peteca spots on lemons (Wild 1991). Commercial packing line treatments of fruit may alter fruit susceptibility to rind disorders by altering of natural waxes on the fruit surface. A study by Albrigo (1972a) showed that wax is brushed down, reorganized, but not removed by normal commercial washing and brushing. Removal and reorganization of natural waxes on the fruit surface have been thought to alter water and osmotic potentials, consequently reducing turgor pressure potential of 'Marsh' grapefruit (Alférez et al. 2010). On fruit stored at 45% RH for 30 days, the percentage of water loss was higher (15%) in packing line-processed fruit than in those hand-washed and waxed (shellac-based wax), which had 9% water loss. In a previous study, the water effect was greater on fruit exposed to prolonged periods of dehydration at lower relative humidity (Alférez and Burns 2004). These authors concluded that waxing the fruit enhanced severity of the damage only if there was a previous dehydration period.

In 'Marsh' grapefruit, 'Fallglo' tangerine, and 'Temple' oranges, waxing has been reported to stimulate postharvest rind pitting and the hypothesis was that the disorder results from decreasing O_2 and increasing CO_2 internal levels (Petracek et al. 1995, 1997, 1998a,b). Later results showed that shellac-based waxes resulted in higher rind pitting disorder, while fruit coated with carnauba- or polyethylene-based wax developed low incidence and nonwaxed fruit did not develop the disorder (Petracek et al. 1998b). Internal O_2 levels were lower (1.8–3.5%) on fruit coated with shellac-based waxes, higher (10%) for carnauba- and polyethylene-based waxes, and highest (19%) for nonwaxed fruit. Conversely, internal CO_2 levels were high for fruit coated with shellac-based waxes (7.8–8.3%), lower for fruit coated with carnauba wax (4.9%) and polyethylene-based wax (5.8%), and lowest for nonwaxed fruit (1.5%). Another finding supporting this idea showed that waxing the fruit on its own is not detrimental for the development of peel pitting, but alteration in RH of waxed fruit may be deleterious (Alférez and Zacarìas 2001). In a later study, 'Marsh' grapefruit under controlled atmosphere storage (5% CO_2 and 14% O_2) did not develop rind pitting if there was no previous dehydration (Alférez and Burns 2004). It is noteworthy that Petracek's group often observed

pitting developing at O_2 levels below 9%; perhaps, 14% O_2 used by Alférez and Burns (2004) was not low enough to cause pitting. In 'Blanco' mandarins, Bajwa and Anjum (2006) reported that polyethylene-based and shellac-based coatings resulted in poor water distribution in the rind and exacerbated rind staining symptoms compared with nonwaxed fruit. As a result, components contained within commercial wax formulations were implicated in causing the disorder, but no work has been conducted to study morphology of commercially applied waxes. However, a comparison of natural wax morphology between healthy and damaged areas of affected 'Navelate' orange fruit, conducted by Agustí et al. (2001), revealed no significant differences in wax morphology, cuticular thickness, or permeability.

These observations supported the idea that postharvest rind pitting was a result of a previous dehydration event followed by a condition of high RH. Commercial wax exacerbates the disorder because wax affects fruit water potential. The above arguments collectively suggest that rind pitting provokes collapse of subepidermal cells without affecting the morphology and water permeability of the cuticle. Exposure of fruit to low RH conditions followed by high RH storage, and possibly unfavorable internal CO_2 or O_2 concentration, promotes rind pitting. It could therefore be concluded that commercial waxes that alter water status and levels of internal gases of the fruit can enhance nonchilling rind pitting if fruit undergo a previous water stress.

3. Ethylene. Ethylene has been reported to play a protective role against stress conditions causing postharvest losses in citrus fruit (Porat et al. 1999). Fruit undergoing nonchilling rind physiological disorders show a marked and transient increase in ethylene production (Lafuente et al. 2001; Sala et al. 2005). Conditioning 'Navelate' fruit with ethylene reduced the incidence of rind pitting (Cajuste and Lafuente 2007). Ethylene increased epicuticular wax content of 'Navelate' oranges and showed that ethylene induces changes in surface wax morphology, thus might be related the formation of new waxes (El-Otmani and Coggins 1985; Cajuste et al. 2010).

V. MOLECULAR AND PHYSIOLOGICAL BASIS OF PHYSIOLOGICAL RIND DISORDERS

To obtain a general picture of the nature of the main postharvest disorders in citrus, it is necessary to delineate the precise function of the identified physiological and molecular disorder-associated response (Lafuente and

Zacarias 2006). In recent years, researchers have turned their focus to study the molecular mechanisms underlying rind physiological disorders of citrus fruit. The classical example of a study conducted to establish the correlation between rind pitting disorder and molecular characteristics of the rind was published by Sanchez-Ballesta et al. (2001). These researchers investigated the expression of cDNAs by screening the cDNA library from nonchilling pitting-sensitive citrus cultivars ('Navelate' and 'Fortune') and nonchilling pitting-tolerant 'Pinatale' fruit. They further isolated a full-length cDNA, named 3c1, which was differentially expressed by different postharvest stress conditions. A small region consisting of 35 residues in 3c1 protein had significant similarity to several proteins known or hypothesized to use an acyl-CoA substrate.

The level of the CrglcQ gene, encoding an acidic class III β-1,3 glucanase isolated from citrus flavedo, increases transiently in fruit exposed to postharvest conditions, favoring both chilling injury and nonchilling rind pitting disorders (Sanchez-Ballesta et al. 2006, 2008). This increase parallels that in ethylene production and the appearance of visible symptoms of damage. Thus, although they are fruit specific, changes in 3c1 and CrglcQ gene expression may serve as biochemical markers for the development of postharvest chilling injury and nonchilling rind pitting disorders. Again, in spite of the disorders being induced by different environmental conditions, different patterns of gene expression in different disorders indicate that they may still be used as good molecular markers of the susceptibility of citrus fruit to develop pitting on the flavedo under different postharvest conditions. These genes are regulated by ethylene exposure, suggesting their association with fruit senescence (Sanchez-Ballesta et al. 2008).

In 'Navel' orange fruit, Gao et al. (2006) and Li et al. (2009) identified differentially expressed genes and showed that genes preferentially expressed in stressed (wounded) fruit had significant similarity to known genes. For instance, the sequence analysis revealed that a full-length cDNA of one of the isolated clones had significant similarities to Ca^{2+} binding protein, named CsCAB. Other isolated sequences were similar to cysteine protease, named *CsCP*, and to *NAC* domain protein known as CsNAC. Gao et al. (2009) further investigated the expression of expasin-like gene, named CsEXP. Quantitative analysis performed to determine the expression pattern of these cDNAs during the wounding revealed the involvement of these genes in the process of rind pitting development.

The expression of *CsNAC* and *CsCP* genes was induced under several postharvest abiotic stresses and was enhanced during the development of

peel pitting (Fan et al. 2007, 2009). The *CsCP* expression was induced by hypoxia (3% O_2), but repressed by anoxia (0% O_2), wounding, ethylene, and high temperature (40°C). Since ethylene treatment can reduce the rind pitting of orange fruit (Lafuente and Sala 2002; Cajuste and Lafuente 2007), the down-regulation of *CsCP* by ethylene might contribute to the suppression of physiological response to stress (Fan et al. 2009). It is important to note that in the studies by Gao et al. (2006, 2009) and Fan et al. (2007, 2009), the physiological and molecular response was studied by wounding fruit using a knife. Therefore, the conclusion to be drawn from these observations is that these genes are involved in stress response related to physical damage and possibly to the disorders. However, the interaction between different rind pitting-related genes would be an interesting aspect in elucidating the molecular mechanism of citrus rind pitting. Furthermore, the cause–result relationship between *CsCP* and rind pitting still needs to be further verified.

The involvement of antioxidant system in the beneficial effect of ethylene conditioning in reducing the disorder was previously investigated by Cajuste and Lafuente (2007), who demonstrated that increased PAL and reduced POD activities play a significant role in the development of nonchilling peel pitting. Change in phenylpropanoid metabolism is an important response to stress. PAL has been shown to be the rate-controlling enzyme in phenylpropanoid synthesis and wounding of citrus fruit such as mandarin and grapefruit (McDonald et al. 2000). Activity of PAL in the albedo and flavedo was high, while that of POD was reduced on fruit affected by the disorder. In addition, higher levels of lignin and phenols were reported on fruit conditioned with ethylene, and these fruit had lower occurrence of the disorder. These findings concur with results reported by Lafuente et al. (2003), who observed a change in PAL activity and ethylene production associated with the development of peel pitting. In a similar study, Sala et al. (2005) reported that at nonchilling temperature (12°C), 'Navelate' orange, a cultivar tolerant to nonchilling but susceptible to chilling peel pitting, had lower PAL activity than 'Pinalate', a chilling-tolerant variety. When stored at chilling temperature (2°C), 'Pinalate' fruit had higher catalase (CAT) than 'Navelate' cultivar.

This suggests that the magnitudes of PAL activity and ethylene differ with the cultivar as well as the type of disorder. These observations give an indication that the activation of PAL in the flavedo and albedo and a rise in lignin and phenols in the flavedo may be used as biochemical indicators that produce more phenylpropanoid products and reduce non-chilling peel pitting (Sala et al. 2005). Furthermore, the decline of POD activity in both albedo and flavedo tissues and also the inability of

albedo to increase lignin and phenolic contents may be indicative of low ability of the fruit to overcome this physiological disorder. CAT activity on the other hand may play a role in protecting both 'Navelate' and 'Pinalate' fruit from conditions promoting chilling and nonchilling peel pitting physiological disorders (Cajuste and Lafuente 2007).

Conditioning 'Navelate' oranges with 10 μl L^{-1} ethylene significantly reduced the incidence of nonchilling peel pitting while inhibiting ethylene action by 1-methylcyclopropene (1-MCP) increased the incidence of nonchilling rind pitting (Estables-Ortiz et al. 2009). Gene ontology analysis conducted from this study revealed that ethylene induced the metabolism of amino acid derivatives, including penylpropanoids. These observations are in agreement with Cajuste and Lafuente (2007) who suggested that phenolic compounds might be involved in ethylene-induced protection against peel pitting.

Rind pitting disorder has also been reported to be related to tonoplast disruption and concomitant accumulation of phenolic substances and volatiles under the cuticle, such as acetaldehyde, ethanol, and ethylene (Sawamura et al. 1984; Cohen et al. 1990; Zaragoza et al. 1996). Limonene and valencene may be related to postharvest nonchilling peel pitting (Dou et al. 1999; Medeira et al. 1999; Dou 2003). The large amount of volatile compounds found in pitted and nonpitted fruit are essential oils such as limonene and valencene (Dou 2003). It was proposed that internal volatile composition of fruit could be used as an indicator of fruit susceptibility to postharvest pitting. By comparing volatile composition of pitted and nonpitted 'Fallglo' tangerines and white 'Marsh' grapefruit, the author showed that pitted fruit had higher volatile concentration than nonpitted fruit. However, of more than 20 volatile compounds, limonene was the only one found in significantly higher concentrations in pitted 'Fallglo' tangerines and 'Marsh' grapefruit as compared with nonpitted fruit. Medeira et al. (1999) further proposed the possibility that limonene in the parenchyma of the flavedo of 'Encore' mandarin is released from its compartments, and is toxic to the cells. Although significant difference in volatile components of the rind occurred during storage, rind pitting was probably caused by means other than changing rind volatile composition (Sun and Petracek 1999).

VI. TECHNIQUES FOR INDUCING RIND DISORDERS

Studies in different citrus growing regions indicate that rind water status is a key factor prevailing in the susceptibility of citrus fruit to postharvest nonchilling peel pitting (Alférez et al. 2005, 2010). In citrus

growing areas, such as Florida during 'Marsh' grapefruit harvesting season and Spain during 'Navelina and 'Navelate' harvesting season, harvested fruit may experience fluctuations in RH from 95% to 25% within a 24 h period (Alférez et al. 2004, 2005). These conditions have been reported to induce postharvest nonchilling disorders in these fruit. Therefore, to reproduce symptoms of postharvest nonchilling pitting disorders such as noxan of 'Shamouti' oranges (Ben-Yehoshua et al. 2001), postharvest peel pitting in 'Navel' oranges (Alférez and Zacarìas 2001) and 'Marsh' grapefruit (Alférez and Burns 2004; Alférez et al. 2010), and rind staining in 'Navel' oranges (Plate 3.3a) (Alférez et al. 2003) under controlled conditions, RH is changed from low to high.

The incidence of rind breakdown (RBD) of 'Nules Clementine' mandarin has consistently been shown to be lower in fruit exposed to the sun than nonexposed fruits, and higher on exposed than the nonexposed side of individual fruits (van Rensburg et al. 2004; Khumalo 2006; Cronje 2009). Light conditions were also reported to have influence on fruit color (van Rensburg et al. 2004; Cronje 2009) and maturity (Barry et al. 2000). Well-colored 'Nules Clementine' mandarin fruit did not suffer from peel pitting or rind breakdown disorder during storage (Cronje et al. 2011a). These observations prompted investigations to gain better insight into the effect of high light/low light on the occurrence of the disorder as a part of testing models that result in an increase in RBD sensitivity.

In order to prove the hypothesis that the fruit flavedo should receive direct sun exposure to ensure good rind conditions, Cronje (2009) and Cronje et al. (2011a) used paper bags to cover individual fruit and to manipulate the duration of direct sun exposure. By covering the fruit positioned on the outside of the canopy during stages II and III (immediately after physiological fruit drop or 4 months before harvest) of fruit development, it was possible to induce RBD in 'Nules Clementine' mandarins. This is the first successful technique to induce a physiological rind disorder during preharvest and has opened new avenues of research toward elucidating the mechanisms involved in the disorder and eventually improving rind condition.

VII. PROSPECTS FOR FUTURE RESEARCH

Significant progress has been made in understanding nonchilling peel pitting and factors associated with the disorder. For instance, Cronje et al. (2011a) showed that the reduction of fruit light interception

during stage II of fruit development, and probably earlier, is detrimental to rind condition and can lead to higher incidence of the disorder. This is one of the major advancements in unraveling the factors predisposing 'Nules Clementine' mandarin fruit rind to rind breakdown disorder.

Although intensive research has been conducted, physiological rind disorders still occur frequently and unpredictably. The difficulty is that these disorders, characteristically, do not manifest during harvest or fruit grading but develop about 1–5 weeks after harvest (Agustí et al. 2003, 2004; Cronje 2007). This delayed phenomenon is, in essence, the difficulty that is faced by the industry and importers alike. The challenge is therefore to develop technology to determine rind quality on the packing line, in order to classify individual fruit for either local or export market, as losses in the postharvest chain can result in a significant reduction of return on investment.

There is therefore, a need to develop an objective, fast, and nondestructive assessment that can be used to accurately determine or predict the susceptibility of presymptomatic citrus fruit to rind disorders. Among nondestructive quality assessment techniques such as near infrared spectroscopy (NIRS) (Zheng et al. 2010), hyperspectral imaging, and multispectral imaging (Blasco et al. 2009), magnetic resonance imaging (MRI), X-ray (Lammertyn et al. 2003), and optical coherence tomography (OCT) (Meglinski et al. 2010), NIRS is arguably the most advanced with regard to instrumentation, applications, accessories, and chemometric software packages (Nicolaï et al. 2007). A review by Magwaza et al. (2012) discusses the recent developments and application of Vis–NIR spectroscopy to nondestructively evaluate the internal and external quality of citrus fruit.

It is worth noting that very limited research has been conducted to develop a technology to assess, predict, and monitor the physiological disorders and rind physiological disorders of citrus fruit (Geeola et al. 1994). This is because until recently, most nondestructive quality measurement technologies were developed to assess fruit according to their internal quality attributes (Butz et al. 2005) rather than external quality. However, the success of NIRS to detect surface bruising in apple (Geeola et al. 1994), surface defects in peach (Miller and Delwiche 1991), storage disorder in kiwifruit (Clark et al., 2004), and internal drying in tangerine citrus (Peiris et al. 1998b) shows the potential of this technology in determining nonchilling physiological rind disorders. One of the recent successes of NIRS application was demonstrated by Zheng et al. (2010) who used NIRS to predict oleocellosis sensitivity of citrus fruit.

Imaging techniques have been developed and successfully applied as inspection tools for quality assessment of a variety of fruits (Xing et al. 2003, 2005; Mehl et al. 2004). Basically, the development of the multispectral and hyperspectral imaging not only provides the possibility to capture images in the visible range but also extends to capture multiple images at different wavelengths in the Vis–NIR regions (Mehl et al. 2004; Qin et al. 2008). These analytical technologies, which combine Vis–NIRS with digital imaging, now allow both spatial and spectral information to be obtained simultaneously. Further information on the principles of these technologies can be found in a review by Gowen et al. (2007).

Internal and external quality defects of onions can be effectively observed and screened by the OCT system, and this noninvasive method is suitable for examining intact plants (Meglinski et al. 2010). OCT produces two-dimensional images of plant tissues at a penetration depth of 1–2 mm from the surface (Sapozhnikova et al. 2003). Detailed aspects of OCT theory and applications have been discussed in comprehensive reviews by Fercher et al. (2003) and Tomlins and Wang (2005). NIRS and OCT offer potential for the noninvasive assessment of the chemical composition such as carbohydrate content in the flavedo and changes in intact fruit that might predispose fruit to the development of rind disorders.

It is possible that rind pigments measured only at harvest cannot be used as indicators for fruit susceptibility to rind breakdown (Cronje et al. 2011a). Studies have also suggested the participation of the antioxidant enzymatic system in the chilling and nonchilling conditions causing rind pitting (Sala and Lafuente 1999; Lafuente et al. 2003; Sala et al. 2005; Cajuste and Lafuente 2007). These investigations have shown that phenolic metabolism may be required for building protecting barriers that would help 'Navelate' fruit to reduce nonchilling peel pitting. However, further investigations are needed to understand the participation of the antioxidant system in protecting citrus fruit against other rind nonchilling physiological disorders, such as RBD on 'Nules Clementine' and rind staining on 'Navel' oranges.

VIII. CONCLUSIONS

Intensive research has been conducted on determining factors that trigger citrus nonchilling rind pitting disorders. Similar to most fruit physiological disorders, nonchilling rind physiological disorders are theoretically associated with preharvest, ecophysiological, and

postharvest factors. Various studies by different groups of investigators have found a correlation between preharvest factors such as cultivar, rootstock, microclimate, nutrient imbalance, and postharvest rind pitting. In addition, stressful postharvest conditions such as low and sudden changes in RH exacerbate the disorder by reducing rind water potential. However, the mechanism governing the occurrence of rind pitting disorder and the manner in which it is related to other physiological rind disorders is still not well understood. Nonetheless, it has been established that different canopy microclimates influence sensitivity of fruit to these disorders. Different research groups maintained that rind pitting disorders affect sun-exposed fruit more than shaded (covered by foliage) fruit. It is hypothesized that solar radiation may be involved in the structural alteration of the cuticle, and a high rind temperature over a long period may induce localized dehydration in the epidermal and subepidermal cells, leading to plasmolysis and membrane collapse. In contrast, 'Nules Clementine' mandarins deviated from this trend whereby inside fruit were more susceptible to RBD. Exposure of 'Nules Clementine' to high (outside) or low (inside) light levels in the canopy affected the rind carbohydrate and carotenoids concentration during fruit development whereby outside fruit had higher rind carbohydrate and carotenoids compared with fruit located inside the canopy. Future research on general rind biochemical changes and antioxidants in particular, incorporating multiple sampling times and postharvest pigment analysis, is suggested.

The incidence of these disorders can be controlled by maintaining mineral nutrient balance, sufficient light penetration within the canopy by pruning, high water potential, and reducing the rate of fruit senescence. Preharvest and postharvest application GA3 (10 mg L^{-1} just before or at fruit color break) has been demonstrated as a practical method to reduce the incidence or delay the appearance of physiological nonchilling rind disorders associated with senescence such as rind staining of navel orange and rind pitting in 'Fortune' mandarin. Incidence and severity of nonchilling pitting disorder can be markedly reduced by several postharvest treatments such maintaining constant humidity and raising the humidity around the fruit to above 95% RH. Basically, postharvest treatments that will reduce weight loss and maintain the turgidity and firmness of the fruit should reduce the incidence of these disorders. Earlier in the chapter, it was shown that posthatvest nonchilling rind disorders are caused by transient exposure of fruit to low RH (<45%), followed by transfer to high RH (90%) and 2 h at low RH are sufficient to induce peel pitting after transfer to RH. It is therefore suggested that commercial impact of

postharvest peel pitting can be reduced by harvesting susceptible cultivars at high RH and minimizing exposure to low RH postharvest. However, it should be borne in mind that excessive turgidity and wetness can also predispose citrus fruit to a different important physiological disorder, oleocellosis. Considering that oleocellosis results from mechanical impact damage that ruptures oil glands, careful handling during harvest and postharvest packhouse operations should be maintained.

ACKNOWLEDGMENTS

This work is based on the research supported by the South African Research Chairs Initiative of the Department of Science and Technology and National Research Foundation. The authors are grateful to the South African Perishable Products Export Control Board (PPECB) and the South Africa/Flanders Research Cooperation Programme (Project UID: 73936) for financial support that made it possible to undertake the study, and to Rosemary Burns and Dr. Kate Cools for technical research support at Cranfield University (CU). Mr. Lembe Magwaza's study visit to CU was partly funded by the Commonwealth Scholarship Commission of the United Kingdom.

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4

Fruit Splitting in Citrus

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ABSTRACT

Various citrus cultivars of 'Navel' and 'Valencia' orange [*Citrus sinensis* (L.) Osbeck], as well as mandarin and mandarin hybrids (*Citrus reticulata* Blanco) are prone to a preharvest physiological rind disorder, known as fruit splitting. Similar disorders occur as fruit cracking and/or splitting in other commercially important horticultural crops, most notably in apple, apricot, cherry, grape, nectarine, prune, and tomato. Fruit splitting in citrus differs from other crops due to the unique morphology of a citrus fruit, consisting of the pulp and rind, which is made up of the spongy white internal layer, the albedo (mesocarp), and the external layer, the flavedo (exocarp). Pressure applied by the rapidly expanding pulp during fruit growth leads to the formation of microcracks in the flavedo and initiation of fruit split at the stylar or navel end of the citrus fruit rind. This area of the rind is the thinnest and/or structurally weaker than other areas of the fruit rind. The episodic nature of fruit split is a good indication that certain environmental and/or cultural cues initiate the incidence of fruit splitting. Such factors include nutrient imbalances, specifically low Ca and K and high P, warm and humid climatic conditions, irregular water supply, and heavy crop loads. The unique anatomical features of certain citrus cultivars, such as presence of a secondary fruitlet (navel), weaken the structure of the

Horticultural Reviews, Volume 41, First Edition. Edited by Jules Janick.
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primary fruit. In addition, the thin rind of the reticulated mandarin and mandarin hybrids increases the susceptibility to fruit splitting. Current horticultural practices to reduce the incidence of splitting include a combination of crop load manipulation by thinning and GA_3 application/girdling, as well as sufficient Ca, K, and P nutrition and consistent irrigation. There is, however, no single commercial technology to consistently reduce the incidence of this disorder. Recent research on mandarin species reported significant reduction of fruit splitting through the application of a synthetic auxin, 2,4-D, as a foliar spray. However, results were erratic when applied to orange cultivars and negative effects on fruit quality, such as increased rind coarseness and reduction in juice content, are some of the major drawbacks of 2,4-D application. This review aims to summarize the unique physiology of citrus fruit splitting, as well as the contributing factors and horticultural practices available to reduce the impact of this disorder.

KEYWORDS: fruit splitting; irrigation; nutrient balance; plant growth regulators; rind disorder

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I. INTRODUCTION

A. Problem and Overview

Fruit splitting is a major preharvest physiological disorder in various citrus species, leading to annual yield losses of up to 30% (Rabe et al. 1990; Barry and Bower 1997). Fruit splitting is caused by pressure resulting from the expanding pulp of an individual fruit on the rind (Erickson 1968; Bower et al. 1992; Almela et al. 1994; Barry and Bower 1997), eventually causing a fissure at the stylar or navel end, and leading to the splitting of the fruit (Fig. 4.1). Split fruit eventually drop from the tree. Not only does fruit splitting negatively affect yield, but it also attracts insects and pathogens that cause decay; subsequently, intense labor is required to sanitize the orchards.

A wide variety of cultural and environmental factors, independent of clonal characteristics, influence and contribute to both the initiation and severity of citrus fruit splitting. These include nutrient imbalances (Erickson 1957; Bar-Akiva 1975; De Cicco et al. 1988), warm and humid climatic conditions (Coit 1915; Almela et al. 1994; Barry and Bower 1997), irregular water supply (Wager 1939; De Cicco et al. 1988;

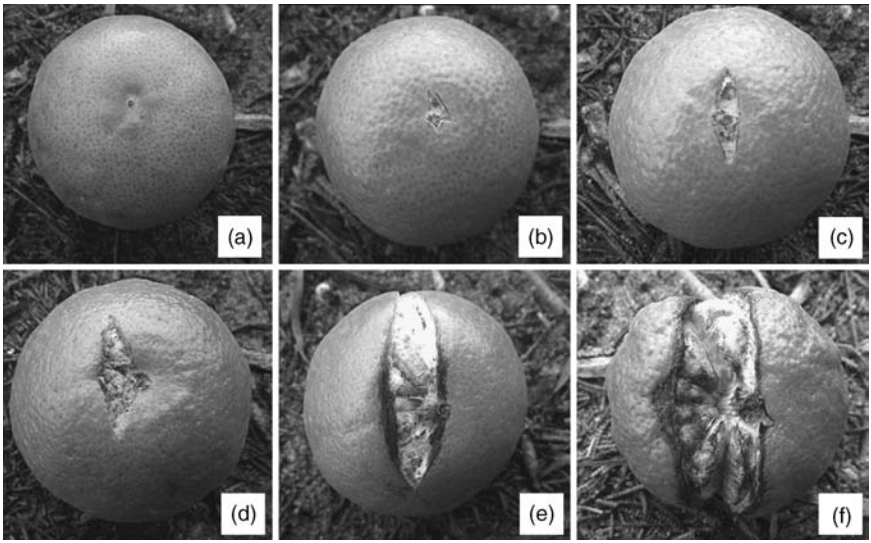

Fig. 4.1. Fruit splitting initiates at the stylar end of the fruit as a small fissure of the rind (a). As the pulp starts to expand, the accompanied increase in volume forces the rind to split open (b–e). Split fruit eventually drop from the tree (f). Labor is required to remove split fruit from trees and abscised split fruit from the orchard floor (sanitation).

Goldschmidt and Galili 1992), and heavy crop load (Rabe et al. 1990; Barry and Bower 1997). Secondary to these factors, fruit growth and morphological features of the fruit, such as the thickness of the rind and large navels, also play an important contributing role in the initiation of the disorder (Wager 1939; Lima et al. 1980). The severity of the disorder may vary considerably between seasons (De Cicco et al. 1988; Almela et al. 1994), making it difficult to predict and control.

Most of the studies on the control of fruit splitting focused on increasing the rind thickness and strength of split-prone species by applying preharvest mineral nutrient sprays to the canopy or plant growth regulator (PGR) foliar sprays. Although results were erratic, PGR applications were generally more successful than mineral nutrient applications for reducing spitting. In this regard, the synthetic auxin, 2,4-dichlorophenoxy acetic acid (2,4-D) (Borroto et al. 1981; Almela et al. 1994; Greenberg et al. 2006; Mupambi 2010), and gibberellic acid (GA_3) (Rabe et al. 1990; Almela et al. 1994; García-Luis et al. 1994) were most successful. Calcium (Ca) (Almela et al. 1994; Barry and Bower 1997; Sdoodee and Chiarawipa 2005) and potassium (K) (Bar-Akiva 1975; Borroto et al. 1981; Greenberg et al. 2006) also reduced splitting, but to a lesser degree. Goldschmidt and Galili (1992) focused on the control of pulp expansion during periods of split initiation, using irrigation management, and achieved a significant reduction in the incidence of split fruit.

B. Cultivars Particularly Susceptible to Split

Fruit splitting occurs worldwide as a preharvest problem in mandarin and mandarin hybrids (Goldschmidt and Galili 1992; Almela et al. 1994; Barry and Bower 1997) as well as 'Navel' (De Cicco et al. 1988) and 'Valencia' orange (Bower et al. 1992) (Table 4.1). Cultivars with genetically thin rinds, especially mandarin and mandarin hybrids (easy peelers), are potentially more susceptible to split than cultivars with thicker rinds. The earliest mandarin species prone to splitting, although at low severity, is 'Owari' satsuma. In Clementine, 'Fino', 'Marisol' (Mupambi 2010), and 'Nules' are cultivars known to be susceptible to severe levels of split fruit, while splitting has been reported in mandarin hybrids of 'Ellendale' (Rabe et al. 1989), 'Murcott' (Goldschmidt and Galili 1992), 'Nova' (Almela et al. 1994), and 'Shogun' (Sdoodee and Chiarawipa 2005) especially in years of heavy fruit load (Rabe and Van Rensburg 1996).

'Navel' orange and certain other mandarin cultivars such as 'Nova' and 'Ellendale' genetically develop a secondary fruitlet (navel) covered

Table 4.1. Susceptibility to fruit splitting in citrus cultivars.

Species	Type	Cultivar	Time of maturity	Prevalence
Mandarin	Satsuma	Owari	Early	Low
	Clementine	Fino, Marisol, Nules, Orogrande	Middle	High
	Hybrid	Murcott, Nova, Mor, Orri, Ellendale, Orlando, Ortanique, Shogun	Middle/late	High
Orange	Navel	Hamlin, Navelina, Washington	Middle/late	High
	Valencia	Campbell, Frost, Leng Midknight, Olinda	Late	Moderate

or protruding at the stylar end of the primary fruit (García-Luis et al. 1994; Rabe and Van Rensburg 1996). The presence of these structures hampers the structural integrity of the fruit rind (García-Luis et al. 1994) and fruit with large secondary fruit (navels) are thus more prone to splitting, as was found with 'Washington navel' orange (Wager 1939; Lima et al. 1980; García-Luis et al. 1994). In addition to the secondary fruitlet, certain cultivars such as 'Navelina' orange and 'Nova' mandarin are more split prone due to their particular oblate shape and the high rate of morphological differentiation from globose to oblate during critical growth periods (De Cicco et al. 1988; García-Luis et al. 2001). 'Valencia' orange is the latest maturing orange variety and generally develops fruit with thin rind and increased susceptibility to split. Cultivars of note include 'Campbell', 'Frost', 'Midknight', and 'Olinda' Valencia (Borroto et al. 1981; Bower et al. 1992).

The wide variety of influencing factors as well as the complexity of their interactions makes it almost impossible to provide a single commercial solution to the disorder. Therefore, an understanding of the physiology of both the tree and of the most important structural components of the fruit in relation to fruit splitting, namely, the rind and the pulp, is required to combat fruit splitting in citrus.

C. Fruit Splitting in Other Horticultural Crops

Fruit splitting or cracking has been reported for almost every horticultural crop of economic importance. This disorder occurs most notably in apple (Visai et al. 1989), apricot (Benson 1994), cherry (Belmans and Keulemans 1996), grape (Considine and Kriedemann 1972), nectarine (Gibert et al. 2007), prune (Milad and Shackel 1992), and tomato

Table 4.2. Summary of factors causing fruit cracking and splitting in commercially important horticultural crops, as well as proposed control measures.

Crop	Cause	Control
Apple	Serious peel russet (Visai et al. 1989)	Foliar GA4 + 7 applications (Byers et al. 1990)
Apricot	B deficiency (Benson 1994); heavy rainfall during fruit growth (Gülşen et al. 1995)	B application (Benson 1994)
Cherry	Excessive water supply at harvest (Belmans and Keulemans 1996)	Ca applications (Meheriuk et al. 1991); GA applications (Cline and Trought 2007)
Grape	High rainfall at onset of ripening (Clarke et al. 2010)	Consistent water supply (Considine and Kriedemann 1972)
Nectarine	Low crop load (Gibert et al. 2007); increased fruit size (Gibert et al. 2007)	Lowering irrigation during rapid fruit growth (Gibert et al. 2007)
Prune	Excessive irrigation following water stress (Milad and Shackel 1992)	Consistent water supply (Milad and Shackel 1992)
Tomato	Excessive irrigation following water stress (Peet 1992); insufficient nutrition (Huang and Snapp 2004); low crop load (increased growth rate) (Peet 1992); harvest at pink stage (late) (Peet 1992)	Use of crack-resistant cultivars (Sperry et al. 1996); consistent water supply (Sperry et al. 1996); GA (Peet 1992) and Ca (Huang and Snapp 2004) application; harvest at green mature stage (early) (Peet 1992)

(Peet 1992) (Table 4.2). Although similarities in certain causal factors as well as certain aspects of the physiological development of the phenomenon exist between these crops and citrus fruit, unique anatomical features of citrus fruit as well as physiology of fruit development separate the phenomenon in citrus from other crops.

Splitting of a fruit is a consequence of cracks developing in the epidermis or in the rind of a developing fruit. In most crops that are prone to cracking or splitting, the spatial distribution of cracks varies. Cracks could develop at the stylar and/or stem end, cheeks, and shoulders of the fruit. Although the tendency to crack is genetically controlled with certain cultivars being crack resistant (Gülşen et al. 1995; Belmans and Keulemans 1996; Sperry et al. 1996), the intensity of the disorder in crack-prone cultivars is episodic, with fluctuations in severity between seasons. This indicates the disorder in other crops to also be induced by either environmental conditions and/or cultural factors (Peet 1992).

Certain causative factors in other fruit crops, namely, cultural and environmental, are also important with citrus. Heavy rainfall during the

period of rapid fruit growth in apricot (Gülşen et al. 1995), grape (Clarke et al. 2010), as well as tomato (Peet 1992) and at harvest in cherry (Belmans and Keulemans 1996) correlates as a causative factor of the phenomenon in citrus fruit (Wager 1939). In addition, as suggested in citrus (Coit 1915), high-volume irrigation after a period of water stress has been shown to result in the development of cracks in prune (Milad and Shackel 1992), tomato (Peet 1992), and nectarine (Gibert et al. 2007). Cultural practices encouraging excessive fruit growth, such as high irrigation during the period of rapid fruit growth of nectarine (Gibert et al. 2007) as well as pruning and thinning of tomato plants in a similar developmental phase (Peet 1992), can lead to the development of cracks of the fruit surface. In terms of mineral nutrient deficiency, cracks develop due to boron (B) deficiency in apricots (Benson 1994) and calcium (Ca) deficiency in cherry (Meheriuk et al. 1991) and tomato (Huang and Snapp 2004).

Even though similarity exists in causes of splitting between citrus and other fruit, the unique morphology and physiology of citrus fruit indicate additional causes. Citrus fruit is known as a Hesperidian berry, with a leathery rind and internal swollen trichomes and juice sacs (Swingle 1943); these aspects as well as the differences in rind thickness and the presence or absence of secondary fruit add factors that could cause the initiation and splitting of citrus fruit.

II. PHYSIOLOGY OF CITRUS FRUIT SPLITTING

A. Relationship Between Fruit Growth, Resulting Shape, and Splitting

Citrus fruit growth follows a sigmoïdal curve as described by Bain (1958), with the rind developing mainly during stages I and II, whereas pulp growth predominantly occurs during stage II. During stage III, very little increase in fruit size occurs as the fruit matures.

García-Luis et al. (2001) linked the chronological development of this disorder with certain morphological changes of the fruit during development, such as an increase in diameter/height ratio (D/H ratio). The physical splitting of the fruit predominantly occurs during stage II of fruit development of split-prone cultivars (Fig. 4.2) (Borroto et al. 1981; Goldschmidt and Galili 1992; García-Luis et al. 1994; Rabe and Van Rensburg 1996). During stage II of fruit development, there is an increase in pulp volume due to the expansion of cells caused by

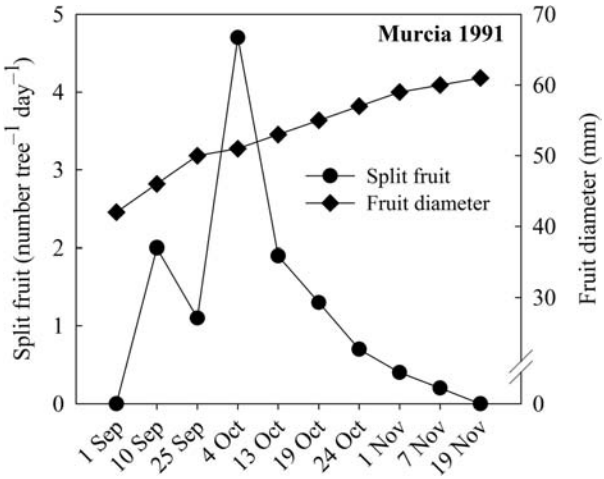

Fig. 4.2. The seasonal pattern of fruit splitting, expressed as number of split fruit per tree per day, as it occurred in 'Nova' mandarin in an orchard in Spain (Murcia) (northern hemisphere) in 1991. The initiation of splitting corresponds with the rapid increase in fruit diameter. *Source*: Adapted from García-Luis et al. (1994).

increase in turgor pressure, resulting in a progressive change in fruit shape.

Fruit shape is classified as the ratio between fruit diameter and fruit height. Fruit with a low diameter to height ratio are generally referred to as globose. During the period of maximum increase in citrus fruit diameter (stage II), fruit transform from globose to oblate in shape (García-Luis et al. 2001) and pressure exerted by the pulp forces the rind to enclose its expanding volume due to the predominant occurrence of the pulp and albedo's cell growth (Bain 1958). The increase in fruit D/H ratio is accompanied by an increase of internal stress exerted on the poles of the fruit (Considine and Brown 1981), namely, the calyx and the stylar end.

While the large intercellular spaces of the albedo absorb some of the pressure exerted by the rapid pulp expansion (Monselise 1986), the flavedo stretches and becomes thinner. The flavedo of split-prone cultivars cannot accommodate the increase in pulp volume (Erickson 1957; Goldschmidt and Galili 1992; García-Luis et al. 2001), and as a result, fruit split at the stylar or navel end, where the rind is thinner and structurally weaker (Coit 1915).

Although fruit shape is specific to a cultivar, certain factors such as warm temperature, relative humidity, as well as rapid water uptake by the tree (Wager 1939; Lima et al. 1980; Goldschmidt and Galili 1992)

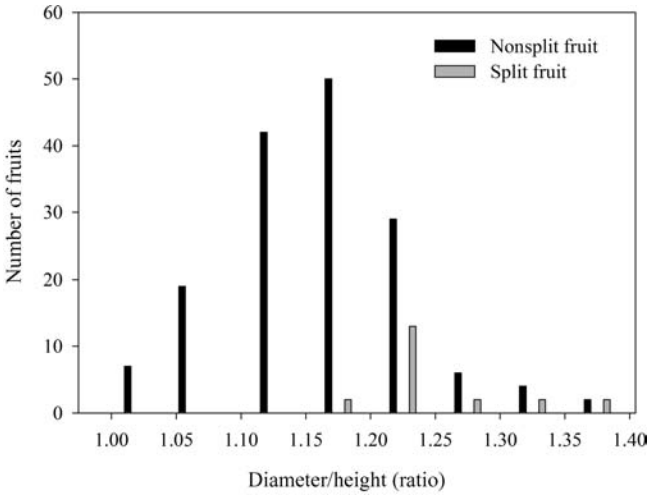

Fig. 4.3. Two hundred fruits from 'Nova mandarin' trees were tagged and their diameter and height periodically measured until the end of fruit development at which they were then classed as split (solid bars) and nonsplit (hollow bars). Final diameter/height ratio of all tagged fruit ranged from 1.02 to 1.37 with split occurrence at ratios $\geq$1.20. *Source*: Adapted from García-Luis et al. (2001).

may accelerate fruit growth. This could alter the fruit shape (increase the *D*/*H* ratio) to such an extent that the rind is unable to accommodate the increasing pulp volume and the fruit splits (Goldschmidt and Galili 1992). In 'Navel' orange, as the *D*/*H* ratio reduced, a lower incidence of fruit splitting occurred (De Cicco et al. 1988). In 'Nova mandarin', the percentage split fruit reached a maximum when the *D*/*H* ratio increased from 1.21 to 1.23 during fruit growth (Fig. 4.3) (García-Luis et al. 2001).

As reported for other crack-prone crops such as tomato (Peet 1992) and nectarine (Gibert et al. 2007), a reduction in irrigation rate during periods of rapid fruit growth, without stressing the tree, holds promise in reducing the likelihood of fruit cracking and splitting. By reducing water supply during stage II of fruit development, fruit splitting was reduced in 'Murcott' mandarin (Goldschmidt and Galili 1992).

Although the physical splitting of the citrus fruit occurs as a consequence of increase in pulp volume during stage II of fruit development, the potential for fruit splitting incidence is, to a large extent, a result of any stress to the tree and young fruitlets during fruit development in stage I (Rabe and Van Rensburg 1996). Factors such as nutritional imbalances, water stress during stage I, and high flower number and

fruit set hamper sufficient cell division and lead to the development of a weak and thin rind. In addition, fruit shape (known to be genetically influenced) and ambient growing conditions affect the initiation and severity of fruit splitting of the rind. Therefore, finding a successful commercial solution to fruit spitting of citrus will require an understanding of how to manipulate not only fruit growth but, in particular, fruit rind development.

B. Splitting as Related to Rind Characteristics

Although fruit with high *D*/*H* ratios are more likely to split, a proportion of fruit from the same tree with similar dimensions or even higher remains structurally intact. Therefore, it could be assumed that additional aspects in the fruit rind development could increase its susceptibility to splitting in reaction to expanding pulp. Cultural as well as environmental factors contribute to the development of citrus fruit with thin or weak rind and, indirectly, the fruit's propensity to split (Fig. 4.4) (Almela et al. 1994). As cell division in the fruit rind predominantly occurs during stage I of fruit development, contribution of these factors to increased susceptibility to splitting predominantly occurs during stage I of fruit development (Rabe and Van Rensburg 1996).

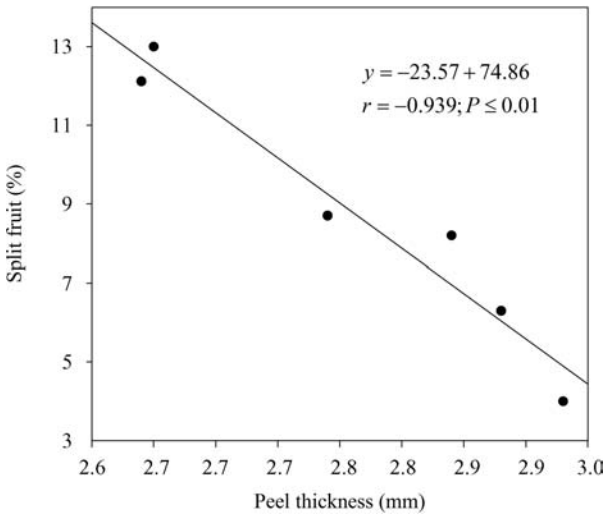

Fig. 4.4. As rind/rind thickness of 'Nova mandarin' hybrid increases, the percentage of split fruit decreases, indicating an inverse relationship between fruit splitting and peel/rind thickness in 'Nova mandarin' fruit. *Source*: Adapted from Almela et al. (1994).

Cultural factors include imbalances of certain mineral nutrients such as K and P (Section III.A.1) (Chapman 1968; Bar-Akiva 1975; Morgan et al. 2005), hormonal imbalances due to production of seedless fruit (Section III.A.2) (Erner et al. 1976; Rabe et al. 1990), and suboptimal irrigation, hampering plant–soil water relations. Any alterations leading to increased interfruit competition in the tree, such as girdling or GA_3 treatments that stimulate a higher percentage fruit set, could lead to the development of fruit with a thin or weak rind and an increase in splitting (Rabe et al. 1990). The most important environmental factors leading to development of fruit with thin rind, and thus also susceptibility to splitting, are warm and humid climatic conditions during stage I of fruit development (Cohen et al. 1972).

III. CAUSES OF CITRUS FRUIT SPLITTING

A. Cultural

1. Mineral Nutrition. With regard to citrus fruit splitting, imbalances in potassium (K) and phosphorous (P) can contribute to thin or weak rind and can therefore, at either too high or low rates, indirectly increase the likelihood of splitting (Bar-Akiva 1975; Borroto et al. 1981; Almela et al. 1994; Morgan et al. 2005).

With an increase in P supply and hence increased leaf P content, a decrease in rind thickness of citrus fruit is found (Chapman 1968). In contrast, an increase in leaf K content results in an increase in rind thickness and coarseness (Chapman 1968; Monselise 1986). This concurs with results found on the mineral composition of split 'Washington navel' oranges, with the rind of split fruit having significantly higher P content than nonsplit fruit (Erickson 1957). Similarly, a decrease in rind thickness of split fruit was found as the leaf P content increased in 'Navelina' orange and a reduced number of split fruit was found as the leaf K content increased (De Cicco et al. 1988). Higher incidence of splitting in trees with low leaf K content was reported in 'Hamlin' (Koo 1961) and 'Valencia' orange (Gilfillan and Stevenson 1982). Morgan et al. (2005), reporting an increase in rind thickness of 'Hamlin' orange with an increase in K nutrition and without evaluating the effect on number of split fruit, hypothesized that an increase in rind thickness could lead to a reduction in fruit splitting of this split-prone cultivar.

One of the aims of fertilizer practices is to ensure an optimum for both P and K in citrus orchards. Optimum for leaf P ranges between 0.10% and 0.16% and for leaf K, between 1.0% and 1.5% (CRI Production

Guidelines 2007). Some orchards with these nutrient levels in leaves still have a high percentage of split fruit. This indicates the involvement of factors other than P and K contributing to the prevalence of this disorder.

2. Hormonal Imbalances. Growth and development of citrus fruit are, to a great extent, dependent on the endogenous hormone content of the fruit. Seeds that develop as a result of pollination serve as a source of these hormones during the critical early development stage of the fruit (Monselise 1977).

However, split-prone mandarin cultivars such as 'Nova' and 'Ellendale' are weakly parthenocarpic and planted in isolated blocks to avoid cross-pollination and resultant seed formation (Barry and Bower 1997). Production of seedless fruit can lead to reduced fruit set but the lack of seeds has also been correlated with a decrease in rind thickness and a resultant higher occurrence of fruit splitting. Cross-pollinated 'Ellendale' mandarin trees had more seeds than noncross-pollinated trees and thus also an increased rind thickness and very few split fruit (Rabe et al. 1990). Pollination and seed formation increase the gibberellin content of weakly parthenocarpic fruit (Ben-Cheikh et al. 1997). It is possible that this increased endogenous gibberellin content leads to an increase in rind thickness. High levels of endogenous GA_3 and cytokinin are responsible for the excessive growth of 'Shamouti' orange fruit rind, which leads to the development of a very thick and rough rind (Erner et al. 1976).

3. Rainfall and Irrigation. Splitting of citrus fruit is a consequence of the pressure of expanding pulp on the rind of citrus fruit (Goldschmidt and Galili 1992; García-Luis et al. 1994, 2001). It could therefore be reasoned that any factor leading to drastic or excessive pulp expansion could increase the incidence and severity of splitting. The influx of water into the pulp during stages II and III of fruit development could exert undue pressure on the developing rind and lead to the eventual splitting thereof (Coit 1915; Wager 1939; Lima et al. 1980; Goldschmidt and Galili 1992).

Avoiding fluctuations in soil water content as well as avoiding depletion of water from deeper soil layers is of critical importance in avoiding fruit splitting. This was illustrated by De Cicco et al. (1988), who reported a significantly higher severity in fruit splitting of 'Navelina' orange when the total available water in the 40–80 cm soil layer was low. With total available water in the 40–80 cm soil layer at an optimum, fruit splitting was significantly lower. In reaction to daytime

drought stress, citrus leaves can withdraw water from the rind (xylem backflow), which leads to cessation of, or decrease in, fruitlet growth (Furr and Taylor 1939; Hilgeman 1977). This is thought to result in a premature strengthening of the flavedo cells, leading to a reduced ability to divide and enlarge as normal (Graebner 1920). Wager (1939) suggested the initiation of splitting of 'Washington navel' orange fruit to be caused by a sudden supply of large amounts of water after a period of water stress, during which the prematurely strengthened cells are unable to react to the sudden resupply of water into the pulp. Large tension exerted on the rind leads to eventual failure of the rind tissue. A similar mechanism was proposed to be responsible for splitting of tomato (Peet 1992) and prune (Milad and Shackel 1992).

Citrus produced in the humid, summer rainfall areas of South Africa have a higher propensity to split, presumably due to the frequent and unavoidable natural water supply during periods of rapid fruit growth. However, Rabe and Van Rensburg (1996) failed to correlate the seasonal rainfall pattern positively with fruit splitting.

4. Crop Load. The severity of citrus fruit splitting is very much dependent on flower number, percentage fruit set (Rabe et al. 1989; Rabe and Van Rensburg 1996), as well as final crop load (Gilfillan and Stevenson 1982; Rabe et al. 1990; Barry and Bower 1997). A high percentage of split fruit occurred at very high crop loads and little or no splitting in years of low crop loads (Gilfillan and Stevenson 1984). However, an increase in the disorder was expected at lower crop loads in tomato (Peet 1992) and nectarine (Gibert et al. 2007), which can be explained by the higher growth rate of individual fruit at lower crop loads and an inability of the fruit epidermis to accommodate for the increase in fruit volume created by these higher growth rates.With an increase in the number of fruit per tree, a linear increase in the interfruit competition for water and assimilates is expected. Lenz and Cary (1969) reported a decrease in fruit size and, more importantly, a decrease in rind thickness of citrus fruit with an increased crop load per tree. As crop load increased, the K concentration, a very important contributing agent to the development of a healthy and thick rind, declined in both the leaves and shoots of citrus trees (Lenz 2000).

Cultural practices such as girdling or GA_3 treatments during the blossom period are generally applied to increase fruit set percentage in citrus, especially in weakly parthenocarpic cultivars (Rabe et al. 1990; Rabe and Van Rensburg 1996; Barry and Bower 1997). However, the higher set percentage results in an increased interfruit competition, leading to a significantly higher number of split 'Nova' and

'Ellendale' mandarin fruit (Rabe and Van Rensburg 1996; Barry and Bower 1997).

5. Canopy Position Microclimate. Growth habit and resulting tree shape of some citrus cultivars as well as ineffective pruning by producers stimulate the development of variation in microclimate within a tree canopy that could lead to the development of fruit that are potentially more prone to physiological disorders such as rind breakdown of 'Nules Clementine' mandarin (Cronjé et al. 2011).

However, the fruit in the outer canopy are exposed to higher temperatures than the inside fruit. The high surface temperature of fruit in the outer canopy can cause the formation of free radicals inside cells of the fruit and their high reactivity leads to a loss in membrane integrity and eventual cell death (Wünsche et al. 2004). In 'Stayman' apple, fruit in the outer canopy are more likely to crack (Verner 1935). In citrus, the cellular damage due to the high heat leads to sunburn in the flavedo (light yellow to brown discoloration) and has been described by Sdoodee and Chiarawipa (2005) as a causal factor of splitting of 'Shogun' mandarin in Thailand.

B. Environmental

Climate has a definitive effect on rind thickness as well as the rate of fruit growth, thereby indirectly affecting the propensity of fruit toward splitting. Almela et al. (1994) reported varying intensities of 'Nova' mandarin fruit splitting between years and linked the variability to seasonal difference in climate.

1. Temperature. Barry and Bower (1997) reported the splitting of 'Nova' mandarin fruit to be less prevalent in cooler production regions. This was in agreement with Coit (1915), who suggested that regions more prone to hot weather are more likely to experience fruit splitting. Reuther et al. (1973) found that 'Valencia' orange exposed to warmer climate during the rapid growth period developed thinner rind and thus experienced higher levels of fruit splitting, compared to fruit exposed to lower temperatures. In these hot areas, the growth rate of citrus fruit during every stage of fruit development is also higher than those in cooler areas. This accelerated growth rate, especially of the pulp during growth stage II of fruit development, may lead to higher pressure being applied to the rind and thus initiate fruit splitting. This is similar to what Peet (1992) found in tomato, when fruit are exposed to high temperatures.

2. Humidity. Citrus fruit grown in humid production regions develop thinner rinds than those grown in drier regions (Cooper et al. 1963) and are, therefore, more likely to split. Rabe et al. (1989) reported severe fruit splitting of 'Ellendale' mandarin specifically in hot and humid citrus-producing regions in Swaziland (Tambankulu) and South Africa (Letaba, Limpopo), compared to regions with lower humidity such as the Western Cape Province of South Africa. However, a high incidence of fruit splitting is often associated with a dry spring followed by a wet period during stages II and III of fruit development.

IV. REDUCING CITRUS FRUIT SPLITTING

A. Foliar Mineral Nutrient Applications

1. Potassium. The mineral nutrient most abundant in a citrus fruit is K, and in K-deficient trees, reduction in size as well as number of fruit is expected (CRI Production Guidelines 2007). The most important effect of increased K nutrition on the quality of citrus fruit is a reduction in the juice content and total soluble solids (TSS) as well as an increase in fruit size, total acidity (TA), and rind thickness. Therefore, supplementing split-prone cultivars with K to achieve leaf K levels of between 1.0% and 1.5% (CRI Production Guidelines 2007) will lead to the development of fruit with thicker rind that are less likely to split (Morgan et al. 2005).

The soil application of K on three-year-old container-grown 'Valencia' orange trees reduced fruit splitting and increased rind thickness of K-treated trees, compared with untreated trees that experienced a higher incidence of fruit splitting (Bar-Akiva 1975). Potassium is readily translocated within a citrus tree and soil fertilization is the most effective cultural practice to address nutrient deficiency in citrus trees. Foliar sprays do, however, result in some nutrient uptake and could be used as a method of supplementing trees with K or correcting any deficiency of K. The time of foliar K application affects its efficacy in terms of influencing the incidence of splitting, and Rabe et al. (1989) reported higher numbers of split fruit per tree when 4% KNO_3 was applied prior to physiological fruit drop. In contrast, later application resulted in a significant reduction in splitting. The higher fruit set and increase in interfruit competition as a result from the earlier K application were thought to have led to the higher splitting (Rabe et al. 1990).

2. Calcium. Calcium is one of the most important structural components of cell membranes and walls and plays an important role in the processes of cell division and growth (Hepler 2005). Transport of Ca from the soil to the developing fruit is a passive process, dependent on the flow of the transpiration stream through the plant. Ca is weakly translocated from old leaves or other plant parts/organs to newly developing leaves, meristems, and fruit (Hanger 1979). Therefore, any deficiency of Ca in the soil, or any factor hampering the transport of Ca (e.g., low VPD) especially during critical periods of cell division and growth, will lead to Ca deficiency in the fruit. Such a deficiency or imbalance could lead to physiological disorders involving the rind, namely, rind breakdown of 'Nules Clementine' mandarin (Cronjé et al. 2011) and fruit splitting of 'Shogun' mandarin (Sdoodee and Chiarawipa 2005). The optimum leaf Ca in citrus production is 2.5–5.5% (CRI Production Guidelines 2007).

Cracking of tomato (Peet 1992; Huang and Snapp 2004) and cherry (Meheriuk et al. 1991) is thought to be a consequence of insufficient Ca supply. Multiple foliar applications of $CaCl_2$ and $Ca(OH_2)$ reduced the incidence of cracking in 'Van' cherry. This concurred with an earlier study by Barry and Bower (1997), in which a single foliar application of 2% $Ca(NO_3)_2$ at 70% full bloom significantly reduced fruit splitting in 'Nova' mandarin, compared with control, untreated trees. Boron (B) and Ca interact to form a stabilizing complex in the middle lamella of plant cells (Blevins and Lukaszewski 1998). By applying these two mineral nutrients in combination as a foliar spray to crack-prone 'Mountain spring' tomato, there was a significant reduction in the number of cracked tomato fruit (Huang and Snapp 2004). A similar significant reduction of split 'Shogun' mandarin fruit was recorded after the foliar application of either 1% $CaCl_2$, boric acid or a combination thereof, applied 4 months after fruit set (Sdoodee and Chiarawipa 2005).

B. Foliar-Applied Plant Growth Regulator (PGR) Applications

Foliar applications of PGRs result in varying amounts of success in reducing fruit splitting of split-prone cultivars. PGRs could strengthen the rind of developing fruitlets (Coggins and Hield 1968) or inhibit rind senescence (García-Luis et al. 1994). Application of PGRs in the form of auxin and gibberellin could potentially substitute for the lack of natural endogenous hormones in seedless cultivars and increase the rind strength of these fruit and their resistance to split.

In a study on the effect of applied hormones on the anatomy and splitting of 'Nova' mandarin, García-Luis et al. (1994) observed a

decrease in fruit splitting attributed to applied GA_3 successfully inhibiting the senescence of the rind, making the fruit less prone to splitting. The application of the synthetic auxin 2,4-D to cultivars prone to develop thin and/or smooth rinds led to an increase in thickness and rind coarseness (Coggins and Hield 1968), which has subsequently been shown to reduce fruit splitting (García-Luis et al. 2001).

However, in some instances, PGR treatments resulted in contrasting results and either promoted fruit splitting in 'Navel' orange (Lima and Davies 1984), had little or no effect on 'Valencia' orange (Gilfillan and Stevenson 1982), or reduced the disorder on a number of mandarin species (Borroto et al. 1981; Almela et al. 1994; García-Luis et al. 1994, 2001; Greenberg et al. 2006; Mupambi 2010).

1. Gibberellic Acid (GA_3). Gibberellins are plant hormones responsible for facilitating cell division and enlargement, and therefore the application of GA_3 is used in many crops, such as grape and cherry, to increase fruit size (Cline and Trought 2007). Apart from its effect on fruit size, GA_3 applications also increase firmness of crack-prone cherry (Cline and Trought 2007) and tomato fruit (Peet 1992). In citrus, GA_3 increases rind resistance to pressure and delay of chlorophyll breakdown (McDonald et al. 1987), which is an indication of delaying of rind senescence (García-Luis et al. 1994) and its potential as a possible control measure of fruit splitting in certain citrus species. In 'Washington navel' orange, Bevington (1973) reported an increase in rind resistance to puncturing as well as a decrease in physiological disorders of the rind, such as puffing and creasing, with May (Southern hemisphere) applications of GA_3.

In 'Nova' mandarin, GA_3 (20 mg L^{-1}) applied after physiological fruit drop was more successful than a foliar spray during full bloom in reducing fruit splitting (García-Luis et al. 1994, 2001). This corresponds with the increase in fruit splitting observed when GA_3 applications at 10 or 20 mg L^{-1} were made during full bloom on 'Ellendale' mandarin (Rabe and Van Rensburg 1996). This can be explained by an increase in fruit set from the earlier application and, therefore, interfruit competition.

2. Synthetic Auxin: 2,4-Dichlorophenoxy Acetic Acid (2,4-D). Expansion of plant cells is facilitated by the important plant hormone auxin, produced in apical meristems and transported to growing tissue (Coggins and Hield 1968). Commercial applications of synthetic auxins in citriculture include 2,4-dichlorophenoxy propionic acid (El-Otmani et al. 1993) and 3,5,6-trichloro-2-pyridyl oxyacetic acid (Greenberg

et al. 2006), and are applied to increase fruit size by facilitating increased cell expansion (Mitchell 1961).

Excessive stimulation of cell expansion can lead to eventual cell and plant death, as is the case with application of the synthetic auxin, 2,4-D as a lethal herbicide. Some crops, such as grape, are very sensitive to this particular PGR and drifts of herbicidal sprays often lead to death of vines (Kasimatis et al. 1968). However, citrus trees are less sensitive to this PGR, and when applied at low rates ($\leq 20\,\mathrm{mg\,L^{-1}}$), an increase in fruit size is expected due to increased sink strength of treated fruit as well as stimulation of rind growth (Guardiola and García-Luis 1997).

In preliminary studies to reduce the size of navel end opening in 'Navel' orange, a significant decrease in fruit splitting of 'Marisol Clementine' by foliar application of 2,4-D at full bloom ($25\,\mathrm{mg\,L^{-1}}$) and petal drop (15 and $25\,\mathrm{mg\,L^{-1}}$) occurred (Mupambi 2010). These treatments, although successfully reducing fruit splitting, negatively increased rind coarseness and led to an increased percentage of fruit with persistent styles. Application of 2,4-D on the same cultivar and site, but at later timing (after physiological fruit drop) and at $15\,\mathrm{mg\,L^{-1}}$, reduced fruit splitting and produced fruit of acceptable rind coarseness and without persisting styles, indicating that the success of this treatment could be dependent on timing as well as concentration (unpublished). García-Luis et al. (2001) observed a significant reduction of fruit splitting with foliar applications of $20\,\mathrm{mg\,L^{-1}}$ 2,4-D at full bloom, and attributed it to an increase in rind thickness at the stylar ends of treated fruit.

3. Combination of PGRs and Mineral Nutrients as Foliar Treatments. The combination of PGRs and mineral nutrients proved successful in reducing the severity of citrus fruit splitting. The disorder was reduced by more than 50%, with a treatment consisting of KCl (150 kg ha) and 2,4-D at $10\,\mathrm{mg\,L^{-1}}$ on 'Olinda Valencia' orange trees (Borroto et al. 1981). Greenberg et al. (2006) found a reduction of fruit splitting when 5% Bonus NPK was applied with 2,4-D foliar sprays on 'Nova' mandarin. Almela et al. (1994) reported that a foliar spray of 2% $Ca(NO_3)_2$, 20 mg L^{-1} 2,4-D, and $20\,\mathrm{mg\,L^{-1}}$ GA_3 reduced fruit splitting by increasing rind strength, but not rind thickness, which could indicate a possible strengthening effect of the citrus fruit rind.

C. Managing Plant Water Relations

Careful and detailed management of irrigation practices during fruit growth periods, with the aim of avoiding fluctuations in soil water

content, is key in controlling fruit splitting in citrus (Rabe 1988). Goldschmidt and Galili (1992) achieved moderate success in reducing splitting of 'Murcott' mandarin when they reduced the normal irrigation during late summer in the period of pulp expansion (stage II) to 50–60% and as much as 30% of normal irrigation, without significantly affecting internal fruit quality. Although deficit irrigation during late stages of fruit development is a standard practice to increase the TSS of early maturing cultivars such as 'Satsuma' mandarin, it is important not to stress trees excessively during the early stages of fruit development, as it may negatively affect fruit growth and final fruit size (Hilgeman 1977).

D. Thinning

Splitting of citrus has been particularly prevalent in years of excessive crop load (Rabe and Van Rensburg 1996), where high competition for water and assimilates between fruit leads to a reduction in total partitioning between fruit and the development of small, thin-rinded, and split-prone fruit. Therefore, thinning of flowers or thinning of fruit prior to physiological fruit drop (stage I) in years of expected excessive crop load is suggested as a possible measure to reduce competition between fruitlets for assimilates and water. This can increase partitioning to individual fruit to eventually produce larger fruit with thicker and stronger rind, and an accompanied lower incidence of splitting (Barry and Bower 1997). In addition, in years where a heavy crop load is expected, both irrigation and nutrition should be adjusted to accommodate for the increased fruit set.

However, excessive thinning of fruitlets or thinning during the period of rapid fruit growth (stage II) may result in a low fruit set percentage and, as a result, increase the growth rate of remaining fruit to such an extent that the rinds of these fruit are unable to accommodate for the increased growth rate and result in fruit cracking or splitting. The thinning of young fruit was proposed as a causative factor in the cracking of nectarine (Gibert et al. 2007) and tomato fruit (Peet 1992) due to the resulting increase in growth rate of remaining fruit.

V. CONCLUSIONS

Fruit splitting in citrus differs from other crops due to the unique morphology of citrus fruit, consisting of the pulp and rind, which is, in addition, made up of the spongy white internal layer, the albedo (mesocarp), and an external layer, the flavedo (exocarp) (Monselise 1986).

During stage I of fruit development (cell division), the majority of the flavedo cells are formed whereafter cell division of the flavedo declines and cells of the pulp start to expand in stage II (Bain 1958). The pressure applied by the rapidly expanding pulp leads to the formation of microcracks and initiation of splitting at the stylar or navel end of the fruit, the area where the rind is the thinnest and/or structurally weaker than other areas of the rind.

Certain environmental as well as cultural factors lead to the development of rind that is thinner and more split prone. Such factors include nutrient imbalances, specifically low K and P (Erickson 1957; Bar-Akiva 1975; De Cicco et al. 1988), warm and humid climatic conditions (Coit 1915; Almela et al. 1994; Barry and Bower 1997), irregular water supply (Wager 1939; De Cicco et al. 1988; Goldschmidt and Galili 1992), and heavy crop loads (Rabe et al. 1990; Barry and Bower 1997). However, stress during stage I of fruit development seems to be the most important factor determining the susceptibility of an orchard to fruit splitting (Rabe and Van Rensburg 1996). During this stage, the majority of the flavedo cells are formed and its structural integrity is determined. With high crop loads, or by insufficient irrigation or fertilization during this critical period, the potential for fruit to split is increased significantly.

Fruit splitting has been reported in a various 'Valencia' as well as 'Navel' orange cultivars, which are more prone due to the presence of a secondary fruitlet (navel) that weakens the structure of the primary fruit. Fruit splitting occurrence is more severe in thin-rind, reticulated mandarin and mandarin hybrids (Goldschmidt and Galili 1992; Almela et al. 1994; Barry and Bower 1997). Consumer preference for easy-peeling, low-seeded mandarins of high internal fruit quality, especially relatively new cultivars such as 'Murcott', 'Nova', 'Mor', and 'Orri', has led to large-scale planting of these cultivars by producers. However, these cultivars are split prone and large quantities of fruit are lost solely due to fruit splitting, especially in 'on' years as these trees are prone to alternate bearing.

Current horticultural practices to reduce the incidence of splitting include crop load manipulation by thinning and GA_3 application/girdling, as well as sufficient Ca, K, and P nutrition and consistent irrigation. However, no single practice consistently reduces the incidence of fruit splitting in a splitting-prone orchard or cultivar.

Recent research on mandarin species reported significant reduction of fruit splitting through the application of a synthetic auxin, 2,4-D, as a foliar spray (Greenberg et al. 2006; Mupambi 2010). Successful reduction of fruit splitting with foliar application of 2,4-D seems more likely

on mandarin cultivars as results were erratic when applied to orange cultivars (Gilfillan and Stevenson 1984; Lima and Davies 1984). Additional negative effects on fruit quality, such as increased rind coarseness and reduction in juice content, are the major drawbacks of 2,4-D application. Successful implementation of 2,4-D application in citrus production in order to reduce splitting would be dependent on elucidating the timing, rate, as well as cultivar sensitivity.

The episodic nature of fruit splitting, however, is a good indication that certain environmental and/or cultural cues initiate the incidence of fruit splitting. The most important causative factors seem to be (1) heavy crop loads and (2) any stress during stage I of fruit development. The goal of future research should be to determine any other contributing factors as well as finding commercially viable methods to manipulate them, to eventually avoid the initiation of the physiological disorder, that is, citrus fruit splitting.

ACKNOWLEDGMENTS

The authors would like to thank Dr. Stephan Verreynne for guidance and information during the preparation of the manuscript. The valuable comments and suggestions to improve the manuscript by Dr. Tim Grout are gratefully acknowledged. Special thanks are due to Dr. Graham Barry for assistance with the section on cultivars as well as suggestions to improve the manuscript.

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5

Postharvest Biology and Technology of Ber Fruit

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ABSTRACT

Ber or Indian jujube (*Ziziphus mauritiana* Lamk.) is generally consumed fresh and is an important fruit of arid regions. Ber fruit has a high nutritive value, being a rich source of provitamin A, vitamin C and B complex, and also of Ca, K, Br, Rb, and La. Galactose, fructose, and glucose are the major sugars found in ber fruit. Fruits have a spongy, sweet-tasting pulp, and are an excellent source of ascorbic acid and carotenoids. The fruits are drupes characterized by a highly lignified and pointed endocarp (stone), fleshy mesocarp (pulp), and a thin pericarp (skin). Ber fruit have a climacteric respiratory behavior. Some maturity indices are in use but color is the most reliable. Standardization of non-destructive maturity indices is needed. Proper postharvest handling practices are yet to be developed. Short shelf life, postharvest rotting, and chilling injury are the most important problems. There has been limited postharvest research on ber fruit in the past two to three decades, and the information is scattered in diverse local and regional sources, especially in India. This review outlines

Horticultural Reviews, Volume 41, First Edition. Edited by Jules Janick.
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some of the important findings on maturity and harvest indices, respiration, ethylene production, pre- and postharvest treatments affecting postharvest life and quality, storage methods, and postharvest pathology.

KEYWORDS: maturity indices; physiological disorders; ripening; *Ziziphus mauritiana*

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I. INTRODUCTION

Ber (*Ziziphus mauritiana* Lamk, Rhamnaceae) is a tropical/subtropical fruit native to the northern hemisphere (Lyrene 1979). It is also known as Indian jujube, desert apple, or Indian plum among other names (Table 5.1). The genus *Ziziphus* has 135–170 species (Islam and

Table 5.1. Vernacular names of ber.

Country/region	Name
Afghanistan	Berra
Bangladesh	Bozoi, kool, kul
Barbados	Dunk, mangustine
Cambodia	Putrea
China	Hong tsao, lang tsao, ta tsao, tsao tse
Dominican Republic	Perita haitiana
England	Desert apple, Indian jujube, Indian plum, Indian cherry, Indian date, jujube; Chinese jujube; Chinese date; Chinese fig; cottony jujube
Ethiopia	Abateri, gaba-artgie, gewa-ortigi
France	Jujubier; (le jujube d' Afrique tropicale), datte chinoise
Greece	Tzintzola
India	Bogori (Assamese); kul (Bengali); ber, bor, bordi, boyed (Gujarati); ber, beri (Hindi); badari, baer, bogari, bore, egasi, elasi, ilanji, ilisi, jelachi, karkhandhu, yolachi (Kannada); ber, bhor, baher, bor, bardi, bora (Marathi); badaram, badari, kolam, lantu, elanda, perintutati (Malayadam); Ber, Beri, Unals (Punjabi); ajapriya, badari, balastha, dridhabija, dviparni, ghonta, gudaphala, kantaki, karkaramadhu, koli, kuvali, madhuraphala, madadebara, nakhi, nripabadari, nripeshta, prithukoli, phalashayashira, rajabadari, rajakoli, rajavallabha, sukshmaphala, sukshmapatrika, srigalakoli, svachha, sukorapriya, suphala, tanubija, ubhayakantaka (Sanskrit); Ber, Jangri (Sindhi); adidarum, attiram, ilandai, iradi, koli, kandai, kullari, kulvali, padari, sivagam, vadari, vettiram, veyam, elanda (tamil); badaramu, badari, gangaregu, gangarenu, karkhanduvu, regu, renu (Telugu); ber (Urdu); barholi, bodokoli, bodori, koli (Uriya)
Indonesia	Widara, dara, bidaru
Iran	Kanar, kunar, nabik
Iraq	Aunnaberhindi, nabig, sidr
Italy	Guiggiolo
Jamaica	Coolie plum or crabapple
Japan	Sanebuto-natsume
Kenya	Mkunazi (Swahili); kwkurrah (Borao); ekalati (Turhana); olongo (Luo); tolumuro (Pokot)
Laos	Than

(*continued*)

Table 5.1. (*Continued*)

Country/region	Name
Malawi	Masawo (Chewa); msondoka (Yao)
Malaya	Bedara
Malaysia	Bidaru, epal siam, jujube
Myanmar	Zi, zee-pen, zizidaw, ziben
Nepal	Baer
Pakistan	Ber (Urdu); ber, berwarter, kunar (Baluchi)
Philippines	Manzanites, manzanas
Portugal	Jujubeira, maceira
Puerto Rico	Aprin, yuyubi
Queensland	Chinese apple
Somalia	Gob, bheb, jujuba
Spain	Azufaifo, yuyuba
Sri Lanka	Ilanda, mahadebara, masaka (Sinhalese)
Sudan	Sidr nabk, nabbag elfil
Tanzania	Mkunazi (Swalihi)
Thailand	Phutsa, putsa, man tan
Trinidad	Dunks
Uganda	Esilang (Karamajong)
Venezuela	Ponsigne, yuyubo
Vietnam	Tao, tao-nhuc
West Africa and Sahel	Domo, ntomono, surgo ntomono, tomboro, tomonou (Bambara); batenluongu, bu sakonhionabu inakpayuani, nan janlwane (Gourmanche); magaria (Haussa); magunuga, mugulga, mugulanga, muegunga, mugunuga, mug-niga (More); djabe, djabi, tabi, n'giobi (Peulh); NGIT (Sere); ajzen (Tamachek); dem, dim, sedem (Wolof)
West Indies	Pomme malcadi, pomme surette, petit pomme, liane croc chien, gingeolier, dindoulier
Zaire	Kankole
Zambia	Masau (Nyanja); musawce (Tonga); akasongole (Bemba)
Zimbabwe	Masua, yanja, musawu (Central Shona, Tangu)

Sources: Sundararaj and Balasubramanyam (1959), Von Maydell (1986), Morton (1987), FAO (1988), Pareek (2001).

Simmons 2006), of which 17 are native of India (Watt 1883; Bailey 1947; Singh et al. 2000). Species having edible fruit found in different parts of India are: *Z. apetala* Hook.f., *Z. funiculosa* Buch.-ham. ex M.A. Lawson, and *Z. incurva* Roxb. in northeastern hills; *Z. mauritiana* Lamk. and *Z. nummularia* (Burm.f.) Wight & Arn. in the drier tracts; *Z. oenoplia* (L.) Mill. and *Z. rugosa* Lamk. in central and eastern India; and *Z. jujuba* Mill. (*Z. vulgaris* Lam.) and *Z. oxyphylla* Edgew. in the northwestern Himalaya region (Singh and Arora 1978; Pareek 1988). *Z. mauritiana* is cultivable ber in drier parts of the Indian subcontinent (Sebastian and Bhandari 1990). Ber is cultivated and found in disturbed areas near

settlements and along the roads in some African countries (Johnston 1972), where fruits are harvested from naturally seeded plantations and sold in local markets. *Z. jujuba* Mill. is cultivated in China, Korea, and in parts of southeast Africa (Lin and Cheng 1995). Ber is considered an underutilized fruit crop in semiarid regions of the world and can be successfully cultivated in the marginal ecosystem of the subtropics and tropics (Pareek 2001).

Z. jujuba Mill. and *Z. mauritiana* Lamk. are the most important species in terms of distribution and economic significance. The former is native of China, where it is known as the Chinese date or Chinese jujube. It is less tropical of the two species, tolerating temperatures as low as −29°C, and is deciduous. *Z. mauritiana* is semideciduous or evergreen, and is commercially most important in India, where it is known as Indian jujube or ber. Ber fruit is a glabrous, globose, or oval edible drupe varying greatly in size from 1 to 2 cm diameter but some oval cultivars can reach 6 × 4 cm. The pulp is acidic and sweet, the fruit is greenish-yellow or sometimes reddish. The Chinese jujube fruit is an ovoid-oblong edible drupe 1.5–2.3 cm long, dark reddish-brown to black, each being short-stalked and may be pendulous and pulp is source to sweet.

Indian ber is a tree with spreading and branching habit (Fig. 5.1). The fruit is a drupe, globose to ovoid in shape, up to 6 × 4 cm in size; skin smooth or rough, glossy, thin but tough, yellowish to reddish or blackish; flesh white, crisp, juicy, sub acid to sweet, becoming mealy

Fig. 5.1. Fruiting ber tree.

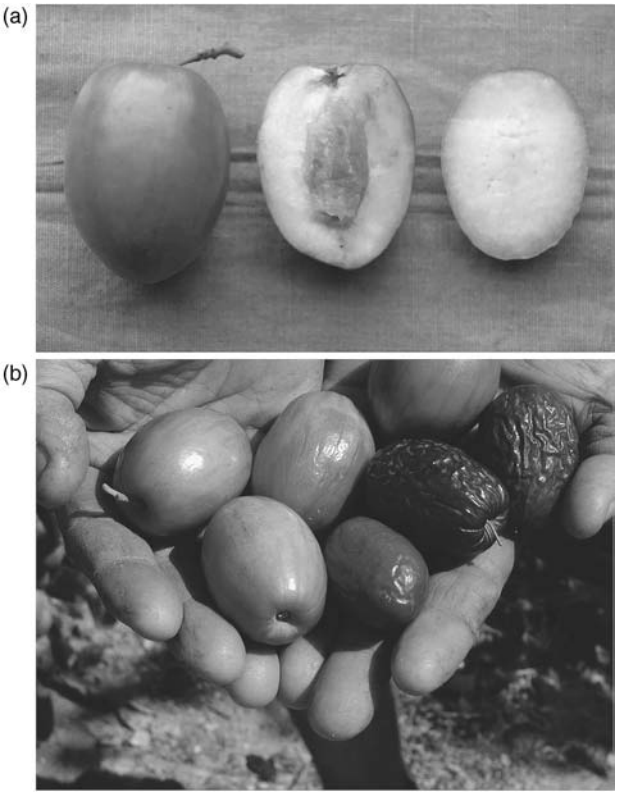

Fig. 5.2. Ber fruits: (a) internal and external appearance; (b) fruits at various stages of ripening.

in fully ripe fruit (Fig. 5.2). Seed is a tuberculate and irregularly furrowed stone, containing 1–2 elliptic brown kernels each 6 mm long. Ber fruit is generally eaten fresh and is a rich source of ascorbic acid, essential minerals, and carbohydrates (Pareek 1983; Abbas et al. 1988; Pareek et al. 2002). It is richer than apple and mango in vitamin C, protein, and minerals, and contains higher phosphorus and iron than orange (Khera and Singh 1976).

Ber is generally eaten as dessert fruit, but has good potential for making processed products such as candy, squash, powder, and syrup (Pareek et al. 2010). Extensive studies have been carried out to prepare various processed products from ber fruit such as candy (Gupta et al. 1980, 1981a,b;

Gupta 1983; Kumar et al. 1992), dehydrated products (Dhawan 1980; Khurdiya 1980a,b; Khurdiya and Roy 1986; Lande et al. 1999), juice and wine (Khurdiya 1980b; Chivero and Mawadza 1998), and shreds and powder (Patil et al. 1999).

In western India, fruit of *Z. nummularia* is dried and powdered with spices to prepare a product called *churn*. A wild species, *Z. oxyphylla* Edgew. (syn. *Z. rotundifolia* DC), is gathered in Pakistan and used as a subsistence food (Saqib and Sultan 1994). In the Zambezi valley in Zimbabwe, *Ziziphus* fruit is eaten fresh from June to September and after dehydration consumed throughout the year (Funkhouser 1998). The dry powder is used in baking and to prepare jam (Maposa and Chisuro 1998), a traditional loaf (Kadzere 1998), and kachaso, a crude spirit (Arndt 2001). An alcoholic drink is also made from the fruit in Malawi and West Africa. *Z. abyssinica* Hochst., a widespread wild African species, is locally cultivated in southern Nigeria. Fruit of *Z. spina-christi* is gathered for use in many parts of West Africa (Hutchinson and Dalziel 1958). Cakes are made out of dried and fermented pulp in Zambia (Kalikiti 1998). In Namibia, wild *Z. mucronata* Willd. is used for making hot liquor (Hailwa 1998).

The *Ziziphus* species are distributed throughout the tropical, subtropical, and temperate regions of both hemispheres (Rendle 1959). Small or large plantations of ber exist in Afghanistan, Iran, Syria, Burma, Australia (Nijjar 1975), France (Evreinoff 1949; Munier 1973), United States (Thomas 1924; Lanham 1926; Riley 1970), and Russia (Mukherjee 1967). Some Mediterranean countries also have ber orchards. The fruit was carried to Europe from Syria by Sextus Pompeius toward the end of the reign of Augustus Caesar, about the beginning of the Christian era, and it soon spread to all countries bordering the shores of the Mediterranean (Bailey 1947).

Ber remained confined to the warmer parts of Italy, France, Spain, and Portugal and in Africa to the northern states of that continent. Its first introduction into the United States at Beaufort, North Carolina, seems to have been done from Europe in 1837 (Lanham 1926). It was introduced to California and neighboring states from southern France in 1876 (Rixford 1917).

The cultivation of ber is said to have started in India when a Muslim grower won a prize by presenting fruits from a budded plant to King Raghoji Bhonsle II (Singh 1964). At present, ber cultivation is practiced all over India. It is estimated that there are about 20,000 ha of ber orchards in India. The major growing states in India are Madhya Pradesh, Bihar, Uttar Pradesh, Punjab, Haryana, Rajasthan, Gujarat, Maharashtra, and Andhra Pradesh. It is also cultivated in Nepal,

Bhutan, Bangladesh, Afghanistan, Sri Lanka, Pakistan, Iran, Iraq, UAE, and other Arabian Gulf countries.

The storage life of ber fruit is very short and its high perishability is a problem. At ambient temperature conditions (15–25°C), a shelf life of 2–4 days is common. Due to the glut of fruits in the local markets during peak season, a substantial quantity is wasted, resulting in heavy postharvest losses (Pareek et al. 2009). The cost and returns analysis show that ber production is highly remunerative, but the highly perishable fruit requires proper handling with respect to preharvest, harvesting and postharvest treatments, packaging, transportation, storage, postharvest pathology, and processing (Salunkhe and Kadam 1995). This review examines the literature related to ber research, much of which have been carried out in India, including important aspects such as nutritional composition, fruit growth and development, chemical variability, maturity indices, respiration and ethylene production, ripening changes, pre- and postharvest treatments to extend the postharvest life, and postharvest diseases, among other important postharvest information.

II. FRUIT COMPOSITION AND NUTRITIONAL VARIABILITY

Much of the data relating to ber fruit are cultivar-specific; however, the information can be summarized to provide a general picture. Ber fruit has a high nutritive value (Table 5.2) and is a rich source of provitamin A, vitamin C and B complex, and also of Ca, K, Br, Rb, and La (Tiwari and Banafar 1995). Galactose, fructose, and glucose are the major sugars found in ber fruit (Muchuweti et al. 2005b). *p*-Hydroxybenzoic, caffeic, ferulic, and *p*-coumaric acids are the most abundant phenolic compounds in ber with concentrations of about 366, 31, 20, and 19 mg kg^{-1} on a dry weight basis, respectively, whereas vanillic acid is the least abundant with a concentration of about 2.5 mg kg^{-1}. Guil-Guerrero et al. (2004) analyzed several ber cultivars from Spain for fatty acid and carotene contents. Tryglycerides having medium chain fatty acids were most abundant in all samples. The main fatty acids were 12:0, 10:0, 18:2 ($n-6$), 16:1 ($n-7$), 16:0, and 18:1 ($n-9$) in total saponifiable oil. The fruit yields about 1.3 g saponifiable oil per 100 g on a dry weight basis. Carotenes were found to be in good agreement with other fruits, varying from 4 to 6 mg per 100 g on a dry weight basis (Guil-Guerrero et al. 2004). Citric, malonic, and malic acids were identified as major organic acids in ber (Muchuweti et al. 2005b). Pareek (1983) recorded 81–97% pulp in fresh, mature fruit, and Jawanda et al. (1980a,b) reported a range of 91–93%.

Table 5.2. Nutritive composition of ber fruit.

Constituents	Amount (per 100 g)
Moisture (g)	81.6–83.0
Protein (g)	0.8
Fat (g)	0.07
Fiber (g)	0.60
Carbohydrates (g)	17.0
Total sugars (g)	5.4–10.5
Reducing sugars (g)	1.4–6.2
Nonreducing sugars (g)	3.2–8.0
Ash (g)	0.3–0.59
Calcium (mg)	25.6
Phosphorus (mg)	26.8
Iron (mg)	0.76–1.8
Carotene (mg)	0.021
Thiamine (mg)	0.02–0.024
Riboflavin (mg)	0.02–0.038
Niacin (mg)	0.7–0.873
Citric acid (mg)	0.2–1.1
Ascorbic acid (mg)	65.8–76.0
Fluoride (ppm)	0.1–0.2
Pectin (% dry basis)	2.2–3.4

Sources: Morton (1987), Pareek and Dhaka (2008), Pareek et al. (2009).

The nutritive richness of the pulp has been widely recognized. Ber is richer than apple in protein, phosphorus, calcium, carotene, and vitamin C (Bakhshi and Singh 1974), and richer than oranges in phosphorus, iron, vitamin C, and carbohydrates, and exceeds them in caloric value. Ripe fruit provides about 21 kcal per 100 g of pulp (Singh et al. 1973). Pulp contains about 12–14% carbohydrates (Singh et al. 1967; Jawanda et al. 1981) of which about 5.6% is sucrose, 1.5% is glucose, 2.1% is fructose, and 1% is starch. Total sugars content differs markedly with cultivar (Singh et al. 1983). The amino acids asparagine, aspartic acid, glycine, glutamic acid, serine, and threonine are found in the pulp (Bal 1981a).

A wide range of variability for quality traits was detected in 30 cultivars of ber (Bisla and Daulta 1986). 'Umran' has about 19% total soluble solids (TSS) and 1.2% acidity. In the case of 'Kathaphal', TSS is about 23% and acidity is about 0.8% while in 'Gola', TSS is about 17–19% and about 0.5% acidity. In 'Kaithli', TSS is about 18% and acidity 0.5% (Daulta and Chauhan 1982). Ber germplasm showed significant variation in physicochemical characteristics of 23 genotypes, and out of them 10 produced fruit of excellent quality (Lal et al. 2003). Variations

in 10 local ber genotypes grown in West Bengal were noted for soluble solids, total sugars, acidity, and ascorbic acid content; ranges of these parameters were 9.5–19.1%, 4.9–12.3%, 0.38–2.60%, and 17.3–52.0 mg per 100 g, respectively (Ghosh and Mitra 2004). Godara (1980) evaluated 16 cultivars for quality characters. The fruit of 'Mundia Murhara' and 'Chhuhara' had the highest TSS content (22.8% and 22.4%, respectively). 'Banarasi Karaka' fruit had the highest nutritive value (Tiwari and Banafar 1995). Some cultivars show variation in acidity (0.23–0.78%) and ascorbic acid (80.9–178.0 mg per 100 g pulp) (Godara 1980). Fruit ascorbic acid content of several cultivars ranged between 70 and 165 mg per 100 g of pulp (Jawanda and Bal 1978). Bisla et al. (1980) observed the highest vitamin C content (120.15 mg per 100 g) in 'Illaichi'. Vitamin C content was highest in 'Narikelee', followed by 'Kaithli', 165 and 125 mg 100 g fruit pulp, respectively (Gupta 1977). Chen et al. (2003) found 'Jinsi 3' and 'Jinsi 4' (both small-fruited) had more than 35% sugar. Gupta et al. (2004) found among the cultivars tested that 'Godhan' was the most nutritive with regard to total soluble solids and ascorbic acid content, whereas 'Kharki' was the sweetest at Hoshangabad, Madhya Pradesh, India. The highest acidity (0.49%) was exhibited by 'Soni', while the lowest acidity (0.25%) was exhibited by 'Kabra' and 'Amrabati'. The highest total sugar content (14.5%) was exhibited by 'Bekanta' and the lowest (8.5%) by 'Karka'. Tomar and Singh (1987) reported that the highest total soluble solids were recorded for 'Umran' and the highest acid content in 'Sanaur 4' in Bhatinda, India.

III. PHYSIOLOGICAL AND BIOCHEMICAL CHANGES DURING MATURATION AND RIPENING

A. Maturity Indices

The time required for ber fruit to develop from fruit set to maturity is dependent on cultivar and location (Table 5.3). Fruits that are allowed to ripen on the tree normally have a shorter shelf life, and the best results are obtained if they are picked before the onset of ripening (Al-Niami and Abbas 1988; Al-Niami et al. 1989; Abbas 1995b). The development of fruit skin color is one of the most reliable maturity indices. Fruits are harvested at the mature golden-yellow stage in 'Umran' (Singh et al. 1981) and 'Kaithli' (Siddiqui and Gupta 1989a), and at the mature green stage in 'Mallasey' and 'Bambawi' (Al-Niami et al. 1992).

Table 5.3. Days from fruit set to maturity in different ber cultivars and species.

Days from fruit set maturity	Cultivar	Reference
65	*Z. rotundifolia*	Joseph and Shanmugavelu (1987)
108	Gola	Singh et al. (1981)
130	Local	Neog et al. (1993)
135	Banarasi Karaka	Pandey et al. (1990)
147	Jogiya	Gupta et al. (1984)
170–180	Kaithali, ZG-2	Jawanda and Bal (1980)
180	Banarasi	Joseph and Shanmugavelu (1987)
	Sanour-2	Bal (1981b)
180–190	Umran	Bal and Singh (1978)
	Umran	Prasad and Babu (1988)

At maturity ber fruit contains sucrose, glucose, and fructose in the ratio of 3:1:1 (Bal 1981a), while TSS, acidity, and ascorbic acid content vary between 12% and 21%, 0.13% and 1.42%, and 39 and 166 mg per 100 g, respectively, on fresh weight basis in different cultivars and regions (Pareek 1983). According to Bhatia and Gupta (1985), TSS, acidity, and TSS:acid ratio at maturity should be 16.7–17.0%, 0.20–0.24%, and 76–84 for 'Gola' and 16.2–17.4%, 0.16–0.17%, and 93–100 for 'Umran', respectively. TSS and polyphenol oxidase (PPO) activity have also been suggested as an index for maturity (Kadam et al. 1993).

Specific gravity is considered a reliable indicator for maturity and harvest, showing a decrease with increasing intercellular spaces. Fruit specific gravity decreased continuously from fruit set to harvest (Bal 1981b), although other reports have indicated that it decreased up to 45 days after fruit set and then stabilized until harvest (Pandey et al. 1990). Values at harvest maturity in 'Kaithli', 'Gola', and 'Umran' fruits have been reported to be 0.88, 0.93, and 0.81, respectively, with corresponding fruit wall pressure values of 2.07, 2.52, and 2.80 N (Bhatia and Gupta 1985). Meel et al. (1991) recommended that fruit of 'Sandhura Narnaul' should have a specific gravity less than 1 for harvest.

Degree-day (DD) heat requirements above a base of 7.2°C for maturity in 'Gola', 'Kaithli', and 'Umran' fruits were 1,980–2,236, 2,236–2,466, and 2,566–2,920, respectively (Gupta et al. 1992). In general, the harvest period in North India is mid February to March for 'Gola', mid March to last week of March for 'Kaithli', and March to April for 'Umran' (Jawanda and Bal 1980; Bhatia and Gupta 1985). Availability periods of ber fruit in India vary from December to March.

B. Physiological Changes

1. Respiration. Ber is characterized as a climacteric fruit on the basis of its pattern of respiratory activity, with the respiration peak preceding the ethylene burst by 1 day (Zhu et al. 2010). It is possible that the high rates of respiration during ber fruit ripening are responsible for the short storage life of the fruit under room temperature conditions (Abbas and Fandi 2002). Rate of respiration of mature green ber fruit of both *Z. mauritiana* and *Z. spina-christi* is low but increases as the fruit matures, reaching a peak value when it enters the ripening phase and then declines rapidly (Abbas 1997). The respiration rate increased from green mature to fully ripe stage, then again declined in overripe fruit (Anuradha et al. 1997). Abbas and Fandi (2002) found that the respiration rate was high 3 weeks after anthesis, but then declined steadily until 12 weeks after anthesis, when it reached 14.2 mg CO_2 kg^{-1} h^{-1}. The rate then began to increase, first slowly and then rapidly to a maximum value of 100.3 mg kg^{-1} h^{-1} as the fruit entered the ripening phase. The rate of CO_2 production declined rapidly as the fruit became overripe. This pattern of respiratory change is characteristic of a climacteric fruit. Contrary to this Kader et al. (1982) observed that respiration rate fluctuated between 15 and 20 mL CO_2 kg^{-1} h^{-1} during 15 days of storage at 20°C, suggesting that ber fruit has a nonclimacteric pattern of respiration. However, at room temperature, a climacteric pattern of respiration was observed by Qiuping and Wenshui (2007). Respiration in control and chitosan-coated fruit began to increase after 1 day of storage at room temperature, where CO_2 production reached a maximum of 54.9 and 53.6 mg kg^{-1} h^{-1} on days 4 and 7, respectively (Qiuping and Wenshui 2007). Singh et al. (1981) observed that on an average the rate of CO_2 production was 52.4 mg kg^{-1} h^{-1} at the green stage and reached up to 127.64 mg kg^{-1} h^{-1} at the red-ripe stage. The rate of respiration at the red-ripe stage among various cultivars was found to be 119.72, 131.54, 137.32, 132.32, and 133.33 mg CO_2 kg^{-1} h^{-1} in 'Umran', 'Rashmi', 'Kaithli', 'ZG-3', and 'Ponda', respectively.

Ber fruits were shown to have a respiration rate of 100.1 mL CO_2 kg^{-1} h^{-1} under ambient conditions and the peak was recorded on the second day of storage (Mishra and Khatkar 2009). Singh et al. (2010) observed a continuous increase in respiratory activity up to the seventh day of storage followed by a decline. Respiratory activity was affected by a coating treatment and storage conditions. The lowest rate of CO_2 production (0.25 mg kg^{-1} h^{-1}) was due to treatment with 1.5% $CaCl_2$ followed by those treated with 1% $CaCl_2$, while it was highest in fruit

without any coating treatment (Singh et al. 2010). Respiration in ber fruit reached a climacteric peak on the third day, but it was significantly inhibited by a 5 μM brassinosteroid treatment (Zhu et al. 2010). Collectively, the data suggest that ber fruit does possess a transient rise in respiration associated with ripening and can be categorized as a climacteric fruit.

2. Ethylene Production. Ber fruit produces high amounts of ethylene and have responses to exogenous ethylene treatments as measured by changes in skin color, juice color, and fruit composition (Kader and Kasmire 1984). The ethylene evolution rate increased from the green mature to the fully ripe stage, and then declined at the overripe stage (Anuradha et al. 1997; Qiuping and Wenshui 2007; Mishra and Khatkar 2009). Gupta et al. (1987) observed that ethylene production increased as the fruit entered the ripening stage, reached a peak, and then declined in the 'Umran' fruit harvested at the color-break stage. A similar trend was also observed in fruit of the cultivar 'Kaithli' by Gupta et al. (1989) and in 'Zaytoni' by Abbas and Saggar (1989). Ber fruit detached from the tree and stored at 20°C have low ethylene production in the mature green stage, but the rate of production increases rapidly as the fruit advances in maturity whereupon it reaches a peak value, then declines rapidly (Abbas 1997). Ethylene production was not detected until the 12*th* week after anthesis and the peak of ethylene production preceded that of CO_2 production by 2 days (Abbas 1995a). It increased rapidly, reaching a maximum of 13 $\mu L\,kg^{-1}\,h^{-1}$ 18 weeks after anthesis and then declined rapidly. Al-Niami et al. (1992) reported that ethylene production increased as the fruit of 'Mallasey' and 'Bambawi' entered the ripening phase. Sharma et al. (2000) also reported that there was no detectable amount of ethylene at the green mature stage (23 weeks after fruit set) but was observed at a later stage. Ethylene rate increased up to full yellow stage (25 weeks after fruit set) and then decreased sharply on further ripening both on the tree as well as in storage in 'Umran' ber. The rise in ethylene coincided with the rise in respiration; however, the magnitude of ethylene evolution was lower during fruit ripening in storage as compared to fruit ripening on the tree. The pattern of ethylene evolution and respiration during ripening confirms the climacteric nature of ber fruit. The rise in ethylene production by ripe ber fruit is considered very high according to the classification of Kader and Kasmire (1984). The rate of ethylene production also had a climacteric pattern during storage at room temperature of *Z. mauritiana* cv. 'Cuimi' (Qiuping and Wenshui 2007). Ethylene evolution peak (85.9 $\mu L\,kg^{-1}\,h^{-1}$) was noted on the second day of storage in control fruit at room

temperature; thereafter, a continuous decrease was observed up to the end of 8 days (26.9 $\mu L\,kg^{-1}\,h^{-1}$) storage (Mishra and Khatkar 2009).

3. Total Soluble Solids. TSS content of the fruit is low during the initial stages of growth, but increases throughout the growth period and reaches a peak in the physiologically mature fruit (Jawanda and Bal 1980; Bal 1981b; Abbas et al. 1988, 1994; Abbas and Saggar 1989). A gradual increase in starch content was observed up to full maturation and then it decreases during ripening in 'Sanaur 2' (Bal 1981a), and in 'Gola', 'Kaithli', and 'Umran' fruit (Bhatia and Gupta 1985), which may contribute to the changes in TSS.

4. Acids. The acid content of the fruit is high during the initial stage of fruit growth and decreased as the fruit matures (Bal and Singh 1978; Bal 1981a; Abbas et al. 1988; Abbas and Saggar 1989). Acidity decreases with advanced maturity. During this period, available organic acids are utilized at faster rate during the respiratory process and thus the acid content decreases considerably (Bal et al. 1995).

5. Ascorbic Acid. Ascorbic acid content of ber fruit is initially low, and continues to increase until the fruit reaches physiological maturity (Abbas 1997). The increase in ascorbic acid with the advancement of ripening reached peak value (559 mg per 100 g) on the 15*th* day of storage at 20°C (Kader et al. 1984). Bal et al. (1995) also noted the increase in vitamin C content as the maturity advanced in 'Umran' fruit.

6. Sugar. Reducing and nonreducing sugars increase up until full maturity (Bal et al. 1979; Jawanda and Bal 1980; Bal 1981a). Total sugars increased gradually up to a certain period of growth and then increased rapidly (Bal and Singh 1978; Jawanda and Bal 1980; Bal 1981a; Gupta et al. 1984; Bhatia and Gupta 1985; Pandey et al. 1990; Kadam et al. 1993). Bal et al. (1979) reported that in 'Umran' fruit sucrose and fructose continued to increase whereas glucose decreased slightly with advancement of ripening. The stages of harvest had a significant effect on total sugars. Delaying fruit picking to later maturity stages resulted in higher sugars afterripening (Bal and Chauhan 1981; Bal 1986). In China, studies on four Indian jujube cultivars ('Gaolangyihao', 'Xinshiji', 'Mizao', 'Miandianchangguo') found that soluble sugars consisted mainly of sucrose, glucose, and fructose (Ling et al. 2008). The sucrose content increased quickly from mid-late stage to ripening, but the rate of sucrose accumulation in 'Gaolangyihao' was faster than that of the other three cultivars. Fructose

and glucose accumulation in 'Gaolangyihao' was similar to that of 'Xinshiji', and fructose content was almost equal to glucose content. The content of fructose was significantly higher than that of glucose in 'Mizao' and 'Miandianchangguo' fruit (Ling et al. 2008).

7. Phenols. Total soluble phenols decrease with the advancement of maturity and ripening (Bal and Singh 1978; Bal 1981b; Al-Niami et al. 1992; Bal et al. 1995). This reduction in phenolic compounds during ripening could be due to its hydrolysis into other compounds or owing to their transformation from a soluble into an insoluble form (Singh et al. 1981). Both on the tree as well as stored 'Umran' fruit had a decrease in total phenols and tannins with the advancement of ripening (Kadam et al. 1993). Total phenolics decreased in Chinese ber fruit after 3 days at 20°C and again increased after 15 days of storage (Kader et al. 1982).

8. Volatiles. The total amount of volatiles was very low in mature green 'Umran' fruit, and fruit at this stage is characterized by the presence of *cis*-3-hexanol, hexanol, and hexanoic acid, while lactones were totally missing (Kovacs et al. 2010). The aroma of yellow (ripe) 'Umran' fruit was characterized by the presence of even carbon number ethyl esters of ethanol and fatty acids ranging in length from C_4 to C_{14}. Different esters (ethyl butyrate, ethyl hexanoate, or ethyl octanoate, -decanoate, -dodecanoate, -tetradecanoate) were present in yellow fruits. The esters with a low carbon chain length have a fruity-floral odor, while those with higher carbon number have a heavy soapy smell. Lactones (gamma-octalactone, gamma-decalactone, gamma-dodecalactone) were present in small amount, which have low odor threshold (Kovacs et al. 2010).

9. Proteins. Soluble protein in fruit on a fresh weight basis ranged from 9.4 to 26.9 $mg\,g^{-1}$ in 42 cultivars of *Z. mauritiana* (Kumar et al. 1999). The number and diversity of free amino acids isolated from fruit pulp of wild taxa and 40 cultivars of *Z. mauritiana* varied (Gill et al. 1997). In wild samples, the number of amino acids per sample was in the range of 4–8. Of the 17 free amino acids represented in wild samples, glutamic acid, amino-butyric acid, threonine, proline, and alanine were well represented. In cultivated ber fruit, the number of amino acids per sample was in the range of 3–10. Of the 22 amino acids quantified in these cultivars, arginine, cysteine, cystine, alanine, and proline were most commonly detected. The amino acids most frequently detected in cultivars (arginine, cysteine, and cystine) were absent in wild taxa. The commonly detected amino acids in wild samples (glutamic acid, amino-

butyric acid, and threonine) were not common in cultivated varieties. 'Umran' fruit has 0.79% protein content that was reported to decrease with the delay in harvesting (Bal et al. 1979). Protein content in 'Umran' and 'Sanaur-2' was high in immature fruit but decreased during maturation (Bal et al. 1978). Gupta et al. (1984) observed that the crude protein content in 'Jogia' decreased rapidly during the first 6 weeks followed by a sharp decrease up to 11 weeks and then a gradual decline until ripening. Total proteins decreased and soluble proteins remained unchanged during ripening on the tree as well as in storage in 'Umran' ber fruit (Sharma 1996). Abbas (1997) found a similar decline in the protein content during development as the fruit becomes physiologically mature, but, in contrast, found that the protein content then rises again to peak value as the fruit enters the ripening phase and finally decreases as the fruit become overripe.

10. Enzymes. The activity of polygalacturonase (PG) and β-D-galactosidase increases with the advancement of ripening of 'Umran' fruit, while the activity of cellulase and pectin methylesterase increases up to the fully ripe stage, and then decreases at the overripe stage, both on the tree as well as in storage (Sharma 1996). The activity of β-D-galactosidase was significantly higher in the mature green 'Umran' ber fruit, and there was no difference between unpeeled and peeled fruit. The high activity of β-D-galactosidase was probably connected to the initiation of ripening (Kovacs et al. 2010). PG activity was not different in mature green and yellow fruit. In the outer part of the fruit (unpeeled), PG activity was significantly higher than peeled fruit. The change in PG activity seems to correlate with the solubilization of pectin in fruit (Kovacs et al. 2010). Ber fruit had a high PG activity, and there was a direct correlation between PG activity and fruit softening (Muchuweti et al. 2005a). Fruit PG activity increased sharply for the first 4 days of storage and reached a maximum value of 4.5-fold higher than initial activity, and then decreased sharply. PG activity in chitosan-coated fruit reached a peak level 3.6-fold higher than the initial activity level after 7 days storage at room temperature. Treatment with the ethylene action inhibitor 1-methylcyclopropene (1-MCP) greatly retarded the rise in PG activity in the first 7 days. The maximum PG levels of 1-MCP and 1-MCP + chitosan-treated fruit were observed on day 13, being 3.0- and 2.6-fold higher than initial levels, respectively (Qiuping and Wenshui 2007).

Increase in peroxidase activity in ber fruit during ripening on the tree and during storage was reported by Kadam et al. (1993). The activities of peroxidase and protease increased, while the activity of amylase

decreased progressively with the advancement of ripening in 'Umaran' ber fruit. The increased activities of peroxidase and protease were responsible for oxidizing phenols and ascorbic acid and decreasing the protein content of fruit, respectively. The activities of polyphenol oxidase and catalase (CAT) first increased up to the fully yellow fruit stage, and then decreased in the later stages of senescence. The activity of catalase was proposed to be linked to changes in respiration and autocatalytic synthesis of ethylene (Sharma 1996).

Ripening of the fruit was associated with increased pectin methylesterase (PME) activity (Bal et al. 1995). Randhawa et al. (1984) reported that artificial ripening of ber fruit with ethephon increased the PME activity. During storage, fruit rotting was reported to partially depend upon the activity of cellulase. A higher activity of this enzyme was thought to promote fruit softening that subsequently promotes fruit decay. In 'Umran' fruit, cellulase activity progressively increased during storage up to 20 days and decreased thereafter (Jawandha et al. 2009a). The cellulase activity is also affected by exogenous application of $CaCl_2$ and GA_3. After 20 days of storage, minimum cellulase activity was recorded in GA_3 (60 ppm)-treated fruit followed by $CaCl_2$ (2%) treatment in 'Umran' ber (Jawandha et al. 2009b).

During plant senescence, lipid membrane peroxidation is the main cause for membrane decomposition (Zhang et al. 2003). Lipoxygenase (LOX) activity is implicated in the onset of membrane lipid peroxidation. LOX activity in Indian jujube fruit increased sharply within the early 4 days, and then remained at high level during 4–7 days storage. LOX activity of chitosan-treated fruit increased slowly during the first 4 days of storage and reached a high peak on day 7, and then decreased. LOX levels of coated and noncoated fruit were completely suppressed by 1-MCP compared to the control throughout 10 days and then increased, reaching a peak value after 13 days of storage at room temperature. Maximum LOX levels in 1-MCP or 1-MCP + chitosan-treated fruit were 15.6% and 13.3% lower than the control and coated fruit, respectively (Qiuping and Wenshui 2007). Sankhla et al. (2006) also observed that 1-MCP-treated fruit of 'Seb' ber had lower LOX activity.

The effect of brassinosteroids (BR) on phenylalanine ammonia-lyase (PAL), PPO, CAT, and superoxide dismutase (SOD) in jujube fruit was reported by Zhu et al. (2010). PAL activity in BR-treated fruit showed a peak on the first day after treatment, and was considerably higher than that of the control fruit. PPO activity in control fruit quickly reached the maximum level on the second day and subsequently dropped. A similar trend was also observed in BR-treated fruit. The control fruit had an

initial increase in CAT activity and a constant decrease afterward. Compared with the control, the increase in CAT activity was higher in BR-treated fruit and was maintained at a higher level. SOD activity declined continuously in control fruit, but there was only a slight decrease in SOD activity in BR-treated fruit (Zhu et al. 2010). The membrane permeability increased, the activity of SOD dropped unsteadily, peroxidase (POD) decreased, and the content of malondialdehyde (MDA) increased during ripening of ber fruit (Cheng-le et al. 2008).

11. Cell Ultrastructure. Kovacs et al. (2010) studied the ultrastructural changes in 'Umran' fruit during ripening and observed that the skin of mature green and yellow fruit consisted of waxy epidermis and a hypodermis with 6–8 cell layers. Cells in this region are flattened and compressed. Intact parenchymatous cells can be found under the hypodermis. Starch granules/grains could be seen in the cells. There were no important differences between mature green and yellow 'Umran' ber fruit according to scanning electron microscopy results. Mesocarp at different ripening stages was associated with the gradual softening of the cell walls. The majority of cells were intact in mature green fruit, but there were no remarkable differences even between neighboring cells. An electron-dense precipitate covered the inner surface of the tonoplast of many cells. Chloroplasts were round and grana were visible, plastoglobuli were rare in this stage, and cell walls were homogeneous. During coloration of the yellow fruit chloroplasts underwent characteristic changes. In the ripe fruit, the number and volume of plastoglobuli increased while the amount of plastid stroma and the stroma thylakoid decreased, the grana disappeared, the density of middle lamellae also decreased, and the three layers in the wall were well distinguishable. The most striking feature was found in the morphology of brown overripe fruit, where the middle lamellae of cell walls broke down, cytoplasm was almost completely destroyed, and the fruit was too soft and not very suitable for eating as fresh fruit (Kovacs et al. 2010).

IV. PREHARVEST TREATMENTS TO EXTEND SHELF LIFE

Weight loss commonly increases with the increase in storage period in ber fruit, but the preharvest use of certain chemicals has been reported to reduce fruit weight loss during storage (Bal et al. 1978; Jawanda et al. 1980a; Bal 1982; Abbas et al. 1990).

A. Calcium Compounds

Efforts have been made to increase shelf life and quality of fruit by using calcium compounds. Ber fruit contains Ca as pectate, carbonate, oxalate, and phosphate (Minamide et al. 1986). Exogenous application of calcium nitrate resulted in reduction of respiration rate (Gupta and Mehta 1988). Preharvest application of 1% $CaNO_3$ at color-turning stage (Gupta et al. 1989; Siddiqui and Gupta 1989b; Siddiqui et al. 1989) and 1.7 g L^{-1} $CaCl_2$ with 1% Teepol 10 days before harvest (Gupta et al. 1987) increased shelf life at room temperature, reduced weight loss, and delayed color development during storage. Jawanda et al. (2009b) also prolonged shelf life in 'Umran' ber fruit for 20 days in storage at 3–5°C and 85–90% RH with preharvest application (at color-break stage) of $CaCl_2$ (2%), and also resulted in minimum cellulase activity and rotting percentage and have also registered high palatability rating as well as high phenolic content. Calcium treatment increased chlorophyll content in ber fruit by maintaining chloroplast membrane integrity and retarding the activities of chlorophyllase and chlorophyll oxidase (Yadav et al. 2003).

B. Growth Regulators

Singh et al. (1989a,b) observed that preharvest spray with 0.03% boron and 0.05% zinc along with 50 ppm NAA on 'Pewandi' ber improved fruit quality. Siddiqui et al. (1989) reported that zinc sulfate at 0.4% and boric acid at 0.1% were more effective than other concentrations on 'Umran' fruit.

Bal and Chauhan (1981) reported advanced ripening by a week in 'Sandhura Narnaul', 'Umran', and 'Gola' with ethephon application. Preharvest spray of ethephon in 'Umran' cultivar increased the TSS and vitamin C and decreased acidity (Chauhan and Gupta 1985; Sandhu et al. 1989). At 400 ppm, ethephon resulted in highest TSS content and also improved the 'Umran' fruit color to golden yellow (Masalkar and Wavhal 1991). Preharvest spray of ethephon at 300 ppm to ber trees induced fruit uniform ripening and fruit harvested at optimum maturity could be stored for up to 40 days at 0–3.3°C and 85–90% RH (Bal et al. 1995).

C. Fungicides

Preharvest sprays with 500 ppm captan, Difolatan, and thiabendazole (TBZ) have been reported to improve the shelf life of 'Kaithli' fruit. The effect of captan was more pronounced in reducing weight loss and that

of TBZ was more pronounced in reducing decay during storage (Gupta et al. 1989). However, the shelf life of 'Gola' fruit was not improved by TBZ (Gupta and Mehta 1987).

V. POSTHARVEST HANDLING AND TECHNOLOGY

A. Fruit Ripening

Some of the postharvest problems of ber fruit include variation in ripening time, failure of immature fruit to ripen after harvest, and poor retention of mature fruit on the tree (Pareek et al. 2009). Ethephon was reported to enhance quick ripening and improvement of ber fruit quality (Bal and Chauhan 1981; Meel et al. 1991; Bal et al. 1992, 1996; Abbas and Fandi 2002). However, the response to ethephon has been variable depending on concentration, cultivar, time of application, and temperature during the ripening period. Kader et al. (1984) found that exposing Chinese ber fruit to 100 ppm ethylene at 20°C for 4 h or dipping in 2,000 ppm ethylene solution for 2 min induces rapid and uniform ripening. Ethephon at 500 mg L^{-1} advanced the ripening by 6–7 days compared with the control. Furthermore, TSS and ascorbic acid content were significantly increased by ethephon treatment, whereas titratable acidity was significantly decreased (Abbas et al. 1994).

B. Grading

Ber fruit may be graded according to maturity, size, shape, and color. At this point in time, proper grading has not been standardized in ber. Ber fruit should be graded into three grades as given in Table 5.4. Grading can either be carried out manually or by passing through sieves of different mesh sizes.

Table 5.4. Grading criteria for ber.

Grade	Standard
A	Shining yellow, large (>35 mm) to medium size (24–35 mm), fruits of uniform size with no blemishes
B	Uneven yellow or yellow red, large (> 35 mm) to medium (25–35 mm) fruits to uniform shape with some blemishes
C	Red, large (>35 mm) to small (<25 mm) fruits. Uneven yellow, small (<25 mm) fruits

Source: Pareek and Gupta (1988).

C. Cold and Hot Water Treatments

Postharvest dipping of ber fruit in cold water reduced respiration, ethylene production, and enzymatic activities, whereas hot water treatment controlled the development of pathogens, thereby prolonging the shelf life and maintained the quality. After harvest, dip treatments of 'Gola' fruit in cold water for 2 h improved their shelf life (Gupta and Mehta 1987).

Hot water dipping treatments did not affect ripening initially, but on the eighth day of storage the ripening was reduced significantly only in the hot water-treated fruit packed in sealed polyethylene bags (Lal et al. 2002). Hot water (40°C) dipping of fruit has been reported to reduce water loss of fruit during storage. The hot water dipping treatment may prevent surface moulds development and decreases decay (Siddiqui and Gupta 1995). Postharvest water dipping at 50°C for 5 min significantly increased the shelf life and maintained the quality of 'Umran' ber fruit, particularly late during a storage period of 8 days. It also retarded enzymatic activity, respiration rate, and activity of postharvest pathogens (Lal et al. 2002).

D. Fungicides

Dipping of fruit in 1–2% of fungicide prolonged the shelf life of 'ZG-3' fruit (Mehta et al. 1985) and reduced weight loss in 'Gola' fruit (Gupta and Mehta 1987). Ripening of harvested 'Umran' fruit was delayed by treatment with $CaCl_2$ (4.5 or 9 g Ca L^{-1}) solution (Siddiqui and Gupta 1989a). Dipping 'Gola' fruit in 500 ppm TBZ, captan, and Dithane M-45 improved the shelf life by reducing the rate of respiration (Siddiqui and Gupta 1988).

E. $KMnO_4$

$KMnO_4$ is an ethylene absorber that reduces ethylene action in storage. Dipping of 'Umran' fruit in 0.05% or 0.1% $KMnO_4$ reduced the decay during storage (Siddiqui and Gupta 1989a). Postharvest dipping of 'Gola' fruit in 1,000 ppm $KMnO_4$ at color-turning stage gave the best result in prolonging the shelf life of fruit to 14 days at room temperature (Ramkrishan and Godara 1994). Fruit of 'Umran' cultivar dipped for 15 min in solution of $KMnO_4$ (0.05%, 0.1%) using Teepol as surfactant reduced weight loss and decay over the control during the sixth day of storage (Siddiqui and Gupta 1995). 'Umran' fruit treated with KMnO4 (5%) and packed in sealed polyethylene bags had the longest shelf life of 9 days, followed by 2.5% $KMnO_4 + 2.5\%$ $Ca(OH)_2$ with sealed polyethylene bags (8 days) (Fageria et al. 2007).

F. Ozone

Ozone is a strong oxidizing agent effectively used to control the growth of microorganisms, oxidizing harmful gases such as ethylene. At normal temperature, ozone delayed decay, reduced respiration rate, and delayed the loss in fruit rigidity and the loss in vitamin C of ber fruit (Yue-hua et al. 2006).

G. Growth Regulators

Plant growth regulators are applied after harvest to hasten or delay uniform ripening, to reduce postharvest decay, to improve the physicochemical characteristics, and to improve the shelf life and keeping quality and marketability of ber fruit (Kudachikar et al. 2000). Treatments with 500 ppm Cycocel (chlormequat) for 15 min (Siddiqui and Gupta 1995), 1,000–2,000 ppm for 10 min (Jain et al. 1979), and 200 ppm (Abbas 1997) have been reported to result in lower weight loss and improvement in quality. Cycocel was found to be more suitable than ascorbic acid and $KMnO_4$ (Siddiqui and Gupta 1995). Siddiqui et al. (1985) and Sandhbhor and Desai (1991) observed that 10–100 ppm benzyladenine reduced weight loss, but increased ethylene evolution in 'Umran' fruit during storage. Postharvest dip in 150 or 300 ppm ascorbic acid solution reduced overripening, increased TSS but had no effect on acidity and ascorbic acid during storage (Siddiqui and Gupta 1988). Postharvest dipping of 'Gola' and 'Umran' fruit in 200 ppm maleic hydrazide increased the marketability percentage and improved the storage life and keeping quality of ripe fruit for up to 12 days (Naik and Rokhade 1994; Bandopadhyay and Sen 1995). Fruit treated with 2% mustard oil with 50 ppm GA_3 stored in perforated polyethylene bags, resulted in reduced weight loss and rotting and better maintenance of physical appearance, color, and quality of fruit for up to 12 days of storage (Meena 1997). GA_3 or Cycocel at 10 and 200 mg L^{-1}, respectively, delayed ripening by 2 days (Abbas 1997). GA_3 at 60 ppm was found to be most satisfactory followed by $CaCl_2$ at 2% as postharvest application to maintain shelf life and quality of 'Umran' fruit (Jawandha et al. 2008). The rate of ethylene evolution by 'Umran' fruit was reduced with the application of ascorbic acid (150 ppm) and Cycocel (500 and 1,000 ppm) throughout the storage period; however, the application of ascorbic acid (300 ppm) and $KMnO_4$ (0.05% and 0.1%) increased ethylene evolution (Siddiqui and Gupta 1995).

H. 1-Methylcyclopropene (1-MCP)

Treatment of 'Seb' ber fruit with 1-MCP (100–400 nL L^{-1}) prevented the decrease in fruit firmness and vitamin C content (Sankhla et al. 2006). 1-MCP-treated fruit remained greener than the control with higher chlorophyll content and lower levels of lipid peroxidation and lipoxigenase activity. In 'Cuimi' ber fruit, 600 nL L^{-1} of 1-MCP, 1.5 g per 100 mL of chitosan, or their combination were effective in retarding senescence during storage at room temperature and 80–90% relative humidity, and in comparison with the control the storage life was extended by 7, 5, and 8 days, respectively. Fruit treated with the combination of 1-MCP and chitosan coating showed better retention of chlorophyll content, TSS, ascorbic acid, and fruit firmness, delayed the climacteric and ethylene evolution, and reduced stem-end rot incidence (Qiuping and Wenshui 2007).

I. Coating

The effect of coating with whey protein concentrate, carboxymethyl cellulose, peanut oil, and bee wax on postharvest life and quality attributes of 'Umran' fruit was studied during storage at ambient (20 ± 1°C, 70 ± 5% RH) and refrigerated (10 ± 1°C, 65 ± 5% RH) storage conditions. The peanut oil-coated fruit had 8 and 16 days of economic shelf life at ambient and refrigerated conditions, respectively (Mishra and Khatkar 2009). The shelf life of fruit lasted for 12 days when coated by an agent made from guar gum, carrageenan, glycerin monostearate, alcohol, and preservatives, and bactericides at room temperature, and lasted for 50 days at 2–5°C (Xiaoning et al. 2006).

J. Irradiation

Irradiation preservation of ber fruit may help delay postharvest ripening and senescence, reduce postharvest spoilage, and extend the shelf life. Ahmed et al. (1972) treated mature, hard green 'Umran-13' fruit with 10, 20, 30, 40, or 50 krad of gamma rays and found that fruits treated with 20–40 krad were relatively firmer and greener than the control during 8 days of storage at room temperature (30 ± 2°C). Irradiation had no detectable adverse effects on taste and flavor of the ripened fruit. Similarly, no significant changes in TSS, titratable acidity, sugars, ascorbic acid, pectic substances, carotenoids, and chlorophyll of the ripe ber fruit occurred as a result of postharvest irradiation (Ahmed et al. 1972). Mature green 'Zaytoni' ber fruits were subjected to gamma

irradiation doses of 0, 10, 30, and 50 krad, and fruits subjected to 30 krad were firmer and greener than nonirradiated control fruit after 6 days of storage (20°C, 85–90% RH), and delayed ripening by 3 days. There was no significant loss in the nutritive value of the fruit due to irradiation (Abbas et al. 1992). Purohit et al. (2003) treated 'Umran' fruit with ultraviolet (UV-C) radiation (4 and 6 h corresponding to 3.6 and 5.4 kJ m^{-2}) and 5 ppm paclobutrazol. Weight loss and rotting were lowest in fruit treated with UV-C radiation for 5.4 kJ m^{-2} + 5 ppm paclobutrazol, following 12 days of storage. Ascorbic acid and TSS were retained in the fruit treated with UV radiation for 5.4 kJ m^{-2} + 5 ppm paclobutrazol.

K. Packaging

Fruit of 'Kaithli' and 'Umran' cultivars packed in hardboard corrugated cartons of 3–9 kg fruit-holding capacity (40 × 45 × 20 cm) with six holes of 1 cm diameter on two sides with a cushion of shredded paper retained good quality for 9–12 days (Gupta et al. 1981c). Decay and weight loss can be reduced by the use of 5 g bleaching powder per kg fruit as a fumigant (Singh and Gupta 1987). Diphenyl impregnated paper lining in boxes improved the shelf life of 'Umran' and 'Gola' fruit (Gupta and Mehta 1987). Paper lining proved a better cushioning material than *Cynodon dactylon* grass (Singh and Gupta 1983). Use of perforated polyethylene bags was recommended for selling ber fruit in local markets (Jain et al. 1979; Jain and Chitkara 1980; Panwar 1981; Sandhbhor et al. 1992; Naik and Rokhade 1996; Lal et al. 2002). Wrapping fruit in brown paper or butter paper followed by bagging in perforated polyethylene promoted storage life and weight loss reduction from fruit of the cultivar 'Narikeli'. The different wrapping materials increased physical barriers to CO_2 and O_2 and maintained a reduced O_2 atmosphere.

For long distance transport (800 km), cardboard containers and mulberry baskets with straw as cushioning material proved to be the best packaging material (Jain and Chitkara 1980). For short distance transport (200 km) of 'Umran' fruit cardboard boxes proved the best resulting in the least weight loss, with the highest losses from the use of gunny bags. Mode of transportation also influenced the fruit weight loss. Transport by rail resulted in lower weight loss than by truck (Anon. 1987). Modified wire-bound boxes, made of cheaper wood, proved better for transporting ber fruit over a distance of 350 km than the traditional boxes (Siddiqui et al. 1993). Small packages of 1–2 kg in perforated polyethylene bags, nylon net bags, and in cardboard

cartons can be used. Fruit are also packed in large packages of 10–20 kg in gunny bags, cloth packages, or wooden or plywood boxes with holes or slits (Pareek and Gupta 1988).

L. Ambient Storage

Ber fruit are commonly stored at ambient/room temperature (25–35°C) from harvest until their consumption. Jawanda et al. (1980a) observed that 'Umran' and 'Sanaur-2' fruit could be stored for up to 10–12 days at room temperature. Panwar (1981) reported that ber fruit remained in marketable condition for about 1 week. Ripe fruit when stored at room temperature without any treatment remained for up to 7 days (Bal 1982). Gupta et al. (1983) observed that shelf life at room temperature was the longest in 'Sanaur-5' followed by 'Ponda', 'Reshmi', and 'Umran'. Pareek and Gupta (1988) observed a shelf life of 'Gola' and 'Kaithli' cultivars at ambient temperature of up to 7 and 10 days, respectively. *Z. spina-christi* fruit could be stored for 6 days at room temperature (Al-Niami and Abbas 1988; Abbas et al. 1990). Golden-yellow ripe fruit of 'Umran' could be stored for about 1 week at 30°C (Anon. 1990). Fruits of 'Gola' were suitable for eating for up to 8 days of storage (Ramkrishan and Godara 1993). Siddiqui and Gupta (1995) observed 38% weight loss, 35.3% overripening, and 13.4% decay loss in 'Umran' fruit at room temperature after 6 days of storage. In contrast, Gupta and Kadam (1995) reported that fruit stored at ambient temperature had a short life of 3 days only. Under ambient conditions, fruit showed high degree of pathological infection and loss in color and could be stored only for 9 days (Nath et al. 1999). Pareek et al. (1999) observed that storage environment did not affect the levels of total sugars in the fruit. It was observed that the fungicides Virosil-Agro (2.5% and 5%) and Bavistin (1%) maintained the original levels of reducing sugars during the storage period. 'Umran' fruit could be stored for up to 8 days at room temperature (Lal et al. 2002).

M. Storage in Zero Energy Cool Chamber

A zero energy cool chamber (ZECC) is designed to enhance the shelf life of fruit and vegetable by lowering the temperature and increasing the relative humidity inside the chamber via passive evaporative cooling (Roy and Khurdiya 1986). Ber fruit of 'Kaithli', 'Umran', and 'Gola' cultivars could be stored in these chambers for 14, 15, and 18 days, respectively (Anon. 1989). Siddiqui and Gupta (1990) stored fruit in these chambers for up to 10 days. Fruit of 'Gola' was in acceptable

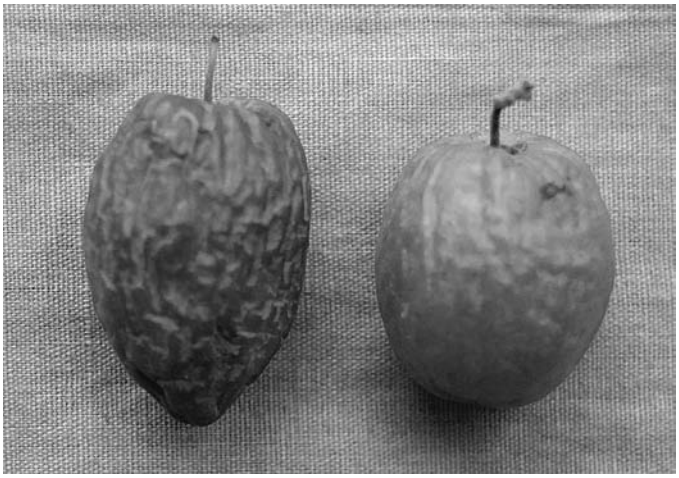

Fig. 5.3. Shriveled ber fruit due to water loss.

condition after 12 days of storage. There was a decrease in fruit firmness, specific gravity, and organoleptic quality with a corresponding increase in acidity of fruit (Ramkrishan and Godara 1993). Fruit weight loss of 10.4% was recorded for 'Umran' after 12 days that were organoleptically acceptable, while weight loss was more than double (24.1%) under ambient temperature (Fig. 5.3) (Fageria et al. 1999; Dhaka et al. 2000). The significant reduction in weight loss under ZECC was due to prevailing higher humidity and lower temperature, which lowered the transpiration rate as well as ethylene production. ZECC + $CaCl_2$ at 1.5% or ZECC alone might be an ideal on-farm storage facility for maintaining the quality of ber fruit under semiarid environment of western India (Singh et al. 2010). 'Gola' fruit treated with 1.5% $CaCl_2$ and stored in ZECC had least weight loss, spoilage loss, respiratory activity, and exhibited 7 days of shelf life (Singh et al. 2010).

N. Low-Temperature Storage

Several researchers have examined the effect of low temperature on postharvest changes and chemical constituents of ber fruit and on their storage behavior (Jawanda et al. 1980b; Jain et al. 1981; Panwar 1981; Al-Niami and Abbas 1988; Abbas and Asker 1989; Al-Niami et al. 1989; Al-Sareh 1989; Kadam et al. 1995). Jawanda et al. (1980b) observed that 'Umran' and 'Sanaur-2' fruit could be stored for up to 30 and 40 days,

respectively, in a commercial cold storage (0–3.3°C). Jain et al. (1981) reported that fruit stored in perforated polyethylene bags and baskets at 13°C retained an acceptable organoleptic quality for up to 3 weeks. Panwar (1981) stored 'Umran' and 'Kaithli' fruit for up to 42 days at 10°C. Shelf life of 'Gola' and 'Kaithli' fruit at 1.7°C was found to be 42 and 28 days, respectively (Pareek and Gupta 1988). In storage at 10°C, 79% RH, 'Gola', 'Kaithli', and 'Umran' fruit remained acceptable for up to 42, 28, and 35 days (Anon. 1989). The golden-yellow ripe fruit of 'Umran' could be stored for about 3 weeks at low temperature ranging from 0 to 4°C (Anon. 1990). Fruit stored at 5°C lost 48% of their weight during 12 weeks storage duration, while the fruit stored at 22°C and 15°C lost 70% and 75% of their weight, respectively. After 3 weeks of storage, more than 40% of the fruit had shriveled at the 22 and 15°C storage temperatures compared to only 3% at the 5°C storage temperature (Tembo et al. 2008). Pareek et al. (2010) reported that best conditions for the maintenance of high organoleptic quality of ber fruit during storage was 7.5°C and 90–95% RH. At this temperature, the fruit developed attractive color and acceptable quality and can be stored for up to 2 weeks. They also observed that fruit stored at 5°C or at lower temperature develop chilling injury on the fifth day of storage. 'Umran' ber fruit stored at 5–8.5°C and 82–85% RH had less weight loss and decay compared to the fruit stored at ambient (17–25°C, 40–65% RH) condition (Meena et al. 2009). Clearly, various preharvest factors (production region, irrigation, and orchard management practices) and postharvest factors (fruit location on tree, maturity stage, harvesttime, and storage conditions) affect storage life and quality of ber fruit.

VI. POSTHARVEST DISEASES AND DISORDERS

A. Disease

Ripened fruits are susceptible to attacks by a various pathogenic fungi and bacteria that are responsible for postharvest diseases. Fruit may be exposed to various decay-causing microflora during packaging, storage, and transport. About 16 fungi belonging to 12 genera have been reported to cause fruit rot in ber fruit during harvest, transit, and storage. Some of the predominant organisms observed on freshly harvested fruit were *Alternaria tenuissima*, *Aspergillus niger*, *A. sydowii*, *Curvularia* spp., *Rhizopus oryzae*, *Penicillium chrysogenum*, and *Phoma* spp.] of which *A. niger* and *R. oryzae* caused the greatest spoilage *in vitro* (Kainsa et al. 1978). Singh and Gupta (1983) found that *Botryodiplodia*

theobromae, Phoma hissarensis, and *Ulocladium chartarum* caused decay losses more frequently in packages. When fruits are weakened by senescence and chilling injury, they are attacked by several pathogens that cause fruit rot (Abbas 1997). A number of minor pathogens include *Geotrichum* spp., *P. herbarum* (Sumbali and Mehrotra 1983), *Phytophthora nicotianae*, and *Sclerotium rolfsii* (Ullasa and Rawal 1986).

The *Alternaria* soft rot starts as light-brown lesions at the site of a cut or incision, and later changes to dark brown or black color with the increase in severity of the symptoms. The outer skin of the spot remains intact but the flesh inside turns dark brown, and appears visibly macerated and water-soaked. As the time of incubation advances rotting penetrates inside the tissue up to the seed in the center and quickly encircles it, emitting a foul smell (Sharma et al. 1983).

Lal et al. (1981) evaluated five fungicides *in vitro* and *in vivo* and found that Bavistin and Difolation performed best and could be recommended as fruit dips at 500 and 1,000 ppm, respectively. Treatment with 1% Bavistin and 5% Virosil reduced both pathological and physiological losses in ambient (30°C) as well as in cold storage (7°C) (Nath et al. 1999). *A. alternata* causes preharvest infection on ber fruit that can result in as much as 25% yield loss (Nallathambi 2001; Nallathambi et al. 2006). Further, the shelf life is reduced as this fungus rapidly colonizes the marketable fruit (Sharma et al. 1993; Nallathambi et al. 1999). Nallathambi et al. (2000) observed fungal pathogens such as *Rhizopus sexualis*, *R. microsporus*, and *R. oligosporus* followed by *Mucerpyriformis*, *A. niger*, *A. flavus*, *A. alternata*, *Trichothecium roseum*, *Tridadium splendens*, *Phoma scrghuia*, *Fusarium culmorum*, and *Penicillium* spp. on stored 'Gola' fruit. However, fruit stored at low temperature (7°C) after treatment with cold water for 30 min, hot water (50°C for 5 or 10 min), and 0.5% calcium chloride suppressed these fungal infections. Fruit stored at room temperature (28 ± 2°C) after treatment with cold water for 15 min, hot water for 5 min, 2,500 ppm Virosil, and 0.5% calcium nitrate had significantly reduced infection rates by 93.3%.

Application of fungicides is a common management strategy to combate the postharvest pathogens on harvested fruits. An alternative fungal control strategy involves the application of isolates of *Trichoderma* spp. from hot-arid regions, fungicides and their combinations were evaluated for the management of ber fruit rot after harvest (Nallathambi et al. 2009). Few of the desert isolates of *Trichoderma* spp. were effective in suppressing ber fruit rot pathogen in both *in vitro* and *in vivo* conditions. Integration of *T. viride* isolate T.v-CIAH240 with several fungicides was very efficient in the control of *A. alternata* in

treated fruit. The latent infection by a few isolates of *Trichoderma* spp. in overripened fruit was suppressed completely when fungicides were added in combination with a bioagent even at low concentration. *A. alternata* can be managed by combined application of *T. viride* (T.v-CIAH240) with an inexpensive fungicide like mancozeb, alcidine, and thiophanate-methyl at low doses of 50–100 $\mu g\, g^{-1}$ (Nallathambi et al. 2009).

Blue mold rot, caused by *P. expansum*, is one of the most important diseases in ber fruit (Qin and Tian 2004). Application of 5 μM brassinosteroids effectively reduced incidence of blue mold rot by stimulating defence-related enzymes, such as phenylalanine ammonia-lyase, polyphenol oxidase, catalase, and superoxide dismutase (Zhu et al. 2010).

B. Disorders

1. Fruit Cracking. Considerable reduction in yield and quality of ber fruit occurs due to preharvest physiological disorders like fruit cracking, fruit skin discoloration, and fruit drop (Kudachikar et al. 2000). These disorders pose serious problems during fruit development. Preliminary studies on the mechanism of fruit cracking in three cultivars indicated that susceptibility increases at maturity, which appears to be due to accumulation of soluble sugars, a decrease in water potential, and a decline in peel toughness. 'Huping Zao' was the most susceptible cultivar, followed by 'Heiye Zao' and 'Lang Zao'. Further studies revealed that all cultivars were susceptible to fruit cracking and the elasticity and plasticity nature of the fruit flesh was the main cause (Li and Gao 1990).

2. Chilling Injury. Being a subtropical fruit, ber is very susceptible to low-temperature injury. The common physiological disorder in ber fruit is pitting (Al-Sareh 1989; Abbas 1995b). Chilling injury symptoms are dependent upon the storage temperature, as well as the duration of these temperatures. These symptoms were greater in fruit held at 0°C than those at 4°C; in addition they become more serious as the time of the storage at 0–4°C was extended. Surface pitting appeared after 5, 7, and 15 days at 0, 4, and 10°C (Abbas 1997).

VII. SUMMARY AND FUTURE PROSPECTS

Ber is grown for its edible fruit in hot dry areas of the tropics and the subtropics and a good source of vitamin C. Fruits are eaten fresh, dried

as dessert, or candied and preserved in various ways. Compared to other fruit trees, ber provides nutritious fruit at relatively low cost, but they remain underutilized despite their multiple uses. In many areas, fruits are still gathered from wild stands. A great deal of know-how exists on production techniques for Indian jujube and Chinese jujube, but most of this information has not been transferred through extension agencies.

Research and development studies on ber were limited until the 1960s to cultivar trials and vegetative propagation studies in the states of Punjab and Uttar Pradesh in India. Since that time studies have expanded much more widely and addressed all aspects of ber cultivation, harvesting, grading, packaging, and processing. Research in India has been paralleled by some research in Pakistan, Bangladesh, and a number of countries in Africa.

Studies on harvesting, grading, and packaging of fruit have resulted in a number of recommendations for growers and packers. However, standard grading related to end use has hardly been implemented and more research is needed, not only on the economics along the production to consumption chain but also on the socioeconomic benefits particularly those affecting the well-being of family producers.

Ber fruit has a climacteric respiration behavior. Various maturity indices have been characterized including color, total soluble solids, days from full bloom to maturity. The postharvest quality and shelf life of ber fruit are influenced by both pre- and postharvest factors particularly plant growth regulators, stage of maturity, composition of fruit, storage conditions, storage type, and packaging. Low storage temperatures (6–10°C) can extend the shelf life beyond 2–3 weeks, but chilling injury is a serious problem. Therefore, some treatments to reduce chilling injury such as salicylic acid, acetylsalicylic acid, 1-MCP, brassinosteroids, and polyamines need to be tested at low temperatures.

Standardized conditions for commercial storages have yet to be developed. Controlled and modified atmospheres have not been commercially applied. More attention should be focused on characterizing the physiology of ber fruit, including ripening, gene expression, protein synthesis, and regulation of enzymes catalyzing sugar formation and translocation. Reliable maturity and international standards, with respect to quality, should be developed. In order to extend the storage period, delay ripening, and maintain fruit quality, low-temperature storage in combination with controlled and modified atmospheres should be evaluated along with methods of ethylene control. Furthermore, additional studies are needed to develop processing of ber.

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Peach Texture

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ABSTRACT

For several thousand years, the peach, *Prunus persica* (L.) Batsch, has undergone extensive development through selection and breeding, resulting in the delectable fruit as we know it today. Depending on cultural background and other factors, the peach "we know" may be yellow and soft with high acidity and pubescence, white and firm with low acidity and smooth skin, or even blood red and crisp with a flat shape. Growing consumer demand for the availability of a wider variety of types of fruits and vegetables has led to peaches with extensive variation in texture appearing on retail market shelves. This texture variation brings about significant challenges for producers, marketers, and even consumers. Harvest maturity, rate of ripening, postharvest performance, bruising, and many other factors change as texture changes. By understanding the biochemical, genetic, and physiological bases of peach texture and texture-related postharvest disorders, and knowing the textures currently in production and development, breeders as well as others involved in the peach industry will be provided the means for developing and producing high-quality cultivars, thereby increasing peach consumption.

KEYWORDS: fruit breeding; mealiness; melting flesh; nonmelting flesh; polygalacturonase; *Prunus persica*; slow ripening; stony hard

Horticultural Reviews, Volume 41, First Edition. Edited by Jules Janick.
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ABBREVIATIONS

ACC	1-Aminocyclopropane-1-carboxylic acid
ACO	1-Aminocyclopropane-1-carboxylic acid oxidase
ACS	1-Aminocyclopropane-1-carboxylic acid synthase

AFLP	Amplified fragment length polymorphism
AVG	Aminoethoxyvinylglycine
CA	Controlled atmosphere
CI	Chilling injury
EDTA	Ethylenediamine-tetra-acetic acid
EGase	β-(1,4)-Glucanase
EJC	Extractable juice content
EndoPG	Endopolygalacturonase
ExoPG	Exopolygalacturonase
MCP	1-Methylcyclopropene
MF	Melting flesh
NIR	Near infrared
NMF	Nonmelting flesh
NSF	Nonsoftening flesh
PCR	Polymerase chain reaction
PG	Polygalacturonase
PME	Pectin methylesterase
RFLP	Restriction fragment length polymorphism
SH	Stony hard
SMF	Slow-melting flesh
SR	Slow ripening
SSC	Soluble solids concentration
TA	Titratable acidity
USDA	U.S. Department of Agriculture

I. INTRODUCTION

Peach, *Prunus persica* (L.) Batsch, is a diploid ($2n = 16$), temperate tree fruit native to China (Monet and Bassi 2008). Archaeological work at a Neolithic village site in the Chinese province of Zhejiang uncovered wild peach pits projected to be 8,000–9,000 years old (Huang et al. 2008). Peach cultivation can be traced back almost 4,000 years through ancient Chinese texts, with the first descriptions of local selections appearing more than 2,000 years ago (Huang et al. 2008). For a review of the origin and dissemination of the peach, see Faust and Timon (1995).

The peach fruit is a drupe that is pubescent or glabrous with a fleshy mesocarp and a very hard (stony) endocarp that is pitted and furrowed (Bassi and Monet 2008). Although the nectarine, peaches' smooth-skin mutant, has subtle differences (e.g., flavor and size) from the peach, the term "peach" is commonly used to refer to both fruit types. Currently, all

commercially grown peaches are *P. persica* (Scorza 2004). The biochemistry, physiology, and genetics of peaches and nectarines are very similar. Excluding skin pubescence, differences within nectarine cultivars themselves are likely as significant as differences among peach and nectarine cultivars (Brady 1993). The wide appeal of the fresh fruit and its quality as a preserved product has facilitated the rapid spread of peach to and across Europe. By the 18th century, *P. persica* had become established in the United States (Crisosto and Kader 2000). In 2010, the top five peach and nectarine producing countries in millions of tonnes (Mt) were China (10.7), Italy (1.6), Spain (1.1), the United States (1.0), and Greece (0.6) (FAO 2010).

The primary goal of breeders, food scientists, producers, distributors, and marketers is the consumer acceptance of fresh and processed peaches (Sistrunk 1985). With U.S. annual per capita utilization of fresh peaches and nectarines at approximately 2.0 kg, peach ranks significantly lower in fresh utilization than several other common fruits including apples (7.4 kg), bananas (11.2 kg), and oranges (4.1 kg) (USCB 2012). In 1987, 24% of U.S. consumers listed peaches as a favorite snack, but by 1991, only 11% considered it a favorite (Bruhn et al. 1991). In their 1991 survey, Bruhn et al. (1991) found that 30% of consumers were dissatisfied with fresh peaches due to too little flavor, while 21% were dissatisfied due to excessive firmness. This trend has been attributed to consumer objections due to poor quality including excessive or insufficient fruit firmness, lack of flavor, low soluble solids concentration (SSC) (i.e., sweetness), and lack of aroma (Crisosto and Kader 2000; Crisosto 2002, 2006; Crisosto et al. 2003; Scorza et al. 2004; Byrne 2005, 2012).

Peach production is divided between fresh and processing markets, although more than 90% of world production is for the fresh market (Byrne et al. 2012). From 1980 to 1992 alone, 475 fresh-market peach, 287 fresh-market nectarine, and 80 processing peach cultivars were introduced worldwide (Bacon 2004; Infante et al. 2006). Within the peach industry there is a trend toward the planting of new cultivars, with over 70% of peach trees sold from 1999 to 2002 being cultivars less than 10 years old. Although yellow, standard-acid, soft-flesh peaches still predominate, the crop area of nontraditional types with atypical flesh color, acidity, shape, and flesh type is increasing (Infante et al. 2006).

Within stone fruit breeding programs, there is a trend toward developing new fruit types and improved postharvest traits, both of which are highly correlated with fruit texture (Byrne 2005). Unlike apples and bananas, peaches are generally not considered to be a convenient fruit

(Jaeger 2006). The inconvenience of the peach fruit, particularly its soft, easily bruised flesh, short storage life, and high incidence of damage from cold storage, has contributed to its flat consumption trend in recent years (Crisosto 2006; Crisosto and Valero 2008; Okie et al. 2008). By understanding the biochemical, genetic, and physiological bases of texture, breeders as well as others involved in the peach industry will be provided the means for developing and producing new cultivars that are of high quality and convenient for consumers, thereby increasing peach consumption.

II. FRUIT TEXTURE

A. Defining Fruit Texture

Texture refers to a wide range of attributes that determine "mouth-feel" and can be measured using sensory and instrumental methods (Harker et al. 1997). Texture is frequently mechanically defined by force, deformation, and elasticity (Abbott et al. 1984). Elasticity is the "rate of change of force with respect to deformation, often calculated as slope from the initial straight portion of a compression force/deformation curve" (Abbott et al. 1984). Additionally, texture is defined as "all physical characteristics sensed by the feeling of touch that are related to deformation under applied forces and are measured objectively in terms of force, distance, and time" (Jackman and Stanley 1995). When describing texture, the terms firmness, flesh firmness, and fruit firmness are widely used by food scientists and horticulturists. Traditionally, horticulturists describe the mechanical properties of fruit tissue as firmness. Fruit firmness can be defined as the force required to compress a fruit tissue sample between the back teeth (Lopez et al. 2011). The texture of fruit has been referred to as hard, soft, crisp, juicy, melting, floury, and gritty, among others (Harker et al. 1997).

Several other terms commonly used to define fruit texture include crispness (the sound sensation when a sample is chewed and the resistance to deformation under load up to the point of sudden fracture), fibrousness (the presence and feel of fibrous structures detected during chewing), juiciness (the amount and perception of juice released by the sample while chewing), and toughness (the resistance to breakdown when chewed) (Abbott et al. 1984; Bourne 2002; Lopez et al. 2011). Consumer perception of texture is determined by many factors, not the least of which are socially and culturally learned expectations, socioeconomic status, and even

gender; however, texture is generally inconspicuous unless it is unexpected, which is usually taken as a sign of poor quality (Szczesniak and Kahn 1971; Jackman and Stanley 1995). Even if a fruit has a high level of flavor, when texture is poor, flavor is irrelevant (Harker et al. 1997). Consumer studies conducted by Abbott et al. (1984) found that crisp, hard, and tough were positively correlated and that relationships of mealy, juicy, and spongy to crisp, hard, and tough were inconsistent, varying among cultivars and panelists. There are many reviews of various aspects of fruit texture (Jackman and Stanley 1995; Harker et al. 1997; Redgwell and Fischer 2002), fruit softening/ripening (Poovaiah et al. 1988; Wakabayashi 2000; Payasi and Sanwal 2010), and cell wall composition and metabolism (Huber 1983; Fischer and Bennett 1991; Vicente et al. 2007).

The fruit industry often imposes regulations based on texture measurements, usually firmness, to facilitate quality management and marketing. The idea behind such regulations is that by requiring specific fruit firmness at harvest and during transportation and storage, consumers will be provided with a uniform, high-quality product. Although these regulations are imposed with good intentions, inadequate firmness measurement standardizations and the lack of correlation between high-quality appearance and high-quality flavor as well as perceived texture can limit the effectiveness of such regulatory efforts (Harker et al. 1997). An additional challenge is defining quality. Quality is comprised of many different properties acting dependently as well as independently. In general, the quality of fruit includes its sensory properties such as appearance, aroma, and taste, as well as nutritive values, mechanical properties, functional properties, and texture, which plays a sensory role as well as a mechanical and functional role (Abbott 1999). For a full review of the measurement of quality in fruits and vegetables, see Abbott (1999).

B. Fruit Texture on a Cellular Level

Jackman and Stanley (1995) reviewed many of the cellular aspects that contribute to texture in foods. The structural integrity of the cell wall and middle lamella as well as the turgor pressure within cells contributes to the texture of plant-based food, specifically fruit (Jackman and Stanley 1995). Turgor pressure provides the hydrostatic component of cell and tissue strength and therefore influences the firmness of ripening fruit (Huber 1983; Harker et al. 1997). As fruits are composed of living cells, texture is affected by the characteristics of these cells. During storage and ripening (physiological and biochemical processes),

textural aspects change at a cellular level. These changes can make the assessment of texture a challenge (Harker et al. 1997).

Juiciness is important as it relates directly with the perception of texture (Szczesniak and Kahn 1984). Juiciness can be defined as the weight or percentage of juice extractable from a fixed weight of fruit tissue (Harker et al. 1997). Although the water content of a tissue dictates its juiciness, the perceived juiciness is attributed to the ability of a cell to release free juice (Szczesniak and Ilker 1988).

1. Cell Walls. In most fruits, the flesh is primarily composed of parenchyma cells, which have thin, nonlignified walls and a large vacuole (Harker et al. 1997). Cell walls are separated by the middle lamella, a region rich in subunits of pectin, a high molecular weight, acidic, complex polysaccharide (Huber 1983; Jayani et al. 2005). Texture, in a broad sense, is dependent upon the attributes of the parenchyma cells and the middle lamella including cell size, wall thickness, turgor pressure, adhesion, and shape, and upon nonparenchyma cells, for example, collenchyma cells, phloem and xylem elements, and epidermal cells (Harker et al. 1997). The properties of the fruit primary cell wall are a result of the mixture of matrix (pectic and hemicellulosic) polysaccharides, cellulose microfibrils, glycoproteins, and water (Huber 1983; Fischer and Bennett 1991; Harker et al. 1997; Redgwell and Fischer 2002). In molecular form, the five polysaccharides that make up 90% of the cell wall are rhamnogalacturonans, xyloglucans, galactoglucomannans, glucuronoarabinozylans, and cellulose, with rhamnogalacturonans (pectic polysaccharides) accounting for 40–60% of the total (Redgwell and Fischer 2002). Variation in texture can be attributed to the process of cells separating or breaking, which is determined by cell wall strength (structural integrity) and cell-to-cell adhesion (Harker et al. 1997). Studying soft and crisp fruit, Redgwell et al. (1997) found that cell wall swelling was pronounced in ripened soft fruit of avocado, blackberry, and strawberry, but not in ripened crisp fruit such as apple and watermelon. Redgwell et al. (1997) suggested that wall swelling occurred as a result of changes to the cell wall during pectin solubilization. During ripening, most fruit cell walls increase in soluble pectin and decrease in noncellulosic neutral sugars due to solubilization, degradation, or polymerization (Fischer and Bennett 1991; Harker et al. 1997). For a specific review of cell wall changes in peaches during ripening, see Ben-Arie et al. (1989).

2. Membranes. Membrane integrity plays a role in fruit texture (Harker et al. 1997). The plasma membrane separates the intracellular

and extracellular compartments of plant tissues and partially regulates the transportation of various materials including enzymes. The plasma membrane plays a key role in the assembly and degradation of the cell wall and osmoregulation, turgor pressure, and ionic composition of extracellular solution (Harker et al. 1997). As a general rule, during ripening, membrane conductivity (permeability) increases (Harker and Maindonald 1994; Harker et al. 1997). Membrane and cell wall changes can occur simultaneously making it challenging to separate their influences on fruit texture (Harker et al. 1997). The structure and role of membranes in relationship to food quality have been reviewed by Huber (1983), Fischer and Bennett (1991), Stanley and Parkin (1991), and Vicente et al. (2007).

C. Evaluating Fruit Texture

The question "Are we measuring what we think we are measuring?" proposed by Jackman and Stanley (1995) highlights the challenge of accurately evaluating texture. Measuring texture is essential in assessing fruit maturity and quality and is important in various areas of fruit research. Assessment of texture usually involves instrumental and/or sensory measurements. The usefulness of instrumental measurements depends on their correlation with sensory attributes, and they are also used to test fruit characteristics that may not be directly associated with consumer acceptability such as harvest maturity (Harker et al. 1997). The study and understanding of the influence of environment, pre- and postharvest factors, breeding, and other factors on texture is based in part on the development of instrumental texture measurement technologies (Harker et al. 1997). The texture of fruit is both elastic and viscous; therefore, its changes, natural or induced (e.g., ripening or under force), are time dependent. This characteristic of texture greatly affects the strategy and capacity of its measurement (Harker et al. 1997).

Several tools and methods can be used to measure changes in fruit texture, with detailed reviews of methods and instruments provided by Abbott (1999) and Bourne (2002). Several standard mechanical tests have been used extensively including pressure and compression testing, and shear and extrusion testing, among others (Harker et al. 1997). Although routinely used, the standard destructive-type tests result in highly variable data due to both physiological and operational factors. Therefore, it is recommended that a combination of multiple, multivariable mechanical measurements based on different principles and that measure properties of differing scale be used for accuracy and

reproducibility (Abbott et al. 1984; Jackman and Stanley 1995). Today, several companies specialize in the production of destructive and nondestructive texture analyzers that use various technologies such as pressure testing, compression, spectroscopy, and proprietary measurement techniques.

III. PEACH TEXTURE

A. Introduction to Peach Texture

There is wide variability in texture of peach grown around the world, especially in regions with extensive domestic production and consumption. Regional preferences such as the North American demand for yellow melting flesh (MF) peaches, the Latin American demand for yellow nonmelting flesh (NMF) (Fig. 6.1a), and the Chinese demand for white MF explain the diversity of peach texture in commerce (Hesse 1975; Byrne 2002, 2005; Monet and Bassi 2008). But, the increased worldwide demand beginning in the 1960s for standardized peach fruit that can withstand harvest and transportation has limited the diversity of peach texture within the commercial market (Hesse 1975).

'Chinese Cling' ('Shanghai Shui Mi') was introduced into the United States in the 1850s and formed the basis of the U.S. peach industry (Okie et al. 2008). 'Elberta', an offspring of 'Chinese Cling', in particular was responsible for the contemporary peach industry and expanded production areas in the early 1900s due to its superior shipping characteristics not previously found in fresh-market peaches. Not only did the texture (firmness) of 'Elberta' or its widely grown progeny 'J.H. Hale' contribute to the modern peach shipping industry, it was also transferred to future cultivars through extensive crossing (Myers et al. 1989; Okie et al. 2008). Thanks to 'Elberta' and the advent of superior harvest, transport, and storage technologies, the globalization of the peach market and the growing demand for new products beginning in the 1980s encouraged the development of a large number of new cultivars and production of nonstandard peach types (Hesse 1975; Byrne 2002, 2005, 2012). Shewfelt et al. (1987) found that firmness was still the most limiting quality attribute in the postharvest handling system. A recent study on U.S. peach breeding priorities found that firmness was one of the most important characteristics in terms of cultivar development and selection, preceded by only appearance, yield, and date of ripening (Gallardo et al. 2012). Among breeders, it was perceived that emphasis

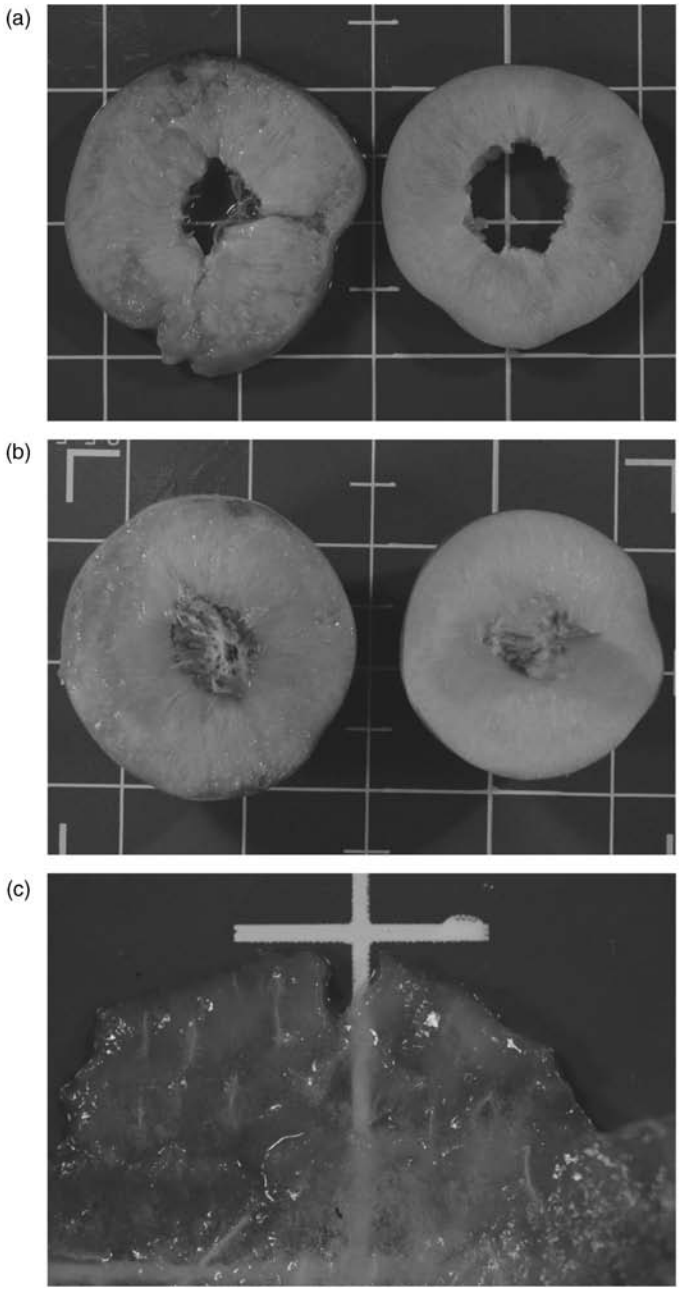

Fig. 6.1. Peach fresh types: (a) melting flesh (left), nonmelting flesh (right); (b) pit adherence, freestone (left); clingstone (right); (c) mealiness gel formation in melting flesh peach. Photographs by P. Sandefur.

on selection for fruit texture was encouraged by both producers and marketers and that selecting new cultivars with improved firmness was limited by the lack of genetic information and available germplasm (Gallardo et al. 2012). Since the early days of peach breeding, breeders have been selecting for increased fruit firmness, with cultivars showing a gradual increase in firmness over time (Scorza 2004). Although breeders may have selected less intensely for taste and adaptability compared to firmness and attractiveness, improving these commercial characteristics was deemed necessary (Monet and Bassi 2008).

According to Crisosto (1994), "stone fruit quality is a combination of attributes and properties that give them value in terms of human consumption." To growers, appearance is essential, to distributors, firmness and storage performance are key, and to consumers, appearance and flavor (quality) are vital (Crisosto 1994). Varying consumer preference for texture types challenges the industry (Sistrunk 1985). Firmness can influence the perception of other aspects of fruit quality such as flavor (Sistrunk 1985). Reeves and Cummings (1970) suggested that it would be logical to assume that the firmest peaches would have the longest shelf-life, but 42 years later, this assumption has been discredited as increased firmness and increased shelf-life are not necessarily correlated. The maturity of peaches can dramatically affect their quality as processed products including characteristics such as drained weight, discoloration, and taste, with most consumers preferring an advanced degree of maturity, but this is complicated by the large variation for firmness that is found at maturity among peach cultivars (Kader et al. 1982; Sistrunk 1985; Iglesias and Echeverría 2009).

B. Measuring Peach Texture

The various aspects of peach texture cannot be fully described without first discussing peach texture measurement. Flesh firmness is frequently used as an indicator of maturity in stone fruit (Lill et al. 1989). Firmness (finger feel) is important for consumers, with fruit that is too firm perceived as under-ripe, and fruit that is too soft perceived as overripe. Consumers generally use sight and touch as the first means of rating a fruit's quality (Sistrunk 1985). Texture of fresh peaches is arguably as important as flavor and aroma for consumers (Sistrunk 1985). But, even with large numbers of fruit sampled, fruit-to-fruit variability makes firmness determination a major challenge, and fruit softening can vary dramatically according to the point of firmness measurement on the fruit, with the suture, tip, or shoulder softening first depending on cultivar (Luchsinger and Reginato 2001; Scorza 2004).

1. Destructive Testing. Magness and Taylor (1925) were the first to publish regarding the use of puncture testing for texture/firmness determination on peaches. Since its development, the puncture test (also referred to as the Magness and Taylor or Effegi test) continues to be the most widely used instrumental method for measuring fruit texture (Sistrunk 1985; Harker et al. 1997). As early as 1957, it was concluded that firmness measured by a pressure tester was the best single index of peach fruit quality (Rood 1957). Abbott et al. (1976) found that after adjusting for operator and instrument, comparable penetrometer firmness readings could be measured with Magness and Taylor, Effegi, and Instron® instruments. Many researchers have recommended specific fruit firmness values based on penetrometer measurements to facilitate proper harvest for quality fruit, but variation in peach texture due to cultivar, maturity, or other factors makes consistency very difficult (Rood 1957; Visagie and Eksteen 1981; Visagie 1984; Sistrunk 1985; Lill et al. 1989). Maness et al. (1992b) concluded, based on variable Instron penetrometer firmness readings within the inner, middle, and outer regions of the mesocarp, that average whole fruit firmness determinations alone do not accurately reflect the firmness of localized individual fruit tissues. Although the accuracy of penetrometer measurements has been questioned, they are frequently used in current research on texture. Murrillo et al. (1997) used a wire probe installed on an Instron machine to generate a force–displacement response from a cylindrical peach tissue core. This response was transferred to the frequency domain and used to measure peach crunchiness (Murrillo et al. 1997). Additionally, compression testing on peach flesh tissue plugs has also been used as a method for determining firmness (Aggarwal et al. 2005).

Flesh and skin color has been used to predict fruit firmness. Lewallen and Marini (2003) concluded in their study that skin ground color alone is not a good indicator of fruit firmness (maturity) as light hue angle (light environment) significantly affected skin color and firmness. Penetrometer firmness measurements have also been frequently used to gauge peach maturity, but along with other types of pressure testing, the ratio of SSC to titratable acidity (TA) has been reported as a good indicator of maturity. Sistrunk (1985) suggested that maturity could accurately be determined using a ratio of SSC to TA and either firmness or background color, although Crisosto (1994) found that wide variation of SSC within fruit and within trees limited its usefulness in maturity determination. Delwiche and Baumgardner (1985) concluded that in the cultivars tested, background color, specifically the Hunter tristimulus 'a' parameter (positive a = red; negative a = green) value

from a colorimeter correlated well with maturity, although this was only tested on yellow-flesh cultivars (Byrne et al. 1991). Byrne et al. (1991) found that fruit firmness was well correlated with 'a' color values from both skin and flesh and that flesh values were less variable than skin values, likely due to the skin's red over-color. It has been found that although ground color and fruit firmness measurements can independently be used to determine fruit maturity, a combination of ground color and firmness measurements is superior (Visagie and Eksteen 1981; Visagie 1984; Crisosto 1994). This is especially true in cultivars with high levels of blush that can mask ground color and in production regions where climatic conditions and cultural practices can dramatically impact firmness (Crisosto 1994).

2. Nondestructive Testing. Crisosto (1994) predicted the development of technologies such as near infrared (NIR), magnetic resonance, light transmittance, and sound detection that could lead to a reliable, nondestructive maturity index for the peach industry. Several nondestructive methods for measuring peach maturity have been tested, including impact response, NIR spectra, acoustic, and optic and image techniques. It was found that optical reflectance (from pigments) when properly optimized could accurately grade peaches into commercial maturity classes (Lleó et al. 2008).

Light transmission measurements have been reported as good indicators of maturity. Watada et al. (1976) demonstrated specific light transmission measurements as the first nondestructive flesh firmness measurement technique. Harker and Dunlop (1994) found that by using electrical impedance techniques, measurements could be made to determine fruit maturity. Hyperspectral scattering using specific wavelengths has also been shown to be potentially useful for the rapid and nondestructive estimation of peach firmness, although a combination of 10 or 11 wavelengths was required to obtain accurate predictions (Lu and Peng 2006). Although NIR spectroscopy has been tested for predicting peach firmness, it was found that its accuracy was not high enough for commercial application by Peano et al. (2006), but Zerbini et al. (2006), Tijskens et al. (2007), and Ziosi et al. (2007b) were able to improve the accuracy of spectroscopy to an acceptable level compared to penetrometer firmness. Vanoli et al. (2007) confirmed that time-resolved reflectance spectroscopy (670 nm absorption coefficient) can be used as an effective index of biological age of nectarines and to predict the rate of fruit softening during ripening. Although a newer device, the Sinclair iQ^{TM} firmness tester, was found to successfully group peaches into commercially important maturity classes,

correlations with penetrometer firmness measurements were low; therefore, it was concluded that the Sinclair device measures a different physical fruit property (tissue elasticity) than the penetrometer (tissue failure) (Valero et al. 2007).

Delwiche et al. (1987) tested several different types of impact force as means of determining firmness and found that they were correlated with the pressure test and could be used to differentiate maturity among different cultivars. Based on this initial work, Delwiche et al. (1989) developed a firmness sorting machine based on impact force response. Although only 74% of peaches tested were sorted correctly into maturity (firmness) groups, the machine required minimal fruit handling, functioned at a commercially acceptable sorting rate, and was the first commercial-grade machine for flesh firmness-based sorting (Delwiche et al. 1989). Scorza et al. (2004) conducted postharvest softening evaluations using a drop-test device that produced repeated measurements on the same fruits during storage. The drop-test device successfully evaluated the effects of harvest stage on postharvest softening and was determined to be a valuable tool for nondestructively evaluating fruit firmness (Scorza et al. 2004). Using a drop test and piezoelectric film sensors, dynamic response characteristics of peach were successfully used to detect firmness at a rate that could successfully be used in a commercial sorting facility (Wang et al. 2006, 2009). Yurtlu (2012) compared low mass impact and acoustic impulse response methods to penetrometer firmness measurements and found a significant, although minimal relationship. Although these nondestructive devices can be used to gauge firmness, they measure a different physical property (tissue elasticity) than the penetrometer (Yurtlu 2012). Diezma-Iglesias et al. (2006) successfully correlated the impact test and an acoustic firmness measurement test with penetrometer testing, and determined that the nondestructive tests were successfully able to differentiate two firmness classes 90% of the time.

Zhang et al. (1994) tested correlations between Effegi penetrometer firmness testing and impact parameters, sonic impulse parameters, and ground color. They found that drop impact and sonic impulse were well correlated with Effegi firmness over a wide range of firmness, but ground color was only slightly correlated and highly cultivar dependent. Besides Effegi testing, the impact parameters were the most sensitive to differences in fruit firmness. Their results indicated that impact and impulse methods were superior to the Effegi method for determining whole fruit firmness with a single measurement, and that although Effegi firmness was most sensitive, wide measurement variation was found in individual fruit, limiting its accuracy (Zhang

et al. 1994). The potential application of objective instrumental impact firmness sensors in commercial canneries was validated by Slaughter et al. (2006), who found that impact firmness sensors successfully evaluated fruit firmness, matching current inspection methods with 83% accuracy.

Lavilla et al. (2002) demonstrated the use of volatile aroma compounds to determine proper maturity harvest in two cultivars. By testing for the presence of volatile components such as propanol, hexyl acetate, limonene, and others, 'Big Top' nectarine and 'Royal Glory' peach were successfully grouped into three stages of maturity, and proper harvest maturity was determined. Many newer nondestructive tests have yet to be fully correlated with more traditional firmness measurement techniques (i.e., penetrometer) to establish the accuracy of these technologies across various peach textures. Infante et al. (2008) reviewed several nondestructive methods for measuring peach texture and more specifically measuring ripening and maturity.

C. Peach Ripening and Its Relationship to Texture

Generally, fruit softens in a distinct pattern as ripening proceeds (Rood 1957; Fischer and Bennett 1991; Harker et al. 1997). Fruit ripening is often determined by changes in fruit firmness, changes in fruit skin or flesh color, and increases in respiration rate, ethylene production, and SSC to acid ratio (Lill et al. 1989; Harker et al. 1997), although newer nondestructive technologies such as time-resolved reflectance spectroscopy have been developed (Tijskens et al. 2007). Ethylene (C_2H_4), the simplest alkene, is a plant growth regulator/plant hormone that affects most aspects of plant growth and plays a vital role in fruit ripening, development, and overall texture. This hydrocarbon can diffuse into and through plant tissues endogenously and exogenously, and strongly influences the initiation and progression of senescence (Watkins 2002).

Common consumer complaints about fresh peaches are that they are too firm, mealy, lack flavor, and fail to ripen, which, in part, is due to consumer misunderstanding of the difference between mature fruit and fruit that is ripe and ready to eat (Crisosto 2006). Harvest maturity is a critical factor in determining storage performance and fruit quality, with immature and overripe fruits being of inferior quality, more susceptible to physiological disorders, and possessing a shorter shelf- and cold-storage life (Lill et al. 1989; Crisosto et al. 1995; Kader 1999, 2002). Reid (1992) (from Crisosto 1994) defined mature as "that stage at which a commodity has reached a sufficient stage of development that after harvesting and postharvest handling, its quality will be at least the

minimum acceptable to the consumer." Maturity at harvest strongly influences quality and shelf-life, with the ideal harvest maturity optimizing yield, fruit size, and consumer acceptability. Fruits from a particular cultivar harvested at early maturity tend to have good storability but reduced size and quality, while the opposite is true for more mature fruits. If fruits are picked too immature they will never ripen to optimal quality, while those too mature will not withstand harvest and transport and are more susceptible to rot (Lill et al. 1989; Ramina et al. 2008). According to the U.S. Department of Agriculture (USDA) standards for grades of peaches, "mature" means that the peach has reached the stage of growth that ensures a proper completion of the ripening process (USDA 2004). Within the 2004 USDA standards for grades of peaches, four grades are listed: U.S. Fancy, U.S. Extra No. 1, U.S. No. 1, and U.S. No 2. In terms of firmness (excluding all other quality characteristics), all four grades consist of peaches that are mature but not soft or overripe. Within the USDA grades, soft or overripe peaches are considered to be "damaged" and "seriously damaged," respectively (USDA 2004).

Compared to most fruits, maturation is highly variable in peaches. Extensive variation for maturity can be found between trees of a single cultivar in one locality or even within a single tree (Marini and Trout 1984). To further complicate fruit maturation and firmness measurements, individual fruits do not soften at the same rate on all parts of the fruit. Peach firmness frequently declines from the stem to the blossom end and from the suture to the cheeks, and this must be taken into account when measuring fruit maturity (Maness et al. 1992b; Crisosto 1994). In work conducted by Marini and Trout (1984), peaches were harvested from one cultivar at the firm-mature stage on five dates. They found that differences among fruits from an individual tree accounted for over half of the firmness variation, while only 3% was due to differences among trees. This variation can make standard peach texture evaluation a major challenge. Fruit perishability and respiration rate are highly correlated, with fruits that have a low respiration rate (e.g., apple) generally having longer postharvest storage potential (over 8 weeks) than fruits with a high respiration rate (e.g., blackberry, less than 2 weeks) (Kader 2002). Peaches are a climacteric fruit with a moderate (11–20 mL $CO_2 kg^{-1} h^{-1}$ at 5°C or ~50 mL $CO_2 kg^{-1} h^{-1}$ at 15°C) respiration rate (Hardenburg et al. 1986; Lill et al. 1989; Kader 2002; Wills et al. 2007; Ramina et al. 2008).

Early work by Connors (1922), Lilleland (1933), Tukey (1933, 1936), and Harrold (1935) clearly demonstrated that peach fruits are climacteric and develop in distinct physiological stages: (I) rapid cell

division and cell expansion leading to a large increase in pericarp volume beginning shortly after bloom (high level of ethylene and respiration); (II) a period of retarded endocarp development and rapid embryo development during mid-season (low ethylene and respiration); and (III) a period of rapid endocarp development (completion) and resumption in pericarp volume increase prior to ripening and senescence (high ethylene and respiration) (Brady 1993). Stage III, the climacteric stage, is generally, depending on genotype, divided into two stages, with stage III being a gradual decrease in firmness and stage IV being a rapid softening/melting (Tonutti et al. 1991, 2001; Fishman et al. 1993; Lester et al. 1994). During and after the melting phase, fruits are very susceptible to physical injury and have a short storage life. It was found that respiration declined during the beginning of stage III, but reached a climacteric peak at stage IV (ripening) (Tonutti et al. 1991).

Physiological stages III and IV encompass several commercial maturity classes that have led to substantial confusion. Attempts to reconcile these classifications have led to one that has five maturity classes: hard, firm, firm-ripe, tree-ripe, and soft-ripe (Shoemaker and Teskey 1959; Hansche et al. 1972); one that has four maturity classes measured as kilogram-force (kgf): immature (>6.7), threshold maturity (>4.5 and ≤ 6.7), firm-ripe (>2.2 and ≤ 4.5), and soft-ripe (≤ 2.2) (Byrne et al. 1991); and another that has three maturity classes: immature, threshold mature, and mature (Delwiche and Baumgardner 1985; Robertson et al. 1989). Many of the earlier studies defined maturity stages simply based on "finger feel" and reduction in the green background color, but over the past 50 years a wide range of tools and techniques have been used to assist in the process. In general, these stages encompass a wide range of potential harvest opportunities, from very immature, where the peach "does not yield to moderate pressure," useful for transport to distant markets, to tree ripe/soft, where fruit "cannot be marketed other than direct from the orchard to the consumer" because the lack of firmness renders fruit prone to bruising and loss of integrity (Shoemaker and Teskey 1959; Scorza 2004). The inconsistency over the exact number of maturity stages is in part due to the wide variation in texture and rate of maturation found among peach cultivars.

In an effort to increase peach quality and meet the various needs of the marketplace, several maturity indices have been developed. The majority of maturity indices are designed as a compromise between the demands of the consumer (high eating quality) and the distributor/marketer (storage and shipping performance) (Kader 1999, 2002). Peaches maintain higher quality when harvested between 4.5 and

5.4 kgf firmness than when harvested at 5.5–6.8 kgf (Crisosto 1994; Lewallen and Marini 2003). For processing peaches, fruits with a firmness greater than 3 kgf but less than 6 kgf (8 mm probe) are recommended to prevent bruising and pit shards, respectively (Gradziel and McCaa 2008). Detailed ripening protocols have been developed to assist distributors and retail managers of fresh-market peaches in optimizing peach fruit quality (Crisosto and Parker 1997). In general, fruit with a firmness of 3.2–5.3 kgf was considered acceptable by consumers, a firmness of 2.7–3.6 kgf had high consumer acceptance (termed "ready-to-buy"), and 0.9–1.8 kgf had the highest eating quality (termed "ready-to-eat") (Crisosto 1999; Crisosto and Valero 2008; Di Miceli et al. 2010). To minimize potential physical damage, a firmness of 2.2–3.6 kgf was suggested as the "transfer point" threshold, before which firmness the peach should be transferred to the retail store, reaching the shelves at a firmness no lower than 1.8–2.3 kgf (Crisosto and Valero 2008).

Peach fruit destined for the fresh market is frequently handpicked using bags, baskets, or totes and then placed into field bins that are transported to the storage/packing facility and volume fill packed or packed into two layer boxes or trays. Fruits picked at advanced maturity stages and bruise-prone white-flesh peaches are generally picked and placed into baskets or totes and packed in the field (Crisosto and Valero 2008).

IV. PEACH FLESH TYPES

A. Introduction

In 221–386 CE, records in China describe peach cultivars with various flesh textures from soft (MF) to "sweet and crispy" (NMF) (Huang et al. 2008). Connors (1922) classified flesh texture into three groups: firm commercial that soften upon ripening ('J.H. Hale'); soft, which is too soft for shipping, with both being MF; and rubbery/resilient or tough, which do not soften upon ripening (NMF) (Bailey and French 1933, 1949; Sherman et al. 1990; Lester et al. 1994). Bailey and French (1933, 1949) suggested that MF is dominant to NMF. Yoshida (1976) confirmed that a single pair of alleles was responsible for flesh type, with MF dominant over NMF (discussed in detail in Section V) (Hesse 1975). Along with MF and NMF, several other flesh types including stony hard (SH), nonsoftening flesh (NSF), and slow ripening (SR) are found within current peach cultivars and breeding program germplasm (Table 6.1).

Table 6.1. Known peach flesh types and associated cultivars, loci, alleles, enzymes, and DNA markers.

Flesh type	Pit adherence	Representative cultivars	Locus	Alleles	Enzyme association	DNA markers	References
Melting	Freestone	Elberta, Loring, Redhaven	*F-M*[z] (*endoPG* gene)	*F-*	endoPG	EndoPG simple PCR	Lester et al. (1994, 1996), Callahan et al. (2004), Peace et al. (2005b, 2007), Peace and Norelli (2009)
	Clingstone	Dixired	*F-M* (*endoPG* gene)	*f-*	endoPG	EndoPG simple PCR	Lester et al. (1994, 1996), Callahan et al. (2004), Peace et al. (2005b, 2007), Peace and Norelli (2009)
Nonmelting	Clingstone	Crimson Lady, UFGold, White Cloud	*F-M* (*endoPG* gene)	f_1f_1 and f_1f_2	endoPG	EndoPG simple PCR	Lester et al. (1994, 1996), Callahan et al. (2004), Peace et al. (2005b, 2007), Peace and Norelli (2009)
Nonsoftening	Clingstone	Amoore Sweet and Bowden	*F-M* (*endoPG* gene)	f_2f_2	endoPG	EndoPG simple PCR	Peace and Norelli (2009)
Slow-melting	Freestone, clingstone	White County, Big Top	None established	None established	ACS	None established	Ghiani et al. (2011a)
Slow ripening	Freestone	Breeding selections only	*Sr*	*sr sr*	None established	AFLP: E-ACT/M-CGG-80bp	Brecht and Kader (1984a,b,d), Ramming (1991), Tataranni et al. (2010)
Stony hard	Freestone, clingstone	Yumyeong, Ghiaccio	*Hd*	*hd hd*	Biochemically upstream of ACS[y]	None established	Haji et al. (2003, 2005), Tatsuki et al. (2006), Peace and Norelli (2009)

[z]*F*, *f*, f_1, f_2 *alleles*. Note: Melting is *F-* and *f-*; melting + freestone is *F-*, (*FF*, *Ff*, Ff_1, Ff_2); melting + clingstone is *f-* (*ff*, $ff_1$$ff_2$); nonmelting + freestone as governed by the *F-M* locus does not exist.

[y]Monogenic recessive with epistatic effect on *F-M* locus.

B. Melting Flesh

The fresh-market peach industry has been and continues to be dominated by peaches of the MF type. In China, the world's largest peach producer, ~80% of peaches grown are MF types, although this percentage is expected to drop as the popularity of NMF is on the rise (Huang et al. 2008). Yoshida (1976) found soft, medium, firm, and SH (further discussed below) textures among MF genotypes. Although Blake (1937) and Bailey and French (1949) suggested soft-MF was dominant to firm-MF, Yoshida (1976) concluded that the firm-MF and soft-MF texture differences were due to multiple gene effects and that linkage is present among the genes involved.

Blake (1937, 1940) found peaches that "possess the NMF character to a partial degree," which he termed semi-melting. Connors (1922), Blake (1937), and Weinberger (1944) all found that the degree of firmness varied within the melting types from very soft to very firm with 'Champion' as a very soft-flesh example and 'J.H. Hale' as a firm-flesh example. The "firm" genotypes of the "semi-melting" flesh type, also referred to simply as "firm," "melting very firm," or more distinctly as "slow melting" flesh (SMF), are less susceptible to bruising than the "soft" flesh, referred to simply as "melting" (MF), due to their increased firmness (Mignani et al. 2006; Bassi and Monet 2008; Ghiani et al. 2011b). Additionally, the SMF types facilitate maturity/harvest management and display a longer shelf-life (Mignani et al. 2006; Bassi and Monet 2008). One of the earliest cultivar examples of SMF may be Babcock, a white freestone peach that was described as having fruits that remain firm 2 weeks after considerable color has developed and possess a characteristic crispness (Weldon and Lesley 1933). Recent work on the SMF types has resulted in selections and cultivars (Big Top, Rich Lady, Diamond Princess, White County, and White Diamond) that are very firm and crisp at early maturity, but eventually soften and develop ethylene (Clark et al. 2005; Iglesias and Echeverría 2009; Ghiani et al. 2011b). 'Big Top' was found to be significantly firmer than the MF 'Bolero' at harvest, but after 5 days at room temperature storage, 'Big Top's' firmness was very low, similar to 'Bolero' (Ghiani et al. 2011b). At the University of Arkansas, MF fruit generally changes from a firm state (3–4 kgf) at harvest (harvest based on firmness and dissipation of 95% green background color) to a very soft state (less than 0.5 kgf) within 2 days at room temperature, while the SMF types harvested at the same firmness require between 4 and 6 days, depending upon genotype, to reach the very soft state (J.R. Clark, unpublished). The precise rate of softening in MF and SMF types is highly dependent upon cultivar/

selection and environmental conditions. The SMF type was likely first commercially introduced in the United States from private breeders in California, but several breeding programs are developing SMF cultivars including substantial work at the University of Arkansas. These fruits are reported to have a long storage and shelf-life, specifically on the tree (Bassi and Monet 2008; Ghiani et al. 2011a). Although MF was initially classified as dominant to SMF, this has not been found to be universally true (Bassi and Monet 2008). While ripe, soft MF 'Bolero' fruit evolved ethylene at harvest, the SMF 'Big Top' did not begin to evolve ethylene until 4 days after harvest (Ghiani et al. 2011a). Ghiani et al. (2011a) found that the SMF trait appeared to be linked to a delayed 1-aminocyclopropane-1-carboxylic acid (ACC) synthase (ACS) expression and the resulting delayed ethylene evolution. Preliminary molecular polymorphisms found in 'Big Top' appeared suitable for the development of a genetic test that could differentiate these flesh types, although further analysis is necessary (Ghiani et al. 2011a). To date, no molecular markers have been developed to differentiate MF and SMF types.

The variation in firmness found within MF types and the array of names given to describe these hints at the complexity of differentiating flesh type based on firmness and assessing a tree's true phenotype (Mignani et al. 2006). Determining a uniform maturity at harvest across flesh types and using a standardized phenotyping protocol is essential. Even the variation in accurate evaluation methods among breeding programs and allied scientists limits the adoption of a universal flesh type classification system and challenges the molecular characterization of the different types.

In addition to various rates of flesh softening within MF types, both coarse and fine flesh characteristics can be found in MF cultivars. Undoubtedly several factors including cell size and growing environment contribute to these differences, but little research has been conducted on the topic. 'Winblo' and 'Loring' exemplify this difference with the flesh of 'Loring' being coarse and the flesh of 'Winblo' being very fine, almost buttery, when grown in similar environments (J.R. Clark, pers. commun.).

C. Stony Hard

The SH trait was first selected ('Jingyu') at the Beijing Forestry and Pomology Institute in the 1970s. The fruits were firm, freestone, white-flesh, "practically freestone-NMF" with good shipping and shelf-life potential, although they were distinct from NMF and MF (Li 1984; Hough 1985). The SH fruits have been noted to have a very crispy flesh

texture (Scorza and Sherman 1996). Yoshida (1976) was the first to publish regarding the SH trait and concluded that MF was dominant over SH, and like MF and NMF, the trait is controlled by a single gene. Goffreda (1992, 1999) and Liverani et al. (2002) also found SH to be recessive and revealed that the fruit produced little or no ethylene, had low respiration rates, and exhibited delayed ripening. SH fruits, including 'Ghiaccio' and 'Yumueong', were found to produce no ethylene, although ethylene production was stress-induced from cold storage (10°C) (Hayama et al. 2003; Tatsuki et al. 2006; Ghiani et al. 2007, 2011a; Begheldo et al. 2008). The biochemical and physiological nature of the SH trait has been extensively studied. Bassi et al. (1998) discovered that, compared to MF fruits, SH fruits have a higher Ca content bound to cell wall pectins (insoluble) (Giovannini et al. 2006), with SH fruits having a high Ca and total pectin content in general (Bassi et al. 1998; Mignani et al. 2006; Bassi and Monet 2008). Limited endopolygalacturonase (endoPG) and expansin accumulation has been found in the SH cultivar Manamoi (Hayama et al. 2007). The failure of SH fruit to produce ethylene has been attributed to the suppression of ACS (*PpACS1* gene) during ripening (Haji et al. 2003; Tatsuki et al. 2006, 2007). Additionally, it was concluded that the induction of ethylene production in cold storage was due to stimulated ACC production (Begheldo et al. 2008). The suppressed ACS and the subsequently reduced ethylene production is likely responsible for the unusual softening pattern found in SH fruit. It was therefore suggested that controlled applications of exogenous ethylene or ACC could be applied commercially to achieve a desired level of softening in SH fruit (Haji et al. 2003; Hayama et al. 2006b, 2008b; Tatsuki et al. 2006).

Further review of the literature on SH reveals conflicting reports on SH firmness and softening pattern. Goffreda (1999) found that all SH fruits were much firmer than MF; however, when exposed to ethylene or cold storage, they softened rapidly. While Haji et al. (2003) reported that the SH fruit never softened to the extent of MF fruit even when exposed to ethylene. These conflicting findings have been subsequently addressed by the hypothesis that the SH trait is independently inherited from MF and NMF (Yoshida 1976; Haji et al. 2001; Begheldo et al. 2008). Recently, this hypothesis has been corroborated as the SH gene (termed *Hd*) has been determined to have an epistatic effect on MF and NMF. In SH fruit, the underlying MF or NMF is revealed by applying exogenous ethylene, as the SH/MF fruit will soften to a melting texture, while the SH/NMF will not 'melt' (Scorza and Sherman 1996; Haji et al. 2001, 2003, 2005; Lu et al. 2008; Okie et al. 2008; Peace and Norelli 2009).

Efforts to incorporate the SH trait into U.S. germplasm began in the 1970s with the work of L.F. Hough and continue today in several breeding programs (Goffreda 1999; Byrne 2005). Several SH cultivars have been developed in Italy, for example, 'Ghiaccio-1' (Liverani et al. 2002; Okie et al. 2008). Ghiaccio is a series of peach cultivars (Ghiaccio 1, Ghiaccio 2, Ghiaccio 3) with no blush (no red pigment on the fruit skin) and very firm flesh with a long shelf-life on the tree (20–25 days). Although fruits of the Ghiaccio series have been reported to hold on the tree at a ripe state for up to 25 days without losing their pulp consistency or developing off colors, the flesh firmness of 'Ghiaccio-1' strongly decreased during the first 2 days of storage. Further, the flesh firmness decreased linearly for 10 days at 20°C, at which point firmness resembled that of standard MF peach cultivars (0.5–0.7 kg) (Nicotra et al. 2002; Testoni and Fibiani 2006). SH selections have been developed with low and high acidity as well as clingstone and freestone, with several promising selections in testing (Goffreda 1992; Liverani et al. 2002), but as of 2005, all SH cultivars were clingstone (Bassi and Monet 2008). Peach breeding programs in Taiwan and Brazil are also breeding with SH in an effort to produce cultivars with improved storage, shelf-life, and dual purpose (fresh market and processing) (Byrne 2005; Lu et al. 2008). Just like attempting to differentiate MF and SMF, distinguishing the SH fruits from other flesh types is a challenge. This challenge makes conducting research on flesh types very difficult as one must consider various changes in firmness, color development, size, flavor, and SSC/TA ratio to reliably judge maturity (Goffreda 1992; Bassi et al. 1998; Bassi and Monet 2008).

D. Nonmelting Flesh

Although historically often referred to as something other than NMF (e.g., clingstone, slow-softening, canning peach, and others), peach fruits with a firm texture when fully mature (does not go through stage IV, i.e., melting), but do soften slightly as ripening proceeds, are referred to as NMF. This flesh type is always associated with clingstone pit adherence and is often described as having rubbery texture. Calling NMF the "canning" flesh type is very misleading though, as wide variation is found within the NMF types and a growing percentage of fresh-market peach cultivars now have NMF (Sherman et al. 1990; Beckman and Sherman 1996; Bassi and Monet 2008). Sensory and chemical testing of MF and NMF determined that even though NMF fruits were firmer, less juicy, and usually rubbery compared to MF fruits, the flavor, phenolic compounds, TA, and SSC were

not significantly different between the flesh types (Brovelli et al. 1999b; Contador et al. 2011). Biggs (1976) and El-Agamy et al. (1981) found limited ethylene production of "slow-softening" peaches (e.g., 'Floridagold') was responsible for the increased firmness after storage at room temperature and was due to a decreased capacity for ethylene production. These findings differed from those of Brovelli et al. (1999a), Haji et al. (2001), and Ghiani et al. (2007) who found that NMF fruit both on and off the tree had more elevated levels of ethylene production compared to MF fruit. Overall, Brovelli et al. (1999a) found that ethylene production was similar for both types and that the climacteric stage was not well defined and difficult to compare.

The peach processing industry is based on NMF cultivars, with over 80% of processing peach cultivars of this flesh type (Gradziel and McCaa 2008). The increased flesh firmness of NMF types allows for the fruit to be handled as a bulk commodity by limiting the degree of damage as would be found if MF types were used. Additionally, the firm flesh allows for the fruit to be harvested with a fuller degree of maturity, improving the quality of the processed product (Pressey and Avants 1978; Gradziel and McCaa 2008). The development of a freestone-NMF peach has been a major goal of breeders for over 50 years. In 1985, Hough stated with enthusiasm "nonmelting clingstones—it must be possible to break this linkage!" (Hough 1985). As early as 1937, reports proclaimed the existence of freestone or semi-freestone-NMF types, although a freestone or semi-freestone-NMF cultivar has yet to be developed (Blake 1937; Gradziel and McCaa 2008). In their 1996 publication, Beckman and Sherman described a semi-freestone-NMF peach found in 1992 from open pollination of two separate sources (Fla. 9-20C and Fla. 9-26C) originating from combining Mexico and North Carolina germplasm, although at the time of their publication the genetic nature of this phenotype was not determined. Both Fla. 9-20C and Fla. 9-26C were clingstone NMF. Seedlings from Fla. 9-20C were additionally described by Van Der Heyden et al. (1997) who found that the population's segregation approached a 1:1 ratio of semi-freestone to clingstone, with the ripe fruit having a more intermediate firmness between the NMF and MF individuals. Although the semi-freestone flesh was softer than the clingstone progeny, it was concluded that it was still firmer than MF (Van Der Heyden et al. 1997). Through a backcross from a peach × almond interspecific hybrid, Gradziel (2002) recovered firm-flesh freestone peaches. But, in contrast to standard NMF types, the seedlings recovered were unstable in flesh type in certain environments and softened when overripe and were therefore not true NMF genotypes (Gradziel and McCaa 2008). Work continues on

developing freestone-NMF cultivars as well as on the incorporation of other flesh types such as SH to develop a freestone peach with enough firmness to withstand the demands of the processing industry (Gradziel and McCaa 2008).

The majority of fresh-market peaches in the United States are MF (Hough 1985; Byrne 2002). By 1985 great progress had been made at developing firm-MF types, but managing harvest to pick fruit at optimal maturity was and continues to be very difficult. This challenge led Hough (1985) to predict that fresh-market peaches with NMF would be developed. NMF was not found in the U.S. fresh market in 1985, but the trait had been used in both Latin America and parts of Europe for centuries (Byrne 2002; Bassi and Monet 2008). In recent years, there has been a progressive shift in the fresh market to the adoption of NMF due to its resistance to bruising and potentially superior storage performance (Scorza 2004). This trend facilitates the improvement of fruit quality by allowing for harvesting more mature fruit with higher levels of sugar and flavor attributes (Scorza 2004). Taste panel testing of MF and NMF peaches found that although the texture was distinctly different between the types, the flavor profile was not distinct between the two (Brovelli et al. 1995). Consumer acceptance trials of peaches cold-stored for 14 days (conducted at a "supermarket") found that NMF was rated higher than MF for texture, appearance, and overall quality (Williamson and Sargent 1999). Beckman et al. (2008) reported that cultivars with NMF had superior poststorage firmness and generally displayed improved cropping, fruit shape, blush, and SSC/TA ratios compared to commercial MF cultivars. The NMF fruits were also of comparable size and had reduced incidence of split pits. These results suggest that incorporating the NMF trait into fresh-market peaches could be successful. Work has been conducted at Louisiana State University and in Brazil to develop cultivars suitable for both the fresh market and the processing industry, with at least one dual purpose cultivar, 'Leonense', having been developed from the Brazil program (Wilson and Boudreaux 1986; Raseira et al. 1998). The University of Florida and the University of Arkansas are breeding for fresh-market NMF peaches with the idea of increased firmness, with the Arkansas program particularly focused on nectarines, allowing for the development of increased flavor while maintaining superior shelf-life (Byrne 2005; J.R. Clark, pers. commun.). Traditionally, NMF fruit has a rubbery flesh, but breeding work is pursuing a crisper, nonrubbery texture. NMF is also easier to breed for as larger populations can be managed without missing the optimum peak in firmness (Sherman et al. 1990). This work has resulted in several releases including

'UFGold', 'UFPrince', 'Springprince', 'Springbaby', 'Crimson Lady', 'White Rock', 'White Cloud', 'Arrington', and 'Bradley' (Clark et al. 2001, 2005, 2011; Byrne 2002). A three-way cooperative regional project involving the USDA Agricultural Research Service, the University of Georgia, and the University of Florida is in part focused on developing fresh-market NMF cultivars for use in moderate-chill areas (Beckman et al. 2008). In addition, breeding programs in Mexico, Brazil, Spain, S. Africa, Australia, and Italy are working to develop fresh-market NMF cultivars (Badenes et al. 1998; Byrne 2002; Byrne and Bassols Raseira 2006; Okie et al. 2008; Topp et al. 2008; Byrne et al. 2012).

E. Nonsoftening Flesh

Although the NSF type has been incorporated into breeding program germplasm and released cultivars, it is one of the least described flesh types. Phenotypically, NSF peaches are much like NMF but with an increased level of firmness that is frequently perceived as a crispness that remains until overripe (Peace and Norelli 2009). Genotypically, NSF peaches can be differentiated from MF and NMF using the endoPG polymerase chain reaction (PCR) test (discussed in Section V.C) (Peace and Norelli 2009). The NSF type has been utilized in the University of Arkansas breeding program in an effort to develop crisp fresh-market peaches with improved cold-storage performance. Several NSF advanced selections have been developed and two cultivars, Amoore Sweet and Bowden, have been released from the program (Clark et al. 2005). Cold-storage performance evaluations of these cultivars and other NSF selections found that the NSF types had improved skin and flesh quality and reduced levels of flesh browning and mealiness compared to MF and NMF types (Sandefur 2011). The development of high-quality NSF cultivars could have a major impact on both the processing and fresh-market industries, but more research on the precise characteristics of NSF is needed.

F. Slow Ripening

Another unique flesh type with a classification pertaining more to its ripening pattern than to its texture is the SR type. In 1984, progeny from a cross using the standard MF nectarine cultivar 'Fantasia' at the Fresno, California USDA-ARS stone fruit breeding program were found to have delayed ripening and increased flesh firmness, subsequently termed SR. The SR flesh is crisp and firm (but not NMF), being 60% firmer at harvest than 'Fantasia', although the rate of softening during storage was

significantly reduced (Brecht and Kader 1984c). The parents of these two types had MF and no intermediate types were found. Generally, fruits of the seedlings demonstrated poor organoleptic qualities, had an undesirable, hard texture, and were susceptible to internal breakdown (Ramming 1991). Based on segregation ratios, the trait was proposed to be monogenic and the symbol *sr* or *slr* was proposed (Brecht and Kader 1984c; Ramming 1991; Begheldo et al. 2007; Tataranni et al. 2010). According to Begheldo et al. (2007), SR fruit growth stops after pit hardening, remaining small with minimal ethylene evolution, no softening, and pale skin color. Although treatment with propylene gas stimulated the onset of ethylene production, the SR genotypes still showed a resistance to ripening with a 14–18 day delay in ethylene production. Brecht and Kader (1984a,b,d) concluded that the ethylene production was limited by the availability of ACC.

Morgutti et al. (2005) studied three SR selections (BO 95021075, BO 95021043, and BO 95021074). Only one selection evolved ethylene and underwent flesh softening (to 1.4 kgf), while the other selections evolved no ethylene and softened to only slightly over 6 kgf. Using the μPEACH 1.0 microarray, Begheldo et al. (2007) found 376 genes to be differentially expressed in 'Fantasia' fruit during the transition from immature to mature, while only 54 genes were differentially expressed during this transition in SR fruit. When treated with propylene, genes involved in ethylene signal perception and transduction were up-regulated in 'Fantasia', but not in the SR fruit (Begheldo et al. 2007). Tataranni et al. (2010) developed an amplified fragment length polymorphism (AFLP) SR molecular marker (E-ACT/M-CGG-80bp) with further studies in progress evaluating the utility of this marker during seedling selection. These studies highlight the potential of SR genotypes as suitable models for studying the genes involved in peach ripening and texture. Like the previous flesh types (MF vs. SMF), the classification of genotypes as SR is a major challenge. The dramatic variability in ethylene production found within SR genotypes complicates accurately defining SR (Morgutti et al. 2005). Although the exact phenotypic characteristics of SR types may not be clarified, ongoing research aims to determine what exactly defines SR and to develop a molecular marker linked to the SR trait in peach (Morgutti et al. 2005, 2006).

G. Pit Adherence

Frank N. Meyer, a USDA plant explorer who traveled in China in the early 20th century, described peaches with many of the phenotypic

characteristics that are commercially used today. Meyer mentioned both freestone fruits, where the mesocarp freely separates from the endocarp, and clingstone fruits, where the mesocarp does not separate from the endocarp, with the wild stands he found being freestone (Fig. 6.1b) (Hesse 1975). Traditionally, in the United States, the majority of fresh-market peaches (MF) have been freestone except for early season types, which are predominantly clingstone. This trend is not universal, with clingstone fruit preferred in several countries (e.g., Italy, Spain, and Mexico) (Bassi and Monet 2008; Okie et al. 2008). Additionally, many late-season fruits are often clingstone due to their high eating quality compared to late-season freestones (Okie et al. 2008).

Bailey and French (1933, 1949) and Blake (1940) described all degrees of adhesion from "air-free" to "semi-clingstone" to very clingstone, the latter of which was found to be particularly evident in early-ripening cultivars (Weinberger 1944). The rapid flesh maturation found in early-ripening cultivars was determined to be responsible for the lack of separation of the mesocarp from the endocarp; therefore, the semi-freestone types are often physiologically classified as clingstone but genetically classified as freestone (Beckman and Sherman 1996; Bassi and Monet 2008). Bailey and French (1933, 1949) suggested that mesocarp–endocarp (flesh to pit) adhesion is a simple Mendelian trait controlled by a single locus, the *Freestone* (*F*) locus, with cultivars classified as either freestone (*F*-) or clingstone (ff). This hypothesis has been validated by many researchers and the locus was much later determined to be located on the G4 linkage group (Lesley 1957; Dettori et al. 2001; Yamamoto et al. 2001; Verde et al. 2002; Peace et al. 2005a,b; Bassi and Monet 2008).

Early work by Bailey and French (1933, 1941, 1949) also pointed out the relationship between pit adherence and variation in flesh texture. They hypothesized that pit adherence and flesh type were controlled by two separate but linked loci [*F* locus and *Melting* (*M*) locus] with epistatic interaction. Later work by Monet (1989), Peace et al. (2005a, b), and many others established that the two traits were controlled by a single locus, *freestone-melting flesh* (*F-M*), with two separate genes (Martínez-García et al. 2012). Although the connections between flesh type and pit adherence and the knowledge that certain flesh types only appear with particular pit adherence (e.g., only clingstone with NMF) have been well established for years, consumers and others involved in the peach industry still have misconceptions regarding these traits. The term "freestone" is frequently and erroneously used to imply "melting" although clingstone-MF peaches are prevalent around the world. While

the fresh peach market is predominantly freestone-MF, early- and late-season fruits are commonly clingstone-MF.

V. RIPENING AND THE ENZYMATIC EFFECTS ON PEACH TEXTURE

A. Pectin and Flesh Softening

Peaches and nectarines are climacteric fruit in that they show respiratory activity and a surge of ethylene production at ripening (Lill et al. 1989). In general, fruit softening can arise from several processes including loss of turgor, degradation of starch, and cell wall breakdown, though the changes in fruit texture during ripening have been largely attributed to cell wall degradation. Using electrical impedance measurements, Harker and Maindonald (1994) found that during ripening, cell wall resistance declined 60%, vacuole resistance declined 26%, and membrane capacitance decreased 9% in MF fruit. These changes in tissue resistance were closely related to flesh firmness (Harker and Maindonald 1994). At the initiation of softening, fibrils appeared in the middle lamella of the cell wall with vascular tissue (xylem and phloem elements) contributing to stringiness in soft fruit (Harker et al. 1997). This flesh stringiness ("pineapple-flesh"), illustrated by the cultivar Encore, is frequently found in both white and yellow flesh fresh-market and processing peach cultivars and can be a major quality concern in Michigan (W. Shane, pers. commun.). Although low soil nitrogen levels have been associated with increased flesh stringiness, more research is needed to determine the genetic and physiological aspects of this trait (Reeve and Neufeld 1959). In peach, the majority of flesh softening is due to the solubilization and depolymerization of pectic polymers that make up a large proportion of the carbohydrate polymers that account for 90–95% of the structural components of cell walls (Dawson et al. 1992; Ramina et al. 2008).

Pectin is a heteropolysaccharide predominantly containing galacturonic acid residues and is located primarily in the cell wall and intercellular spaces (Zhang et al. 2012). For a review of pectin and pectinolytic enzymes, see Jayani et al. (2005). Fresh peach fruit is composed of 0.1–0.9% pectic substances (Jayani et al. 2005). In their work, Zhang et al. (2010) determined that peach firmness was closely related to the precise contents and nanostructure of pectin and its hydrolyzation by enzymes. As ripening proceeds, pectin is depolymerized and solubilized, which plays a major role in cell wall

loosening and disintegration (Zhang et al. 2012). Changes in hemicellulose, an additional carbohydrate polymer in the cell wall, have also been associated with flesh softening, specifically decreasing tissue cohesion (Hedge and Maness 1998; Ramina et al. 2008). The decline in flesh firmness as fruit matures is related to a decrease in the molecular weight of soluble pectin, an increase in the content of water-soluble pectin and uronic acids, decreasing ethylenediamine-tetra-acetic acid (EDTA)-soluble pectin, protopectin, and cellulose, and a decrease in the esterification of pectin, although, in general, the pectins of peach fruit are highly esterified (Shewfelt 1965; Ben-Arie and Lavee 1971; Pressey et al. 1971; Chang and Smit 1973; Pressey and Avants 1978; Huber 1983; Sistrunk 1985; Lill et al. 1989; Dawson et al. 1992; Maness et al. 1993; Karakurt et al. 2000). Although pectin disassembly occurs throughout the ripening process, it is amplified during the final melting stage (stage IV) (Dawson et al. 1992; Hadfield and Bennett 1998). Shewfelt (1965) found that the changes in total pectin content during ripening were cultivar dependent. It was later found that higher cold-storage temperatures (4.4°C vs. 1.1°C) were directly related to the degree of softening, as well as increased cellulase activity, and increased ethylene evolution (Vakis et al. 1970; Lill et al. 1989). Yoshioka et al. (2011) suggested that pectic polysaccharides are potentially solubilized during peach ripening without depolymerization. In MF fruit, solubilization of pectin polysaccharides is potentially required for pectin depolymerization by degrading enzymes (Yoshioka et al. 2011). The complexity of apparent molecular mass changes in pectin and hemicellulose extracts of peaches implicates the action of a number of different enzymes capable of degrading both pectin and hemicellulose cells (Hedge and Maness 1998).

B. Ripening-Related Enzymes

Numerous enzymes play a role in pectin modification and other biochemical changes related to flesh softening and texture. The most extensively studied pectinolytic enzymes are protopectinases, which degrade insoluble protopectin to soluble pectin, polygalacturonases (PG), pectin methylesterases (PMEs), and lyases, which breakdown pectate and pectin, respectively, and pectin esterases, which catalyze deesterification of pectin (Jayani et al. 2005). The most characterized enzymes in relation to peach softening and texture are ACS (EC 4.4.1.14) and 1-aminocyclopropane-1-carboxylate oxidase (ACO) (EC 1.14.17.4), PME (EC 3.1.1.11), PG (EndoPG—EC 3.2.1.15 and ExoPG—3.2.1.67), and β-(1,4)-glucanase (EGase) (EC 3.2.1.4)

(Rexová-Benková and Markovic 1976; Hadfield and Bennett 1998; Jayani et al. 2005; Ramina et al. 2008). For an overview of several pectic enzymes, see Rexová-Benková and Markovic (1976) and Jayani et al. (2005). Using a cell wall–oriented genomic approach, Trainotti et al. (2003) reported that fruit softening begins well before the ethylene climacteric rise and continues thereafter. Additionally, it has been proposed that the degradation of other, yet undiscovered components of the cell wall may be required for the induction of the softening process (Wakabayashi 2000). The genes expressed, and therefore enzyme activity, prior to the climacteric ripening stage are generally down-regulated by ethylene compared to ripening-specific genes that are generally up-regulated by the hormone, although some genes appear to be insensitive to ethylene (Trainotti et al. 2003; Ramina et al. 2008). The enzyme/gene associations and representative cultivars for each peach flesh type are summarized in Table 6.1.

1. 1-Aminocyclopropane-1-carboxylate Synthase and Oxidase. 1-Aminocyclopropane-1-carboxylate synthase and oxidase are required for the biosynthesis of ethylene in peach (Tonutti et al. 1991; Ramina et al. 2008; Borsani et al. 2009). At least three ACS isogenes have been found in peach, but not all are associated with ripening (Mathooko et al. 2001; Ruperti et al. 2001; Tatsuki et al. 2006, 2007). The enzymes ACO and ACS are up-regulated in the climacteric phase, accumulating during ripening (Trainotti et al. 1997, 2006b, 2007; Mathooko et al. 2001; Lurie et al. 2002; Tatsuki et al. 2006; Vecchietti et al. 2009; Lombardo et al. 2011). It was found that ACO underwent a large change in relative abundance during the fruit transition from the preclimacteric to the climacteric phase and was stimulated by propylene (Prinsi et al. 2011; Ruperti et al. 2001). The activity of ACO has been observed in the mesocarp as well as the skin of ripening peach fruit (Vecchietti et al. 2009). As precursors to ethylene, ACS and ACO are directly related to peach texture. Ethylene activity is required for the expression of the MF, NMF, and NSF phenotypes; therefore, ACS and ACO activity is also required. Additionally, the transcription suppression of ACS (Pp-ACS1) has been found to result in the lack of ethylene evolution in SH cultivars (Tatsuki et al. 2006, 2007; Bassi and Monet 2008).

2. Pectin Methylesterase. Although several researchers (Chang and Smit 1973; Dawson et al. 1992) found little or no decrease in the activity of PME (also referred to as pectin esterase, pectase, or pectin methoxylase) during ripening, several studies found that PME activity decreased during ripening (Sterling and Kalb 1959; Shewfelt

et al. 1971; Hobbs et al. 1991; Lurie et al. 2002). All above-mentioned studies reported a high level of PME at an early-ripening state (e.g., at commercial harvest). Glover and Brady (1995) found that PME activity was much higher in early-mature fruit than in fully ripe fruit and concluded that the strong association of PME with pectic polymers may regulate enzyme activity/turnover. In their studies on tomato and pear, Pressey and Avants (1976, 1982) found that PME (which catalyzes the deesterification of pectin) stimulated the depolymerization of pectin by PG. Additionally, it was found that PME activity appeared to be more intimately related to flesh softening than PG as PME increased markedly during initial flesh softening, but was down-regulated by ethylene before the highest activity of PG (Artés et al. 1996; Lurie et al. 2002; Trainotti et al. 2003; Ramina et al. 2008; Kao et al. 2012). Like ACS and ACO, PME is directly related to flesh texture with PME activity required for expression of the MF, NMF, and NSF phenotypes. Little research has been conducted on the precise differences in PME activity in the different flesh types, but Manganaris et al. (2006) reported PME activity to be significantly lower in NMF fruit than MF fruit before and after the ripening process.

3. Polygalacturonase. Pressey and Avants (1973, 1978) established the relationship between pectin solubilization, fruit softening, and PG, which is also referred to as pectin depolymerase, pectinase, D-galacturonase, and glycanohyrolase (Huber 1983). Two types of PG were identified, an endoPG that cleaved the rhamogalacturonan chain and an exopolygalacturonase (exoPG) that removed galacturonosyl residues (Pressey and Avants 1976). According to Rexová-Benková and Markovic (1976), the term "endo" denotes a random-action pattern and "exo" denotes a terminal-action pattern. Both the exo- and endoPG require deesterified galacturonic residues to hydrolyze the pectin chain (Rexová-Benková and Markovic 1976; Glover and Brady 1995). The enzyme exoPG is activated by Ca ions while endoPG activity is reduced by Ca ions (Pressey and Avants 1973; Poovaiah et al. 1988; Ferguson and Boyd 2002). It has been suggested that Ca binding likely reduces the susceptibility of the pectic substrate to enzyme attack.

Brady et al. (1985) found that firm tomato cultivars generally contained less PG activity at all stages of maturity compared to soft cultivars. Further work conducted by Giovannoni et al. (1989) determined that endoPG plays an essential role in the degradation of pectin during fruit (tomato) ripening. It was concluded that endoPG was required for pectin degradation but did not initiate softening in tomato (Hadfield and Bennett 1998). In peach, this role had been suggested by

Pressey and Avants (1973, 1978) and Pressey et al. (1971) who found that when peach fruits were immature and firm, no PG activity was found and that the increase in water-soluble pectin was paralleled by the development of PG activity. This was not due to different levels of total PG, but rather to the enzyme composition (exo- vs. endoPG). This is in agreement with the hypothesis that PME is more responsible for flesh softening than PG (Artés et al. 1996; Lurie et al. 2002; Trainotti et al. 2003; Ramina et al. 2008; Kao et al. 2012). The activity of PG was low at harvest and increased during ripening in MF peach fruit, demonstrating a typical ripening-related pattern, with expression increasing throughout ripening (Lurie et al. 2002; Trainotti et al. 2003). With continued softening, large, intercellular areas, which develop largely as a result of PG-catalyzed degradation of pectic rhamnogalacturonan, became filled with fibrils (King et al. 1989). Additionally, fruit treated with 1-methylcyclopropene (MCP) had reduced levels of PG activity (Lurie et al. 2002; Tonutti et al. 2007).

It was found that when ripe, "clingstone" fruit had mostly insoluble pectin and exoPG activity, while ripe "freestone" fruit had both exo- and endoPG activity along with high levels of water-soluble pectin (Pressey et al. 1971; Pressey and Avants 1978). Although these findings appeared to be significant, it was concluded that fruit firmness began to decrease before any PG activity was detected; therefore, PG was suggested not to be responsible for the initiation of softening. Two forms of exoPG were found in the mesocarp tissue of ripe freestone peaches and their activity increased dramatically only when the tissue was already very soft, again indicating that exo- and endoPG activity may not be fully associated with flesh softening (Downs et al. 1992; Orr and Brady 1993). At least three distinct PG-related genes have been described in peach (Lester et al. 1996). Lester et al. (1996) confirmed the role played by endoPG during the melting stage in peach fruit and identified an endoPG cDNA involved in flesh texture differences. A restriction fragment length polymorphism (RFLP) was detected for the prevalent endoPG (PRF3)-related gene, confirming it as a marker for the *M* locus (Lester et al. 1996). An endoPG protein was detected in both NMF and MF fruits, although it was higher in MF and increased as the flesh softened, while it remained low in NMF fruit (Morgutti et al. 2006). It was concluded that there was differential expression of endoPG in NMF and MF fruits with the NMF possibly resulting from a deletion in the endoPG gene (Callahan et al. 2004; Morgutti et al. 2006). EndoPG has received substantial attention due to its impact on flesh texture and is discussed in more detail in Section V.C.

4. β-(1,4)-Glucanase. EGase (also known as cellulase or β-1,4-endoglucan hydrolase) hydrolyzes the β-1,4-glucan linkages of plant cell wall polymers, weakening the wall structure during ripening (Ramina et al. 2008). The activity of EGase has been clearly associated with peach fruit abscission and the activity of EGase was also found to increase prior to any significant flesh softening (Hinton and Pressey 1974; Hadfield and Bennett 1998). At least three members of the peach EGase family have been discovered, with one differing from the others by having a decreased expression during ripening and is down-regulated by ethylene (Trainotti et al. 1997, 2006a,b; Begheldo et al. 2008). Lurie et al. (2002) found that EGase mRNA was only minutely detected at harvest and showed no increase during ripening, while after cold storage and subsequent ripening a small increase in EGase activity was observed. Additionally, treating peach fruit with propylene increased EGase activity in association with flesh softening. Using a cDNA whose cognate gene is *ppEG1*, Trainotti et al. (1997) found that *ppEG1* codes for EGase and that it is expressed during abscission of fruits and during the very late stage of fruit ripening, thus cooperating with other enzymes in fruit mesocarp softening. Work published a year later (Bonghi et al. 1998) found two forms of EGase in peach, with one demonstrating involvement in early fruit growth and one with the initial phases of softening before the ethylene climacteric stage, which could be stimulated by propylene. This research demonstrated that EGase is intimately involved in the initial phase of flesh softening, preceding the activity of PME and PG.

5. Additional Enzymes and Related Proteins. Expansins, which are nonenzymatic proteins, have been found to be associated with peach flesh softening (Hayama et al. 2001, 2003; Ramina et al. 2008). At least three expansins have been detected in peach fruit, with two being up-regulated during the onset of ripening and one being expressed prior to ripening (Hayama et al. 2003, 2007; Trainotti et al. 2003). One expansin (PpExp3) was found only in MF cultivars (very low in NMF) and therefore has been suggested to be related to the differences in MF and NMF, although high levels of expression were found in the SH cultivar 'Yumyeong' (Hayama et al. 2001, 2003, 2007; Morgutti et al. 2005; Ramina et al. 2008). NMF fruit treated with ethylene had increased expansin expression equal to that of MF (Hayama et al. 2006a).

Hayama et al. (2006a) reported a putative peach β-D-xylosidase (EC 3.2.1.37) gene (*PpARF/XYL*) that was proposed to be associated with flesh softening and was ethylene dependent. Continued work with

this gene found that ethylene plays a major role in β-D-xylosidase expression, but β-D-xylosidase accumulated prior to the ethylene climacteric stage, suggesting that it may play a role in the initial ripening process (before melting) and may be regulated by factors other than ethylene (e.g., auxins) (Di Santo et al. 2009).

Using a cell wall–oriented genomic approach, Trainotti et al. (2003) uncovered the activity of several cell wall–related genes during peach fruit ripening. It was found that β-galactosidase (EC 3.2.1.23) showed a typical ripening-related pattern, being up-regulated by ethylene with expression increasing throughout ripening (Trainotti et al. 2003). In this same study, pectate lyase expression was initiated at the onset of ripening, and reached a maximum during the initial softening phase, and it was concluded that pectate lyase is responsible for early coarse pectin degradation providing for its breakdown by other degrading enzymes (Trainotti et al. 2003). In a later study, Trainotti et al. (2007) found that with the onset of ripening, at least nine different auxin-related genes were found to increase expression with the initiation of ripening. Several of these genes were found to have decreased expression as late ripening (melting stage IV) proceeded (Trainotti et al. 2007).

C. EndoPG and the Differentiation of Flesh Types

MF peaches have a larger decrease in intrinsic viscosity and apparent molecular weight of pectins, increased dissolution of the middle lamella, and increased intercellular spaces than NMF peaches during the late stages of ripening (Chang and Smit 1973; Brovelli et al. 1998). Orr and Brady (1993) hypothesized that these changes and the depolymerization of pectin to soluble oligomers creating the MF texture may be the main function of endoPG. The activity of endoPG was not observed in mature NMF fruit, but as MF fruit softened, endoPG activity increased (Orr and Brady 1993; Karakurt et al. 2000). Callahan et al. (1993) found no PG-related RNA in firm, unripe peaches, found low levels in fruit that had started to soften, and found high levels in soft-ripe (melting) fruit, with this change coinciding with the peak in ethylene evolution. Although no endoPG activity was found in NMF fruit, Lester et al. (1994) found that transcription of the endoPG gene may still occur in NMF fruit, although the small RNA transcript size may be due to sequence aberration that affects the translation or production of the active enzyme.

More recent work has cemented the relationship between endoPG and pit adhesion and flesh type, with Ghiani et al. (2011b) concluding that endoPG function was essential to achieve the MF texture. It was

found that the *F* locus is less than 50 kbp upstream from the *M* locus with both genes being identical, apart from slight variation in their introns and promoter region (Peace et al. 2005a,b, 2007; Peace and Norelli 2009). In conclusion, the *Freestone* and *Melting* endoPG genes were classified as one pleiotropic locus, *Freestone-Melting flesh* (*F-M*) and it is located at the end of peach linkage group 4 (Dettori et al. 2001; Peace et al. 2005a,b, 2007; Ogundiwin et al. 2009; Peace and Norelli 2009). Four functional alleles have been found of *F-M*, and additivity, dominance, pleiotropy, and epistasis interactions are found at this locus (Peace and Norelli 2009). The first allele is *F* and is dominant over the other three, the second allele is *f* and is dominant over the third (f_1) and the fourth allele (f_2); therefore, *F*- results in freestone-MF; ff, ff_1, and ff_2 results in clingstone-MF; f_1f_1 and f_1f_2 results in clingstone-NMF; and f_2f_2 results in clingstone-NSF (Peace and Norelli 2009). It was hypothesized that the f_1 allele arose from a deletion in the *Freestone* gene, while the null allele arose from a deletion of both the *Freestone* and *Melting flesh* genes. Additionally, it was determined that the f_1 allele's *Melting flesh* gene is either impaired through an undetected mutation or the freestone-MF phenotype requires the presence of both the *Freestone* and *Melting flesh* genes, as the f_1 allele result in clingstone-NMF rather than the expected clingstone-MF phenotype (Peace and Norelli 2009). From this work, a simple endoPG PCR test for distinguishing clingstone-MF, freestone-MF, and clingstone-NMF, which can successfully be used for phenotype detection in peach, has been developed (Peace et al. 2005b; Peace and Norelli 2009).

VI. PRODUCTION AND HANDLING EFFECTS ON PEACH TEXTURE

A. Irrigation and Pruning

Environmental and cultural management practices greatly influence peach texture. Although Reeves and Cummings (1970) found a slight reduction in peach firmness with increased irrigation, Crisosto et al. (1997) found that irrigation had no influence on fruit firmness. Deficit irrigation (no irrigation) was found to increase the perception of increased firmness and crispness, but increased perception of texture was not always correlated with increased penetrometer firmness measurements (Lopez et al. 2010). Using deficit irrigation during only the second stage of peach fruit development, Vallverdu et al. (2012) found that the sensory perception of firmness and crispness by a panel of trained judges was reduced. As deficit irrigation tended to result in

smaller fruit, it was hypothesized that smaller fruit would generally be firmer due to higher cellular density compared to larger fruit, explaining the increased firmness in deficit irrigation. However, this was contradicted by the findings that firmness decreased due to deficit irrigation (Lopez et al. 2010, 2011; Behboudian et al. 2011). Behdoudian et al. (2011) reviewed the impact of reduced irrigation on peach fruit quality.

Pruning has a dramatic effect on the tree light environment; therefore, it has been hypothesized that this change in light environment can impact fruit firmness, though, like irrigation, the precise effect is debated (Lewallen and Marini 2003). Early work by Schneider et al. (1958) found that heavy pruning increased peach fruit firmness. Marini (1985) observed that peaches from summer-topped trees were firmer than those from summer-pruned and dormant-pruned trees and that fruit harvested from tree tops had reduced firmness compared to fruit harvested from the canopy interior. Additionally, deviating from routine pruning practices has been reported to increase fruit firmness (Reeves and Cummings 1970).

B. Nutrient Management

The influence of Ca on physiological and biochemical changes during fruit ripening was reviewed by Poovaiah et al. (1988). Robson et al. (1989) found that foliar Ca applications tended to increase firmness and improve storage performance. By increasing firmness, the onset of the melting stage was significantly delayed, and therefore, the authors suggested that Ca applications could be used as a method of postponing harvest (Robson et al. 1989). But, Crisosto et al. (2000) found that Ca foliar sprays had no effect on fruit firmness (Gradziel and McCaa 2008). Although postharvest fruit Ca application was shown to increase firmness during storage, fruits treated with Ca were found to have an undesirable taste (Prussia et al. 2005) and resulted in skin injury (Wills and Mahendra 1989).

High levels of N fertilization were found to decrease the size of cells from the outer and inner flesh compared to lower N rates (Reeve and Neufeld 1959). Reeves and Cummings (1970) found that increased N levels (from 0.15 to 0.30 kg N per tree) decreased shelf-life and firmness in MF fruit, but only in minimal irrigation environments. Despite this, Proebsting (1957) found that high N levels increased fruit quality. Although high N content has been shown to be associated with decreased firmness, there is no clear explanation for such effects. Possibly the N effect on rate of fruit growth affects cell properties such as cell turgor and cell wall strength resulting in variations in fruit

firmness (Ferguson and Boyd 2002). Liu et al. (2010) found that increased suture size and softening were greater in trees with high levels of N fertilization compared to low levels.

Reeves and Cummings (1970) found that soil-applied Mg fertilization decreased shelf-life and firmness, while P and K applications increased firmness (Sistrunk 1985). When peach trees were sprayed with a foliar formulation of Ca, Mg, and Ti, fruit firmness at harvest and during storage (7–28 days) was higher than in fruit from un-sprayed trees (Serrano et al. 2004). The foliar/exogenous application of jasmonates and the infiltration of putrescine was found to delay ripening and therefore reduced the rate of softening of peach fruit (Martínez-Romero et al. 2000; Tonutti et al. 2001; Ziosi et al. 2007a; Payasi and Sanwal 2010).

C. Bruising

Peach bruising results in substantial textural changes on and within damaged fruit. Yield losses in both the fresh and processed markets generally occur during harvest and transport as a result of physical or mechanical bruising damage, with up to 50% of fruits sustaining damage (Gradziel and McCaa 2008). Generally, peach fruits are dense with a low volume of intracellular air space and, therefore, are susceptible to deep bruises, which develop in cone-shaped and radial fractures that are not necessarily visible on the fruit surface directly after impact (Maness et al. 1992a). The lack of firmness in ripe peaches, which makes the fruit very vulnerable to bruising, is a major problem in fruit handling (Lill et al. 1989). Although delaying harvest can increase fruit size, blush, and SSC, it also decreases fruit firmness, making the fruit more susceptible to bruising and potentially incapable of maintaining quality during harvest, transport, and storage (Crisosto 2007). Within the USDA standards for grades of peaches, all four grades require fruit to be free from damage caused by bruises, except "U.S. No. 2" that requires fruit only be free from serious damage caused by bruises (USDA 2004).

Fruit bruises commonly result from impacts (dropping, bouncing, or jarring), compression (over-filled bins or displays), and vibration (abrasion between fruit or surfaces) (Brusewitz et al. 1992; Crisosto and Valero 2008). Peach and nectarine cultivars differ in their response to impact. Maness et al. (1992a) found that when impacted with various levels of force, negligible changes were found in fruit respiration and ethylene production. Ripeness and drop height were directly correlated with the percentage of fruit bruised and bruise volume, but the characteristics necessary for peaches to be highly resistant to bruising are not

known (Brusewitz et al. 1992). Hung and Prussia (1989) found that bruise volume and susceptibility increased with maturity and storage time. They also concluded that bruise susceptibility could be predicted by failure stress or puncture force, and could be used to predict bruise volume when a specific impact energy was used. Critical impact bruising thresholds have been developed that identify the minimum firmness required to prevent impact bruising (Crisosto et al. 2001b; Crisosto 2007). For nectarine cultivars, bruising was significantly enhanced when fruit softened below 4.5 kgf, and for peach cultivars, bruise potential was significant when softened below 3.6 kgf (Crisosto 2007). Bruising thresholds vary among cultivars, with maturity, degree of pubescence, and fruit size affecting bruise expression and development.

Along with postharvest cold storage, the treatment of peaches with plant growth regulators (i.e., polyamines and gibberellic acid) prior to harvest and/or before handling and storage has been shown to be effective in reducing fruit susceptibility to bruising by increasing firmness (Crisosto and Valero 2008; Ahmadi et al. 2010). Postharvest treatment of peaches with aminoethoxyvinylglycine (AVG) has been found to delay softening during storage at room temperature and in cold storage (Garner et al. 2001; Hayama et al. 2008a; Ramina et al. 2008). Preharvest AVG treatment also resulted in delayed softening during room temperature storage (Bregoli et al. 2002), but after 1 week the treatment effects were no longer noticeable (McGlasson et al. 2005). Treatment of peaches with MCP resulted in higher levels of firmness during storage (Grima-Calvo et al. 2005; Hayama et al. 2008a). The MCP treatment inhibited ACS activity, in turn reducing ethylene production and slowing flesh softening (Mathooko et al. 2001). Although MCP treatment slows softening, the effects vary with fruit maturity, generally decreasing as ripening proceeds (Ziosi et al. 2007b). Additionally, Tonutti et al. (2007) found that MCP treatment at the s3 phase down-regulated ACO, induced expansin (contig 941), and had a negative effect on PG, PME, and expansin (contig 938) expression. Preharvest treatment of peaches with polyamines (spermidine) significantly delayed flesh softening as well (Bregoli et al. 2002). Although several chemical treatments can be used to reduce flesh softening, developing cultivars with resistance to bruising is likely the most effective means of reducing fruit loss due to bruising.

D. Cold Storage and Its Effects on Peach Texture

Peach fruits are highly perishable. Even under perfect storage conditions the cold-storage life ranges from 2 to 6 weeks depending upon

cultivar (Lill et al. 1989). Without cold storage, peaches ripen and senesce rapidly, having a shelf-life of 1 day to 1 week depending on picking maturity, flesh type, and cultivar (Lill et al. 1989). Although cold storage is essential for commercial production, low temperatures can dramatically affect fruit texture as well as flavor, color, and skin quality (Lill et al. 1989; Harker et al. 1997). Chilling injury (CI), also known as internal breakdown, has been found to affect numerous horticultural crops after cold storage at temperatures above freezing but below 10°C (Luchsinger and Walsh 1998). The symptoms of CI in peach include the development of mealiness (Fig. 6.1c), skin and flesh browning, flesh translucency, color bleeding from skin and pit, and loss of flavor (Crisosto 1999). CI in stone fruit has been reviewed by Lill et al. (1989). Although there are many symptoms of CI, the most pertinent to texture is the development of mealiness.

1. Mealiness. Mealiness, also referred to as woolliness, is perceived as a dry, coarse, gel-like quality/feeling when peach fruit is chewed. Since there is no noticeable external appearance difference between mealy and nonmealy peaches, the detection of mealiness can be a major challenge (Von Mollendorff et al. 1992b; Luchsinger and Walsh 1998). However, detecting and understanding mealiness and its causes are very important to commercial peach production because it is highly negatively correlated with consumer acceptance of fresh fruit (Luchsinger and Walsh 1998). Apart from simply visually assessing the mesocarp, the level of extractable juice content (EJC) is the most common method for assessing mealiness.

Harker and Maindonald (1994) found that a higher resistance of the cell wall was present in mealy nectarine fruit compared to nonmealy tissue, indicating that membrane permeability is reduced in mealy fruit although the membranes remain structurally intact. Along with reduced membrane permeability, reduced levels of EJC were found in mealy peaches (King et al. 1989; Zhou et al. 1999). Von Mollendorff et al. (1992a,b) found that maximum woolliness paralleled minimal EJC and that storage at −0.5°C resulted in less CI than storage at 3°C. King et al. (1989) concluded that mealy texture was associated with an incomplete degradation of the cell wall during ripening and likely resulted from the pressure necessary to break the cell walls during mastication. Based on these studies, the loss of EJC and appearance of thick juice that does not flow freely can be used as a measure of fruit mealiness, although this method was not always found to be reliable (Von Mollendorff et al. 1992a). Several methods have been used to measure juiciness and therefore EJC (Harker et al. 1997). Lill and Van

Der Mespel (1988) developed a method of rating mealiness based on juice content after gentle homogenization and centrifugation that correlated well with taste-panel assessment. A simple and reliable method for determining juice content that can be used for evaluating mealiness development was also developed by Infante et al. (2009).

Early work by Guelfat-Reich and Ben-Arie (1966) on mealiness found that no differences in mealiness or other chilling symptoms were found among peaches of different cultivars and harvest maturities. Later work by Visagie and Eksteen (1981), Eksteen (1984), and Lill et al. (1989) found a higher level of mealiness after storage in early mature (green) harvested fruit, although Valero et al. (1997) found CI to be more severe at a late stage of harvest maturity. Luchsinger and Walsh (1998) found no relationship between maturity stage and wooliness in controlled atmosphere (CA)-stored fruit. Additionally, it was reported that the incidence of mealiness was highest directly after cold storage and decreased during subsequent storage (10, 15, and 20°C) until no symptoms were observed, although EJC remained low (Von Mollendorff et al. 1989). This indicates that holding peaches at ~20°C prior to retail display could reduce the incidence of mealiness, but the reduction in mealiness subsequent to cold storage appears highly cultivar dependent (Von Mollendorff et al. 1989, 1992b). During on-tree ripening, water-soluble pectin increased and EDTA-soluble pectin and protopectin decreased, although the total amount of pectin remained constant (Ben-Arie and Lavee 1971; Pressey et al. 1971; Shewfelt et al. 1971; Sistrunk 1985; Lill et al. 1989). In comparison, Ben-Arie and Lavee (1971) found that after 2 weeks of cold storage, the insoluble pectin fractions within peach fruit increased, and as a result, the total amount of pectic substances increased. This increase in total pectic substances was attributed to the continued activity of PME during storage and inactivity of PG. Not only has PME activity been found to continue during storage, it may even increase, while PG activity is completely inhibited (Artés et al. 1996).

Buescher and Furmanski (1978) and Furmanski and Buescher (1979) concluded that reduced activity of PG during subsequent ripening along with a reduced electrolyte leakage and internal conductivity was responsible for mealiness in peach. The imbalance caused by the continued activity of PME during cold storage with decreased activity of PG resulted in the accumulation of deesterified pectate, which would provide for the development of pectate gel in the presence of Ca (Ben-Arie and Lavee 1971; Furmanski and Buescher 1979; Lill et al. 1989; Zhou et al. 1999, 2000; Peace et al. 2005a). Work by Dawson et al. (1992, 1993) found that Ca uptake and efflux was greater in mealy

fruit tissue than in normally ripened tissue, supporting the earlier findings that the formation of Ca pectate gel in the cell wall is responsible for mealiness. The dissolution of the middle lamella, cell separation without substantial cell fracturing (increased intercellular spaces), thickening of the primary wall, and irregular cell shape were found in mealy fruit as CI developed, all of which supported the idea that Ca pectate gels were formed and responsible for the mealy texture (Lill et al. 1989; Luza et al. 1992). Additionally, cell walls in mealy fruit appeared to thicken over two times that of nonmealy fruit (Luza et al. 1992). Based on tensile testing of mealy fruit, Sistrunk (1985) found that fractured cell surfaces were covered in a layer of juice, but with no visible cell damage. Although the fractured cell surfaces were covered with juice, Harker and Sutherland (1993) found that in mealy tissue the exudation of juice into extracellular spaces was inhibited compared to nonmealy tissue.

In some cultivars, mealiness was found to be greater in the inner than the outer mesocarp (Zhou et al. 2000). Although different from mealiness, Luza et al. (1992) reported a leathery texture in NMF fruit with CI. During cold storage of NMF fruit, uronic acid and cellulose content were reduced, neutral sugars increased, and PG and PME activity was low (Manganaris et al. 2006). After cold storage, EGase, endo-1,4-β-mannanase, β-galactosidase, α-arabinosidase, and endoPG activity was lower in mealy fruit than in nonmealy fruit. These changes were suggested to cause tissue breakage along enlarged air spaces, reducing the levels of EJC (Brummell et al. 2004). It was found that spermidine (free polyamine) concentrations increased in mealy peaches, but decreased in nonmealy peaches (Valero et al. 1997). Obenland et al. (2003) found a correlation between expansin expression and mealiness and suggested that expansins possibly play a role in the development of this disorder.

Susceptibility to mealiness is cultivar dependent, with MF fruit being significantly more susceptible to mealiness development than NMF fruit as seen through the expansion of intercellular spaces in MF mesocarp tissue but not NMF tissue (Brovelli et al. 1998). The NMF and NSF fruits are essentially resistant to mealiness (Infante et al. 2009; Peace and Norelli 2009). The SH cultivar 'Ghiaccio-1' showed good cold storage performance with fruit maintaining high eating quality for 30 days of cold storage, but little work has been done on mealiness development in SH or SR cultivars (Testoni and Fibiani 2006). Although not quantified until recently, the association of reduced PG activity and the development of mealiness has been well established since the 1970s (Buescher and Furmanski 1978; Furmanski and Buescher 1979;

Sistrunk 1985). A large QTL for mealiness was detected at the *F-M* locus, indicating that mealiness occurred in freestone-MF progeny, but was absent in clingstone-NMF progeny (Peace and Norelli 2009). Peace et al. (2005a) confirmed that endoPG plays a critical role in mealiness development, as endoPG activity is required for the expression of other gene(s) controlling mealiness, and found that endoPG is epistatic in the genetic control of mealiness (Peace and Norelli 2009). This finding was corroborated by Martínez-García et al. (2012) who concluded that the lack of mealiness in NMF fruit is directly correlated with the lack of a functional *Melting* gene.

Melting-flesh cultivars exhibit wide variability in mealiness susceptibility (Crisosto 1999). Peace et al. (2006) concluded that within MF cultivars, heritability of mealiness susceptibility was high, which led to the hypothesis that there is potential for as few as two loci being responsible for this disorder. QTLs accounting for almost 50% of mealiness variation in MF progeny have been identified and work is being conducted to verify the QTLs and develop diagnostic genetic tests (Peace et al. 2005b, 2006; Ogundiwin et al. 2007). Additional work is under way to identify other genes associated with mealiness, with researchers using comparative expressed sequence tag transcript profiling to find genes associated with mealiness (Ogundiwin et al. 2007; Peace and Norelli 2009; Vizoso et al. 2009).

2. Methods for Limiting Mealiness. It has been found that lower storage temperatures, the optimum being $0 \pm 0.6°C$, improve storability (Luchsinger and Walsh 1998). Although mealiness developed at 0°C, symptoms took significantly longer to appear than when fruits were stored at 5°C (Luchsinger and Walsh 1998). Although Von Mollendorff (1992b) found that after 4 weeks of cold storage mealiness was greater than after 1–3 weeks and that mealiness dissipated as ripening progressed after storage, this was highly cultivar dependent. Several methods have been developed to reduce CI, specifically mealiness development in cold storage, including preconditioning, intermittent warming, CA storage, ethylene application, and several other chemical application treatments.

By exposing cold-stored fruit to intermittent warming (~20°C) from 2 days every 3 weeks to 1 day per week, CI was successfully reduced and nectarine eating quality was maintained for 6 weeks (Anderson and Penney 1975; Lill 1985). But, intermittent warming resulted in flesh softening, which could limit fruit shipping potential (Lill 1985). The delayed development of mealiness after intermittent warming was directly associated with an increase in PG activity, which was normally

limited in cold storage (Ben-Arie and Sonego 1980; Peace et al. 2005a). Preconditioning fruits by exposing them to ~20°C for 12–48 h after harvest, but prior to cold storage, has also been shown to delay the development of CI and is successfully being used commercially in California and Chile (Crisosto et al. 2003, 2004; Crisosto and Valero 2008). Preconditioned fruits were more tolerant to poor storage temperatures and developed significantly less mealiness (Zhou et al. 2000; Crisosto et al. 2003). Additionally, after storage, preconditioned fruits were generally of higher eating quality with increased market life, which was attributed to the increased PME and PG activity (Choi and Lee 2001; Crisosto et al. 2003, 2004; Crisosto and Valero 2008; Martínez-García et al. 2012).

CA storage has been shown to reduce CI (Wade 1981). The addition of CO_2 to the storage atmosphere not only reduced mealiness development, but also increased firmness up to 6 days after removal from cold storage (Wade 1981). With CA storage, retention of fruit firmness and ground color was improved, although the precise impact of CA was dependent on cultivar, maturity, preharvest factors, temperature, and fruit size (Crisosto 1999; Garner et al. 2001). Although modified atmosphere packaging provided partial reduction of CI in peaches, mealiness symptoms were found to be the least affected with only 33% of fruit showing reduced levels of mealiness from modified atmosphere packaging (Zoffoli et al. 2002). For a review of the potential impact of CI and modified atmosphere packaging on peach quality, see Crisosto et al. (2009). Ethylene application during storage has been recommended as a method for controlling mealiness development in cold-stored fruit (Lurie et al. 2002). Several studies found that ethylene application during cold storage or CA storage with high levels of ethylene delayed the onset of mealiness, reduced mealiness symptoms, and increased the level of EJC in the fruit (Crisosto et al. 2001a; Lurie et al. 2002). Although the effects of AVG postharvest dip treatment and high CO_2 CA storage on mealiness development were not studied, it was found that fruit treated with AVG had a significantly increased level of firmness throughout storage (Garner et al. 2001). Postharvest application of MCP and N_2O had no measurable effect on mealiness development during storage, but treated fruit maintained high quality during extended storage and had higher levels of firmness than the control (Grima-Calvo et al. 2005).

A total of 106 genes were found to be differentially expressed between juicy and mealy peach fruit. Data analysis indicated that the activity of most of these genes (>90%) was repressed in the mealy fruit. In cold-stored peaches, the expression level of selected genes (*cobra, endoPG,*

cinnamoyl-CoA reductase, and *rab11*) was lower than in juicy fruit, and remained low in woolly peaches after ripening (González-Agüero et al. 2008). Borsani et al. (2009) conducted a detailed evaluation of the enzymes and biosynthetic pathways operating during postharvest ripening, and several enzymes (e.g., neutral invertase) not yet correlated with fruit ripening were identified as important components of the postharvest ripening process. Further research on these enzymes and the biochemical changes associated with mealiness are needed to develop procedures for the prevention of mealiness development. The only long-term solution to CI, particularly mealiness, is the development of cultivars with a high level of resistance. Although progress is currently being made through traditional breeding practices, a better understanding of the mechanisms and inheritance of mealiness is needed to solve this important problem (Martínez-García et al. 2012).

VII. SUMMARY

The peach has been and continues to be a popular fruit in countries across the world. As long as 2,000 years ago, peaches have encompassed a diversity of textures. This diversity can still be found today in cultivars and breeding program germplasm. Consumer satisfaction with peaches has not increased in recent years while other fruit have had dramatic increases in consumption, and it is at least partially due to inconsistent peach fruit quality. With one of the main goals of everyone involved in the peach industry being to provide consumers with a high-quality product, understanding what constitutes quality from the perspective of texture is of utmost importance.

The term texture refers to a wide range of attributes that determine "mouth-feel," with the texture of peaches encompassing the qualities of hard, soft, crisp, juicy, melting, floury, and gritty among others. Texture is dependent upon the attributes of cells and cell walls, with cell size, cell wall thickness, cell turgor pressure, cell adhesion, and cell shape all playing a role. In addition, environment and cultural management practices can affect the precise expression of peach texture. Numerous enzymes have been identified as playing a role in pectin modification and other biochemical changes related to peach flesh texture, specifically the ripening and softening pattern. Of these enzymes, endoPG has received substantial attention as it has been found to be responsible for several of the major differences in peach flesh texture.

Within peach breeding programs, there is a trend toward developing new fruit types and improved postharvest traits, both of which are

highly correlated with fruit texture. Within these programs, firmness is ranked in the top three of most important characteristics in terms of cultivar development and selection. The fresh-market peach industry has been and continues to be dominated by peaches of the MF type, while the processing industry is made up predominantly of the NMF type. Additional flesh types including SMF, SH, NSF, and SR have been and are currently in development and could potentially become prominent in either industry due to their unique characteristics including such qualities as bruising resistance, extended shelf-life, and superior cold-storage performance. One cold-storage disorder directly related to peach texture is mealiness, which dramatically reduces fruit quality. Thanks to years of work combating mealiness, several methods have been developed for limiting its development, and work is in progress to develop cultivars with a high level of resistance.

The diversity of peach texture dramatically complicates industry regulations based on texture measurements designed to facilitate quality management and marketing. Texture measurement is of primary importance and a major challenge, due in part to fruit-to-fruit variability and within-fruit differences. Measuring texture is essential in assessing fruit maturity and quality, and the understanding of the influence of environment, preharvest and postharvest factors, breeding, and other factors on texture is based in part on the development of instrumental texture measurement technologies.

Although the routine application of molecular markers in peach breeding programs has yet to develop, marker-assisted breeding for texture characteristics is seeing its first use. By understanding the biochemical, genetic, and physiological bases of texture, breeders as well as others involved in the peach industry will be provided the means for developing and producing new cultivars that are of high quality and convenient for consumers, thereby increasing peach consumption.

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7

High-Density Olive Plantations

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ABSTRACT

Hand-harvested traditional plantations with 70–100 trees ha^{-1} are being replaced by high-density mechanically harvested orchards. Diverse typologies of high-density orchards are currently planted. Intensive orchards (150–250 trees ha^{-1} under rainfed conditions to 200–400 trees ha^{-1} under irrigation) are harvested with trunk shakers and catching frames. Wide hedgerow (450–800 trees ha^{-1} and up 4 m wide) is harvested with self-propelled trunk shakers with slanted canvas or with big sized continuous harvesters. Narrow hedgerow (800–1,000 trees ha^{-1} in rainfed conditions and >1,500 trees ha^{-1} with rows less than 1.5 m wide under

Horticultural Reviews, Volume 41, First Edition. Edited by Jules Janick.
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irrigation) is harvested with straddle harvester. Earliness of bearing and cumulated productivity is related to plant density. Interception of radiation by sunlit canopy becomes a major factor determining productivity and oil rate. In hedgerows of continuous canopies, the link between cover and light interception is determined by row distance, orientation, and porosity (i.e., permeability of incident radiation to penetrate into the canopy). A few traditional early-bearing and productive cultivars are planted in intensive and large hedgerows, while only three cultivars ('Arbequina', 'Arbosana', and 'Koroneiki') are mainly planted in narrow hedgerows. Cultivar standardization and specific requirements of new high-density systems are objectives of breeding programs. Interaction between cultivar, irrigation strategies, plantation design, training and pruning, and general orchard management is critical to maintain canopy size and shape allowing optimal light interception, and ease of access to fruits by harvesting systems. *Verticillium* wilt has been a problem in high-density orchards due to various factors associated with intensification. High-density orchards may also be more affected by some other pests and diseases than traditional systems. Integrated pest management, including tolerant and/or resistant cultivars and pathogen-free certified nursery plants, is recommended. Comparative costs indicate that all high-density orchards are able to produce benefits over traditional orchards. High-density olive plantations development will represent a threat to the continuity of traditional plantations, an opportunity for a competitive olive oil industry, and a challenge for the research and development.

KEYWORDS: breeding; canopy hedgerow; irrigation strategies; management; mechanical harvesting; *Olea europaea*; production costs; verticilium wilt

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ACKNOWLEDGMENTS
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I. INTRODUCTION: OLIVE GROWING IN A TIME OF CHANGE

Olive groves are mainly located in the Mediterranean Basin and have played a major role in the culture there for thousands of years. However, a progressive transformation in olive growing techniques is under way in response to changing socioeconomic conditions and advances in technology. Traditional, manually harvested nonirrigated olive plantations are being replaced by new irrigated orchards designed for mechanized harvesting.

Several factors have converged to shape traditional olive plantations. First, the olive is a species that is well adapted to Mediterranean climates, which are characterized by long, dry summers, irregular rainfall for the rest of the year, and relatively mild winter temperatures.

Most plantations were established to provide widely spaced, long-lived trees of considerable size on nonirrigated land. This form of olive monoculture remains the most common farming system in many regions. Management techniques are generally based on local age-old empiricism, productivity per hectare is low, and the gradual increase in demand for olive oil and table olives has been met with new plantings on progressively poorer and more fragile soils. Manual harvesting is still practiced in many farms and continues to be a major source of employment and income for numerous people during the 2–3 month harvesting period.

After the Second World War, olive production underwent a profound change in the northern regions of the Mediterranean and in new olive-producing areas throughout the world. Rural emigration to cities required more productive olive plantations that became increasingly mechanized and required increased capital investment. The accumulated changes since that time have resulted in a new type of olive growing. New olive orchards bear earlier and their lifespan are shorter than traditional plantations. Tree densities are also higher, and trees are smaller and more adapted to mechanical harvesting than in traditional plantations. Good Agricultural Practices (GAP) to limit soil erosion and environmental contamination and attempts to increase crop quality have been progressively introduced. Annual management, including harvesting and pruning, which are the two most labor-demanding activities of the production cycle, has been mechanized and simplified. Productivity has been increased through irrigation, higher tree densities, and the selection of early-bearing trees using high-yielding cultivars propagated by a dynamic nursery industry. Breeding programs to produce new cultivars are under way in various countries. Finally, olive oil and, to a lesser extent, table olives are progressively being accepted as a healthy food. The result is a gradually increasing world demand for these products. A general overview of the current state and recent advances in the olive industry within and outside Mediterranean countries was reported in the Second International Seminar Olivebioteq held in Sicily [Caruso et al. (eds.) 2006] and in *Acta Horticulturae* 924 (Tous et al. (eds.) 2011). A monographic issue of *Advances in Horticultural Sciences* 24(1) edited by Fiorino (2010), including various papers on olive intensification and mechanization, has also been published.

This review focuses on the intensification of olive plantations with particular emphasis on high-density orchards. Several preliminary comments are required. First, it is necessary to clarify the concept of high density. In traditional olive groves and orchards, tree density may range from 17 to more than 300 trees ha^{-1}, with an average density of

less than 100 trees ha^{-1}, mainly in response to rainfall. The density in new intensive irrigated mechanized orchards, in contrast, ranges from 200 to over 2,000 trees ha^{-1}. Thus, although intensification is not necessarily achieved through higher density, an increase in plant density has clearly occurred in the orchards over the last 60 years. Therefore, we propose a typology of olive orchards based on various criteria for planting intensification. Second, the recent progress in olive plantations has been propelled by private industry more than by research and development (R&D) systems, which required two sources of information for this review, especially for the recently developed high-density hedgerows, where empirical information on the fast development of these orchards precedes reports in scientific journals. Third, the new production paradigm presents challenges for stability in traditional olive oil and table olive industries and in R&D systems in olive-growing countries.

II. TYPOLOGIES OF OLIVE PLANTATIONS

The designation of olive plantations is diverse in different countries based on tradition and historical changes in the olive plantations. For instance, the terms grove, orchard, and plantation are often generically used as synonyms, though they may refer to specific olive plantings. We will use the term grove only for irregular, low-density rainfed olive plantations that are also devoted to cattle feeding, whereas the term orchard will refer to olive plantations associated with other crops or specialized for oil or table olive production. Plantation refers generically to any land with planted olives.

We propose a specific typology for the current olive planting systems based on the following criteria: (1) olive specialization or association with other growing species, (2) continuity or discontinuity of the canopy, (3) plant density, (4) water availability (rainfed or irrigated), and (5) method of harvest. Table 7.1 shows the proposed typologies for specialized olive plantations, ranging from traditional to continuous hedgerow orchards. It also summarizes the structure of the orchard (e.g., the continuity or discontinuity of the canopy, cultivars, volume of the canopy, density, and tree training and trunks per tree); production (e.g., years to full bearing, average crop at full bearing and years of full bearing); and method of harvesting and the overall quality of the oil. In this review, we will focus on high-density specialized orchards (intensive and hedgerow) and use traditional specialized orchards as a reference.

Table 7.1. Typologies of specialized olive plantations (orchards): planting systems, productivity, and methods of harvest.

	Typology of plantings						
	Discontinuous canopy				Continuous canopy (hedgerow)		
	Traditional orchards (T)		Intensive orchards (I)		Wide (WH)	Narrow (NH)	
Variable	Rainfed (RT)	Irrigated (IT)	Rainfed (RI)	Irrigated (II)	Irrigated (IWH)	Rainfed (RNH)	Irrigated (INH)
Cultivars	Diverse and local		Selected by high yield, early bearing, and adapted to mechanical harvest				
Density (trees ha^{-1})	17–300[a]	70–120	150–250	200–400	450–800	800–1,000	>1,500
Volume (10^3 m^3 ha^{-1})	6.3–9.8	11.0–13.0	8.0–10.5	12.0–15.0	14.0–18.0	No data	6.0–7.0
Tree training	Diverse, vase		Open vase and central leader		Wide wall	Narrow wall	Narrow wall
Trunks per tree	1–4	1–4	1	1	1	Variable	Variable
Production							
Years to full bearing	10–15	8–10	6–8	5–7	4–6	4–5	3–4
Yield at full bearing (t ha^{-1})	1–5	5–10	4–6	8–10	>10	4–6	>10
Years of bearing	>100	>100	>40	>40	>20	>15	>15
Oil quality and harvest method							
Oil quality	Irregular and PDO[b]		High standard quality		High standard quality		
Harvest method	Manual, branch shakers and poling		Shakers and catching frames		Diverse	Straddle harvesters	

Other obsolete plantations are not included in this table (see text).

[a]Related to rainfall.

[b]PDO (Protected Denomination of Origin).

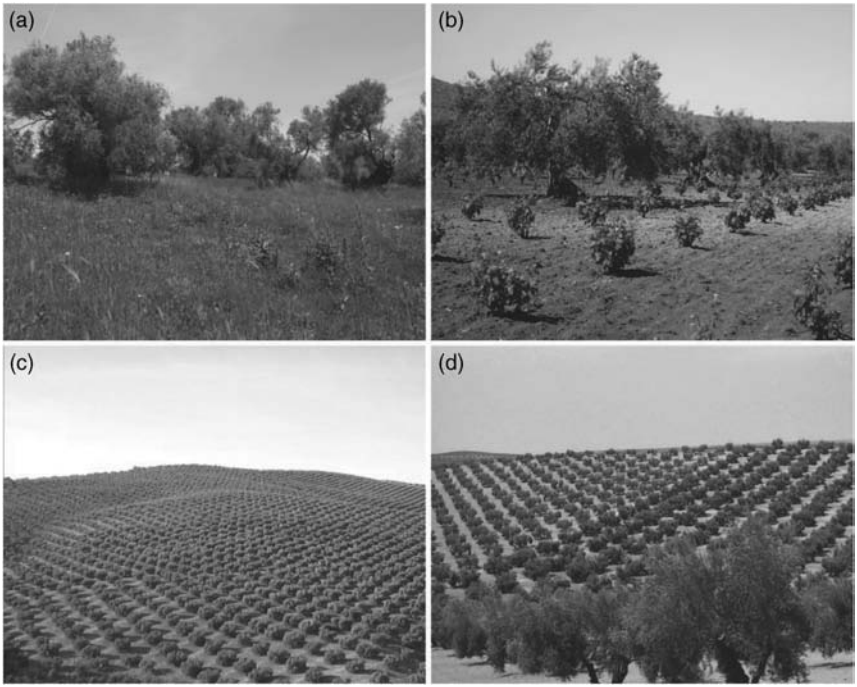

Fig. 7.1. Typologies of traditional olive plantations. (a) Grove (G). (b) Traditional associated orchard (TA) (courtesy of J.R. Guzmán-Alvarez unpublished). (c) Traditional rainfed specialized orchard (TR) (courtesy of J.R. Guzmán-Alvarez unpublished). (d) Traditional rainfed (T) (left) and irrigated (right) (TI) specialized orchards (courtesy of M. Pastor et al. 2005). (See text for further discussion).

A. Discontinuous Canopy

1. Traditional Olive Grove (G). These plantations (Fig. 7.1a) are composed of an irregular and scarce number of scattered olive trees in rainfed soil, which is often poor and shallow and located on high-slope land. Olive trees are usually planted at irregular distances associated with shrubs, annual crops, or pastures for grazing. Many of these plantations are started by thinning out wild olives to grow natural pastures or by sowing a mixture of annual or perennial species of cereal and legumes for grazing and top grafting with local cultivars onto wild olives. Groves may also be started by planting local cultivars using large cuttings or sphaeroblasts at low densities that are scattered or placed within the borders of plots used for husbandry activities. Both types of plantations seem to correspond to the first steps of olive growing as

indicated by current centennial olive plantations (Díez et al. 2011) and classical references (Holgado Redondo 1998; Foxhall 2007). These olive groves are, therefore, characterized by their longevity, middle- or large-sized trees, low planting density (between 17 and 50 trees ha^{-1}), rainfed farming, low input and yield, and high labor demand for manual harvest by hand, poling, or picking of naturally shed fruits.

2. Traditional Associated Orchards (TA). The Roman term *Hortus* refers to middle-sized family farms (*fundus*), fully cultivated with different species of fruits, vegetables, and ornamentals and annual crops that are systematically allocated into the farm, which may be irrigated. This term is extensively referred to in classical treatises by Theophrastus, Varro, Cato, Columella, Gaius Plinius (cited by Hooper and Bash 1993; Holgado Redondo 1998; Foxhall 2007). Olive orchards that include a mixture of other crops (e.g., fruit species, vines, vegetables, and cereals) have been continuously described since that time. Multicropping farms can now be found in the Mediterranean, which have a mixture of olives and other fruit crops (e.g., citrus, almond, or vines), vegetables, ornamentals, cereals, and leguminous species in both rainfed and irrigated farms (Fig. 7.1b). These species may share the same plot or occupy adjacent plots.

Olive plants usually belong to local cultivars propagated by large cuttings or sphaeroblasts in nurseries or *in situ*. Plants are propagated less frequently by grafting local cultivars onto seedlings in nurseries and planting them several years later in the orchards at a low or very low density (<50 trees ha^{-1}). Until the 1950s, multicropping olive orchards were cultivated in many Mediterranean countries (Morettini 1950; Pansiot and Rebour 1961). The main advantages of this type of orchard are that they provide some income to the farmers until full bearing in traditional olive farming and in off years because of the biennial bearing habit of this species.

3. Traditional Specialized Orchards (T)

Rainfed Traditional (RT). Orchards containing only olive trees have also been described since Classical times. Cato reported large farms with more than 6,000 trees exclusively planted with olives at low density (<100 trees ha^{-1}) in Rome (Hooper and Bash 1993). Similar specialized orchards with the same density were also reported in Greece during the Classical period (Foxhall 2007). Specialized orchards have been planted in Andalusia since Roman times. For instance, this type of orchard was reported in El Aljarafe, which was a permanent

olive-growing county close to Seville in the Roman Empire, by Columella (Holgado Redondo 1998), in Middle Age Muslim kingdoms by Al Awan (Cubero Salmerón 2002) and in the Modern Period (Guzmán-Álvarez 2004). El Aljarafe is currently a production site for table olives in specialized low-density traditional olive orchards.

Most traditional specialized orchards are planted with local cultivars in rainfed farms (Fig. 7.1c,d, left). Plants are propagated as described for multicropping orchards. The density ranges from 17 to more than 300 trees ha^{-1} and in exceptional cases up to 200–600 trees ha^{-1} (Pisani olive forest) (R.Gucci, pers. commun.), in different Mediterranean regions based on amount of the rainfall (Morettini 1950). Tree size is influenced by biological, environmental, and management factors. Training and renewal pruning are used to reduce tree size and enhance harvesting. The spacing of olives in traditional specialized orchards is adjusted for the expected final size of the olive relative to the training of the trees. For instance, rainfed orchards in Andalusia are vase-shaped either with one or several trunks rising from the ground. One-trunk trees are smaller than 3–4-trunk trees. The plant density of these orchards ranges from approximately 65 trees ha^{-1} (3–4 trunks $tree^{-1}$) to 120 trees ha^{-1} (1 trunk $tree^{-1}$). The 3–4-trunk trees, which are largely planted in Andalusia, show increased permeability of solar radiation into the lobe-shaped canopy and the traditional harvest is facilitated by beating the canopy with poles, which is possible because of the proximity of the canopy to the ground. The periodic pruning of adult olives (Ortega-Nieto 1969) allows the gradual renewal of the whole canopy over a period of more than 12 years by biennial removing half of the canopy on any individual trunk. Therefore, trees maintain at least 5/6 of their yield potential when compared with a full canopy during this period. This pruning system can be used therefore to adjust trees to the desired size for enhanced harvest and adapt the tree canopy size of local cultivars to suit the soil, rainfall, and site.

Irrigated Traditional (IT). This system (Fig. 7.1d, right) is similar to the system discussed above. Cultivars, tree density, tree spacing, and training were initially designed and established for rainfed conditions. After irrigation was established, when the trees were fully developed. The water applied in irrigated traditional orchards varies with availability from scarce seasonal application (50 mm) to regular (150–300 mm $year^{-1}$) deficit irrigation schedules throughout the season. Increases in tree size, canopy volume, and cropping correspond to the available water (rainfall + irrigation). In Spain, this system has been expanded in traditional orchards since the 1970s, especially after Spain entered the

EU, which subsidizes yield (Consejería de Agricultura y Pesca 2003). The difficulty of applying efficient mechanical harvesting is the main drawback of the rainfed and irrigated traditional systems (Gil-Ribes et al. 2008).

4. Intensive Orchards (I). Intensive olive growing appeared in Italy at the beginning of the 1960s (Breviglieri 1961), although its development was slow over the next 20–30 years (Scaramuzzi 1976; Fontanazza 1993). Fontanazza (1993) defined specific traits for intensive specialized olive orchards as follows:

- Advance bearing by high-density plantations. The density is higher than that in traditional specialized orchards and reaches 800 trees ha^{-1}. Bearing begins by the 3rd–4th year after planting, and the full crop is obtained by the 7th–10th year. A high crop yield is obtained throughout the full crop period. The yield for the central region of Italy is typically higher than 4,000–5,000 kg ha^{-1}in rainfed orchards and higher than 5,000–6,000 kg ha^{-1} in irrigated farms.
- Reduced longevity. The orchard lifespan should not be longer than 40–50 years.
- Simplified and mechanized management techniques, particularly training, pruning and harvesting. Labor requirements should be reduced from 300–400 h ha^{-1} in traditional orchards to 100–110 h ha^{-1} when harvesting and pruning are mechanized.
- Choice of cultivars that permits early, high, and regular cropping, good olive oil quality and adaptability to available mechanical harvesting and pruning.

By the middle of the 1960s, intensive olive growing started to be introduced in Spain and other Mediterranean countries. A manual was published by the FAO and INIA (Phillippe et al. 1976) to promote new methods of growing olive trees, particularly new planting systems. The proposed intensification followed the previous Italian experience. In Spain, irrigation becomes the major factor for intensifying olive plantations with, simultaneously, increasing density, intercepted radiation, and yield (Mariscal et al. 2000a). Based on water availability, we propose two types of intensive olive plantations.

Rainfed Intensive Orchards (RI). These orchards (Fig. 7.2a) have previously been reviewed in both Spain (Pastor and Humanes 1990; Pastor et al. 1993; Navarro and Parra 2008) and Italy (Fontanazza 1993; Vitagliano and Sebastiani 2003). Increasing the density from less than

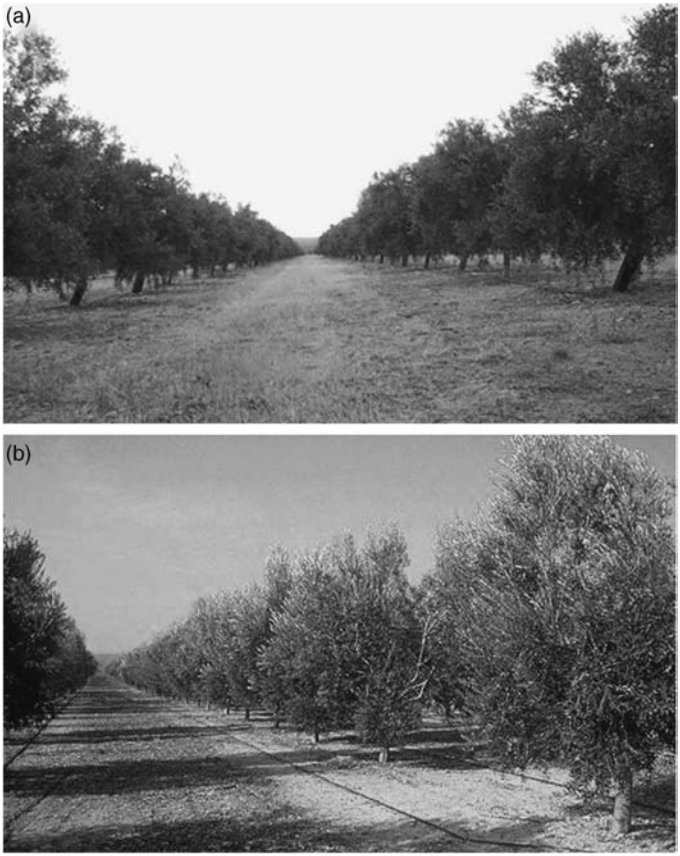

Fig. 7.2. Typologies of intensive plantations. (a) Intensive rainfed orchard (IR). (b) Intensive irrigated (II). (See text for further discussion). *Source*: Courtesy of M. Pastor (ed.) (2005).

100 trees ha^{-1} to 150–250 trees ha^{-1}, arranging plants in rectangular arrays (9×7 m to 7×6 m), and training trees in an open vase configuration with one trunk is currently recommended (Navarro and Parra 2008) for rainfed intensive and for mechanized orchards based on long-term experiments performed in Andalusia between 1966 and 1975 at densities ranging from 100 to 400 trees ha^{-1} (Guerrero 1988; Pastor and Humanes 1990; Pastor et al. 1993). These experiments were performed in different soils with an average rainfall between 400 and 550 mm $year^{-1}$. The cultivars planted were the best producers for olive oil and table olives among those traditionally grown in the region, and the oil cultivars were adapted to mechanical harvesting with trunk shakers.

The average time to full bearing ranges from 6 to 8 years after planting time. The yield of olives at full bearing ranges between 4 and 6 trees ha^{-1}, and the average oil content for a high oil yielding cultivar such as 'Picual' is approximately 20–22%, although oil content varies depending on the soil and annual rainfall.

Adjustment of this system to other olive-producing regions or cultivars should be based on the experience of previous orchards and experimental data. However, few experimental data have been available for most new olive-producing regions around the world until recently (Section III). The available water and incident radiation for rainfed intensive orchards are the main limiting factors for crop yield, fruit size, and oil content (Vitagliano and Sebastiani 2003; Navarro and Parra 2008). Fontanazza (1993) proposed that temporary trees be planted in rainfed orchards at a density of 400–600 trees ha^{-1} and removed when competition among the trees for water or incident radiation is observed. Eliminating half of the planted trees is justified only if the return income yielded by the crop produced until the time of removal of these temporary trees is higher than the investment cost of planting. Reducing tree size by periodic pruning is recommended as a better option for orchards with a tree density higher than 300 trees ha^{-1} when a reduction in incident radiation appears in the adult phase of the orchards (Pastor et al. 1993). A critical canopy volume of 8,000 m^3 ha^{-1} has been used as a reference for rainfed orchards in the most productive areas of Andalusia (Pastor 2005; García-Ortiz et al. 2008).

Irrigated Intensive Orchards (II). These orchards (Fig. 7.2b) have been largely developed during the last few decades (Fontanazza 1993; Vitagliano and Sebastiani 2003; Pastor 2005; Lavee 2006; Tous et al. 2006; Navarro and Parra 2008; Gómez-del-Campo et al. 2010; Vieri and Sarri 2010). The density ranges from 200 to 400 trees ha^{-1}. Planting distances range from 8×6 m to 6×4 m. Trees are trained in an open vase configuration with one single trunk and are harvested using trunk shakers and diverse catching frames. This system takes 5–7 years to reach full bearing with an average crop higher than 10 t ha^{-1}. The lifespan of these orchards is more than 40 years.

Irrigation has concomitantly increased the volume, external area of the canopy, and yield relative to the total water applied (rainfall + irrigation) up to 12,000–15,000 m^3 ha^{-1} (García-Ortiz et al. 2008). Shading reduces flowering and fruit size and delays ripening in the lower portion of the tree canopy in adult trees (plantations with an age > 15 years). This volume corresponds to the minimal distance between trees (4–5 m) within the row. At a density of 300–400 trees ha^{-1} for middle-vigor

cultivars, the total water applied was over 800 mm (rainfall + irrigation) (Pastor 2005). In Argentina, at low latitudes (30–35°S), when the total water applied was higher than 1,000 mm year^{-1} for middle and high-vigor cultivars planted at a density of 200–250 trees ha^{-1}, the exuberant vegetative growth of the trees built up continuous canopies with more than 14,000 m^3 ha^{-1} resulting in severe shading in the canopy and causing serious management difficulties for the orchard, particularly during harvesting (Gómez-del-Campo et al. 2010). Pruning and restricting water application have been suggested to control tree size and reduce shading when this critical volume value is exceeded (Pastor 2005; Correa-Tedesco et al. 2010).

B. Continuous Canopy (Hedgerow)

Sporadic use of hedgerows in olive orchards has been reported since the 1950s (Breviglieri 1961; Scaramuzzi 1976; Lavee 2010). Chronologically, the development of the olive industry based on narrow hedgerows (continuous canopy with a width less than 1.00–1.50 m) in irrigated olive orchards was triggered by the use of the vine straddle harvester for very-high-density orchards (>1,500 trees ha^{-1}) in the early 1990s (Tous et al. 2003; Rius and Lacarte 2010). The high investment required for establishing this system and the possibility of reducing these costs by decreasing the density (i.e., by increasing the distance between rows) promoted the expansion of very-high-density (800–1,000 trees ha^{-1}) hedgerows in rainfed farms with an annual rainfall of over 500 mm by the mid-2000s (www.todolivo.es, www.olint.com).

The previously described intensive olive plantations also tried to decrease the time to bearing and increase return on investment by increasing the density of the planting system and/or the amount of water applied to the orchard (Fontanazza 1993; Pastor 2005; Lavee 2006; Tous et al. 2006; Gómez-del-Campo and Fernández 2007). The concomitant increase in tree size causes the canopies of adjacent trees to merge, thus giving way to large continuous hedgerows. The difficulty of continuous harvesting in these tall and wide hedgerows results from the need for a large specific harvester, such as a straddle harvester with a rigid frame of 4 × 4 m (Lavee 2010; Ravetti and Robb 2010) or by a lateral hedge harvester and side-by-side shaker (Galán 2004; Vossen 2007; Ferguson et al. 2010; Lavee, 2010; Vieri and Sarri, 2010). Another shortcoming of this system is caused by the porosity (i.e., the permeability to incident radiation into the canopy) of the wide hedge (Connor 2006) is that it reduces the proportion of well-illuminated canopy area typical of narrow hedgerows. Limiting the size, height, and

width of the hedge by including existing low-vigor and early-bearing cultivars, breeding for low vigor, a compact habit of growth and for early bearing (Lavee 1990; Rallo 1995) or controlling deficit irrigation and pruning become critical for orchard management (Connor 2006; Gómez-del-Campo and Fernández 2007; Correa-Tedesco et al. 2010; Cherbiy-Hoffmann et al. 2012). The following three types of hedgerows have been developed in the past 20 years:

1. Irrigated Wide-Hedgerow Orchards (IWH). This orchard type (Fig. 7.3a,c) is also designed as high-density (HD) (Tous 2011). The system was derived from orchards with a discontinuous canopy, frequent and high volume irrigation, and high density (450–800 tree ha^{-1}) and designed to be harvested by trunk shakers, or it was derived from intensive (250–450 trees ha^{-1}), high volume irrigated orchards (Gómez-del-Campo et al. 2010; Cherbiy-Hoffmann et al. 2012) in subtropical areas. The decreasing efficiency of classical trunk shakers when more than 400 trees ha^{-1} are planted and the excessive tree size for vine straddle harvesters create a need for other harvesters. These orchards are harvested continuously by large straddle harvesters, lateral hedge, or side-by-side shakers (Ferguson et al. 2010; Lavee 2010). The planting distances are usually 7×3.5 m to 6×2 m. The total irrigated water ranges from 100 to 350 mm and is usually less than 250 mm in Mediterranean areas with moderate rainfall (400–550 mm). Monocone, ypsilon, and open vase training configurations with a trunk height of more than 0.60 m are common. Moderate vigor and early-bearing cultivars are used. An interval of 4–6 years is required before these orchards are full bearing, and they produce more than 10 t ha^{-1} $year^{-1}$ for 20–30 years. In subtropical arid areas of Argentina (200–450 mm of rainfall), highly irrigated orchards (>900 mm) with medium density (200–300 trees ha^{-1}) create very wide hedgerows that are difficult to manage in the long term (Cherbiy-Hoffmann et al. 2010; Correa-Tedesco et al. 2010; Gómez-del-Campo et al. 2010).

2. Narrow Hedgerow Orchards (NH)

Irrigated Narrow Hedgerow (INH) (Fig. 7.3b,d). This system is also called super high density (SHD) (Tous 2011) or superintensive (Rius and Lacarte 2010), and it was the first developed industrial hedgerow. The first orchard was planted at Valonga farm in Binefar (NE of Spain) in 1994 (Rius and Lacarte 2010). In this system, the plant density is higher than 1,500 trees ha^{-1}, and planting distances are 4×1.75 m to 3.5×1.35 m. Trees are trained in a central leader with 0.40 m of trunk

Fig. 7.3. Typologies of hedgerow plantations. (a and c) Irrigated wide hedgerow (IWH) also designed as high density (HD). (b and d) Irrigated narrow hedgerow (INH) also designed as super high density (SHD) or superintensive. (See text for further discussion).

height. The total irrigated water is limited to 100–250 mm in the Mediterranean climate (400–550 mm rainfall). Topping is also essential from 4 to 5 years after planting to limit the height and width of the hedgerow and allow the straddle harvester to pass over the hedge. The most planted cultivar, 'Arbequina', is an early-bearing low-middle-vigor cultivar. Other early-bearing cultivars such as 'Arbosana' and 'Koroneiki' have also been planted as complementary cultivars. Recently bred cultivars (e.g., 'Sikitita', Tosca', and 'Askal') are also being planted (Rius and Lacarte 2010; Tous 2011). These orchards require 3–4 years to reach full bearing and they produce more than 10 t ha^{-1}, on average, for more than 15 years.

Rainfed Narrow Hedgerow Orchards (RNH). This system is very similar to the NH orchard system described above. The concept of the narrow hedgerow is extended to rainfed orchards by increasing the distance

between rows and trees, particularly the former (www.todolivo.es). Density ranges from 800 to 1,000 trees ha^{-1}, and distances range from 6 to 7 m between rows and 1.5 to 2 m between trees within a row. The cultivars used are the same as in irrigated narrow hedgerows and canopy volume and external area are reduced correspondingly. Trees are also trained in a central leader with 0.4 m of trunk height. Orchards require 3–5 years to reach full bearing and they produce an average of 4–6 t ha^{-1}, depending on annual rainfall, for more than 15 years.

III. EFFECTS OF DENSITY ON PLANT PERFORMANCE

This section addresses the performance results related to tree density obtained from commercial orchards and field trials. Although increased tree density in olive orchards has been widely adopted in most olive-growing countries since the 1960s, little information is available regarding the influence of planting density on different aspects of olive tree performance and even less is known about high densities. A few reports have compared different planting densities; however, the orchard conditions range greatly from rainfed low tree density plantations (51 trees ha^{-1}) (Guerfel et al. 2010a) to very-high-density plantations with drip irrigation (2,581 trees ha^{-1}) (León et al. 2007b). In some cases, the results are derived from commercial orchard surveys (Pastor et al. 2005; UC Davis Olive Center 2009) (www.olint.com) and in a few cases from established specific density trials (Psyllakis et al. 1981; Pastor and Humanes 1990; Pastor et al. 1998; Tous et al. 1999; León et al. 2007b; Pastor et al. 2007; Msallem et al. 2008; Tous et al. 2010; Tous 2011; Guerfel et al. 2012).

The most relevant publications on this topic, including papers and congress proceedings are summarized in Table 7.2. The most important results regarding the different traits studied are highlighted below.

A. Size and Growth Habit of the Tree

Controlling tree size to prevent shading problems (competition for light between neighboring trees) and to accommodate straddle harvesters are the main challenges in the development and long-term viability of olive hedgerow orchards. Nevertheless, the effect of density on tree growth has been poorly studied.

In a planting density trial with the 'Arbequina' cultivar (Tous et al. 2005), significant differences were found in tree growth only between the lowest density (238 trees ha^{-1}) and the remaining studied

Table 7.2. Planting density trials in olive tree.

Year planted	Conditions	Density (trees ha^{-1}) and layouts (m × m)	Cultivar	Traits evaluated	Reference
El Carpio and Motalbán, Córdoba (SW Spain)					
1974	Open vase with 1–3 trunks per tree, rainfed conditions	Six densities: 100 (10 × 10), 156 (8 × 8), 200 (7.07 × 7.07), 312 (8 × 4), 400 (5 × 5), 400 (7.07 × 3.51)	Picual	Fruit yield, fruit size, oil content	Pastor and Humanes (1990)
Crete (Greece)					
1967	Open vase, irrigation	Four densities: 280 (6 × 6), 400 (5 × 5), 560 (6 × 3), 620 (4 × 4)	Koroneiki	Fruit yield	Psyllakis et al. (1981)
Jemmel (Center Tunisia)					
1988	Rainfed (250 mm)	Four densities: 51 (14 × 14), 69 (12 × 12), 100 (10 × 10), 156 (8 × 8)	Chemlali	Fruit yield, plant water status, gas exchange	Guerfel et al. (2010a); Kmicha et al. (2008)
				Fatty acid composition, fruit fresh weight, oil content, olive oil quality parameters, phenolic profile	Guerfel et al. (2010b)
				Triacylglycerols, volatile compounds	Guerfel et al. (2012)
Córdoba (SW Spain)					
1984	Open vase, irrigation (4,000 m^3 ha^{-1})	Six densities: 200, 250, 300, 350, 400, 450	Arbequina	Fruit yield, oil content	Pastor et al. (1998)
Reus (NE Spain)					
1984	Rainfed (500 mm)	Six densities: 179, 220, 227, 280, 312, 385	Arbequina	Fruit yield	Tous et al. (1999)

(*continued*)

Table 7.2. (*Continued*)

Year planted	Conditions	Density (trees ha^{-1}) and layouts (m × m)	Cultivar	Traits evaluated	Reference
1995	Trees trained to monocone (central leader), open vase in lowest density, Irrigation (1,500 m^3 ha^{-1})	Five densities: 238 (7 × 6), 555 (6 × 3), 666 (6 × 2.5), 740 (4.5 × 3), 888 (4.5 × 2.5)	Arbequina	Tree growth, yield, fruit traits	Tous et al. (2005, 2008a)
Córdoba (SW Spain)					
1999	N–S rows, open vase in three first densities, central leader in highest density, fertigation	Four densities: 204 (7 × 7), 408 (7 × 3.5), 816 (3.5 × 3.5), 1.904 (3.5 × 1.5)	Arbequina	Fruit yield, oil content, fruit distribution, and vegetative growth along canopy height layers	Pastor et al. (2005, 2007)
Pedro Abad, Córdoba (SW Spain)					
2000	N–S hedgerow, trees trained to a central leader, fertigation.	10 densities 780 (5.7 × 2.25), 909 (5.5 × 2), 952 (5.25 × 2), 1,143 (5 × 1.75), 1,203 (4.75 × 1.75), 1,481 (4.5 × 1.5), 1,569 (4.25 × 1.5), 2,000 (4 × 1.25), 2,254 (3.55 × 1.25), 2,581 (3.1 × 1.25)	Arbequina	Fruit yield, oil content, moisture	León et al. (2007b); Muñoz-Díez et al. (2010)
Takelsa (NE Tunisia)					
2003	–	Four densities: 312, 416, 600, 1,250	Arbequina	Tree vigor (trunk cross-section, canopy volume, and width), fruit yield	Msallem et al. (2008)

Year of plantation, trial conditions, plant densities, layouts, cultivar, and traits evaluated are indicated when available in the original reference.

layouts (over 555 trees ha^{-1}) 10 years after planting. Trees grown under the lowest density conditions were larger, with wider trunk sectional area and greater canopy volume per tree; however, the total canopy per hectare was significantly lower (6,500 m^3 ha^{-1} vs. 14–18,000 m^3 ha^{-1} at higher densities).

Similarly, Msallem et al. (2008) reported increased tree size in terms of trunk cross-sectional area, canopy volume, and canopy width at lower densities (312 and 416 trees ha^{-1}) when compared with higher densities (1,250 trees ha^{-1}). Furthermore, the tree spacing seemed to influence the growth habit, as trees in wider layouts (lower density) tended to grow horizontally (low height/width ratio) when compared with trees under super-high-density cultivation. The canopy volume per hectare was higher in the highest densities. Moutier et al. (2010) also reported an effect of planting density on tree architecture when studying unpruned trees in two layouts (6×5 m and 6×2.5 m). When the density was doubled, a significant decrease in trunk basal diameter, canopy diameter along and across the row and canopy volume per tree was observed, but the tree height increased. A trend for fast vertical growth was also observed in unpruned trees planted at high densities (1,904 trees ha^{-1}) and irrigated over 6,000 m^3 ha^{-1} in Córdoba, where the average rainfall is 512 mm (Pastor et al. 2007). This paper described vegetative growth in two trees by dividing the canopy into five aboveground layers. The highest level of photosynthetically active radiation (PAR) was intercepted by shoots placed higher than 2.50 m (over 80%), whereas two layers below (between 1.50 and 2.50 m), the PAR never exceeded 40%. The PAR was very low (10%) in canopy layers below 1.50 m. Shoot growth expressed as the relative length increase mainly occurred in the uppermost layer where radiation levels were higher.

B. Fruit Crop

Olive production expressed as fruit and/or oil yield has been the most common trait evaluated in existing density trials.

Differences in production were observed in low to medium density trials under both rainfed and irrigated conditions. Whereas low densities usually showed higher production at the tree level, the highest yield per hectare was usually obtained via high densities (Pastor et al. 1998; Tous et al. 1999; Kmicha et al. 2008; Guerfel et al. 2010a). Nevertheless, a decrease in fruit yield and a higher alternate bearing for densities over 450 trees ha^{-1} have been reported 10–12 years after planting by Psyllakis et al. (1981) and Pastor et al. (1998), who suggested that this finding

could be attributed to a lower efficiency because of shading when the trees grow older (Pastor et al. 1998). In rainfed conditions, especially under high drought stress, tree-to-tree water competition increases with density and has a negative effect, similar to the more pronounced alternate bearing observed at higher planting densities (Guerfel et al. 2010a).

Tree density had a negative influence on fruit and oil yield per tree; however, the yield per hectare increased along with density. Similarly, Tous et al. (2005, 2008a,b) reported a higher average yield (approximately 10,000 kg ha^{-1}) in the highest densities (740 and 888 trees ha^{-1}) after 10 years of observation. No differences in productivity (kg cm^{-2} of trunk cross-section) or yield efficiency (kg m^{-3} of canopy volume) were found among the planting densities. Therefore, it seems that competition among trees in high-density treatments was not severe enough after 10 years to reduce production. According to Msallem et al. (2008), the yield efficiency and productivity were not influenced by the planting density.

A clear effect of planting density on fruit and oil yield was also observed in a narrow irrigated hedgerow (SHD) trial. Although a reduction in oil yield per tree was observed in their experiment, a significant positive linear regression between the density and cumulated oil yield per hectare was found at 7 (León et al. 2007b) and 12 years after planting (C. Muñoz-Díez, pers. commun.) for densities up to 2,581 trees ha^{-1}. Clearly, with adequate pruning and water management, the critical factor for cumulated oil yield is the number of meters of hedgerow per hectare within a range of row length from 1,754.4 m ha^{-1} (780 trees ha^{-1}) to 3,225.8 m ha^{-1} (2,581 trees ha^{-1}) (Fig. 7.4).

Different results were found by Pastor et al. (2005, 2007) in an experiment performed in Córdoba (537 mm of rainfall) with 600 mm of water applied by drip irrigation. In this trial, the accumulated fruit and oil yield 7 years after planting significantly increased with tree density up to 816 trees ha^{-1}, but in the layout with the highest density (1,904 trees ha^{-1}), the accumulated oil yield decreased because of a significant reduction in production beginning in the sixth year. In the same trial, the fruit distribution within the height of the canopy was studied in the fifth year using four different layers from the bottom to the top of the tree (0–75; 75–125; 150–125; 225–300). In the layout with the highest density, the highest portion of fruit production (over 68% of the total crop) was found in the upper and better illuminated portions of the canopy, whereas in trees planted at 408 trees ha^{-1}, the fruit was more evenly distributed. In both cases, higher oil content was found in the upper and better-illuminated layers. According to these authors, the

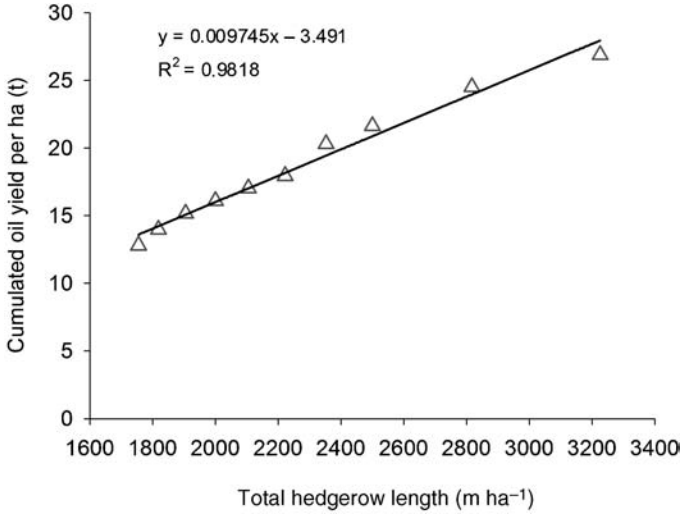

Fig. 7.4. Linear regression between cumulated oil yield per hectare 12 years after planting and linear meters of row in narrow hedgerow. *Source*: From data by León et al. (2007b) and Muñoz-Diez et al. unpublished.

shading problems became severe in super-high-density (irrigated narrow hedgerow) orchards soon after planting.

Fruit distribution within the canopy was also studied by Larbi et al. (2008) in a commercial olive orchard with 'Arbequina' and 'Arbosana' cultivars planted at 1,250 trees ha^{-1}. In both cultivars, the fruit yield was similar in the bottom (0–1 m) and middle (1–2 m) layers. In 'Arbequina', fruit was also found in the top layer, but none was found in 'Arbosana'. Significant differences in oil content were found among canopy heights, with lower oil content in the bottom layer.

C. Oil Rate

Oil production per hectare increases with planting density in most trials (Pastor and Humanes 1990; Tous et al. 1999; León et al. 2007b; Msallem et al. 2008; Muñoz-Díez et al. 2010). A positive linear regression between oil yield and density was found by León et al. (2007b), with accumulated oil rates ranging from 4,705 to 9,732 kg ha^{-1} in the 7th year and from 12,803 to 26,880 kg ha^{-1} in the 12th year (C. Muñoz-Díez, pers. commun.). This increase in oil yield seems to be a direct consequence of the fruit yield increase, as oil content seems to be barely influenced by tree spacing (Tous et al. 2005; León

et al. 2007b; Msallem et al. 2008), even under rainfed conditions in a semiarid area (Guerfel et al. 2010b).

In contrast, Pastor et al. (2007) found that oil yield increases along with density only during the first three years of production. Later, oil content was drastically reduced in the treatment with the highest density (1,904 trees ha^{-1}) because the trees had to be topped to suit the harvester, which resulted in a lower cumulative oil yield 6 years after planting. Furthermore, the fruit oil content was lower at the highest density. In a commercial orchard survey, the same authors (Pastor et al. 2005) reported low or moderate oil yield (1,300–2,100 kg ha^{-1}) in an irrigated narrow hedgerow (SHD) when compared with intensive orchards with 250–400 trees ha^{-1} (mean 1.727 kg ha^{-1} for the first six harvests, and mean 2.412 kg ha^{-1} for the adult stage).

D. Oil Composition

To date, the influence of planting density on oil chemical attributes has been reported by Guerfel et al. (2010b, 2012) in a low to medium density trial under rainfed conditions using the 'Chemlali' cultivar in Jemmel (Tunisia). Some olive oil quality traits were affected by the planting density, including fatty acid composition, pigment content (chlorophyll and carotenoids), phenolic concentration, and composition. The oils were more stable and had a higher antioxidant, pigment, and oleic acid concentration when the trees were grown at higher densities (100 and 156 trees ha^{-1}). The authors suggested that the differences observed may be the result of different soil water availability among the planting densities. The volatile compounds of virgin olive oil also seemed to be affected by tree spacing; however, no clear tendency was observed for any compound (Guerfel et al. 2012). Because the variability of these compounds is very high, the results should be confirmed. With respect to other analytical parameters (e.g., free fatty acid content, peroxide value, and extinction coefficients at 230 (K230) and 270 nm (K270)), planting density had little influence. All oil samples obtained in the trial were classified as extra virgin oils.

E. Fruit Size and Quality

Some fruit traits (e.g., fresh fruit weight (FW), pulp to stone ratio, and oil and water content) have been evaluated in a few density trials. In most cases, the planting density seems to have had little influence on these traits. Pastor and Humanes (1990) did not find significant differences in the oil content or fruit size in two different trials.

Tous et al. (2005, 2008a) reported similar results for fruit weight and pulp to stone ratio, and León et al. (2007b) made similar observations for oil content and moisture in the 4 years recorded. Similar observations for fruit oil and water content were obtained by Msallem et al. (2008). In contrast, in rainfed conditions and low to medium tree density, Guerfel et al. (2010b) found great variability in fresh fruit weight that was significantly higher for the lower densities (51 and 69 trees ha^{-1}) than for the higher densities (100 and 156 trees ha^{-1}). Slight differences among the planting densities were found for oil content, which was significantly higher in the lowest density treatment. These results may be caused by the semiarid conditions of the trial. Water availability is crucial under these conditions, and lower plant densities result in more available water per tree that leads to increased fruit size.

IV. CRITICAL FACTORS FOR HIGH-DENSITY ORCHARDS

A. Cultivars

Cultivars represent a critical factor for any olive plantation. The performance of any cultivar at the adult stage is determined by genotype, adaptation to climate and soil, and orchard management. Final size is critical for choosing planting distances in high-density plantations. These planting systems require very early and high-bearing cultivars, tolerance to abiotic and biotic stresses, tolerance to bruising (table olives), amenability to mechanical harvesting and high fruit size (table olive) or high oil yield (oil olives) to produce high-quality virgin olive oil. Therefore, the process of intensifying olive plantations requires specific cultivars that may differ from the local cultivars currently used in traditional plantations.

1. Cultivars Used

Traditional Local Cultivars. Only some of the traditional cultivars from a range of Mediterranean countries (Table 7.3) are being used in new intensive orchards. In fact, the current expansion of new intensive olive orchards within and outside the Mediterranean Basin has modified cultivar distribution and use in all countries. In traditional producing countries, only some of the best-suited cultivars for new systems are now planted. For instance, in Andalusia, Spain, among the 24 main cultivars planted in Spain (Barranco et al. 2005), 'Arbequina', 'Picual', and 'Hojiblanca' represent 92% of the plants produced in nurseries in

Table 7.3. Main number of cultivars, diffusion, and major traditional cultivars in olive-producing countries ranked according to their cultivated area.

Country	No. cvs.	Distribution[a]	Major cultivar [synonym] (Use)[b]	Reference
Albania	–	–	Kalinjot (O)	Barranco et al. (2000); Belaj et al. (2004)
Algeria	5	R, L	Sigoise [Picholine Maroccaine] (O)	Barranco et al. (2000)
Argentina	1	R	Arauco [Azapa, Sevillano] (D)	Barranco et al. (2000)
Chile	1	R	Azapa [Arauco, Sevillano] (D)	Barranco et al. (2000)
Croatia	3	R, L	Oblica (O)	Barranco et al. (2000)
Cyprus	1	N	Ladoelia (O)	Mile (2006)
Egypt	11	R, L	Aggizi Shami (T), Ahmed (T), Toffahi (T), Maraki (O)	Laz (2006)
France	10	R,L	Picholine du Languedoc (D)	Moutier et al. (2011); Roussos et al. (2006)
Greece	16	N, R, L	Koroneiki (O), Konservolia [Amphissis] (D), Mastoidis (D), Adramintini (O), Kalamon (D)	Metzidakis and Koubouris (2006)
Iran	10	R, L	Zard [Roghanil] (O), Dezful (D), Mavi (D),	Zeinanloo (2006)
Israel	1	N	Soury (O)	Lavee (2006)
Italy	16	R, L	Coratina (O), Ogliarola Salentina (O), Cellina di Nardo (D), Carolea (D), Frantoio (O), Leccino (O), Ogliarola Barese (O)	Deidda et al. (2006)
Jordan	3	N, L	Nabali (D)	Ayoub (2006)
Lebanon	5	R, L	Soury (D)	Bassal (2006)
Morocco	2	N	Picholine Marocaine [Haouzia, Menara] (D)	Ismaili-Alaoui (2006); Barranco et al. (2000)
Palestina	1	N	Nabali Baladi (O)	Barranco et al. (2000)
Peru	1	R	Sevillano[Arauco, Azapa](T)	Barranco et al. (2000)

Portugal	7	R, L	Galega (O), Carrasquenha (D), Cobrançosa (O), Azeitera [Manzanilla Cacereña] (D)	Pinheiro (2006); Barranco et al. (2000)
Slovenia	1	R	Bianchera [Belica](O)	Barranco et al. (2000)
Spain	24	R, L	Picual (O), Cornicabra (O), Hojiblanca (D), Lechín de Sevilla (O), Manzanilla de Sevilla (T), Morisca (O), Empeltre (O), Arbequina (O), Manzanilla Cacereña [Azeitera] (D)	Barranco et al. (2008)
Syria	9	R, L	Zaity (O), Sorani (D), Doebli (D), Khoderi (D), Kaissy (T)	Al Ibrahem (2006)
Tunisia	8	R, L	Chemlali (O), Chetoui (O), Meski (T), Ouslati (O)	Jardak (2006)
Turkey	16	R, L	Memecik (D), Ayvalik [Edremit Yaglik] (O)	Zafer Can and Isfendiyaroglu (2006)
USA	5	N	Mission [Picholine Marocaine)] (O), Manzanilla de Sevilla (T)	Sutter (1994); I.Trujillo (pers. commun.)
Yugoslavia			Zutica (O)	Barranco et al. (2000)

[a]N = National, R = Regional, L = Local.

[b]O = Oil, T = Table, D = Dual.

2006 (Consejería de Agricultura y Pesca. Junta de Andalucía, cited by De la Rosa and León 2009). All three cultivars are adapted to intensive orchards, and only 'Arbequina' is well suited for use in hedgerows.

This reduction and standardization of the cultivars planted is a general trend for any new intensive plantation. The choice of the best local cultivars within a region or country and the selection of cultivars from other countries are common for new plantations. In Mediterranean countries, new intensive orchards are planted using the best suited local and/or foreign cultivars for the systems used in Egypt (Laz 2006), Greece (Metzidakis and Koubouris 2006), Iran (Zeinanloo 2006), Israel (Lavee 2006), Italy (Deidda et al. 2006), Jordan (Ayoub 2006), Lebanon (Bassal 2006), Morocco (Ismaili-Alaoui 2006), Portugal (Pinheiro 2006), Spain (Rallo 2006), Syria (Al Ibrahem 2006), Tunisia (Jardak 2006), and Turkey (Zafer Can and Isfendiyaroglu 2006). Some countries, such as France, promoted national and local cultivars focusing on the uniqueness of their olive oil (Roussos et al. 2006; Moutier et al. 2011). The introduction of cultivars from Mediterranean countries allowed the development of plantations in a number of new olive-producing countries (Sweeney 2003; Sebastiani et al. 2006). Due to an increasing risk of genetic erosion, a major emphasis on the exploration, cataloging, conservation, and evaluation of olive genetic resources has recently been developed (Barranco et al. 2000; Bartolini et al. 2005; Rallo et al. 2005; Rallo et al. 2011), including network initiatives by the International Olive Council (Essid 2010).

Cultivar Field Trials. New cultivars have often been planted in new areas without previous comparative field trials. Frequent failures of cultivar adaptation to these new areas have been attributed to frost damage, insufficient chilling for releasing potential reproductive buds from dormancy and then flowering, early ripening and modified oil composition and the excessive vigor of trees or hedgerows for mechanical harvesting. The failure of some established orchards has garnered more attention in comparative cultivar field trials in high-density plantations (Table 7.4).

However, only limited information is available from field trials on cultivar performance under intensive or super-high-density (irrigated narrow hedgerow) orchards (De la Rosa et al. 2007; Camposeo et al. 2008; Maia et al. 2008; Tous et al. 2008a,b; Allalout et al. 2011; Dias et al. 2011; Godini et al. 2011; Larbi et al. 2011; Proietti et al. 2011; Tombesi et al. 2011a). Most of the cultivars considered in these trials are low-vigor and early-bearing ones that suit hedgerow conditions, such as 'Arbequina', 'Arbosana', 'Koroneiki', and 'Fs-17', among others.

Table 7.4. Comparative cultivar trials in high density.

Year planted	Conditions	Planting density (trees ha^{-1}) and layout (m)	Cultivar	Traits evaluated	Reference
La Canonja, Tarragona (NE Spain)					
1998	NE–SW hedgerows, trees trained to central leader, drip irrigation, very small doses of N	2,469 (1.35 × 3)	Arbequina i-18, Arbosana i-43, Canetera, Joanenca, Koroneiki, Fs-17	Tree vigor, growth habit and precocity, yield, fruit traits, oil content, pest and disease incidence, harvesting efficiency	Tous et al. (2008b, 2011)
Pedro Abad, Córdoba (SW Spain)					
2000	N–S hedgerows, trees trained to central leader, fertigation	1,975 (3.75 × 1.35)	Arbequina, Arbequina i-18, Arbosana, Koroneiki, Fs-17	Fruit yield, oil content, moisture, fatty acid composition	De la Rosa et al. (2007); Muñoz-Díez et al. (2010)
Mornag (North Tunisia)					
2000	Commercial orchard	1,250	Arbequina, Arbosana	Fruit yield, fruit distribution in the canopy	Larbi et al. (2008)
Cassano Murge, Apulia (South Italy)					
2002	Trees trained to central leader, drip irrigation	1,667 (4 × 1.5)	Arbequina, Arbosana, Cipressino, Coratina, Frantoio, Fs-17, Leccino, Urano	Tree growth, precocity	Camposeo et al. (2008)

(*continued*)

Table 7.4. (*Continued*)

Year planted	Conditions	Planting density (trees ha^{-1}) and layout (m)	Cultivar	Traits evaluated	Reference
Safara-Moura (Portugal)					
2002	Trees trained to central leader	1,850 (4 × 1.35), 1,250 (4 × 2)	Arbequina, Azeitera, Cobrançosa, Cordovil de Serpa, Galega Vulgar, Redondil	Tree growth, physiological traits (photosynthesis, stomata conductance, transpiration, water use efficiency), yield	Maia et al. (2008); Dias et al. (2011)
Valenzano, Apulia (South Italy)					
2006	N–S hedgerows, trees trained to central leader, drip irrigation	1,667 (4 × 1.5)	Arbequina, Arbosana, Carolea, Cima di Bitonto, Coratina, Don Carlo®, Frantoio, Fs-17®, I/77®, Koroneiki, Leccino, Maurino, Urano®	Tree growth, fruit yield, oil yield, harvesting efficiency	Camposeo and Godini (2010); Godini et al. (2011)
Abruzzo Region (Central Italy)					
2006	Central leader, drip irrigation	1,250 (2 × 4)	Arbequina, Arbosana, Don Carlo, Fs-17	Tree growth, photosynthesis efficiency, fruit traits, oleic acid, polyphenol content	Tombesi et al. (2011a)
Umbria Region (Central Italy)					
2006	Hedgerow, central leader	1,482 (4.5 × 1.5)	Arbequina, Leccino, Maurino, Frantoio, Moraiolo	Tree growth, photosynthesis efficiency, precocity, yield, harvester efficiency	Proietti et al. (2011); Tombesi et al. (2011b)

Northern Tunisia					
Not specified	Drip irrigation	1,250 (2 × 4)	Arbequina, Arbequina i-18, Arbosana, Koroneiki	Oil accumulation during ripening, fatty acid and TAG composition, total phenol and *o*-diphenol content, olive oil quality parameters (acidity, PV, K232, K270, stability), pigment content	Allalout et al. (2011)
2003	Central leader, irrigation (1,500–2,000 $m^3 ha^{-1}$)	1,250 (2 × 4)	Arbequina i-18, Arbosana, Chemlali, Chetoui	Tree growth (trunk diameter, height, canopy volume), Fruit yield, alternate bearing index, fruit traits (fruit weight, dry weight, oil content), fatty acid composition	Larbi et al. (2011)
Southern France					
1997	Free trained	333 (6 × 5), 666 (6 × 2.5)	Boutellain, Picholine, Aglandou, Olivière	Tree vigor (trunk basal diameter, canopy volume and width, tree height), Fruit yield	Moutier et al. (2010)

Year of plantation, trial conditions, plant densities, layouts, cultivar, and traits evaluated are indicated when available in the original reference.

However, many traditional cultivars are not well suited for super-high-density hedgerow orchards because of excessive vigor and tree architecture.

In comparative cultivar trials at high density (Table 7.4), fruit size and other fruit quality traits were also evaluated. Generally, significant differences among the cultivars were observed for many of these characteristics (e.g., fruit weight, pulp to stone ratio, water content, and oil content) in each of the trials. These differences appeared to be consistent when comparing the same cultivars in different countries and in different layouts (De la Rosa et al. 2007; Tous et al. 2008b; Larbi et al. 2011; Tombesi et al. 2011b). Moreover, the previous authors reported very similar values for fruit weight, oil content, and moisture in those cultivars that were coincident in the different locations ('Arbequina', 'Arbosana', 'Koroneiki', or 'Fs-17). Therefore, the cultivar seemed to be the main source of variation for fruit weight and oil content, although slight differences were observed among trials.

High quality extra-virgin oils have been obtained in comparative cultivar trials in super-high-density conditions. These trials have shown differences among cultivars and indicate that many oil quality parameters are largely influenced by cultivar (De la Rosa et al. 2007; Allalout et al. 2011).

Trials have shown that although some traditional cultivars from different countries are well adapted to intensive orchards, few are well adapted to hedgerow orchards. Tous (2011) concluded that the most outstanding cultivars from Spain ('Picual', 'Arbequina', and 'Hojiblanca'), Italy (e.g., 'Frantoio', 'Leccino', 'Coratina', and 'Carolea'), Greece ('Koroneiki'), and France ('Picholine du Languedoc') are well adapted to densities in the range of 200–700 trees ha^{-1}. In contrast, only a few traditional cultivars ('Arbequina', 'Arbosana', and 'Koroneiki') are well adapted and extensively used in hedgerows with more than 1,500 trees ha^{-1}. The 'Arbosana' cultivar is a scarcely distributed local cultivar from L'Arboc, a small village in Catalonia (Tous and Romero 1993) that has shown low vigor and early and high bearing in hedgerow plantings. This example illustrates that some relatively unimportant traditional local cultivars may be used in new intensive hedgerow orchards. In summary, the diversity of climatic factors within the Mediterranean Basin, new growing areas and specific requirements for cultivar traits in high-density orchards highlight the need for cultivar trials in different countries and regions.

Clonal Selection. Clonal selection within leading cultivars was a first step in the initial olive improvement. Trees selected within major

cultivars were tested for performance stability after multiplication and elite selection became the basis for establishing improved clones of the mother trees in the 1980s (Lavee 2011). This method has been used for many cultivars, such as 'Frantoio' and 'Leccino' (Baldoni and Fontanazza 1990; Bartolini and Guerriero 1995); 'Picual' (García-Berenguer 1988); 'Manzanilla de Sevilla' (Suarez et al. 1990); 'Arbequina', 'Arbosana', 'Koroneiki', and 'Empeltre' (Tous et al. 1998; Tous 2011); 'Chemlali' (Khlif and Trigui 1986); 'Picholine Marocaine' (Lansari and Bouchra 1996); and 'Souri' and 'Nabali' (Lavee 1990; Lavee et al. 2008). The distribution and use of these selections are usually unknown, except for those that have been registered as trademarks [i.e., 'Arbequina' (clone IRTA-i-18), 'Arbosana' (clone IRTA-i-43), and 'Koroneiki' (clone IRTA-i-38)] and recommended for hedgerow planting (Rius and Lacarte 2010). However, De la Rosa et al. (2007) did not find any differences in performance between a standard 'Arbequina' and 'Arbequina' clone IRTA-1–18 in a comparative trial planted in 1999–2000. In general, there is no experimental or empirical evidence of differential performance between the selected clones and the original cultivar. Minimal differences in molecular markers among different mother trees of the leading cultivars provided evidence for high genetic homogeneity among potential mother trees (Belaj et al. 2004).

In summary, only data from experiments in different environments and from established plantations will provide information on the real agronomic comparative value of these selections. Currently, no significant improvement might be expected from clonal selection within major traditional cultivars.

2. Breeding. The first olive-breeding programs were initiated in 1960 in Israel (Lavee 1990) and in 1971 in Italy (Bellini et al. 2002a). Since the mid-1980s, new breeding programs have been developed in France (1986), Spain (1991), Morocco (1994), Tunisia (1994), Turkey (1994), Greece (1996), Australia (1997), Iran (1999), and Portugal (2002) (De la Rosa and León 2009). These programs search for traits suitable for intensive and sustainable olive growing, such as early bearing, high yield, tolerance to abiotic stresses, resistance to biotic stresses, adaptation to mechanical harvesting, oil composition for health and sensorial quality. Most of these programs are based on planned cross-breeding, selection within the progeny and cloning. However the Australian program is based on selection from local populations derived from spontaneous crosses among the first-introduced cultivars or from feral genotypes and their ulterior cloning (Sedgley and Wirthensohn 2000). Most of these programs were aimed at obtain cultivars for olive oil, but a

few programs were for table olives or both. Only the programs from Israel, Italy, and Spain have yielded new releases to date (De la Rosa and León 2009). A new cultivar for high-density narrow hedgerow orchards, 'Sikitita' ('Chiquitita' in the United States) was released in 2008 (Rallo et al. 2008a). This release is early bearing, has low vigor, and has a compact growth habit. These traits make this cultivar suitable for the new hedgerow system harvested with a continuous overhead straddle harvester. The 'Sikitita' cultivar has been protected in the UE and nine other countries. More information is available at www.sikitita.es. Only 'Barnea' and Askal' (Lavee et al. 1986; Lavee et al. 2003), 'Fs-17' (Fontanazza et al. 1998), and 'Sikitita' ('Chiquitita' in the United States) (Rallo et al. 2008a; Rallo et al. 2011) are currently planted.

Breeding programs have provided some relevant advances in shortening the Juvenile Period (JP). Efficient germination protocols and forced growth (Lavee et al. 1996; Santos-Antunes et al. 2005; Moreno-Alias et al. 2010; El Riachy et al. 2011a,b), criteria for early selection (Pritsa et al. 2003; De la Rosa et al. 2006; Rallo et al. 2008b), and the influence of the parents on the length of the JP (Santos-Antunes et al. 2005; Moral et al. 2011) provide useful tools for a selection among within progeny in less than 4–5 years. An unproductive period of advanced selection in a field trial and JP of the corresponding seedlings has also been reported (León et al. 2007a). Therefore, selection for short JP provides genotypes with a short unproductive period, and parents with short unproductive periods seem to transmit a short JP to their progeny.

Other relevant factors that emerge from these breeding programs include the establishment of a minimum time for evaluating factors such as oil content components, fatty acid composition, fruit weight, fruit removal force (FRF) to fruit weight ratio (León et al. 2004b, 2008; De la Rosa et al. 2008), and indirect selection (León et al. 2004a). The high variability among genotypes for any measured characteristic in a breeding program for oil or table cultivars represents a valuable advantage in a vegetative propagated species such as olive (Rallo et al. 2011a). Screening of large numbers of progeny from different crosses for resistance to *Verticillium dahliae* that is currently a major limiting factor for intensive and hedgerow orchards in olive-producing countries, indicates that 'Frantoio' is resistant to this disease and is a suitable genitor for breeding (Trapero et al. 2011). Very few comparative trials among advanced selections have been reported to date (Bellini 1993; Bellini et al. 2002b; León et al. 2008; De la Rosa et al. 2008). Only Bellini et al. (2002a) reported trials at

different sites. New cultivars have been released prior to the results of extensive networks of field trials.

Comprehensive reviews on the current state of genetic resources and breeding have recently been published (Lavee 2011; Rallo et al. 2011).

In summary, the advances of new breeding programs in many countries will certainly provide the olive industry with new cultivars suitable for high-density plantations for oil and table crops in the years to come.

B. Irrigation

Olive is a species that is well adapted to drought but increases its fruit and oil production with limited addition of irrigation water (Pastor et al. 1999; Patumi et al. 1999; Moriana et al. 2003). Orchard water consumption depends on sunlit leaf area that is determined by plant density as well as canopy size and shape. In this regard, olive intensification is a limited option in areas where irrigation water is scarce.

More intensive orchards develop more sunlit leaf area, which means that potential transpiration will increase proportionately. In this sense, water availability will determine the most profitable orchard density. Thus, olives are cultivated at 17 trees ha^{-1} in the Sfax desert of Tunisia, where the annual rainfall is less than 50 mm. In Andalusia, which has a rainfall of 550 mm and deep soil with high water retention capacity, technical experts recommend plant densities of 478–833 olives ha^{-1} to produce 950–1,368 kg oil ha^{-1} on dry land. With scarce irrigation of 15–70 mm, with the same density and oil production will be 1,100–1,718 kg ha^{-1}. When the water irrigation is 70–150 mm, production may reach 1,520–2,829 kg ha^{-1} (www.todolivo.es).

It appears that no field data exist relating to the irrigation requirements of orchards with different densities. Information regarding the irrigation requirements of intensive orchards was estimated using models of water demand in response to orchard density and canopy volume (Bonachela et al. 2001; Orgaz et al. 2007; Orgaz and Fereres 2008). An example of the application of this method to olive orchards of various densities and ages under the climatic conditions of Córdoba (Spain) is shown in Table 7.5, which shows how irrigation water requirements for maximum transpiration increase with time after planting as trees grow, canopies develop, and the interception of radiation increases.

In practice, such irrigation requirements are commonly not commercially available. In fact, growers of high-density orchards usually apply

Table 7.5. Irrigation for maximum transpiration (mm).

	Irrigation (mm)			
Plant density (trees ha^{-1})	Year 1	Year 2	Year 3	Year 4
200	74	84	101	149
400	71	94	134	238
1,000	73	170	310	594

Calculated by (Orgaz et al. 2007) in Cordoba (Spain). ETo = 1,382 mm, rainfall = 396 mm, irrigation without soil water reserves.

approximately 200 mm of irrigation per season. Because growth is the most drought-sensitive process for the tree, full irrigation for maximum transpiration is only appropriate during the initial years when maximum canopy growth is required for orchard establishment. Once canopies are completely developed, maximum production, as in other fruit crops, can be successfully achieved with less applied water using regulated deficit irrigation during certain periods of fruit growth (Chalmers et al. 1986; Ruiz-Sánchez et al. 2010; Behboudian et al. 2011). During the summer, olive trees are least affected by water deficit, and production is not greatly reduced (Goldhamer 1999; Alegre et al. 2002; Moriana et al. 2003; Grattan et al. 2006). However, even during this period, water stress should be managed to prevent excessive yield reduction (Goldhamer 1999; Moriana et al. 2003).

Irrigation management specifically developed from within density trials would assist in determining suitable practices for commercial production. Thus, the interpretation of such results should take into account the fact that trees in some experiments were not irrigated (Pastor et al. 1998; Tous et al. 1999; Guerfel et al. 2010a), while in others experiments irrigated trees planted at all densities received the same amount of water per unit land area (Pastor et al. 1998, 2005, 2007; Tous et al. 2005; León et al. 2007). These trials give preliminary information regarding water availability, density, canopy size and shape, and production.

The density trial of Pastor et al. (2005, 2007) in Córdoba, Spain shows how high water availability (1,137 mm) can advance the time to production decline as soon as 6 years after planting in the highest density (1,904 trees ha^{-1}) when compared with a lower density (408 trees ha^{-1}). Excessive growth due to excessive water volume applied cause more competition among trees and canopy shading in the highest density than in the lower density. Under the same conditions, León et al. 2007b found a positive correlation between yield and tree density after the

seventh year at higher densities than those used by Pastor et al. (2005, 2007), but only with 200 mm of seasonal irrigation. High water availability can produce excessive vigor in high-density orchards, which causes shading, reduces production, and causes management problems (Correa-Tedesco et al. 2010).

In summary, available water is a key element in the production and management of high-density orchards. More experimental effort is needed to determine the relationship between water requirements and density for sustainable management.

C. Training and Pruning Systems

The initial planting pattern is a critical factor for orchard profitability not only because it must be suited to the growing conditions and the cultivars but also because of the subsequent impact on management, especially harvest machinery and the maintenance of the desired size and shape of the canopy of the mature orchard for continuing fruit productivity and quality. The actual canopy shape will be obtained by adopting specific training systems and canopy management for particular growing conditions, as determined by the climate, soil, and cultivar.

1. Training. A training system is the design and development of a tree framework or skeleton that supports the canopy. Pruning during the initial years determines the skeleton of the tree. The length of the trunk, insertion, orientation, length of main branches, and number of primary and secondary branches determine the skeleton and canopy shape. Once the structure of the plant is fully formed, pruning is used to renew fruiting surfaces and contain the size of the mature tree. Similar canopy shapes can be achieved using different training systems. Hedgerows can be achieved in vigorous conditions using trees trained in the vase configuration with a trunk of 0.80 m and three main branches. In less vigorous conditions, hedgerows can be developed at a spacing of 4×1.5 m with trees trained to a central leader.

The canopy characteristics depend not only on the training system but also on its management. The objectives of efficient canopy management are to achieve full canopy development at an early tree age, sustain fruit production over the projected life of the orchard, to produce high-quality fruit, and facilitate the efficient use of machines and hand labor. Canopy management requires a range of practices to reduce canopy shading and increase ventilation. Works in vines (Shaulis et al., 1966; Smart et al. 1988) and in fruit trees (Palmer and Jackson 1977; Jackson

and Palmer 1980; Palmer 1989) were pioneer in canopy modeling and management. Canopy management techniques can be divided into the techniques that modify canopy size and form and those that modify leaf density. In the first group, the design decisions include planting distance, cultivar and trellis system. Pruning, irrigation, and nitrogen fertilization are considered to be shoot density management techniques.

The orchard-planting pattern incorporates specific aspects of orchard design and management for a desired canopy shape. When deciding on a planting pattern, careful consideration of cultivar, spacing, training system, canopy shape, and management of the climatic and soil conditions of the orchard should be considered. Such management will depend on the desired product and the structure and economy of the farm. Furthermore, these factors interact with each other. For a grower, the chosen system should be based on general cropping efficiency balanced with the cost of establishing and maintaining the crop. One of the most important decisions in the planting pattern is the spacing between trees and tree density. The objective of orchard spacing is to ensure maximum bearing potential per hectare in a minimum amount of time but arranging the trees in such a way that maintenance can be performed easily and efficiently. Tree density mainly affects production during the first years, and higher tree densities have higher production until the canopies fill the space available and start to cause both internal and mutual shading. Spacing and row width must be chosen to account for the inherent vigor. The distance between rows will depend on canopy depth to allow radiation to penetrate to the lower layers of the canopy and allow machinery to move easily. The distance between trees in each row must allow the desired canopy shape and take into account the cultivar growth characteristics, orchard conditions, and management.

2. Canopy Shape. The canopy is the leaf area and shoots system including the fruit that is supported by the woody skeleton of the tree. The characteristics of the skeleton (i.e., trunk, primary and secondary branches) and the growth of vegetative organs determine the shape and other canopy characteristics. In orchards, these characteristics are modified by tree density. Tree canopy shape can be greatly modified by density and spacing, so canopy shape reflects the interrelationship among trees grown in an orchard. The canopy can be described by its geometry (i.e., depth, width, external surface area, and volume) and leaf density that can be described as leaf area per canopy volume, leaf area per external surface area, and leaf area per soil surface (LAI: leaf area index), or defined indirectly using sunfleck

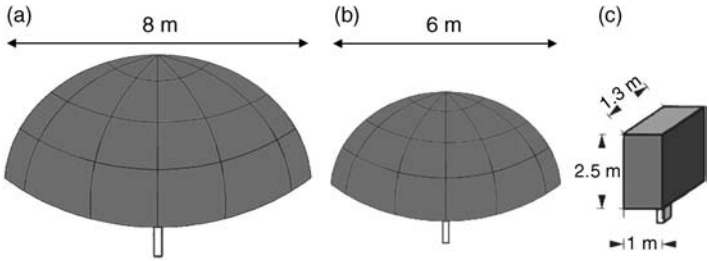

Fig. 7.5. Canopy shapes of different planting pattern. (a) Hemispherical shape at 12×12 m (69 olives ha^{-1}), 6,933 m^2 ha^{-1} of external surface, and 9,244 m^3 ha^{-1} of volume. Covered soil 53%. (b) Hemispherical shape at 8×7 m (179 olives ha^{-1}), 7,588 m^2 ha^{-1}, and 10,117 m^3 ha^{-1}. Covered soil 50%. (c) Parallelepiped narrow hedgerow at 4×1.3 m (1,933 olives ha^{-1}), 14,999 m^2 ha^{-1}, and 6,250 m^3 ha^{-1}. Covered soil 25%. *Source*: From Gómez-del-Campo and Fernández (2007).

density and porosity (i.e., permeability of incident radiation to penetrate into the canopy). Canopies can be described as continuous or discontinuous and, depending on leaf density, as dense or porous. The canopy shapes of olive trees are not as variable as those of apple or pear trees or vines due to specific morphological and physiological characteristics. In particular, the perennial leaves of olive trees do not permit the restructuring of the canopy every year. Rather, canopy development occurs slowly with many small leaves. Shoots have a basitonic growth habit with proximal parts growing more than distal parts. Thus, the natural growth habit of the olive is a bush with different branches appearing from adventitious buds of the crown. No dominant trunk develops in olive trees, and lateral expansion exceeds vertical expansion. Canopies are inherently spherical, hemispherical, or ellipsoidal in unpruned plants (Gucci and Cantini 2000). Branch appearance determines the natural size and shape of the olive tree, for which there is wide genetic variation between cultivars.

The various canopy shapes used in olive orchards have been well described by Gucci and Cantini (2000) and Morettini (1972). The most common shapes are spherical (e.g., vase, globe, and bush), conical (mainly monocone), and hedgerow. Canopy shape data from a globe training system, spacing and hedgerow are shown in Fig. 7.5.

The spherical shape is a natural canopy shape that has a large shaded center core that is either not productive or produces fruit of poor quality. The vase is the most common olive training system. One stem is allowed to develop a trunk of variable, but generally, low height, from which laterals are left to form main branches that surround an open,

illuminated central space. For such trees, canopies are discontinuous, and all of the outside surfaces are well illuminated. When the center of a vase canopy is occupied by branches, it is considered to be a globe vase.

The vase shape varies considerably depending on environmental conditions, cultivars, and orchard management. Godini (2002) described traditional rainfed orchards in Apulia, which is the most important olive growing region in Italy, where different globe canopy shapes were developed which had different density, tree size, branch inclination, trunk width, and yield. These differences resulted from different soil depth, fertility, rainfall and cultivar habits, but in all cases, the trees were maintained as discontinuous canopies. In other situations, vigorously grown canopies of globe- or vase-pruned trees leave no space between the trees within rows and form continuous hedgerow canopies. Such orchards can be mechanically harvested by trunk shakers if the height of the trunks exceeds 0.80 m. Branches should be vertical, and the canopy should be porous. Continuous over-row harvesting and side-by-side shaker systems can also harvest tall discontinuous and continuous canopies.

The bush system is a small version of the large globe-shaped tree that was developed in the 1950s and 1960s (Cantini et al. 1998). The canopy was lowered to 50 cm above the ground, and each tree was pruned with 3–6 branches. These orchards require virtually no pruning during the first 5–7 years, when the central branches must be eliminated to allow light to penetrate the canopy. After 10 years, heavy pruning is required to reform the bush, which delays production for 3 years, but high yield is achieved again 4–5 years later (Vitagliano and Bartolini 2003). The main problem with this orchard design is a lack of suitable harvesting machinery.

The conical shape (multiple or monocone) is not the natural growth habit of olive trees but has some important advantages. This shape provides good light distribution through the canopy by limiting the width of the treetop. Higher tree densities can be used, and higher production can be obtained during early years. The monocone was proposed by Roventini in 1936 for high-density orchards (cited by Gucci and Cantini 2000). Fontanazza (1993) recommended this training system for mechanical harvesting with tree shakers. The monocone is trained to a central leader with a height of 3.0 m and has a trunk with a height of 0.80–1.00 m. Branches appear from the central leader at various heights to provide every stem with good illumination. In other fruit trees, this shape is considered to be a slender spindle. However, this training system does present some disadvantages. It is not suited for some cultivars, such as 'Maurino', because a central leader

is difficult to maintain (Palliotti et al. 1999) and vegetative growth is reduced. Furthermore, no advantage in production or fruit quality has been reported over vase-shaped canopies (Preziosi et al. 1994; Palliotti et al. 1999; Silvestri et al. 1999).

A hedgerow is a continuous canopy shape with two parallel faces. Breviglieri (1961) proposed this training system for high production in Italy before solutions for mechanical harvesting were identified. Commercial narrow hedgerow orchards, also called super-high-density (800–1,975 trees ha^{-1}) orchards, have been planted in Spain since the early 1990s. Narrow hedgerows can be obtained when the trees are trained to a central leader using palmette or ypsilon shape or when they are nearly free form. At planting, the tree must be supported vertically to form the central leader, and branches that grow horizontally must be removed. A wider hedgerow can be obtained by training the tree as a vase.

D. Intercepting Radiation: From Separated Trees to Continuous Canopy

The typology of orchards (Table 7.1) shows how the trend toward greater tree density has been achieved by gradually changing the tree and orchard structure. Together with density, these factors determine the interception of radiation with determinant impacts on productivity, water requirements, and management, particularly machinery for harvesting. Measurements and models of radiation interception continue to play important roles in interpreting these effects in olive orchards; however, much of this work was adapted from earlier general works orchards of other fruit crops. Canopy cover is a first and powerful approximation for low-density orchards where tree crowns are well separated, but in plantings that form hedgerows of continuous canopies, the link between cover and interception is also determined by row orientation.

1. Orchards of Spaced Trees

Radiation Interception. The literature on orchards with spaced trees concentrates on tree number and canopy volume. These studies have led to simple estimates of vertical canopy cover and thus provide a first approximation of the radiation intercepted for photosynthetic production and for estimating irrigation requirements (Villalobos et al. 2000) and to calculate of crop coefficients (Orgaz et al. 2006). However, the actual radiation interception of these orchards is more complex for

individual orchards and varies throughout the year depending on the solar trajectory. Mariscal et al. (2000a) accounted for solar trajectory and characteristics of individual tree canopies in terms of leaf distribution, transmittance, and reflectance, thus providing a general model validated for a wide range of orchard structures with measurements obtained using a plant canopy analyzer (LI-COR Ltd, 4647 Superior Street, Lincoln, Nebraska USA). The results apply to calculations of photosynthetic productivity and water requirements.

Productivity. In a further study, Mariscal et al. (2000b) combined the estimated radiation interception with tree growth measurements and partitioning to component organs to estimate the radiation use efficiency of photosynthetic production. From these calculations, estimates of radiation-limited yield can be obtained for a wide range of orchard types. Earlier estimates of olive productivity obtained from a range of olive groves in Andalusia estimated the radiation use efficiency of dry biomass and oil production to be 0.35 and 0.16 g MJ^{-1} PAR (photosynthetically active radiation), respectively, which is 80% of the efficiency obtained by sunflowers in similar environments (Villalobos 1999).

2. Hedgerow Orchards. The strict geometry of hedgerows leads to easier analyses of light interception. The basic parameters of orchard structure are row orientation, canopy width (at base), canopy depth (from top), and canopy shape (e.g., rectangular or rhomboidal). Tree height is greater than canopy depth because the bases of the trees are kept clear of foliage (0.5–1.0 m) to facilitate management, especially for mechanical harvesting. These parameters permit deriving the parameters of row length, canopy surface area and canopy volume per hectare, and fractional (vertical) orchard cover. At a greater level of detail, porosity (ρ) is determined by canopy width (w), leaf area density (d, leaf area per unit volume, $m^2\,m^{-3}$), and the distribution of leaves within the canopy. Porosity is important for the penetration of radiation into canopies for photosynthesis and for ventilation to reduce disease outbreaks and ensure the effective penetration of sprays to control pests and diseases.

Radiation Interception by Hedgerow Canopies. Interest in this subject is now concentrated in computer modeling (Palmer and Jackson 1977; Jackson and Palmer 1980; Palmer 1989; Friday and Fownes 2001; Annandale et al. 2004; Connor 2006; Olsen et al. 2007; Oyarzun et al. 2007). The diurnal progression of the sun is accurately captured

using several equations, which allows interception patterns of direct beam radiation and allowances for diffuse sky radiation and porosity to be readily calculated for hedgerow structures, depending on structure, location (latitude), and day of the year. The results of these calculations are presented for individual rows in Fig. 7.6 and for orchards in Figs 7.7 and 7.8. Important features include the following:

- Diurnal symmetry of incidence patterns for either canopy wall of N–S orchards and similar patterns throughout the year for individual orchards.
- Diurnal asymmetry of incidence patterns for orchards in other orientations. The greatest difference for the canopy walls of E–W orchards that vary markedly during the year and between latitudes. S-facing (S hemisphere) and N-facing (N hemisphere) canopy walls only receive direct illumination for short periods, early morning and late afternoon, in midsummer.
- The depth of the canopy wall that receives direct sunlight depends on its distance from the wall of the adjacent row (i.e., alley width).
- Annual interception by E–W hedgerows is less than that by N–S hedgerows of the same structure, which has implications for the water requirement during summer irrigation seasons.

Productivity and Management. An optimum structure for a hedgerow orchard is one that provides high productivity with facility and economy of management. Management refers to the ease of access to the orchard and the cost of suitable equipment. For an individual orchardist, the challenge is to plant productive cultivars (i.e., in terms of yield and quality) in a pattern that will most quickly achieve the intended structure and then maintain it. For orchards that are irrigated and fertilized, productivity is most closely related to the interception of radiation and the efficiency with which the radiation is converted to yield. Management concerns scale, human operatives, and the machinery required for pruning and harvesting.

Hedgerow Productivity. Connor and Gómez-del-Campo (2013) have extended the illumination model of olive hedgerows (Connor 2006) to include measured responses of oil yield and quality to incident radiation in hedgerow orchards (cv. Arbequina) in various N–S-oriented structures (Connor et al. 2012). The result is a model that can be extrapolated to simulate yield and quality of a wide range of hedgerow structures exposed to varying radiation that depends on the location

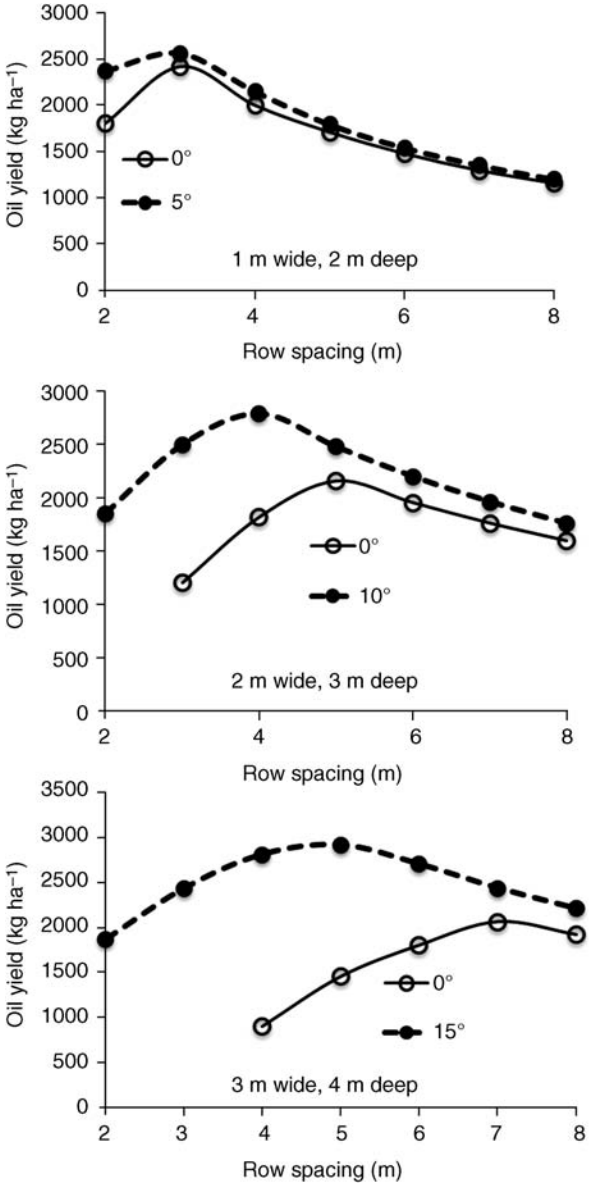

Fig. 7.6. Simulated response of oil yield to row spacing and canopy slope for various hedgerow structures. *Source*: From Connor et al. (2012), and Connor and Gómez-del-Campo (2013).

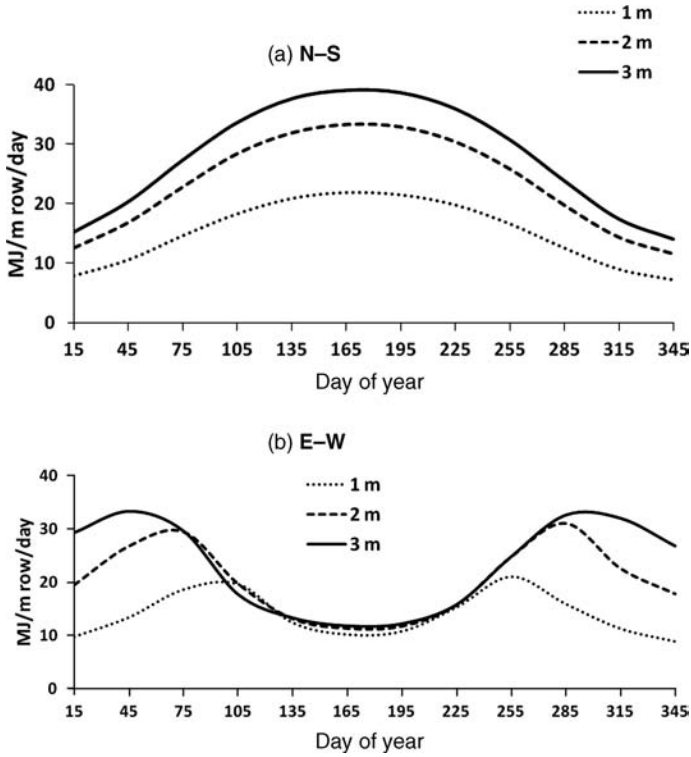

Fig. 7.7. Impact of row orientation (N–S) and (E–W) and alley width (1, 2, and 3 m) at 35°N on seasonal interception of horizontally incident radiation by hedgerow orchards with canopies 2 m deep and 1 m wide. *Source*: From Connor et al. (2012), and Connor and Gómez-del-Campo (2013).

and time of year. The objective is to provide a framework for research and development of optimum structures across a wide range of hedgerow types limited by the NH (SHD) and WH (HD) (Table 7.1) extremes. The following results are instructive:

- Analyses confirm that for rectangular-shaped hedgerows, the important structural feature is the ratio of canopy depth (top to base of canopy) to alley width (= row spacing − canopy width).
- Maximum radiation-limited yield is achieved when the ratio is close to unity (1:1) because this structural arrangement optimizes illumination of the canopy walls and row length per unit area.

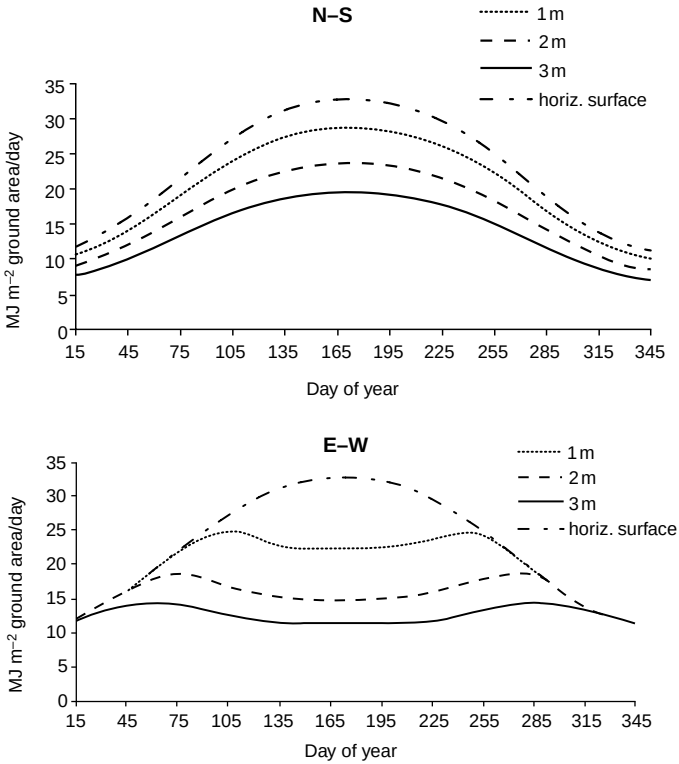

Fig. 7.8. Impact of row orientation (N–S and E–W) and alley width (1, 2, and 3 m) at 35°N on seasonal interception of direct beam radiation by both walls per unit row length of individual rectangular hedgerows with canopies 2 m deep and 1 m wide. *Source*: From Connor et al. (2012), and Connor and Gómez-del-Campo (2013).

- Narrow hedgerows that are sufficiently wide to intercept most incident radiation provide the greatest orchard yield because they form more row length per unit area (Fig. 7.4).
- Substantial yield benefit can be realized in wide canopies by pruning to sloping canopy walls (rhomboid hedgerow shape). In orchards managed in this way, yield increases because of greater interception of radiation and also because of greater row length per unit area arising from the optimal ratio of canopy depth, as the alley width is reduced.

The results from Fig. 7.6 suggest that various combinations of canopy width, depth, and slope together with row spacing can provide similar radiation-limited yields.

3. Hedgerow Management. The practical consequence of this analysis is to demonstrate that row spacing is the key initial decision in establishing hedgerow canopies. Tree density within rows will determine the form of individual trees and how quickly the hedgerow is achieved, but row spacing will determine the tree height needed to obtain maximum productivity. Wider row spacing requires deeper canopies and taller trees. Harvesters are becoming available for a wide range of orchard types, but over-row harvesters seem better for short hedgerows than for tall hedgerows. Advantages are provided with regard to human scale and cost, but little is known about the longevity and ease of maintaining reproductive capacity in hedgerows of various structures. The optimum combination of structure and machinery will vary from place to place depending on the location and economies of scale (Freixa et al. 2011).

E. Plant Protection

Hall (2011) has reviewed the current challenges for plant protection in olive plantations and highlighted the following aspects: (1) The effective control of *Verticillium* is a priority for crop growth, (2) Several pests and diseases have a regional or local presence in new olive-growing countries and thus require specific control measures, (3) The use of certified olive plants is essential to prevent the spread of important pests and pathogens in new orchards, (4) The availability of pesticides is limited by national and international regulations, (5) Olive cultivars and new genotypes have high variability with respect to pest and disease tolerance/resistance, and (5) Control methods should be integrated into the general crop management systems.

The expansion of new intensive plantations has been associated with an increase in the incidence of pests and diseases. Different incidences of diseases in traditional, intensive and hedgerow rainfed and irrigated plantations have been reported by Trapero (2007) and Moral et al. (2012). In most cases, observational data prevail over experimental ones, which at times are not conclusive. Evaluating the incidence of *Verticillium* wilt and other diseases and pests could illustrate which factors are more important for spread and severity of various diseases and pests in plantations and how orchard plant density may affect their incidence and plant protection management.

1. The Case of *Verticillium* Wilt of Olive (VWO)

Etiology and Spreading. *Verticillium* wilt is considered to be the most serious biotic threat to olive orchards. The causal agent is *Verticillium*

dahliae Kleb, which is a species with a broad range of hosts and diverse pathotypes that affects olive orchards (see reviews by López-Escudero and Mercado-Blanco 2011; Jiménez-Díaz et al. 2012; Mercado-Blanco and López-Escudero 2012). These pathotypes have been classified based on their pathogenicity as defoliating (D) (highly virulent) and not defoliating (ND) (less virulent) groups (Rodríguez-Jurado et al. 1993). VWO was reported for the first time in olive trees in Italy (Ruggieri 1946). Diverse surveys have illustrated the rapid spread of this disease in Spanish olive-growing areas over the past 30 years (Blanco-López et al. 1984; López-Escudero et al. 2010) and in other Mediterranean countries (Thanassoulopoulos et al. 1979; Al-Ahmad and Mosli 1993; Serrhini and Zeroual 1995; Bellahcene et al. 2000; Levin et al. 2003a; Nigro et al. 2005; Dervis et al. 2010). The expansion of this disease in olive orchards of nonMediterranean countries has also been reported (Nicolini and Traversi 1950; Schnathorst and Sibbett 1971; Sergeeva and Spooner-Hart 2009; Pérez et al. 2010).

The persistence of this disease is caused by the longevity of microsclerotia, which is the soil survival structure present during the non-parasitic infection of the life cycle of *V. dahliae*. Wilhelm (1955) found that this latent structure can remain viable for up to 15 years in infested soil. Therefore, dormant microsclerotia will remain in soils until suitable conditions favor germination and new infections trigger a new parasitic phase. The presence of microsclerotia in soils is associated with previous cultivation of susceptible crops and the use of infested water for irrigation.

In Andalusia, the expansion of irrigation in olive orchards (Consejería de Agricultura y Pesca, 2003), the establishment of new olive plantations on soils previously cultivated with *Verticillium* wilt susceptible crops (such as cotton), the prevalence of susceptible cultivars in new orchards and the infection of nursery plants are recognized as major causes of VWO incidence and distribution (Trapero and Blanco-López 2008).

A survey of the presence of VWO in CAC plants (the compulsory category of the EU for commercial production of olive trees by nurseries) was performed in Andalusia (Consejería de Agricultura y Pesca 2007, unpublished internal paper)). On average, 15% of the plants sampled were infected. This average was dependent on cultivar: an infection rate of 8.8% was found in 'Arbequina', 16% in 'Picual', 17.5% in 'Hojiblanca', and 27.3% in the rest of the sampled olive trees. In the same survey, up to 28% of olive trees were positive for *Pseudomonas savastanoi* pv. *savastanoi*. In Apulia, Italy, 50% of the soils sampled in nurseries were infested with *V. dahliae* (Nigro

et al. 2005). These data indicate that infected plants represent a major threat for the spread of disease into newly planted areas and suggest the need for a certification scheme for olive nurseries that guarantees that the trees are free of known viruses, *V. dahliae* and *P. savastanoi* pv. *savastanoi* to improve the protocols currently implemented (Martelli et al. 1995, Martelli 1999).

Cultivar Susceptibility. López-Escudero and Mercado-Blanco (2011) have summarized the work on cultivar susceptibility in naturally infested soil and in artificial inoculation with D and ND pathotypes. In field surveys, three of the most highly planted cultivars in Spain in intensive orchards ('Picual', 'Hojiblanca', and 'Manzanilla') were found to be susceptible; however, 'Arbequina', which is the most highly planted cultivar in hedgerows and is commonly planted in intensive orchards, is moderately resistant to VWO (L. Roca, pers. commun.). All four cultivars are, however, highly susceptible under conditions of artificial inoculation.

Influence of Plant Density. Recently, olive growers have increased the tree density in olive plantations from 70–100 trees ha^{-1} to >1,500 trees ha^{-1} (Table 7.1). For many pathosystems, microclimates changes resulting from higher plant density usually enhance improve the conditions for disease development (Burdon and Chilvers 1982; López-Escudero et al. 2010). However, there is no clear evidence that tree density alone affects VWO incidence. Rather, other factors associated with the process of intensification of new olive orchards, such as cultivar susceptibility, infected planting material, and infested irrigation water as previously discussed. These factors affect disease incidence by increasing inoculums density in the soil (L. Roca, pers. commun.).

Plant Protection. Management of plant protection against VWO should be based on an integrated approach that considers the ability of the plants to recover from the disease (Trapero and Blanco-López 2008; López-Escudero and Mercado-Blanco 2011; Jiménez-Díaz et al. 2012). This approach has decreased disease incidence in different countries. The disease can develop in successive years from new infections through the roots. Therefore, measures to prevent infection before planting and to prevent new annual infections in affected trees should be the basis for integrated protection.

Jiménez-Díaz (2010) recommend the following measures as an Integrated Control Management (ICM) strategy for VWO: (1) site selection to prevent the use of infested soils or soils containing the pathogen and/or

exposed to herbaceous crops susceptible to *Verticillium* wilt, particularly cotton, (2) deinfestation of planting sites infested with the D pathotypes or high inoculums density of the ND pathotype, (3) use of cultivars moderately susceptible to the D pathotypes, (4) use of planting stock certified to be free of *V. dahliae*, and (5) protection of planting stock root systems from infection by residual inocula. Jiménez-Díaz (2010) also recommends the use of molecular protocols for the detection and identification of *V. dahliae* pathotypes, as well as root treatment with biological agents that have been demonstrated to be efficient in reducing the severity of infection by the D pathotypes.

2. Other Diseases. A high incidence of different foliar mycoses that induce defoliation (*Spilocaea oleagina, Pseudocercospora cladosporioides*, and *Colletotrichum* spp.) and of root mycoses that cause tree wilt (*Verticillium dahliae* and *Phytophthora* spp.) has been reported in intensive, hedgerow and traditional orchards (Trapero 2007; Trapero and Blanco-López 2008; Moral et al. 2012). Increased plant density and irrigation are likely to increase the duration of wetness of host tissues, which could result in a higher incidence of these diseases in high-density olive orchards, as occurs in many pathosystems (Burdon and Chilvers 1982).

Mechanical harvest with over-row straddle harvesters has also been related to a high incidence of olive knot (*P. savastanoi* pv. *savastanoi*) in hedgerow orchards (Tous 2011). This increase in disease incidence has been related to shoot lesions produced during mechanical harvesting that facilitate the penetration of this epiphytic bacterium (Trapero 2007). Nevertheless, hedgerow orchards can be successfully managed by increasing the pruning intensity and the number of copper fungicide treatments (J. Moral and A. Trapero unpublished data).

Some experimental data provide information on the differential incidence of some diseases. Moral et al. (2012) observed the incidence of fruits affected by *Colletotrichum acutatum* in trees of 'Arbequina', which is a moderately resistant cultivar (Moral and Trapero 2009), in an experiment in Córdoba where the trees were planted at four plant densities (i.e., 1,904, 816, 408, and 204 trees ha^{-1}) in a N/S orientation and irrigated yearly with 6,000 m^3 ha^{-1}. This is higher than the standard irrigation amount (2,000 m^3 ha^{-1}) that it is typically used in olive orchards in Córdoba. The incidence of affected fruits was the highest at 1,904 olive trees ha^{-1} and severe epidemics were observed at this density of planting in comparison to the other three densities. There was, however, no difference among the planting densities with regard to total fruit infection (symptomatic plus latent infections).

Some environmental changes and cultural practices may also influence the incidence of some diseases in high-density olive orchards. For instance, Viruega et al. (2011) observed an increase in the incidence of *Spilocea oleagina* with an extended leaf wetness period of the leaves and with more lesions as a consequence of the frequent pruning used to control hedgerow size. These lesions also represent an important factor for olive knot caused by *P. savastanoi* pv. *savastanoi*. Furthermore, more young leaves were found to be affected by *P. cladosporioides*.

Finally, a high incidence of fungal species (mainly Botryosphaeriaceae species) in pruning wounds has been reported for different tree crops (Michailides and Morgan 2004). In olive trees, the species *Neofusicoccum mediterraneum* has been isolated from cankers on branches surrounding pruning wounds. The mechanical harvest system that has been newly implemented in Spanish olive orchards and is increasingly being implemented in California orchards is expected to create more wounds on the shoots and branches of the trees and may result in a greater risk for infection by the Botryosphaeriaceae species and other wound-associated pathogens (Moral et al. 2010).

3. Pest Incidence. To the best of our knowledge, there have been no specific studies related to the effect of increasing tree density on the incidence of olive pests. Therefore, it is only possible to predict some possible issues based on the existing knowledge.

In most cases, high-density olive plantations have irrigation-related high soil humidity that, combined with the large fruits, may create a favorable environment for pests (Metzidakis et al. 2008). Similarly, it has been demonstrated in 10 Spanish cultivars that the susceptibility of olive trees to the olive fly (*Bactrocera oleae* Gmel) is higher under irrigated conditions that under rainfed conditions, where the high relative humidity is favorable for olive fly biology and the large olive fruits seem to be more attractive for oviposition (Santiago-Álvarez et al. 2010). Furthermore, there are several reports about the need to control *Margaronia unionalis* Hübn in high-density olive plantations (León et al. 2007b).

Pruning is a key operation to control tree vigor in traditional and high-density plantations. Even if regular pruning following established codes of practice is performed, pruning wounds are targets for oviposition by the olive pyralid moth *Euzophera pinguis* Haworth (Lepidoptera: Pyralidae). Furthermore, this pyralid is becoming a serious pest for olive crops in Spain, Portugal, and other countries.

There is considerable interest in the selection of cultivars that are well adapted to high-density plantations. As a result, the susceptibility of

such new cultivars to key olive pests such as *B. oleae* should be determined. Most olive hedgerow plantations are now based on the use of the cultivars 'Arbequina', 'Arbosana', and 'Koroneiki', which have a very low susceptibility to olive fly attacks (Quesada-Moraga et al. 2010b).

As a result of the relatively high soil moisture, low biodiversity, and high productivity, high-density olive plantations may be highly prone to pests. Thus, it is essential to monitor selected trees that are well distributed throughout the orchard, throughout the season. Susceptibility to pests is of great importance when deciding which cultivar to plant. Choosing a tolerant cultivar makes integrated pest management easier and reduces production costs by reducing chemical inputs. However, a limited number of susceptible trees in the orchard could act as "traps" for monitoring or controlling pests.

F. Mechanical Harvesting

The need to reduce reliance on manual promoted progressive changes in the systems used for olive planting and harvesting. In addition, new requirements for environmental sustainability and for enhanced quality of both olive oil and table olives have also stimulated change. An increasing demand for technology and capital investment has been associated with these new systems. The rate of development of mechanical harvesting for olives has been continuous and progressive since the 1960s. The following three main approaches have been developed since that time: (1) fruit removal from the tree, (2) collection, cleaning, and transport of fallen fruits, and (3) integration of all of these harvest operations into a single operation using continuous harvesters.

1. Fruit Removal from the Tree. Most of the labor demand for traditional manual harvesting was focused on the removal of fruits from the trees, either by hand or with poles (Fig. 7.9a). Humanes-Guillén (1976) measured the time required for the different single operations included in the whole process of olive harvesting. Whereas the total demand for harvesting represented 80% of the total manual labor for annual olive orchard management, 40–60% of this demand corresponded to fruit removal by poling or by hand.

Two different complementary approaches were designed to achieve fruit removal: (1) fruit loosening products and (2) mechanical devices.

Fruit Loosening Products. Spraying different chemicals to reduce the fruit attachment force was explored on table olives. The first

Fig. 7.9. Hand olive harvesting and devices to facilitate fruit removal process. (a) Hand harvest (courtesy of d'Abrunhosa family). (b) Hand-held combing. (c) Trunk shaker mounted in tractor. (d) Self-propelled trunk shaker. (See text for further discussion).

experiments were applied to table olives (Hartmann et al. 1968; Lavee et al. 1973) and oil olives (Collina and Zucconi 1966) to facilitate harvesting. At that time, plant growth regulators were considered potential agents for modulating fruit ripening and for controlling other associated processes such as fruit abscission. Many different products were tested but Ethrel showed the most promise (Hartmann et al. 1970; Ben-Tal and Lavee 1976) and large-scale experiments were performed in most olive countries to determine the appropriated concentrations and environmental conditions for its commercial use (Lavee 2010).

However, leaf drop was associated with ethylene-releasing compounds at concentration that were effective for fruit abscission, which therefore presented a major drawback for the commercial use of such

compounds. Different additives (Ben-Tal 1987; Shulman et al. 1982) were applied to restrict the effect of ethephon on the abscission zone of fruits and leaves and overcome or reduce the induction of leaf drop. Some promising initial responses to new formulations (Vitagliano 1975; Birger et al. 2008) and other additives such as monopotasium phosphate (Barranco et al. 2004) and 1-methylcyclopropene (Burns et al. 2008) did not provide consistent results in extensive commercial applications. Consequently, no reliable fruit abscission agents with commercial potential for both oil and table olives have been identified (Ferguson et al. 2010). In a recent review, Lavee (2010) concluded that using fruit-attachment-loosening agents is currently very limited in the olive industry. The problems of leaf drop and variability of response across different years and locations have not yet been solved.

Mechanical Harvest Aids. Many different devices have been designed to facilitate fruit removal. Ferguson et al. (2010) indicated that different hand-held harvesting units are used in small, hilly orchards in California but cannot be considered to represent mechanical harvesting because the speed and efficiency of the unit is determined by the operator and there is no collection mechanism. Different units (such as pneumatic, hand-held combing, and clamping shaking) have been described (Gil-Ribes et al. 2008; Ferguson et al. 2010; Lavee 2010) (Fig. 7.9b). Branch shakers and combing units are still widely used in small olive orchards in many countries because of their low cost and high rate of fruit removal (>90%) (Gil-Ribes et al. 2008; Lavee 2010) (Fig. 7.9b). These devices increase the fruit collection to 350–400 kg per worker per day (Ferguson et al. 2010).

Inertia Trunk Shaker. Scaffold shakers were initially developed for traditional vase-trained trees with low or nondefined trunks (Lavee 2010). Inertia head trunk shakers were designed by the University of California for table olive harvesting by the end of the 1960s (Fridley et al. 1971). Since that time and for many years, trunk and scaffold shakers have been considered the most efficient method for fruit removal. Shakers are composed of a head and a clamp that attaches the shaker to the trunk (Fig. 7.9c). Three types of trunk shaker heads have been designed to date: linear, multidirectional, and orbital. Three types of clamps (i.e., three-point, scissors, and pincers) are used. Three-point clamps are well suited for cylindrical trunks, whereas scissors and pincers are better adapted to the trunks of old trees with irregular shaped cross-section. The efficiency of the clamp that attaches the shaker to the trunk is a critical point for all shaker heads, as any

movement between the clamp and the trunk during shaking can tear the barks and causes severe trunk wounding (Affeldt et al. 1988; Castro-García et al. 2007; Lavee 2010). Shaker heads of different sizes are mounted on heavier or lighter tractors as front, lateral, or back modules. Self-propelling shakers are also widely used (Fig. 7.9d). A review of shakers used for olives has recently been published (Gil-Ribes et al. 2008).

Many factors influence the efficiency and side effects of shakers and these factors determine the choice of shaker and its operation (Visco et al. 2008a,b). Internal factors refer to the shakers themselves. Shakers transform mechanical energy from a diesel engine to hydraulic energy that is transmitted to the shaker head to be transformed again into a mechanical force vibration that is applied to the tree branch or trunk. This vibration is transmitted by the tree frame, according to its dynamic properties, to detach the fruits. The energy of the trunk vibration used to detach olive fruits could damage the bark, shoot, branches, and even the machine. Blanco-Roldán et al. (2001) reported that the energy leak was higher than 33% during energy transformation from a 80 to 100 HP tractor to a multidirectional shaker under regular harvesting conditions indicating that improvements in the design of the shaker to increase its energy efficiency is needed.

The frequency, acceleration, stroke, vibration time, and desired degree of fruit removal are major parameters that affect the vibration transmitted from the shaker to the tree. Most commercial orbital trunk shakers operate at frequencies between 20 and 40 Hz (1,200–2,400 cycles min^{-1}) (Gil-Ribes et al. 2007). Intensively planted olive trees have an interesting vibration response when they are excited between 28 and 30 Hz (1,680–1,800 cycles min^{-1}). In this frequency range, the force vibration excites the first and second tree modes (20.2 and 37.7 Hz, respectively), which reduces vibration damping and prevents large resonance phenomena in the tree (Castro-García et al. 2008). Klonsky (2009) found that a short stroke of less than 2.5 cm and a frequency of 42 Hz (2,520 cycles min^{-1}) or a long stroke of 10 cm at low frequency of 17 Hz (1,020 cycles min^{-1}) is required to remove 80% of the fruits for green table olives. In these studies, long strokes also increase trunk wounding, cause branches to break, and decrease the lifespan of the shaker.

The time of vibration is also a critical parameter for efficient shaker operation. Studies on cumulative olive detachment using artificial vision techniques indicate that more than 50% of the olives drop in the first 3 s of vibration and that shaking the olive tree beyond 5 s causes progressive damage to both the tree and the shaker (Gil-Ribes

et al. 2008). Further studies indicate that two vibrations of 10 s were more effective for fruit removal at the beginning and mid-ripening but not at later harvesting dates and that these vibrations caused negligible damage to the trees (Blanco-Roldán et al. 2009). These results have resulted in modifications to the usual time of vibration that was 20 s.

In summary, the mode and time of vibration are critical factors for safe fruit removal and to maximize the lifespan of the shaker and tractor. Therefore, the design, choice, and operation of the shaker should consider these critical factors.

Agronomical Factors. The introduction of shakers stimulated many studies to define the influence of agronomic factors on the efficiency of shakers for fruit detachment and the accompanying side effects. Tree size and architecture are related to the transmission of vibration to the canopy. Fridley et al. (1971) stated that vibration was transmitted well throughout an upright scaffold and that the vibration was damped in low-hanging branches, thus requiring complementary fruit removal by poling. The training of trees and their distances became recognized as a major problem for efficient fruit removal in traditional olive plantings in Spain (Humanes-Guillén 1976). A one-trunk medium-sized vase configuration with 3–4 main limbs (20–40 m^3 volume) has been found to be an adequate training system that is for suited to mechanical harvesting under experimental conditions studies in both Spain and Italy (Humanes-Guillén 1976; Pastor and Humanes 2000; Gucci and Cantini 2003; Tombesi 2006; Visco et al. 2008a,b). In Italy, orchards trained in monocone (Gucci and Cantini 2003) have also been harvested using shakers, although the fruit removal efficiency was less than that in young vase-trained trees.

Currently, tree density in orchards to be harvested with trunk shakers ranges between 150 and 400 trees ha^{-1}, and corresponds to planting distances of 9×7 m to 7×6 m in rainfed plantations and 8×6 to 6×4 m in irrigated plantations (Table 7.1). In a preliminary study on vibration, D'Agostino et al. (2008) determined that shaker should maximize the vibration effects and that the shaker should only be applied to small tree that have a rigid structure. Ferguson (2006) further determined that the lifespan of the orchard should be less than 20 years to avoid excessive tree size and poorly structured trees that are not suited to mechanical harvesting.

Fruit removal force (FRF), fruit fresh weight (FW), oil content, and variation throughout ripening are critical parameters for efficient mechanical harvesting when using shakers. In all cases, the fruit removal force decreases, and the natural fruit drop increases with

the progress of ripening, whereas the fruit oil content and fruit weight remain constant or decrease slightly once the color of the fruit begins to change progressively from green to black. These changes determine the optimum period for mechanical harvesting using shakers (Humanes-Guillén 1976). Extensive variability has been reported among traditional cultivars (Humanes-Guillén 1976; Lavee et al. 1982; Kouraba et al. 2004; Visco et al. 2008a,b,c; Farinelli et al. 2012) and among genotypes from breeding progenies that further increase the variability inherited from the progenitors (De la Rosa et al. 2008). These data indicate the advantages of establishing several cultivars that have fruits that detach readily by shaking and that ripen at different overlapping times to extend the period of harvesting and the annual use of the shaker, thus reducing the cost of harvesting. The possibility of obtaining new suitable cultivars by breeding remains also a challenge.

Differences in oil composition and quality throughout ripening have been extensively reported. A recent review (El Riachy et al. 2011a) indicated that the type of cultivar and the progress of ripening represent the main sources of variability in virgin olive oil composition and sensorial profiles. In general, harvesting at the beginning of fruit ripening is related to a high level of antioxidants, bitterness, pungency, and fruity flavor. Late harvesting is associated with the occurrence of natural drop of the fruit, the severity of which varies with the cultivar (Beltrán et al. 2008). High acidity and deterioration of sensorial quality of olive oil have been found when dropped fruits collected late from the ground are processed (Uceda et al. 2008). Early mechanical harvesting prior to the occurrence of natural fruit drop is therefore recommended as a good husbandry practice.

2. Collection, Cleaning, and Transport of Fallen Fruits. Traditional olive harvest includes several successive single operations. First, naturally dropped fruits are hand-collected from the ground, cleaned, bagged, and transported to the oil mill. Then, fruits from the trees are collected manually or detached by poling. For table olives, fruits are manually collected, whereas fruits for oil are usually detached by poling and subsequently collected using shade cloths (Fig. 7.9b). These fruits are then cleaned and loaded into trailers to be transported to oil mills or table olive processing factories. Fruit removal by shakers represents only the first step toward mechanical harvesting of olives. The olives fall from the shaken trees into nets, shade cloths, or on the ground, and then the same steps used for fruits removed by poling are followed for cleaning, loading, and transport.

The time required for different harvest operations has been extensively recorded in many oil olive plantations since the first field trials of shaker mechanical harvesting. Humanes-Guillén (1976) summarized data from this extensive field experimentation. The time required for fruit removal by shakers is constant without respect to tree crop, whereas the time required for other operations is related to tree crop load. The working time for fruit removal by shakers ranges between 3.8% and 1.2% of the total time required for the whole harvest operation, according to the tree crop load.

This substantial reduction should be complemented by mechanization of other operations. Different approaches to mechanize the collection of fruits from the ground, extension and moving of nets, and cleaning and loading of fruits into bins or the simultaneous integration of fruit falling and catching have been developed to complement the mechanical removal of fruits by shakers (Gil-Ribes et al. 2008; Lavee 2010).

The collection of fruits from the ground requires previous preparation of the soil by rollers to facilitate subsequent operations. Picking these dispersed fruits from the ground involves grouping them into rows and gathering them up, followed by cleaning and loading into containers for transport to the mill. Mechanical and pneumatic sweepers and sweeper gatherers are currently used for these operations (Gil-Ribes et al. 2008). The main drawback of collecting fruits from the ground is the damage incurred to the fruits, which can severely reduce the oil quality (Uceda et al. 2008).

Lavee's (2010) review describes methods developed to facilitate fruit collection. A catching frame in the form of an inverted umbrella and a conveyer carrying the harvested fruits to a tank mounted in the same rig with the shaker was the initial approach and represent the first step toward a continuous harvester (Fig. 7.10a). These systems have been used largely in widely spaced, traditional, and intensively planted commercial orchards and are highly efficient for plant densities <250 trees ha^{-1}. In more industrial orchards with higher densities, the higher number of trees per hectare increases the cost of harvest. The insufficient space between trees also impedes the use of the inverted umbrella connected to the shaker (Fig. 7.10a). A winding catching canvas deployed from a drum has been the most common catching frame and is still used. Both systems require a large amount of manual labor and two individual mechanical devices. A step forward to integrated mechanical harvest was therefore needed for orchards with densities greater than 250 trees ha^{-1}.

3. Continuous Harvesters. The tendency to increase the plant density above 250 trees ha^{-1} drove the search for alternative mechanical harvest

Fig. 7.10. Olive harvesters: (a) trunk shaker with an inverted umbrella catch frame, (b) side-by-side trunk shaker, (c) modified vineyard straddle harvester, (d) canopy shaker straddle harvester. (See text for further discussion).

systems. Several systems have been developed in the past 15 years, and some of them are based on the association of trunk shakers and contact-head machines with slanted canvas working in tandem. The integration of both machine and catching frames in a single unit (side-by-side systems) (Fig. 7.10b) or straddle harvesters for wide and narrow hedgerows that integrate all operations (i.e., removing, cleaning, and loading the fruits into bins), from which the fruits are poured into a tractor trailer or truck to be transported to the oil mill (Fig. 7.10c and d) are now typically used (Gil-Ribes et al. 2008; Ferguson et al. 2010; Lavee 2010; Ravetti and Robb 2010; Tous et al. 2010; Vieri and Sarri 2010; Tous 2011).

These continuous harvesters have been designed to address the requirements of high-density orchard typologies (Table 7.6), and each one is best suited for different circumstances. Trunk shakers and inverted umbrellas are very well adapted to medium-sized orchards with fewer than 250 trees ha^{-1} and tree trunk heights of approximately 0.8–1.0 m. Fruit removal efficiency is influenced by fruit and tree sizes, the position of fruits within the canopy, and the ripening process. The

Table 7.6. Hand and mechanical harvest systems in olive for current orchard typologies elaborated by Castro-García et al. (2007), from published and unpublished own data.

Typology[a]	Harvesting system	Harvesting efficiency (% fruits per tree)	Harvesting efficiency (kg or trees h^{-1})	Harvesting cost (€ kg^{-1})	Oil quality
RI	Hand (poles, sticks, nets)	>90	15–25 kg h^{-1} per worker	>0.20	Irregular
IT	Mechanical harvest aids	>90	30–50 kg h^{-1} per worker	0.18–0.24	Good
RI	Mounted or self-propelled tree shakers	80–90	30–60 trees h^{-1}	0.12–0.20	Good
II	Over-the-row harvester	>90	40–60 trees h^{-1}	0.09–0.12	Good
IWH (HD)	Self-propelled trunk shaker and tandem canvas	70–85	90–180 trees h^{-1}	0.05–0.10	Good
RNH (SHD)	Over-the-row harvester	90	60–180 trees h^{-1}	0.05–0.10	Good
INH (SHD)	Adapted grape harvester	95	300–600 trees h^{-1}	0.03–0.08	Good

[a]RT = rainfed traditional, IT = irrigated traditional, RI = rainfed intensive, II = irrigated intensive, IWH = irrigated wide hedgerow, RNH = rainfed narrow hedgerow, INH = irrigated narrow hedgerow, HD = high density, SHD = super high density.

adaptation of cultivars, tree training, and pruning are therefore critical factors for this system that have required relevant experimental study in most countries.

Narrow hedgerow orchards have been designed to be harvested with the modified grape straddle harvester (Rius and Lacarte 2010). This machine is well suited for harvesting in many farms, as it may work efficiently in diverse slopes and soils and may move easily from farm to farm. The size of the farm is not currently a problem, as many companies offer harvesting services to farmers. The harvest efficiency is very high and does not depend on the size of the fruit, the position of the fruit within the canopy, or the ripening index (Tous 2011). The most common self-propelled machines have variable sizes, depending on the model, and are between 2.5–4 m tall and 0.5–1.5 m wide. The speed of the modified vineyard straddle-harvesting machine ranges between 1 and 2 $km\,h^{-1}$, and the area covered is approximately 3–4 $ha\,day^{-1}$ (Lavee 2010; Tous et al. 2010). Maintaining the same size of tree becomes a critical point for this system, and only a few early-bearing traditional and new cultivars are well adapted to this harvester (Section IV.A.1). However, this harvester has been efficiently used to date in the oldest narrow hedges planted in 1994 by adjusting the height and width of the hedge through deficit irrigation and through pruning trees to suit the shape and size of the harvester.

Side-by-side shakers, lateral-contact hedge harvesters, and large overhead straddle harvesters are currently being tested or are already used in farms in California (Ferguson 2006; Vossen 2007; Ferguson et al. 2010), Italy (Vieri and Sarri 2010), Argentina, Australia (Ravetti and Robb 2010), Spain, and Portugal (Gil-Ribes et al. 2008; Tous et al. 2010; Tous 2011) for intensive and large hedgerow plantations [high density] or orchards with a density higher than 250 trees ha^{-1}, particularly on the range of 450–800 trees ha^{-1}. Ravetti and Robb (2010) compared the performance of a large straddle harvester and side-by-side shakers in full-canopy trees with a total volume of 16,000 $m^3\,ha^{-1}$ in an orchard planted at 7×4 m and trained in a free palm form at Boort, Australia, where large farms on flat lands are common. This paper evaluated the speed of operation, efficiency of fruit removal, canopy damage, trunk damage, and net harvesting time and cost of operation, and concluded that both types of machine are competitive and safe alternatives. Whereas shakers are viable options for small-scale operations in light cropping or late harvest situations, straddle harvesters are more competitive for large-scale modern intensive plantations with high levels of production. The maneuverability of the large straddle harvester is a main limiting factor when it is used on small farms within

sloping terrains. These machines offer the possibility to harvest a wider range of cultivars with different levels of vigor when compared with the modified grape harvester.

In summary, olive mechanical harvesting began with harvest shakers for removal of fruits off of trees in the early 1960s. The association of diverse devices with shakers to provide complementary operations for the whole process of harvesting as well as the integration of all operations into a single machine since the early 1990s has opened many possibilities and has led to the design and use of integrated continuous harvesters. These changes in mechanical harvesting have been associated with contemporary modifications of olive planting systems.

V. ORCHARD ESTABLISHMENT COSTS, MANAGEMENT COSTS, AND ECONOMICAL INDICES

Several books describe the current operational practices in olive growing from plant establishment to harvesting [Fiorino (ed.) 2003); Barranco et al. (eds.) 2008, 2010]. The narrow hedgerow system (super high density or superintensive) has also been extensively described by Rius and Lacarte (2010). This chapter summarizes the costs of standard practices for the establishment and annual management of the different plantation typologies defined in this review. Our data are based on a study performed by reputed experts for AEMO (2010) in Spain, which data are actualized yearly. We have also data from Todolivo (www.todolivo.es), which is a company that has established and managed thousands of hectares of narrow hedgerows in many countries. Our data are also based on our own experiences and are relevant to Spain in 2012. Some reviews on comparative costs of establishment and annual management as well as the cost of production in different countries have been published in recent years (García et al. 2008; AEMO 2010; Ait Hmida 2010; Pannelli 2010; Freixa et al. 2011), which may be helpful for readers as comparative references to the data presented here.

A. Establishment Costs

The approximate comparative cost of establishing the current typologies of plantations (Table 7.2) in Spain for 2012 are shown in Table 7.7. The costs have been estimated based on the average costs on different olive farms according to the information provided by advisors from different service companies working in the olive sector. Here, the

Table 7.7. Estimated establishment cost of olive plantation typologies.

	Cost (€ ha^{-1})						
	Orchard typology[a]						
Operation description	RT	IT	RI	II	IWH (HD)	RNH (SHD)	INH (SHD)
Irrigation establishment	–	2,000	–	2,250	2,500	–	3,000
Soil preparation, nursery plants acquisition, staking and planting, training and annual management	500	500	750	750	2,500	3,000	4,000
Total cost	500	2,500	750	3,000	5,000	3,000	7,000

[a]RT = rainfed traditional, IT = irrigated traditional, RI = rainfed intensive, II = irrigated intensive, IWH = irrigated wide hedgerow, RNH = rainfed narrow hedgerow, INH = irrigated narrow hedgerow, HD = high density, SHD = super high density.

investment per hectare only refers to the strict cost of establishment, that is, costs incurred during soil preparation, plant acquisition, staking, planting, training, and management for the first year. Investment for irrigation systems is also included in the corresponding typologies. These costs are highly variable from farm to farm depending on the proximity and ease of availability of the source of water, topography of the land, and size of the farm among other factors. The values presented are therefore useful for comparisons among planting typologies.

In summary, investment cost increases with planting density and the specificity of the irrigation system.

B. Annual Costs

The approximate comparative annual costs of production at full bearing for the different typologies in Spain for 2012 are shown in Table 7.8. The costs have been estimated based on the average costs on different olive farms according to the information provided by advisors from different service companies working in the olive sector. Annual production costs at full bearing include the following:

- Winter pruning, removal of trunk suckers, and removal of pruning debris. There are no substantial differences among typologies, except for the removal of suckers, which is an operation that is not usual in hedgerow plantations.

Table 7.8. Estimated annual costs of olive plantation typologies.

	Cost (€ ha^{-1})						
	Orchard typology[a]						
Operation	RT	IT	RI	II	IWH (HD)	RNH (SHD)	INH (SHD)
Winter pruning	150	150	150	150	150	150	150
Picking debris	80	80	80	80	80	80	80
Summer sucker removal	50	50	40	40	0	0	0
Soil fertilization	80	100	100	120	120	100	120
Soil management	240	240	240	240	240	240	240
Plant protection and fertilizers	170	170	200	200	250	250	250
Irrigation	–	250	–	300	300	–	300
Harvesting	500	900	600	800	600	300	400
Transport and milling	150	300	300	480	600	360	600
Indirect costs	80	80	80	80	80	80	80
Total cost	1,500	2,320	1,790	2,490	2,420	1,560	2,220

[a]RT = rainfed traditional, IT = irrigated traditional, RI = rainfed intensive, II = irrigated intensive, IWH = irrigated wide hedgerow, RNH = rainfed narrow hedgerow, INH = irrigated narrow hedgerow, HD = high density, SHD = super high density.

- Soil fertilizer application. This cost is usually related to the expected yield of the orchard.
- Phytosanitary and fertilizer foliar sprays: This involves 2–3 foliar applications to control peacock (*Spilocaea oleagina*) and other diseases (copper) and applying insecticides for fruit flies and moths (*Prays oleae*) that are common in traditional plantations. However 3–4 applications are commonly required in intensive orchards and 4–5 to hedgerow orchards and these include preventive application of copper after mechanical harvesting to prevent olive knot. Foliar fertilizers rich in N and K are frequently incorporated in some of the foliar sprays.
- Soil management is variable among farms but similar among plantation typologies. Minimum tillage and herbicides applications are common general practices.
- There are minimal differences among typologies related to the administrative canon for water. In general, traditional plantations are irrigated with 1,500 m^3 ha^{-1} and intensive and hedgerow orchards are irrigated with 2,000 m^3 ha^{-1} water.
- Harvesting costs obviously differ significantly among plantation typologies. The costs of harvesting for plantation typologies have

Table 7.9. Economical Indices of olive plantation typologies.

Typology[a]	Investment (€ ha^{-1})	Average fruit yield (t ha^{-1})	Harvesting cost (€ t^{-1})	Total costs (€ ha^{-1})	Oil cost (€ kg^{-1})	Payback (years)
RT	500	2.5	200	1,500	3	–
IT	2,500	5	180	2,320	2.32	20
RI	750	5	120	1,790	1.79	10
II	3,000	8	100	2,490	1.55	7
IWH(HD)	5,000	10	60	2,420	1.42	8
RNH(SHD)	3,000	6	50	1,560	1.52	7
INH(SHD)	7,000	10	40	2,220	1.3	9

[a]RT = rainfed traditional, IT = irrigated traditional, RI = rainfed intensive, II = irrigated intensive, IWH = irrigated wide hedgerow, RNH = rainfed narrow hedgerow, INH = irrigated narrow hedgerow, HD = high density, SHD = super high density.

previously been defined (Table 7.6). These costs represent the main cost for traditional and intensive orchards harvested with trunk shakers and complementary methods for collecting, cleaning, and transporting the fruits removed from the trees.

- Costs of transport to the processing plant and milling are set according to the amount of olives in tons. In Spain, this cost is approximately 60€ t^{-1}. Taxes, insurance, and management costs are a fixed amount per hectare. In Spain, this amount is approximately 80€ ha^{-1}.

C. Economical Indices

Some relevant economic indices for plantation typologies in Spain for 2012 are shown in Table 7.9. The oil content per kilogram of olives is estimated to be 20% for traditional and intensive systems and 17% for hedgerow plantations. The payback has been calculated based on the average price of olive oil, that is, 2.2€ kg^{-1}. Traditional olive plantations are marginal at this current olive oil price. The data indicate that the cost of producing olive oil in intensive and hedgerow plantations and the cost of producing table olives are all below the current prices for olive oil and table olives.

VI. THE FUTURE

Major social and economical transformations in olive-growing countries have steadily reduced the available manpower for agriculture since the end of World War II. In addition, consumption of virgin olive oil and

table olives has been increasing around the world since the late 1970s because consumers have recognized the benefits of olive oil on health. Thus olive-producing countries will continue to see an increase in demand for both commodities. As a consequence, new high-density olive plantation systems have been designed to be mechanically harvested and to have high productivity to meet the growing global demand for olive oil and table olives.

Looking toward the future some critical points that will impact on the global olive industry are presented below.

A. Impact of the New Planting Systems

New intensive and hedgerows plantings are currently increasing in most traditional and new olive-growing countries. There are essentially three main types of mechanically harvested, early-bearing and highly productive systems: intensive, wide hedgerow, and narrow hedgerow. Whereas intensive and narrow hedgerow plantations may be either rainfed or irrigated, all wide hedgerow orchards are irrigated. These plantation systems are able to produce olive oil at competitive prices to meet increasing global demand. Choice among these planting systems will depend on the different ecological, financial, social, economic, and cultural circumstances of farmers. Current trends indicate that high-density planting systems will continue to be developed in traditional and new olive-growing areas. These new plantations will produce an increasing fraction of the total worldwide yield of olive oil and table olives in the future.

However, the impact of high-density systems on traditional olive-growing areas must be considered. Traditional olive growing is utilized by most olive plantations in the world, particularly in the Mediterranean region. The comparative cost of production and the current prices of olive oil based on Spanish data indicate that most traditional olive plantations are marginal. However, traditional plantations continue to partially sustain the economic activity of the population living in the related areas. Although some of these plantations can be converted to mechanization following new technologies, there are natural (steep slopes), structural (small farm sizes), economic (low income), and sociocultural (e.g., old age and labor unavailability) factors that impede conversion to new competitive planting systems. In addition, various policies have been implemented in European Union and other Mediterranean countries to subsidize the olive sector to sustain traditional olive farming as well as to reconvert it to more intensive systems. In the long term, reconversion and/or conservation of traditional olive

growing represents a major economic, social, and political challenge in most olive-growing countries.

Advances in the harvester manufacturing industry and in R&D systems and public–private cooperation have provided the increasing availability of partially or fully mechanical harvesting systems and mechanical pruning machines for high-density plantations. The availability of new mechanical harvesting systems will provide new possibilities for already established traditional orchards and new high-density plantations. Intensive mechanized planting systems represent the future of olive growing in developed countries. The mechanical harvesting of traditional orchards is currently limited by the topographical (particularly steep slope) and socioeconomic characteristics inherent to most traditional olive farms. Advances in the design of new machines for traditional plantations are in progress but more effort is needed.

B. The Need for Research and Development

Scientific research and development in most traditional olive-growing countries have been limited. Empirical knowledge has been a major source of the current technology in traditional olive orchards. Only in the past 30 years has experimental research increased its role in olive and oil research and innovation, as evidenced by databases such as WOK and Scirus. For instance, a survey on olive growing references in the WOK from 1899 to date done by the first author of this review shows an insignificant number of references from 1899 to 1956, then an steady increase from 1957 to 1986, and finally an exponential increase from 1987 to date. The development of new planting systems requires an increase R&D efforts and support for these systems will become more critical than it was in the past for traditional olive growing. This review has identified some critical aspects for the continuous development of intensive and sustainable olive growing in the world that require strong R&D commitment.

1. Cultivar Field Trials. The expansion of intensive and hedgerow planting systems has generally not been preceded by informative field trials in traditional olive-growing areas or in new olive-growing countries. This review indicates that the best producers of traditional cultivars are usually well suited for intensive orchards in their areas of growth, but few of them are well adapted to very-high-density hedgerows. Furthermore, the uneven adaptation of traditional olive cultivars in new climatic areas, both in the Mediterranean region and in new

subtropical olive-growing areas has been reported. Although field trials of some cultivars for intensive orchards have been published in the past 20 years (Table 7.4), more experimental effort is needed. Therefore, field trial networks should be used to identify the best cultivars for optimizing production in intensive and hedgerow orchards in both traditional and new olive-growing areas.

2. Breeding. Recent changes in olive intensification indicate that many traditional cultivars are unsuitable for use in the new growing systems. In the future, cultivars should be early-bearing and high-yielding, efficient in the use of the available water, tolerant to other biotic stresses, resistant to major pests and diseases (particularly to *Verticillium* wilt), well adapted to the new mechanically harvested planting systems, and be able to yield high-quality olive oil and table olives. Such requirements resulted in classical breeding programs for olive trees being initiated in 1965–1975. Although only a few cultivars have been obtained to date, the new breeding programs have provided notable methodological advances such as the shortening of the juvenile period, new criteria for early and simplified selection elite genotypes within progenies, and improved understanding of the heritability of some relevant traits. These breeding programs are yielding an increasing number of preselections and advanced selections. The first projects in functional genomics will also provide useful tools for MAS (marker-assisted selection). These efforts will enhance the opportunity for introducing new releases in the future.

3. Pests and Diseases. Irrigation in traditional and in high-density plantations in the Mediterranean region and in new growing areas has been associated with the development of specific soil-borne and defoliating diseases. The spread of *Verticillium* wilt in most olive-growing countries is a major threat for new plantations. Olive knot should be strictly controlled because of its ease of penetration into lesions on branches and shoots during mechanical harvesting. Inconclusive data also exist regarding the higher incidence of some diseases in high-density plantations compared with that in traditional orchards. The risk of disease transmission by plants from the nursery industry has been observed in several countries. Integrated plant protection management strategies should be implemented, including preventive (e.g., the exclusion of infested soil and irrigation water, quarantine and certification of nursery plants, and use of tolerant/resistant cultivars) and postplanting control techniques in whole crop management systems. This strategy should also consider

the international context of international regulation for available pesticides.

4. Canopy Management. The interaction of many factors such as climate, soil, cultivar, planting distances and row orientation, training systems and available water determine tree and hedgerow volumes and external canopy surfaces. The interception of radiation depends on the sunlit leaf area and is a major factor in determining productivity and quality (i.e., oil yield and composition). The sequential processes that occur in the biennial reproductive cycle of olive trees are also influenced by most of these factors. Furthermore, mechanical harvesting requires a critical size and specific geometry of the trees and hedgerows for efficient fruit collection. Consequently, managing the canopy and reproductive processes is critical for the success of any high-density olive plantation, as different combinations of any of these critical factors may determine the success or failure of a high-density planting system.

This review demonstrates that most publications on high-density plantations contain scattered information from commercial orchards or experiments in which only a single factor was studied, thus limiting the value of the results. However, some experiments have provided critical information. For example, the linear relationship between accumulated oil yield up to 12 years after planting and the total linear meters of narrow hedgerows in an orchard indicates the need to limit the height and width of the hedgerow via manual or mechanical pruning to reduce canopy shading. Particularly relevant is the use of computer models for radiation interception that has been determined to be a critical factor for productivity in separated trees and hedgerows. More research effort aimed at testing some potentially critical factors, including the distance between rows and available water (rainfall + irrigation), row orientation and row spacing for specific latitudes, and the porosity of the large and narrow hedgerows, should provide useful local information for producers. Validated computer models to forecast yield productivity based on geographical and environmental conditions will also be valuable.

C. Conservation of Cultivars and Rootstocks

Although propagation by farmers in traditional olive plantations conserved a huge diversity of traditional local cultivars, the expansion of intensive and hedgerow orchards has been associated with the expansion of the nursery industry for the propagation of the required plant material. Few cultivars are now planted, and many traditional local cultivars are no longer propagated. The consequent risk of genetic

erosion necessitates the conservation, cataloging, and sustainable use of olive genetic resources by including existing cultivars in available *ex situ* germplasm banks.

In addition increasing genetic diversity through the exploration and *in situ* and *ex situ* conservation of relict cultivars, wild olives and related species are required. The effort undertaken in the past 40 years in this regards should be strongly supported in the future, including the initiative launched by the International Olive Council in 1994 to establish a network of germplasm banks. New molecular tools may also facilitate studies into understanding and defining genetic variability and the establishment of core collections will assist the study of genotype–environment interactions for relevant agronomic characteristics. Furthermore, germplasm banks will provide critical information for cultivar and rootstock evaluation and for the choice of progenitors in breeding programs.

ACKNOWLEDGMENTS

The valuable comments and suggestions for improvement of the manuscript by our fellows G.L. Blanco-Roldán, J.A. Gil-Ribes, F.J. López-Escudero, J. Moral, A. Moriana, and E. Quesada-Moraga are gratefully acknowledged. We also thanks to Todolivo S. L. and their technical advisors for providing valuable data in establishment and management costs of high-density plantations. Finally, we are deeply in debt to Jules Janick, Ian Warrington, and Ricardo Fernández-Escobar for their final and valuable editing.

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8

The Carob Tree: Botany, Horticulture, and Genetic Resources

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ABSTRACT

The carob tree, *Ceratonia siliqua* L, is a characteristic constituent of the evergreen, "maquis" and "garigue" vegetation type in low-altitude areas in the Mediterranean Basin. All over these territories, this dioecious and thermophilous tree has been extensively cultivated for its pods. These trees are used for both human consumption and as a sugar-rich animal feed. However, currently the main interest is seed production for gum extraction from the endosperm, which is used as a stabilizer in numerous commercial food products. Most cultivars are female, and require the presence of pollen donors in the orchards. The carob is mainly insect-pollinated (flies, bees, and wasps), but is also wind-pollinated, depending on the habitat. The carob tree shows some outstanding features, like rusticity and drought resistance, and produces under reduced orchard management, and thus is well suited for part-time farming. Carob's main limitation is its frost sensitivity. In addition, modern carob orchards start bearing earlier (fourth year after budding) than traditional carob plots, and they increase yield steadily in response to minimum cultural care and deficit irrigation. This crop has received little attention until now, but currently it is being reemphasized as an alternative in dryland (500 mm) or in supplementary drip irrigation areas with a Mediterranean climate for diversification and revitalization of coastal agriculture. This chapter describes carob's economic

Horticultural Reviews, Volume 41, First Edition. Edited by Jules Janick.
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importance worldwide and their genetic resources and it also reviews various aspects of its taxonomy, botany, origin, ecology, properties, uses, diversity, and breeding. All the life cycle descriptions are referred to the northern hemisphere climatic conditions. In addition, a full account of the crop-producing areas, agronomy, limitations, industry market, and prospects is presented.

KEYWORDS: carob cultivars; *Ceratonia siliqua*; genetic variability; orchard management; propagation

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I. INTRODUCTION

The carob tree (*Ceratonia siliqua* L., Fabaceae) has been grown since antiquity in most countries of the Mediterranean Basin, usually in mild places and in rainfed orchards with poor soils. Its value was recognized by the ancient Greeks, who brought it from its native Middle East to Greece and Italy, and by the Arabs, who disseminated it along the North African coast and toward the north, into Spain and Portugal. It was spread in the 19th century to other regions such as California, Arizona, Mexico, Chile, and Argentina by Spaniards, to parts of Australia by Mediterranean emigrants, and to South Africa and India by English people.

Carob has long been recognized by farm peoples of the Mediterranean region as a valuable substitute for grains in times of drought and famine. The period when carob was first cultivated remains unclear, but archaeological evidence suggests that the Egyptians may have been one of the first settled farming peoples to cultivate the tree. Seafaring Semite traders may have introduced the carob, along with the grape and olive, into Egypt around 18th century BCE from Palestine or Syria (Esbenshade and Wilson 1986). The Pharaoh Thutmosis III of Egypt (1490–1436 BCE) mentioned carob wood trophies from Palestine, and by the time of Rameses III (1190–1164 BCE) it was used for the construction of temples (K. Mitrakos 1968, unpublished). The seeds provided an extract (gum) used in the preparation of the strips of cloth that bound the mummies of the Pharaohs in the sarcophagus (Rol 1973, Winer 1980). The carob is not mentioned in the Old Testament. In contrast, carob cultivation and uses are soundly documented in later Jewish sources, namely, the Mishna (first century BCE–second century CE) and the Talmud (third–fifth centuries CE), as a source of good feed for domestic animals (cattle, horses, and pigs) and human food; also some agronomic and pod store comments are given (Moldenke and Moldenke 1952; Liphschitz 1987; Zohary 2002). The carob beans as food are only some noted in the New Testament of the Bible (gospels Matthew, Mark,

and Luke) (Moldenke and Moldenke 1952; Daris 1964). John de Baptist, while preaching in the desert, was said to have consumed "locust" and wild honey. The locusts are believed to have been carob pods rather than insect (grasshoppers). Thus, the pods came to be called "Saint John's Bread" or "locust bean" in many countries (e.g., UK, Germany, and the Netherlands). The same can be said of the husks mentioned in the parable of the Jesus hungry prodigal son "who would fain have filled his belly with husks that the swine did eat" is believed by some to have been referring to carob pods. In Roman times, two writers, Columella (4 BCE–65 CE) and Pliny the Elder (23–79 CE), describe the carob and its cultivations at some length. In addition, numerous charred carob pods were uncovered in Herculaneum and Pompeii ruins destroyed in 79 CE (Spina 1986; Zohary 2002). For centuries, the pods of the carob have found favor as a livestock feed. Arab jewelers in the Middle Ages used the uniform seeds as a unit of weight (200 mg) for gold and precious stones, and called them "karat." The carob tree is an important part of the Mediterranean vegetation and it is often interplanted with olives, grapes, almonds, and barley in low-intensive farming systems. Carob pods with their sugary pulp have been a staple in the diet of farm animals and were eaten by children as snacks or by people in times of famine. However, currently the main interest is seed production for gum extraction from the seed endosperm. Worldwide, carob bean gum (CBG) (or syn. locust bean gum (LBG)) is now widely used by the food industry as a thickener or stabilizer in the production of a large number of commodities such as ice cream and soups. Kibbled pods have been shipped from producing countries to all over Europe and the United States. Because of low orchard management requirements, the carob tree is suitable for part-time farming and shows potential for planting in semiarid Mediterranean or subtropical regions. The trees are also useful as ornamentals and for landscaping, windbreaks, and afforestation. Cattle can browse on leaves and the wood is suitable for fuel. Carob cultivation is sustainable and eco-friendly mainly due to several features such as drought resistance, salt tolerance, atmospheric pollution resistance, pest and disease and fire resistance, and suitable to low-input horticulture. Carob's main limitation is its frost sensitivity.

A. Origin, Domestication, and Distribution

The origin of carob is unclear and several centers of origins have been proposed. De Candolle (1883) and Vavilov (1951) suggested Turkey and Syria. Zohary (1973, 2002) reported the origin in the Arabian Peninsula and demonstrated from archaeobotanical evidences (most of them from

Israel) that carob existed in the eastern Mediterranean Basin long before the start of agriculture, and this region has been at least one of its domestication centers, which needs further clarification as the status of the wild-growing carobs in the western Mediterranean region. *C. oreothauma*, the only known carob-related species, is considered to have its center of origin in the southeast of Arabia (Oman) and around the African horn (north of Somalia), and Hillcoat et al. (1980) suggested it to be the wild ancestor of the cultivated *C. siliqua*. Early literary sources indicate that its domestication took place relatively late (only in Roman times). The reason for this late date probably is that the carob does not lend itself to simple vegetative propagation, and its cultivation had to wait until the introduction of scion grafting into the Mediterranean Basin. Carob culture reached its peak in this region in early Islamic times (Zohary 2002). Spontaneous carobs occur and thrive in many places around the western Mediterranean Basin, but they are regarded as feral derivatives of the fruit crop that probably evolved under domestication. Most carob cultivars were probably selected during the Middle Ages by Muslims (Ramon-Laca and Mabberley 2004).

Zohary (1996, 2002) suggested that similar to most Old World fruit crops (olive, grape-vine, date-palm, and fig), domestication of *C. siliqua* was based on shifting from sexual reproduction (in the wild) to vegetative propagation (under cultivation). In carob, as in other fruit and nut trees, the shift to vegetative propagation is the cultivator's solution to the problem of wide variability that is characteristic for sexual reproduction in cross-pollinated plants. In addition, as a predominantly dioecious tree, carob includes half staminate and pistillate trees, and about 1% hermaphrodites in natural conditions (Condit 1919). Zohary (2002) proposed that under domestication, hermaphroditic clones were favored, causing a partial breakdown of dioecy in carob culture. Spontaneous promising seedlings showing superior features have been empirically selected by growers and were then clonally propagated. As a consequence, wild carob trees currently growing in Mediterranean countries are not identical to the species type (Mitrakos 1988). Hillcoat et al. (1980) reported that cultivation in ancient times would have been unnecessary since wild trees were common in the eastern Mediterranean.

Wild and feral carobs reproduce by seed, while cultivated varieties are propagated vegetatively as clones. The carob does not root easily by cuttings and is only easily multiplied by scion budding. The propagation of pistillate clones changes the sex ratio in carob-producing areas. The three main fruit traits that distinguish domesticated carobs from their wild relatives are larger bean size, more pulp, and higher

sugar content. Increased size and a higher number of seeds are less evident. These pod traits together with productivity and environmental adaptation seem to have been the most important selection criteria for growers.

As a food source, carob pods could be stored and transported to long distances. In most of the Mediterranean region, wild and naturalized carobs are distributed in more or less the same geographic and climatic belt as the cultivated trees. Forms of spontaneous carobs are particularly common at low altitudes along the Spanish Mediterranean coast, southwest of Spain and south of Portugal, the Balearic Islands, southeast of France, Corse, and Sardinia islands, the shores on the south of Italy including Sicily, the Adriatic coast of Croatia, the Aegean region in Greece and Turkey, along the northern and southern ranges of the isle of Cyprus, in the Malta Islands, in the maritime belt of Lebanon and Israel, the coastline in Tunisia and Algeria, and the north and south of Morocco (Fig. 8.1).

The carob tree was likely introduced into the United States from Spain in 1854. In the 1950s, W. Rittenhouse and J.E. Coit promoted this species in California and introduced budwood of selected Mediterranean cultivars, but currently only few seedling trees are grown for shade on the streets of cities in southern California and Arizona (Ferguson and Arpaia 1990). In Australia, they were introduced by the Mediterranean immigrants in the 19th century (Tous 1995), mainly for agroforestry uses and recently for pod production. Finally, in China, carob seedling trees have been planted in some forest regions, as Sichuan and Yunnan (Tous and Chunqian 2004), basically for forestation and animal feeding.

Fig. 8.1. Carob tree distribution in the Mediterranean Sea. Carob production is 260,000 t.

In Mediterranean countries, the distribution of this evergreen sclerophyllous species is controlled by winter cold stress (Mitrakos 1981). The carob is one of the most characteristic and dominant trees in the low-altitude zone (0–500 m) warm weather vegetation of the Mediterranean evergreen "maquis" and "garigue" (Zohary and Orshan 1959; Folch Guillen 1981) and rarely up to 800 m asl (there are some exceptions in the Atlas mountains in Morocco and some hills in Lebanon). In some areas along the Mediterranean sea coast, wild carobs cover undisturbed hilly landscape.

B. World Production and Market

1. Production. Commercial carob production is currently based in the Mediterranean Basin. The only significant recent plantings outside this region are in Australia. World production of carob pod is estimated at about 220,000 t per year produced from some 127,000 ha, with variable yields depending on cultivar, region, and farming practices. Spain producing on average 60,000 t per year (MARM 2008) is the leading carob producer and exporter followed by Morocco, Italy, Portugal, Greece, Turkey, Cyprus, Algeria, and some other countries (Tables 8.1 and 8.2). The southern countries of the European Union (Spain, Italy,

Table 8.1. Carob production area in Mediterranean countries (2008).

Country	Area (ha)	%
Spain	50,000[a]	38.5
Morocco	30,000[b]	23.1
Italy	15,000[c]	11.5
Portugal	15,000	11.5
Greece	5,000	3.8
Turkey	4,000	3.1
Cyprus	3,000	2.3
Algeria	2,000	1.5
Israel	1,500	1.2
Other[d]	4,500	3.5
Total	130,000	100.0

[a]*Source*: MARM (2008); FAOSTAT (2009).

[b]*Source*: Aitchitt et al. (2007).

[c]*Source*: Istat (2009) and others.

[d]Includes Lebanon, Tunisia, Croacia, Malta, Australia, South Africa, USA (California), and Mexico.

Table 8.2. Average carob pod and seed production in the world (2007–2008).

Country	Pod (t)	%	Seed (t)	%
Spain	60,000[a]	27.3	6,000	23.3
Morocco	40,000	18.2	7,600	29.6
Italy	35,000[b]	15.9	3,500	13.6
Portugal	30,000	13.6	3,000	11.7
Greece	19,000	8.6	1,900	7.4
Turkey	15,000	6.8	1,500	5.8
Cyprus	7,000	3.2	700	2.7
Algeria	6,000	2.7	700	2.7
Other[c]	8,000	3.6	800	3.1
Total	220,000	100.0	25,700	100.0

[a]*Source*: MARM (2008); FAOSTAT (2009).

[b]*Source*: Istat (2009) and others.

[c]Lebanon, Tunisia, Israel, Croacia, Australia, South Africa, USA, and so on.

Portugal, Greece, and Cyprus) with some 85,000 ha account for 70% of the growing area and about 69% of the world pod production. Morocco is the most important country (average 7,600 t) for seed production, followed by Spain (6,000 t). There is some production in Lebanon, Tunisia, Australia, Croatia, and Israel and small amounts are produced in Malta, California, Mexico, and South Africa. Pod and seed production in different countries are not parallel because the differences in seed yields of cultivars and wild types (Table 8.2). The market for carob pods is quite stable; about 54,000 t of pods per year are used in Spain (MARM 2008). The potential world demand for gum (LBG) is estimated around 10,000–12,000 t per year, which are produced from about 30,000 to 35,000 t per year of carob seeds.

In Spain, the largest carob-growing area (190,000 ha) was reached toward the 1930s, but production has halved between 1970 and 1995 (MARM 2008). The current Spanish growing area and production (50,000 ha and 60,000 t, respectively) is distributed in five regions: C. Valenciana (22,000 ha and 23,500 t), Catalonia (9,600 ha and 12,000 t), Balearic Islands (12,950 ha and 12,700 t), Andalusia (1,477 ha and 15,000 t), and Murcia (975 ha and 1,240 t) (MARM 2008). There are estimated to be 54,000 isolated trees (not in orchards), some of which are intercropped with other species such as almonds, olives, figs, and grapevines. An important number of wild and feral trees thrive in Andalusia (Batlle and Tous 1994; Tous et al. 1995).

Carob production in Italy (30,000–35,000 t) is mainly located in Sicily (provinces of Ragusa 18,700 t, Siracusa 9,800 t, and elsewhere

1,350 t) and in Puglia region 700 t (Istat 2009). Production in Sardinia is negligible (550 t). The current total surface is about 15,000 ha (10,800 ha in regular orchards). Italian production has halved between 1955 and 1995. The current tendency is to reduce even more the area devoted to carob.

The carob-growing region in Portugal is concentrated in the south with some 12,000 ha and 20,000–40,000 t of production depending on years. The Algarve is the main producing region of this country, and around 60% of the total surface is located in four places, Silves, Faro, Loulé, and Tavira. In the Alentejo region, there are also some orchards in Mértola (Martins-Louçâo and Brito de Carvalho 1989). The Portuguese carob production has declined over the past 20 years and the cultivated area reduced at least 25% (Droste 1993). Recently, there is an integrated planning to increase the surface in the Algarve region (DRAALG 2006).

In Greece, the carob exists in the southeast Peloponnese, in Attiki, the islands of southern Aegean (mainly Samos and Chios), the Ionian Islands (Kefallonia) and in Crete, where 80% of the total Greek carob production is concentrated (Androulakis 1994). Currently, the carob tree areas are used as pasture lands and the pod production ranges between 15,000 and 20,000 t. In Cyprus, the carob was a major crop (50,000 t) in the 1960s–1970s, but afterward the surface declined as a result of the expansion of irrigated crops (Orphanos 1980); currently, there are about 3,000 ha with an annual average production of 7,000 t.

Carob production in Morocco, dependent on annual rainfall, has increased over the past 15 years and ranged from 26,000 (Sbay 2008) to 60,000 t (Aitchitt et al. 2007). The main spontaneous populations are concentrated in the four rugged mountain chains: the Rif in the north, parallel to the Mediterranean coast, and three mountain chains in a northeastern to southwestern axis, the Middle Atlas (Taza, Fes, Beni Mellal), High Atlas (Azilal, Marrakech), and Anti-Atlas (Agadir, Tafraout). Crop area of wild and feral carob in Morocco is estimated around 30,000 ha (Aitchitt et al. 2007). Some new orchards have recently been planted in the south (Tiznit), and Moroccan production is expected to rise moderately in the coming years. In Tunisia, carob pod production is also from spontaneous trees and was estimated in the 1950s to be about 2,800 t (Crossa-Raynaud 1960). Recently (2006), there were planted around 500 ha giving an average production of 1,000 t that are mainly used for domestic consumption and *in situ* animal feeding (Tous et al. 2006). Turkish total production is about 12,000–15,000 t that is collected from isolated trees (354,000) as there are no carob orchards. The production is concentrated along the coast in the Aegean (4%) and Mediterranean (96%) regions from Urla (Izmir) to Samandag (Hatay)

(Vardar et al. 1980). The main producing provinces are Içel, Antalya, Mugla, Adana, Burdur, and Aydin.

In Israel, Goor et al. (1958) reported some 250,000 carob trees scattered in forests. In the early 1950s, about 2,000 ha were planted either as groves, on grazing land, as forests, or as roadside trees. Currently, some plantings are still productive (1,500 ha), but yield seems to be decreasing (200 t). In Lebanon, carob is cultivated in the coastal areas up to 800 m in different agricultural systems (about 300 ha); it can be found in olive and almond orchards, where carob is mainly planted and grafted. These are mostly wild trees that have been maintained and grafted (Breugel and Stephan 1999). Furthermore, carob is planted in monoculture orchards.

In Croacia, carob production is extensive, based on some 500 ha (FAOSTAT 2009) located in parts of central and southern Dalmatia (region placed along the Adriatic coast). The main producing areas are the islands of Vis, Lastovo, Solta, Korcula, and the area of Dubrovnic. The annual carob crop is estimated in 400–500 t and it is collected from scattered trees and groves, and it is exclusively processed into carob flour (Kaleb 1998).

In California, during the 1950s, there was a well-publicized "carob crusade" promoting this species as a dryland crop requiring little irrigation, and several orchards were established throughout the south. However, mainly owing to low crop productivity under dryland conditions and high land and processing costs, the project failed (Ferguson and Arpaia 1990). Currently, there are a few isolated trees for shade in gardens and streets in southern California.

In Australia, the crop was introduced around 1850 by Mediterranean emigrants. However, it was only in the 1980s that interest in carob led to planting some orchards (Esbenshade and Wilson 1986; Tous 1995; Race et al. 1999). The Australian carob-growing area is about 500 ha and there are also some 30,000 isolated trees, mainly in South Australia (50% of total surface) and Western Australia (30%) but also in Queensland, New South Wales, and Victoria. Production is estimated around 1,000 t per year. Ripe pods have potential as a high-energy stock feed and also seeds satisfy the increase of domestic demand for LBG (Race et al. 1999).

2. Market. From the market situation over the past 20 years, it can be deduced that carob pod prices tend to be cyclic with long gaps and high peaks, as in the years 1984 (0.25 US$ kg^{-1}), 1994 (0.8 US$ kg^{-1}), and 2006 (0.40 € kg^{-1}). Currently (2011), in Spain and Italy, the prices for carob pods, carob kernels, and carob gum (food quality) are 0.20–0.25, 1.65–2, and 6–7, respectively. This makes the market prices unsettled

and produces a negative effect on demand. In addition, highly variable prices favor market speculation. Carob production assessment worldwide is difficult for the following reasons: (a) lack of proper statistic records; (b) natural variations of the annual yields (frost, drought, etc.); and (c) variation of the amount harvested between years due to the course of the market price.

The overall carob production trends are stationary in some countries (North Africa, Lebanon, and Portugal) and decreasing in others (Spain, Italy, and Cyprus). Usually farmers harvest and collect the carob fruits and bring to the cooperative or private kibbler, but there are other peculiar ways to market carobs, for example, in Sicily, where price is determined after fruits are placed and kept in the kibbler, and in Magreb region (mainly Morocco), most harvesting is under contract with forest state owner paid a previously agreed price per hectare based on estimated yield. Also, there is some variability in the quality of carob pods, in traditional European Union countries the kernel yield is about 10%, but in Morocco, the average kernel yield of wild and feral trees is in the range of 18–20%. All these aspects are influencing global prices. However, the industry needs a steady and regular raw supply and stable prices on which customers can rely. In addition, carob seed prices are even more fluctuating than carob kibbled prices. As the main industrial application is the CBG, this recurrent situation affects carob demand and thus its multiple uses and usually CBG producers buy other gum substitutes, such as guar, tara, and xanthan, to make several commercial products. For improving the stability of the farmer's pod prices, the potential carob pulp demand should be increased to reduce the final dependency of the kernel price.

II. BOTANY

A. Taxonomy and Nomenclature

The scientific name of carob tree (*C. siliqua*) derives from Greek *keras* (horn), and Latin *siliqua*, alluding to the hardness and shape of the pod. The common name originates from the Hebrew *kharuv*, from which are derived the Arabic *kharrub* and later *algarrobo* or *garrofero* (Spanish), *carrubo* (Italian), *caroubier* (French), *karubenbaum* (German), *alfarrobeira* (Portuguese), *charaoupi* (Greek), *charnup* (Turkish), *garrofer* or *garrover* (Catalan), *tikida* (Bereber), and *chaito-tou-shu* (Chinese). The carob is also known as St. John's bread or locust bean in reference to the presumed use as food by St. John the Baptist and translated in German as

johannisbrotbaum. The common term "carob" is sometimes misused to indicate other species such as those of *Prosopis*.

The genus *Ceratonia* belongs to the Fabaceae (syn. Leguminosae) of the order Rosales. Legumes are important members of tropical, subtropical, and temperate vegetation throughout the world. This is one of the largest families of blooming plants and includes 650 genera and over 18,000 species (Polhill et al. 1981) and is extremely variable in morphology and ecology. The carob tree is generally placed in the tribe Cassieae of the subfamily Caesalpinoideae; however, several authors doubt *Ceratonia*'s position in the Cassieae (Irwin and Barneby 1981; Tucker 1992a,b). The diploid chromosome number for *Ceratonia* is $2n = 24$, whereas many members of the Cassieae complex have $2n = 48$ and Goldblatt (1981) suggested it might be aneuploid. The genus *Ceratonia* is regarded as one of the most archaic of the legume genera (Tucker 1992a). Taxonomically, *Ceratonia* is completely isolated from all other genera of its family (Zohary 1973). Hillcoat et al. (1980) and Tucker (1992a) considered the carob as a very isolated remnant of a part of the Fagaceae now largely extinct.

A second species *C. oreothauma*, Hillcoat, Lewis and Verdc., was only described in 1980. Two subspecies were distinguished, subsp. *oreothauma*, native to Arabia (Oman), and subsp. s*omalensis*, native to the north of Somalia. *C. oreothauma* is morphologically very distinct from *C. siliqua*. In addition, *C. oreothauma* has slightly smaller pollen grains than *C. siliqua*, and they are tricolporate rather than tetracolporate (Ferguson 1980). As pollen grains are more evolved than tricolporate grains, *C. oreothauma* was suggested as the wild ancestor of the cultivated *C. siliqua* (Hillcoat et al. 1980).

B. Morphology

1. Tree. The carob tree grows as a sclerophyllous evergreen shrub or tree up to 8–17 m high, with a broad semispherical crown and a thick trunk with brown, rough bark, and sturdy branches (Fig. 8.2). All seed-rooted trees will sucker to some degree at ground level. Leaves are 10–20 cm long, alternate, pinnate, with or without a terminal leaflet. Leaflets are 3–7 cm long, ovate to elliptic, in 4–10 normally opposite pairs, coriaceous, dark green and shiny above, pale green beneath and finely veined with margins slightly ondulate, and tiny stipules. The leaves are sclerophyllous and have a very thick single-layered upper epidermis, the cells of which contain phenolic compounds in the large vacuoles; stomata are present only in the lower epidermis and arranged in clusters (Mitrakos 1988). Carob trees shed second year leaves in early

Fig. 8.2. Carob tree growing in Catalonia coastal areas (NE of Spain).

summer, and they renew leaves in spring. The strong taproot is deep, penetrating in the deeper soil where it can absorb the nutrients and water that the plant needs. Relevant parts of the plant are shown in Fig. 8.3.

The tree has a cyclic vegetative growth. Two flushes take place in spring and autumn, the latter being weaker or sometimes missing at all (Fadl et al. 1979; Diamantoglou and Meletiou-Christou 1980). At low temperatures ($\leq$10°C), vegetative growth is reduced. However, intensity and beginning of shoot growth in spring also depend on the bearing status of a tree or branch (Haselberg 2000). In fruit-bearing trees ("on" status), vegetative growth is delayed and reduced. Compared to nonfruit-bearing trees ("off" status), the flushes are associated with higher levels of shoot growth. Single leaves are shed after 2 years in summer (July) and partially renewed in spring (Diamantoglou and Mitrakos 1981).

Although the carob tree is a legume, like most Cesalpinoideae, it does not nodulate, and thus it is unable to fix nitrogen (Martins-Louçâo and Rodríguez-Barrueco 1982; Martins-Louçâo 1985; La Malfa et al. 2010). Arbuscular mycorrhizal (AM) fungi have been shown to colonize carob roots; however, no ectomycorrhizal association was found (Martins-Louçâo et al. 1996). The colonization by AM may increase nitrogen uptake by the plant.

The carob is a dioecious species with some hermaphroditic forms. The flowers are initially bisexual and become functionally unisexual by

Fig. 8.3. Shoots, leaves, male and female inflorescences, and pods. *Source*: Zohary (1973).

subsequent organ suppression (Tucker 1992a); dioecy is not common among Fagaceae. In evolutionary terms, unisexuality is generally regarded as a derived character from bisexual ancestral state. There is some evidence in many cultivars such as 'Bugadera' and 'Sfax' that environmental factors modify sex expression in the course of the floral differentiation. Caruso et al. (2008a) propose a role of ethylene in carob sex expression.

Flowers are small (6–12 mm long) and numerous, green tinted and red colored, appearing in late autumn, and show pentamerous symmetry with calyx but not corolla placed on a short pedicel. The inflorescences, usually bearing 15–40 single flowers, arise as short

lateral racemes mainly on 2 year-old or older branches and on the trunk (cauliflorous and ramiflorous flowering). Cultivars vary considerably intheir blooming characteristics (Haselberg 2000). Flower numbers and density in female inflorescences are lower than that in male and hermaphrodite inflorescences (Crescimanno et al. 1988; Retana et al. 1994).

Pistillate flowers consist of a pistil (6–8.5 mm) on a disk and rudimentary stamens, surrounded by five hairy sepals. The ovary is bent, consisting of two carpels (5–7 mm long) and several ovules. The stigma has two lobes. Staminate flowers consist of a nectarial disk with five stamens with delicate filaments surrounded by hairy sepals. Hermaphrodite flowers contain a pistil and a complement of five stamens.

2. Fruit and Seed. The fruit is an indehiscent pod, elongated, compressed, straight or curved, thickened at the sutures, 10–30 cm long, 1.5–3.5 cm wide, and about 1 cm thick with blunt or subacute apex (Fig. 8.4). Pods are brown with a wrinkled surface and leathery when ripe. The pulp comprises an outer (pericarp) leathery layer and softer inner region (mesocarp). Seeds occur in the pod transversally, separated by mesocarp (Fig. 8.4). Seeds are numerous (4–15), rather uniform, and smooth, glossy, brown color, and ovate-oblong (8–10 cm long, 7–8 mm wide, and 3–5 mm thick), and the testa is hard. The seeds of grafted cultivars usually comprise 8–12% of the pod weight, and 16–20% for ungrafted wild types. The approximate composition of the seed (weight) is coat (30–33%), endosperm (42–46%), and embryos or germ (23–25%).

Carob pods are rich in sugars, but poor in protein. Most of the protein is found in the seed germ. The seed endosperm contains high percentage of galactomannan (carob bean gum powder) that has high commercial value and many industrial uses. A wide variation in fruit characteristics has been reported among cultivated genotypes (Caja et al. 1988; Crescimanno et al. 1988; Tous and Batlle 1990; Barracosa et al. 2007).

C. Reproductive Biology

Condit (1919) reported that the ratio of pistillate to staminate individuals is about 1:1 including a few hermaphrodites, but this relation changes depending on the regions. In the Balearic Islands, the frequency of hermaphrodites is higher than over the Iberian Peninsula (Tous et al. 2001), and Morocco, where the proportion staminate to pistillate

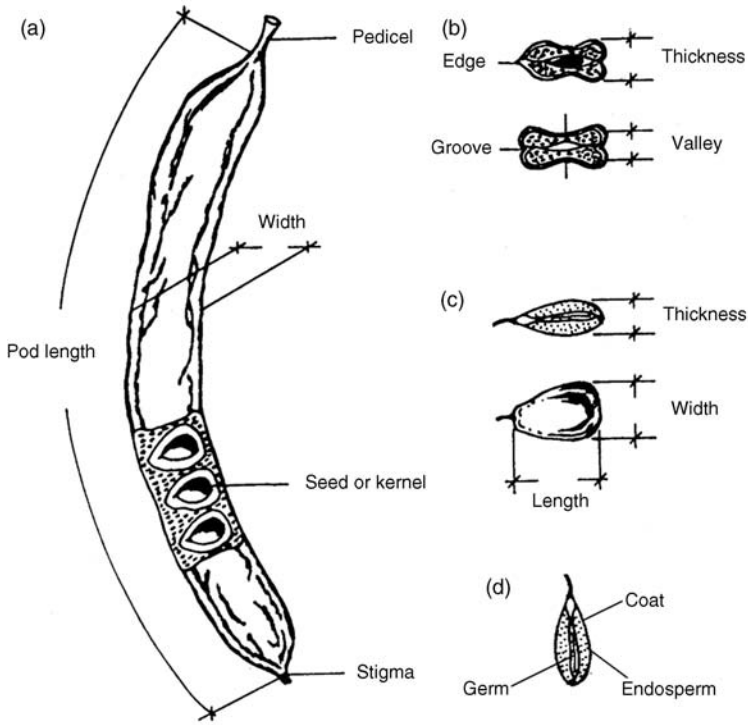

Fig. 8.4. (a) Important parts of the carob pod, (b) crosssection of pod, (c) seed, (d) crosssection of seed. *Source*: Tous et al. (2009).

trees in the natural populations is 3:1 (Sbay 2008). In countries like Spain, Italy, and Cyprus, in grafted orchards the ratio of male to female trees ranged from 1:3 to 1:6 (Russo 1954; Orphanos 1980). Floral morphology is complex. Schroeder (1959) grouped 59 carob cultivars growing in California into five floral classes based on sex expression throughout the season: pistillate, pistillate with occasional perfect flowers (hermaphroditic), perfect with occasional staminate flowers, perfect, and staminate. He reported that while adult trees maintained their floral types, young trees showed variation in the development of stamens. The provision of pollinators will prove to be essential for cultivars in the first three groups in order to ensure adequate commercial fruit set. Early season hermaphrodite cultivars showed some tendency toward pistil development failure later in the season.

There are many different forms of staminate trees; however, the two main types observed in Italy, Portugal, and Spain are often locally named after their anther color as red or yellow. This feature has revealed to be insufficient for their classification as it is determined independent of other flower characteristics (Haselberg 1988). It appears that blooming of red males is more extended than yellow males. Pollen grains released from the anthers possess a spheroidal shape and they are tetracolpate (Ferguson 1980). Their diameter at the polar is 28–29 μm and at the equator is 25–28 μm (Ferguson 1980; Liskens and Scholten 1980). Pollen tube growth and fertilization has been described by Haselberg (2000).

The carob is the only Mediterranean tree with the main blooming season at the end of the summer and autumn, similar to many truly tropical plants. However, the time and length of the flowering period depend on local climatic conditions and the ecotype trees. In some places, its blooming period overlaps partially with that of the loquat tree (*Eriobotrya japonica*). The extended flowering season in carob compensates for the unstable weather at this time of the year, and ensures that at least some flowers will be pollinated in a spell of good weather and insect activity (Retana et al. 1994).

Pollen transport from staminate to pistillate flowers is affected not only by insects, mainly bees, flies, wasps, and night-flying moths (Retana et al. 1990, 1994; Ortiz et al. 1996), but also by wind (Passos de Carvalho 1988; Tous and Batlle 1990). Flowers of all three sexes secrete nectar, although nectar volume and sugar content are higher in pistillate flowers than in staminate (Ortiz et al. 1996). Different insect groups tend to visit flowers at different hours. Bees are scarce in autumn when carobs are blooming, but many flies are present. How far wind-borne pollen is effective is unknown, but isolated pistillate trees have produced small crops.

The time of flower induction in carob still remains unclear. It has been speculated to take place in spring (Tous and Batlle 1990) or early summer, but these hypotheses need further verification (Haselberg 2000). Floral induction and differentiation processes are considered to be restricted due to competing growing organs, such as terminal vegetative shoots or the existence of developing fruits (May–June), which set in the previous season (Haselberg 2000). Leshem and Ophir (1977) reported that vegetative spring growth is related to enhanced gibberellin activity in the leaves and inflorescences of pistillate than of staminate carob trees. In addition, they observed in June a low concentration of endogenous gibberellins in a multihormone complex including auxin and ethylene, presumably required for flower

induction. In July, seeds growth as well as growing vegetative shoots and normally gibberellins are produced in large amounts. Gibberellic acid is a primary inhibitor for floral initiation in temperate woody perennials (Westwood 1993), it was found to restrain or delay floral induction (Haselberg 2000). The developmental stages of both pistillate and staminate flowers (Fig. 8.5) were first defined and described by Haselberg (1988).

The tree follows a 2 year cycle of reproductive and vegetative growth (Fig. 8.6). Carob is characterized by an extended blooming period. In Mediterranean countries, blooming mainly occurs between end-August and mid-November with a peak in October; however, some receptive

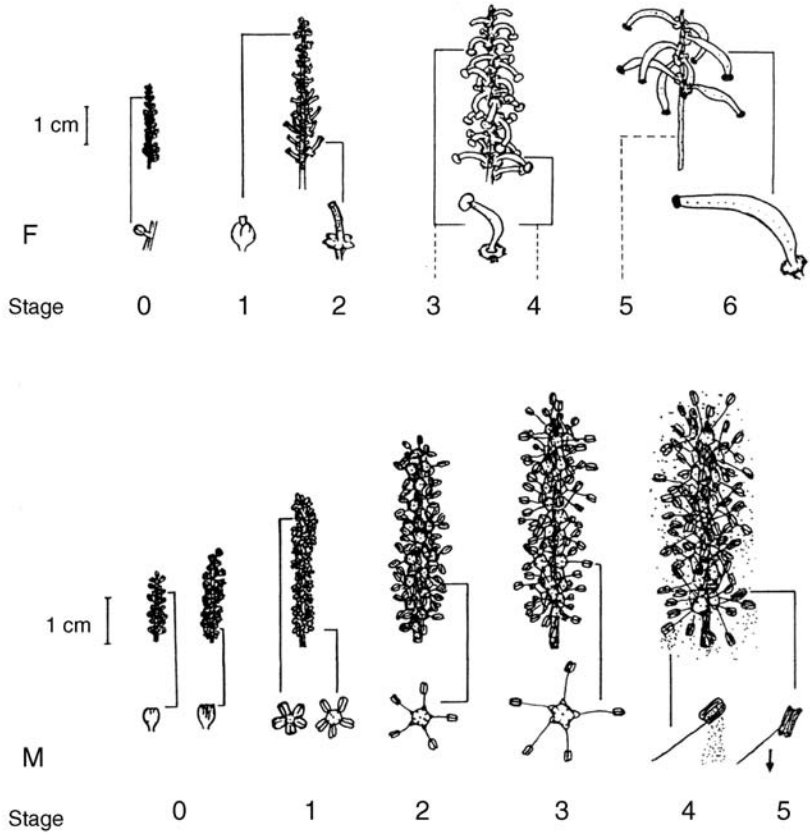

Fig. 8.5. Stages of development of female (F) and male (M) flowers of carob. *Source*: Haselberg (1988).

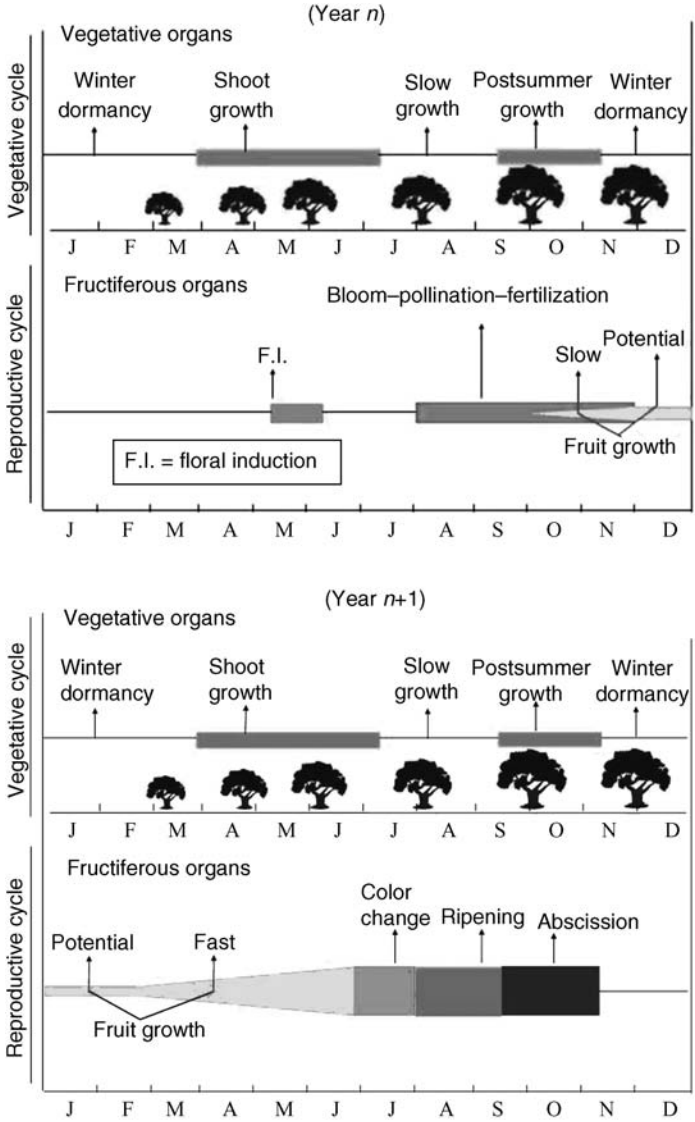

Fig. 8.6. Two-year cycle of growth in *C. siliqua*, L. *Source*: Tous and Batlle (1990).

flowers may as well be found in July and December (Orphanos 1980; Martins-Louçâo and Brito de Carvalho 1989; Retana et al. 1994). Blooming period shows great variability between sexes and is determined by genetic and environmental factors (Tous and Batlle 1990; Retana et al. 1994; Bosch et al. 1996). Development of inflorescence periods is wider in pistillate and hermaphrodite clones (2 months or more) than in staminate clones (about 1 month).

Ferguson (1980) reported up to 36% of morphologically abnormal pollen grains in staminate carob plants, although this appeared unrelated to a reduction in pollen fertility. Sfakiotakis (1978) observed high pollen germination variability *in vitro* among wild staminate trees in Crete. Their germination percentages ranged from 4% to 69%. However, Ciampolini et al. (1986) found less differences on pollen germinability from 5% to 39% in staminate and from 7% to 26% in hermaphrodite types. High variability and low values for pollen germinability in carob can thus presumably be related with extreme climatic conditions (rainy weather or temperatures exceeding 40°C).

Pistillate and hermaphrodite inflorescences carry a mean of 17 and 20 flowers, respectively, but few of them produce pods and only a small proportion of inflorescences set more than two fruits (Retana et al. 1994). Fruit set rate as influenced by the bearing status; in Mediterranean cultivars, the overall fruit set is normally around 1–3% in "on"-trees to 8–10% in "off"-trees (Russo 1954; Rovira and Tous 1996; Haselberg 2000). Haselberg (1996) found a positive correlation between blooming intensity and fruit drop and also that pods with a low number of seeds aborted more frequently.

D. Fruit Growth and Development

Fruit growth follows a sigmoid curve (Ilahi and Vardar 1976). For complete fruit development, 10–11 months are needed. Between 5,000 and 6,000 h above 10°C are required for pods to ripen (Esbenshade and Wilson 1986). Since the inflorescences appear in late summer and autumn, the development of fruit occurs slowly during the late winter, in spring fast pod growth period start (April–May), and, finally, in the last stage, the fruit grows slowly, ripens, and starts becoming dry in June and changes color from green to brown in July–August (Ilahi and Vardar 1976; Bosch et al. 1996). Fruit ripening was affected by the carob cropping status; in "on"-trees, fruits began to change color earlier than in "off" trees (Haselberg 2000). The ripeness of fruit is indicated by the complete darkening of the pedicel just prior to natural detachment from the branch and at this period fruit also have reached their full sugar

content. The green pods moisture in May–June are much heavier than the ripe ones, containing about 70% of water, whereas pod water content at maturity harvested is about 12–18%.

Shedding of carob flowers and young fruits occurs mainly from October to December, then slows down during January–February, and rarely occurs from June to early August (Bosch et al. 1996; Rovira and Tous 1996). Bosch et al. (1996) observed that on larger inflorescences of the two pistillate cultivars ('Negra' and 'Rojal'), higher rates of fruit initiation, fruit set, and seed set per flower produced than on smaller inflorescences. Haselberg (1996) reported that variations in flowering intensity and pod yield are likely to be more influenced by endogenous factors related to alternate bearing than by climatic conditions. However, unfavorable environmental conditions may significantly reduce yield by fruit set reduction, thus increasing production risk in marginal growing sites.

Alternate bearing and a biennial growth pattern have been reported for carob in general (Martins-Louçâo and Brito de Carvalho 1989; Tous and Batlle 1990; Tous et al. 2009). A heavy crop load reduces blooming and causes a light crop in the following year. This physiological habit has produced lower effect with selected cultivars choice, adequate ratio of pollinators used, and more care as to cultural practices such as irrigation and fertilization.

E. Ecology

The carob grows well in warm temperate and subtropical areas, and tolerates hot and humid conditions of coastal areas. Carob and orange trees have similar temperature requirements, but carob tolerates poorer soils and needs much less water. The carob tree is more tender than the olive. For resistance to dry environments, it is surpassed only by pistachio (Evreinoff 1955). Carob is a xerophytic species well adapted to the ecological conditions of the Mediterranean region because of its efficient hydric regulation by stomatic adjustment and its foliar structure and anatomy (Catarino et al. 1981). Carob, together with *Pistacia lentiscus* and *Olea europaea* ssp. *oleaster*, forms one of the most characteristic associations of the low-altitude zones of the Mediterranean vegetation, and thus is considered to be a climax community (*Oleo-Ceratonion* and *Ceratonio-Pistacion lentisci*) (Zohary and Orshan 1959; Folch Guillen 1981).

1. Growing Periods. The two main growing periods are in spring and autumn as in most Mediterranean trees. Vegetative growth slows below

10°C. Thus, it seems that this species enters some kind of "light" dormancy, at least in the coolest latitudes. However, in some very warm places and under favorable conditions, carob grows without becoming dormant either in winter or in summer (Liphschitz and Lev-Yadun 1988). The cambium can be active throughout most of the year (Fahn 1953) or all over the year with low rates of activity in January (Arzee et al. 1977). Investigations on the annual rhythm of cambial activity in Italy by Scaramuzzi et al. (1971) showed that cambium is active from February to the end of September and inactive during winter months due to low temperatures.

The rooting habit of carob is similar to pistachio; its extensive root system penetrates the soil deeply. Carob develops roots under stressful conditions to explore deeper soil layers where water may be available. It can thus survive long periods of drought. In addition, Nunes et al. (1989) reported that carob leaves are able to maintain turgor under situations of soil drought, using different strategies according to the season.

2. Climate. Suitable areas for this thermophilous species should have subtropical Mediterranean climate with cool (not cold) winters, mild to warm springs, and warm to hot dry summers. These Mediterranean-like areas range from approximately 30 to 45°C in northern latitudes (Mediterranean Basin, California, and Arizona) and between 30 and 40°C in southern latitudes (Australia, South Africa, and Chile).

Young carob trees and their flowers do not stand winter chilling; they can be damaged when temperatures fall below −4°C and adult trees can only withstand winter temperatures of −7 to −10°C. However, trees can withstand summer temperatures of 40°C and hot dry winds. Strong winds can break adult tree branches and detach pods, and also damage young trees (Tous and Batlle 1990). Autumn rains can interfere with pollination and affect fruit set. High humidity in spring promotes *Oidium* infection on both leaves and young pods, and also *Pseudocercospora ceratoniae* that affected leaflets and the trees appeared defoliated.

Carob, as a xerophyte, can survive dry climates without irrigation and is well adapted to dry environments with annual average rainfall between 250 and 500 mm per year (Tous and Batlle 1990). It has developed some drought resistance mechanisms (Nunes et al. 1989; Salleo and Lo Gullo 1989). Although drought resistant, carob trees do not bear commercial crop unless they receive at least 500–550 mm of rainfall per year (NAS 1979), although 350 mm of annual rainfall is considered enough for fruit set (Coit 1949; Ticho 1958; Crescimanno 1982).

3. Soil. Carob trees are grown in a wide range of soil types, from poor, sandy soils and rocky hillsides to deep soils. Trees do not withstand waterlogging, although the root system is usually deep. In areas with shallow rocky soils, tree size and productivity are reduced. The best soils are sandy well-drained loams, with alkaline or neutral pH, and calcareous with high lime content. Carob can tolerate up to 3% of sodium chloride in the soil (Winer 1980).

III. HORTICULTURE

A. Propagation and Planting

Carob may be propagated by seed, budding, cuttings, and micropropagation. Seedling rootstocks vary widely in vigor, habit, and cold resistance, but no selections are available. Seeds are removed from the ripe pods of the last harvest. Sowing should be done early in spring. Seeds germinate easily (70–80%), but the seed coats are very hard and require scarification with acid or hot water treatment. Carob seeds do not need to be stratified in a cold store to break dormancy. Good results were obtained with any of the following methods (Batlle and Tous 1997): soaking in tap water at room temperature for 15 days; soaking in boiling water, stirring briskly for 10 min, and then put in cold water for 24 h; soaking in concentrated sulfuric acid (80%) for 1 h and then rinsing with tap water to prevent complete digestion of the seed coat; or soaking in gibberellic acid (25 ppm) for 24 h.

After soaking, water is drained away and the seeds are sown either into polyethylene trays on greenhouse benches and kept at 20–30°C or directly into tall plastic pots (12–15 cm diameter and 35–40 cm deep) placed outside under shading. Optimum temperature for carob seed germination was found to be 25°C (De Michele and Occorso 1988) and 27.5°C (Mitrakos 1981). Different potting mixtures can be used. They usually contain soil, humus, perlite, and peat moss in various ratios, and are usually amended with sand to improve drainage and structure. The germinated seed should be watered regularly, but not overwatered, as this can result in damping off and root rot diseases.

Budding onto seedling rootstocks is the most common vegetative propagation method. Seedlings are budded in the nursery 1–2 years after germination, or 2–3 years after planting in the orchard. Bud grafting normally is carried out during late spring to early summer, care being taken that the rootstock bark opens easily. The type of budding depends of the rootstock size, and the most used are

"T-bud" (rootstocks of 1–2 cm of diameter), "chip bud" (less than 1 cm), and "patch bud" (bigger than 2 cm) (Brito de Carvalho and Graça 1988; Tous and Batlle 1990). When planting a new carob orchard, rootstocks are planted in late February or March and usually budded the following year in spring.

Vegetative propagation by cuttings and tissue culture are not yet commercially available for nurseries. Carob has been described by Lee et al. (1977) and Hartmann and Kester (1983) as difficult to root. Its adventitious rooting potential is low, but rooting has been obtained on subterminal hardwood cuttings (2 or 3 years old), after treatment with sulfuric acid and a high concentration of hormone (IBA or IBA combined); a rooting bench containing perlite and fitted with bottom heat ($24 \pm 1°C$) and mist (once every 2 min during the day) was used (Alorda et al. 1987). It appears that three aspects of the cuttings are important for rooting: time of collecting (seasonal variation), type of shoot (age and position), and genotype (rooting potential). Alorda and Medrano (1988) in Majorca (Spain) and Cabrita et al. (1988) in Algarve (Portugal) observed the highest rooting percentage in March cuttings, while for Fadl et al. (1979) in Egypt it was in April. Regarding genotype, the best rooting percentages were obtained by Alorda and Medrano (1988) using 'De la Mel' (syn. 'Negrillo') (85%) and one local hermaphrodite selection (45%) and by Cabrita et al. (1988) using 'Galhosa' (44%) rather than 'Mulata' (27%). Alorda and Medrano (1988) reported success after transplanting to the field with irrigation, while Cabrita et al. (1988) described plant failure after transplanting to a soil mixture under greenhouse conditions. De Michele and Occorso (1988) obtained a good rooting percentage (57.9%) in Sicily, using semihardwood cuttings with leaves taken in March and treated with IBA (8,000 ppm).

Carob micropropagation using both juvenile and adult tissues has been attempted by several authors (Sebastian and McComb 1986; Vinterhalter et al. 1992; Androulakis 1994; Alorda and Medrano 1996). Protocols have been established from axillary buds of mature pistillate trees (Romano et al. 2002; Brugaletta et al. 2009) and from protoplast (Haq 2006), with adequate nutrient medium (Gonçalves et al. 2005), and plants were successfully established in the field. Also a micrografting technique was developed for carob using *in vitro* germinated seedlings as rootstocks and apex or shoot cultures of pistillate cultivars as microscions (Hsina and El Mtili 2009). However, trials at IRTA (Institut Recerca Tecnologia Agralimentàries) comparing 'Rojal' cultivar plants, either micropropagated or grafted onto seedling rootstocks, indicated that micropropagated plants had a vegetative period of 4 years after

planting with rapid vegetative growth and were less expensive than the grafted plants. However, disadvantages included a 1 year delay in pod bearing and reduced root system development, requiring the need of staking as well as windbreaks.

Planting and transplanting of seedling rootstocks, before or after budding, are usually done directly from containers into the orchard. As carob is an evergreen tree and seedlings are very sensitive to frost and root drying, late transplanting in February or March (northern hemisphere) is recommended after frost danger has past; the use of bare rooted trees is not advisable. Young seedlings are very sensitive to frost damage, and thus in frosty places they should be protected.

Trees with well-developed roots should be used for transplanting and proper care during and after planting is essential. Unlike other fruit trees, usually carobs are not budded in the nursery. Trees should be well watered immediately after planting, and soil moisture should extend below the root zone. A second irrigation should follow within 2 weeks, followed by regular fertilization, using mainly nitrogen in the ammonium form rather than nitrate because of its easier uptake (Cruz et al. 1993). Rootstocks should be staked on the downwind side to ensure straight tree growth for budding and to protect them from excessive wind that is common in coastal areas around the Mediterranean.

B. Orchard Design

1. Layout. Traditionally, tree densities in carob orchards of Mediterranean countries have been low and variable, within the range of 25–45 trees ha^{-1} that means square tree spacing from 20×20 m to 15×15 m. Rectangular planting has also been a common design. Intercropping with species like olive, grape vines, or almond is frequently found. A well-designed orchard should ensure early bearing, adequate pollination, and maximum production potential, but with sufficient space for mechanical management.

Currently, for dryland orchards on poor soils or with support drip irrigation on the Mediterranean coast, tree densities between 100 and 200 trees ha^{-1} are recommended; that is, spacing from 9×10 m to 6×8 m (Tous and Batlle 1990). High-density planting in fertile soils may require thinning later. In California, Coit (1951) suggested a spacing of 9×4.5 m and tree removal some 10 years after planting to obtain a spacing of 9×9 m. In good soils of the Algarve (Portugal), an initial density of 6×4 m, later thinned to a density of 6×8 m and, finally (about 20 years old) with a layout of 12×8 m, was proposed (Brito de Carvalho 1988a).

However, most new orchards are being planted at permanent tree density (about 150–200 trees ha^{-1}) as tree removal is often inconvenient for most growers.

2. Pollinators. The need for pollination in carob has been clearly shown by Russo (1954). The carob is mainly (70–85%) insect-pollinated (by hover flies, solitary bees, and wasps), but is also wind-pollinated (30–15%), depending on the habitat (Zohary 2002). All pods contain seeds, and where a seed is missing, the pod does not grow to its full width (Orphanos and Papaconstantinou 1969). There is no evidence of apomixis.

The arrangement of pollinating trees in carob orchards has been traditionally disregarded by growers. This may have caused low yield or even contributed to the crop abandoning. In the island of Crete, Sfakiotakis (1978) reported crop failure due to unfruitfulness resulting from lack of pollination. Pollination has traditionally been achieved either by keeping a staminate branch from the rootstock in the center of the tree, if the rootstock is staminate, or by budding a staminate or hermaphrodite into the tree if the rootstock is pistillate. Spontaneous trees (half of which are staminate) may be found in the neighborhood, near paths or tracks, but generally in insufficient number. If staminate or hermaphrodite trees are planted as pollinators, they must be interspersed around and within the orchard in a regular pattern. It is important to use different types of staminate or hermaphrodite pollinators to overlap with pistillate cultivars' bloom, as main cultivars often display a long blooming season (3–4 months between August and November). Since male trees have a shorter flowering period than hermaphrodites, the latter usually show better overlapping and also bear fruits.

The ideal ratio of staminate or hermaphrodite to pistillate trees presumably depends on insect and wind activity in the orchard during flowering and also on pollen germinability. The proposed range varies from 4% of "Coit" (1949) to 20% of "Merwin" (1981). However, it seems enough to plant around 12% of pollinating trees (Tous and Batlle 1990), for example, a ratio of eight pistillate to one staminate or hermaphrodite, with pollinators planted in every third row and separated by two pistillate trees within the row (as shown in Fig. 8.7). Additional pollinators could also be planted in border rows upwind of the orchard. In California, Thomson (1971) recommended an orchard pollination design of hermaphrodites on alternate or every third row of trees for adequate pollination. In existing groves showing pollination deficiencies, some pistillate trees can be top-worked and grafted with hermaphrodite scion wood.

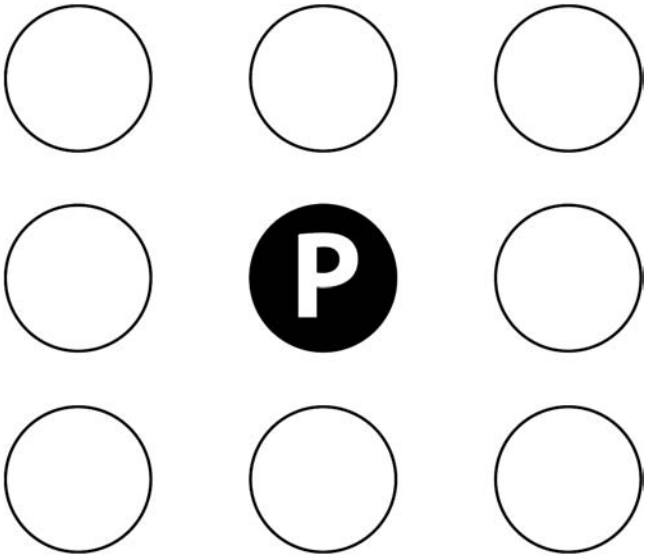

Fig. 8.7. Distribution of pollinators at a 1:8 ratio.

C. Training and Pruning

The carob tree requires little pruning, unlike many fruit and nut trees, which require pruning annually. After the basic framework of the tree has been established, only light pruning is necessary. This is due to the fact that carob fruits on 2 year and older wood.

In young trees, the traditional training methods were usually based on spherical or open vase forms, with a tall trunk and branching (first scaffold) from about 0.8–1.0 m above the ground. Currently, training pruning is simple and straightforward. Short trunks (low first scaffold) favor vegetative growth and early bearing, whereas taller trunks are advisable for mechanical orchard management. At the end of the third or fourth year after planting, it is also important to remove all lower vigorous side branches for tree training.

Usually adult trees are slightly pruned after harvest (October in northern hemisphere) or early spring (March), and light pruning is required every 3–4 years. Normally, dead wood and thin branches are removed (up to about 5–7 cm in diameter) and the annual shoot length should be beneath 25–30 cm. This operation should be carried out particularly in years when a significant crop is expected. Also it is common to apply manual sucker removal at the trunk base.

Rejuvenation pruning can be done in old neglected orchards or abandoned trees by severe thinning to increase and regularize production. If branches are broken in gales, they should be removed with a clean cut and mastic ought to be applied to the cut surface to keep out rain, as rotting can start easily, especially in mature trees at the peak of production.

D. Soil Management

Soil maintenance in carob orchards has traditionally been carried out by tilling weeds to reduce evapotranspiration and to improve water penetration. It is advisable to till the soil only up to 15–20 cm depth with a harrow or a cultivator, to prevent disrupting the shallow and active root system as this soil zone is generally the most fertile and best aired. Farmers in Spain usually till two times during the year: in early spring and when the green pods are developed and in the late spring.

In some orchards in Spain, weed control is accomplished through the mixed system of tillage and herbicide applications with good results (Tous and Batlle 1990), but in Catalonia some growers apply natural plant green cover between rows and herbicides under the trees. The most commonly used chemicals have been oxyfluorfen (pre- and postemergent) and glyphosate (postemergent). It is advisable to avoid the application of the last mentioned herbicides before the fourth year. Weed control is especially important in young plantations, since heavy weed competition for water and nutrients can significantly reduce tree vigor and early productivity.

E. Nutrition and Fertilization

Traditionally, carob orchards have scarcely been fertilized. However, in recent years, the revaluation of the crop has led some farmers to apply various types of fertilizer. As for other crops, carob tree nutritional evaluation relies on leaf and soil analysis. For nutritional assessment, leaf sampling should be taken during vegetative rest, between December and January in northern hemisphere. Correia et al. (2002) indicate that leaf mineral composition is related to yield in carob tree orchards. Results from these foliar analyses (% dry weight) should indicate optimum levels of 2.20–2.70% nitrogen, 0.10–0.15% phosphorus, and 0.9–1.30% potassium (Correia 2007).

Most workers highlight the benefits of nitrogen in increasing development and fruit production in old carob tree plantations (Lloveras and Tous 1992; Correia and Martins-Louçâo 1993). It has been shown that

this leguminous tree is unable to fix atmospheric nitrogen (Martins-Louçâo and Rodríguez-Barrueco 1982; Martins-Louçâo 1985). In traditional Spanish orchards, with average production of 2,500–3,000 kg ha^{-1}, an application of 50 kg of N per hectare is recommended for a density of 50 trees ha^{-1} (Tous and Batlle 1990). Another suggestion is the application of a P/K-based fertilizer and 25% of nitrogen after harvesting (autumn); the remaining nitrogen fertilizer can be applied in February. In orchards receiving some drip irrigation, N and K may be applied in the months of May and June, coinciding with the fast fruit growth stage. Recent field experiments, conducted in different calcareous soil types, show that ammonium nitrate and urea have been used with good results (Correia 2007). Phosphorus deficiency is not clearly seen in leaves or fruits of carob trees. Carob pods are important potassium sinks, particularly during the stage of high fruit growth (April and June) and ripening period (July and August). Potassium may be applied as potassium sulfate or potassium chloride. At field level, the response to other essential nutrients, like Ca, Mg, S, and micronutrients are not known (Correia 2007).

The first four planting years, the $N:P_2O_5:K_2O$ concentrations may be used at a proportion of 2:1:1, but after the fifth year from budding it should be changed to 2:1:2 due to the importance of K for fruit development and drought resistance (Correia 2007). Adult trees 15–20 years old are expected to achieve their maximum potential yield. At this stage, in Algarve (Portugal) in a field experiment conducted during 4 years, mature trees received 0.9 kg of N (as ammonium nitrate) each year. Leaf N concentration was around 2.50% (dw) in winter sampling and tree growth and fruit production increased each year (Correia et al. 2002). Lloveras and Tous (1992) also tested several N amounts (0–5 kg per tree per year) on large trees (more than 40 years old and with an average height of 5 m) and the pod yield increased with rising N fertilization levels.

Foliar fertilization (urea and potassium nitrate) and fertigation practices in new intensive carob orchards should be considered. It is important to stress the benefit of applying organic matter as with all other fruit and nut trees; it is recommended to apply 30–40 kg of manure per tree, every 3–4 years during autumn tilling. The use of mycorrhiza improved the uptake of nitrogen (Cruz et al. 2004).

F. Irrigation

In the Mediterranean region, where water resources are scarce, irrigation is reserved for the more profitable horticultural crops. Therefore, the

carob tree is mostly planted in rainfed land. However, carobs have rarely been intensively cropped and there is little information available on optimum water requirements. In this drought-resistant species, water supply should be considered as occasional irrigation and within certain dose limits and periods over the year. Some experiments on young trees resulted in a positive drip irrigation effect on vegetative growth and early pod production (Esbenshade and Wilson 1986; Tous and Batlle 1990; Correia 2007). For 2–3-years-old carob trees, Correia (2007), based on climatic conditions of Algarve, proposes 360 L of water supply per year for each tree, distributed between April and, September. This water supply promotes the start of tree growth and cropping.

Some authors indicate that, in order to ensure a good harvest, approximately 500 mm of rainfall per year is required (NAS 1979), and thus when rainfall is below 400 mm some complementary water supply is needed (Tous and Batlle 1990). The main irrigation periods in this species are considered to be spring (vegetative development), the beginning of summer (probable floral induction and fast pod growth), and autumn (flowering and accumulation of reserves).

In Mediterranean areas of the northern hemisphere with scarce water supply, drip irrigation shows goods results. In mature orchards with water doses of 100 mm per year (1000 m^3 ha^{-1}), one or two applications per month are proposed between April and August, which benefits are clearly reflected in the yield (Tous and Batlle 1990). In Algarve (Portugal), Correia and Martins-Louçâo (1995) using mature trees of 'Mulata' tested three irrigation levels (0%, 50%, and 100%) based in water loss by class A pan evaporation and two N amounts, as ammonium nitrate (21 and 63 kg ha^{-1} $year^{-1}$), and the results suggested that the fertigation increased yield and vegetative growth.

G. Pests and Diseases

The carob tree is normally free from severe insect and disease troubles and is a crop that traditionally has not been sprayed. In Spain, the most damaging insect is the polyphagous larva of the leopard moth (*Zeuzera pyrina*) that attacks the wood of trunk and branches, causing severe damage to young trees. Cultivars tested in Spain were all susceptible in some degree (Martorell 1987; Tous and Batlle 1990). In isolated cases, it can be controlled by introducing a wire into the galleries to destroy the larvae or by filling the holes with pesticide paste. Other control methods are applied like chemical sprays (pyrethroids) and biological methods, as sexual confusion trap causing mating disruption (Torá et al. 2009).

The pods of many cultivars sometimes become infested with the small and polyphagous larva of the carob moth (*Ectomyelois ceratoniae*) while maturing and before the harvesting period is complete. It also attacks stored carobs extensively, where it can be controlled by fumigating. Coit (1961, 1967) reported different susceptibility of several cultivars to the carob moth in California. Black aphids attack mainly the terminal shoots of young trees, and some hermaphrodite cultivars appear to show more susceptibility than females (Tous et al. 1996). In some areas, sporadic attacks of the white scale (*Aspidiotus hederae*) occur in mature carobs, mainly in trunk, branches, and leaves. In Cyprus, Orphanos (1980) reported carob midge (*Asphondylia* spp.) attacks pods at a very early stage, which caused stunting. High humidity seems to soften the pods, making it much easier for worms to get in.

Carob mildew caused by *Oidium ceratoniae* C. attacks pods, leaves, and twigs in different periods of the year, mainly in spring and in autumn and is the most important carob disease. Severe damage occurs only in some cultivars. For example, 'Rojal', 'Matalafera', 'Duraió', 'Amele di Bari', and 'Racemosa' are fairly tolerant to this disease, while 'Negra', 'Melera', 'Costella', 'Santa Fe', and 'AA-2' are susceptible (Goor et al. 1958; Graniti 1959; Martorell 1987; Tous and Batlle 1990; Tous et al. 2003). Thus, a cultivar grading to *Oidium* susceptibility exists (Table 8.5). Another fungus, *P. ceratoniae*, occasionally induces leaf-yellow spotting, and the trees appeared defoliated (Perrotta et al. 1998; Varo et al. 2005). Also, *Polyporus sulphureus* can destroy wood branches in old trees. Young carob trees growing under greenhouse conditions have shown resistance to root rot caused by *Armillaria mellea* infection (Loreto et al. 1993).

Other pests that occasionally cause severe damage to carob orchards are small rodents like gophers (*Pitymys* spp.), rabbits, and rats (*Rattus* spp.). Gophers can severely damage the root system of young trees. In California, Thomson (1977) reported that it was almost impossible to establish a young orchard unless gophers are controlled. Rabbits and deer graze on the young trees. In several Mediterranean countries (Spain, Portugal, Cyprus, etc.), rats are major pests. Rats can strip the bark, not only of young shoots but also of older branches and even limbs and by girdling a limb or branch they can kill it. Several types of baits in traps can be used to control these rodents. However, the best control is natural predation by the wild native fauna, conservation of which is essential. Cattle, horses, sheep, and goats all browse on the foliage of young and adult trees and can destroy young unprotected trees.

H. Harvesting

Carob harvesting is usually carried out at the end of summer or the beginning of autumn depending on cultivar and region. Harvesting can be manual or mechanical. Fruit ripeness, and therefore its optimal harvesting time is indicated by the complete darkening of the pedicel just prior to natural pod detachment from the branch. Sometimes, pod drop is hastened by the wind.

Most of the carob in the Mediterranean countries is harvested by hand, which represents about 50–70% of total production costs. The ripe fruits are knocked down with the help of long bamboo poles or wooden sticks and collected under the trees on fiber nets or from the ground by plastic rakes to cumulate fruits. This operation needs careful handling since at this time of the year carobs are in full bloom. The striking action of the poles can damage flowers and next crop might be partially destroyed. In Spanish orchards, the quantity of pods manually harvested, in average crop years, varies between 250 and 300 kg per day per worker (Tous and Batlle 1990). Most of the land used for carob is rocky and steep with small size and irregular orchard designs, making conditions unsuitable for mechanical harvesting. However, few carob orchards in flat areas of Australia, Portugal, and Spain (Catalonia) are adapting conventional harvesters used for other tree crops (olive, almond, hazelnut, walnut) as trunk or branch shakers that drop the pods on the ground or platforms, sweepers and vacuum machines to collect the fruit under the trees. The carob working capacity of the vacuum prototypes in Catalonia varies according to soil preparation and crop amount on the ground ranging between 1,000 and 1,500 kg ha^{-1} of harvested pods. In order to reduce harvesting costs, all pods of the same cultivar should be harvested in one or two times.

The harvest period usually coincides with autumn rainfall. This may cause an increase in pod moisture of as much as 20% and lead to a consequent loss of fruit quality (molds and sugar fermentations). Carobs should be harvested when they have 12–18% of water content (when the sample exceeds 18% moisture the kibbler penalizes the crop prize). After harvesting, carobs are either delivered to the processor or stored under shelter.

I. Postharvest Processing

Most of the carob pods harvested is brought to the processing plant (kibbler). When carobs arrive, moisture content is variable (10–20%) depending on harvesting conditions and autumn rainfall. Pods require

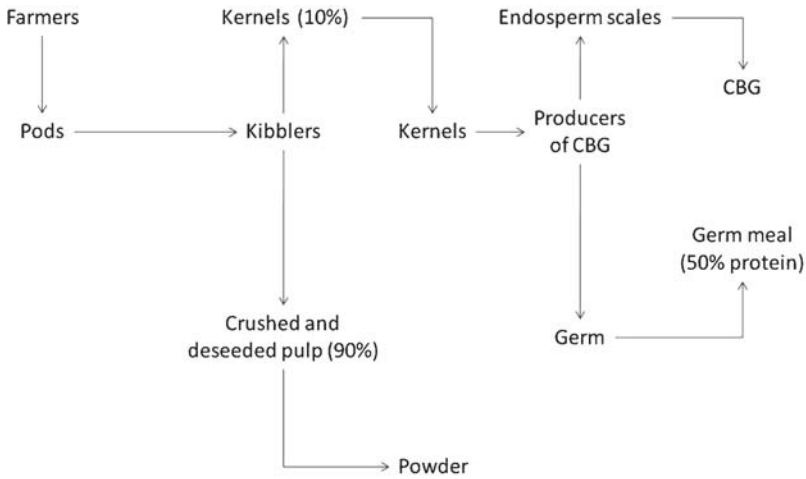

Fig. 8.8. Processing of the carob pod. *Source:* Batlle and Tous (1997).

further drying and thus are stored under shelter in dry and ventilated places to reduce moisture to around 8% and to avoid rotting. Pods are kibbled to separate the two main components: pulp and seeds.

Carob pods are crushed mechanically using a kibbler, then they are separated from the kernels (Fig. 8.8). The pod is processed differently, depending on whether it is used for animal feed or for food products. The feed factory grinds the deseeded pulp to different sizes in relation to the kind of livestock to be fed. The food industry processes the pulp further by roasting and milling to obtain a fine powder that is traded as carob powder.

The carob seeds are transported in bulk by lorry to the gum factories. The kernels are difficult to process, since the seed coat is very hard. Kernels are peeled without damaging the endosperm and the embryo (germ). The two main procedures applied to remove seed coat (Z. Puhan and M.W. Wielinga 1996, unpublished) are acid (seeds treated with sulfuric acid to carbonize the coat) and roasting (kernels roasted in a rotating furnace to peel off the coat). After the peeling process, the endosperm can be split from the cotyledons because of their different friabilities. When the peeled seeds are forced through a "splitting machine," the brittle embryos turn out as a fine powder (germ meal) and can be separated from the unbroken endosperm scales by a sifting operation. Subsequently, the endosperm is ground on roller mills to the desired particle size (gum). The CBG is the ground endosperm and the carob germ meal is a by-product of the seed processing.

Grower's payout is calculated in relation to the pod moisture and kernel yield of the cultivar delivered and also on amount of debris. Before carobs are stored, a grading sample is drawn from each delivery. This sample is processed individually using a small kibbler to determine kernel percentage. The two major components in determining return to the grower are weight delivered and percentage kernel weight.

J. Yield

Carob orchards are known to start producing slowly. This has two main causes: the slow tree growth and its long vegetative period, and other environmental and cultural factors are also involved. In plantations located in marginal areas, the unbearing period is long, from 6 to 8 years, while in others, where the growing conditions in new orchards are better, some selected cultivars start cropping 3 or 4 years after budding. The production of these clones increases to achieve full bearing at the age of 10–20 years and then it stabilizes (Tous et al. 2008, 2009). Goor et al. (1958) reported that carob trees start to bear fruit on the fifth to sixth year after budded trees are planted and in the seventh or eighth year when seedlings are used for planting and budded later.

It is also important to recognize that mature carob trees show alternate or biennial bearing (Fig. 8.9). The causes, in addition to genetics, include

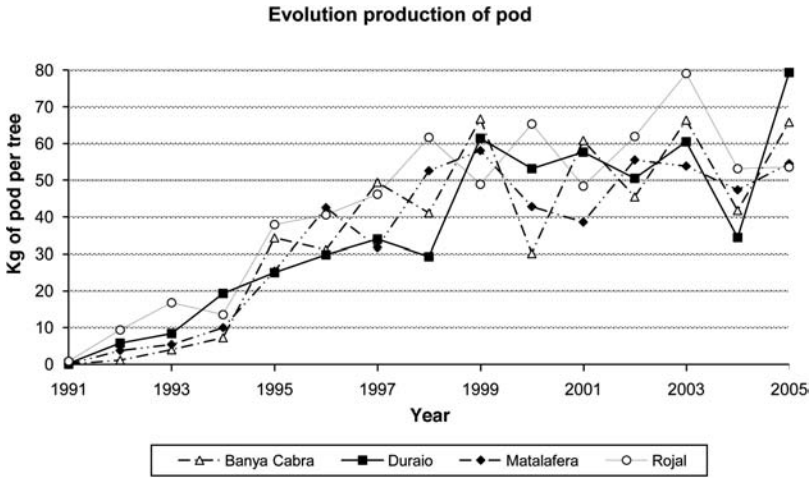

Fig. 8.9. Annual average yields 1991–2005 for four Spanish carob cultivars grafted in 1987. *Source*: Tous et al. (2009).

climatic conditions such as scarce and variable rainfall, frosts, fogs, and deficiencies in orchard design (lack of pollination) and management (fertilization, pruning, damage of the inflorescence during harvesting, etc.). In any 4 year production period, usually there are one poor, two medium, and one heavy crop (Hills 1980). In Algarve (Portugal), Haselberg (1996) observed in 30–40 years old 'Mulata' trees that the presence of pods in "on" years has an inhibitory effect on current season's flower differentiation, mainly during the period of most intensive fruit and seed growth (April–June). Regarding the yield efficiency of this cultivar in mature orchards, it normally ranged between 0.20 and 0.54 kg pods m^{-3} canopy (Haselberg 2000). In other cultivar trials located in coastal northeastern part of Spain, this yield index is similar, about 0.40–0.45 kg m^{-3}, in the best cultivars, such as 'Duraió', 'Matalafera', 'Rojal', and 'Aida' (Tous et al. 2008, 2009).

The productive potential of carob is variable and scarcely known under good cultivation conditions. In Spain, average traditional orchard productivity is around 1,300 kg ha^{-1} (MARM 2008), which is very low. In Portugal, the average yield per hectare is 1,700–2,700 kg (Droste 1993). In Tarragona, traditional orchards that receive minimum management tend to produce 2,000–3,000 kg ha^{-1} with 50 trees ha^{-1}, giving an average yield of 50–70 kg per tree (Tous and Batlle 1990).

Some modern orchards 10–20 years old in Spain and Portugal give average high yields, of about 6,000 kg ha^{-1} in dry conditions (500 mm) and 8,000–10,000 kg ha^{-1} with deficit-regulated irrigation and densities of 150 trees ha^{-1} (Tous et al. 2009). In Israel, in fully bearing trees in nonirrigated groves but with some 550 mm of annual rainfall, the yield can be about 7,400 kg ha^{-1} and in irrigated orchards an average of 12,300 kg ha^{-1} can be reached (Goor et al. 1958). Both examples were higher than the average production of traditional orchards cited above. A well-grown adult tree could yield about 100–200 kg per year. Some big isolated trees can produce 250–300 kg in good crop years. With respect to the carob industrial yields, 1,000 kg of pods yields about 100 kg of seed that produces 35–38 kg of gum.

IV. VARIABILITY AND GENETIC RESOURCES

A. Cultivars

Wild carob forms are still frequently found all over the eastern Mediterranean Basin and are naturalized in the west. Throughout the Mediterranean region, wild or feral carob trees were often used as stocks for

budding *in situ* with selected cultivars. In some areas, such as in Mediterranean Turkey or in the south of Spain and countries like Morocco, pods from ungrafted spontaneous trees are collected.

Since antiquity, the cultivated carob has been propagated first by seeds and later by budding. Thus, carob cultivars originated from chance seedlings selected from local populations and later propagated by scion budding into commercial orchards. Zohary (2002) reported that *C. siliqua* cultivars and wild-growing trees frequently grow side by side and intercross freely. He proposed that under domestication, hermaphroditic clones were favored by growers, causing a partial reduction of dioecy in carob culture. The main changes in this fruit tree under domestication were increases in pod size, fleshiness, and sugar content. In contrast, the climatic requirements of the cultivars still closely resemble those of the wild forms (Zohary 2002).

Centuries of cultivation have originated a number of local cultivars differing in habit, vigor, pod size and quality, seed yield, productivity, and pest and disease resistance. Most cultivars are of unknown origin and represent the germplasm of each region. All over the world, not even 50 named cultivars of limited distribution are reported in the literature (Tous and Batlle 1990; Batlle and Tous 1997). Commercial cultivars and wild types differ largely in terms of pulp production, seed yield, and LBG content (Crescimanno et al. 1988; Kalaitzakis et al. 1988; Sánchez-Capuchino et al. 1988a; Tous et al. 2001, 2006). The main cultivars grown in orchards in Spain and other traditional Mediterranean countries have a high pulp content and low seed yield and are consequently not suitable for the new industrial uses aimed at kernel production (Tous and Batlle 1990; Batlle 1997). For this reason, some genotype collecting from wild and feral populations has been carried out in Andalusia (South of Spain) (Tous et al. 1995), Tunisia (Tous et al. 2006), and Morocco (IRTA's surveys in 2007–2010).

Previous studies on carob cultivars have focused on genetic variability (Tous et al. 1992; Batlle et al. 1996; Talhouk et al. 2005; Afif et al. 2006; Caruso et al. 2008b; Barracosa et al. 2008), tree and fruit description (Schroeder 1952; Orphanos and Papaconstantinou 1969; Spina 1986; Tous and Batlle 1990; Russo and Polignano 1996; Batlle and Tous 1997), correlation studies between morphological fruit and seed characters (Albanell et al. 1988, 1996; Caja et al. 1988; Barbagallo et al. 1997; Barracosa et al. 2007; Naghmouchi et al. 2009; Sidina et al. 2009), pulp chemical composition (Binder et al. 1959; Davies et al. 1971; Vardar et al. 1980; Caja et al. 1988; Marakis et al. 1988; Biner et al. 2007), and gum rheological properties (MacCleary et al. 1985; Lazaridou et al. 2000; Rizzo et al. 2004), but there is very little information on the agronomical

performance of carob cultivars (Tous and Batlle 1990). Thus, there is renewed interest in carob germplasm banks and cultivar trials.

Pistillate plants have always been selected in preference to the hermaphrodite ones, as they are better pod bearers. Hermaphrodites are never the main producing trees in orchards, and often, staminate pollinators are isolated seedling trees or branches left on the rootstocks after budding female cultivars. However, hermaphrodites are of interest as pollinators; and some Italian types like 'Bonifacio' and 'Tantillo' were selected for this purpose (Russo 1954) and some Spanish types were introduced at IRTA's experimental plots ('A-19', 'BN-1', '2–12', 'Aleixà i·158', 'Punt Inglés', and 'Vivall i·133').

The main cultivars grown in Spain and other countries are listed in Tables 8.3 and 8.4, respectively. Spanish cultivars are largely characterized by high pulp content and medium seed yield (8–10%). Some cultivars from the Balearic Islands give a medium-high seed yield (15%) and spontaneous ecotypes from Andalusia even higher (18%), but the main cultivar 'Negra' yields only around 8%. Italian cultivars tend to have medium pulp and seed content. Most Portuguese cultivars produce medium seed yield (12–14%) and beans with round kernels well suited for gum extraction. In Cyprus, carob trees constitute a remarkably uniform group for some features but produce low to medium seed content (8–14%) having relatively flat seeds, such as 'Tylliria' that is widely grown (Orphanos and Papaconstantinou 1969). In Turkey, where carob distribution is restricted to the Aegean and the Mediterranean coast, two pod types can be found (cultivated and wild) (Biner et al. 2007).

Table 8.3. Main carob cultivars growing in different regions of Spain (from NE to south coast).

Region	Province	Cultivars (in order of crop importance)
Catalonia	Barcelona	Negra, Banya de Cabra, Banya de Marrà, Molla Negra
	Tarragona	Negra, Rojal, Costella de Ruc, Llei dAldover
Balearic islands	Majorca	Bugadera, De la mel, Duraió, Vera, Costella, Rossa
	Ibiza	Panesca, Boval, Uraiona, Fina, Rotja[a]
C. Valenciana	Castellón	Negra, Ralladora, Banyeta, Casuda, Del pom, Murtera
	Valencia	Matalafera, Melera, Costella, Llisa, Casuda, Catxa
	Alicante	Lindar, Costella de Bou, Vera, Borrera, Sta. Maria, Fornera
Murcia		Mollar, Ramillete,[a] Mojonera
Andalusia	Málaga	Sayalonga, Rubia, Bravia wild trees
	Granada	Fina, Laesa, Vacta
	Huelva	Blanca

[a]Hermaphrodite.

Table 8.4. Main carob cultivars grown in other countries.

Country	Region or district	Cultivar or type (in order of importance)
Italy	Sicily	Gibiliana (syn. Latinissima), Racemosa, Saccarata
	Puglia	Amele di Bari, Cavallaro, Schiovinesca
Portugal	Algarve	Mulata, Galhosa, Canela, Aida
Morocco	Rif, Fes, Marrakech, Agadir	Ungrafted wild trees (90%)
Greece	Crete	Hemere (80%, syn. Imera), ZacharoharupaKatsunia
Cyprus		Tylliria, Koundourka, Koumbouta
Turkey	Mediterranean and Aegian basin	Wild and Cultivated (fleshy and sisam) types
Tunisia	Coastal and inland areas	Sfax, and wild types
Israel	Coastal and inland areas	Tylliria, Sandalawi, Habati, Aaronsohn
Lebanon	Coastal area	Ahmar, Makdissi, Sandali, Khachabi
Croacia	Adriatic coast	Komiski, Sipanski, Mekis
USA[a]	California	Sta. Fe[b], Clifford[b], Bolser[b], Gabriel[b], Molino
Mexico[a]	Northwest region (Baja Calif.)	Badam, Santa Fe[b], Amele, Tylliria
South Africa[a]	Western Cape	Tylliria, Sfax, Aaronshon, Sta. Fe[b]
Australia[a]	South Australia	Sfax, Clifford[b], Sta. Fe[b], Tylliria, Irlam, Wait
	Western Australia	Sfax, Sta. Fe[b], Kp-1, Clifford[b], Tylliria

[a]USA, Mexico, South Africa, and Australia, carobs are considered a new crop.
[b]Hermaphrodite.

Turkish production is 70% wild type and the rest cultivated (fleshy and "sisam" types) that are considered to be grafted carob trees (Vardar et al. 1980). The Greek production is concentrated in the island of Crete (around 80%) where carob trees grow wild and cultivated. Most bean production comes from 'Hemere' that gives a seed yield of 9% (Kalaitzakis et al. 1988). Spontaneous populations from Morocco produce high seed-yielding (16–26%) pods with round kernels and scanty flesh (M. Ouchkif, unpublished; Sbay 2008; Sidina et al. 2009). In Tunisia, most trees are wild (Crossa-Raynaud 1960; Tous et al. 2006; Naghmouchi et al. 2009), with seed yield about 15–18%, and 'Sfax' is the most important grafted cultivar with high pulp and lower seed content (8–10%).

Carob cultivars vary widely in a number of characteristics that are of interest for growers (Tables 8.5 and 8.6). To assess and select cultivars for commercial production in Mediterranean countries, several traits should be considered, such as the sex (pistillate clones, usually the main cultivar, and pollinators), production (precocity, yield, and

Table 8.5. Agronomic characteristics of main carob cultivars growing at the IRTA's CGB[a] in Catalonia (NE of Spain) (in alphabetic order and according to the importance of the producing countries).

Origin	Cultivar	Sex[b]	Growth habit	Precocity	Resistance to fruit abscission	Susceptibility to *Oidium*
Spain	A-19	H	Semierect	Very early	Medium	Low
	Banya Cabra	F	Semierect	Late	Medium	Medium–low
	Bugadera	F	Open	Medium	Medium	Low
	Duraió	F	Open	Early	Medium	Medium–low
	Matalafera	F	Open	Medium	Very low	Low
	Negra	F	Open	Medium	High	High
	Ramillete	H	Weeping	Very early	Very high	Medium–high
	Rojal	F	Erect	Very early	Low	Low
	Sayalonga	F	Open	Late	High	Low
Italy	Gibiliana	F	Open	Medium	High	Medium
	Amele di Bari	F	Erect	Medium	Medium	Low
Portugal	Aida	F	Semierect	Early	Medium	High
	Galhosa	F	Open	Late	Medium	Low
	Mulata	F	Open	Early	Low–medium	Low
Cyprus	Tylliria	F	Erect	Medium	Very high	High
Tunisia	Sfax	F	Open	Early	Low–medium	Low
California	Santa Fe	H	Open	Very early	High	High

[a]CGB (Carob Germplasm Bank).
[b]F: female; H: hermaphrodite.

alternate bearing), resistance to biotic and abiotic conditions, harvesting ease (low fruit removal force), and fruit quality (as pulp and kernel).

1. Sex. On the basis of the flower structure, staminate, pistillate, and hermaphrodite cultivars are recognized. Pistillate cultivars are the most important trees in commercial groves of Mediterranean countries. Staminate and hermaphrodites are normally used as pollinators. There is no agreement between the different authors on the best density of pollinators for commercial orchards. However, there is sufficient information to recommend around 12% (1:8) of pollinators distributed regularly (Tous and Batlle 1988, 1990). Hermaphrodite clones, provided they are self-fertile and cross-compatible with the main cultivar, are most desirable and could be used instead of unproductive staminate pollinators.

2. Resistance to Environmental Stress. Carob trees grow best in calcareous soils, preferably near to the sea. They are drought resistant but

Table 8.6. Commercial characteristics of main carob cultivars growing at the IRTA's CGB[a] in Catalonia (NE of Spain).

Origin	Cultivar	Pod size[a]	Pod shape[b]	Pulp content[c]	Sugar content (%)[d]	Seed yield (%)[e]	Endosperm content (%)[f]
Spain	A-19	Long	S	Medium	–	12–13	46.6
	Banya Cabra	Long	T	Low	–	12–16	54.3
	Bugadera	Medium	S	Medium	–	15–17	51.4
	Duraió	Medium	S	Low-medium	–	15–17	58.0
	Matalafera	Medium	S	Medium	–	10–13	58.0
	Negra	Short	S	High	–	7–9	52.0
	Ramillete	Medium-long	C	High	–	8–10	50.6
	Rojal	Long	S-C	Medium	–	10–11	56.2
	Sayalonga	Long	S	Medium	–	14–17	56.0
Italy	Gibiliana	Medium	C	High	38–40	7–10	53.1
	Amele di Bari	Medium	S	High	53–54	8–9	52.0
Portugal	Aida	Long	S	Medium	–	12–13	58.0
	Galhosa	Short-medium	S	Low	–	14–16	58.3
	Mulata	Medium	S	Medium	40–50	10–12	55.8
Cyprus	Tylliria	Medium-long	S-C	High	51–52	8–10	49.0
Tunisia	Sfax	Long	S-C	High	51–52	7–11	52.6
California	Santa Fe	Long	S-C	Medium	47–48	6–8	51.5

[a]Medium pod length about 15 cm.
[b]S = straight; C = curved; T = twisted.
[c]Pulp dry weight.
[d]Dates from references.
[e]Medium seed yield = 10%.
[f]% of dry seed weight.

tolerate only light frost. Sensibility to frost and fog is a serious problem in this crop. The extent of frost damage depends on the temperature within the orchard and the physiological state of the trees. As several frost spells have occurred in various places since records are taken, some cultivar differences have been observed. The Portuguese cultivar 'Galhosa' seems to be more cold tolerant than 'Mulata' (Brito de Carvalho 1988b). In Andalusia, ungrafted local types known as 'Bravia' seem more tolerant than the grafted cultivars (Tous et al. 1995). In Portugal, a correlation was found between the number of foggy days during the blooming period and yields. Susceptibility to wind is revealed by broken branches after storms; it is related to wood health, tree shape, and size, and thus to cultivar branching density and management.

3. Production (Precocity, Yield, and Alternate Bearing). High yield is an important characteristic for farmers, but regular bearing is also to be considered, as most cultivars show alternate bearing, such as 'Amele di Bari' in Italy (Crescimanno 1982), 'Tylliria' in Israel (Goor et al. 1958), 'Mulata' in Portugal (Haselberg 2000), and 'Cacha', 'Negra', and some hermaphrodite cultivars in Spain (Martorell 1987; Tous and Batlle 1990). In addition to these genetic traits, other factors affecting yield, such as pollination amount, effect of cultural practices, and environmental conditions (dry or irrigated orchard), are also to be considered.

Precocity is highly desirable in carob to reduce the otherwise unproductive vegetative phase of the first years and to pay off quickly the planting costs investment. Some cultivars start to bear early, 4–5 years after budding ('Rojal', 'Duraió', 'Ramillete', 'Mulata', 'Aida', some Spanish hermaphrodites selections), while others come to bear some years later ('Banya de Cabra', 'Sayalonga', 'Cacha', 'Galhosa', 'Sandalawi'). In Spanish, carob collections hermaphrodite types normally bear sooner (third year after budding) than pistillate cultivars (V. Navarro, unpublished; Tous et al. 1993, 2003, 2008). Most cultivars come into bearing early when orchard management and rainfall, or supplementary irrigation, are adequate.

4. Fruit Quality (Pulp and Seed). The quality of fruits depends mainly on seed and pulp yield. Currently, seeds are the most important part of the pods as they are used to extract the valuable carob bean gum. Pulp value depends on its use (livestock feed or human food industry) and sugar content, fiber, tannins, and flavor (Coit 1961). Chemical carob pod composition differs widely according to cultivar and climate.

Thomson (1971) found in 40 cultivars the following percentage weight ranges at 10% moisture: total sugars (37–62%), crude protein (2.2–6.6%), crude fiber (4.2–9.6%), and ash (1.5–2.4%). Pods also contain from 0.46% to 1.46% crude fat (Binder et al. 1959) and 2.6–6.7% tannins by dry weight (Louca and Papas 1973; Marakis et al. 1988).

The pulp is the main pod constituent. Pulp content in the pod ranges from 73% to 95% (Caja et al. 1988; Crescimanno et al. 1988; Marakis et al. 1988), with corresponding seed content. In Turkey, the pods of cultivated varieties had a higher total sugar concentration of 531 g kg^{-1} dry weight than the wild-type selections that had 437 g kg^{-1} (Biner et al. 2007). Seed yield is an important fruit characteristic that varies with climatic and soil conditions but is also strongly cultivar related (Brito de Carvalho 1988b). Table 8.6 shows important differences between cultivars. Wild carobs usually produced higher seed yield than cultivated carobs (Marakis et al. 1988; Di Lorenzo 1991; Tous et al. 1995). In Mediterranean ecotypes, the seed yield variation recorded ranges from 5% to 29% (Caja et al. 1988; Crescimanno et al. 1988; Marakis et al. 1988; Sbay 2008; Sidina et al. 2009). Albanell et al. (1996) observed a positive correlation coefficient between total kernel weight and pod length and negatively between seed yield and fruit weight; in relation to gum content they found that seeds should be heavy, thick, and short. Also, Haselberg (2000) in 'Mulata' carob orchards found highest correlations between fruit length and number of seeds per pod ($r = 0.90$), fruit length and pod weight ($r = 0.85$), and pod weight and number of seeds per pod ($r = 0.79$).

The gum content and quality are also important features. They vary with climate, soil, and cultivar (Brito de Carvalho 1988b). Endosperm, from which the gum is derived, ranges from 38% to 60% in dry weight (Albanell et al. 1988; Crescimanno et al. 1988; Rizzo et al. 2004). Ungrafted seedling trees seem to produce seeds with more gum content than grafted cultivars (Marakis et al. 1988). Gum content differs considerably between cultivars. Under the same environmental conditions, 'Duraio', 'Banya de Cabra', 'Matalafera', and 'Galhosa' produce more gum than 'Rojal', 'Melera', and 'Negra' (Tous et al. 1996, 2009). There are also cultivar-related differences in gum quality, especially regarding viscosity grade, gel strength, and galactomannan content (Lazaridou et al. 2000; Rizzo et al. 2004). The current trend is to grow good dual-purpose cultivars (pulp and kernel), so that high production of carob kernel can be avoided in the future to stabilize prices in the CBG market.

Pulp flavor is also important for carobs grown for the food industry. A test on pod flavor of 31 cultivars, ranging from 37.1% to 51.6% of total sugar (reported as glucose), indicated that flavor preference is not

directly related to high sugar content (Binder et al. 1959). The hermaphrodite cultivar 'Santa Fe' was rated highest having a sweet, nutty flavor, and high sugar content (47.5%). The best carob cultivars contain 45–55% of total sugar, while poor cultivars reached 35–45%.

5. Harvesting Ease. Harvesting is the main cost in carob production due to the expensive and scarce labor in most developed countries. Manual pod harvesting represents 50–70% of the total orchard production cost. This cost can be divided between knocking (or shaking) and collecting operations. "Knocking" is a traditional operation performed with thin long poles to knock down ripe pods. Manual or mechanical harvesting by trunk shakers and manpower shakers is affected on size and tree growth habit, pod distribution in the branches, and pod abscission proneness. Collecting operations depend on yield, pod size and shape, and orchard density. The main criterion for the establishment of new carob orchard should be mechanical harvesting. Some horticultural tree features are important to improve mechanical carob harvesting.

Tree Vigor and Growth Habit. Current cultivars, especially when well managed in warm coastal climates, can reach a large size, 6 m high, and fruit-bearing branches usually droop, obstructing trunk shakers used in mechanical harvesting. Small trees make harvesting easier. As to growth habit and branching density, there are big differences between cultivars (Table 8.5). The current need, if shakers are to be used, is to grow rather small trees (orchard density about 150 trees ha^{-1}), with upright growth habit and rigid fruit-bearing branches (Tous et al. 1996).

Fruit Ripening and Abscission. In the Mediterranean Basin, the physiological pod ripening starts in July–August and it is a gradual process closely related to natural fruit drop. These two phenomena can affect harvest efficiency. Some cultivars are more prone to fruit abscission than others when knocked or shaken. For example, 'Matalafera' showed earlier ripening (at the end of August in Valencia) and good natural fruit drop, while other cultivars ripened 1 month later ('Rojal', 'Banya de Cabra', and 'Duraió') showing a rather good fruit abscission. Contrarily, other cultivars, such as 'Amele di Bari', 'Negra', 'Mollar' (from Murcia), 'Ramillete', 'Sayalonga', and 'Tylliria', showed high resistance to natural fruit abscission making mechanical harvesting difficult. The main consideration should be the selection of cultivars-producing pods ripening simultaneously during the period of maximum abscission, to ease collection from the ground.

In agroforestry systems, in which pods are grazed by livestock, the shed of pods is a valuable characteristic, and it is preferable that it occurs progressively over a long period (Brito de Carvalho 1988b). A complete management scheme, regarding livestock and cropping systems, should be developed for each particular circumstance.

Fruit Shape and Size. Carob bean size is a highly variable genetic character influenced by many environmental factors as well as pollination level and fruit set. Generally, grafted cultivars produce larger fruits than unselected wild types. This trait makes both manual and mechanical harvesting easier. Pod shape is also highly variable (Table 8.6; Fig. 8.10). For easier and cheaper collection, straight fruits are preferred to curved or twisted pods (Brito de Carvalho 1988b). The easiest pods to be collected are large and straight. Carob pod size is also an important trait for resistance to strong winds in spring, being less prone to drop short pods, to prevent premature fruit dropping.

The current trend is to choose dual-purpose carob cultivars having acceptable seed and pod yield and suited to mechanical harvesting. Such cultivars will require small–medium canopies, an erect-open growth habit, early bearing age, high and regular yield, harvesting ease (uniform fruit ripening, large pod size, and good abscission), diseases tolerance (oidium), and trees should be planted on regular spacings at an orchard density of about 150–200 trees ha^{-1} to rise overall economic returns. Regarding these characteristics, the most promising pistillate cultivars studied at IRTA collections and trials in northeastern Spain are 'Duraió', 'Aida', 'Rojal', and 'Matalafera' (Tous et al. 2008, 2009). Other cultivars such as 'Banya de Marrà', 'Negra Gata', 'Bugader', and 'Rotja' also show some agronomic and commercial interesting characteristics in southeastern Spain (Lloret et al. 2007). Outstanding hermaphrodite pollinating ecotypes include 'BN-1', '2–12', 'Aleixà i·158', and 'Vivall i·133'.

B. Descriptors

Carob cultivar classification has been a primary concern for carob growers and curators. The number of carob genotypes cultivated in the Mediterranean region is considerable, and its assessment using an easy and clear classification system has become necessary. A high number of existing synonyms and homonyms make classification even more difficult. Apart from a few classic carob works written by interested pomologists like Rullán and Estelrich (1882) in Majorca, Bassa (1896) and Lleó (1901) in Spain, Pereira (1900) and Da Matta

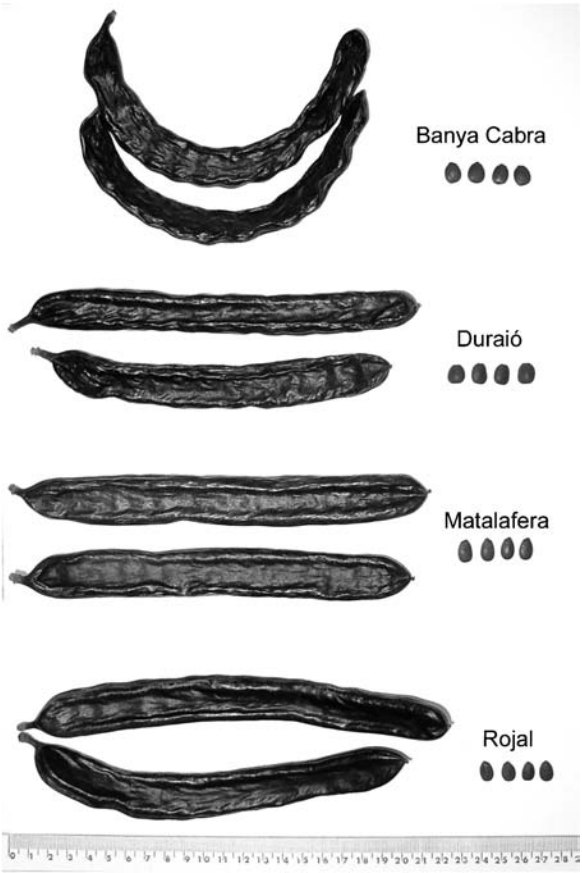

Fig. 8.10. Variation in pod morphology of four Spanish carob cultivars. *Source*: Tous et al. (2009).

(1952) in Portugal, Russo (1954) and Donno and Panaro (1965, 1966) in Italy, Orphanos and Papaconstantinou (1969) in Cyprus, Evreinoff (1960) in Greece, and various reports especially from Israel (Goor et al. 1958) and the United States (Condit 1919; Coit 1967), references on carob classification are scarce. In the last decades (after 1970s), some other pomological studies have been published in the main Mediterranean productive areas after assessing the variation of several carob cultivar traits (Thomson 1971; Tous 1985; Carlson 1986; Spina 1986; Brito de Carvalho 1988b; Crescimanno et al. 1988; Sánchez-Capuchino et al. 1988b; Batlle and Tous 1990; Tous and Batlle 1990; Melgarejo and Salazar 2003).

Although several pomological outlines have been proposed for carob, the development of a generally accepted scheme for cultivar characterization and evaluation, preferably with the support of Bioversity International, is much needed. A first valid framework for a descriptor list would be the last scheme proposed by Batlle and Tous (1997) and Bellini et al. (2007), based on information regarding trees, leaf, inflorescence, fruit, seed, and horticultural–commercial features. Table 8.7 shows the improved proposal of these descriptor characteristics, with some modifications on categories and ranks. Passport, management, and environmental and site descriptors are omitted.

Molecular markers can be useful in carob for genotyping cultivars and for genetic diversity analysis among or within natural populations and cultivated genotypes, clarifying cases of homonyms and synonyms, conserving rational *ex situ* field collections, and investigating new sources of variation for breeding to improve agronomic performance and increase seed yield.

C. Conservation

The main aim of the carob conservation is the preservation and study of the genetic resources kept in the gene pools available. Currently, there are few field carob collections in the world (Table 8.8). The most important is maintained at IRTA-Mas de Bover (Spain) and supported by the Spanish Instituto Nacional de Investigación y Tecnología Agraria y Alimentaria (INIA). This Carob Germplasm Bank (CGB) comprises living collections placed in two coastal sites of Tarragona: Constantí (Mas de Bover) and Vila-seca (Mas Barber), being the last plot warmer than Constantí. Currently, the adult tree collection of the CGB of IRTA gathers 216 accessions from 12 countries: Algeria (1), Australia (7), Cyprus (1), Croatia (2), Israel (1), Italy (7), Morocco (12), Portugal (7), Spain (158), Tunisia (13), Turkey (4), and the United States (3). There is some duplication to safeguard against potential frost damage losses.

Most native resources introduced have been the result of surveys undertaken on Catalonia's Mediterranean coast (Batlle and Tous 1986, 1990), Andalusia (Tous et al. 1995), and the Balearic Islands (Tous et al. 2001), while foreign resources from other surveys in Tunisia (Tous et al. 2006; Naghmouchi et al. 2009) and Morocco, as well as from collaborations with several national and foreign institutions. The characterization of phenological, agronomic, and some commercial varieties has been presented in several works (Tous and Batlle 1990, Tous et al. 1992, 1996, 2003; Batlle et al. 1996; Rovira and Tous 1996; Batlle and Tous 1997).

Table 8.7. Basic descriptor list for carob (*C. siliqua* L.) cultivars.[a]

Characteristics	Category and rank
Tree	
Sex	Male, female, or hermaphrodite
Vigor	Very high, high, medium, low
Growth habit	Upright, open, weeping
Foliage density	Most dense, dense, less dense
Branching	Dense, intermediate, sparse
Leaf	
Rachis length (cm)	Short (<11), medium (11–14), long (>14)
Number of leaflets	Many (>10), medium (8–9), few (<8)
Leaflet shape	Elliptic, oval, round
Leaflet area (cm^2)	Small (<10), medium (10–15), big (>15)
Length/width relation (L/W)	Short, long, narrow
Leaf color	Light green, green, dark green
Inflorescence	
Length (cm)	Short (<6), medium (6–8), long (>8)
Flowers per inflorescence	Many (>30), medium (15–30), few (<15)
Color raquis	Green, yellow, red
Nodosity insertion	yes, no
Fruit pod or bean	
Shape	Straight, curved, twisting
Surface	Smooth, rough, very rough
Color	Black, brown, reddish
Length (cm)	Short (<14), medium (14–18), long (>18)
Width (mm)	Small (<18.5), medium (18.5–22.5), big (>22.5)
Valley (mm)	Thin (<5.1), medium (5.1–6.6), thick (>6.6)
Thickness (mm)	Thin (<7.5), medium (7.5–9.5), thick (>9.5)
Pedicel length	Short, medium, long
Weight (g)	Small (<12), medium (12–17), high (>17)
Number of seeds per pod	Many (>10.5), medium (8.5–10.5), few (<8.5)
Seed yield (%)	Low (<10), medium (10–15), high (>15)
Sugar content (%)	Low (<40), medium (40–50), high (>50)
Seed or kernel	
Shape	Round, oval, elliptic
Surface	Smooth, rough, very rough
Color	Red, brown, blackish
Length (L) (mm)	Short (<8.5), medium (8.5–9.5), long (>9.5)
Width (W) (mm)	Narrow (<6.75), medium (6.75–7.25), wide (>7.5)
Thickness (T) (mm)	Thin (<3.8), medium (3.8–4.5), wide (>4.5)
L/W relation	Low (<1.2), medium (1.2–1.4), High (>1.4)
Seed weight (g, avg 100 seed)	Small (<0.17), medium (0.17– 0.2), high (>0.2)
Gum content (% dry wt endosperm)	Low (<48), medium (48–52), high (>52)

(*continued*)

Table 8.7. (*Continued*)

Characteristics	Category and rank
Agronomic	
Yield, regularity of production, precocity, sensitivity to frost, wind, pests, and diseases susceptibility (*Oidium* and *Cercospora ceratoniae*), ripening time and uniformity, ease of harvesting, and so on	
Commercial	
Uses of carob pods (animal feed or human food), tannin content, sugar, fibre, and so on, quality of CBG (viscosity and gel strength), and germ content	

Source: Adapted from Batlle and Tous (1997).

[a]Passport, management, and environmental and site descriptors are omitted.

Once field collections were established and accessions identified, the main aim has been to characterize the material and assess the genetic variability of important characters, particularly morphological, and agronomic traits (precocity, vigor, growth habit, production, and pest and disease resistance) or commercial aspects (kernel yield, pulp, and gum quality). These results can be used to select clones for adaptation trials or to choose parent trees for breeding to obtain new cultivars. After recording passport data for each new accession, identification and characterization are carried out according to an adapted version of the descriptor list developed by the authors (Table 8.7) and completed with molecular markers.

In Spain, apart from the main carob germplasm bank at IRTA, there are three other carob collections in Lliria-Valencia (Instituto Valenciano

Table 8.8. Carob germplasm collections.

Country	Place, district, and area	Planting year	Accessions		Evaluation
			Native	Foreign	
Spain	Constantí and Vilaseca (Tarragona) 3 ha	1987, 1993, 1998, 2000	158	58	Phenological, agronomic, commercial characteristics
	Lliria (Valencia) 1 ha	1999	109	–	Yield and fruit quality
	Sa Pobla (Majorca) 0.5 ha	2005	14	1	Agronomic and fruit quality
	Torrepacheco (Murcia) 0.2 ha	1997	17	–	None
Portugal	Tavira (Algarve) 0.5 ha	1988	13	2	Yield and fruit characteristics
Italy	Catania (Sicily) 0.5 ha	2000, 2006	10	9	Bioagronomic characteristics
Tunisia	Kairouan 0.5 ha	2006	20	–	None

Investigaciones Agrarias, IVIA), Sa Pobla, Majorca (Conselleria d'Agricultura del Govern Balear) and Torrepacheco, Murcia (Consejeria de Agricultura y Agua of the Murcian Region). They were started after surveying and cataloging carob genetic resources in Comunidad Valenciana (V. Navarro, unpublished), the Balearic Islands (Tous et al. 2001), and Murcia in the southeast of Spain (Rodríguez and Frutos 1988), respectively. The Valencian collection is located in Lliria and holds 109 accessions (with an important number of hermaphrodite types), the other is placed in Sa Pobla (Majorca) having 15 accessions, and finally in Murcia where 17 accessions are kept. Records of these three collections are scarce and generally limited to their origin.

In Portugal, the carob field collection of the Regional Agricultural Center of Algarve (DRAALG) located in Tavira (Portugal), which holds 15 cultivars, is documented with passport and fruit evaluation data (Barracosa et al. 2007). Regarding the other two living collections (Kairouan and Catania), it should be noted that only very limited information is available. In the Tunisian collection at Kairouan (INRGREF experimental farm), in 2006 some ecotypes from surveys made in this country were included (Tous et al. 2006, Naghmouchi et al. 2009), and also 'Sfax', the main grafted cultivar of this country. In Italy (Sicily), the University of Catania began carob activities in 2000. Researches are aimed at establishing a germplasm collection, *ex situ* conservation, characterization of local and foreign cultivars, and evaluation of genetic diversity through molecular markers (La Malfa et al. 2007).

D. Selection and Breeding

In most commercial groves, all over the Mediterranean Basin many of the seeds produced by female clones derived from cultivated by wild hybrid combinations. In some sites, contact between wild forms and carob cultivars provide natural seedling populations where selection can be applied.

Agronomic and technological evaluation of existing cultivars is the quickest procedure for renewing stock in any given carob-growing area. However, this approach has hardly been used in the Mediterranean carob-producing countries. The gradual expansion of the area introducing the most outstanding cultivars ('Sfax', 'Santa Fé', 'Tylliria', 'Casuda', 'Amele di Bari', 'Rojal', and 'Duraió') shows that carob cultivars are able to adapt outside their native areas better than previously thought. Nevertheless, new carob orchards deserve systematic studies of the existing genetic variability, focused on capitalizing positive results

straight away, if possible. Two approaches are foreseen: cultivar trials and clonal selection.

Comparative trials are designed to determine which cultivars are best suited to a particular area, but only a few studies have been published (Coit 1961, 1967; Batlle and Tous 1998; La Malfa and La Rosa 2006; Tous et al. 2008, 2009). Only very few new cultivars and clones, such as 'AIDA' (DRAALG 2006), 'Ibla' (La Malfa and La Rosa 2006), and 'Duraio-IRTA-i·40' (Tous et al. 2009) were selected so far and commercially released for the new orchards of Algarve (Portugal), Sicily (Italy), and Catalonia (Spain), respectively.

Clonal selection is a valuable approach when applied in an old cultivar population that has achieved commercial success. In Spain, clonal selection work was made with 'Rojal' (clone i·211) and 'Duraió' (clone i·40) cultivars.

Little information is available on breeding programs as no controlled crosses and selection has been carried out on carob (Batlle and Tous 1997; Haq 2006). Identification of superior clones (or ecotypes) in natural populations has been the basis of carob stock development. Most cultivars have been obtained from growers who select promising seedlings and propagate them through budding. Use of hermaphrodite types in mass selection after intercrossing or crossing with the best female cultivars is one of the simplest breeding methods. This is based on the relatively high additive variance affecting the inheritance of most traits in fruit and nut trees. No inheritance of a character has been described in carob. Choice of parents with complementary characters from diverse geographical origin and available in *ex situ* collections should be the criteria to be considered. There have been limited attempts to use interspecific hybridization between the two related species *C. siliqua* and *C. oreothauma* (Haq 2006).

V. PROPERTIES AND USES

Carob tree has multiple uses including fruit production, agroforestry, and as ornamentals. In the wild, carob shelter, foliage, and beans attract browsing animals. Carob timber is hard and close-grained, and has been used to make tools as well as fuel, while wood was also traditionally used to make slow burning charcoal. In Mediterranean countries, carob pods have traditionally been used for both animal feed and human consumption; currently, the most valued fraction is the seed for gum extraction. Carob pod pulp is used as feedstuff not only for ruminants (Louca and Papas 1973) but also for nonruminants

Table 8.9. Main products derived from the carob pod (pulp and seed) and some major uses.

Product	Processing	Uses
Pulp		
Kibbles	Any	Animal feed (horses and ruminants)
	Milled	Human food and animal feed (ruminants and nonruminants)
	Extraction and purification	Sugar and molasses
	Fermentation and distillation	Alcohol and microbial protein production
	Extraction	Tannins as antidiarrheal
Powder	Washing, drying, roasting, and milling	Food ingredient; cacao substitute; preparation of dietary and pharmaceutical products
Seed		
Endosperm	Grinding	LBG or E-410; food additive (stabilizer and thickener); dietary fiber; pet food; pharmaceuticals; cosmetics; mixed feed
Embryo	Grinding	Germ meal; human and animal nutrition
Coat	Extraction	Tannins for leather tanning

Source: Batlle and Tous (1997).

(Sahle et al. 1992). However, the pods contain indigestible but valuable seeds.

The pods are crushed to separate seed (10% by weight) and pulp (90%). Each fraction shows particular composition and properties. The main products and uses derived from the carob pod are presented in Table 8.9.

A. Pulp Composition and Properties

Chemical composition of the carob pulp depends on cultivar, origin, and harvesting time (Orphanos and Papaconstantinou 1969; Davies et al. 1971; Vardar et al. 1972; Calixto and Cañellas 1982; Albanell et al. 1991).

On average (Table 8.10), carob pulp is very rich in carbohydrates (80%), with both a significant level of fiber and a high concentration in sugars (46%). Sucrose represents 75% of total sugars, but also contains fructose, glucose, and pinitol. Most polysaccharides are bind to cell walls, with very low starch content (1%) and high levels of dietary fiber (NDF 35%). This fiber is highly lignified and also contains cellulose, while hemicelluloses content is very low. Tannins are fiber components (4–6%) that are condensed in fresh pods but seem to be partially

Table 8.10. Average composition of the carob pulp.

Constituent	$mg\,g^{-1}$
Water	100–110
Dry matter	890–900
Organic matter	860–880
Ash	20–30
Crude protein	20–70
Fat	2–6
Crude fiber	75–180
Nitrogen-free extract	600–780
Total sugars	450–560
Sucrose	315–435
Fructose	60–115
Glucose	30–55
Pinitol	50–70
Neutral detergent fiber (NDF)	360
Acid detergent fiber (ADF)	120–330
Cellulose	30–120
Lignin (ADL)	210
Tannins	45–70
Total polyphenols	15–30 (mg gallic acid equivalent [GAE] per g)
Proanthocyanidin	0.35 (mg GAE per g)
Gallotannins	0.40 (mg cathechin equivalents [CE] per g)
Flavonols	3.20 (mg CE per g)

Source: Whiteside (1981); Z. Puhan and M.W. Wielinga (1996, unpublished); Yousif and Alghzawi (2000); Haq (2006); Turhan et al. (2006); Ayaz et al. (2007); Biner et al. (2007); Ozcan et al. (2007).

hydrolyzed after drying. Ripe carob pods contain large amount of polyphenols (13–30 mg gallic acid equivalent per g dry weight) (Ayaz et al. 2007; Biner et al. 2007).

Crude protein content is very low (4%), the same than essential amino acids. Main amino acids reported are alanine, glycine, leucine, proline, valine, tyrosine, and phenylalanine (Charalambous and Papaconstantinou 1966; Vardar et al. 1972). In addition, almost half of crude protein is linked to acid detergent fiber (ADF) with a low digestibility, even for ruminants (Loo 1969).

Fat content is very low (0.5%), with equal proportions of saturated and unsaturated fatty acids (Rendina et al. 1969). Ash content is also very low, with relevant deficit for many minerals. Mineral composition (in mg per 100 g of pulp) is K = 1,100, Ca = 307, Mg = 42, Na = 13, Cu = 0.23, Fe = 104, Mn = 0.4, and Zn = 0.59 according to Z. Puhan and M.W. Wielinga (1996, unpublished).

In food value, carob pods were considered similar to most cereal grains (NAS 1979) but this is not true (R. Lizardo, pers. commun.) as tannins reduce digestibility of major dietary components and animal growth, limiting its use as stuff. On the other hand, tannins have some beneficial effects since they inhibit microbial growth and activity and can be used to treat some diarrhea in preruminant calves, young rabbits, and postweaning pigs (Lizardo 2001). Carob pulp is appropriate for equine and rabbits, but also for pigs or ruminants if diets are well balanced. In addition, carob is suitable for pets feeding and organic animal production.

In growing-finishing pigs (25–100 kg body weight), no detrimental effect of tannins or fiber from carob pulp is observed when diets are correctly balanced in nutrients (up to 20% of carob pulp). In weaning piglets roasted carob pulp could replace common sugar feedstuffs even in extreme diets. Several studies, cited by Lizardo (2001), reported no significant differences for weight gain in postweaning piglets with 3–5% of carob pulp inclusion in well-balanced diets. In addition, carob tannins improve health of piglets lowering the prevalence of postweaning diarrhea and mortality associated with postweaning colibacilosis (Lizardo et al. 2002).

Carob and its by-products are fiber-rich feedstuffs and seem suitable for ruminant, although little information is available. In dairy, cows carob pulp substitution of 25% of forage or 30% of crushed barley do not reduce significantly milk production, indicating that females partially use their body reserves to compensate the low-energy content of carob pulp. The same was observed for Friesian calves and growing kids that must compensate the low-energy contents of carob pulp by increasing feed consumption or by reducing body reserves. Anyway, animals fed on carob show a poor feed conversion ratio. For lambs, moderate substitution of cereals (up to 20%) or fibrous feedstuff (up to 30%) allowed a good enough grow, although meat sensorial quality could be affected.

Lizardo (2001) also reported that animal feeding on carob diets did not reduce growth performance if they can compensate the deficit energy by an increase of feed intake. In addition, in some cases, carob tannins could reduce growth performance but in some others tannins could contribute to an improvement of animal health. Lizardo (2001) concludes that carob and its by-products are suitable for animal feeding (with differences between ruminants, monogastrics, and postgastric), but their nutritional value and the upper limit of their inclusion in the diet remains unknown.

The pulp can be ground into a fine powder for use in human nutrition. After getting roasted, the powder can be added to cakes, bread, sweets, ice

creams, or drinks as a flavoring agent (NAS 1979; Yousif and Alghzawi 2000). Carob powder "cocoa" has advantages over chocolate, since it has less calories and has neither caffeine nor theobromine (Whiteside 1981; Craig and Nguyen 1984; Yousif and Alghzawi 2000; Youssef et al. 2009). Its flavor is not as rich as dark chocolate but resembles milk chocolate. Also in some countries like Egypt, carob syrup is a popular drink obtained by extracting carob kibbles with water, resulting in a lower energy value than carob flour or pods (Ozcan et al. 2007).

Finally, due to the high sugar content of the pod and its relatively low cost, carob pulp was among the first horticultural crops used as stocks for the production of industrial alcohol by fermentation in several Mediterranean countries (Merwin 1981), with ethanol production between 10 and 95 $g\,L^{-1}$ (Pardao et al. 2008; Sánchez et al. 2010). In addition, carob pod is considered as a pinitol sugar source with an antihyperglycemic effect (Kim et al. 2005). There are other uses for consideration. Milled and chopped carob pomace, two by-products of the carob molasses industry, were tested in Lebanon as a potting medium for plants and have shown promise as substitutes for peat-based mixes in nurseries (Rishani and Rice 1988).

B. Seed Composition

Constituents of the seed are as follows (by dry weight): coat (20–24%), endosperm (54–57%), and embryo or germ (20–22%) (Tous et al. 2009). The seed coat contains antioxidants (Batista et al. 1996), while the germ is rich in protein (Table 8.11) with high amount of glutamic acid, aspartic acid, and arginine (Bengoechea et al. 2008). The carob germ flour is also suitable to produce gluten-free products of high quality (Miñarro et al. 2010).

Endosperm is the most valued seed fraction. After grinding, it is commercialized as CBG or LBG. Several degrees of purity are offered,

Table 8.11. Average composition of commercial carob germ meal.

Constituent	%
Loss on drying (at 105°C)	7
Lipids (neutral)	8
Minerals	6
Crude protein (N × 6.25)	52
Carbohydrate (by difference)	27

Source: Z. Puhan and M.W. Wielinga (1996, unpublished).

Table 8.12. Functional properties of carob bean gum (CBG).

Function	Example	Use level (%)[a]
Adhesion	Glaces, juices	0.2–0.5
Binding agent	Pet foods	0.2–0.5
Bodying agent	Dietetic beverages	0.2–1.0[b]
Crystallization inhibitor	Ice cream, frozen foods, bread	0.1–0.5
Clouding agent	Fruit drinks, beverages	<0.1
Dietary fiber	Cereals, bread	0.2–0.5
Foam stabilizer	Whipped topping, ice cream	0.1–0.5
Gelling agent	Pudding, desserts, confectionery	0.2–1.0
Molding	Gum drops, jelly candies	0.5–2.0
Protective colloid	Flavor emulsions	0.2–0.5
Sterilizing agent	Salad dressings, ice cream	0.1–0.5
Suspending agent	Chocolate milk	<0.1
Swelling agent	Processed meat products	0.2–0.5
Synergistic agent	Soft cheeses, frozen foods	0.2–0.5
Thickening agent	Jams, pie fillings, sauces, baby food	0.2–0.5

Source: Z. Puhan and M.W. Wielinga (1996, unpublished).

[a]As such or as component in an appropriate blend.

[b]Depending on degree of polymerization or viscosity of CBG.

depending on how well the endosperm is separated from the embryo and seed coat. Specks of cotyledons and testa are usually present in commercial LBG preparations. For use as a natural food additive, known as E-410, only high grade is admitted, while more residues are allowed for pet food.

This mucilaginous gum, also known as "tragasol," is used in a wide range of commercial products as a thickener, stabilizer, binder, and gelling or dispersing agent (Table 8.12). LBG is a commodity used by the food industry for the production of a large number of different food products (Camacho et al. 1999), such as ice creams, soups, sauces, cheese, fruit pies, canned meats, confectionery, bakery products, and pet foods. Technical applications of LBG, pure or blended with other gums, include cosmetics, pharmaceuticals, film emulsions, paints, polishes, ceramics, adhesives, and mixed feed (Salari 1982; Johnsen et al. 1988; Oyofo et al. 1988; Neukom 1989; Tous and Batlle 1990, 1997; García-Ochoa and Casas 1992; Z. Puhan and M.W. Weilinga 1996, unpublished; Batlle 1997; Lazaridou et al. 2000; Rizzo et al. 2004; Gonçalves et al. 2005; Vega and Goft 2005) and are summarized in Table 8.13. Recently, a new potential use of LBG, rich in galactomannans and specially mannose, is related to mixed feed (poultry, pig, and cattle), and it is a preventive element in the diet for the

Table 8.13. Carob bean gum uses and technical applications.

Industrial use	Applications
Pharmaceuticals	Anticoeliac products, pomades, pills, toothpaste
Cosmetics	Emulsions and foams, shaving foam
Textiles	Coloring thickener
Paper	Flotation product for recovering material. Thickener for surface treatment
Chemicals	Glues, coloring, polishing, dyeing, matches, pesticides
Petroleum	Flocculation additive to increase stability and thickness of welling
Mining	Flotation product
Boring	Wall reinforcement, moisture absorbent
Concrete	To strengthen solidification
Explosives	Water binder for explosives
Mixed feed	Preventive element to reduce the incidence of *Salmonella* and *E. coli*

Source: Droste (1993); Batlle and Tous (1997); Becker and Galletti (2008).

reduction of prevalence of *Salmonella* and *E. coli* (Oyofo et al. 1988; Becker and Galletti 2008). In the 1980s, LBG applications were food industry (ca. 75%) and technical (ca. 25%); however, this has changed in the 1990s, due to an increase in the LBG price, now food industry is 90% and technical is 10% (Batlle and Tous 1997). Consumption of hydrocolloids in some European countries and in the United States is presented in Table 8.14.

The endosperm is the galactomannan CBG or LBG. It is a polysaccharide molecule composed of linear (1 → 4) β-D-mannose backbone (Man) and D-galactose (Gal) sugar units linked to it by (1 → 6) α-glycosidic bonds (ratio M:G between 3:1 and 4:1) rather similar to tara gum (ratio 3:1) and higher than guar gum (ratio 2:1) (Fig. 8.11). Lazaridou et al. (2000) reported relevant data on intermolecular associations related to Man/Gal ratio and relative frequencies for Man-Man, Man(Gal)-Man(Gal), Man (Gal)-Man, and Man-Man(Gal) dyats that varies from each carob tree cultivar. The rheological properties of aqueous solutions are related to these galactomannan structures. Although carob gum is a nongelling polysaccharide, it shows a strong synergistic interaction with other gums like xanthan or carrageenan (Camacho et al. 2005). The rheological properties of such gels are also related to fine structure of galactomannan backbone. It appears that interaction between the carob and xanthan gums occurs in the unsubstituted backbone regions of the gel (Viera and Gil 2005). Finally, the possible use by the food industry of natural antioxidants contained in the carob seed coat as a by-product of the LBG industry has shown promise (Batista et al. 1996).

Table 8.14. Hydrocolloids consumed as food additives per head in different countries.

Hydrocolloids	Main function	World production (t year^{-1})	Consumption (g year^{-1})[a]	
			USA	D, F, I, UK
Starch products	Thickener + gelling	1,200,000	1,300	1,281
Gelatin	Gelling	138,900	65	122
Agar	Gelling	8,100	2	3
Alginates	Gelling	9,300	10	10
Carrageenans	Gelling	25,500	11	18
Guar gum	Thickener	35,400	34	39
Arabic gum	Emulsifier	23,100	22	59
Carob bean gum (CBG)	Thickener	11,700	8	18
Carboxy methyl cellulose (CMC)	Thickener	11,100	23	6
Other cellulose derivatives	–	–	6	1
Xanthan gum	Thickener	13,800	13	3
Pectin	Gelling	23,100	11	19
Total	–	1,500,000	1,505	1,579

Source: Z. Puhan and M.W. Wielinga (1996, unpublished); Phillips and Williams (2000); Prochile (2007).

[a]D = Germany, F = France, I = Italy.

C. Environmental Benefits

Carob is widely planted as an ornamental and shade tree on the streets of California, Australia, and elsewhere; staminate trees are preferred, as they do not provide litter from pod fall. However, the carob's value as a drought-tolerant, air pollution tolerant, low-maintenance tree for street, and landscape planting could be limited by the large mature size and strong, invasive roots (Coit 1951; NAS 1979). Carob is now being used in xerogardening in Mediterranean countries. And since it requires little of any cultivation, tolerates poor soils and salinity, and is long-lived, carob tree is often recommended for reforestation of degraded coastal zones threatened by soil erosion and desertification. It has also been recommended for planting as windbreak around orchards (NAS 1979; Esbenshade and Wilson 1986) and could have some use for buffering noise from factories, roads, and railways, because of its dense foliage.

The use of carob for afforestation and soil conservation in warm Mediterranean areas with degraded vegetation or to prevent erosion is often raised but has not yet been investigated. It seems that the carob is not a forest species as it thrives in the maquis; however, its role and potential

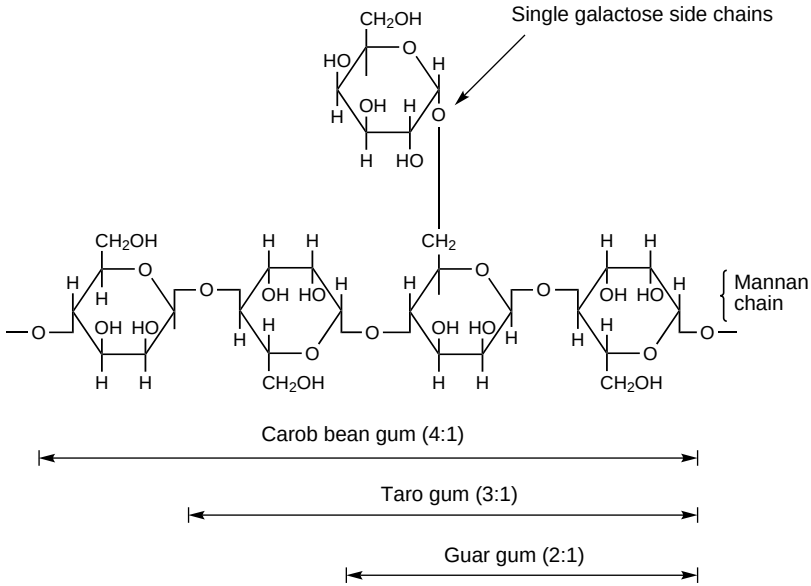

Fig. 8.11. Molecular structure of three galactomanans: carob, tara, and guar gums. *Source*: Neukom (1989).

suitability to cover bare land will be worth assessing. In addition its response to fire, common in the Mediterranean region, to which carob is quite more tolerant than other forest species. Sprouting ability would be a determining factor in natural regeneration. The carob tree showed some regeneration capacity after aerial killing by deep frost (−15°C) on the Mediterranean Spanish coast in 1956 and 1985 (Batlle and Tous 1997). However, carob cannot withstand competition with other forest, "garigue" or "maquis" trees and shrubs, and its germination in nature is rare. It thrives well and regenerates by seeds on dry and warm sites in Israel (Liphschitz 1987). In addition, the development of mycorrhiza inoculation in carob nurseries could improve the establishment and growth of new orchards and afforestation plantings. Overall, the carob has proven its utility as multipurpose production and environmental benefits for warm dryland areas of world Mediterranean climates.

VI. CONCLUDING REMARKS

Since the start of the 1980s, this crop has raised a considerable interest because of generally sustained demand and increase carob pod prices

(mainly the seed). However, this trend has been sharply modified three times in the past 20 years. Carob reached high prices in 1984–1985, 1994–1995, and 2005–2006. Cyclic high pod prices led to a loss of competitivity of carob bean gum versus other natural (guar and tara) or artificial hydrocolloid substitutes. These alternative substances produced a subsequent decline of pod prices. In addition, carob seed prices became even more fluctuating than carob pulp kibbled prices.

Carob price stabilization on the market would improve the prospects of this crop. The revaluation of carob pulp in animal feeding and in carob powder as human food could contribute to an increasing carob demand and reduce the final dependency of the pod price on the kernel. Currently, seed constitutes about 10% of the pod weight but it represents up to 50–60% of its value. In addition the functional, healthy, and light components of carob pulp products (confectionery, bakery, and drinks) should be fully explored.

The carob tree shows some outstanding features like rusticity, drought resistance, and reduced orchard management, and it is also well suited for part-time farming. In addition, modern carob orchards start bearing earlier (fourth year after budding) than traditional carob plots, and they increase yield steadily in response to minimum cultural care and deficit irrigation. The development of a useful propagation method (by cuttings or *in vitro*) would have a favorable impact on carob industry.

Agricultural sustainability has become more important over the years. Although carobs produce reduced yields in old plantations (1,500–3,000 kg ha^{-1}), in modern orchards production potential is higher (6,000–10,000 kg ha^{-1}). In addition, in optimum conditions carob requires minimum inputs compared to most other fruit and nut trees or vegetable crops. In many semiarid regions and marginal soils where carob is well adapted and cultivated, the quantity and quality of irrigation water are the main limitations for production. This crop has received little attention until now, but currently it is being reemphasized as an alternative in dryland (500 mm) or in supplementary drip irrigation areas with a Mediterranean climate for diversification and revitalization of coastal farming.

In the 1980s–1990s, the overall world carob production trend was rather stationary, around 330,000 t (Tous and Ferguson 1996), but currently it seems that the production of carob pods is decreasing until 220,000 t. Some traditional countries will continue reducing their production (Spain, Italy, and Cyprus) while a few of them will probably increase the amount they are producing (Morocco, Portugal, Lebanon, and Australia).

Another factor to be considered is the total harvested carob production that is partially affected by the price level. In isolated trees and marginal orchards of Spain, Italy (Sicily), and Cyprus, it was estimated that only 20% of the whole production is collected when pod prices are attractive for growers and more than 75% is harvested in the case of commercial groves. The main production is usually harvested every year in standard crop market situation. Alternate or biennial bearing causes problems to both the farmers and the stock market. Kibbler and CBG factory managers need to know the potential carob pod production every year to plan their purchases.

The reviewed information on genetic resources shows that carob cultivars vary widely in many pomological and commercial characteristics, such as yield, fruit ripening, tolerance to pest and disease, precocity, harvest ease, sugar content, kernel yield, gum content, quality, and so on. The current trend is to establish mechanically harvestable carob orchards with dual-purpose cultivars having acceptable seed and pod yield and high gum quality. Such cultivars will require relatively small–medium canopies, an erect-open growth habit, rigid fruit-bearing branches, harvesting ease, and they should be planted on regular spacing at an orchard density of about 150–200 trees ha^{-1} (Fig. 8.12). Mechanical harvesting has the potential to halve the current harvesting cost and it will considerably increase the viability of carob orchards.

Most CBG factories are placed in Mediterranean countries of the European Union (Spain, 4, Italy, 2, and Portugal, 1), as it is the world's leading carob-producing region and this is expected to remain the same

Fig. 8.12. Carob modern orchard in Tarragona, Catalonia, Spain.

in the future. Other industries are operating in Switzerland (1) and developing countries like Morocco (1) and Turkey (1). The current CBG world demand by food and pet food industries of around 12,000 t should be supplied yearly, otherwise the consumer industry will look for a suitable substitute gums, causing a consequent loss of the market.

A feature of the carob industry in the main producing countries is that it is fairly well organized. Thus, although growers, cooperatives, kibblers, factory managers, the agrofood industry, and R&D institutions have some different interests, all rely on proper prices for pods and kernels, and they are aware that a more organized sector (from producer to consumer) would be mutually beneficial. Many of the carob kibbler industries belong to the Mondial Carob Group (MCG) since 2000. This organization is placed in Santa Bárbara (Spain). Most carob bean gum-producing companies are members since 1972 of the Institut Europeen des Industries de la Gomme de Caroube (INEC), which is located in Brussels (Belgium). INEC has a Technical Committee and a General Secretariat, whose headquarters are at ETH in Zürich (Switzerland).

At present, mainly growers of Spain, Portugal, Italy, Morocco, Lebanon, and Australia seem to be interested in carob as a crop. Most remaining Mediterranean countries maintain carob as a native tree, useful environmentally and for landscape recreation. Currently, this tree crop is included in the EU support program. Actions are considered in the Nut and Carob Production Organizations scheme (European Regulation Number 2159/89). In addition, the carob tree was included in forestry actions of the European Union (European Regulation Number 2080/92).

A decision to establish, expand, or replant a carob orchard requires knowledge of current and potential consumption (domestic and abroad) and price evolution (variability and projection). It is also important to know competition and market volatility. Its future possibilities in a steadily more competitive horticulture with high costs and low inputs (labor, water, fertilizers, sprays, etc.) are promising, provided that the CBG market prices stabilize. In addition, its use in agroforestry and as an ornamental species for xerogardening and for landscaping is increasingly recognized.

ACKNOWLEDGMENTS

The information presented in this chapter has been compiled by the authors since 1984 when work on carob was started at IRTA Mas de

Bover. From the start, several Spanish agencies supported the work. Since 1988, IRTA and the INIA of the Spanish Ministry of Economy and Competitiveness and some private companies are financing the work on carob at IRTA. The carob germplasm collection placed at IRTA is also funded by INIA.

We are very grateful to A. Martorell (Conselleria d'Agricultura Balear) and V. Albert (IVIA of Valencia) for the information provided about the two carob collections placed in these two Spanish regions. We also thank H. Esbenshade (Carobs Australia, WA) for valuable information provided on carob growing in Australia. We are indebted to our IRTA colleagues: J. Fco. Hermoso, M. Rovira, and A. Ninot for their helpful collaboration on many tasks of the carob program. The authors are pleased to acknowledge the helpful comments and improvements on the chapter by J. Janick and also the thorough correction of the final version made by anonymous reviewers.

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9

Snake Gourd and Pointed Gourd: Botany and Horticulture

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ABSTRACT

Trichosanthes is the largest genus of the family Cucurbitaceae. Its center of diversity exists in southern and eastern Asia from India to Taiwan, The Philippines, Japan, and Australia, Fiji, and Pacific Islands. Two species, *T. cucumerina* (snake gourd) and *T. dioica* (pointed gourd), are widely cultivated in tropical regions, mainly for the culinary use of their immature fruit. The fruit of these two species are good sources of minerals and dietary fiber. Despite their economic importance and nutritive values, not much effort has been invested toward genetic improvement of these crops. Only recently efforts have been directed toward systematic improvement strategies of these crops in India.

Horticultural Reviews, Volume 41, First Edition. Edited by Jules Janick.
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KEYWORDS: cucurbits; *Trichosanthes*; *Trichosanthes cucumerina*; *Trichosanthes dioica*

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I. INTRODUCTION

Snake gourd (*Trichosanthes cucumerina* L. var. *anguina* (L.) Haines) and pointed gourd (*T. dioica*) Roxb. are widely cultivated in tropical regions and used as a vegetable. *Trichosanthes cucumeroides* (Ser.) Maxim. (Japanese snake gourd) is also grown in Japan and China as a source of starch. Snake gourd has high economic importance among vegetables in India and is commonly grown in Southeast Asia, Indo-Malaysia, China, Japan, and northern Australia (Paris and Maynard 2008) as well as parts of Latin America, the Caribbean islands, tropical Africa, and Mauritius (Mini Raj et al. 1993). Pointed gourd is extensively cultivated in the northern and eastern states of India (Uttar Pradesh, West Bengal, Orissa, Bihar, and Assam), Bangladesh, Sri Lanka, and Nepal. Young, tender fruit of snake gourd and pointed gourd are consumed after cooking. Twenty-four species of *Trichosanthes* are found in India, principally along the Malabar Coast of the Western Ghats, in the low and medium elevation zones of the Eastern Ghats, and North Eastern Hills (NEH) region. These gourds also are important in the traditional medicine of China, Thailand, and India.

II. THE GENUS *TRICHOSANTES*

A. Origin and Distribution

Trichosanthes L. is the largest genus of the Cucurbitaceae with 91 species (Jeffrey 1980, 1990; Yueh and Cheng 1980; Huang et al. 1997,

1998, 2007; Rugayah and de Wilde 1999; de Boer and Thulin 2012). The wild species of *Trichosanthes* are restricted to southern and eastern Asia, tropical Australia, and Fiji, while India or the Indo-Malayan region is considered the center of origin (De Candolle 1882). The genus has its center of diversity in southeast Asia from India eastward to Taiwan, the Philippines, Japan and southeastward to Australia, Fiji, and Pacific islands (de Wilde and Duyfjes 2010). There has been no comprehensive revision for the whole range of its distribution, but there have been regional revisions for India (Chakravarty 1959, 1982); China (Lu et al. 2011); Thailand (Duyfjes and Pruesapan 2004); Cambodia, Laos, and Vietnam (Keraudren-Aymonin 1975); Malaysia, Indonesia, and The Philippines (Rugayah and de Wilde 1997, 1999; de Wilde and Duyfjes 2004, 2010); Australia (Telford 1982; Cooper and de Boer 2011); and Japan (Ohba 1984). Of the 91 species (de Boer and Thulin 2012), 24 have been reported from India (Chakravarty 1959), 17 from Thailand (Duyfjes and Pruesapan 2004), 18 from Malaysia (Backer and Brink 1963), 4 from northern Australia, and 4 from Japan. Pointed gourd is cultivated on a small scale in the United States to supply ethnic farmers' markets and ethnic grocery stores (Singh and Whitehead 1999). *Trichosanthes kirilowii* and *T. rosthornii* are cultivated as medicinal crops. It is difficult to estimate the area and production since these crops are raised mostly for local market use and seldom enter the large commercial channels. Several other wild species of *Trichosanthes* are cultivated locally in India, Pakistan, Nepal, China, and Japan for various purposes (Jeffrey 2001). *Petola* or *patala*, the common name for snake gourd (*T. cucumerina*) in the Malay Peninsula, the Moluccas, and the Philippine Islands, is possibly of Sanskrit origin, indicating that the genus *Trichosanthes* may be indigenous to India (Seshadri 1986).

Because of monoecy and dioecy, the species of *Trichosanthes* are highly cross-pollinated. Pollination is strictly entomophilous; the pollen is sticky and cannot be dispersed by wind. The pyrillid moth is reported to be the main pollinator.

B. Taxonomy

Trichosanthes pollen studies have been carried out by Erdtman (1952), Ikuse (1956), Marticorena (1963), Keraudren (1968), Keraudren-Aymonin et al. (1969, 1984), Huang (1972), Mandal and Chanda (1981), Yue and Zhang (1986), Beevy and Kuriachan (1996), Huang et al. (1997), Khunwasi (1998), and Pruesapan and Van der Ham (2005). Generally the pollen grains are 3(4)-porate, 3(4)-colporate, psilate, perforate, (micro) retic, rugulate, and verrucate (Jeffrey 1990). Pollen grains of

all the species were starchy and germinated readily in Brewbaker and Kwack's medium.

Revisions have been made to the subgenera and sections within *Trichosanthes*. The genus is in the subtribe Trichosanthinae, tribe Trichosantheae, subfamily Cucurbitoideae of the Cucurbitaceae (Jeffrey 1980; Duyfjes and Pruesapan 2004; Kocyan et al. 2007). The genus has been revised for India by Kundu (1942) and Chakravarty (1959); for Cambodia, Laos, and Vietnam by Keraudren-Aymonin (1975); and for Malaysia by Rugayah and de Wilde (1997, 1999) and Rugayah (1999); taxonomic keys have been provided in some cases. It is a difficult genus to work with, since the herbaria materials are generally insufficient due to dioecious sex expression; also, the fragile corollas that bloom at night are difficult to collect, preserve, and study (Duyfjes and Pruesapan 2004). Rugayah and de Wilde (1999) found that seed characters are useful to characterize species and groups of species. de Wilde and Duyfjes (2004) studied 21 species from Sabah, including 4 new species. Duyfjes and Pruesapan (2004) discovered 7 new species among the 17 already described in Thailand. Huang et al. (2007) described 33 species from China, of which 14 species are endemic. In India, 24 species have been described by Chakravarty (1959). The description of some *Trichosanthes* species is still problematic.

Yueh and Cheng (1974, 1980) have subdivided *Trichosanthes* on the basis of the male bract, fruit pulp, and seed characters into subgenus Cucumeroides (with two sections: Cucumeroides and Tetragonosperma) and subgenus Trichosanthes (with five sections: Foliobracteola, Involucraria, Pedatae, Trichosanthes, and Truncata). Jeffrey (1980) divided the genus into five sections (Cucumeroides, Foliobracteola, Involucraria, Trichosanthes, and Truncata), without any subgenera. He considered Tetragonosperma to be a synonym of Cucumeroides and placed under section Pedatae as a subsection in Involucraria, proposing subsection Bracteatae for the other species in this section. On the basis of pollen morphology, Huang et al. (1997) subdivided section Foliobracteola into the subsections Foliobracteola and Villosa. Huang et al. (1998) revised the genus again, using morphological, cytological, pollen, and anatomical characters, and reinstalled the subdivision into the two subgenera: Cucumeroides, with two sections (Cucumeroides and Tetragonosperma), and Trichosanthes, with three sections (Involucraria, Foliobracteola, and Trichosanthes). Later, Rugayah and de Wilde (1999) used the staminate bract, fruit pulp, and seed characters to distinguish five sections (no subgenera) in Malaysia: Cucumeroides (subsections Cucumeroides and Tetragonosperma), Foliobracteola, Involucraria (subsections Involucraria and Pedatae),

Trichosanthes, and Edulis, a new section from New Guinea. In Sabah, de Wilde and Duyfjes (2004) distinguished five sections (Cucumeroides, Foliobracteola, Involucraria, and Trichosanthes) that are more or less the same groups as those of Rugayah and de Wilde (1999), plus the new section Asterosperma.

One reason for the difficulty of *Trichosanthes* classification is the lack of a recent monographic revision. So far, the sections are largely based on regional studies with little coordination of the classification of the widely distributed species. However, all authors distinguish several sections, usually grouped into two subgenera: Cucumeroides and Trichosanthes. Recently, de Boer and Thulin (2012) revised the infrageneric classification of the genus, merging Gymnopetalum and Trichosanthes. The genus has 2 subgenera with 11 sections, which are as follows: Asterospermae, Cucumeroides, Edulis, Foliobracteola, Gymnopetalum, Involucraria, Pseudovarrifera, Villosae, Trichosanthes, Tripodanthera, and Truncata.

The genus is endemic in Asia and Australia, except for *T. amara*, a species from the Caribbean island of Hispaniola in the Greater Antilles. However, Schaefer et al. (2008) placed this species in a new genus, *Linnaeosicyos*, using molecular and morphological data. *Trichosanthes* has long been seen as closest to the Asian genera *Hodgsonia* (Muller and Pax 1889) or *Gymnopetalum* (Jeffrey 1962; de Wilde and Duyfjes 2006), and also close to African/Madagascan groups such as Peponium (Jeffrey 1962). The different species of *Trichosanthes* have similar protein patterns. However, a few high-molecular-weight proteins are detected only in *T. dioica* and absent in other *Trichosanthes* species and also in *Gymnopetalum*, which belongs to the same tribe. The protein pattern of *Gymnopetalum cochinchinense* has considerable similarity with that of *T. cucumerina* (Pasha and Sen 1998).

C. Cytogenetics

The basic chromosome number of *Trichosanthes* is $x = 11$ with many diploid and some polyploid species (Table 9.1). Unlike the majority of taxa of the Cucurbitaceae, the chromosomes of *Trichosanthes* are large enough to allow karyotypic analysis. The metacentric to submetacentric chromosomes range from 5.74 to 1.48 μm. The sporophytic chromosome number of *T. cucumerina* and *T. dioica* is $2n = 22$ (Singh and Roy 1979a) with 11 bivalents at meiosis (McKay 1931; Banerji and Das 1937; Sen 1976; Datta and Basu 1978). Giemsa C-banding patterns for intraspecific differentiation have been carried out in *T. dioica* (Sarkar and Datta 1987). The great similarity observed

Table 9.1. Gametophytic and sporophytic chromosome number of *Trichosanthes* species.

Species	Chromosome number		References
	Gametic	Sporophytic	
T. anamalaiensis	11	22	Beevy and Kuriachan (1996)
T. anguina [z]	11	22	Mckay (1931), Sen (1976), Datta and Basu (1978), Beevy and Kuriachan (1996)
T. bracteata	22	44	Thakur (1973), Thakur and Sinha (1976)
T. bracteata var. *bracteata*	11	22, 44	Beevy and Kuriachan (1996)
T. cucumerina	–	22	Roy and Misra (1982), Huang et al. (1994), Beevy and Kuriachan (1996)
	11	22	Sen (1976), Datta and Basu (1978)
T. dioica	11	44	Banerji and Das (1937)
	11	22	Bhaduri and Bose (1947), Sen and Datta (1975), Sen (1976)
	–	33	Singh (1979)
T. japonica [y]	11	22	Nakajima (1937), Sinoto (1929)
T. kirilowii	44	88	Huang et al. (1994)
T. lepiniana	22	44	Huang et al. (1994)
T. lobata	11	22	Singh and Roy (1979a)
T. multiloba	11	22	Kurita (1939)
T. nervifolia	11	22	Beevy and Kuriachan (1996)
T. truncata	11	22	Huang et al. (1994)

[z] *T. anguina* is a var. of *T. cucumerina*.

[y] *T. japonica* is a synonym of *T. kirilowii*.

between the plant morphology of *T. cucumerina*, *T. lobata*, and *T. anguina* is reflected in the chromosomes since they have the same frequency of chiasmata and the same terminalization coefficient per PMC (Singh and Roy 1979a). These species are cross-compatible, with high pollen fertility in the three interspecific hybrids (Singh and Roy 1979b).

It has been suggested that the cultivated snake gourd (*T. cucumerina* var. *anguina*) might have arisen directly from *T. cucumerina* var. *cucumerina* (Singh 1990). Pointed gourd (*T. dioica*) is a dioecious perennial species with karyomorphology different from snake gourd. A heteromorphic pair of chromosomes associated with dioecy has been reported in *T. japonica* (Sinoto 1929; Nakajima 1937) and *T. dioica* (Patel 1952; Sarkar and Datta 1988), but the heteromorphic pair in *T. dioica* was not confirmed in later studies (Singh 1990). Polyploids were also induced in *T. anguina* but have not been commercially successful

so far (Singh and Roy 1975). A natural autotriploid from *T. dioica* was also reported (Singh 1990).

D. Medicinal Use

Trichosanthes species in southeast Asia are traditionally used to treat skin diseases, intestinal disorders, coughs, ulcers, and malaria (Sivarajan and Balachandran 1994). They are considered to be abortifacient, vermifuge, stomachic, refrigerant, purgative, laxative, hydragogue, hemagglutinant, emetic, cathartic, and anthelmintic (Nadkani 2002). The species and plant parts used to treat various diseases are listed in Table 9.2.

Trichosanthes species are also used in Chinese herbal medicine (Dou and Li 2004) and Thai traditional medicine (Kanchanapoom et al. 2002). Species such as *T. dioica* Roxb., *T. nervifolia* L., *T. tricuspidata* Lour., and *T. cucumerina* were known from the earlier times (Monier-Williams 1899; Sivarajan and Balachandran 1994; Decker-Walters 1998) as herbal medicine. *T. cucumerina* has a prominent place in alternative systems of Indian medicine (Ayurveda and Siddha) due to its various pharmacological activities involving antidiabetic, hepatoprotective, hypoglycemic, cytotoxic, antiinflammatory, antifertility, and larvicidal effects (Sandhya et al. 2010). *T. kirilowii* is commonly used in Chinese herbalism, where it is considered to be one of the 50 fundamental herbs (Duke and Ayensu 1985). The tubers and fruit of *T. kirilowii* have been a traditional herbal resource due to its novel pharmaceutical components (Oh et al. 2002; Fei et al. 2004; Kondo et al. 2004). Its tuber traditionally has been prescribed for patients with diabetes, rigorous coughing, breast abscesses, and cancer-related symptoms (Shin et al. 2008). *T. kirilowii* roots are used in Japan for pyretolysis, diuresis, and as an antitussive and antiinflammatory drug. In China the fruit, peel, and seeds are used to treat pneumonia, pleurisy, intercostal neuralgia, tonsillar pharyngitis, and angina pectoris (Ozaki et al. 1996). The seeds are used as an antiinflammatory and expectorant, and to treat coughs (Akihisa et al. 1994). It is purported that *T. dioica* possesses the medicinal property of lowering total cholesterol and blood sugar. These claims were supported by preliminary clinical trials with rats (Chandrasekar et al. 1988) and rabbits (Sharma and Pant 1988; Sharma et al. 1988). Roots of *T. dioica* are traditionally used in India as a hydrogouge, anthelmintic, cathartic, tonic, and febrifuge, and in the treatment of jaundice, anasarca, and ascites (Bhattacharya et al. 2010). The aqueous extract of its leaves has hypoglycemic potential along with a high antidiabetic profile (Rai et al. 2008b).

Table 9.2. Traditional medicinal uses attributed to *Trichosanthes* species.

Species	Use (part used)	References
T. cucumeroides	Abortifacient (plant)	Yeung and Li (1987)
T. anguina	Anthelmintic (fruit), cooling (seed), emetic (fruit), purgative (fruit)	Chopra et al. (1956)
	Blood sugar lowering principle (plant)	Chandrasekar et al. (1988)
T. cucumerina	Anthelmintic and vermifuge (seed, plant), bilious disorder (leaf, stem, seed), boils and carbuncles (plant), cardiac tonic (plant), cathartic (root juice), emetic (leaf juice), emmenagogue (leaf, stem), febrifuge (plant), labor women laxative (fruit), skin eruption (leaf, stem)	Chopra et al. (1956)
	Abortifacient, vermifuge, refrigerant, purgative malaria, laxative, hemagglutinant, emetic, cathartic, bronchitis, anthelmintic	Nadkani (2002)
	Tonic (plant)	Chopra et al. (1956)
	Diabetes, inflammatory (stem, leaf decoction)	Kar et al. (2003)
T. bracteata	Asthma (fruit-smoked), cathartic (fruit), headache (root-boiling with mustard oil), hydragogue (fruit)	Chopra et al. (1956)
	Boils and carbuncles (root)	Kirtikar and Basu (1988), Chopra et al. (1956)
T. dioica	Bilious fever (leaf), cooling (fresh juice, unripe fruit), febrifuge (leaf with equal part of coriander), labor women laxative (leaf, juice from unripe fruit), hydragogue (root), spermatorrhoea (fruit)	Chopra et al. (1956)
	Blood sugar lowering principle (plant)	Chandrasekar et al. (1988)
	Tonic (bitter)	Chopra et al. (1956)
T. cordata	Enlargement of spleen and liver (root dried and powdered), leprosy and leprous ulcers (root mixed with oil), stimulant (dried powder)	Chopra et al. (1956)
	Tonic (bitter)	Chopra et al. (1956)
T. nervifolia	Febrifuge (plant), purgative (root)	Chopra et al. (1956)
	Tonic (bitter)	Chopra et al. (1956)
T. kirilowii	Hypoglycemic activity	Hikino et al. (1989)

(*continued*)

Table 9.2. (*Continued*)

Species	Use (part used)	References
T. tricuspidata	Asthma, ear ache, ozoena, carminative, purgative, abortifacient, to lessen inflammation, cure migraines, and reduce heat of the brain; as a treatment for opthalmia, leprosy, epilepsy, and rheumatism (fruit); emetic and purgative (seeds)	Bhandari et al. (2008)
	Antifever remedy, a laxative, an anthelmintic as well as in migraine treatments	Kanchanapoom et al. (2002)
	Bronchitis	Gaur (1999)
T. lobata	Leprosy (whole plant)	Jeeva et al. (2007)

Species of *Trichosanthes* are well known for their production of biologically active triterpenes (Kanchanapoom et al. 2002) that have been isolated from the highly polar fraction of the nonsaponifiable lipids of saponified *T. kirilowii* seed extracts (Homberg and Seher 1977; Kimura et al. 1997). Multiflorane-type triterpenes such as (3*a*)-multiflora-7,9(11)-diene-3,29-diol, known as karounidiol and its 3-*O*-benzoate were identified as major components of the saponified extract of *T. kirilowii* seeds (Akihisa et al. 1988). The former compound was found to suppress tumor production in mice, as induced by 12-*O*-tetradecanoylphorbol-13-acetate (Yasukawak et al. 1994), and it showed cytotoxic activities against human cancer cell lines, especially renal-cancer cells (Akihisa et al. 2001). The abortifacient proteins trichosanthin (from *T. kirilowii*), and β-trichosanthin (from *T. cucumeroides*) have been isolated. Trichosanthin (TCS) is a type I ribosome-inactivating protein (RIP) isolated from root tuber of *T. kirilowii*. Trichosanthin is of particular interest because of its multiple pharmacological properties such as abortifacient, anti-HIV, immunoregulatory, antiviral, and anti-tumor activities (Leung et al. 1986; McGrath et al. 1989; Zheng et al. 1995, 2000; Lu et al. 2001; Zhao et al. 2006). These trichosanthin-derived pharmaceutical activities, including antitumor effects, were assumed to be connected to its biochemical activities, disrupting the binding of elongation factors to the P-complex as well as *N*-glycosidase activity for ribosome inactivation (Zhang and Liu 1992; Chan et al. 2001; Shaw et al. 2005). The drug trichosanthin is obtained from *T. kirilowii*, which was used locally in China to induce abortion and for the treatment of cancer (Heiser 1979). Anticancer mechanisms of *T. kirilowii* tuber linked to the inhibition of tubulin polymerization, through which it exerts cell cycle arrest at the G_2/M phase in the HepG2

cell line (Shin et al. 2008). An antihuman immunodeficiency virus (anti-HIV) protein (TAP 29) has also been isolated and purified to homogeneity from *T. krilowii* (Huang et al. 1991).

In vitro and *in vivo* studies in animals have shown that aqueous extract of *T. cucumerina* has improved glucose tolerance in noninsulin-dependent diabetes mellitus (NIDDM) animals (Kirana and Srinivasan 2008; Arawwawala et al. 2009), and decreased the sugar level in streptozotocin-induced diabetic rats (Rai et al. 2008a). Hot aqueous extract of root tubers of *T. cucumerina* has been investigated against carrageenin-induced mouse's hind paw edema and it exhibited significant antiinflammatory activity (Kolte et al. 1997). Root extract of *T. cucumerina* L. inhibited human breast cancer cell lines and lung cancer cell lines and one colon cancer cell line (Kongtun et al. 1999). Methanolic extract of the whole plant of *T. cucumerina* showed good hepatoprotective activity against carbon tetrachloride–induced hepatotoxicity (Sathesh et al. 2009). Ethanol extract of whole plant of *T. cucumerina* L. var. *cucumerina* showed antiovulatory activity in female albino rats (Devendra et al. 2009). Hot water extract of *T. cucumerina* showed a significant protection against ethanol-or indomethacin-induced gastric damage, increasing the protective mucus layer, and decreasing the acidity of the gastric juice and antihistamine activity (Arawwawala et al. 2010).

III. SNAKE GOURD

A. Quality Attributes and Human Nutrition

Immature fruit of snake gourd (Fig. 9.1) are used as a vegetable in southeast Asian countries, while in the eastern part of Nigeria, the ripe pulp is consumed. The red pulp can be used to improve food appearance as it can be blended and used to produce a paste for stew, which tastes like and serves the role of tomato (Enwere 1998). The use of snake gourd as a replacement for tomato is reported from Sierra Leone, Liberia, Côte d'Ivoire, Ghana, Benin, and Nigeria (Soladoye and Adebisi 2004). The fruit have poor nutrient content when compared to other common vegetables but do have vitamins C and A (Ojiako and Igwe 2008) as well as proteins, fat, fiber, carbohydrates, and vitamin E. The total phenolic and flavonoid contents are 46.8% and 78.0%, respectively (Adebooye 2008). The predominant mineral elements per 100 g are potassium (122 mg) and phosphorus (135 mg). Other elements found in fairly high amounts are sodium, magnesium, and zinc. The nutritive value of snake gourd is presented in Table 9.3.

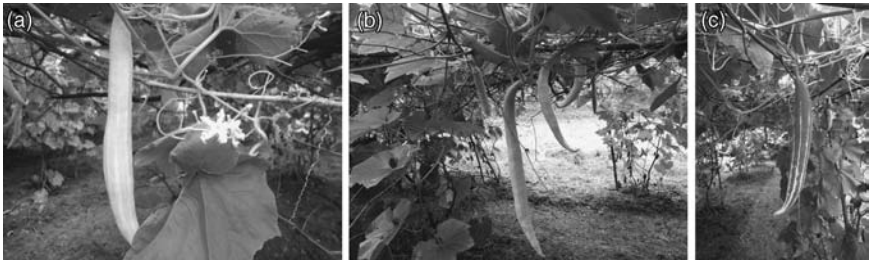

Fig. 9.1. Snake gourd (a) inflorescence and immature fruit of snake gourd; (b) immature fruit; and (c) marketable fruit.

Table 9.3. Proximate analysis and nutritive value of snake gourd and pointed gourd.

	Snake gourd[a]		
Nutrient component	Tender fruit	Ripe fruit	Pointed gourd[b]
Moisture (g)	94.60	93.15	92.00
Protein (g)	0.50	1.85	2.00
Fat (g)	0.30	0.23	0.30
Minerals (g)	0.50	–	0.50
Fiber (g)	0.80	0.81	3.00
Carbohydrates (g)	3.30	3.48	4.20
Energy (kcal)	18.00	–	20.00
Calcium (mg)	50.00	–	30.00
Magnesium (mg)	53.00	–	9.00
Phosphorus (mg)	20.00	–	40.00
Iron (mg)	1.10	–	1.70
Sodium (mg)	25.40	–	2.60
Potassium (mg)	34.00	–	83.00
Copper (mg)	0.11	–	1.11
Sulfur (mg)	35.00	–	17.00
Chlorine (mg)	21.00	–	4.00
Vitamin A	160.00 (IU)	347 (μg 100 mL)	255.00 (IU)
Thiamine (mg)	0.04	–	0.05
Riboflavin (mg)	0.06	–	0.06
Nicotinic acid (mg)	0.30	–	0.50
Vitamin C (mg)	5.00	18.90 (mg 100 mL)	29.00
Oxalic acid (mg)	34.00	–	7.00

[a]*Source*: Ojiako and Igwe (2008).

[b]*Source*: Gopalan et al. (1989).

B. Reproductive Biology

Snake gourd is a monoecious annual with nontuberous roots. Perfect (hermaphroditic) flowers have been observed but were nonfunctional (Singh 1953). Flowers open from bud stage in 8–16 days, with anthesis starting in early evening, that is, between 5 and 7 pm. The stigma remains receptive from 12 h before anthesis to 12 h after anthesis, but maximum receptivity remains at the time of anthesis (Deshpande et al. 1980; Singh et al. 1989). The sex ratio (ratio of staminate to pistillate flowers) in the monoecious species of snake gourd varies from 25:1 to 225:1 (Singh 1953). The major pollinators are bees (*Apis florae* and *A. dorsata*) and beetles (*Conpophilus* sp.)

C. Ecology

Wild snake gourd grows in scrub vegetation, along forest edges and in open forest, from sea level to 1,500 m altitude. Snake gourd performs well in warm and humid climate and is best suited to places is where rains are abundant. High humidity favors growth and fruit development. Temperatures between 30 and 35 °C are considered optimum for growth and fruiting, and temperatures below 20 °C restrict growth. Plants are susceptible to frost. Loamy to sandy loam soils rich in organic matter and having pH range of 6.0–7.0 are best suited. Plants do not tolerate dry soil and require a good moisture reserve in the soil. However, plants are sensitive to waterlogged soils, and heavy soils are unsuitable for cultivation.

D. Culture

1. Propagation. Snake gourd is grown in Kharif (rainy) as well as summer seasons. In northern India, snake gourd seeds are sown from the end of the winter season, that is, late February (Paul 1959) for summer crop and in June and July for the rainy season crop. Various methods of sowing are adopted, depending on season and system of cultivation. In the rainy season, plants are supported on trellises (Bastin and Khader 1985; Seshadri 1986). Seeds (5–6 kg seed per ha) are sown in the hills near the edges of raised beds or pits. Between-row spacings are 1.5–2.5 m, and within-row spacings are 0.6–1.2 m (Nath et al. 1987). For rapid germination, the seeds may be soaked in water for 1 day before sowing (Paul 1959). Normally, the seeds will germinate and emerge in 1 week, unless the soil is too dry or the weather is too cold. Seedlings can be raised in the nursery and transplanted to the field

at the two-true-leaf stage. However, direct seeding is often preferred due to the delicate nature of transplants. Zhang et al. (2000) tested different cytokinins for bud induction *in vitro* and reported that a mixture of benzyladenine and IAA was the best combination.

2. Nutrient Management. Snake gourd responds well to manuring and fertilizer application, but too much nitrogenous fertilizer leads to excessive stem production at the expense of fruit production. In Asia, 20–25 t ha^{-1} farmyard manure incorporated into the soil, supplemented with N (35 kg), P (11 kg), and K (21 kg) per ha, provided good plant growth. N should be applied in several split doses at 2-week intervals for optimum fruiting and yield. Syriac and Pillai (2001) reported maximum fruit yield using 105 kg N ha^{-1}, 200 ppm ethephon, and drip irrigation at 5 mm cumulative pan evaporation.

3. Water Management. For the initial stages of growth, irrigation at an interval of 3–4 days is essential. In the dry season, plants should be irrigated on alternate days during flowering and fruiting periods. Flooding and soil waterlogging should be avoided to reduce the incidence of *Fusarium* wilt and root rots.

4. Training. The bower system of training is most commonly used in growing of snake gourd in India. When seedlings start producing tendrils, they are staked to thin bamboo poles using string or banana fibers to enable the vines to spread on the trellis. In long-fruited types, a small stone is tied to the tip of the developing fruit 5 days after fruit set to prevent coiling; short-fruited types do not require such training. Maximum fruit length and diameter, number of fruit/plant, and yield have been obtained by training to a single stake followed by the bower system (Prakash et al. 2003). However, vines that are allowed to spread over the ground are more vigorous, bear more fruit, and are less damaged by fruit fly. The vines dry up at the cessation of fruiting during October and November. Vines can then be pruned to leave 30–35 cm of stem above the soil.

5. Weed Management. Weed control is important, particularly during the initial stages of plant growth. Use of paddy straw or black polyethylene as a mulch will reduce heat and moisture stress, as well as weed incidence. Two weedings by hand or machine, supplemented with fluchloralin (1.0 kg ha^{-1}) or paraquat (0.5 kg ha^{-1}), effectively controls weeds (refer to the chemical handbook for your area for registered treatments).

6. Use of Growth Regulators. In snake gourd, application of ethephon to seedlings at the two- and four-true-leaf stage reduces the days to first pistillate flowering, and increases the number of pistillate flowers (Kohinoor and Mian 2005).

E. Harvest and Postharvest Management

The harvest of snake gourd starts 78–80 days after sowing and about 2 weeks after fruit set when they are 30–100 cm in length depending on the cultivar. Fruit may weigh up to 1 kg. Harvesting should be done at an interval of 5–6 days with a total of 6–8 harvests per cropping season. Fruit are usually picked when immature. When fruit pulp production is the objective of cultivation, the harvest of the fruit takes place at full maturity. The same ripe fruit may be used for seed extraction. The average plant yields 50 fruit. Yield ranges from 18 to 25 t ha^{-1}.

F. Pests and Diseases

1. Melon Fly (*Dacus cucurbitae*). The female adult punctures the young ovary and lays eggs below the epidermis. The maggots bore deeply into the fruit and feed, making the fruit unmarketable. The fruit become distorted, begin to rot, and fall from the vine. Control is through registered pesticides such as methyl eugenol and malathion.

2. 28-Spotted Potato Beetle (*Epilachna vigintioctopunctata*). Grubs and adult cause severe damage to leaves by feeding on the green tissue between the veins, giving a lace-like appearance. Control is through registered pesticides such as Sevin 50 WP.

3. Red Pumpkin Beetle (*Aulacophora foveicollis*). The insect feeds on seedlings. Adults feed on the cotyledons. Control is through registered pesticides such as Sevin 50 WP.

4. Mite (*Tetranychus kanzawai*). Spider mites colonize the undersurface of the leaves. Both nymphs and adults feed on the sap, which results in yellowish specks on the upper surface of the leaves in pointed gourd. The leaves gradually turn pale and dry up. Control is through registered pesticides such as Dicofol (0.05%).

5. Anthracnose (*Colletotrichum lagenarium*). Leaf spots that are round, reddish-brown, and dry form on the young infected leaves, starting near the veins. The spots may coalesce and leaves become

blighted. The center of leaf spots falls off giving a shot-hole appearance. In advanced stages, there is shriveling and death of the leaf. Affected fruit have brown to black water-soaked round spots with ash-colored centers. High humidity and moist weather are favorable for spread of this disease. The pathogen is both soil- and seedborne. Destruction of the plant debris after harvest is recommended. Crop rotation with nonhost crops helps in minimizing the incidence of disease. Control is through registered pesticides for seed treatment and foliar application. Seed treatment chemicals include Dithane M-45 or Thiram ($2\,g\,kg^{-1}$ seed). Foliar control pesticides include Dithane M-45 (0.2%) at 5–7 days interval controls the disease.

6. Alternaria Blight (*Alternaria cucumerina*). Initially, small spots appear on the leaves, rapidly increasing in number and size. The adjoining spots on severely affected leaves coalesce and have a burned appearance. Use of disease-free seed, seed treatment before sowing, and crop rotation help in minimizing disease incidence. Control is through registered pesticides such as captan (0.2–0.3%) or mancozeb (0.3%) at 10–15-day intervals. Destruction of plant debris after harvest is recommended.

7. Downy Mildew (*Pseudoperonospora cubensis*). Symptoms appear as yellow to brown angular spots on the leaves with purplish growth on the lower surface, causing significant defoliation. High rainfall and moderate temperature (20–22 °C) are favorable for spread of this disease. Control is through registered pesticides such as Ridomil MZ 72 ($2.5\,g\,L^{-1}$) or Dithane M-45 ($3\,g\,L^{-1}$). Destruction of the plant debris after harvest is recommended.

8. Fruit Rots (*Pythium aphanidermatum*, *P. butleri*, *P. debaryanum*, and *P. ultimatum*). Soft, water-soaked lesions appear on the fruit surface, becoming extensive fruit rot. Training of the vines should be done on a trellis or bower to avoid contact of fruit with the soil. Removal and destruction of all affected plant parts including the fruit is required. Control is through registered pesticides such as a soil drench using copper oxychloride (0.2%).

9. Cucumber Green Mottle Mosaic Virus. Cucumber green mottle mosaic virus causes leaf mosaic, leaf distortion, reduction of internode length, and fruit distortion. The virus is mechanically transmitted to several cucurbit hosts, and is seedborne. Infected plants should be removed and destroyed as soon as they are observed.

10. Cucumber Mosaic Virus. Cucumber mosaic virus (CMV) causes plants to have stunted growth with fewer flowers and fruit, resulting in yield reduction. Chlorosis, vein banding, blistering, and deformation of the leaves are the other symptoms of the disease. The virus spreads by mechanical inoculation and by aphid vectors (*Aphis gossypii*, *Myzus persicae*). Infected plants should be removed and destroyed as soon as they are observed.

G. Crop Improvement

1. Genetics. A multiple allelic series controls fruit skin color, which segregated in a monohybrid ratio in the F_2 generation. Deep green was dominant over green, yellow, and white; green was dominant over yellow and white; and yellow was dominant over white (Sardar and Mukherjee 1987). Mini Raj et al. (1993) reported the monogenic inheritance of fruit color [white (WW) dominant over green-white stripes (ww)], fruit size (partial dominance), and fruit pericarp color (deep green dominant over green, yellow, and white; green dominant over yellow and white; and yellow dominant over white). Characters such as node of first pistillate flower, fruit length, fruit weight, fruit diameter, number of pistillate flowers per plant, and fruit per plant are polygenic and positively correlated with yield.

Kumaresan et al. (2006b) reported that days to first staminate flower opening, days to first pistillate flower opening, main vine length, number of fruit per vine, fruit length, fruit diameter, fruit weight, and yield per vine were controlled by both additive and nonadditive gene action with predominance of additive gene action.

Snake gourd has high broad-sense heritability and high genetic gain for plant growth and yield components such as mean fruit weight, fruit length, days to first staminate flower, fruit per plant, and fruit yield so substantial improvement can be made (Joseph 1978; Varghese 1991; Varghese and Rajan 1993; Mathew and Abdul Khader 1999; Rajkumar and Karuppaiah 2007; Banik et al. 2009). Rajkumar and Karuppaiah (2007) observed high heritability for ascorbic acid content of the fruit, crude fiber content, and node number of first pistillate flower. Fruit yield was strongly correlated with fruit weight, fruit per plant, fruit diameter, fruit length, days to first harvest, flesh thickness, and days to first pistillate flower opening (Narayanankutty et al. 2006). Fruit yield was also correlated with vine length, number of seeds per fruit, seed weight per fruit, and ascorbic acid content of the fruit (Kumaresan et al. 2006a).

Path coefficient analysis showed that individual fruit weight, fruit diameter, number of fruit per plant, and node of first pistillate flower are

the most important characteristics contributing to yield due to high direct effects (Pynadath 1978; Kumaresan et al. 2006a; Narayanankutty et al. 2006). On the basis of correlation and path coefficient analysis, proper weight must be given to pistillate flowers per plant, number of fruit per plant, and fruit weight by virtue of their high contribution to yield (Kondalraj et al. 1984). Analysis of combining ability showed significance of general and specific combining ability variances for all characters except sex ratio, number of fruit per plant, and crop duration, indicating the role of both additive and nonadditive gene action (Varghese 1991).

2. Plant Genetic Resources. The southern peninsular tract of India was identified as the first priority region for collection of *T. cucumerina* var. *anguina* based on germplasm distribution, variability, extent of gene erosion, and a survey of existing collections (Toll and Vausloten 1982). Wide variability of snake gourd exists in South India, and institutions such as Tamil Nadu Agricultural University, Coimbatore and Kerala Agricultural University, have made a diverse collection of germplasm. A wide range of variability exists in Bangladesh (Ahmed et al. 2000; Rahman 2004; Khatun et al. 2010) and in India (Pynadath 1978; Mathew 1996; Ashok 2000). N.I. Vavilov Research Institute of Plant Industry (VIR), St. Petersburg, Russian Federation collected 15 genotypes of *T. cucumerina* var. *anguina*.

3. Breeding. There are various goals for plant breeding programs. These include vigorous and highly branched plants, earliness (lower node of appearance of first pistillate flower), high pistillate to staminate flower ratio, high fruit quality and appearance including green or white color depending on consumer preference, and a range of fruit sizes such as short (30–35 cm), medium long (60–70 cm), long (160–180 cm), or extra long (180–200 cm). Fruit should be thick, heavy, as well as non-fibrous and tender at marketable stage. There is a need for resistance to insects (fruit fly) and diseases (fruit rot and mosaic virus).

Variability exists for earliness, size of fruit, fruit/plant, and yield. Local strains have been selected by several institutions and many cultivars have been developed using pure line selection, including CO-1, CO-2, TA-19, and 'Baby' (Table 9.4). Prakash (1953) reported that F_1 hybrids of snake gourd are superior to their parents in plant vigor, fruit number, and fruit size. Natarajan et al. (1985) reported a hybrid snake gourd 'MDU 1' (Panni Pudal × Sel.1).

Mutation breeding holds promise in snake gourd improvement. Datta (1987) isolated a mutant with yellow striped fruit in M_2, following

Table 9.4. Important cultivars of snake gourd (*T. cucumerina* var. *anguina*) from India and their characters.

Cultivar name	Characteristics	Yield (t ha^{-1})
APAU Swetha	Fruit long with whitish background and green stripes	28–30 in 125–130 days
CO-1	Fruit long (160–180 cm), dark green with white stripes	18 in 135 days
CO-2	Fruit short (30 cm long), stout, pale greenish white with ashy bloom on surface; vines less spreading	25
CO-4	Early maturing; fruit long (160–190 cm), dark green with white stripes	25 q ha^{-1}
MDU-1	F_1 hybrid; fruit medium in length (50–60 cm) with white stripes over a green background	35
PKM-1	Fruit extra long (200 cm), dark green with white stripes outside and light green inside, 700 g	25 in 135–140 days
TA 19	Fruit 60 cm long and average fruit weight is 600 g; ready for harvest in 63–70 days from sowing	25
Konkan Sweta	Fruit medium long (90–100 cm) and white	15–20 in 120–130 days
Baby	Fruit small, 22 cm diam., 30–40 cm long, 474 g, elongated and uniformly white	56 (potential)
Manushri	Medium long, white fruited	25–30
Kaumudi	Fruit white, long (100 cm); suited to acid alluvial soils.	500 q ha^{-1}

treatments with 18 KR X-rays of seeds from a white striped cultivar and the mutant was superior to its parent for yield and punicic acid in the seed oil. Datta (1994) induced a short thick fruit with 30 KR X-rays which proved to be a monogenic recessive mutant. The cultivar PKM-1 was developed through induced mutation (Pillai et al. 1979).

IV. POINTED GOURD

A. Quality Attributes and Human Nutrition

The immature fruit, leaves, and new tender shoots of pointed gourd (Fig. 9.2) are used as vegetables in Asia. The fruit are also used in the preparation of pickles and confectionary products. Singh (1989) reported that pointed gourd is rich in vitamins and minerals (Table 9.3).

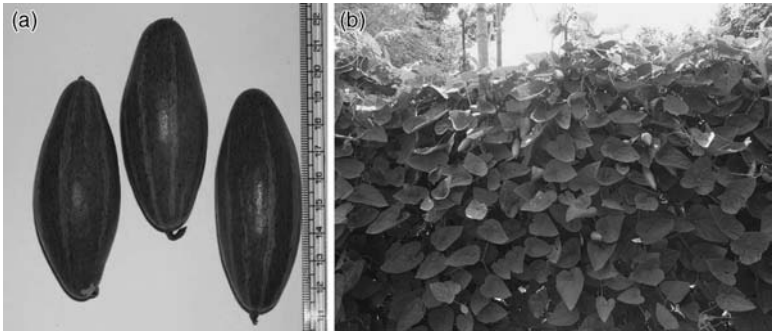

Fig. 9.2. Pointed gourd (a) fruit of 'CHPG 22'; and (b) plant of 'Swarna Alaukik'.

B. Reproductive Biology

T. dioica is a dioecious, tuberous perennial. Occasional perfect flowers are nonfunctional (Singh 1953). A gynodioecious intersex variant with fertile anthers in *T. dioica* was reported by Baillon (1922). Three types of perfect flowers have been reported in *T. dioica*: (1) long style with stigma protruding out of corolla tube with rudimentary stamens; (2) shorter style with stigma lying at the mouth of corolla tube with fully developed anthers, and (3) short style that did not reach up to the mouth of corolla tube with stamens extending slightly above the stigma (Singh et al. 1992).

In the production areas of southern Asia such as India, flowering generally starts in February and continues until November. The opening of a flower from the time of its appearance as a bud takes 16–19 days in staminate flowers and 10–14 days in pistillate flowers. Anthesis begins in the evening, that is, between 7 and 8 pm. The stigma remains receptive from 12 h before anthesis to 12 h after anthesis but maximum receptivity remains at the time of anthesis (Deshpande et al. 1980; Singh et al. 1989). Because of dioecy the pointed gourd is highly cross-pollinated and pollinizers are essential. Pollination is strictly entomophilous; pollen is sticky and therefore unsuitable for wind pollination. There are four insect species visiting the staminate and pistillate flowers of pointed gourd; the red brown beetle (*Carpophilus dimidiatus*) contributes appreciably to pollination (Sachan et al. 1990) as do small ants (*Componotus compressus*).

Natural parthenocarpy has been observed in pointed gourd, and a parthenocarpic line (IIVRPG-105) was developed at the Indian Institute of Vegetable Research, Varanasi, Uttar Pradesh, India. The percentages

of parthenocarpic fruit set in *T. dioica* following natural pollination and pollination with the pollen of *Lagenaria leucantha*, *Momordica charantia*, and *L. leucantha* + *M. charantia* were 58%, 67%, 71%, and 85%, respectively (Singh 1978). Parthenocarpy can be induced with 100–1,000 mg L^{-1} of $AgNO_3$ (Houqe et al. 2002) or 100–500 ppm naphthalacetic (NAA) (Dubey and Nair 1972).

C. Ecology (Climate and Soil)

Pointed gourd performs best in a warm and humid climate where rains are abundant. High humidity favors growth and fruit development. Temperatures between 30 and 35 °C are considered optimum for growth and fruiting, while temperatures below 20 °C restrict growth. Pointed gourd is susceptible to frost. Sandy loam to loam soils rich in organic matter and having a pH of 6–7 with good moisture reserves are best. The crop is sensitive to waterlogging, so heavy soils are unsuitable. Pointed gourd becomes dormant during winter but will sprout and begin growing from the perennial base in the summer.

D. Culture

1. Propagation. Pointed gourd is usually propagated through vine cuttings, root suckers, layered plants, and tissue culture. Seeds are generally not used for commercial propagation owing to poor germination and unpredictable sex expression. Plants raised from seeds are weak, have small leaves, and require 1 year to produce fruit. In the root sucker method, the small roots at the nodes of stems growing along the soil surface are uprooted in October and set in single-plant hills (Seshadri 1986). Pointed gourd can also be multiplied through layering (Singh 1989). Cuttings from the basal portion of mature vines are collected in October when fruiting is nearly complete. The vine cuttings can be planted October to November or February to March in any one of the following methods: (1) vine cuttings of 1–1.5 m having 8–10 nodes are folded in the shape of an 8 and planted in pits filled with farmyard manure and soil; (2) vine cuttings are made into a ring shape and planted in pits keeping the ends above the ground; (3) straight vine cuttings are planted in furrows filled with farmyard manure and soil, keeping the ends of the cutting above the ground; (4) vine cuttings 60–90 cm long are wrapped in moist soil and planted 10 cm deep in furrows.

In areas where there is risk of frost damage during the winter, 20 cm long cuttings taken from mature vines are planted in a protected nursery

in October to November, and the rooted cuttings are transplanted to the field in February to March. Dipping the vine cuttings in 100 mg L^{-1} indole-3-butyric acid (IBA) increases rooting (Pandey and Ram 2000).

Pointed gourd should be planted at 1.5×1.5 m or 2×2 m spacing in the well-prepared pits. A spacing of 1.5×1.5 m is optimum when the vines are trained on trellis (Yadav 1985; Singh 1989). Since pointed gourd is dioecious, sufficient pollinizers must be planted. One staminate plant for every 10 pistillate plants should be planted for proper pollination and high yield.

Houqe et al. (1998) achieved shoot formation in seedling explants on Murashige and Skoog (MS) medium supplemented with 4.44 μM BA. Debnath et al. (2000) developed an efficient *in vitro* protocol for direct plant regeneration, multiplication, and rooting. Efficient rooting was obtained on half strength of MS + 0.5 mg L^{-1} NAA. Kumar et al. (2003) reported that a low concentration of IBA (0.49 μM) produced a significantly higher number of roots per shoot, whereas higher concentrations of IBA favored formation of malformed and thick roots. They reported the highest number of shoots per explant (5.78), highest number of nodes/shoot (6.11), and longest shoots (3.57 cm) on a medium containing 8.88 μM BA, a five- to sixfold multiplication rate compared with earlier studies. Mythili and Thomas (1999) successfully multiplied pointed gourd by culturing of shoot tip and node explants on MS medium containing indole-3-acetic acid (1.0 μM) and indole-3-butyric acid (0.2 μM). Abdul-Awal et al. (2005) micropropagated pointed gourd on MS media supplemented with different concentrations of cytokinins (BA and 2ip) under various combinations of NAA, GA_3, and coconut water. In order to reduce the cost and time of *in vitro* raised plants of pointed gourd, Komal (2011) formulated a minimal medium by substituting costly growth regulators from the MS medium with coconut water. A semisolid MS medium supplemented exclusively with 15% coconut water showed the highest percentage of plantlet regeneration (99%) in the explants.

2. Nutrient Management. Basal application of farmyard manure at 20–25 t ha^{-1} in pits is essential for better growth and fruiting in pointed gourd. In West Bengal, 90 kg N, 26 kg P, and 33 kg K ha^{-1} was found to be optimum (Das et al. 1987). Another study reported that application of 150 kg N, 35 kg P, and 67 kg K ha^{-1} gave the highest yield and high fruit quality (Misra et al. 1994). In river bed production areas, application of 20–25 t farmyard manure, 40 45 kg N, 17 kg P, and 33 kg K ha^{-1} is recommended (Nath and Subramaniyam 1972). Singandhupe et al. (2006) reported that fertigation with 75% of recommended dose of fertilizers

on the basis of 80% potential evapotranspiration (PE) produced the maximum fruit yield of 5.46 t ha^{-1}, which was similar to the yield obtained when 100% of the recommended dose of fertilizer was applied using soil application. Prakash et al. (2003) reported that the use of organic mulch (paddy straw) produced higher number of fruit per plant, maximum fruit length, and yield.

3. Water Management. Irrigation (or rainfall) at an interval of 3–4 days is essential during initial stages of growth. Irrigation on alternate days is carried out during flowering and fruiting periods; no irrigation is required during rainy season when waterlogging may increase the incidence of *Fusarium* wilt. Singandhupe et al. (2006) reported that irrigation at 80% PE saves water and checks weed growth.

4. Training. Pointed gourd vines require training onto an aerial support system (bowers, arches, trellis) to achieve maximum fruit production (Prasad and Singh 1987; Yadav et al. 1989) and facilitate effective pollination. In the bower system, horizontal netted galvanized iron wire is supported above 2.5 m from ground on iron or wood stakes or concrete pillars. Yield was increased 14% when vines were trained on bower system compared with production on the ground (Singh 1989).

5. Weed Management. Weed control is essential during early stages of growth. Control is through registered herbicides such as Fluchloralin 1.0 kg ha^{-1}. Herbicide treatment plus one hand weeding was the most economical weed control method resulting in the highest cost benefit ratio of 1:2 (Gogoi and Gogoi 1997). Dwivedi et al. (1999) obtained high profit with the use of paddy straw mulch instead of herbicides.

6. Pollination Problems. Drying of flowers 1–2 days after anthesis, or yellowing and drying of fruit 5–7 days after anthesis is a common problem during summer. This has been attributed to the lack of pollination and subsequent ovule fertilization during summer months. Both problems underscore the importance of maintaining a ratio of 1 staminate to 10 pistillate plants (Maurya et al. 1985; Mehta et al. 1999).

7. Growth Regulators. Foliar application of gibberellic acid (GA_3) at 40 mg L^{-1} increased the number of pistillate flowers by 230% and decreased flower abortion by 20%, resulting in increased fruit set (by 18.7%). It also increased the length, diameter, and weight of the fruit and also the amount of carbohydrate and ascorbic acid in the fruit (Basu et al. 1999). Application of 30 ppm kinetin increased the protein

content, total soluble carbohydrates, and ascorbic acid content in fruit. Singh et al. (2005) reported an increase in total fruit per plant with the application of 1,000 ppm Alar.

E. Harvest and Postharvest Management

Pointed gourd has uneven fruit maturation due to nonsynchronous fruit set. Fruit become ready for first harvest in 80–90 days after planting (DAP). The full-grown, physiologically mature green fruit are harvested once or twice per week. The average yield of 12–15 t ha^{-1} can be obtained from well-managed plantings. Pointed gourd produces maximum yields for 3–4 years, after which yield gradually declines (Samal and Parida 1983).

As fruit become mature, the exterior turns orange. Harvested fruit have a short shelf-life: only 3–4 days. During long-distance transportation, fruit turn yellow and shrivel, and the seeds harden. The shelf life of pointed gourd increases by 4 days when stored in a zero energy cool chamber [90% relative humidity (RH) and temperature 10–15 °C less than ambient conditions; Chakraborty et al. 1991]. Storability of pointed gourd fruit can be increased to 8 days by coating with waxol (wax emulsion containing 12% solids) + maleic hydrazide (1,000 mg L^{-1}) (Singh 1989) and for 5 days by coating with carnauba wax + sodium hypochlorite (100 mg L^{-1}) + potassium metabisulphite (500 mg L^{-1}) (Koley et al. 2009).

F. Pests and Diseases

1. Melon Fly (*D. cucurbitae*). The female adult punctures the young ovary and lays eggs below the epidermis. The maggots bore deeply into the fruit and feed, making the fruit unmarketable. The fruit become distorted, begin to rot, and fall from the vine. Control is through registered pesticides such as methyl eugenol and malathion.

2. White Fly (*Bemisia tabaci*). The adult flies suck the sap from tender leaves, stunting plant growth. This pest can be controlled by spraying dimethoate 1.5 mL L^{-1} (before flowering) and malathion (2 mL L^{-1}) after flowering).

3. Red Pumpkin Beetle (*A. foveicollis*). The insect feeds on seedlings. Adults feed on the cotyledons. Control is through registered pesticides such as Sevin 50 WP.

4. Node Borer (*Apomecyna saltator*). Borers initially damage the nodal region, and then larvae cause stem swelling and sap oozing by boring into the main stem; their tunnels are filled with glutinous waste material (Singh et al. 2008). Yellow gum exudes from infected nodes, and the stem above the infected node dries. A spray with malathion ($2\,mL\,L^{-1}$) controls the insect. Experiments conducted at the Regional Research Station, Chiplima, India showed that 25–30% of the planting material (roots) contained grubs of the vine borer, which causes significant yield loss at later stage. Control is by soaking of 'seed' (planting stock) in 0.05% Ekalux, Dimecron or 0.067% Thiodan for 15 min before planting.

5. Root Knot Nematode (*Meloidogyne incognita*). Pointed gourd is highly susceptible to root knot nematode. Infected roots are short and stubby, and covered with galls. Application of carbofuran 3 g/plant during August to September and 200 g/plant of neem cake with farmyard manure during January and February reduces nematode incidence. Khan et al. (2009) reported a reduction of root galling by dipping vines in monocrotophos 36SL at 1,000 ppm followed by soil inoculation of *Trichoderma viride* at 10 g/pit once at planting and a second dose 40 DAP. Mukhopadhyay et al. (2006) reported effective control of *M. incognita* by dipping vines in carbosulfan 25 EC at 500 ppm for 6 h followed by application of carbofuran 3G at 2.5 g/pit 45 DAP. Biological control can be done using *Paecilomyces lilacinus* (50 g) along with *Trichoderma harzianum* (100 g), neem cake (250 g), and marigold (*Tagetes erecta*) (3 plants per pit) to control *M. incognita* (Verma et al. 2005).

6. *Fusarium* Wilt. The causal organism is *Fusarium oxysporum* f. sp. *niveum* (Smith) Snyder and Hansen. Symptoms include leaves wilting suddenly and vascular bundles in the collar region becoming yellow or brown. The fungus persists in the soil, making it difficult to control this disease. Use of disease-free planting material and drenching with Captan ($1.5\,g\,L^{-1}$) and Bavistin ($2\,g\,L^{-1}$) around the root zone, followed by application of *Trichoderma* at the rate of 100 g/pit, are recommended for disease control. Soil treatment with 0.5 g Bavistin/pit is also effective.

7. Stem and Fruit Rot. This soilborne disease is associated with *Phytophthora malonis* and *P. cinnamomi*, *Pythium* spp. (*P. aphanidermatum* and *P. cucurbitacearum*), and *Rhizoctonia solani*. This disease is severe during rainy season. Water-soaked lesions appear on the fruit

skin, resulting in fruit rot. Fine mycelial growth is observed on the fruit surface in advanced stages. Vine rotting also occurs. Vines should be trained onto a trellis or bower to avoid contact of fruit with the soil. Removal and destruction of all affected plant parts and fruit is advised. It is important to prevent injury of the fruit skin. Soil drenching with copper oxychloride (0.2%) is recommended. Three sprays of metalaxyl 8% + mancozeb 64% wettable powder both at 0.25% at 8–10 days interval can control this disease effectively (Naskar et al. 2006).

8. Powdery Mildew. Symptoms of powdery mildew caused by *Sphaerotheca fuliginea* appear as nearly white or powdery growth, somewhat circular patches or spots on the lower surface of leaves. More advanced symptoms include leaves becoming brown and shriveled, and plants becoming defoliated. Application of Carbendazim (0.1%) at 2-week intervals and removal of plant debris after harvest are recommended.

9. Watermelon Mosaic Virus (WMV). Affected plants have fewer flowers and fruit resulting in yield reduction. Mild mottling of the leaves as well as vein banding may be observed. The virus spreads by mechanical sap inoculation and vectored by aphids (*A. gossypii* and *M. persicae*). Rapid removal and destruction of infected plants is recommended.

G. Crop Improvement

1. Genetics. A RAPD band OPC 07_{567} was reported as a molecular marker for sex expression (Singh et al. 2002). Isozymatic patterns make it possible to identify sex expression before flowering (Sardar et al. 1994). Kumar et al. (2008) studied the inheritance of stem and leaf morphological traits, and reported that stem shape (angular vs. round), stem pubescence, tendril coiling, tendril branching, and leaf pubescence are governed by a single genes.

Characters such as fruit weight, length and diameter, fruit pulp content, fruit number per plant, fruit volume, number of primary branches per plant, number of leaves per plant, and leaf length are the major yield contributing factors in pointed gourd (Singh et al. 1993, 2007; Sarkar et al. 1999; Hazra et al. 2003). High heritability was reported for fruit length, fruit volume, yield per plant, primary branches per plant, number of fruit per plant, and skin thickness, suggesting that these characters are governed by additive gene action (Singh et al. 1985, 1986, 1992; Sarkar 1989). Significant positive correlations exist between

fruit yield per plant and late flowering (Sarkar and Datta 1987; Prasad and Singh 1990); number of fruit (Singh et al. 1986, 1993; Sarkar 1989; Singh and Prasad 1989; Dora et al. 2003); fruit volume and fruit weight (Singh et al. 1986; Sarkar 1989; Singh and Prasad 1989; Sarkar et al. 1999); fruit diameter (Singh et al. 1987; Sarkar et al. 1999); and fruit length (Singh et al. 1987). However, there was a significant negative correlation between fruit diameter and yield (Singh and Prasad 1989). Yadav et al. (1998) suggested selecting high yielding pistillate clones bearing more fruit per plant in combination with early maturity.

2. Plant Genetic Resources. Extensive collections of pointed gourd germplasm are maintained at multiple locations in India. These include Narendra Dev University of Agriculture & Technology, Faizabad, Uttar Pradesh; Rajendra Agricultural University, Sabour, Bihar; Bidhan Chandra Krishi Viswavidyalaya, Mohanpur, West Bengal; National Bureau of Plant Genetic Resources (NBPGR), New Delhi; Krishna Chandra Mishra Research Institute of Wild Vegetable Crops, Bandanwar, Godda, Bihar; and Central Horticultural Experiment Station, Bhubaneswar.

RAPD (Goswami et al. 2009; Khan et al. 2009; Goswami and Tripathi 2010) and ISSR markers (Goswami and Tripathi 2010) have been used to estimate genetic diversity of pointed gourd germplasm (Hazra et al. 1998; Dora et al. 2001; Ram 2001; Ram et al. 2001; Bharathi and Nath 2010–2011). Kabir et al. (2009) studied the genetic diversity of pointed gourd in Bangladesh and grouped the germplasm based on nine characters.

3. Breeding. The goals for cultivar development in pointed gourd include increased productivity (increased branching, earlier maturity, and more fruit per plant), high fruit quality (proper size, darker color, reduced seed content, longer shelf life), and high insect and disease resistance. Variability exists for earliness, fruit size, number of fruit/plant, and yield. Efficient breeding methods should take advantage of the fact that pointed gourd is cross-pollinated and clonally propagated. Thus, clonal selection is an important part of developing high yielding cultivars. The existing clones of pointed gourd are highly heterozygous, and biparental crosses produce segregating populations for the selection of improved clones. Cultivars such as ‘Arka Neelachal Kirti’, ‘Swarna Rekha’, ‘Swarna Alaukik’, ‘FP 1’, ‘FP 3’, and ‘FP 4’ have been developed through clonal selection (Table 9.5). Induced polyploidy has not been promising because of lack of fertility (Hazra and Ghosh 2001).

Table 9.5. Important cultivars of pointed gourd (*Trichosanthes dioica*) from India and their characters.

Cultivar	Characteristics	Yield (q ha^{-1})
CHES Hybrid 1	First hybrid developed, resistant to fruit fly. The solid, green striped fruit each weigh 30–35 g	280–320
CHES Hybrid 2	Dark green striped fruit with average fruit weight of 25–30 g	300–400
Faizabad Parwal 1	Fruit round, green, and attractive	150–170
Faizabad Parwal 3	Fruit are spindle shaped, green, and less striped	125–150
Faizabad Parwal 4	Fruit are light green, spindle shaped with tapering ends. Recommended for reclaimed sodic soils	125–150
Rajendra Parwal 1	Highly suitable for *diara* land cultivation. Fruit are big-sized striped and green	140–150
Rajendra Parwal 2	Highly suitable for *diara* land cultivation. Fruit are large, dark green with whitish stripes	150–170
Swarna Alaukik	Fruit light green with blunt ends, 5–8 cm long, solid, thin skinned, and good for vegetable as well as sweets	230–280
Swarna Rekha	Fruit greenish white, striped, 8–10 cm long and tapering on both sides	200–230
Shankolia	Fruit are medium long (7.56 cm × 2.94 cm), resembling those of shell; greenish with white stripes, slightly beaked toward distal end and bulged toward stalk	125–150
Konkan Harita	Fruit dark green with white stripes, thin skinned, and good for vegetable	140–170
Arka Neelachal Kirti	Fruit dark green with 3–4 fragmented stripes of cream color; long, elongated spindle shaped with solid core, approximately 45–50 g	250–260

V. FUTURE PROSPECTS

Most of the genetic improvement in snake gourd and pointed grourd has been the result of selection within landraces by farmers in local habitats. However, over the last two decades, increasing emphasis has been placed on more systematic improvement strategies in India. This has resulted in the release of many improved open-pollinated cultivars in these crops by state agricultural universities and the Indian Council of Agricultural Research.

Hybridization programs are expected to create improved recombinants and transgressive segregants. The early identification of staminate and pistillate plants in pointed gourd would be advantageous to help farmers to obtain desirable ratios for optimum yield. Future efforts in snake gourd and pointed gourd breeding should emphasize the development of nutritious, high-yielding cultivars with superior resistance to major diseases and exceptional fruit quality for both domestic and foreign markets.

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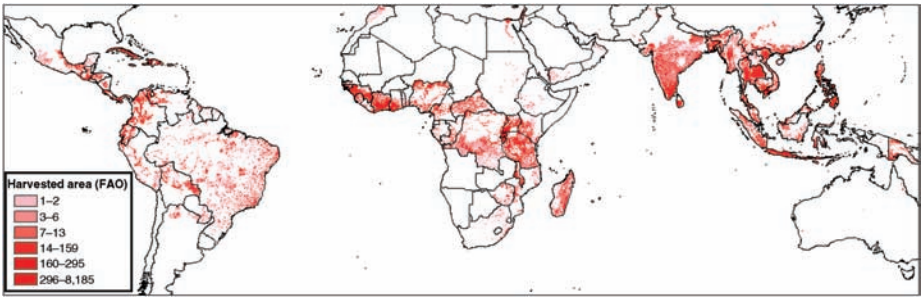

Plate 2.1. Distribution of banana area harvested as in You et al. (2007). Raw data are derived from FAOSTAT (FAO 2010). Grid cell values are tens of hectares per 100 km^2.

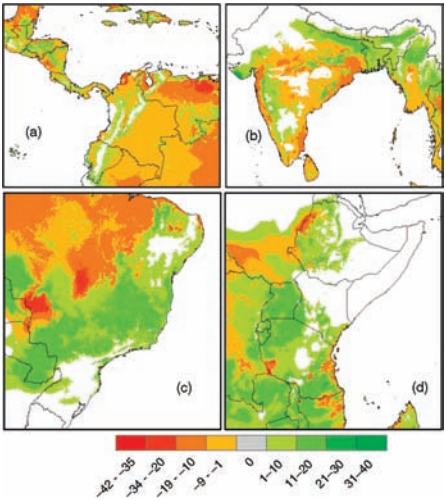

Plate 2.2. Predicted changes in climatic suitability from the study of Ramirez et al. (2011) for the four most important banana-growing regions of the world: (a) Central America and Andean countries, (b) India, (c) Brazil, and (d) East Africa. Values are percent changes in climatic suitability, as predicted by the EcoCrop model (Ramirez-Villegas et al. 2013)

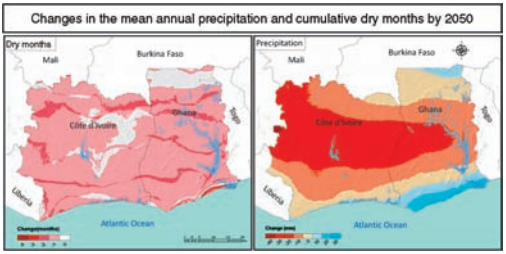

Plate 2.3. Predicted mean annual precipitation and cumulative dry month changes by 2050 according to 19 GCM models (SRES A2) for Ghana and Côte d'Ivoire. *Source*: Adapted from Läderach et al. (2011).

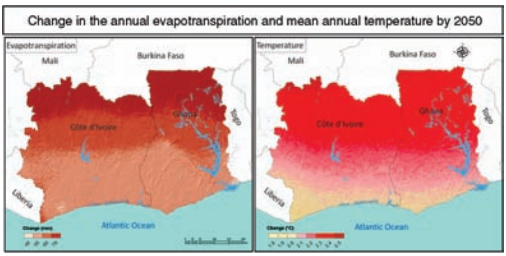

Plate 2.4. Predicted mean annual temperature and evapotranspiration changes by 2050 according to 19 GCM models (SRES A2) for Ghana and Côte d'Ivoire. *Source*: Adapted from Läderach et al. (2011).

Horticultural Reviews, Volume 41, First Edition. Edited by Jules Janick.
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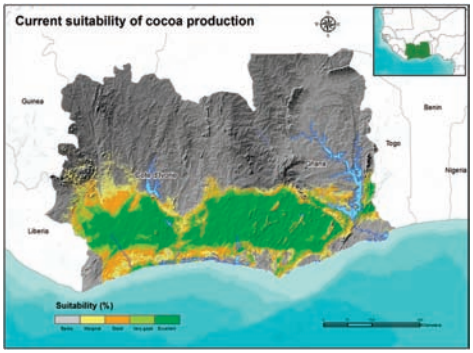

Plate 2.5. Current climatic suitability for cocoa production within cocoa-growing regions of Ghana and Côte d'Ivoire. *Source*: Adapted from Läderach et al. (2011).

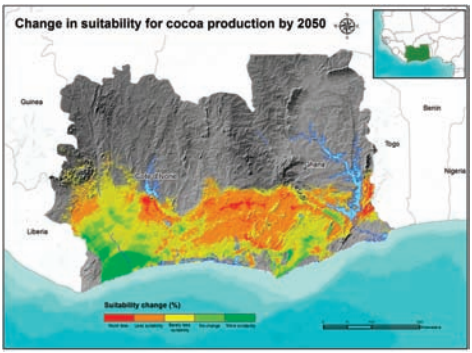

Plate 2.6. Climatic suitability for cocoa production in 2050 according to 19 GCM using the MAXENT crop prediction model. *Source*: Adapted from Läderach et al. (2011).

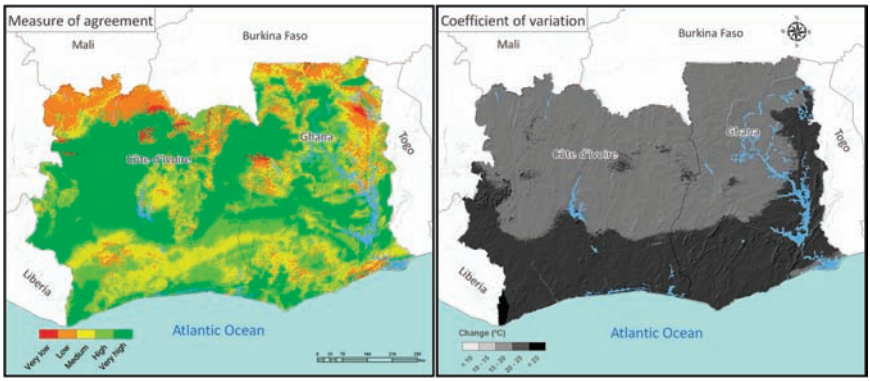

Plate 2.7. Suitability change for cocoa-growing regions by 2050 and measurements of agreement and coefficient of variation of results. *Source*: Adapted from Läderach et al. (2011).

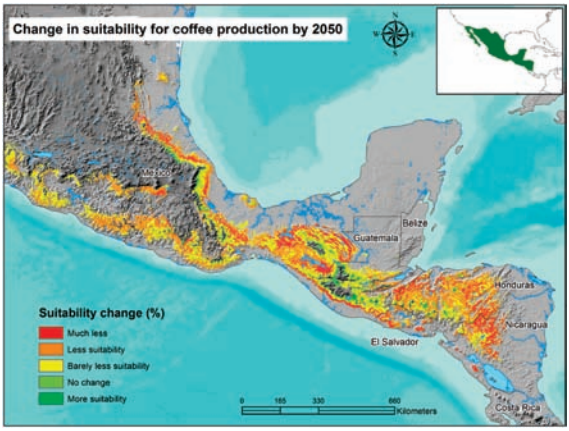

Plate 2.8. Projected changes in coffee suitability in Mesoamerica by 2050 (Läderach et al. 2010b).

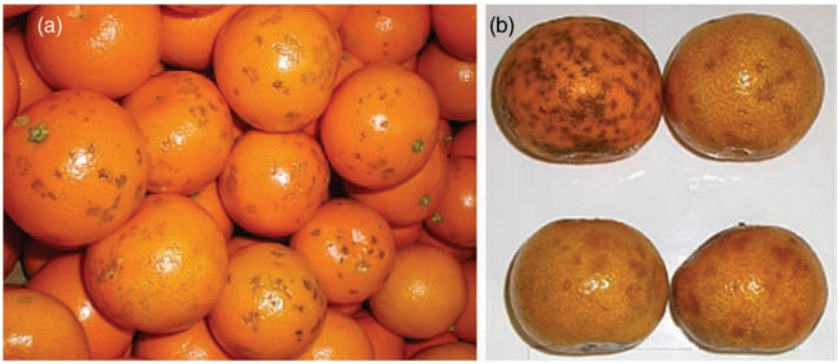

Plate 3.1. Visual symptoms of nonchilling postharvest pitting of 'Nova' mandarin (a) and rind breakdown of 'Nules Clementine' mandarin (b) (Cronje et al. 2011a).

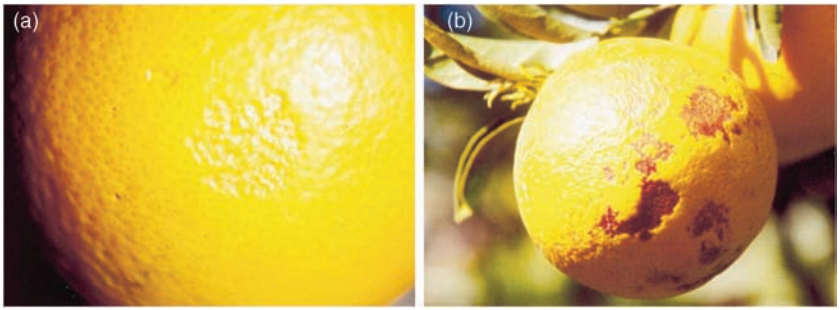

Plate 3.2. Rind staining or peel pitting at nonchilling temperature in 'Navelate' (a) and 'Navelina' (b) oranges is aggravated by transference of dehydrated fruits to high RH (Alférez et al. 2003).

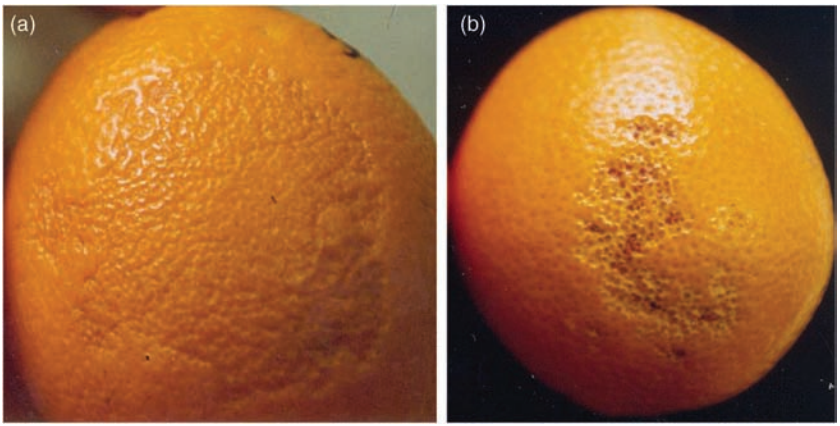

Plate 3.3. Rind staining in 'Navel' orange (a) and peteca spots of lemon (b).

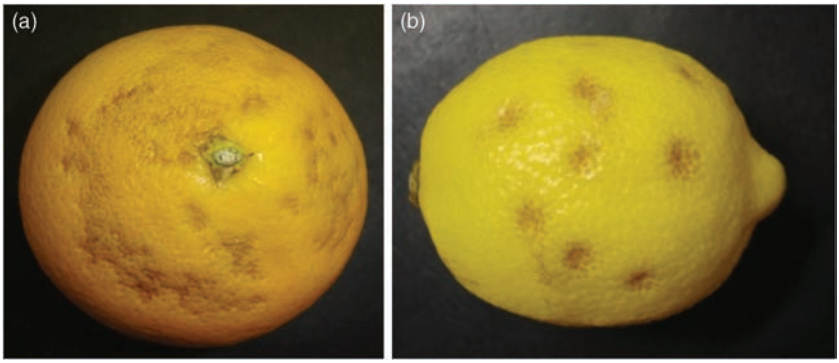

Plate 3.4. Chilling injury in 'Navel' orange (a) and 'Satsuma' mandarin (b).

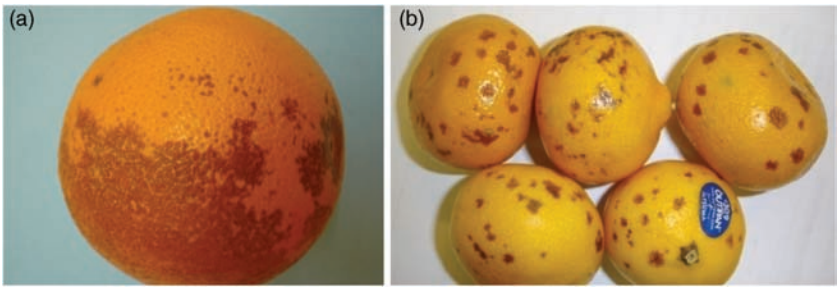

Plate 3.5. Rind breakdown of 'Navelate' sweet orange: (a) first symptoms are characterized by depressed colorless areas; (b) fruits with severe symptoms of preharvest peel pitting develop reddish-brown and dry areas (Agustí et al. 2001).

Plate 3.6. Symptoms of stem end rind breakdown on 'Marsh' grapefruit (Ritenour and Dou 2003).