

14 Challenges of Climate Change to Strawberry Cultivation: Uncertainty and Beyond

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14.1. Climate Change and Forecasting the Impact on Strawberry

The United Nations (UN) Framework Convention on Climate Change, which was opened for signature during the 1992 UN Conference on the Environment and Development in Rio, was the first attempt to deal

with the threat of global climate change. In June 2008, the UN Food and Agriculture Organization (FAO), together with International Fund for Agricultural Development (IFAD), UN World Food Programme (WFP) and Consultative Group on International Agricultural Research (CGIAR) system, convened the High-Level Conference on World

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Food Security: the Challenges of Climate Change and Bioenergy, and 181 countries adopted a declaration that 'It is essential to address the question of how to increase the resilience of present food production systems to challenges posed by climate change' (<http://www.fao.org/foodclimate>). Recently, it was again reiterated in the UN Sustainable Development Goals: 'by 2030, ensure sustainable food production systems and implement resilient agricultural practices that increase productivity and production, that help maintain ecosystems, that strengthen capacity for adaptation to climate change, extreme weather, drought, flooding and other disasters and that progressively improve land and soil quality' (<http://www.un.org/sustainabledevelopment/climate-change-2/>).

What actually constitutes climate? Climate is an extraordinarily complex system with many delicately interrelated components that have significant roles in forming climate through their interactions with the atmosphere (FAO, 2008) (Fig. 14.1). Climate is the statistical aggregate of weather conditions such as temperature, precipitation, wind, cloudiness and storms over a period of time (Glover *et al.*, 2008). Five primary environmental factors are critical for plants to germinate, grow and reproduce, and strawberry is no exception. These factors are carbon dioxide, sunlight, water, an optimal temperature range

and nutrients. Of these, the first four are directly related to climate and vary spatially, diurnally and seasonally. In the context of global climate change, these factors behave erratically and therefore need to be considered foremost when designing strawberry plants adapted to changing climatic conditions.

Strawberry is cosmopolitan in distribution, and therefore predicting the precise impact of climate change on strawberry across all current areas of distribution is very complex and perhaps not possible. The cultivated strawberry, *Fragaria × ananassa* Duch., is a natural hybrid of *Fragaria chiloensis* (L.) P. Mill. and *Fragaria virginiana* (Duch.) and is octoploid ($2n = 8x = 56$). There are about 34 other species of *Fragaria* found in Asia, North and South America, and Europe, of which two are cultivated commercially for their fruit: *Fragaria moschata*, the musky or hautboy strawberry, and *Fragaria vesca*, the wood or alpine strawberry. These species have been cultivated for centuries, but there is little production of them today, due to the success of *Fragaria × ananassa*. About a dozen diploid strawberry species are distributed in Eurasia, although one of them, *F. vesca*, has a wider distribution and is also found in America. Tetraploid species, namely *Fragaria corymbosa*, *Fragaria orientalis*, and *Fragaria moupinensis*, are mostly restricted

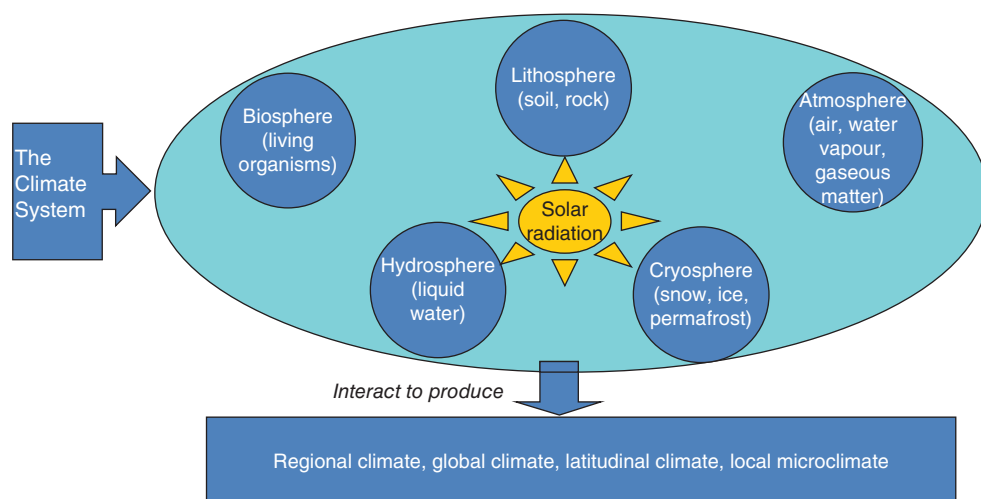


Fig. 14.1. The climate system.

to East Asia, while *F. moschata*, the only hexaploid species, is found in Europe. The octoploid species *F. virginiana* L. is native to North America, north of Mexico, while *F. chiloensis* Duch. is native to west coastal North America and the west coast and Andes Mountains of South America. *Fragaria iturupensis* is the only Asian octoploid species, as described by Staudt (1973). Given the lack of sufficient detail regarding climatic variations and their interactions, as well as the precise climate changes for each of these regions/localities, the impact of climate change on strawberry can be predicted only in general terms. Broadly speaking, global climate change will alter many elements of future strawberry production, primarily because atmospheric carbon dioxide concentration, average temperature and tropospheric ozone concentration will be higher, droughts will be more frequent and severe, more intense precipitation events will lead to increased flooding, some soils will degrade and weather extremes will be more frequent. Climate change will also affect host–pathogen interactions, in particular by: (i) increasing pathogen development rates (the number of generations per year); (ii) relaxing overwintering restrictions on pathogen life cycles due to milder winters; and (iii) modifying host susceptibility to infection (Harvell *et al.*, 2002). Changes in temperature, precipitation and humidity influence the growth, spread and survival of plant diseases, as climate and weather have a major role in influencing disease epidemiology (Rosenzweig *et al.*, 2001). This means that knowledge of how climate change will bring about specific changes in regional weather patterns is crucial in determining how plant disease outbreaks will change in the future. Many disease prediction models have been published in the last decade (Booth *et al.*, 2000; Bergot *et al.*, 2004; Francesca *et al.*, 2006; Evans *et al.*, 2008). By combining these models with climate change models, it becomes possible to study the change in likelihood of the diseases occurring and assess the probability of disease outbreaks. However, most of these studies do not take into account factors such as changes in agricultural and environmental

policy, mitigation activity and consumer preferences. Furthermore, being simplistic in form, these models assume disease inoculum to be present equally throughout the region and everything else to be constant except the weather. In a real case scenario, even though the predictions of disease potential might be valid, the likelihood of actual outbreaks occurring would also depend on the availability of inoculum. In an interesting study about the effect of climate change on strawberry production in the UK, Calleja (2011) predicted that the incidence of powdery mildew in strawberries will increase under climate change projections across most of the UK, with disease incidence increasing more in Scotland, western Wales and the north of England. Similarly, grey mould incidence was predicted to change across most of the UK, with increases north of the Midlands and slight decreases in the south. The incidence of strawberry black spot was predicted to increase drastically across most of the UK, with potential disease incidence increasing most in Scotland and on the west coast of the UK. However, Calleja (2011) cautioned on the usefulness of these disease prediction models, because of their simplicity and assumptions that inocula are present throughout the area being studied and that the same production and disease management practices are used throughout. Thus, while being indicative of potential changes in disease incidence in the UK for these three diseases, more work needs to be done to build more detailed disease models that can provide further information for policymakers and the industry. Additionally, the predictions of these models depend on the appropriateness of the chosen conditions for infection, and might vary slightly if a different temperature range, precipitation level or duration is chosen.

14.1.1. Photoperiod and vernalization

Photoperiod and temperature are major environmental signals affecting flowering in plants. Although molecular pathways mediating these signals have been well characterized in the annual model plant

Arabidopsis, much less information is known in perennials. One of the primary ways of classifying strawberry is on the basis of photoperiod requirements on the seasonal flowering characteristics of the cultivars. Shortening days and lower temperatures normally induce flower development in the crown. However, different genotypes have a wide range of growth habits, from the single fruiting habit of short-day plants to the almost continually blooming and fruiting habit of day-neutral plants. Two main types of cultivar are recognized based on environmental control of flowering:

- Short-day or June-bearing: plants that flower in the spring, produce a single crop and form flower buds in the autumn. These short-day plants require photoperiods under 14 h and/or temperatures under 17°C for floral initiation.
- Ever-bearing: plants that flower and fruit two or more times per season. The ever-bearing habit is governed by long photoperiods. These cultivars fruit throughout the growing season provided temperatures are not too high.

There are two types of ever-bearing plants: (i) Long-day plants, in which lengthening days promote more-or-less continuous flowering during the summer, provided temperatures are not too high; and (ii) Day-neutral plants, in which photoperiod has no effect on flowering; they will also flower several times per year, but do so during short as well as long days.

The flowering habit of the strawberry is directly related to temperature, and strongly interacts with photoperiod. These factors affect induction, initiation and differentiation of flower buds. It has been shown that cool summer temperatures (17°C) allow induction to occur under long photoperiods, even in short-day cultivars. This means that some cultivars considered as short-day types behave as remontants in cool climates. High temperatures generally inhibit flowering under any condition (regarding photoperiod or cultivar), although it has been observed that critical temperature is higher in day-neutral cultivars (Manakasem and Goodwin, 2001; Stewart and Folta, 2010). Thus, cool temperatures

promote flowering, while warm temperatures inhibit flowering, and temperature sensitivity is greater in short-day cultivars and least in day-neutral cultivars.

The day-neutral characteristic, introduced by Bringhurst and Voth (1984) using the genotype *F. virginiana* subsp. *glauca*, collected from the Wasatch Mountains in Utah (Hancock and Luby, 1993), has been investigated widely to elucidate its mode of inheritance. Most studies indicate it to be governed by a dominant locus affected by some minor genes (Ahmadi *et al.*, 1990; Shaw and Famula, 2005), although some suggest it to be a quantitative character having polygenic inheritance (Serçe and Hancock, 2005b; Weebadde *et al.*, 2008). In recent decades, some wild accessions of *F. virginiana* have been identified with varying degrees of photoperiod insensitivity or continuous flowering, but more information and crosses are needed to incorporate these new sources into commercial varieties (Hancock *et al.*, 2001a; Serçe and Hancock, 2005a,b), as the diversity of responses to photoperiod and the interaction with other environmental and epigenetic factors make the analysis difficult. Nevertheless, through the availability of *F. vesca* genomic information and through its genetic manipulation, it has been possible to characterize a gene that inhibits photoperiod sensitivity, named *Terminalflower1* (*FvTFL1*), and to develop molecular markers for its assisted selection (Koskela *et al.*, 2012). By using transgenic lines and gene expression analyses, Rantanen *et al.* (2015) recently observed that the temperature-mediated changes in the *FvTFL1* mRNA expression set critical temperature limits for the photoperiodic flowering in strawberry. Although *F. × ananassa* and *F. vesca* show similar environmental responses, they seem to differ in the genetic control of the perpetual flowering trait. It has been shown that perpetual flowering is controlled by a single dominant locus (Morishita *et al.*, 2012) in *F. × ananassa*. One major quantitative trait locus, namely *FaPFRU*, has been identified in *F. × ananassa*, and is not orthologous to the *Seasonal Flowering Locus* (*SFL*) or *Runnering locus* (*R*) of *F. vesca*, and is positively linked to

perpetual flowering but negatively linked to runner in *F. × ananassa* (Gaston *et al.*, 2013). In another recent development, Castro *et al.* (2015) found a marker showing association with day-neutral flowering and runner in a population derived from a cross of cultivars 'Tribute' × 'Honeoye'. The marker ChFaM148-184T was derived from an expressed sequence tag (EST) (GenBank accession no. GU815864) with homology to *GalUR* (Zorrilla-Fontanesi *et al.*, 2011), a gene that encodes an NADPH-dependent d-galacturonate reductase. This finding supports the hypothesis that photoperiod is mainly a monogenic or oligogenic character.

The chilling requirement (accumulation of chilling hours at 0–7°C) is an important factor affecting reproductive and vegetative growth in strawberry plants. This vernalization period is required to break bud dormancy, and varies with genotypes. It is a mechanism to prevent plants from budding and flourishing early in the season, when chance of spring frost is still high. Therefore, in areas where climate change may cause a drop in temperature during the spring, high-chilling-requirement cultivars may be suitable for cultivation. In Norway, the *F. vesca* cultivar 'Alta', with a much delayed budding and flowering, was discovered. This characteristic was attributed to a high winter chilling requirement, compared with other studied populations of the same species (Heide and Sønsteby, 2007), and therefore it might be possible that such a population will adapt better to regions where climate change has caused prolonging of the winter season.

14.1.2. Disease and pest outbreaks

Climate change will undoubtedly modify pest dynamics. Changes in disease incidence and movement of diseases to areas where they were previously not a problem can lead to substantive regional impacts. Moreover, the impacts of climatic change on crop physiology could affect the interaction between pathogen and host, and potentially also induce changes in the epidemiology of the pathogen (Garrett *et al.*,

2006). The current understanding of these changes is quite limited, despite some past attempts of modelling these changes (Aggarwal *et al.*, 2006; Easterling *et al.*, 2007). The greatest impact of climate change on pathogens is related to the altered condition of the plant host in the changed environment, rather than to any direct impact on the organisms (Chakraborty *et al.*, 2002; Ziska and Runion, 2007). A strawberry plant (host) stressed by the environment could have an altered physiology and chemical composition, which may render it more susceptible to pests or diseases due to altered concentrations of defensive compounds (Ziska and Runion, 2007).

There is a complex interaction between biotic and abiotic factors in disease incidence, development and spread. For example, in recent years, an increase in collapsed and dead strawberry plants due to crown rot has been observed in several fields in central Chile, an important area for strawberry cultivation in this country (Sánchez *et al.*, 2013). According to this study, this disease, caused by *Macrophomina phaseolina*, has also been reported recently in Spain, the USA and Argentina. The microsclerotia of *M. phaseolina* are produced in the host tissue and released into the soil as the infected plant decays. These multi-celled structures allow persistence of the fungus under adverse conditions such as low soil nutrient levels and temperatures above 30°C. Germination of the microsclerotia occurs when temperatures are between 28 and 35°C. Soil moisture content is considered a major factor that affects survival of *M. phaseolina* in soil (Pratt, 2006). Zveibil *et al.* (2012) reported that high soil moisture content and flooding caused a decline in sclerotia viability compared with dry soils. Olaya and Abawi (1996) reported that high temperatures and low soil water potentials are important factors in causing this disease, which is important from the perspective of climate change.

Cool climates will favour the development of diseases such as root rot. *Pythium* spp., especially *Pythium ultimum*, are the most widespread strawberry root pathogens and their growth is favoured by cool climates. This species is a major cause of

black root rot disease in strawberry and can also attack many other crops. In strawberry, *Pythium* spp. destroy juvenile root tissue, such as feeder rootlets. In contrast, *Fusarium* wilt development in strawberry is favoured by high temperatures, which cause the infected leaves to wilt and die rapidly (Maas, 1998). With an increase of temperature from 17 to 27°C, the disease severity of plants infected with *Fusarium oxysporum* increases significantly, causing severe disease symptoms in the crown, root and vascular tissues, along with poor development of roots, eventually resulting in death of the plants within 4 weeks (Fang *et al.*, 2011).

Warmer winters will also have a large influence on the survival of insect pests. The main effect of temperature in temperate regions is on the winter survival of pests. With warmer winters, the natural shield that protects the strawberry industry in cooler areas of Europe will be eliminated, subjecting plants to the invasion of insect pests. In the absence of improved varieties, growers will need to resort to other effective methods of controlling disease, such as increased dependence on pesticides. This will not be a sustainable solution, as access to chemical pesticides is likely to be restricted in the future. As a result of the enactment of legislations such as EC Regulation No. 1107/2009 (this regulation repealed Council Directives 79/117/EEC and 91/414/EEC in 21 October 2009 and applied the precautionary principle to 'ensure that industry demonstrates that substances or products produced or placed on the market do not have any harmful effect on human or animal health or any unacceptable effects on the environment' (<http://eur-lex.europa.eu/legal-content/EN/TXT/?uri=celex:32009R1107>), the availability of pesticides for the strawberry sector has been reduced, making this crop more vulnerable to the impacts of plant disease and climate change.

Calleja (2011) found evidence that climate change is already affecting the strawberry sector in the UK. Many farms have already been adversely affected and have suffered financial loss. However, this has driven innovation within the sector, sometimes as a direct result of companies

involved in strawberry production funding research and development to develop new products, either by the company themselves or through collaboration with universities by funding their research. The need to minimize the use of chemical pesticides for environment-friendly cultivation will require the development of improved cultivars containing pest- and disease-resistant genes. Furthermore, the need to maintain production in different areas and to face changing climates will also require the presence of abiotic stress-resistance genes.

14.2. Major Environmental Factors of Critical Importance

It is evident from the above discussion that one of the major environmental factors affecting plant growth and productivity is temperature, with optimum growth temperatures between 10 and 26°C for strawberry (Ledesma *et al.*, 2004). Field-grown strawberry plants are often exposed to fluctuating temperatures and soil moisture, which have profound effects on plant metabolism. These factors are discussed further in the following sections.

14.2.1. Temperature rise

The increase in temperature above a threshold level for a period of time sufficient to cause irreversible damage to plant growth and development is called 'heat stress'. Heat stress is a complex function of heat intensity (temperature in degrees), duration (seasonal compared with daily temperature extremes) and rate of increase in temperature (Wahid *et al.*, 2007). According to Bray *et al.* (2000), a heat-stress response is observed in plants exposed to temperatures at least 5°C above optimal conditions. Studies on the mechanism of stress tolerance in each species or cultivar are very important for the development of heat-tolerant plants. However, knowledge about the mechanisms of heat tolerance in common strawberry cultivars is limited.

Heat acclimation studies in strawberry plants by Gulen and Eris (2004) revealed that gradually heat-stressed plants showed less membrane injury and exhibited greater heat-stress tolerance than shock heat-stressed plants. Thus, gradual high-temperature stress with long exposure increases heat tolerance in strawberry leaves. Increased heat tolerance was correlated with the accumulation of several heat-stable proteins in the gradually heat-stressed plants. In addition, significant differences between gradual and shock heat-stressed plants were reported in leaf relative water content, loss of turgidity, and total protein and DNA content. Surprisingly, heat stress increased the chlorophyll content in strawberry plants (Gulen and Eris, 2003; Kesici *et al.*, 2013). Moreover, high temperatures increased the activities of antioxidant enzymes ascorbate peroxidase (APX), peroxidase (PRX) and catalase (CAT) (Ergin, 2012). While no effect on glutathione reductase (GR) activity was reported under heat stress, the activity of PRX enzyme was closely related to cell membrane stability and lignification, thus, qualifying as a potential enzyme marker (Gulen and Eris, 2004; Ergin *et al.*, 2012). Heat-shock proteins (HSPs) under the control of heat-stress transcription factors play a central role in the heat-stress response. These were first identified as proteins that are strongly induced by heat stress and subsequently were shown also to be essential for normal growth and metabolism. The role of HSPs in heat tolerance of strawberry is described in a limited number of studies. Ledesma *et al.* (2004) reported 19–29 kDa HSPs in leaves and 16–26 kDa HSPs in flowers of the strawberry cultivars ‘Nyoho’ and ‘Toyonaka’ at high temperatures. Ergin (2012) detected a 23 kDa HSP in leaf tissues during heat acclimation of strawberry cultivars. Accumulation of this 23 kDa HSP was found to be higher in heat-tolerant cultivars than in heat-sensitive cultivars, and thus correlated with heat tolerance in strawberry.

Recently, Kesici *et al.* (2013) evaluated the heat tolerance of 15 commonly grown strawberry cultivars, and found that ‘Elsanta’, ‘R. Hope’ and ‘Camarosa’ were relatively heat tolerant, while ‘Whitney’, ‘Fern’, ‘Festival’ and

‘CG3’ were relatively sensitive. More such studies need to be undertaken to identify cultivars suitable for different temperature regimes.

14.2.2. Temperature drop

Strawberry is a moderately cold-hardy species. Barney *et al.* (1992) report the cold hardiness of strawberry cultivars over a wide range (from -3.8 to -45.0°C). It is one of the most important small fruit crops in several northern parts of the world (Ndong *et al.*, 1997). Genotypes collected in cold environments usually possess greater hardiness and are usually more tolerant to spring frost damage during flowering. In a study on germplasm collections of *F. chiloensis* and *F. virginiana*, a high degree of cold resistance was found in clone PI 552091 of *F. chiloensis*, collected in Chile at an elevation of 1900 m (Hancock *et al.*, 2001a). However, in a study that compared accessions of native American octoploid genotypes, it was determined that those of *F. virginiana*, regardless of their origin, had a greater resistance to cold weather than those of *F. chiloensis*. Within the latter, clones collected in North America were more resistant than those collected in South America (Hancock *et al.*, 2001b).

Chilling injury of strawberry is a serious problem in particularly subtropical cultivated areas (Zhang *et al.*, 2008). Freezing tolerance is evaluated by an ion-leakage test at the cell membrane (Arora *et al.*, 1992). The level of LT_{50} shows the cold-hardiness level of a cultivar and is defined as the temperature killing 50% of the whole plant or tissues. For strawberry cultivars, the LT_{50} of ‘Chamly’, ‘Red Coat’ and ‘Oka’ was reported as -12°C , while the LT_{50} of the freezing-sensitive ‘Chandler’ was -2°C (Ndong *et al.*, 1997). Carbohydrate metabolism is also very important in determining the cold hardiness of plants. Sugars increase the intracellular osmotic potential and reduce the freezing point (Levitt, 1980; Paquin *et al.*, 1989). Seasonal alteration of apoplastic and symplastic sugar metabolism occurs in plants. Symplastic sugar metabolism was found to be more effective in cold tolerance, as the total soluble

sugar, reducing sugar and sucrose contents of the symplast were higher in the cold-acclimated stage than in the non-acclimated stage (Turhan, 2012). Turhan *et al.* (2012a) evaluated the cold hardiness of eight strawberry cultivars and reported that 'Ventane' was the most cold hardy, while 'Kabarla' was the least cold hardy among the eight cultivars.

Strawberries differ considerably in their 'ability' to develop cold or freezing tolerance through a process known as cold acclimation. Thus, understanding the mechanisms involved in cold acclimation has great importance in enhancing the cold tolerance of species, and would be of considerable interest for preventing cold damage. Biochemical changes associated with cold acclimation in various plant species include alterations in lipid composition, increased sugar and soluble protein content, expression of specific proteins, the appearance of new isozymes and alterations in the activity of antioxidative enzymes (Thomashow, 1999; Sarnighausen *et al.*, 2004; Eris *et al.*, 2007; Gulen *et al.*, 2008; Cansev *et al.*, 2009). Zhang *et al.* (2008) reported that chilling acclimation at 0°C resulted in enhancement of superoxide dismutase, CAT, PRX, dehydroascorbate reductase, monodehydroascorbate reductase, APX and GR activities and an increase in reduced ascorbate, dehydroascorbate and reduced glutathione (GSH) contents in the strawberry cultivar 'Toyonaka'. They concluded that the ascorbate-GSH cycle plays an important role in the detoxification of H₂O₂, thereby enhancing chilling resistance in strawberry. As ice formation occurs primarily in the intercellular spaces during freezing injury, Turhan *et al.* (2012b) studied apoplastic antioxidant enzymes in the leaves of two strawberry cultivars, 'Aromas' and 'Diamante'. The activities of apoplastic CAT, PRX and APX varied significantly depending on the cold-hardiness level of the cultivar. Considerable increases in APX and GR enzyme activity in the cold-acclimated stage might serve as markers of cold hardiness in strawberry plants (Turhan *et al.*, 2012a). All these biochemical processes are regulated at the gene expression level and many cold-induced genes/proteins have been characterized in many species. These proteins

accumulate at a high level under cold stress. Recently, Koehler *et al.* (2012) reported stress-responsive proteins in crown tissue of strawberry plants exposed to cold treatments. Ndong *et al.* (1997) conducted a study to identify genes associated with cold acclimation and reported that the expression of *Fcor1* (*Fragaria Cold-Regulated1*) correlated with the freezing tolerance of the strawberry cultivars 'Champly', 'Red Coat', 'Oka' and 'Chandler' and wild strawberry (*F. virginiana*), suggesting that *Fcor1* might serve as a molecular marker for cold tolerance.

14.2.3. Water scarcity/surplus

Another factor that determines the degree of a plant's hardiness towards climate change is its ability to adapt to extreme drought or flooding conditions. Strawberry plants are known for their high demand for water because of their shallow root system (almost all of the roots are in the 0–15 cm depth zone), large leaf area and high water content of the fruit (Chandler and Ferree, 1990; Klamkowski and Treder, 2006). According to Li *et al.* (2010), strawberry plant water stress occurs on the slope and shoulder areas, where there is high irradiance and temperature and low soil water content, resulting in significantly lower fruit yield. Drought stress has a negative effect on strawberry plant growth and yield (Chandler and Ferree, 1990; Husaini and Tuteja, 2012). While drought stress decreases strawberry leaf water potential, transpiration rate and water channel activity, flooding does not cause any change in leaf water potentials and water channel activity in strawberry plants (Blanke and Cooke, 2006). Stomata close more rapidly in flooded strawberry leaves than in drought-stressed ones. The evidence suggests that strawberry plants are generally more adversely affected by drought than by flooding.

In order to develop drought-tolerant strawberry varieties, knowledge about species-level and cultivar-level tolerance is imperative for a successful breeding programme. However, there are limited studies on this aspect in strawberry. The most

drought-tolerant species within the genus *Fragaria* is reported to be *F. chiloensis* (Zhang and Archbold, 1993). Hancock *et al.* (2001a) selected plants of *F. chiloensis* from extremely arid zones, in coastal regions of Chile or the USA (PI 602567, PI 612317, PI 551728 and PI 612490), and used them as donors for tolerance to water/salt stress for modern cultivars. Grant *et al.* (2010) compared the performance of ten strawberry cultivars under water deficit and reported that osmotic adjustment, small leaf area and transpiration rate were some of the drought-tolerant characteristics useful in breeding programmes. Strawberry plants exposed to water stress show a tolerance mechanism based on high elasticity of tissues as a morphological adaptation. The changes in whole-plant morphology and canopy architecture, from monolayer to polylayer leaf distribution, and leaf orientation from south to north, have been reported as an indication of stress-avoidance mechanisms. Based on such morphological and physiological measurements, Klamkowski and Treder (2008) report that the cultivar 'Elsanta' was the most drought tolerant among the three strawberry cultivars evaluated in their study.

Annual average temperatures are showing an upward trend, and evapotranspiration requirements for water are growing. Moreover, water deficit/drought usually causes inhibition of transpiration, because of which the plants fail to dissipate heat, and thus heat stress can also ensue (Buchanan *et al.*, 2000). Studies on the combined effects of heat and water stress, using physiological and molecular tools, have indicated a direct relationship between heat and drought tolerance of strawberry cultivars (Çetinkaya, 2013). In this study, the heat-tolerant cultivars 'Redlands Hope' and 'Camarosa' also showed drought tolerance, while the heat-sensitive 'Festival' and 'CG3' were also drought sensitive.

14.3. Engineering Strawberry with 'Adaptive' Advantages

Plants respond to extreme levels of environmental conditions in a wide variety of ways depending on the species, cultivar, age and

physiological stage of the plant. While it is important to continue striving to reduce greenhouse gas emissions, developing resilient plants that can adapt to climate change is equally important. Abiotic stress conditions can make a difference between having a crop to harvest and crop failure. Tolerance to heat, drought, water-logging and frost, resistance to pests and diseases, and water-use and nitrogen-use efficiency are the most important traits for adaptation to climate change. One way could be through a steady search for new genes among wild strawberry populations, which could then be employed through classical breeding or recombinant DNA technology to develop plants with better built-in resistance to adverse conditions.

14.3.1. Classical breeding

It is not always possible to find the desired characteristics in commercial varieties of the hybrid *F. × ananassa*; therefore, searching for and characterization of wild genotypes is required. The species mostly used as sources of genetic variability are the octoploid species *F. chiloensis* and *F. virginiana*, as these species are of the same ploidy level and easily can be crossed with *F. × ananassa*. These species act as a source of biotic and abiotic stress-resistance genes because of their geographical distribution over a wide area and having been subjected to selection pressure in extreme environments. These genotypes therefore have a long history of involvement in strawberry improvement programmes. Albert Etter, in the early 20th century (1903–1920) in California, obtained more than 50 strawberry cultivars by crossing plants of *F. × ananassa* with wild accessions of *F. chiloensis*, while C.L. Powers and A.C. Hildreth, from the US Department of Agriculture, Beltsville, Maryland, used *F. virginiana* subsp. *glauca* in their programmes (1930s and 1940s). R.S. Bringham and V. Voth, from the University of California, used *F. virginiana* to produce day-neutral varieties, and used *F. chiloensis* to increase fruit size in short-day cultivars (Hancock and Luby, 1993). Thus, strawberry cultivars were developed

by plant breeders to fit particular environmental or marketing niches, and generally, no single cultivar is grown worldwide or even nationwide.

According to Sjulín and Dale (1987), *Fragaria* spp. that have shown cold tolerance are *F. viridis* (Europe, Asia), *F. daltoniana* J. Gay (Himalayas), *F. nipponica* Makino (Japan), *F. mandshurica* Staudt (Manchuria), *F. orientalis* Losinsk (West Asia), *F. moupinensis* (Fr.) Card. (South-west China) and *F. moschata* (North Europe). *F. virginiana* (North America) has been shown to possess disease resistance (red stele, *Verticillium* wilt, powdery mildew, leaf spot, scorch, leaf blight), nematode resistance (root-knot nematode, root-lesion nematode), stress tolerance (waterlogged soil, heat, drought, high soil pH, cold, frost) and photosynthetic efficiency at high temperatures. Similarly, *F. chiloensis* (North and South America) has been shown to possess disease resistance (red stele, *Verticillium* wilt, powdery mildew, leaf blight, viruses), nematode resistance (root-lesion nematode, pest resistance (two-spotted mite, strawberry weevil, black vine weevil) and stress tolerance (drought, high soil pH, salinity, cold). In relation to pest and disease resistance, *F. vesca* could be a natural genetic source of resistance against important diseases, such as powdery mildew, *Verticillium* wilt, and root and crown rot (Gooding *et al.*, 1981; Hancock and Luby, 1993; Korbin, 2011). Powdery mildew-resistant *F. moschata* and red stele-, powdery mildew- and leaf spot-resistant clones of *F. chiloensis* could act as donors for these traits (Hancock *et al.*, 1989).

The US National Clonal Germplasm Repository in Corvallis, Oregon, houses a collection of native germplasms from *F. virginiana* and *F. chiloensis*, which have been characterized for resistance against several foliar diseases, black root rot, root-knot nematode (*Meloidogyne hapla*) and root-lesion nematode (*Pratylenchus penetrans*). Studies have been able to identify various genotypes resistant to a number of important pathogens (Hancock *et al.*, 2003). Similarly, extensive studies carried out at the US Department of Agriculture helped to identify various sources of resistance to different pathogens. For example, they found resistance to

Xanthomona fragariae in a clone of *F. virginiana* from Minnesota and in a hybrid between *F. virginiana* and *F. × ananassa* (Maas *et al.*, 2000), and identified germplasm tolerant to red stele (*Phytophthora fragariae*), *Verticillium* wilt, leaf spot (*Mycosphaerella fragariae*), leaf scorch (*Diplocarpon earliarum*), leaf blight (*Phomopsis obscurans*), powdery mildew (*Sphaerotheca macularis* f. sp. *fragariae*), fruit rot or grey mould (*Botrytis cinerea*) and crown rot (Galletta *et al.*, 1997). For successful use of these wild germplasms to be implemented, much effort will be needed in terms of collection, maintenance and particularly morphological, physiological and biochemical characterization of the different accessions collected in the areas of origin. Detailed information needs to be generated regarding genotypic and phenotypic characterization of collections in germplasm banks and the study of hereditary mechanisms involved in each characteristic. This wild material has great potential to be used as source of genes for developing varieties with enhanced adaptive abilities.

14.3.2. Advanced genetics

Recombinant DNA technology can play a significant role in enabling strawberry farmers to develop plants that cope with the challenges of climate change. Genetic modification techniques are becoming increasingly feasible due to improved techniques and demystification of the various side effects of transgenic technology (Husaini, 2010; Husaini *et al.*, 2011b; Husaini and Tuteja, 2012).

Agrobacterium-mediated gene transfer is the most widely used method for developing transgenic strawberry plants (Husaini *et al.*, 2011a). This genetic transformation protocol has been standardized and perfected for higher transformation success (Husaini and Srivastava, 2006a,b; Husaini, 2010). Several traits that confer adaptive advantage to strawberry plants with regard to global climate change have been improved using this genetic transformation technique (Table 14.1). Transgenic strawberry plants

Table 14.1. Genes conferring an adaptive advantage to transgenic strawberry plants against biotic and abiotic stresses.

| Gene | Resistance against: | Cultivar | Reference |
|--|---|------------------------------------|----------------------------------|
| Fungal resistance | | | |
| Chitinase from rice (<i>rcc2</i>) | <i>Sphaeroteca humuli</i> | 'Toyonoka' | Asao <i>et al.</i> (1997) |
| Chitinase from <i>Lycopersicon chilense</i> (<i>pcht28</i>) | <i>Verticillium dahliae</i> | 'Joliette' | Chalavi <i>et al.</i> (2003) |
| Thaumatin II from <i>Thaumatococcus danielli</i> (<i>thauII</i>) | <i>Botrytis cinerea</i> | 'Firework' | Schestibratov and Dolgov (2005) |
| Chitinase and glucanase from <i>Trichoderma harzianum</i> | <i>Colletotrichum acutatum</i> | 'Camarosa' | Mercado <i>et al.</i> (2005) |
| Chitinase from <i>Phaseolus vulgaris</i> (<i>ch5B</i>), Glucanase (<i>gln2</i>) and thaumatin-like protein (<i>ap24</i>) from <i>Nicotiana tabacum</i> | <i>Botrytis cinerea</i> and <i>Colletotrichum acutatum</i> | 'Pajaro' | Porcel <i>et al.</i> (2006) |
| <i>Bgn13.1</i> from <i>Trichoderma harzianum</i> | <i>Colletotrichum acutatum</i> and <i>Rosellinia necatrix</i> | 'Camarosa' | Mercado <i>et al.</i> (2015) |
| <i>AtNPR1</i> from <i>Arabidopsis thaliana</i> | <i>Anthraco</i> se, Powdery mildew | <i>Fragaria vesca</i> ^a | Silva <i>et al.</i> (2015) |
| Insect resistance | | | |
| Cowpea protease inhibitor (<i>CpTi</i>) | <i>Otiorynchus</i> spp. | 'Rapella' | James <i>et al.</i> (1992, 1993) |
| | | 'Symphony' | Graham <i>et al.</i> (1995) |
| Virus resistance | | | |
| Coat protein | Strawberry mild yellow edge virus | | Finstad and Martin (1995) |
| Cold tolerance | | | |
| Cold-induced transcription factor (<i>CBF1</i>) from <i>Arabidopsis</i> | | 'Honeoye' | Owens <i>et al.</i> (2002, 2003) |
| Acidic dehydrin from wheat (<i>wcor410a</i>) | | 'Chambly' | Houde <i>et al.</i> (2004) |
| Antifreeze protein from Antarctic fish (<i>AFP</i>) | | 'Tioga' | Khammuang <i>et al.</i> (2005) |
| Salt tolerance | | | |
| Late embryogenesis abundance (<i>LEA3</i>) from barley | | 'Toyonaka' | Wang <i>et al.</i> (2004) |
| <i>Osmotin</i> from <i>Nicotiana tabacum</i> | | 'Chandler' | Husaini and Abdin (2008) |
| Drought tolerance | | | |
| <i>Osmotin</i> from <i>Nicotiana tabacum</i> | | 'Chandler' | Husaini <i>et al.</i> (2012) |
| <i>P5CS</i> from <i>Nicotiana tabacum</i> | | 'Camaros', 'Kurdistan' | Bahramnejad <i>et al.</i> (2015) |

^a*Fragaria vesca* is diploid and is not a cultivar of *F. × ananassa*.

overexpressing *pcht28* chitinase from *Lycopersicon chilense* show enhanced resistance to *Verticillium* wilt (*Verticillium dahliae*) (Chalavi *et al.*, 2003), while plants containing a rice chitinase gene (*RCC2*) exhibit improved resistance to powdery mildew (*Sphaerotheca humuli*) (Asao *et al.*, 1997). There are some reports that present the possibility of using pathogenesis-related (*PR*) genes to decrease

the severity of fungal diseases (*Rhizoctonia solani*, *Phytophthora fragariae*, *B. cinerae*) in strawberry (Schestibratov and Dolgov, 2005; Vellicce *et al.*, 2006). In a recent study, Mercado *et al.* (2015) expressed the gene *bgn13.1* from *Trichoderma harzianum* CECT 2413 in strawberry plants and reported that the constitutive expression of *bgn13.1* improved strawberry tolerance to crown rot diseases

caused by *Colletotrichum acutatum* or *Rosellinia necatrix*. In an interesting recent study, Silva *et al.* (2015) showed that ectopic expression of *AtNPR1* from *Arabidopsis thaliana* in strawberry increased resistance to anthracnose, powdery mildew and angular leaf spot, which are caused by different fungal or bacterial pathogens. Consistently, most of the transgenic lines constitutively expressed the defence gene *FvPR5*, suggesting that the systemic acquired resistance activation mechanisms in strawberry and *Arabidopsis* are different. Nevertheless, these findings indicate that increasing the transcript levels of *AtNPR1* or its strawberry orthologues may be a promising approach for development of strawberry cultivars with enhanced broad-spectrum disease resistance.

Genes conferring tolerance to viruses, such as strawberry mild yellow edge virus coat protein (Finstad and Martin, 1995) and cowpea trypsin inhibitor (*CpTi*) (Graham *et al.*, 1995) have also been transferred successfully into strawberry. Coincidentally, the overexpression of *CpTi* also resulted in significantly higher root mass than in control plants.

Transgenic strawberry with enhanced salinity tolerance has been developed using the late embryogenesis abundance (*LEA3*) gene (Wang *et al.*, 2004) and osmotin gene (Husaini and Abdin, 2008). Houde *et al.* (2004) transferred the acidic dehydrin gene of wheat, *Wcor410a*, into strawberry, and this modification prevented membrane injury and greatly improved frost resistance in the leaves. The transfer of cold-induced transcription factor (*CBF1*) and antifreeze protein genes into strawberries has also been reported (Owens *et al.*, 2002; Khammuang *et al.*, 2005). Transfer of the *Nicotiana* osmotin gene into strawberry has been shown to confer drought tolerance to the transgenic plants of strawberry cultivar 'Chandler' (Husaini *et al.*, 2012). Recently, two economically important cultivars of strawberry ('Camarosa' and 'Kurdistan') were transformed with the *P5CS* gene, which encodes $\Delta 1$ -pyrroline-5-carboxylate synthetase, the key enzyme in proline biosynthesis (Bahramnejad *et al.*, 2015). Overproduction of *P5CS* increased proline content, chlorophyll content, shoot length, shoot fresh and

dry weight in the transgenic plants under drought-stress conditions.

Under climate change conditions, crop plants will often experience more than one biotic and abiotic stress. An array of genes, available for use in both cisgenic and transgenic approaches, can be used for the development of varieties with better resilience to the vagaries of climate. Transgenes encoding reactive oxygen species scavenger proteins, transcription factors and protein kinases will be the most suitable candidate genes for conferring adaptive advantages to strawberry against multiple stresses. Moreover, a good strategy would be to use major-effect multirole genes to develop climate resilience in strawberry. In our opinion, one such major-effect multirole gene is osmotin (from *Nicotiana tabacum*). A brief description of the possible role of this gene in developing plants with better resilience through a single gene transfer is described below.

Osmotin: a multirole PR-5 protein

Osmotin can be used effectively in designing plants resilient to multiple stresses (Husaini and Rafiqi, 2012). Osmotin is a stress-responsive multifunctional tobacco PR-5c protein isolated from tobacco (*N. tabacum* var. Wisconsin 38; Singh *et al.*, 1985). The tertiary structure of osmotin is similar to thaumatin and other PR proteins, and is composed of three domains (Min *et al.*, 2004). Domain I consists of an 11-strand, flattened β -sandwich (residues 1–53, 82–125 and 175–205), which forms the compact core of the molecule. Domain II consists of several loops extending from domain I and is stabilized by four disulphide bonds (residues 126–174). Domain III consists of a small loop (residues 54–81) with two disulphide bonds. Osmotin has a pronounced cleft formed by domains I and II.

Osmotin acts as compatible osmolyte that enhances the osmotic potential of the cells and upregulates the levels of proline (Barthakur *et al.*, 2001; Sarad *et al.*, 2004; Sokhansanj *et al.*, 2006; Husaini and Abdin, 2008), another compatible osmolyte and scavenger of reactive oxygen species. Identification of an osmotin-like protein from the intercellular space of the halophyte

Mesaembryanthemum crystallinum and the association of osmotin with the tonoplast of tobacco (Singh *et al.*, 1987; Yen *et al.*, 1994) indicate that osmotin plays a role in the intracellular compartmentation of Na^+ ions to both the intercellular space and the vacuole, thereby minimizing the build-up of Na^+ ions in the cytoplasm (Yen *et al.*, 1994).

In addition to providing salt tolerance (Singh *et al.*, 1989; Bol *et al.*, 1990; Zhu *et al.*, 1993), drought tolerance (Parkhi *et al.*, 2009; Husaini *et al.*, 2012) and cryoprotection (D'Angeli and Altamura, 2007), osmotin also provides protection from fungal pathogens (Raghothama *et al.*, 1993; Zuker *et al.*, 2001). The protein has shown antifungal

activity *in vitro* against a broad range of fungal pathogens (Yun *et al.*, 1998). Specifically, osmotin and osmotin-like proteins have demonstrated antifungal activity against *Phytophthora infestans* (Woloshuk *et al.*, 1991; Zhu *et al.*, 1993; Liu *et al.*, 1994), *Phomopsis viticola* and *B. cinerea* (Monteiro *et al.*, 2003), *Fusarium solani*, *Neurospora* sp. and *Colletotrichum gloeosporioides* (de Freitas *et al.*, 2011a). The fungal growth inhibition by osmotin and osmotin-like proteins is correlated with plasma membrane permeabilization and dissipation of the plasma membrane potential of sensitive fungi (Abad *et al.*, 1996; de Freitas *et al.*, 2011b) (Fig 14.2).

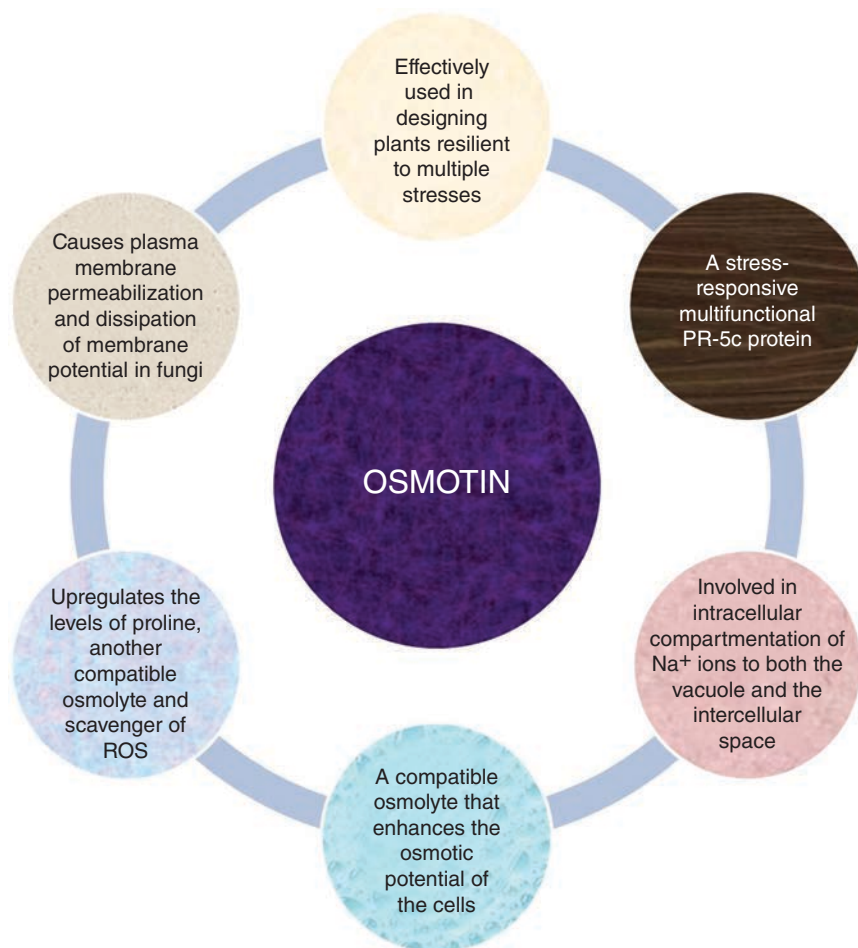


Fig. 14.2. Roles of osmotin.

Clustered regulatory interspaced short palindromic repeats (CRISPRs) and CRISPR-associated (Cas) systems are other emerging techniques that can be employed to introduce useful genome modifications by genome engineering of plants (Sander and Young, 2014). However, no published report about the use of this technology in strawberry is available so far.

14.4. Microorganisms for Enhancing Resilience

The European Commission's working document on *Adapting to Climate Change: the Challenge for European Agriculture and Rural Areas*, published in April 2009, states that high water-stress areas are expected to increase from 19 to 35% by 2070, implying 'significant changes in the quality and availability of water resources' (http://ec.europa.eu/health/ph_threats/climate/docs/com_2009_147_en.pdf). The predicted severe drought conditions will also affect the soil nutrient status. Drought will lead to diminished plant uptake of nutrients such as phosphorus and potassium, causing an additional stress on plants, as both phosphorus and potassium are necessary for high water-use efficiency and stomatal control (Sardans and Peñuelas, 2007). This will influence crop establishment, the crop stand maturation period and total production. Symbiotic soil microorganisms can play a crucial role in buffering crop production against these adverse effects (Husaini, 2014).

Mycorrhizal technology has been used to improve growth of a number of micropropagated horticultural crops, as well as to enable host plants to tolerate or withstand the impairing effects of abiotic and biotic stresses (Borkowska, 2002; Yin *et al.*, 2010). Mycorrhization strongly affects growth and tolerance of plants to water deficiency. Mycorrhizal fungi influence the development of a superior root system, enhance the water-conducting capacity, increase the uptake of macro-, micro- and immobile nutrients, and result in higher photosynthetic rates due to better carbon dioxide assimilation

(El-Tohamy *et al.*, 1999; Estrada-Luna *et al.*, 2000; Augé, 2001).

14.4.1. Arbuscular mycorrhizal fungi

About 90% of vascular plants establish a symbiotic relationship with arbuscular mycorrhizal fungi (AMF) (Gai *et al.*, 2006). The association between AMF and a plant makes the host plant more tolerant to drought in terms of plant growth (Ruiz-Lozano, 2003; Wu and Xia, 2006; Bolandnazar *et al.*, 2007). Generally, AMF-colonized plants have higher activities of several antioxidant enzymes compared with non-colonized plants (Wu *et al.*, 2006ab), but this depends on the enzyme activity, plant organ and AMF genotype involved (Lambais *et al.*, 2003; Wu *et al.*, 2006ab). One of the main benefits of AMF symbiosis for strawberry plants is increased phosphorus uptake under both low-phosphorus fertigation regimes (Boyer *et al.*, 2015) and a high-phosphorus soil environment (Stewart *et al.*, 2005). Opinion on the beneficial effects of AMF inoculation on strawberry is not, however, unanimous. Some studies have reported the beneficial effects of mycorrhiza on strawberry plant growth and yield (Hršelová *et al.*, 1989; Niemi and Vestberg, 1992; Borkowska, 2002; Vestberg *et al.*, 2004; Stewart *et al.*, 2005; Castellanos-Morales *et al.*, 2010; Fan *et al.*, 2011). Yin *et al.* (2010) showed that inoculation of AMF in drought-stressed strawberry plants increased the enzymes associated with the plant's protective system against water stress. Borkowska (2002) indicated that application of AMF strongly affected growth and tolerance to drought stress of the strawberry cultivar 'Senga Sengana' under greenhouse conditions. However, other studies have shown either limited (Garland *et al.*, 2011) or no (Vestberg *et al.*, 2004) beneficial effects. Borowicz (2010) examined the effect of AMF inoculation on water stress in wild strawberry (*F. virginiana*) and reported no strong effects of AMF on strawberry tolerance to drought.

In a recent study, it was found that the water-use efficiency of AMF-colonized strawberry plants was greater under a regulated deficit irrigation (water-stressed) regime than

under a fully watered regime (Boyer *et al.*, 2015). The most notable consequence of inoculation with AMF (*Funneliformis mosseae* BEG25, *Funneliformis geosporus* BEG11 or a 50:50 mixed inoculation) was a significant increase in the survival time of the plants when water was not provided: mycorrhizal plants survived on average 4.4 days longer than control plants. Inoculation with AMF increased all growth characteristics of the strawberry plants measured under both fully watered and water-stressed conditions, regardless of single- or mixed-species inoculation. The addition of AMF inocula (in any combination) to plants subjected to reduced irrigation of up to 40% restored plant growth back to the same or higher values as the non-mycorrhizal, fully watered plants.

In an interesting study, Matsubara *et al.* (2004) investigated the tolerance to *Fusarium* wilt (*Fusarium oxysporum* f. sp. *fragariae*) in response to inoculation with five AMF species (*Glomus margarita*, *Glomus fasciculatum*, *Glomus mosseae*, *Glomus aggregatum*, *Glomus* sp. R10) in strawberry. At 30 days after pathogen inoculation, *Fusarium* wilt incidence ranged from 22% in *G. mosseae* plots to 100% in non-mycorrhizal plots. The incidence and severity of infected roots and vessels were lower in AMF-inoculated than in non-inoculated plots. Non-inoculated and AMF-inoculated plants had higher shoot and root weights compared with non-mycorrhizal plants. The authors claimed that inoculation with AMF improved *Fusarium* wilt tolerance in strawberry.

14.4.2. Vesicular–arbuscular mycorrhiza

Many studies have shown that the drought resistance of crops can be improved by vesicular–arbuscular mycorrhiza (VAM) (Sylvia and Williams, 1992; Al-Karaki, 1998; Li *et al.*, 1999; Liang *et al.*, 2003; Lu *et al.*, 2003; Zhang and He, 2007). Recently, VAM were reported to improve plant drought resistance abilities in strawberry. VAM fungi inoculation slowed down the reduction of chlorophyll and increased the drought resistance of plants by promoting the defence

response of the protective enzyme system in host plants (Yin *et al.*, 2010). The formation of VAM enhanced the activity of the anti-oxidant enzymes superoxide dismutase, PRX and CAT, and H⁺-ATPase in host plants, and reduced the content of malondialdehyde and electrical conductivity of the plasma membrane significantly (Wu and Xia, 2003; Wu *et al.*, 2007), but the exact mechanism of enhancing drought resistance in plants is still not clear.

14.4.3. Plant growth-promoting rhizobacteria

Plant growth-promoting rhizobacteria (PGPR) are free-living bacteria present in the rhizosphere or on the root surface, or inhabiting spaces between cortical cells (Gray and Smith, 2005). Several free-living soil bacteria induce drought tolerance in plants (Arkhipova *et al.*, 2007; Sziderics *et al.*, 2007). Timmusk and Wagner (1999) report that inoculation of *Arabidopsis* plants with the PGPR *Paenibacillus polymyxa*, prior to drought stress, caused an elevation in mRNA copies of abscisic acid-related genes (*ERD15* and *RAB18*), and that these plants were more tolerant to drought than non-inoculated ones. The authors hypothesized that inoculation with the bacteria caused a mild biotic stress, preparing the plants to cope with subsequent drought stress. Sziderics *et al.* (2007) reported that, after a mild osmotic stress, pepper plants inoculated with several PGPRs showed lower expression of genes related to abiotic stresses than non-inoculated plants, probably because the inoculated plants suffered less stress and therefore had a lower expression of stress-related genes.

Recently, there was a report discussing the effects of five PGPRs (*Bacillus subtilis* EY2, *Bacillus atrophaeus* EY6, *Bacillus sphaericus* GC subgroup B EY30, *Staphylococcus kloosii* EY37, and *Kocuria erythromyxa* EY43) on the growth, chlorophyll content, nutrient element content and yield of strawberry plants under natural field salinity stress conditions (Karlidag *et al.*, 2009). PGPR inoculation significantly increased

the growth, chlorophyll content, nutrient element content and yield of the strawberry plants, while lowering the electrolyte leakage of the plants under saline conditions. The highest efficiency in terms of alleviating salinity stress on the yield and nutrient uptake of strawberry plants was obtained from *K. erythromyxa* EY43 (228 g per plant) and *Staphylococcus kloosii* EY37 (225 g per plant) treatment, and the yield increasing ratio of plants was 48% for *K. erythromyxa* EY43 and 46% for *Staphylococcus kloosii* EY37 compared with the control treatment (154 g per plant).

14.4.4. *Piriformospora indica*

Piriformospora indica (Basidiomycota) is an axenically cultivable phytopromotional endosymbiont, which mimics the capabilities of AMF and shows pronounced growth-promotional effects (Varma *et al.*, 1999, 2001). *Piriformospora indica* promotes the synthesis and expression of defence-related proteins and enzymes (isoflavonoid phytoalexins, isoflavonoid glyceollin coumestrol, coumestrol isosojagol) that provide protection and result in higher plant survival (Sahay and Varma, 1999, 2000). In addition, *Piriformospora indica* produces significant amounts of acid phosphatases for the mobilization of a broad range of insoluble, condensed or complex forms of phosphate, enabling the host plant the accessibility to adequate phosphorus from immobilized reserves in the soil (Sahay and Varma, 2000).

Piriformospora indica is a root-colonizing endophytic fungus with a wide host range and helps plants to grow under extreme physical and nutrient stress conditions. This symbiotrophic fungal endophyte was discovered in the Great Indian Desert of Western Rajasthan in India (Varma *et al.*, 1999). The fungus colonizes the roots of the desert plants growing under water-scarcity conditions. It has been established that the fungus promotes the acquisition of drought tolerance in plants (Waller *et al.*, 2005; Sherameti *et al.*, 2008). Strawberry plants inoculated with *Piriformospora indica* or

Sebacina vermifera show a higher percentage of survival under drought conditions with increased chlorophyll contents, total soluble proteins and relative water content, and higher biomass. *Piriformospora indica*-inoculated plants showed a markedly higher tolerance level than *Sebacina vermifera*-inoculated plants (Husaini *et al.*, 2012). The use of *in vitro* and *ex vitro* co-culture systems verified that *Piriformospora indica* possesses pronounced plant growth-stimulating capacity and induces plant secondary metabolite accumulation (Rai *et al.*, 2001; Baldi *et al.*, 2008).

Piriformospora indica has a wide geographical distribution and is reported from Asia, Australia and South America. The fungus seems to have promising potential under changing climate scenarios because it functions as a biofertilizer in nutrient-deficient soils, as a bioprotector against biotic and abiotic stresses, as a bioregulator for plant growth development and enhanced seed production, and as a bioagent for the hardening of plants (Oelmüller *et al.*, 2009).

14.5. Extreme Events, Policy Response and Social Action

Although the climate is warming, the incidence of inter-annual climate variability (extreme events) accompanying the mean climate changes is actually increasing. It has been widely accepted by the Intergovernmental Panel on Climate Change that increases in the frequency of climate extremes may lower crop yields beyond the impacts of 'mean' climate change (Easterling and Apps, 2005; Easterling *et al.*, 2007). According to the World Development Report on *Development and Climate Change* commissioned by the World Bank in 2009, the public in the 15 countries polled (both developed and developing) saw climate change as a serious problem: either as very serious or somewhat serious (WorldPublicOpinion.org, 2010).

From a social and economic point of view, climate impact studies should take into consideration the geographical dimensions of the area of study, as different climatic

patterns affect regions differently, as well as local policies and legislations. For example, the introduction of polytunnels (in the mid-1990s) was one of the most important factors affecting the expansion of strawberry cultivation in the UK from being a minor crop to becoming an industry with a specialist supply chain. The use of polytunnels decreased the impact of weather on the crop, thus bridging the difference in yields obtained between Scottish and English farms. As a result, growers in areas previously disadvantaged by the weather could now grow strawberries competitively. This brought a shift in the geography of strawberry cultivation in the UK. However, damage to polytunnels by extreme weather events such as floods and wind could have a worse impact on strawberry growers in the absence of crop insurance; thus, any damage to the structures would result in a year's worth of investment being lost in one event, the cost of which would be borne by the grower. Crop insurance cover may be a viable solution for strawberry growers, which they may opt for voluntarily. However, policy support or legislation can often act as a driver for such changes. For instance, according to Calleja (2011), in Kent, UK, the county council puts water bans on agricultural enterprises during periods of drought, due to them being close to a large metropolitan area where a constant water supply is needed for human consumption. In response to this, growers in this area have been building water-storage facilities to eliminate their dependency on the council's supply of water. This is an interesting case, whereby the growers have not built water-storage facilities as a conscious response to climate change, but are responding to pressures caused by man-made policies in response to water shortages during periods of drought.

Keeping this in mind, there can be positive ways of using the increased soil temperature in strawberry cultivation. With increasing temperature, soil solarization may become a more feasible option for pest control. The drawback of solarization is that it is restricted in some areas by the length and intensity of sunshine, as well as by the

temperature (Berg, 2007). Solarization is recommended for 30–45 days during the months when the soil temperatures exceed 50°C, although when combined with biofumigation, the soil temperature could be as low as 40°C (Medina-Mínguez, 2002). Solarized soils are often more suppressive to certain soilborne pathogens than non-solarized soils, while *Trichoderma* spp., which act as biocontrol agents against several diseases, are among the microorganisms that can survive the solarization process (Pinkerton *et al.*, 2002).

14.6. Future Perspective

The projections of global climate changes on the earth predict a rise in the concentration of greenhouse gases, an increase in temperature, increased frequency of extreme weather events and aridization of the environment. The implications of these changes on horticulture in general, and on the ability of plants such as strawberry in particular, to adapt to such changes need rigorous analysis. With a view to ensuring the sustainability of strawberry cultivation under these changing climatic conditions, the possible roles of different technological interventions need to be evaluated. The diploid strawberry *F. vesca* is an attractive model plant for genomic analysis because of its small genome. The *F. vesca* EST collection and recent data from proteomic studies in abiotic stresses could also be very useful for further investigations. Unlike in the past, multidisciplinary studies focusing on the effect of multiple stress factors are necessary to understand the impact of stressful conditions on plant growth and development in the open field. Scientists with expertise in climatology, biochemistry, microbiology, pathology, entomology, agricultural physics, plant breeding, biotechnology and systems biology need to collaborate and develop multipronged strategies to address these challenges. Such research studies should not only be based on the current climate conditions but also planned according to the potential future challenges.

Using genetic engineering approaches, transgenic strawberry plants with tolerance

against certain stress factors have already been developed. However, these studies are mostly at the laboratory level, and there is an urgent need to test and evaluate these plants under field conditions. A detailed understanding of the complex mechanisms involved the genome, epigenome, transcriptome and metabolome levels will be useful in designing better strategies for improving stress tolerance in plants. Screening studies, investigating the stress tolerance of genotypes for each biotic/abiotic stress factor, should also be undertaken in parallel for successful breeding programmes. Establishment of a symbiotic relationship between microorganisms and plants also shows

promising potential in enhancing the tolerance of plants to drought and temperature stresses. The beneficial effect of mycorrhization on plant drought tolerance, resulting from the development of a superior root system, enhanced water-conducting capacity and increased uptake of macro-, micro- and immobile nutrients, will be very helpful in understanding the impact on carbon dioxide assimilation and higher photosynthetic rates. Through these technologies, we can aim to develop strawberry plants that have better water- and nutrient-use efficiencies, and that are resilient to high or low temperatures, and to water scarcity or flooding.

References

- Abad, L.R., D'Urzo, M.P., Liu, D., Narasimhan, M.L., Reuveni, M., Zhu, J.K., Niu, X., Singh, N.K., Hasegawa, P.M. and Bressan, R.A. (1996) Antifungal activity of tobacco osmotin has specificity and involves plasma membrane permeabilization. *Plant Science* 118, 11–23.
- Aggarwal, P.K., Banerjee, B., Daryaei, M.G., Bhatia, A., Bala, A., Rani, S., Chander, S., Pathak, H. and Kalra, N. (2006) InfoCrop: a dynamic simulation model for the assessment of crop yields, losses due to pests, and environmental impact of agro-ecosystems in tropical environments. II. Performance of the model. *Agricultural Systems* 89, 47–67.
- Ahmadi, H., Bringham, R.S. and Voth, V. (1990) Modes of inheritance of photoperiodism in *Fragaria*. *Journal of the American Society for Horticultural Science* 115, 146–152.
- Al-Karaki, G. (1998) Benefit, cost and water-use efficiency of arbuscular mycorrhizal durum wheat grown under drought stress. *Mycorrhiza* 8, 41–45.
- Arkhipova, T.N., Prinsen, E., Veselov, S.U., Martinenko, E.V., Melentiev, A.I. and Kudoyarova, G.R. (2007) Cytokinin producing bacteria enhance plant growth in drying soil. *Plant and Soil* 292, 305–315.
- Arora, R., Wisniewski, M.E. and Scorza, R. (1992) Cold acclimation in genetically related (sibling) deciduous and evergreen peach (*Prunus persica* [L.] Batsch): I. seasonal changes in cold hardiness and polypeptides of bark and xylem tissues. *Plant Physiology* 99, 1562–1568.
- Asao, H., Nishizawa, Y., Arai, S., Sato, T., Hirai, M., Yoshida, K., Shinmyo, A. and Hibi, T. (1997) Enhanced resistance against a fungal pathogen *Sphaerotheca humuli* in transgenic strawberry expressing a rice chitinase gene. *Plant Biotechnology* 14, 145–150.
- Augé, R.M. (2001) Water relations, drought and vesicular-arbuscular mycorrhizal symbiosis. *Mycorrhiza* 11, 3–42.
- Bahramnejad, B., Nasri, S., Mozafari, A. and Siosemardeh, A. (2015) *Agrobacterium tumefaciens*-mediated transformation of two economically important strawberry cultivars with *P5CS* gene. *Journal of Plant Physiology and Breeding* 5, 55–66.
- Baldi, A., Jain, A., Gupta, N., Srivastava, A. and Bisaria, V. (2008) Co-culture of arbuscular mycorrhiza-like fungi (*Piriformospora indica* and *Sebacina vermifera*) with plant cells of *Linum album* for enhanced production of podophyllotoxins: a first report. *Biotechnology Letters* 30, 1671–1677.
- Barney, D.L., Davis, B.B. and Fellman, J.K. (1992) *Strawberry Production: Overview*. College of Agriculture, University of Idaho, Moscow, Idaho.
- Barthakur, S., Babu, V. and Bansal, K.C. (2001) Over-expression of osmotin induces proline accumulation and confers tolerance to osmotic stress in transgenic tobacco. *Journal of Plant Biochemistry and Biotechnology* 10, 31–37.
- Berg, G. (2007) Biological control of fungal soilborne pathogens in strawberries. In: Chincholkar, S.B. and Mujerki, K.G. (eds) *Biological Control of Plant Diseases*. Haworth Press, Binghamton NY, pp. 1–17.

- Bergot, M., Cloppet, E., Pérarnaud, V., Déqué, M., Marçais, B. and Desprez-Loustau, M.L. (2004) Simulation of potential range expansion of oak disease caused by *Phytophthora cinnamomi* under climate change. *Global Change Biology* 10, 1–14.
- Blanke, M.M. and Cooke, D.T. (2006) Water channels in strawberry, and their role in the plants response to water stress. *Acta Horticulturae* 708, 65–68.
- Bol, J.F., Linthorst, H.J.M. and Cornelissen, B.J.C. (1990) Plant pathogenesis-related proteins induced by virus infection. *Annual Review of Phytopathology* 28, 113–138.
- Bolandnazar, S., Aliasgarzad, N., Neishabury, M.R. and Chaparzadeh, N. (2007) Mycorrhizal colonization improves onion (*Allium cepa* L.) yield and water use efficiency under water deficit condition. *Scientia Horticulturae* 114, 11–15.
- Booth, T.H., Jovanovic, T., Old, K.M. and Dudzinski, M.J. (2000) Climatic mapping to identify high-risk areas for *Cylindrocladium quinqueseptatum* leaf blight on eucalypts in mainland South East Asia and around the world. *Environmental Pollution* 108, 365–372.
- Borkowska, B. (2002) Growth and photosynthetic activity of micropropagated strawberry plants inoculated with endomycorrhizal fungi (AMF) and growing under drought stress. *Acta Physiologiae Plantarum* 24, 365–370.
- Borowicz, V.A. (2010) The impact of arbuscular mycorrhizal fungi on strawberry tolerance to root damage and drought stress. *Pedobiologia* 53, 265–270.
- Boyer, L.R., Brain, P., Xu, X.M. and Jeffries, P. (2015) Inoculation of drought-stressed strawberry with a mixed inoculum of two arbuscular mycorrhizal fungi: effects on population dynamics of fungal species in roots and consequential plant tolerance to water deficiency. *Mycorrhiza* 25, 215–227.
- Bray, E.A., Bailey-Serres, J. and Weretilnyk, E. (2000) Responses to abiotic stresses. In: Gruissem, W., Buchanan, B. and Jones, R. (eds) *Biochemistry and Molecular Biology of Plants*. American Society of Plant Physiologists, Rockville, Maryland, pp. 1158–1249.
- Bringhurst, R.S. and Voth, V. (1984) Breeding octoploid strawberries. *Iowa State Journal of Research* 58, 371–381.
- Buchanan, B.B., Gruissem, W. and Jones, R.L. (2000) *Biochemistry and Molecular Biology of Plants*, American Society of Plant Physiologists, Rockville, Maryland.
- Calleja, E.J. (2011) The potential impacts of climate change on diseases affecting strawberries and the UK strawberry industry. PhD thesis, University of Warwick, Coventry, UK.
- Cansev, A., Gulen, H. and Eris, A. (2009) Cold-hardiness of olive (*Olea europaea* L.) cultivars in cold-acclimated and non-acclimated stages: seasonal alteration of antioxidative enzymes and dehydrin-like proteins. *Journal of Agricultural Science* 147, 51–61.
- Castellanos-Morales, V., Villegas, J., Wendelin, S., Vierheilig, H., Eder, R. and Cárdenas-Navarro, R. (2010) Root colonisation by the arbuscular mycorrhizal fungus *Glomus intraradices* alters the quality of strawberry fruits (*Fragaria × ananassa* Duch.) at different nitrogen levels. *Journal of the Science of Food and Agriculture* 90, 1774–1782.
- Castro, P., Bushakra, J.M., Stewart, P., Weebadde, C.K., Wang, D., Hancock, J.F., Finn, C.E., Luby, J.J. and Lewers, K.S. (2015) Genetic mapping of day-neutrality in cultivated strawberry. *Molecular Breeding* 35, 1–16.
- Çetinkaya, C. (2013) Physiological effects of drought and recovery treatments in some strawberry cultivars. MSc thesis, Uludag University, Bursa, Turkey.
- Chakraborty, S., Murray, G. and White, N. (2002) *Impact of Climate Change on Important Plant Diseases in Australia*. Rural Industries Research and Development Corporation, Canberra, Australia.
- Chalavi, V., Tabaeizadeh, Z. and Thibodeau, P. (2003) Enhanced resistance to *Verticillium dahliae* in transgenic strawberry plants expressing a *Lycopersicon chilense* chitinase gene. *Journal of the American Society for Horticultural Science* 128, 747–753.
- Chandler, C.K. and Ferree, D.C. (1990) Response of ‘Raritan’ and ‘Surecrop’ strawberry plants to drought stress. *Fruit Varieties Journal* 44, 183–184.
- D’Angeli, S. and Altamura, M. (2007) Osmotin induces cold protection in olive trees by affecting programmed cell death and cytoskeleton organization. *Planta* 225, 1147–1163.
- de Freitas, C.D.T., Lopes, J.L.d.S., Beltramini, L.M., de Oliveira, R.S.B., Oliveira, J.T.A. and Ramos, M.V. (2011a) Osmotin from *Calotropis procera* latex: new insights into structure and antifungal properties. *Biochimica et Biophysica Acta – Biomembranes* 1808, 2501–2507.
- de Freitas, C.D.T., Sousa Nogueira, F.C., Vasconcelos, I.M., Abreu Oliveira, J.T., Domont, G.B. and Ramos, M.V. (2011b) Osmotin purified from the latex of *Calotropis procera*: Biochemical characterization, biological activity and role in plant defense. *Plant Physiology and Biochemistry* 49, 738–743.

- Easterling, W. and Apps, M. (2005) Assessing the consequences of climate change for food and forest resources: a view from the IPCC. In: Salinger, J., Sivakumar, M.V.K. and Motha, R.P. (eds) *Increasing Climate Variability and Change*. Springer, The Netherlands, pp. 165–189.
- Easterling, W.E., Aggarwal, P.K., Batima, P., Brander, K.M., Erda, L., Howden, S.M., Kirilenko, A., Morton, J., Soussana, J.F., Schmidhuber, J. and Tubiello, F.N. (2007) Food, fibre, and forest products. In: Parry, M.L., Canziani, O.F., Palutikof, J.P., van der Linden, P.J. and Hanson, C.E. (eds) *Climate Change 2007: Impacts, Adaptation and Vulnerability: Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, pp. 273–313.
- El-Tohamy, W., Schnitzler, W.H., El-Beahry, U. and El-Beltagy, M.S. (1999) Effect of VA mycorrhiza on improving drought and chilling tolerance of bean plants (*Phaseolus vulgaris* L.). *Angewandte Botanik* 73, 178–183.
- Ergin, S. (2012) Effects of high temperature stress on enzymatic and non-enzymatic antioxidants and protein metabolism in strawberry plants. PhD Thesis, Uludag University, Bursa, Turkey.
- Ergin, S., Kesici, M. and Gulen, H. (2012) Changes in H₂O₂ and peroxidase activities in strawberry plants under heat stress. *Harran University Journal of the Faculty of Agriculture* 16, 25–35.
- Eris, A., Gulen, H., Barut, E. and Cansev, A. (2007) Annual patterns of total soluble sugars and proteins related to cold-hardiness in olive (*Olea europaea* L. ‘Gemlik’). *Journal of Horticultural Science and Biotechnology* 82, 597–604.
- Estrada-Luna, A.A., Davies F.T. Jr and Egilla, J.N. (2000) Mycorrhizal fungi enhancement of growth and gas exchange of micropropagated guava plantlets (*Psidium guajava* L.) during *ex vitro* acclimatization and plant establishment. *Mycorrhiza* 10, 1–8.
- Evans, N., Baierl, A., Semenov, M.A., Gladders, P. and Fitt, B.D.L. (2008) Range and severity of a plant disease increased by global warming. *Journal of the Royal Society Interface* 5, 525–531.
- Fan, L., Dalpé, Y., Fang, C., Dubé, C. and Khanizadeh, S. (2011) Influence of arbuscular mycorrhizae on biomass and root morphology of selected strawberry cultivars under salt stress. *Botany* 89, 397–403.
- Fang, X., Phillips, D., Li, H., Sivasithamparam, K. and Barbeti, M.J. (2011) Comparisons of virulence of pathogens associated with crown and root diseases of strawberry in Western Australia with special reference to the effect of temperature. *Scientia Horticulturae* 131, 39–48.
- FAO (2008) *Climate Change and Food Security: a Framework Document*. Food and Agriculture Organisation, Rome, Italy.
- Finstad, K. and Martin, R.R. (1995) Transformation of strawberry for virus resistance. *Acta Horticulturae* 385, 86–90.
- Francesca, S., Simona, G., Francesco Nicola, T., Andrea, R., Vittorio, R., Federico, S., Cynthia, R. and Maria Lodovica, G. (2006) Downy mildew (*Plasmopara viticola*) epidemics on grapevine under climate change. *Global Change Biology* 12, 1299–1307.
- Gai, J.P., Christie, P., Feng, G. and Li, X.L. (2006) Twenty years of research on community composition and species distribution of arbuscular mycorrhizal fungi in China: a review. *Mycorrhiza* 16, 229–239.
- Galletta, G.J., Maas, J.L., Finn, C.E., Smith, B.J. and Gupton, C.L. (1997) The United States Department of Agriculture strawberry breeding program. *Fruit Varieties Journal* 51, 204–210.
- Garland, B.C., Schroeder-Moreno, M.S., Fernandez, G.E. and Creamer, N.G. (2011) Influence of summer cover crops and mycorrhizal fungi on strawberry production in the southeastern United States. *HortScience* 46, 985–991.
- Garrett, K.A., Dendy, S.P., Frank, E.E., Rouse, M.N. and Travers, S.E. (2006) Climate change effects on plant disease: genomes to ecosystems. *Annual Review of Phytopathology* 44, 489–509.
- Gaston, A., Perrotte, J., Lerceteau-Köhler, E., Rousseau-Gueutin, M., Petit, A., Hernould, M., Rothan, C. and Denoyes, B. (2013) *PFRU*, a single dominant locus regulates the balance between sexual and asexual plant reproduction in cultivated strawberry. *Journal of Experimental Botany* 64, 1837–1848.
- Glover, J., Johnson, H., Lizzio, J., Wesley, V., Hattersley, P. and Knight, C. (2008) *Australia's Crops and Pastures in a Changing Climate – Can Biotechnology Help?* Australian Government Bureau of Rural Sciences, Canberra, Australia.
- Gooding, H.J., McNicol, R.J. and MacIntyre, D. (1981) Methods of screening strawberries for resistance to *Sphaerotheca macularis* (Wall ex Frier) and *Phytophthora cactorum* (Leb. and Cohn). *Journal of Horticultural Science* 56, 239–245.
- Graham, J., McNicol, R.J. and Greig, K. (1995) Towards genetic based insect resistance in strawberry using the cowpea trypsin inhibitor gene. *Annals of Applied Biology* 127, 163–173.

- Grant, O.M., Johnson, A.W., Davies, M.J., James, C.M. and Simpson, D.W. (2010) Physiological and morphological diversity of cultivated strawberry (*Fragaria × ananassa*) in response to water deficit. *Environmental and Experimental Botany* 68, 264–272.
- Gray, E.J. and Smith, D.L. (2005) Intracellular and extracellular PGPR: commonalities and distinctions in the plant-bacterium signaling processes. *Soil Biology & Biochemistry* 37, 395–412.
- Gulen, H. and Eris, A. (2003) Some physiological changes in strawberry (*Fragaria × ananassa* ‘Camarosa’) plants under heat stress. *Journal of Horticultural Science and Biotechnology* 78, 894–898.
- Gulen, H. and Eris, A. (2004) Effect of heat stress on peroxidase activity and total protein content in strawberry plants. *Plant Science* 166, 739–744.
- Gulen, H., Çetinkaya, C., Kadioğlu, M., Kesici, M., Cansev, A. and Eris, A. (2008) Peroxidase activity and lipid peroxidation in strawberry (*Fragaria × ananassa*) plants under low temperature. *Journal of Biological and Environmental Science* 2, 95–100.
- Hancock, J.F. and Luby, J.J. (1993) Genetic resources at our doorstep: the wild strawberries. *Bioscience* 43, 141–147.
- Hancock, J.F., Flore, J.A. and Galletta, G.J. (1989) Variation in leaf photosynthetic rates and yield in strawberries. *Journal of Horticultural Science* 64, 449–454.
- Hancock, J.F., Callow, P.W., Dale, A., Luby, J.J., Finn, C.E., Hokanson, S.C. and Hummer, K.E. (2001a) From the Andes to the Rockies: native strawberry collection and utilization. *HortScience* 36, 221–225.
- Hancock, J.F., Finn, C.A., Hokanson, S.C., Luby, J.J., Goulart, B.L., Demchak, K., Callow, P.W., Serçe, S., Schilder, A.M.C. and Hummer, K.E. (2001b) A multistate comparison of native octoploid strawberries from North and South America. *Journal of the American Society for Horticultural Science* 126, 579–586.
- Hancock, J.F., Callow, P.W., Serçe, S. and Son, P.Q. (2003) Variation in the horticultural characteristics of native *Fragaria virginiana* and *F. chiloensis* from North and South America. *Journal of the American Society for Horticultural Science* 128, 201–208.
- Harvell, C.D., Mitchell, C.E., Ward, J.R., Altizer, S., Dobson, A.P., Ostfeld, R.S. and Samuel, M.D. (2002) Climate warming and disease risks for terrestrial and marine biota. *Science* 296, 2158–2162.
- Heide, O.M. and Sønsteby, A. (2007) Interactions of temperature and photoperiod in the control of flowering of latitudinal and altitudinal populations of wild strawberry (*Fragaria vesca*). *Physiologia Plantarum* 130, 280–289.
- Houde, M., Dallaire, S., N’Dong, D. and Sarhan, F. (2004) Overexpression of the acidic dehydrin WCOR410 improves freezing tolerance in transgenic strawberry leaves. *Plant Biotechnology Journal* 2, 381–387.
- Hršelová, H., Vejsadová, H., Příkryl, Z., Váňová, J., Vančura, V. and Vít, A. (1989) Effect of inoculation with vesicular-arbuscular mycorrhizal fungi on growth of strawberries. In: Vlastimil, V. and František, K. (eds) *Developments in Soil Science*. Elsevier, Amsterdam, The Netherlands, pp. 109–114.
- Husaini, A.M. (2010) Pre- and post-agroinfection strategies for efficient leaf disk transformation and regeneration of transgenic strawberry plants. *Plant Cell Reports* 29, 97–110.
- Husaini, A.M. (2014) Challenges of climate change. *GM Crops and Food* 5, 97–105.
- Husaini, A.M. and Abdin, M.Z. (2008) Development of transgenic strawberry (*Fragaria × ananassa* Duch.) plants tolerant to salt stress. *Plant Science* 174, 446–455.
- Husaini, A.M. and Rafiqi, A.M. (2012) Role of osmotin in strawberry improvement. *Plant Molecular Biology Reporter* 30, 1055–1064.
- Husaini, A.M. and Srivastava, D.K. (2006a) Plant regeneration and *Agrobacterium*-mediated gene transfer studies in strawberry tissues (*Fragaria × ananassa*). *Asian Journal of Microbiology Biotechnology and Environmental Sciences* 8, 671.
- Husaini, A.M. and Srivastava, D.K. (2006b) Genetic transformation in strawberry – a review. *Asian Journal of Microbiology Biotechnology and Environmental Sciences* 8, 75–81.
- Husaini, A.M. and Tuteja, N. (2012) Biotech crops: imperative for achieving the Millenium Development Goals and sustainability of agriculture in the climate change era. *GM Crops and Food* 4, 1–9.
- Husaini, A.M., Mercado, J.A., Schaart, J.G. and Teixeira da Silva, J.A. (2011a) Review of factors affecting organogenesis, somatic embryogenesis and *Agrobacterium tumefaciens*-mediated transformation of strawberry. In: Husaini, A.M. and Mercado, J.A. (eds) *Genomics, Transgenics, Molecular Breeding and Biotechnology of Strawberry*. Global Science Books, UK, pp. 1–11.
- Husaini, A.M., Rashid, Z., Mir, R.u.R. and Aquil, B. (2011b) Approaches for gene targeting and targeted gene expression in plants. *GM Crops* 2, 150–162.
- Husaini, A.M., Abdin, M.Z., Khan, S., Xu, Y.W., Aquil, S. and Anis, M. (2012) Modifying strawberry for better adaptability to adverse impact of climate change. *Current Science* 102, 1660–1673.

- James, D.J., Passey, A.J., Eastbrook, M.A., Solomon, M.G. and Barbara, D.J. (1992) Transgenes for pest and disease resistance: progress in the introduction of transgenes for pest and disease resistance into strawberries. *Phytoparasitica* 20, S83–S87.
- James, D.J., Uratsu, S., Cheng, J., Negri, P., Viss, P. and Dandekar, A.M. (1993) Acetosyringone and osmoprotectants like betaine or proline synergistically enhance *Agrobacterium*-mediated transformation of apple. *Plant Cell Reports* 12, 559–563.
- Karlidag, H., Yildirim, E. and Turan, M. (2009) Salicylic acid ameliorates the adverse effect of salt stress on strawberry. *Scientia Agricola* 66, 180–187.
- Kesici, M., Gulen, H., Ergin, S., Turhan, E., Ipek, A. and Koksai, N. (2013) Heat-stress tolerance of some strawberry (*Fragaria* × *ananassa*) cultivars. *Notulae Botanicae Horti Agrobotanici Cluj-Napoca* 41, 238–243.
- Khammuang, S., Dheeranupattana, S., Hanmuangjai, P. and Wongroung, S. (2005) *Agrobacterium*-mediated transformation of modified antifreeze protein gene in strawberry. *Songklanakarin Journal of Science and Technology* 27, 693–703.
- Klamkowski, K. and Treder, W. (2006) Morphological and physiological responses of strawberry plants to water stress. *Agriculturae Conspectus Scientificus* 71, 159–165.
- Klamkowski, K. and Treder, W. (2008) Response to drought stress of three strawberry cultivars grown under greenhouse conditions. *Journal of Fruit and Ornamental Plant Research* 16, 179–188.
- Koehler, G., Wilson, R.C., Goodpaster, J.V., Sønsteby, A., Lai, X., Witzmann, F.A., You, J.-S., Rohloff, J., Randall, S.K. and Alsheikh, M. (2012) Proteomic study of low-temperature responses in strawberry cultivars (*Fragaria* × *ananassa*) that differ in cold tolerance. *Plant Physiology* 159, 1787–1805.
- Korbin, M. (2011) Molecular approaches to disease resistance in *Fragaria* spp. *Journal of Plant Protection Research* 51, 60–65.
- Koskela, E.A., Mouhu, K., Albani, M.C., Kurokura, T., Rantanen, M., Sargent, D.J., Battey, N.H., Coupland, G., Elomaa, P. and Hytönen, T. (2012) Mutation in *TERMINAL FLOWER1* reverses the photoperiodic requirement for flowering in the wild strawberry *Fragaria vesca*. *Plant Physiology* 159, 1043–1054.
- Lambais, M.R., Ríos-Ruiz, W.F. and Andrade, R.M. (2003) Antioxidant responses in bean (*Phaseolus vulgaris*) roots colonized by arbuscular mycorrhizal fungi. *New Phytologist* 160, 421–428.
- Ledesma, N.A., Kawabata, S. and Sugiyama, N. (2004) Effect of high temperature on protein expression in strawberry plants. *Biologia Plantarum* 48, 73–79.
- Levitt, J. (1980) *Responses of Plants to Environmental Stresses*, 2nd edn. Academic Press, New York.
- Li, H., Li, T., Gordon, R.J., Asiedu, S.K. and Hu, K. (2010) Strawberry plant fruiting efficiency and its correlation with solar irradiance, temperature and reflectance water index variation. *Environmental and Experimental Botany* 68, 165–174.
- Li, M., Jiang, D., Meng, X., Liu, R. and Li, X. (1999) Effects of arbuscular mycorrhizal fungi on growth, yield and quality of *Phaseolus vulgaris* L. in field. *Eco-Agriculture Research* 7, 43–46.
- Liang, J., Zhang, Y., Jia, X.Z., Lv, Q. and Zhang, X.Y. (2003) Effects of ectomycorrhizae on growth and resistance of poplar. *Journal of Nanjing Forestry University* 27, 39–43.
- Liu, D., Raghothama, K.G., Hasegawa, P.M. and Bressan, R.A. (1994) Osmotin overexpression in potato delays development of disease symptoms. *Proceedings of the National Academy of Sciences USA* 91, 1888–1892.
- Lu, J.Y., Mao, Y.M., Shen, L.Y., Peng, S.Q. and Li, X.L. (2003) Effects of VA mycorrhizal fungi inoculated on drought tolerance of wild jujube (*Zizyphus spinosus* Hu) seedlings. *Acta Horticulturae Sinica* 30, 29–33.
- Maas, J.L. (1998) *Compendium of Strawberry Diseases*. American Phytopathological Society, St Paul, Minnesota.
- Maas, J.L., Hartung, J.S., Gouin-Behe, C. and Hokanson, S.C. (2000) Sources of resistance for two differentially pathogenic strains of *Xanthomonas fragariae* in *Fragaria* genotypes. *HortScience* 35, 128–131.
- Manakasem, Y. and Goodwin, P. (2001) Responses of dayneutral and Junebearing strawberries to temperature and daylength. *Journal of Horticultural Science and Biotechnology* 76, 629–635.
- Matsubara, Y., Hirano, I., Sassa, D. and Koshikawa, K. (2004) Increased tolerance to *Fusarium* wilt in mycorrhizal strawberry plants raised by capillary watering methods. *Environmental Control in Biology* 42, 185–191.
- Medina-Mínguez, J.J. (2002) Soil solarization and biofumigation in strawberries in Spain. In: *Proceedings of International Conference on Alternatives to Methyl Bromide*, 5–8 March, Seville, Spain, pp. 108–110.
- Mercado, J.A., Martín-Pizarro, C., Pascual, L., Quesada, M.A., Pliego-Alfaro, F., Santos, B.d.l., Romero, F., Galvez, J., Rey, M., Viña, G.d.l., Llobell, A., Yübero-Serrano, E.-M., Muñoz-Blanco, J. and Caballero, J.L. (2005) Evaluation of tolerance to *Colletotrichum acutatum* in strawberry plants transformed with *Trichoderma*-derived genes. *Acta Horticulturae* 738, 383–388.
- Mercado, J.A., Barceló, M., Pliego, C., Rey, M., Caballero, J., Muñoz-Blanco, J., Ruano-Rosa, D., López-Herrera, C., de los Santos, B., Romero-Muñoz, F. and Pliego-Alfaro, F. (2015). Expression of the β -1,3-glucanase gene

- bgn13.1* from *Trichoderma harzianum* in strawberry increases tolerance to crown rot diseases but interferes with plant growth. *Transgenic Research* 24, 979–989.
- Min, K., Ha, S.C., Hasegawa, P.M., Bressan, R.A., Yun, D.J. and Kim, K.K. (2004) Crystal structure of osmotin, a plant antifungal protein. *Proteins: Structure, Function, and Bioinformatics* 54, 170–173.
- Monteiro, S., Barakat, M., Piçarra-Pereira, M.A., Teixeira, A.R. and Ferreira, R.B. (2003) Osmotin and thaumatin from grape: a putative general defense mechanism against pathogenic fungi. *Phytopathology* 93, 1505–1512.
- Morishita, M., Honjo, M., Hamano, M., Yamazaki, H. and Yano, T. (2012) Genetic analysis of the everbearing habit in strawberry cultivars under 24-hour daylength condition. *Horticultural Research* 11, 301–307.
- Ndong, C., Ouellet, F., Houde, M. and Sarhan, F. (1997) Gene expression during cold acclimation in strawberry. *Plant and Cell Physiology* 38, 863–870.
- Niemi, M. and Vestberg, M. (1992) Inoculation of commercially grown strawberry with VA mycorrhizal fungi. *Plant and Soil* 144, 133–142.
- Oelmüller, R., Sherameti, I., Tripathi, S. and Varma, A. (2009) *Piriformospora indica*, a cultivable root endophyte with multiple biotechnological applications. *Symbiosis* 49, 1–17.
- Olaya, G. and Abawi, G.S. (1996) Effect of water potential on mycelial growth and on production and germination of sclerotia of *Macrophomina phaseolina*. *Plant Disease* 80, 1347–1350.
- Owens, C.L., Thomashow, M.F., Hancock, J.F. and Iezzoni, A.F. (2002) *CBF1* orthologs in sour cherry and strawberry and the heterologous expression of *CBF1* in strawberry. *Journal of the American Society for Horticultural Science* 127, 489–494.
- Owens, C.L., Iezzoni, A.F. and Hancock, J.F. (2003) Enhancement of freezing tolerance of strawberry by heterologous expression of *CBF1*. *Acta Horticulturae* 626, 93–100.
- Paquin, R., Bolduc, R., Zizka, J., Pelletier, G. and Lechausser, P. (1989) Frost tolerance, sugar and proline content of strawberry (*Fragaria ananassa* Duch) during winter. *Canadian Journal of Plant Science* 69, 945–954.
- Parkhi, V., Kumar, V., Sunilkumar, G., Campbell, L.A.M., Singh, N.K. and Rathore, K.S. (2009) Expression of apoplastically secreted tobacco osmotin in cotton confers drought tolerance. *Molecular Breeding* 23, 625–639.
- Pinkerton, J.N., Ivors, K.L., Reeser, P.W., Bristow, P.R. and Windom, G.E. (2002) The use of soil solarization for the management of soilborne plant pathogens in strawberry and red raspberry production. *Plant Disease* 86, 645–651.
- Porcel, R., Aroca, R., Azcón, R. and Ruiz-Lozano, J. (2006) PIP aquaporin gene expression in arbuscular mycorrhizal *Glycine max* and *Lactuca sativa* plants in relation to drought stress tolerance. *Plant Molecular Biology* 60, 389–404.
- Pratt, R.G. (2006) A direct observation technique for evaluating sclerotium germination by *Macrophomina phaseolina* and effects of biocontrol materials on survival of sclerotia in soil. *Mycopathologia* 162, 121–131.
- Raghothama, K.G., Liu, D., Nelson, D.E., Hasegawa, P.M. and Bressan, R.A. (1993) Analysis of an osmotically regulated pathogenesis-related osmotin gene promoter. *Plant Molecular Biology* 23, 1117–1128.
- Rai, M., Acharya, D., Singh, A. and Varma, A. (2001) Positive growth responses of the medicinal plants *Spilanthes calva* and *Withania somnifera* to inoculation by *Piriformospora indica* in a field trial. *Mycorrhiza* 11, 123–128.
- Rantanen, M., Kurokura, T., Jiang, P., Mouhu, K. and Hytönen, T. (2015) Strawberry homologue of TERMINAL FLOWER1 integrates photoperiod and temperature signals to inhibit flowering. *The Plant Journal* 82, 163–173.
- Rosenzweig, C., Iglesias, A., Yang, X.B., Epstein, P. and Chivian, E. (2001) Climate change and extreme weather events; implications for food production, plant diseases, and pests. *Global Change and Human Health* 2, 90–104.
- Ruiz-Lozano, J.M. (2003) Arbuscular mycorrhizal symbiosis and alleviation of osmotic stress. New perspectives for molecular studies. *Mycorrhiza* 13, 309–317.
- Sahay, N.S. and Varma, A. (1999) *Piriformospora indica*: a new biological hardening tool for micropropagated plants. *FEMS Microbiology Letters* 181, 297–302.
- Sahay, N.S. and Varma, A. (2000) Biological approach towards increasing the survival rates of micropropagated plants. *Current Science* 78, 126–129.
- Sánchez, S., Gambardella, M., Henríquez, J.L. and Díaz, I. (2013) First report of crown rot of strawberry caused by *Macrophomina phaseolina* in Chile. *Plant Disease* 97, 996–996.
- Sander, J.D. and Joung, J.K. (2014) CRISPR-Cas systems for editing, regulating and targeting genomes. *Nature Biotechnology* 32, 347–355.

- Sarad, N., Rathore, M., Singh, N.K. and Kumar, N. (2004) Genetically engineered tomatoes: new vista for sustainable agriculture in high altitude regions. In: *Proceedings of the 4th International Crop Science Congress*, 26 September–1 October, Brisbane, Australia, pp. 234–238.
- Sardans, J. and Peñuelas, J. (2007) Drought changes phosphorus and potassium accumulation patterns in an evergreen Mediterranean forest. *Functional Ecology* 21, 191–201.
- Sarnighausen, E., Karlson, D.T., Zeng, Y., Goldsbrough, P.B., Raghothama, K.G. and Ashworth, E.N. (2004) Characterization of a novel Y_nSK_n class of dehydrin-like cDNAs from cold acclimated red-osier dogwood (*Cornus sericea* L.) xylem. *Journal of Crop Improvement* 10, 17–35.
- Schestibratov, K.A. and Dolgov, S.V. (2005) Transgenic strawberry plants expressing a thaumatin II gene demonstrate enhanced resistance to *Botrytis cinerea*. *Scientia Horticulturae* 106, 177–189.
- Serçe, S. and Hancock, J.F. (2005a) The temperature and photoperiod regulation of flowering and running in the strawberries, *Fragaria chiloensis*, *F. virginiana*, and *F. × ananassa*. *Scientia Horticulturae* 103, 167–177.
- Serçe, S. and Hancock, J.F. (2005b) Inheritance of day-neutrality in octoploid species of *Fragaria*. *Journal of the American Society for Horticultural Science* 130, 580–584.
- Shaw, D.V. and Famula, T.R. (2005) Complex segregation analysis of day-neutrality in domestic strawberry (*Fragaria × ananassa* Duch.). *Euphytica* 145, 331–338.
- Sherameti, I., Tripathi, S., Varma, A. and Oelmüller, R. (2008) The root-colonizing endophyte *Piriformospora indica* confers drought tolerance in *Arabidopsis* by stimulating the expression of drought stress-related genes in leaves. *Molecular Plant–Microbe Interactions* 21, 799–807.
- Silva, K.J.P., Brunings, A., Peres, N.A., Mou, Z. and Foltá, K.M. (2015) The *Arabidopsis* *NPR1* gene confers broad-spectrum disease resistance in strawberry. *Transgenic Research* 24, 693–704.
- Singh, N.K., Handa, A.K., Hasegawa, P.M. and Bressan, R.A. (1985) Proteins associated with adaptation of cultured tobacco cells to NaCl. *Plant Physiology* 79, 126–137.
- Singh, N.K., Bracker, C.A., Hasegawa, P.M., Handa, A.K., Buckel, S., Hermanson, M.A., Pfankoch, E., Regnier, F.E. and Bressan, R.A. (1987) Characterization of osmotin: a thaumatin-like protein associated with osmotic adaptation in plant cells. *Plant Physiology* 85, 529–536.
- Singh, N.K., Nelson, D.E., Kuhn, D., Hasegawa, P.M. and Bressan, R.A. (1989) Molecular cloning of osmotin and regulation of its expression by ABA and adaptation to low water potential. *Plant Physiology* 90, 1096–1101.
- Sjulin, T.M. and Dale, A. (1987) Genetic diversity of North American strawberry cultivars. *Journal of the American Society for Horticultural Science* 112, 375–385.
- Sokhansanj, A., Sadat Noori, S. and Niknam, V. (2006) Comparison of bacterial and plant genes participating in proline biosynthesis with *Osmotin* gene, with respect to enhancing salinity tolerance of transgenic tobacco plants. *Russian Journal of Plant Physiology* 53, 110–115.
- Staudt, G. (1973) *Fragaria iturupensis*: a new species of strawberry from East Asia. *Willdenowia* 7, 101–104.
- Stewart, L.I., Hamel, C., Hogue, R. and Moutoglou, P. (2005) Response of strawberry to inoculation with arbuscular mycorrhizal fungi under very high soil phosphorus conditions. *Mycorrhiza* 15, 612–619.
- Stewart, P.J. and Foltá, K.M. (2010) A review of photoperiodic flowering research in strawberry (*Fragaria* spp.). *Critical Reviews in Plant Sciences* 29, 1–13.
- Sylvia, D.M. and Williams, S.E. (1992) Vesicular-arbuscular mycorrhizae and environmental stress. *ASA Special Publication* 54, 101–124.
- Sziderics, A.H., Rasche, F., Trognitz, F., Sessitsch, A. and Wilhelm, E. (2007) Bacterial endophytes contribute to abiotic stress adaptation in pepper plants (*Capsicum annuum* L.). *Canadian Journal of Microbiology* 53, 1195–1202.
- Thomashow, M.F. (1999) Plant cold acclimation: freezing tolerance genes and regulatory mechanisms. *Annual Review of Plant Physiology and Plant Molecular Biology* 50, 571–599.
- Timmusk, S. and Wagner, E.G.H. (1999) The plant-growth-promoting rhizobacterium *Paenibacillus polymyxa* induces changes in *Arabidopsis thaliana* gene expression: a possible connection between biotic and abiotic stress responses. *Molecular Plant–Microbe Interactions* 12, 951–959.
- Turhan, E. (2012) Seasonal alteration of sugar metabolism in strawberry (*Fragaria × ananassa*) plants during cold-acclimated and non-acclimated stages. *African Journal of Biotechnology* 11, 4558–4565.
- Turhan, E., Aydogan, C., Akoglu, A., Baykul, A. and Evrenosoğlu, Y. (2012a) Relationship of seasonal changes in antioxidative enzymes and cold-hardiness in strawberry plant. *Journal of Food, Agriculture and Environment* 10, 445–450.
- Turhan, E., Aydogan, C., Baykul, A., Akoglu, A., Evrenosoğlu, Y. and Ergin, S. (2012b) Apoplastic antioxidant enzymes in the leaves of two strawberry cultivars and their relationship to cold-hardiness. *Notulae Botanicae Horti Agrobotanici Cluj-Napoca* 40, 114–122.

- Varma, A., Verma, S., Sudha, N.S., Bütehorn, B. and Franken, P. (1999) *Piriformospora indica*, a cultivable plant-growth-promoting root endophyte. *Applied and Environmental Microbiology* 65, 2741–2744.
- Varma, A., Singh, A., Sudha, Sahay, N.S., Sharma, J., Roy, A., Kumari, M., Rana, D., Thakran, S., Deka, D., Bharti, K., Hurek, T., Bleichert, O., Rexer, K.H., Kost, G., Hahn, A., Maier, W., Walter, M., Strack, D. and Kranner, I. (2001) *Piriformospora indica*: an axenically culturable mycorrhiza-like endosymbiotic fungus. In: Hock, B. (ed.) *Fungal Associations*. Springer, Berlin/Heidelberg, pp. 125–150.
- Vellicce, G., Ricci, J.D., Hernández, L. and Castagnaro, A. (2006) Enhanced resistance to *Botrytis cinerea* mediated by the transgenic expression of the chitinase gene *ch5B* in strawberry. *Transgenic Research* 15, 57–68.
- Vestberg, M., Kukkonen, S., Saari, K., Parikka, P., Huttunen, J., Tainio, L., Devos, N., Weekers, F., Kevers, C., Thonart, P., Lemoine, M.C., Cordier, C., Alabouvette, C. and Gianinazzi, S. (2004) Microbial inoculation for improving the growth and health of micropropagated strawberry. *Applied Soil Ecology* 27, 243–258.
- Wahid, A., Gelani, S., Ashraf, M. and Foolad, M.R. (2007) Heat tolerance in plants: an overview. *Environmental and Experimental Botany* 61, 199–223.
- Waller, F., Achatz, B., Baltruschat, H., Fodor, J., Becker, K., Fischer, M., Heier, T., Hückelhoven, R., Neumann, C., von Wettstein, D., Franken, P. and Kogel, K.H. (2005) The endophytic fungus *Piriformospora indica* reprograms barley to salt-stress tolerance, disease resistance, and higher yield. *Proceedings of the National Academy of Sciences USA* 102, 13386–13391.
- Wang, J.L., Ge, H.B., Peng, S.Q., Zhang, H.M., Chen, P.L. and Xu, J.R. (2004) Transformation of strawberry (*Fragaria ananassa* Duch.) with late embryogenesis abundant protein gene. *Journal of Horticultural Science and Biotechnology* 79, 735–738.
- Weebadde, C.K., Wang, D., Finn, C.E., Lewers, K.S., Luby, J.J., Bushakra, J., Sjulín, T.M. and Hancock, J.F. (2008) Using a linkage mapping approach to identify QTL for day-neutrality in the octoploid strawberry. *Plant Breeding* 127, 94–101.
- Woloshuk, C.P., Meulenhoff, J.S., Sela-Buurlage, M., van den Elzen, P. and Cornelissen, B. (1991) Pathogen-induced proteins with inhibitory activity toward *Phytophthora infestans*. *Plant Cell* 3, 619–628.
- WorldPublicOpinion.org (2010) *Public Attitudes Toward Climate Change: Findings From a Multicountry Poll*. The World Bank, Washington, DC.
- Wu, Q.S. and Xia, R.X. (2003) Research and application on vesicular-arbuscular mycorrhiza of fruit trees. *Plant Physiology Communications* 39, 536–540.
- Wu, Q.-S. and Xia, R.-X. (2006) Arbuscular mycorrhizal fungi influence growth, osmotic adjustment and photosynthesis of citrus under well-watered and water stress conditions. *Journal of Plant Physiology* 163, 417–425.
- Wu, Q.S., Xia, R.X. and Zou, Y.N. (2006a) Reactive oxygen metabolism in mycorrhizal and non-mycorrhizal citrus (*Poncirus trifoliata*) seedlings subjected to water stress. *Journal of Plant Physiology* 163, 1101–1110.
- Wu, Q.S., Zou, Y.N. and Xia, R.X. (2006b) Effects of water stress and arbuscular mycorrhizal fungi on reactive oxygen metabolism and antioxidant production by citrus (*Citrus tangerine*) roots. *European Journal of Soil Biology* 42, 166–172.
- Wu, Q.S., Zou, Y.N. and Wang, G.Y. (2007) Effect of inoculation with arbuscular mycorrhizal fungal on citrus under water stress conditions. *Journal of Yangtze University (Natural Science Edition)* 4, 18–21.
- Yen, H.E., Edwards, G.E. and Grimes, H.D. (1994) Characterization of a salt-responsive 24-kilodalton glycoprotein in *Mesembryanthemum crystallinum*. *Plant Physiology* 105, 1179–1187.
- Yin, B., Wang, Y., Liu, P., Hu, J. and Zhen, W. (2010) Effects of vesicular-arbuscular mycorrhiza on the protective system in strawberry leaves under drought stress. *Frontiers of Agriculture in China* 4, 165–169.
- Yun, D.-J., Ibeas, J.I., Lee, H., Coca, M.A., Narasimhan, M.L., Uesono, Y., Hasegawa, P.M., Pardo, J.M. and Bressan, R.A. (1998) Osmotin, a plant antifungal protein, subverts signal transduction to enhance fungal cell susceptibility. *Molecular Cell* 1, 807–817.
- Zhang, B. and Archbold, D.D. (1993) Solute accumulation in leaves of a *Fragaria chiloensis* and a *F. virginiana* selection responds to water deficit stress. *Journal of the American Society for Horticultural Science* 118, 280–285.
- Zhang, H.S. and He, X.L. (2007) Effect of AM fungal on the protective system in leaves of *Artemisia ordosica* under drought stress. *Biotechnology Bulletin* 3, 129–133.
- Zhang, Y., Luo, Y., Hou, Y.-X., Jiang, H., Chen, Q. and Tang, H.-R. (2008) Chilling acclimation induced changes in the distribution of H₂O₂ and antioxidant system of strawberry leaves. *Agriculture Journal* 3, 286–291.
- Zhu, B., Chen, T.H.H. and Li, P.H. (1993) Expression of an ABA-responsive osmotin-like gene during the induction of freezing tolerance in *Solanum commersonii*. *Plant Molecular Biology* 21, 729–735.

- Ziska, L.H. and Runion, G.B. (2007) Future weed, pest and disease problems for plants. In: Newton, P.C.D., Carran, R.A., Edwards, G.R. and Niklaus, P.A. (eds) *Agroecosystems in a Changing Climate*. CRC Press, Boca Raton, Florida, pp. 261–287.
- Zorrilla-Fontanesi, Y., Cabeza, A., Domínguez, P., Medina, J., Valpuesta, V., Denoyes-Rothan, B., Sánchez-Sevilla, J. and Amaya, I. (2011) Quantitative trait loci and underlying candidate genes controlling agronomical and fruit quality traits in octoploid strawberry (*Fragaria × ananassa*). *Theoretical and Applied Genetics* 123, 755–778.
- Zuker, A., Shklarman, E., Scovel, G., Ben-Meir, H., Ovadis, M., Neta-Sharir, I., Ben-Yephet, Y., Weiss, D., Watad, A. and Vainstein, A. (2001) Genetic engineering of agronomic and ornamental traits in carnation. *Acta Horticulturae* 560, 91–94.
- Zveibil, A., Mor, N., Gnyem, N. and Freeman, S. (2012) Survival, host–pathogen interaction, and management of *Macrophomina phaseolina* on strawberry in Israel. *Plant Disease* 96, 265–272.