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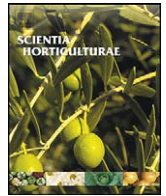
Review

Grafting as a tool to improve tolerance of vegetables to abiotic stresses: Thermal stress, water stress and organic pollutants

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ABSTRACT

Due to limited availability of arable land and the high market demand for vegetables around the world, cucurbit (cucumber, melon, and watermelon) and solanaceous (eggplant, pepper and tomato) crops are frequently cultivated under unfavourable soil and environmental conditions. These include thermal stress, drought and flooding, and contamination by persistent organic pollutants. Plants exposed exhibit various physiological and pathological disorders leading to stunted growth and severe loss in fruit quality and yield. One way to avoid or reduce losses in production caused by adverse soil chemical and physical conditions and environmental stresses in vegetables would be to graft them onto rootstocks capable of reducing the effect of external stresses on the shoot. This review gives an actual overview how grafting can alleviate the adverse effects of environmental stresses on vegetable's crop performance at agronomical, physiological, and biochemical levels. Implications for the selection and breeding of stress-tolerant rootstocks are discussed.

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Contents

1. Introduction

Environmental stresses represent the most limiting conditions for horticultural productivity and plant exploitation worldwide. Important factors among those are water, temperature, nutrition, light, oxygen availability, metal ion concentration, and pathogens.

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One direction out of these problems is to develop crops that are more tolerant to such stresses. This is carried out with tremendous efforts particularly at breeding companies; however, due to a lack of practical selection tools like genetic markers, it is a slow and inefficient process so far. As one effect, each year a high number of new cultivars is released which can be used by the growers. A special method of adapting plants to counteract environmental stresses is by grafting elite, commercial cultivars onto selected vigorous rootstocks (Lee and Oda, 2003). Grafting is nowadays regarded as a rapid alternative tool to the relatively slow breeding methodology aimed at increasing environmental-stress tolerance of fruit vegetables (Flores et al., 2010). In vegetable production, grafting is already used for more than 50 years in many parts of the world. Grafting is not associated with the input of agrochemicals to the crops and is therefore considered to be an environment-friendly operation of substantial and sustainable relevance to integrated and organic crop management systems (Rivard and Louws, 2008). The cultivated area of grafted *Solanaceae* and C*ucubitaceae* has increased tremendously in recent years because the objective of grafting has been greatly expanded (Lee et al., 2010). Nowadays, grafting is used to reduce infections by soil-borne pathogens and to enhance the tolerance against abiotic stresses. Among those are saline soils (Colla et al., 2010), soil-pH (alkalinity) stress, nutrient deficiency, and toxicity of heavy metals (Savvas et al., 2010). Other abiotic conditions for the application of rootstocks are thermal stress, drought and flooding, and persistent organic pollutants. This review focuses on these particular stress conditions and considers the root-derived molecular and physiological mechanisms involved in optimised rootstock–scion interaction and scion performance. Given the complexity of these traits, suggestions for efficient selection and breeding of stress-tolerant rootstocks are discussed as well.

2. Thermal stress

2.1. Chilling and suboptimal temperature

2.1.1. Background

Temperature is one of the most important environmental factors inflicting heavy economic relevant yield losses by reducing plant growth and development, causing wilt and necrosis, and retarding the rate of truss appearance and fruit ripening (Ahn et al., 1999). The production of vegetables in areas of cold and even mild climate conditions has to face during the winter, and to some extend also during the spring and autumn, chilling and suboptimal-temperature conditions. Depending on the crop species, the temperature threshold for growth of most of the chilling-sensitive fruit vegetables, such as pepper (*Capsicum annuum* L.), eggplant (*Solanum melongena* L.), cucumber (*Cucumis sativus* L.), tomato (*S. lycopersicum* L.) and melon (*C. melo*, *cucrbita*), is about 8–12 °C (Hansen et al., 1994; Criddle et al., 1997). In the range above (approx. up to 25–30 °C), metabolic rates increase exponentially with temperature. Below this threshold, many horticultural crops originating from (sub)tropical areas suffer from physiological disorders which, depending on the intensity and length of exposure, subsequently lead to irreversible dysfunction, cell death and finally plant death (see reviews Allen and Ort, 2001; Venema et al., 2005). In this section the focus is on suboptimal-temperature stress. This is defined as any reduction in plant performance that results in limitation to the yield potential caused by exposure to temperatures between the threshold for optimal biochemical/physiological activity or morphological development and the threshold at which the plant can successfully complete its life cycle (Greaves, 1996). Each aspect of growth, development and/or fruit formation has its own temperature optimum which varies among and within species as well with plant age.

During the vegetative growth phase suboptimal temperatures mainly result in slower leaf expansion and initiation rate of new leaves. The delay in the build-up of the crop and interception of irradiation both contribute to loss of (early) crop productivity. The reduction in leaf expansion and appearance rate at suboptimal temperature is not limited by the supply of assimilates, since the leaves accumulate large amounts of starch (Venema et al., 1999, 2008). More likely, root hormonal signals associated with water and nutrient uptake in combination with a decreased elasticity of the epidermal cell walls are involved. During the generative growth phase of tomatoes suboptimal temperature (i) reduces fruit set as a result of poorer pollen quality, (ii) increases the period between anthesis and maturity of the fruit, (iii) increases fruit size, and (iv) decreases truss appearance rate (see review by Van der Ploeg and Heuvelink, 2005). The slower fruit development and truss initiation rate of new trusses at suboptimal temperatures mainly reduces the yield early in the season when the prices for tomatoes are the highest. In addition to early yield, fruit quality characteristics are severely affected by temperature as well (Adams et al., 2001; Dorais et al., 2001). These both aspects do not make it economically profitable for the production in greenhouses to reduce the temperatures, despite reduction of the heating costs. However, due to increasing energy prices and public concern about environmental problems related with CO_2 emissions from the combustion of fossil fuel, the greenhouse industry is forced to improve its energy-efficiency, defined as the amount of fruits produced per unit energy input ($kg\,MJ^{-1}$). Although traditional breeding over the last 30 years has led to the generation of cultivars with a twofold improved energy-efficiency as a result of increased production levels, there is now also need to reduce the absolute amount of energy input (Van der Ploeg and Heuvelink, 2005). The successful cultivation of vegetables in the field and in (unheated) greenhouses under lower mean temperatures requires the breeding of new cultivars that are better adapted to low temperatures. The fact that low-temperature tolerance is developmentally regulated and growth stage-specific makes this trait a fairly complex one in which many genes are involved. This is probably the reason that breeders have been put limited efforts to the characterization of genetic control of cold tolerance (Foolad and Lin, 2001). As a fast and efficient alternative for the relatively slow breeding process aimed at lowering the heat demand of vegetables, grafting of existing elite commercial cultivars onto selected low-temperature tolerant rootstocks is regarded as a promising tool (den Nijs, 1980; Zijlstra et al., 1994; Rivero et al., 2003c; Venema et al., 2008). Worldwide a high percentage of the cultivated fruit vegetables under intensive production is already grafted (see Lee et al., 2010). However, the main general objective of using rootstocks is to increase scion growth and development rate, endurance and, ultimately, crop production. Recently, the effectiveness of grafting with respect to upgrading fruit quality is increasing (Davis et al., 2008; Flores et al., 2010; Rouphael et al., 2010). The next section reviews grafting studies in which rootstocks were evaluated as a tool to alleviate the impact of suboptimal (root-zone) temperatures. The practical benefits of increased suboptimal-temperature tolerance in vegetables for the open cultivation would be: (i) extension of the growing season, which would increase production over time; (ii) adaptation to growing areas with shorter growing seasons; (iii) prevention of plant and fruit damage from low temperatures (Rick, 1983); (iv) a decreased need for irrigation because earlier plant establishment makes a better use of the early-season rains and water availability (Foolad and Lin, 2001); and for the protected cultivation, (v) a better use of greenhouse facilities (CO_2 applications and heat storage), (vi) less combustions of fossil fuel, and (vii) decrease in CO_2 emissions (Venema et al., 2008).

2.1.2. Rootstocks as tool to increase low-temperature tolerance

Since the late sixties of the last century rootstocks have been used to enhance fruit yield as a common practice in open-ground and in unheated polythene greenhouses for *Cucurbitaceae* cultivation (cucumbers, squash, and melon) during the cold seasons in Japan and Korea, when low soil temperatures seriously affect seedling performance or even kill them (Ahn et al., 1999; Lee et al., 2005b). Experimental work on this topic started in the late sixties of the last century by Hori et al. (1970) with cucumber. However, grafting does not automatically improve tolerance to low temperature. In several grafting experiments with *Cucurbitaceae* or *Solanaceae* different scion-rootstock combinations did not respond with an advantageous growth or yield under lower temperatures (Okimura et al., 1986; Bulder et al., 1987). Tomato (cv. Big Red) grafted onto cv. Heman [*S. lycopersicum* L. × *L. hirsutum* (Vahl) Dunal] and Primavera (*S. lycopersicum* L.) produced more fruits than the control in the greenhouse, however, under low-temperature conditions in the field the positive effect almost disappeared (Khah et al., 2006). On the other hand Zijlstra and den Nijs (1987) demonstrated under low day- and night-temperature conditions of 18/7 °C a high variability in the contribution of 29 tomato rootstocks to earliness of flowering, fresh weight of trusses and shoots, and fruit production. A main reason of success seems, not surprisingly, the selection of rootstocks with a significant higher tolerance to suboptimal temperatures. However, as a consequence of inbreeding during domestication, the genetic diversity, and therefore also the variation in adaptability to low temperatures, is very small among the many cultivars of e.g. tomato (Paul et al., 1984; Nieuwhof et al., 1999; Van der Ploeg et al., 2007). The variation in low-temperature tolerance in related wild species, particularly in accessions thriving at high-altitudes with large diurnal variations in day/night temperatures, is much larger (Tachibana, 1982; Venema et al., 2005).

For cucumber, figleaf gourd (*Cucurbita ficifolia* Bouché) and bur cucumber (*Sicos angulatus* L.) are used as rootstocks. Figleaf gourd is unique among cucurbit species with an optimal root temperature at approximately 15 °C, thus 6 °C lower than that of cucumber roots (Tachibana, 1982; Lee, 1994; Ahn et al., 1999; Rivero et al., 2003c). Several studies demonstrated that these two rootstocks improved vegetative growth and early yield at suboptimal temperatures (den Nijs, 1980; Tachibana, 1982; Bulder et al., 1991; Zhou et al., 2007) and also when only the roots are subjected to chilling temperatures <8 °C (Ahn et al., 1999). Recently it was tested that grafting of a cucumber scion onto a squash rootstock (*Cucurbita moschata* Duch) could tolerate suboptimal temperatures compared with a self grafted cucumber when the squash rootstock cutting was exposed to a bottom heat treatment, which involved soaking the cut end of the cutting in warm nutrient solution of 30 °C for one day (Shibuya et al., 2007).

For tomato, rootstocks of the high-altitude accession LA 1777 of *S. habrochaites* (synonym *L. hirsutum* Dunal, Venema et al., 2008), 'KNVF' (the interspecific hybrid of *S. lycopersicum* × *S. habrochaites*, Okimura et al., 1986), and chill-tolerant lines from backcrossed progeny of *S. habrochaites* LA 1778 × *S. lycopersicum* cv. T5 (Bloom et al., 2004) were able to alleviate low root-temperature stress for different scions. All these experiments were performed on a relative short-term basis; no production data are available from long-term grafting experiments.

For watermelon, grafting onto Shin-tosa-type (an interspecific squash hybrid, *Cucurbita maxima* × *C. moschata*) rootstocks is used to advance the planting date during cool periods (Davis et al., 2008). The same rootstocks can also be used to improve the vegetative growth rate of eggplants at suboptimal temperatures (Gao et al., 2008). Another rootstock which may be used for this purpose is 'Torvum vigor' (Okimura et al., 1986).

The breeding of vigorous rootstocks with a broad abiotic stress resistance is hampered by the lack of practical selection tools like genetic markers because the knowledge about the physiology behind a successful rootstock (root–shoot interaction) is still very limited. In addition, a trait like thermal-stress resistance is complex and the identified QTL's have hardly any value for practical breeding purposes. Rootstock selection for e.g. tomato is mainly determined by high vigour what seems somehow related to resistance to thermal fluctuations and suboptimal-temperature tolerance (Rivero et al., 2003a; Venema et al., 2008). Current methods for rootstock breeding are relying on a trial-and-error approach to construct interspecific hybrids of selected well-rooted wild species and vigorous cultivated species. Rather than focusing on identification of single allele specific markers for desirable traits that are expressed in a particular hybrid combination, it is necessary to identify physiological characteristics that reflect the complex underlying genetic make-up. These physiological characteristics, which are ideally easy to measure, can be used as generic tools to develop a reliable method which supports the selection of vigorous rootstocks with an, in this case, broad thermal-stress resistance. With this approach rootstock selection can be done more efficiently with regard to time, labour and space. In the next section, therefore, molecular and physiological mechanisms underlying rootstock performance and root–shoot interaction at low temperature are reviewed.

2.1.3. Mechanisms involved in rootstock performance at low temperatures

Low (root-zone) temperatures both affect root growth, size, and architecture, as well as its functioning. The importance of root functioning at decreased (root-zone) temperatures in controlling shoot (scion) growth and productivity has been attributed to the viscosity of water, root pressure and hydraulic conductance, metabolic activity, production and upward transport of phytohormones, as well as the ability of the root to absorb nutrients. To what extent rootstocks are able to alleviate the negative effects of low root-zone temperatures on scion performance is a combination of how its growth and functioning are affected, the interaction between rootstock and scion, the physiological age of the graft combination, and the duration and intensity of the stress episode.

2.1.3.1. Root growth and architecture.
Mainly because of the hidden nature of roots, there are relatively few studies on the impact of temperature on root phenotype. It is expected that the recent development of imaging technologies will help us to increase our knowledge how root architecture is affected by changing temperature conditions (Nagel et al., 2009). Particularly under suboptimal temperatures low-temperature tolerant rootstocks maintain higher root growth rates than sensitive ones (Tachibana, 1982, 1987; Venema et al., 2008). Tomato grafted onto a cold-tolerant rootstock revealed a higher capacity to adjust their root/shoot ratio to suboptimal root-temperature (Venema et al., 2008). The physiological mechanism(s) involved in this shift in assimilate partitioning from source leaves to roots is not clear and may be regarded as energetically wasteful from an agronomic point of view (Perez-Alfocea et al., 2010). However, this adaptive response recovers the functional equilibrium between root and shoot, allowing the root system to overcome restrictions in water and/or nutrient uptake. The faster growth of cold-tolerant tomato rootstocks seems to be associated with the growth of more first order laterals (Nakano et al., 2002; Lee et al., 2005a). However, Lee et al. (2004a) did not find significant differences in root architecture comparing cold-sensitive cucumber and – tolerant figleaf gourd roots. Another striking difference in root growth between chilling-sensitive and – tolerant tomato species is the extent in which root elongation rate was inhibited by low temperature (Zamir and Gadish, 1987; Venema et al., 2008). The root elongation rate, k, is

described by the Lockhart (1965) equation: $k = \Phi(P - Y)$. According to this equation reduction in elongation rate can result from a drop in turgor pressure (P), or from changes in cell wall architecture decreasing the extensibility (Φ) or increasing the yield threshold, i.e. the minimum pressure required for growth (Y). It turned out that k is mainly affected by hormones and other effectors which influence cell wall properties, whereas turgor pressure recovers very quickly and remain rather constant after the onset of a stress (De Cnodder et al., 2006). Root cell elongation is characterized by the ability to undergo wall extension in acidic apoplastic conditions. According to the acid-growth theory protons play a primary role in wall loosening enabling cell elongation (Rayle and Cleland, 1992). A low apoplastic pH (<5) activates expansins in the cell wall, which probably break the hydrogen bonds between the cellulose chains and the cross-linking glycans (Cosgrove, 2000). The apoplastic pH is determined by the H^+-efflux through the plasma membrane H^+-ATPases and the H^+-influx through H^+-coupled symporters (Tanner and Caspari, 1996). The activity of H^+-ATPases can be affected by hormonal signals such as auxin (Rayle and Cleland, 1992) and environmental cues such as temperature (Sze et al., 1999).

Besides auxin, which decelerates root elongation in a concentration-dependent way (Rayle and Cleland, 1992; Tanimoto, 2005), cell elongation in roots is sensitive to many other endogenous factors like ethylene (Le et al., 2001; De Cnodder et al., 2005), abscisic acid (Sharp and LeNoble, 2002), cytokinin (Werner and Schmülling, 2009) and gibberellic acid (Tanimoto, 2005), as well as external root conditions like calcium (Kiegle et al., 2000), phosphate and iron concentrations (Ward et al., 2008). It is clear that there are a lot of (unknown) cross talks among plant hormones involved in acidification, formation and modification of the cell wall. In addition to cell wall properties, variation in root elongation rate among *Arabidopsis* ecotypes was positively correlated with cyclin-dependent kinase (CDK) activity. This suggests that cell cycle activity, i.e. production rate of new cells, might be an important determinant of root elongation rate as well (Beemster et al., 2002). In the case of suboptimal root-zone temperatures, there is very little knowledge about the key-physiological mechanisms which underlie the inhibitory effect on the cell cycle and cell elongation in roots (Walter et al., 2009).

2.1.3.2. Nutrient absorption. Remarkably, not many data are published on nutrient uptake and transport related to suboptimal-temperature stress of grafted horticultural crops. Most of them are for *Cucurbitaceae* and linked with figleaf gourd. It was shown, that both uptake (Masuda and Gomi, 1984; Tachibana, 1982, 1987) and transport (Choi et al., 1995) of the macro-nutrients, particularly nitrate and phosphate, increased in figleaf gourds compared with cucumber rootstocks in response to decreased root-zone temperatures. Among the micro-nutrients, Mn-, Cu-, and Zn-contents increased since these are diminished strongly with decreasing temperature (Li and Yu, 2007). Iron is not much affected by temperature and thus also not changed in cucumber grafted onto figleaf gourd. Nutrient uptake per unit root is reduced for most nutrients because of the larger root system of the rootstocks at lower temperature (unpublished data). In tomato, P is the macro-nutrient which uptake is most depressed at decreasing root temperatures (Starck et al., 2000), which may limit photosynthesis by decreasing the availability of P_i (Zhou et al., 2009). It is apparent that current tomato cultivars need higher P supply at suboptimal than at optimal root temperatures (Starck et al., 2000; Zhou et al., 2009). P starvation may induce ethylene production, as mentioned above, and decrease cytokinin content in the root (Marschner, 1995). No data are available from grafting studies with tomato indicating that chilling-tolerant rootstocks can diminish the decrease in P-availability in the shoot in response to low-temperature stress.

A model after Silberbush and Barber (1983) clearly implied that root elongation rate is a key trait for optimizing the efficiency of phosphorus uptake. Observations that root elongation rate of *S. habrochaites* is less inhibited by low temperatures (Zamir and Gadish, 1987; Venema et al., 2008) make this accession an interesting candidate as rootstock to improve P-uptake of tomato at lower temperatures. In addition, this wild tomato species also revealed less reduction in NH_4^+ absorption and the xylem sap transport rate in response to chilling stress (Brunet et al., 1990; Bloom et al., 1998). In general, root systems which nutrient uptake is less inhibited by low temperatures show a significant higher metabolic activity (Li et al., 2008), higher respiration rates (Masuda and Gomi, 1982), and higher actions of the plasmamembrane H^+-ATPase that provides the energy by an extrusion of protons from the root at low temperatures (Choi et al., 1995; Ahn et al., 1999; Lee et al., 2005a).

2.1.3.3. Absorption and translocation of water, and osmoregulation. Studies analysing the effects of low temperature on root systems were mostly focused on water uptake, causing chilling-sensitive species to suffer from water stress (Choi et al., 1995; Ahn et al., 1999). The most common and rapid visible consequence is wilting of the leaves (Bloom et al., 2004; Lee et al., 2005b). Cold-tolerant rootstocks may overcome restrictions to water absorption at chilling temperatures by an increase of the root hydraulic conductance, decreased induction of cell wall suberin layers, lipid peroxidation, and closure of the stomata (Bloom et al., 2004; Lee et al., 2005a). However, as Bloom et al. (2004) demonstrated with two independent methods, the root hydraulic conductance in two tomato species differing in low-temperature tolerance declined equally with temperature. Thus, increase in water uptake seems to be more related to the increase in biomass partitioning towards the roots as an adaptive mechanism to compensate for the decrease in water movement through the roots when these are subjected to suboptimal temperatures. In contrast, the hydraulic conductance of figleaf gourd roots dropped less (twofold) compared with cucumber rootstocks (24-fold) at 8 °C, indicating that the radial transport of water was less reduced (Lee et al., 2004b, 2005b, 2008). While water permeability of cortical cells of chilling-sensitive cucumber decreased by a factor of 10, there was only a slight decrease in chilling-resistant figleaf gourd (Lee et al., 2005c). From the studies of Lee et al. (2005a,b,c) it is clear that the aquaporins of cucumber were much more sensitive to low-root temperature than those of figleaf gourd. The authors suggested that both species possess different aquaporin families (Lee et al., 2005c) and differ in the ability to maintain a low level of H_2O_2 in the cytoplasm and to detoxify reactive oxygen species (ROS) at low root temperatures (Lee et al., 2004a; Zhou et al., 2007; Rhee et al., 2007). Besides aquaporins, the H^+-ATPase activity of root plasma membrane is closely involved in low root temperature-tolerant characteristics of plants lowering the osmotic potential for subsequent water uptake. The hypothesis has been that low root temperature-tolerant species are likely to possess the ability of water uptake at low root temperature through active proton pumping (Ahn et al., 1999, 2000; Lee et al., 2004b, 2005b). Studies elucidating the differences in biochemical characteristics of both H^+-ATPases and aquaporins between figleaf gourd and cucumber are in progress (Rhee et al., 2007).

Scions grafted onto low-temperature tolerant cucurbita rootstocks close the stomata much later compared with scions grafted onto sensitive ones, or scions grafted onto their own. Thus, transpiration is maintained and such plants perform better and experience cell death later (Yu et al., 1999). The stomatal resistance of figleaf gourd was not affected until the root temperature was lowered to 8 °C while it decreased significantly in cold-sensitive cucumber rootstocks (Ahn et al., 1999, 2000; Yu et al., 1999). In contrast, cold-tolerant tomatoes, such as *S. habrochaites* (LA 1778), decline the stomatal conductance resulting in a stomatal closure, while the

stomata of cold-sensitive species remain open until chilling temperatures of 5 °C. Not till then, they became flaccid and suffered damage (Bloom et al., 2004). Grafting experiments indicated that this differential stomatal behaviour during root chilling has distinct shoot and root components.

Since leaf water content decreased less at low temperatures in cucumbers grafted onto figleaf gourd, osmoprotectants, such as amino acids, quartenary ammonium compounds, polyols and sugars accumulated to osmotically significant levels without disrupting plant metabolism (Tachibana, 1982). Functions range from acting as an energy source to help the cells overcome oxidative stress to act as an osmoprotectant by stabilising both the quaternary structure of proteins and the highly ordered structure of membranes against the adverse effects of thermal stress.

2.1.3.4. Lipid peroxidation and antioxidants. Low-temperature stress on roots of chilling-sensitive plant species increases the production of ROS, such as superoxide, hydrogen peroxide, and hydroxyl radicals, which may cause peroxidation of unsaturated membrane lipids (Tachibana, 1982; Guy et al., 2008). This increases the membrane rigidity and results in a later stage in the leakage of electrolytes, water and soluble materials out of the cell into the intercellular space of the roots (Yu et al., 1997; Liu et al., 2004; Lee and Chung, 2005; Gao et al., 2008).

By measuring the malondialdehyde concentration in studies with cucumbers and watermelons it became clear that grafting onto low-temperature tolerant rootstocks may decrease the degree of lipid peroxidation and electrolyte leakage induced by cold stress (Gao et al., 2008). Comparing chilling-sensitive and -tolerant cucumber rootstocks indicated that this difference is related to differences in ROS accumulation (Zhou et al., 2004, 2006, 2007; Rhee et al., 2007). For tomato it was found that grafting can almost completely prevent the chill-induced accumulation of H_2O_2 in leaves (Rivero et al., 2003b).

When ROS are increasing with decreasing temperature, a profound up-regulation in the capacity to detoxify these compounds via antioxidants can be expected (Guy et al., 2008). However, the results of the many studies on antioxidant concentrations and enzyme activities of ROS-scavenging enzymes in cold-stressed (grafted) plants are not always in agreement and seem to depend on the actual temperature and if the whole plant or only the rootstock was exposed to low temperatures (Feng et al., 2002; Li and Yu, 2007; Li et al., 2008; Rivero et al., 2003b; Zhou et al., 2009; Gao et al., 2009). One reason for the higher activity of the ROS-scavenging enzymes in scions grafted onto cold-tolerant rootstocks might be due to a higher delivery of abscisic acid (ABA) and cytokinins since both ABA and cytokinins up-regulate the ROS-scavenging system in plants (Jiang and Zhang, 2002; Pogany et al., 2003).

2.1.3.5. Sink-source relations. The inhibition of the metabolic and growth capacity at decreasing (root) temperature contribute to a decrease of the sink strength of the root, i.e. the ability to draw photosynthates from the phloem. This will decrease the transport of carbohydrates out of the source leaves which contributes to the accumulation of carbohydrates in the leaves (Venema et al., 2008) and thus, reduces the specific leaf area (Venema et al., 1999, 2008). Together with an increase of the cell size in transverse direction (Hoek et al., 1993) this results in the production of thicker leaves which intercept less light and therefore negatively affect photosynthesis and biomass production. The accumulation of carbohydrates may also inhibit photosynthesis by down-regulation of genes involved in photosynthesis (Paul and Foyer, 2001). The extent in which temperature-stress inhibits the sink strength of the rootstock is therefore an important factor for leaf morphology, photosynthesis and finally the growth capacity of the shoot (Tachibana, 1987; Venema et al., 2008). There are indeed many grafting studies

with different species which indicate that low-temperature tolerant rootstocks have a stimulating effect on photosynthesis at decreased (root) temperatures (Ahn et al., 1999; Zhou et al., 2007; Li et al., 2008; Gao et al., 2008; Miao et al., 2009). Besides the higher sink capacity, cold-tolerant rootstocks may supply the scion with more water, nutrients and hormones under low-temperature stress, factors which may all affect photosynthesis. In addition, stimulation of photosynthesis by cold-tolerant rootstocks may also be explained by a decreased concentration of ROS in chloroplasts responsible for the degradation of RuBisCO and the D_1 protein (Zhou et al., 2009). More details on the impact of low temperature on photosynthesis can be found in the reviews of Allen and Ort (2001), Venema et al. (2005), and Van der Ploeg et al. (2007).

Maintaining rootstock growth (sink strength) under abiotic stresses, like cold and salinity, seems to be both related to stress tolerance (Venema et al., 2008; Perez-Alfocea et al., 2010). In spite of this stress-induced shift in assimilate partitioning to the root, the aim of grafting is that scion growth should be maintained as high as possible in order to increase plant production. Our physiological knowledge, however, about root-to-shoot signalling is still very low. Besides phytohormones, recent studies demonstrated that some specific RNA molecules are transported through phloem tissue as genetic information to execute coordinated growth and development between rootstock and scion (Harada, 2010).

2.1.3.6. Phytohormones (see Aloni et al., 2010). Low-temperature-induced changes in root phytohormone production influence not only root growth (sink strength), but affect also root-to-shoot hormone signalling which changes shoot physiology and thus productivity. A comprehensive study on this topic, like recently published for tomato under salt stress (Albacete et al., 2008, 2009; Perez-Alfocea et al., 2010), is lacking. Instead, only studies in which different plant species and stress treatments were used are currently available. From these it appeared that the severe inhibition of shoot biomass accumulation of tomatoes at low root temperatures stem from slow upward transport of root-born phytohormones, such as cytokinins and gibberellins, due to reduced water flow through the plant rather than reduction in their rate of biosynthesis (Ali et al., 1996). The growth limiting effects of low-root temperature on tomato shoots, i.e. leaf expansion and stem elongation, could partly be reversed by application of a low dose of gibberellins (GA_3) either to the apex (Menhenett and Wareing, 1975) or to the rooting medium (Bugbee and White, 1984). However, application of kinetin or benzylaminopurine (BAP), a synthetic cytokinin, only slightly improved tomato shoot growth at low root temperatures (Menhenett and Wareing, 1975). In addition to lower upward transport of cytokinins and gibberellins, low-root temperatures increased the upward transport of absicic acid (ABA) (Atkin et al., 1973) and induced accumulation of ABA in the shoot (Daie and Campbell, 1981). There is now convincing evidence that ABA functions in the roots to allow better uptake of water by affecting the conformation of aquaporins (water channels) in root cell membranes (Lee et al., 2005c). In the shoot, ABA controls transpiration by regulating the opening of the stomata (Hetherington and Davis, 1998). Recent experiments provided compelling evidence that ABA is required to maintain root (Spollen et al., 2000) and shoot growth, particularly leaf expansion (Hussain et al., 2000; Sharp and LeNoble, 2002). The latter is in contrast to the general view that ABA acts as an inhibitor of leaf expansion. The mechanism behind this action is partly by suppressing ethylene synthesis and partly by another mechanism that is independent of ethylene (LeNoble et al., 2004). The production of ethylene (ACC) increased in response to cold stress (Abeles et al., 1992; Huang and Lin, 2003). Low root temperature-

induced shoot growth inhibition was also reported to be associated with IAA accumulation due to reduced export from shoot to cooled roots (Veselova et al., 2005). This subsequently promoted cytokinin oxidase activity resulting in a decreased shoot cytokinin concentration.

Grafting studies with cucumber demonstrated that the more cold-sensitive rootstocks have a higher and sharper increase in ABA content in the xylem sap after a chill at 7 °C (Zhou et al., 2007). This was accompanied by lower amounts of cytokinins. In contrast to *C. sativus* L. which cytokinin concentrations in the xylem sap decreased, figleaf gourd stimulated cytokinin biosynthesis at suboptimal temperatures resulting in higher cytokinin concentrations in root xylem exudates (Tachibana, 1987). Higher cytokinin concentrations might be responsible for the increase in mRNA levels of the large and small subunits of RuBisCO and the activities of RuBisCO and FBPase. Results suggest also that some signals coming from chilling-resistant roots (i.e. ABA and cytokinins) protect leaf photosynthesis in shoots of chilling-sensitive plants (Zhou et al., 2007). Interestingly, the root nitrate concentration was positive related to xylem sap cytokinin and gibberellin concentrations in the roots (Tachibana, 1987), suggesting that the enhanced cytokinin synthesis of temperature-tolerant figleaf gourds at suboptimal temperature may be related to higher nitrate uptake.

2.1.4. Genetic basis and breeding of low-temperature tolerant rootstocks

Studies on the genetic basis of low-temperature tolerance were reviewed for tomato by Venema et al. (2005). In a BC_1 population derived from *S. lycopersicum* cv. T3 × *S. habrochaites* LA1777, three quantitative trait loci (QTLs) controlling the plastochron index were detected (Vallejos and Tanksley, 1983). In another study, analysis of multiple generations derived from a cross between *S. lycopersicum* cv. T5 and a primitive *S. lycopersicum* tolerant to cold temperature showed that growth under suboptimal temperatures was genetically controlled by at least two genes that are predominantly additive in nature (Foolad and Lin, 2001). Truco et al. (2000) identified several QTLs controlling shoot wilting under root chilling in an interspecific (*S. lycopersicum* cv. T5 × *S. habrochaites* LA1778) BC_1 mapping population. The QTL accounting for the largest percent of the phenotypic variation (33%) was designated *stm9* for shoot turgor maintenance. A segregating BC_1S_1 population derived from a selected plant from this mapping population also showed an association between the presence of *S. habrochaites* alleles at *stm9* and a significantly faster relative growth rate after chilling (Goodstal et al., 2005). This study is a nice example how existing introgressed backcross populations of *S. lycopersicum* with *S. habrochaites* may allow identification of gene loci connected to traits involved in low-temperature tolerance of roots. After identification of important QTLs, supported by studies which elucidate the underlying key-molecular and physiological mechanisms, the introgression of desirable genes related to low-temperature tolerance into appropriate rootstock genotypes could be made more efficient by Marker Assisted Selection. However, as mentioned in a previous section, rather than focussing on identification of single allele specific markers for low-temperature tolerance that are expressed in a particular hybrid combination, it is first necessary to identify physiological characteristics that reflect the complex underlying genetic make-up. This knowledge may deliver appropriate selection criteria which can be used for the breeding of low-temperature tolerant rootstocks.

2.2. Supraoptimal temperature

2.2.1. Background

Fruit vegetable production can also be constrained by high temperature under hot (semi)arid conditions (Abadelhafeez et al., 1975; Abdelmageed and Gruda, 2009) and during the hot-wet and hot-dry season in the lowland tropics (Palada and Wu, 2008). Production in greenhouses, particularly under soilless cultivation, is concerned as well because the root environment, such as soil, substrate, or nutrient solution, might be heated by high temperature and/or radiation under protected conditions (Wang et al., 2007). Levels above 35 °C limit the cultivation of *Solanaceae* rather than *Cucurbitaceae*.

Supraoptimal temperatures cause, similar to other abiotic stresses, a series of complex morphological, physiological, biochemical and molecular changes that adversely affect plant growth and productivity (see review in Wang et al., 2003). Among the many deleterious effects described are growth reduction, decrease in the photosynthetic rate and increase in respiration, assimilate partitioning towards the fruits, osmotic and oxidative damage, reduced water and ion uptake/movement, cellular dehydration. On the other hand, plants activate stress-responsive mechanisms, such as shifts in protein synthesis (e.g. heat shock proteins), detoxification, osmoprotection, and stabilization of enzymes and membranes. It is the question if rootstocks are able to improve these defence processes and finally contribute to enhance heat tolerance of the whole plant.

2.2.2. Rootstocks as tool to increase high-temperature tolerance

Contrary to the grafting of cucurbit rootstocks at suboptimal temperature, practical applications at supraoptimal temperature are insignificant. However, since 1990 the grafting technology was initiated and developed by the Asian Vegetable Research and Development Center (AVRDC) beginning for tomato and extended on pepper to improve the production in the Asian lowland tropics (AVRDC, 1995; Palada and Wu, 2008). Guides were published for grafting tomatoes and peppers, but the application is described to minimize not the aftermath of high temperature rather the problems of flooding and soil borne diseases which often accompany heat periods in the tropics (AVRDC, 2003, 2009).

Moreover, experimental results are published testing the success of *Solanaceae* rootstocks selected against supraoptimal temperature ranges. Based on these results, the use of grafted tomato may confer a certain degree of resistance against thermal stress (Rivero et al., 2003b). Since eggplants are better adapted to hot arid climate and have a better tolerance against supraoptimal soil temperature, the use of eggplants as rootstocks for tomato at higher temperature seemed to be more promising (Abadelhafeez et al., 1975; Abdelmageed and Gruda, 2009). Although it was tested that eggplant rootstocks enhanced vegetative growth at 28 °C, they had no advantage rather they decreased total fruit dry weight. The use of a heat-tolerant tomato (cv. Summerset) as a rootstock also failed to improve the yield. However, testing eggplants (*S. melongena* cv. Yuanqie) grafted onto a heat-tolerant rootstock (cv. Nianmaoquie) seemed to be promising and resulted in a prolonged growth stage and yield increase up to 10% (Wang et al., 2007). Comparing different lines of chilli pepper rootstocks (*C. chacoense*, *C. baccatum*, *C. frutescens*, *C. annuum*) confirmed highest yields under high-temperature conditions for rootstocks recommended by the AVRDC (*C. annuum* cv. Toom-1 and 9852-54; Palada and Wu, 2008).

2.2.3. Mechanisms involved in rootstock performance at high temperatures

Comparable to suboptimal temperatures, supraoptimal rootzone temperatures severely reduce root elongation and increase average root diameter (Qin et al., 2007). Increased ethylene production seems to play a role as well in this stress response (Abeles et al., 1992). Ethylene biosynthesis inhibitors could partly alleviate the effects of supraoptimal-temperature stress on root elongation and radial expansion, and had positive effects on leaf water

status and stomatal opening (Qin et al., 2007). However, photosynthesis and biomass production were not improved, probably due to non-stomatal limitation of photosynthesis mediated by nutrient deficiency. It is known that supraoptimal temperatures may develop multiple mineral deficiencies (P and Fe) in roots and shoots, which both can increase ethylene production (Tan et al., 2002; Ward et al., 2008). Overcoming the supraoptimal temperature-induced changes in nutrient uptake and transport to the shoot will be necessary before the positive effects of reduced root ACC production are to improve shoot growth (Qin et al., 2007).

The injury at high temperature has been ascribed as for low temperature to lipid phase transitions that decreased membrane stability accompanied by inactivation of metabolism (Hansen et al., 1994). Grafting tomato onto a heat tolerant rootstock (*L. esculentum* cv. RX-335) resulted in a decreased hydrogen peroxide concentration indicating the lower oxidative stress (Rivero et al., 2003a). Hydrogen peroxide was probably catalyzed by antioxidant enzymes, such as GPX and catalase showing higher concentrations. The activity of other antioxidative enzymes from the ascorbate/gluthation cycle increased as well but SOD activity was lower. It could also be shown that grafting of tomato onto eggplants reduced electrolyte leakage under supraoptimal temperature stress, indicating less membrane damage and a higher ability to retain solutes and water (Abadelhafeez et al., 1975; Abdelmageed and Gruda, 2009). The tomato grafted onto eggplants exhibited also a lower proline level but higher ascorbate concentrations compared with self-grafted tomato (Abadelhafeez et al., 1975).

3. Water stress

3.1. Drought

Water is quickly becoming an economically scarce resource in many areas of the world, especially in arid and semiarid regions, such as the Mediterranean basin. The increased competition for water among agricultural, industrial, and urban consumers creates the need for continuous improvement of irrigation practices in commercial vegetable production. One way to reduce losses in production and to improve water use efficiency under drought conditions in high-yielding genotypes would be grafting them onto rootstocks capable of reducing the effect of water stress on the shoot as observed in tree crops (García-Sánchez et al., 2007; Satisha et al., 2007).

Sanders and Markhart (1992) have shown in beans (*Phaseolus vulgaris* L.) that the osmotic potential of dehydrated scions of grafted bean plants was determined by the rootstocks, while the osmotic potential of non-stressed scions was governed by the shoot. Drought tolerance provided by either the rootstock or the scion resulted in enhanced nitrogen fixation in soybean (*Glycine max* L.) (Serraj and Sinclair, 1996). Other grafting experiments on drought with fruit, such as kiwi and grapes, proof that drought-tolerant rootstocks are available and useable under commercial growth conditions (Clearwater et al., 2004). In contrast, only a few studies exist on grafted fruit vegetables. Since eggplants are more effective to water uptake than tomato root systems, it would be interesting to see their grafting potential under water-stress conditions. Experimental results did not confirm the advantage of eggplants when used as a rootstock for tomato (Abadelhafeez et al., 1975). Grafted mini-watermelons onto a commercial rootstock (PS 1313′: *Cucurbita maxima* Duchesne × *Cucurbita moschata* Duchesne) revealed a more than 60% higher marketable yield when grown under conditions of deficit irrigation compared with ungrafted melons (Rouphael et al., 2008). The higher marketable yield recorded with grafting was mainly due to an improvement in water and nutrient uptake, indicated by a higher N, K, and Mg concentration in the leaves, and higher CO_2 assimilation. Grafting experiments with ABA deficient mutants of tomato showed that stomata can close independently of the leaf water status suggesting that there is a chemical signal produced by the roots that controls stomatal conductance (Holbrook et al., 2002). Moreover, transgenic tobacco plants were successfully generated maintaining high water contents and retaining photosynthetic activity during drought (Rivero et al., 2007). Combined use of genetic and agronomic technologies to sustain water status may maintain plant growth under conditions where yield would otherwise be significantly reduced.

3.2. Flooding

Flooding and submergence are major abiotic stresses and are serious problems for the growth and yield of flood sensitive crops. Flooding conditions cause oxygen starvation, which arises from the slow diffusion of gases in water and from oxygen consumption by microorganisms and plant roots. Problems caused by flooding may be solved by growing flood-tolerant crops or grafting intolerant plants onto tolerant ones. For instance, grafting improved flooding tolerance of bitter melon (*Momordia charanthia* L. cv. New Known You #3) when grafted onto luffa (*Luffa cylindria* Roem cv. Cylinder#2) (Liao and Lin, 1996). A milder depression of photosynthetic rate, stomatal conductance, transpiration, soluble proteins, and/or activity of RuBisCO was possibly related to this difference in flooding tolerance. In contrast, the reduction of the chlorophyll content in cucumber leaves induced by waterlogging was enhanced by grafting onto squash rootstocks (Kato et al., 2001). A chemical signal present in xylem sap stimulates ethylene biosynthesis in the shoot and thus may be responsible for the decreases. When grafting watermelon [*Citrullus lanatus* (Thunb.) Matsum and Nakai cv. 'Crimson Tide'] onto *Lagenaria siceraria* SKP (Landrace) the decrease in chlorophyll content was less pronounced compared with non-grafted water melons (Yetisir et al., 2006; Liao and Lin, 1996). Moreover, adventitious roots and aerenchyma formation were observed in grafted but not in ungrafted watermelon under flooding. Flooding occurs also during the heat period in the lowland tropics. Here, the AVRDC recommends growing tomatoes on eggplants 'EG195' or 'EG203' and pepper on chili accessions 'PP0237-7502', 'PP0242-62' and 'Lee B' (AVRDC, 2003, 2009). Mode of action described for watermelons are also valid for the eggplant and chili pepper rootstocks. Moreover, cultivation manuals mention that these rootstocks are tolerant against bacterial or fusarium wilt, southern or *Phytophthora* blight, and/or root-knot nematodes. Since waterlogging is often escorted by an increased tolerance of such diseases explains the indirect tolerance against flooding.

4. Organic pollutants

Drins (aldrin, dieldrin and endrin) have been categorized as a group of persistent organic pollutants because of their high toxicity, high bioaccumulation and persistency in the environment. Otani and Seike (2007) examined the effect of grafting on dieldrin and endrin uptake from the soil in cucumber plants. They chose four varieties each of *Cucurbita* spp. and cucumber, made up of 16 combinations of grafted plants by combining the *Cucurbita* spp. as rootstocks and the cucumber as scions, and then compared the dieldrin and endrin concentrations in the aerial tissues of the grafted plants with those of self-grafted *Cucurbita* spp. and cucumber plants. The results indicated that dieldrin and endrin concentrations in the grafted plants were mainly influenced by the rootstock variety. The highest dieldrin concentration was found in 'Schintosa-1gou' (*Cucurbita maxima* Duchesne × *Cucurbita moschata* Duchesne), which was 1.6 times lower than the value

recorded in the 'Yuyuikki-black' rootstock (*Cucurbita moschata* Duchesne). Similar results were observed for the endrin concentration but the variations among plants grafted onto *Cucurbita* rootstocks were smaller than those for the dieldrin concentration. These results were confirmed in another experiment where Otani and Seike (2007) compared the effect of three *Cucurbita* spp. rootstocks ('Yuyuikki-black', 'Shintosa-1gou', and 'Hikaripower-gold') on the dieldrin concentration in fruits of grafted cucumber (*C. sativus* L.) plants grown in contaminated soils. The dieldrin concentration in cucumber fruits grafted onto 'Yuyuikki-black' decreased by 50–70% compared with those grafted onto 'Shintosa-1gou' (*Cucurbita maxima* Duchesne × *Cucurbita moschata* Duchesne), and by 30–50% compared with those grafted onto 'Hikaripower-gold' (*Cucurbita moschata* Duchesne). Therefore, it is possible to reduce drin pollution in cucumber by about 50% using a low-uptake rootstock like 'Yuyuikki-black'. Selecting low-uptake rootstock varieties is a promising practical technique to reduce dieldrin concentration in cucumber fruits grown in contaminated fields. However, further studies are needed to evaluate if these rootstocks are also able to prevent the uptake of other toxic compounds.

5. Conclusions and perspectives

Grafting is a promising tool to enhance plant performance of both *Cucurbitaceae* and *Solanaceae* under growth conditions in which plants (roots) have to deal with suboptimal and/or supraoptimal temperatures, water stress and organic pollutants. Several effective rootstocks are mentioned and already in practical use, or used in breeding programs. Since desired rootstock traits mentioned in this review are fairly complex, multi-gene ones, practical selection tools like genetic markers are lacking. For this reason the breeding of appropriate rootstocks is still a matter of trial and error and the use of specific physiological parameters (biomarkers) to select plants in the breeding process is unprecedented for future rootstock breeding. This review illustrates that the molecular and physiological mechanisms involved in the advantageous response of specific stress-tolerant rootstocks are manifold and partly still unknown. Future research should focus, therefore, on identification of the key-physiologically root-derived processes (biomarkers) that are highly correlated to the rootstock traits of interest. The identified biomarkers can then be used as generic tools to develop an effective method for the selection of rootstocks which improve the adaptability of fruit vegetable crops to either thermal or water stress, organic pollutants, or other abiotic stresses.

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