



Review

# Role of grafting in vegetable crops grown under saline conditions

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ABSTRACT

Salinity is one of the major abiotic stresses that reduce plant growth and crop productivity in many vegetable production areas of the world. Grafting can represent an interesting tool to avoid or reduce yield losses caused by salinity stress in high-yielding genotypes belonging to *Solanaceae* and *Cucurbitaceae* families. Grafting is an integrative reciprocal process and, therefore, both scion and rootstock can influence salt tolerance of grafted plants. Grafted plants grown under saline conditions often exhibited better growth and yield, higher photosynthesis and leaf water content, greater root-to-shoot ratio, higher accumulation of compatible osmolytes, abscisic acid and polyamines in leaves, greater antioxidant capacity in leaves, and lower accumulation of Na<sup>+</sup> and/or Cl<sup>-</sup> in shoots than ungrafted or self-grafted plants. This report gives an overview of the recent literature on the salinity response of grafted plants and the mechanisms of salt tolerance in grafted plants related to the morphological root characteristics and the physiological and biochemical processes. The review will conclude by identifying several prospects for future researches aiming to improve the role of grafting in vegetable crops grown under saline conditions.

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1. Introduction

Salinity in soil or water is one of the major abiotic stresses that reduce plant growth and crop productivity worldwide (Arzani,

2008). More than 800 million hectares of land throughout the world are salt-affected (including both saline and sodic soils), corresponding to more than 6% of the world's total land area (FAO, 2009). Low rainfall, high evaporation, poor water management and the indiscriminate use of huge quantities of chemical fertilizers have also exacerbated growing concentrations of salts in the rhizosphere (Mahjan and Tuteja, 2005).

Most of the vegetable crops are glycophytes and, therefore, highly susceptible to soil salinity even at low electrical conductivity

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in the saturated soil extract (Shannon and Grieve, 1998). Moreover, the salinity response of crops throughout their growth cycle may change in relation to several interacting variables, including the cultural environment, the plant developmental stage and the magnitude (salt concentration and time of exposure) of the stress experienced over time (Munns, 2002). The deleterious effects of salinity on plant growth are associated with (1) low water potential of the root medium which causes a water deficit within the plant; (2) toxic effects of ions mainly  $\text{Na}^+$ ,  $\text{Cl}^-$ , and  $\text{SO}_4^{2-}$ ; (3) nutritional imbalance caused by reduced nutrient (e.g.,  $\text{K}^+$ ,  $\text{Ca}^{2+}$ ,  $\text{Mg}^{2+}$ ) uptake and/or transport to the shoot (Munns and Termaat, 1986; Ashraf, 1994; Marschner, 1995; Serrano et al., 1999; Hasegawa et al., 2000).

Numerous attempts have been made to improve the salt tolerance of crops by traditional breeding programmes. However, commercial success has been very limited due to the complexity of the trait: salt tolerance is complex genetically and physiologically (Flowers, 2004). At present, major efforts are being directed towards the genetic transformation of plants in order to raise their tolerance (Borsani et al., 2003) and in spite of the complexity of the trait, the transfer of a single gene or a few genes has led to claims of improvement in salt tolerance, such as occurs with the expression of some genes involved in the control of  $\text{Na}^+$  transport (Gaxiola et al., 2001; Rus et al., 2001; Zhang and Blumwald, 2001). However, the nature of the genetically complex mechanisms of abiotic stress tolerance, and potential detrimental side effects, make this task extremely difficult (Wang et al., 2003; Flowers, 2004). Solving a problem as complex as the profitable use of saline water in irrigated agriculture requires more than one strategy. In addition to tolerant cultivars, several cultural practices, each contributing to a small extent to allow plants to withstand better the deleterious effects of salt, needs to be applied (Cuartero and Fernandez-Muñoz, 1999). Some of the proposed practices, like the application of chemical fertilizers at levels somewhat above the optimum in freshwater irrigation, the application of chemical amendments or leaching salts to deeper soil layers, are hardly compatible with the urgent need to preserve the environment (Cuartero et al., 2006). One environment-friendly technique for avoiding or reducing losses in production caused by salinity in high-yielding genotypes belonging to *Solanaceae* and *Cucurbitaceae* families would be to graft them onto rootstocks capable of ameliorating salt-induced damage to the shoot (Santa-Cruz et al., 2002; Fernández-García et al., 2002, 2004; Estañ et al., 2005; Colla et al., 2005, 2006a,b; Wei et al., 2007; Goreta et al., 2008; Martínez-Rodríguez et al., 2008; Zhu et al., 2008a,b; He et al., 2009; Huang et al., 2009a,b,c, 2010; Uygur and Yetisir, 2009; Yetisir and Uygur, 2010; Zhen et al., 2010). This strategy could also enable plant breeder to combine desired shoot characteristic with good root characteristic (Zijlstra et al., 1994; Pardo et al., 1998). Proposed explanations for grafting-induced salt tolerance are: (1) higher accumulation of proline and sugar in the leaves (Ruiz et al., 2005); (2) higher antioxidant capacity in the leaves (López-Gómez et al., 2007); (3) lower accumulation of  $\text{Na}^+$  and/or  $\text{Cl}^-$  in the leaves (Fernández-García et al., 2004; Estañ et al., 2005; Goreta et al., 2008; Zhu et al., 2008a,b).

Grafting is an integrative reciprocal process and, therefore, both scion and rootstock influence salt tolerance of grafted plants (Etehadnia et al., 2008). Romero et al. (1997) observed that root characteristics are of primary importance in determining the salt tolerance of melon plants. In addition, the importance of the root system in the regulation of salt tolerance has also been documented in salt-sensitive and salt-tolerant potato genotypes (Shaterian et al., 2005). In contrast, Chen et al. (2003) concluded that scion genotypes play an important role in the growth of grafted tomato plants, regardless of the salinity in the growing media, whereas rootstock has little influence. Studies on tomato plants suggest that the characteristics of the rootstock conferring salt tolerance on the shoot

depend also on the salt tolerance of the shoot genotype (Santa-Cruz et al., 2002). Moreover, a recent work on cucumber also suggested that the salt tolerance of grafted cucumber seedlings is related to the shoot genotype (Zhu et al., 2008a,b). Therefore, more studies are necessary to investigate the primary factor that determines the salt tolerance of grafted plants.

The aim of this paper is to review the recent literature on the salinity response of grafted plants and the mechanisms of salt tolerance in grafted plants related to the morphological root characteristics and the physiological and biochemical processes. The review will conclude by identifying several prospects for future researches aiming to improve the role of grafting in vegetable crops grown under saline conditions.

## 2. Salinity response of grafted plants

### 2.1. Growth and yield

Grafting tomato (*Solanum lycopersicum* L.) plants for increased salinity tolerance is a promising practice to improve the crop performances in saline soil conditions. Santa-Cruz et al. (2001) found an increase in growth and fruit yield when a salt-sensitive tomato cultivar 'Moneymaker' was grafted onto a tolerant rootstock 'Pera' and irrigated with water containing 50 mM NaCl as compared to self-grafted plants. Estañ et al. (2005) also found that grafting provides an alternative way to improve salt tolerance, determined as fruit yield, in a commercial tomato hybrid ('Jaguar') grafted onto several tomato rootstocks ('Radja', 'Volgogradskij', 'Pera', and 'Volgogradskij' × 'Pera') with different potentials to exclude saline ions and grown at different NaCl concentrations (0, 25, 50, and 75 mM of NaCl). Estañ et al. (2005) reported that the positive effect on salt tolerance caused by the rootstocks was lower at 25 mM NaCl than at 50 and 75 mM NaCl indicating that the tolerance induced by the rootstock in the shoot was related to ionic rather than osmotic stress caused by salinity. In a recent study, Martínez-Rodríguez et al. (2008) addressed the question whether shoot genotype with an 'excluder' character ('Moneymaker') is able to increase its salt tolerance when grafted onto rootstocks ('Radja' and 'Pera') with excluder character. Grafting onto either 'Radja' or 'Pera' improved tomato fruit yield compared to self-grafted plants of 'Moneymaker' when plants were grown at 50 mM NaCl, whereas there was no effect of either rootstocks or grafting *per se* on fruit yield in the absence of salinity or at 25 mM NaCl. The yield increase in heterografted over self-grafted plants was around 40% whereas in an earlier study (Estañ et al., 2005) the increase was 80% for the same salt level, albeit with a different scion. The shoot genotype used in the Martínez-Rodríguez et al. (2008) study ('Moneymaker') is a better excluder than that used in the Estañ et al. (2005) study ('Jaguar'), so the different yield increases may be due to a lower shoot ion concentration induced by the same stress level when a genotype with higher exclusion ability as 'Moneymaker' is used. Taken together, these results support the conclusion that the salt tolerance of the shoot depends on the root system, independently of the genotype used as a scion, although the positive effect of rootstock may show to a different degree depending on the higher or lower exclusion ability of the shoot genotype.

Similarly to tomato, the growth performance of the eggplant cultivar 'Suqiqie' (*Solanum melongena* L.) was improved under saline stress conditions when the 'Torvum Vigor' (*Solanum torvum* Swartz) was used as rootstock (Liu et al., 2007; Wei et al., 2007). The results showed that the inhibiting extent of stem elongation of grafted seedlings was significantly lower than that of own-root seedlings under saline conditions (80 mM NaCl). Moreover, the growth of grafted seedlings was more vigorous than that of own-root seedlings, especially in roots.

The better crop performance of grafted *Solanaceae* crops in comparison with self-rooted plants when grown under saline conditions has been also observed in several Cucurbits such as watermelon, melon and cucumber. As reported by Goretta et al. (2008), when watermelon ('Fantasy') was grafted onto 'Strongtosa' rootstock (*Cucurbita maxima* Duch. × *Cucurbita moschata* Duch.) the reductions in shoot weight and leaf area due to exposure to salinity were lower than in ungrafted plants. Moreover, other experiments demonstrated that grafted 'Crimson Tide' watermelon [*Citrullus lanatus* (Thunb.) Matsum et Nakai] onto *C. maxima* and two *Lagenaria siceraria* rootstocks resulted in higher growth performance than ungrafted plants under saline conditions (8.0 dS m<sup>-1</sup>, Yetisir and Uygur, 2010). Reduction in shoot dry weight was 41% in ungrafted plants while it varied from 22% to 0.8% in grafted plants under the same saline conditions.

Romero et al. (1997) compared the effect of salinity (4.6 dS m<sup>-1</sup>) on two varieties of melon (*Cucumis melo* L.) grafted onto three hybrids of squash (*C. maxima* Duch. × *C. moschata* Duch.) with its effects on ungrafted melons and found that grafted melons were more tolerant to salinity and gave higher yields than ungrafted ones. However, Edelstein et al. (2005) and Colla et al. (2006b) showed that the sensitivity to salinity was similar between grafted and ungrafted melon plants, and the higher marketable yield from grafted plants was mainly due to grafting *per se*. It was demonstrated that grafting *per se* affects directly plant yield (Rivero et al., 2003). Its influence can be exerted by the interaction of some or all of the following processes: increase of water and nutrient uptake due to the rootstock's vigorous root system (Lee, 1994; Ruiz et al., 1997), enhanced production of endogenous-hormones (Zijlstra et al., 1994) and enhancement of scion vigor (Leoni et al., 1990). The joint action of some or all of these processes could explain the higher yield often observed in grafted plants at any level of salinity in the root zone. These conflicting results may be attributed to different effects of the *Cucurbita* rootstocks that were used in these studies: 'TZ-148' was used by Edelstein et al. (2005), 'P360' by Colla et al. (2006b), and 'Shintoza', 'RS-841', and 'Kamel' by Romero et al. (1997), which open the possibility of site-specific rootstock selection.

Huang et al. (2009a) showed that reduction of cucumber (*Cucumis sativus* L. 'Jinchun No. 2') shoot dry weight can be alleviated by grafting onto bottle gourd rootstock 'Chaofeng 8848' (*L. siceraria* Standl.). In a similar study, Huang et al. (2009b) determine the fruit yield of cucumber plants 'Jinchun No. 2', either self-grafted or grafted onto the commercial salt tolerant rootstock 'Fingleaf Gourd' (*Cucurbita ficifolia* Bouché) and 'Chaofeng Kangshengwang' (*L. siceraria* Standl.) under saline conditions (0, 30, or 60 mM NaCl). Plants grafted onto 'Fingleaf Gourd' and 'Chaofeng Kangshengwang' had higher fruit number and marketable fruit yield compared to the self-grafted plants at all salt levels. The total fruit yield of plants grafted onto 'Fingleaf Gourd' increased by 15%, 28%, and 73%, under 0, 30, and 60 mM NaCl stress, respectively, whereas the respective values were 14%, 33%, and 83% in the plants grafted onto 'Chaofeng Kangshengwang', with respect to self-grafted plants. Moreover, a lower percentage of unmarketable fruit was also observed on the plants grafted onto 'Fingleaf Gourd' and 'Chaofeng Kangshengwang' under 60 mM NaCl compared to the self-grafted plants (Huang et al., 2009b).

## 2.2. Leaf gas exchange and water relations

A wide range of morphological and physiological characteristics are affected by rootstocks, scions and their interactions (Santa-Cruz et al., 2002; Fernández-García et al., 2002, 2004; Estañ et al., 2005; Colla et al., 2006b; Yang et al., 2006; Martínez-Rodríguez et al., 2008; Huang et al., 2009b; He et al., 2009). Some of these characteristics have the potential for improvement of plant water relations,

growth and development during salt stress. In watermelon Colla et al. (2006a) observed that the net assimilation of CO<sub>2</sub> decreased with increasing salinity from 2.0 to 5.2 dS m<sup>-1</sup> in all grafting combinations (Tex/Macis, and Tex/Ercole), especially in ungrafted Tex treatment. Yang et al. (2006) demonstrated that grafted cucumber plants exhibit higher net photosynthesis, stomatal conductance, and intercellular CO<sub>2</sub> concentrations under NaCl stress than self-rooted plants. In another study, He et al. (2009) determined the leaf gas exchange of tomato plants 'Hezu903', ungrafted, self-grafted or grafted onto 'Zhezhen' and exposed to 0, 50, 100, or 150 mM NaCl, over a two-week period. As reported by He et al. (2009), the net CO<sub>2</sub> assimilation rate (*A*) declined with increasing level of salt stress. In rootstock-grafted plants, the decrease was accompanied by a significant decrease in stomatal conductance (*G<sub>s</sub>*) and intercellular CO<sub>2</sub> concentration (*C<sub>i</sub>*), implying that stomatal limitations were responsible for the reduction in *A* by salt treatment (Farquhar and Sharkey, 1982). In ungrafted and self-grafted plants, *C<sub>i</sub>* decreased under moderate stress conditions, but did not change under severe conditions, while *A* and *G<sub>s</sub>* decreased dramatically, implying the occurrence of non-stomatal limitations. This might indicate that, when exposed to 150 mM NaCl, the ungrafted and self-grafted plants suffered from severe stress (Flexas and Medrano, 2002). Under moderate and severe salt stresses, the rootstock-grafted plants showed higher *A* than non-grafted and self-grafted plants. This was in agreement with previous findings that grafting onto some rootstocks improves the photosynthesis performance of plants under salinity (Moya et al., 2002; Massai et al., 2004). Water use efficiency (WUE), calculated as the ratio of *A* (net assimilation) to *E* (transpiration), increased in moderately salt-stressed tomato plants, owing to the fast decrease of transpiration rate. Compared with the ungrafted and self-grafted plants, rootstock-grafted plants had a higher WUE under saline conditions, which might result from the milder reduction of the photosynthetic performance in rootstock-grafted plants (He et al., 2009). The higher WUE is of importance for salt tolerance, since high WUE may reduce the uptake of salt and alleviate the water deficiency induced by salinity (Moya et al., 1999; Karaba et al., 2007).

Santa-Cruz et al. (2002) found that, under saline conditions, leaf water content increased by 35% in grafted plants when the scion had a salt inductor character in comparison with self-grafted plants. This capacity to increase the leaf water content was related to a lesser reduction of shoot growth (Neumann, 1997; Rus et al., 1999). Also, leaf water content remained similar under control conditions in several grafting combinations of tomato, but increased to dissimilar levels with salinity, thereby indicating that specific combinations were more resistant to salinity (Martínez-Rodríguez et al., 2008). However, salinity had no significant effect on relative leaf water content in cucumber and tomato grafted onto different rootstocks (Huang et al., 2009b; Estañ et al., 2005), compared with the self-grafted plants, which could be attributed to changes in the soluble components contributing to osmotic adjustment (Huang et al., 2009b).

## 3. Mechanisms of salt tolerance in grafted plants

### 3.1. Morphological root characteristics

Root characteristics which may play an active role in ions and water uptake are root length and density (Gahoonia and Nielsen, 1997; Krasilnikoff et al., 2003), number of root hairs and their length and hence their surface area (Dvorlai and Jens, 1999; Itoh and Barber, 1983). The enhanced salt tolerance of grafted vegetables has often been associated with the root system. In fact, the root systems are the most critical parts of the plant faced with soil-related stress factors such as salinity. Therefore, root characteristics are the main

**Table 1**  
Na<sup>+</sup> and Cl<sup>-</sup> exclusion and/or inclusion in grafted vegetables under saline conditions.

Scion species	Rootstock species	Ion exclusion and/or inclusion in the scion	Ion exclusion and/or inclusion in the rootstock	References
<i>Cucumis sativus</i> L.	<i>Cucurbita moschata</i> Duch.	Na <sup>+</sup> exclusion		Chen and Wang (2008)
<i>Cucumis sativus</i> L.	<i>Cucurbita ficifolia</i> Bouché	Na <sup>+</sup> exclusion		Chen and Wang (2008)
<i>Cucumis sativus</i> L.	<i>Cucurbita moschata</i> Duch.	Na <sup>+</sup> exclusion and Cl <sup>-</sup> inclusion	Na <sup>+</sup> and Cl <sup>-</sup> inclusion	Zhu et al. (2008a)
<i>Cucumis sativus</i> L.	<i>Lagenaria siceraria</i> Standl.	Na <sup>+</sup> and Cl <sup>-</sup> exclusion	Similar Na <sup>+</sup> and Cl <sup>-</sup>	Huang et al. (2009a)
<i>Cucumis sativus</i> L.	<i>Lagenaria siceraria</i> Standl.	Na <sup>+</sup> and Cl <sup>-</sup> exclusion		Huang et al. (2009b)
<i>Cucumis sativus</i> L.	<i>Cucurbita ficifolia</i> Bouché	Na <sup>+</sup> and Cl <sup>-</sup> exclusion		Huang et al. (2009b)
<i>Cucumis sativus</i> L.	<i>Cucurbita moschata</i> Duch.	Na <sup>+</sup> exclusion, similar Cl <sup>-</sup>	Na <sup>+</sup> inclusion	Zhen et al. (2010)
<i>Citrullus lanatus</i> (Thunb.) Matsum and Nakai	<i>Cucurbita maxima</i> Duch. × <i>C. moschata</i> Duch.	Na <sup>+</sup> exclusion	Na <sup>+</sup> inclusion	Goreta et al. (2008)
<i>Citrullus lanatus</i> (Thunb.) Matsum and Nakai	<i>Lagenaria siceraria</i> Standl.	Na <sup>+</sup> exclusion	Na <sup>+</sup> inclusion	Zhu and Guo (2009)
<i>Citrullus lanatus</i> (Thunb.) Matsum and Nakai	<i>Cucurbita maxima</i> Duch. × <i>C. moschata</i> Duch.	Na <sup>+</sup> exclusion and Cl <sup>-</sup> inclusion		Colla et al. (2006a)
<i>Citrullus lanatus</i> L. (Thunb.) Matsum and Nakai	<i>Lagenaria siceraria</i> Standl.	Na <sup>+</sup> exclusion and Cl <sup>-</sup> inclusion		Colla et al. (2006a)
<i>Citrullus lanatus</i> (Thunb.) Matsum and Nakai	<i>Lagenaria siceraria</i> landrace	Na <sup>+</sup> exclusion		Yetisir and Uygur (2010)
<i>Citrullus lanatus</i> (Thunb.) Matsum and Nakai	<i>Cucurbita maxima</i> Duch.	Na <sup>+</sup> exclusion		Yetisir and Uygur (2010)
<i>Cucumis melo</i> L.	<i>Cucurbita maxima</i> Duch. × <i>C. moschata</i> Duch.	Na <sup>+</sup> exclusion and Cl <sup>-</sup> inclusion		Colla et al. (2006b)
<i>Cucumis melo</i> L.	<i>Cucurbita maxima</i> Duch. × <i>C. moschata</i> Duch.	Na <sup>+</sup> exclusion, similar Cl <sup>-</sup>		Edelstein et al. (2005)
<i>Cucumis melo</i> L.	<i>Cucurbita maxima</i> Duch. × <i>C. moschata</i> Duch.	Na <sup>+</sup> and Cl <sup>-</sup> exclusion		Romero et al. (1997)
<i>Solanum melongena</i> L.	<i>Solanum torvum</i> Swartz	Na <sup>+</sup> exclusion	Na <sup>+</sup> inclusion	Bai et al. (2005)
<i>Solanum melongena</i> L.	<i>Solanum torvum</i> Swartz	Na <sup>+</sup> and Cl <sup>-</sup> exclusion	Na <sup>+</sup> and Cl <sup>-</sup> inclusion	Wei et al. (2007)
<i>Solanum lycopersicum</i> L.	<i>Solanum lycopersicum</i> L.	Similar Na <sup>+</sup> and Cl <sup>-</sup>		He et al. (2009)
<i>Solanum lycopersicum</i> L.	<i>Solanum lycopersicum</i> L. × <i>S. cheesmaniae</i> L. Riley	Similar Na <sup>+</sup>		Albacete et al. (2009)
<i>Solanum lycopersicum</i> L.	<i>Solanum lycopersicum</i> L.	Na <sup>+</sup> and Cl <sup>-</sup> exclusion		Fernández-García et al. (2002)
<i>Solanum lycopersicum</i> L.	<i>Solanum lycopersicum</i> L.	Na <sup>+</sup> and Cl <sup>-</sup> exclusion		Fernández-García et al. (2004)
<i>Solanum lycopersicum</i> L.	<i>Solanum lycopersicum</i> L.	Na <sup>+</sup> and Cl <sup>-</sup> exclusion		Santa-Cruz et al. (2002)
<i>Solanum lycopersicum</i> L.	<i>Solanum lycopersicum</i> L.	Na <sup>+</sup> and Cl <sup>-</sup> exclusion		Estañ et al. (2005)
<i>Solanum lycopersicum</i> L.	<i>Solanum lycopersicum</i> L.	Na <sup>+</sup> and Cl <sup>-</sup> exclusion		Martinez-Rodriguez et al. (2008)

reason for the alleviation of deleterious effect of salt stress on the shoot growth. In tomatoes, He et al. (2009) observed that root dry mass declined at 100 and 150 mM NaCl, in comparison with non-saline conditions, but the decrease was smaller in rootstock-grafted plants. Similarly, Zhu et al. (2008a,b) and Huang et al. (2009a) reported that the reduction in the root dry weight of grafted cucumber plants was significantly lower than that recorded in ungrafted plants under NaCl stress. Moreover, in comparison with ungrafted cucumber plants, the partitioning of biomass between shoot and root showed that the grafted plants tended to accumulate more biomass in root, resulting in a greater root-to-shoot ratio in the grafted plants (Huang et al., 2009a). Finally, using squash and bottle gourd rootstocks under saline stress conditions, the reduction in root dry weight in comparison to non-saline conditions was significantly lower in grafted than ungrafted watermelon plants (Colla et al., 2006a; Yetisir and Uygur, 2010). Therefore, the better growth performance of grafted in comparison to ungrafted vegetable crops exposed to salinity stress might be attributed, at least to some extent, to differential root growth under salinity stress.

### 3.2. Physiological and biochemical mechanisms

High salt concentrations cause ion imbalance, ion toxicity, and hyperosmotic stress in plants. As a consequence of these primary effects, secondary stresses such as oxidative damage often occur (Zhu, 2001a). Grafted plants develop numerous physiological and biochemical mechanisms to cope with salt stress. These strategies include (i) salt exclusion in the shoot and retention of salt ions in the root, (ii) better maintenance of potassium homeostasis, (iii) compartmentation of salt ions in the vacuole, accumulation of compatible solutes and osmolytes in the cytosol, (iv) activation

of an antioxidant defense system, and (v) induction of hormone-mediated changes in plant growth.

#### 3.2.1. Salt exclusion in the shoot and retention of salt ions in the root

The most common effect of soil salinity is the growth inhibition due to direct Na<sup>+</sup> and Cl<sup>-</sup> toxicity at biochemical level. For some plants, particularly woody perennials such as citrus and grapevines, Na<sup>+</sup> is retained in the woody roots and stems, while Cl<sup>-</sup> is accumulated in the shoot and causes the most damage to the plant (Flowers, 1988). However, for many plants, including vegetables such as cucumber, melon, watermelon, tomato, and eggplant, Na<sup>+</sup> is the primary cause of ion-specific damage (Tester and Davenport, 2003; Varlagas et al., 2010). Plants grafted onto appropriate rootstocks restricted the transport of Na<sup>+</sup> from root to shoot (Romero et al., 1997; Estañ et al., 2005; Goreta et al., 2008; Zhu et al., 2008a). However, it is unknown whether grafting can reduce the uptake of Na<sup>+</sup> by the plant.

Salt tolerance mechanisms can occur in a wide range of organizational levels from the cellular level (e.g., compartmentation of Na<sup>+</sup> within cells) to the whole plant (e.g., exclusion of Na<sup>+</sup> from the plant and exclusion of Na<sup>+</sup> from the shoot) (Tester and Davenport, 2003; Møller et al., 2009). The enhanced salt tolerance of grafted vegetables has often been associated with lower Na<sup>+</sup> and/or Cl<sup>-</sup> contents in the shoot (Table 1). In tomatoes, the Na<sup>+</sup> and Cl<sup>-</sup> concentrations in the xylem and leaves of NaCl-treated plants are higher in self-rooted plants than in grafted plants (Santa-Cruz et al., 2002; Fernández-García et al., 2002, 2004; Martinez-Rodriguez et al., 2008). The salt tolerance of tomatoes are enhanced by grafting, but the rootstocks have a different capability in regulating the transport of Na<sup>+</sup> and Cl<sup>-</sup> to the tomato shoot, suggesting the impor-

tance of rootstock selection (Estañ et al., 2005). Eggplant grafted onto *S. torvum* had lower leaf  $\text{Na}^+$  and  $\text{Cl}^-$  contents than self-rooted plants under NaCl stress (Bai et al., 2005; Wei et al., 2007). In watermelons, the capacity of 'Strong Tosa' (*C. maxima* Duch.  $\times$  *C. moschata* Duch.) to withstand salt stress better than other tested rootstocks is partially due to efficient  $\text{Na}^+$  exclusion from the watermelon shoot (Goreta et al., 2008). Cucumber plants grafted onto *C. moschata* had lower  $\text{Na}^+$  and higher  $\text{Cl}^-$  contents in the leaves (Zhu et al., 2008a). Probably the accumulation of  $\text{Cl}^-$  play an important role in osmotic adjustment under salt stress (Flowers, 1988). Grafting decreases the concentrations of  $\text{Na}^+$ , but not  $\text{Cl}^-$  in the leaves of melon and watermelon (Colla et al., 2006a,b). However, the salt tolerance of grafted and self-rooted plants is similar, and the higher yield from grafted plants is mainly due to the improved vigor of plant (Colla et al., 2006a,b). In an earlier study, the enhanced salt tolerance of melon plants grafted onto *C. maxima*  $\times$  *C. moschata* was associated with lower leaf  $\text{Na}^+$  and  $\text{Cl}^-$  contents (Romero et al., 1997). Thus, grafted plants appear to have developed various mechanisms to avoid the physiological damage that can be caused by excessive accumulation of salt ions in the leaf, suggesting that other ion mechanisms (e.g.,  $\text{Cl}^-$  exclusion) may also be implicated in some cases.

Apart from the level of  $\text{Na}^+$  in the shoot, another component of plant salinity tolerance is the capability of the tissue to tolerate  $\text{Na}^+$  (Munns and Tester, 2008). This is especially true in the case of salt tolerance of grafted plants. In contrast to the exclusion of saline ions in the shoot, the root of rootstocks generally includes more  $\text{Na}^+$  and  $\text{Cl}^-$  compared with self-rooted plants, as has been reported for eggplants (Bai et al., 2005; Wei et al., 2007), watermelons (Goreta et al., 2008; Zhu and Guo, 2009), and cucumbers (Zhu et al., 2008a; Zhen et al., 2010). Tissue tolerance to  $\text{Na}^+$  involves the storage of  $\text{Na}^+$  in vacuoles, which can protect cytosolic enzymes from the toxic action (Apse et al., 1999). Electrochemical  $\text{H}^+$  gradients, generated by  $\text{H}^+$ -pumps at the plasma membrane ( $\text{H}^+$ -ATPase) and the tonoplast ( $\text{H}^+$ -ATPase,  $\text{H}^+$ -PPase), provide the energy used by the plasma membrane- and tonoplast-bound  $\text{Na}^+/\text{H}^+$  antiporters to couple the passive movement of  $\text{H}^+$  to the active movement of  $\text{Na}^+$  out of the cell and into the vacuole, respectively (Blumwald, 1987). The  $\text{H}^+$ -ATPase and  $\text{H}^+$ -PPase activities of root tonoplast membrane are inhibited under NaCl stress, but the inhibition in grafted tomato seedlings occurs at a later stage and is significantly milder than in self-rooted seedlings. This mechanism suggests that the roots of grafted plants have a higher capacity for vacuolar  $\text{Na}^+$  sequestration (Chen et al., 2008).

### 3.2.2. Better maintenance of potassium homeostasis

The metabolic toxicity of  $\text{Na}^+$  is largely a result of its capability to compete with  $\text{K}^+$  for binding sites essential for cellular function. More than 50 enzymes are activated by  $\text{K}^+$ , and  $\text{Na}^+$  cannot be used as a substitute in this role (Bhandal and Malik, 1988). It should be emphasized that a decrease in the  $\text{K}^+/\text{Na}^+$  may result in a deficiency of K. Therefore,  $\text{K}^+$  homeostasis is an important factor in salt tolerance (Munns and Tester, 2008). Grafted plants have a higher  $\text{K}^+$  content which seems to relate to the higher salt tolerance compared with self-grafted plants (Zhu et al., 2008a; Huang et al., 2009a). The salt tolerance of grafted tomato plants was associated with xylem  $\text{K}^+$  but not  $\text{Na}^+$  (Albacete et al., 2009). However, the direct relationship between leaf  $\text{K}^+$  homeostasis and salinity tolerance of grafted plants has not yet been established.

### 3.2.3. Accumulation of compatible solutes and osmolytes

Plants need to maintain internal water potential below that of the soil in order to maintain turgor and water uptake for growth. This requires an increase in osmotica either through uptake of inorganic ions or synthesis of metabolically compatible solutes. The compounds that most commonly accumulate include sucrose, proline, and glycine betaine (Munns and Tester, 2008). Unlike inor-

ganic solutes such as  $\text{Na}^+$  and  $\text{Cl}^-$  ions, however, these organic solutes are not harmful to enzymes and other cellular structures even at high concentrations. They are often referred to as compatible osmolytes (Zhu, 2001b). At high concentrations, compatible solutes function in osmotic adjustment. The high concentrations of compatible osmolytes accumulate in the cytosol and organelles to balance the osmotic pressure of the ions in the vacuole (Munns and Tester, 2008). In addition, data suggest that an increased amount of compatible osmolytes may protect plants by scavenging oxygen-free radicals caused by salt stress (Zhu, 2001b; Huang et al., 2009c).

Tomato plants grafted onto *S. lycopersicum* have a higher soluble sugar and proline content than self-rooted plants under NaCl stress (Chen et al., 2005). Similarly, grafted cucumber plants have a higher soluble sugar and proline content, but they have a lower  $\text{Na}^+$  and  $\text{Cl}^-$  content in the leaves than self-rooted plants under NaCl stress, suggesting that the enhanced salt tolerance of grafted plants is related to the change in osmotic component (Yang et al., 2006; Chen and Wang, 2008; Huang et al., 2009a). In addition, cucumber plants grafted onto *C. ficifolia* have higher soluble sugar content than self-rooted plants under macronutrient-induced saline conditions. Although compatible solutes have a higher energy requirement, grafted plants can still benefit from the higher accumulation of compatible solutes. The over-accumulation of  $\text{Na}^+$  in the leaf tissue can cause premature leaf senescence or even death, while a higher soluble sugar and proline content can prevent, to some extent, the detrimental effect induced by salinity (Tester and Davenport, 2003).

### 3.2.4. Induction of the antioxidant defense system

Salt stress reduces stomatal conductance, thereby limiting  $\text{CO}_2$  supply to the leaf (Apel and Hirt, 2004). This in turn causes the over-reduction of the photosynthetic electron transport chain, resulting in the production of reactive oxygen species (ROS) such as superoxide radicals ( $\text{O}_2^-$ ) and hydrogen peroxide ( $\text{H}_2\text{O}_2$ ). These ROS are highly reactive and can seriously disrupt normal metabolism through oxidative damage to lipids, proteins, and nucleic acids (Apel and Hirt, 2004). Plants have the capability to scavenge or detoxify ROS by producing different types of antioxidants. Antioxidants can generally be categorized into two different types: enzymatic and non-enzymatic compounds. Enzymatic antioxidants include superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), monodehydroascorbate reductase (MDHAR), dehydroascorbate reductase (DHAR), and glutathione reductase (GR). The most commonly known non-enzymatic antioxidants are glutathione (reduced form, GSH), ascorbate (reduced form, AsA), carotenoids, and tocopherols (Apel and Hirt, 2004; Ashraf, 2009).

Antioxidants can be used as markers of salinity tolerance in grafted vegetables (Table 2). Grafted cucumbers have a higher relative expression of Cu/Zn-SOD, Mn-SOD, and CAT mRNA, and higher activities of SOD, Cu/Zn-SOD, Mn-SOD, and CAT, thereby a higher salt tolerance under NaCl stress than self-rooted plants as well (Gao et al., 2008). The increased salt tolerance of cucumber plants grafted onto *C. ficifolia* was found to be linked to the increased SOD and POD activities under saline conditions induced by major nutrients (Huang et al., 2010). Under excessive  $\text{Ca}(\text{NO}_3)_2$  stress, grafted eggplants have a lower  $\text{O}_2^-$  production rate and  $\text{H}_2\text{O}_2$  and malondialdehyde content (a lipid peroxidation product, MDA). They also have higher SOD, POD, APX, and GR activities than self-rooted seedlings (Wei et al., 2009). Higher antioxidant capacity in grafted plants under salt stress has been observed also in other fruit-bearing vegetables. In watermelons, for instance, the activities of SOD, POD, and CAT in the leaves of grafted watermelon seedlings were significantly higher than those of self-rooted seedlings under NaCl stress (Zhu et al., 2008b). In tomatoes, the alleviation of oxidative damage in grafted tomato plants under NaCl stress originated from the increase in activities of CAT and the enzymes involved in

**Table 2**  
Antioxidants as markers of salinity tolerance in grafted vegetables.

Scion species	Rootstock species	Antioxidant	References
<i>Cucumis sativus</i> L.	<i>Cucurbita maxima</i> Duch. × <i>C. moschata</i> Duch.	SOD, POD, CAT, APX	Yang et al. (2006)
<i>Cucumis sativus</i> L.	<i>Cucurbita ficifolia</i> Bouché	SOD, Cu/Zn-SOD, Mn-SOD, CAT	Gao et al. (2008)
<i>Cucumis sativus</i> L.	<i>Cucurbita ficifolia</i> Bouché	SOD, POD	Huang et al. (2010)
<i>Cucumis sativus</i> L.	<i>Cucurbita moschata</i> Duch.	SOD, POD, CAT	Zhen et al. (2010)
<i>Citrullus lanatus</i> (Thunb.) Matsum and Nakai	<i>Cucurbita maxima</i> Duch. × <i>C. moschata</i> Duch.	SOD	Goreta et al. (2008)
<i>Citrullus lanatus</i> (Thunb.) Matsum and Nakai	<i>Lagenaria siceraria</i> Standl.	SOD, POD, CAT	Zhu et al. (2008b)
<i>Solanum lycopersicum</i> L.	<i>Solanum lycopersicum</i> L.	SOD, POD, APX, AsA	Chen et al. (2005)
<i>Solanum lycopersicum</i> L.	<i>Solanum lycopersicum</i> L.	SOD, POD, CAT	Zhang et al. (2008)
<i>Solanum lycopersicum</i> L.	<i>Solanum lycopersicum</i> L.	CAT, APX, DHAR, GR	He et al. (2009)
<i>Solanum melongena</i> L.	<i>Solanum torvum</i> Swartz	SOD, POD, CAT, AsA, GSH	Liu et al. (2007)
<i>Solanum melongena</i> L.	<i>Solanum torvum</i> Swartz	SOD, POD, APX, GR	Wei et al. (2009)

Abbreviations: SOD, superoxide dismutase; CAT, catalase; POD, peroxidase; APX, ascorbate peroxidase; DHAR, dehydroascorbate reductase; GR, glutathione reductase; AsA, ascorbate (reduced form); GSH, glutathione (reduced form).

the ascorbate-glutathione cycle such as APX, DHAR, and GR (He et al., 2009).

In addition to enzymatic antioxidants, non-enzymatic antioxidants were also found to contribute to the salinity tolerance in grafted vegetables. The AsA and GSH contents in the leaves of grafted eggplant seedlings were found to be significantly higher than those in self-rooted seedlings under NaCl stress (Liu et al., 2007). Compared with those on the leaves, there have been fewer studies on the antioxidant system in the roots of grafted vegetables under salt stress. Cucumber grafted onto salt tolerant rootstocks have lower root H<sub>2</sub>O<sub>2</sub> content, and higher root SOD, POD, and CAT activities than plants grafted onto salt sensitive rootstocks under NaCl stress (Zhen et al., 2010). Under excess Ca(NO<sub>3</sub>)<sub>2</sub> stress, grafted tomato plants have a lower root O<sub>2</sub><sup>-</sup> production rate and lower H<sub>2</sub>O<sub>2</sub> and MDA contents than self-rooted plants. The SOD, POD, and CAT activities in roots of grafted plants were significantly higher than in self-rooted plants (Zhang et al., 2008). Therefore, an efficient antioxidant system is an important factor for the enhanced salt tolerance of grafted plants. This is achieved by obtaining higher activities of anti-oxidative enzymes and contents of non-enzymatic antioxidants to scavenge ROS, thereby reducing oxidative damage.

### 3.2.5. Induction of hormones-mediated changes in plant growth

Hormones or their precursors have been hypothesized to regulate leaf growth inhibition under salt stress because decreased leaf growth rate is independent of carbohydrate supply, water status, nutrient deficiency, and ion toxicity (Munns and Tester, 2008). Abscisic acid (ABA) plays a central role in root-to-shoot and cellular signaling in salt stress, as well as in the regulation of stomatal conductance (Zhu, 2001b). Cytokinins are assumed to be synthesized mainly in the roots and transported to the shoots via the xylem. They are also implicated in several aspects of plant development, particularly the regulation of leaf senescence (Gan

and Amasino, 1995; Balibrea et al., 2004). Polyamines are small, cationic molecules ubiquitously present in prokaryotic and eukaryotic organisms. These molecules are involved in the regulation of many basic cellular processes such as DNA replication and transcription, cell proliferation, modulation of enzyme activities, membrane rigidity, and stabilization (Liu et al., 2004).

The ABA and total polyamine (putrescine, spermidine, spermine) contents of grafted tomato and eggplant seedlings are significantly higher than those of self-rooted seedlings under NaCl stress (Chen et al., 2006; Zhang et al., 2007; Liu et al., 2008a,b). In addition, the Spd and Spm contents, as well as (Spd + Spm)/Put value, were higher in grafted melon and cucumber plants than in self-rooted plants under NaCl stress (Xu et al., 2006; Yang et al., 2007). Similar results were also observed under other types of salt stress. Under excess Ca(NO<sub>3</sub>)<sub>2</sub> stress conditions, a higher polyamine content is consistent with higher arginine decarboxylase (an important enzyme responsible for putrescine biosynthesis) activity, suggesting that grafted tomato plants have a stronger capability to synthesize polyamines compared with self-rooted plants (Zhang et al., 2008). The activities of the polyamine degradative enzymes (diamine oxidase and polyamine oxidase) in grafted eggplant seedlings were significantly lower than in self-rooted seedlings, and the polyamine content in grafted seedlings were significantly higher than in self-rooted seedlings under excess Ca(NO<sub>3</sub>)<sub>2</sub> stress conditions (Wei et al., 2009).

The maintenance of shoot vigor dilutes toxic ions, but it also generates new (energetic) resources for defense against stress, which may allow root functioning to delay, minimize, or avoid toxic ionic effects (Munns and Tester, 2008). Tomato crop productivity under NaCl stress depends not only on "ionic message" delivery from the root to the shoot (salt-specific traits), but also on "hormonal message" [root-derived hormones: Z (zeatin), Z/ZR (zeatin riboside), Z+ZR/ACC (the ethylene precursor 1-

**Table 3**  
Morphological and physiological aspects involved in the tolerance of grafted plants to salinity and corresponding main site of action.

	Root-soil continuum level	Root level	Leaf level	References
Better root-to-shoot ratio	•			Huang et al. (2009a)
Root Na <sup>+</sup> accumulation		•		Bai et al. (2005); Wei et al. (2007); Zhu et al. (2008a); Zhu and Guo (2009)
Accumulation of compatible osmolytes		•	•	Ruiz et al. (2005); Huang et al. (2009a)
Potassium homeostasis			•	Zhu et al. (2008a); Albacete et al. (2009); Huang et al. (2009a)
Reduced Na <sup>+</sup> and/or Cl <sup>-</sup> translocation to the shoot			•	Santa-Cruz et al. (2002); Fernández-García et al. (2002, 2004); Estañ et al. (2005); Bai et al. (2005); Wei et al. (2007); Martínez-Rodríguez et al. (2008); Zhu et al. (2008a); Goreta et al. (2008)
Induction of anti-oxidative defense		•	•	Liu et al. (2007); Gao et al. (2008); Zhang et al. (2008); Wei et al. (2009); Zhu et al. (2008b); Zhen et al. (2010)
Synthesis of plant hormones		•	•	Chen et al. (2006); Xu et al. (2006); Yang et al. (2007); Zhang et al. (2007); Liu et al. (2008a,b); Zhang et al. (2008); Wei et al. (2009)

aminocyclopropane-1-carboxylic acid)]; these hormonal message can regulate leaf growth and senescence (vigor-related traits) (Albacete et al., 2009). Grafting results in an interactive relationship between a rootstock and a scion, overall, more root-to-shoot signals should be identified to elucidate the salt tolerance mechanism in grafted plants.

#### 4. Conclusions and future perspectives

For decades, vegetable grafting has been successfully practiced in many Asian countries, and it is becoming increasingly popular in Europe as well. This review concludes that grafting is an effective way to improve the salt tolerance of fruit-bearing vegetables. The grafting process itself had no obvious effect on plant salt tolerance. The increased salt tolerance of grafted plant was due to “the use of salt tolerant rootstock”, plants grafted onto different rootstocks respond more or less differently to salinity (Estañ et al., 2005; Ruiz et al., 2005). Grafting is also a well established technique for the growth and production of fruit trees under saline conditions (Rivero et al., 2003). Citrus grafted onto Cleopatra mandarin (*Citrus reshni* Hort. ex Tan) are more salt tolerant than those grafted onto Carrizo citrange [*Citrus sinensis* (L.) Osb. × *Poncirus trifoliata* (L.) Raf.] (Moya et al., 2002). Peach grafted onto GF<sub>677</sub> (*Prunus persica* × *Prunus amygdalus*) than Mr.S<sub>2/5</sub> (a natural hybrid of *Prunus cerasifera*) are more efficient in protecting plants from the deleterious effects of NaCl stress (Massai et al., 2004). Loquat plants grafted onto quince rootstock are more salt tolerant than self-rooted ones (López-Gómez et al., 2007). All the above leads to the conclusion that the selection of appropriate rootstocks could strengthen plant tolerance to salt stress.

Grafting can alleviate ion toxicity by limiting the transport of Na<sup>+</sup> and in some cases also of Cl<sup>-</sup> to the shoot while storing these in the roots, which are typical tissue tolerance mechanisms. The higher accumulation of compatible solutes and osmolytes in the cytosol of leaf cells can increase plant survival and delay leaf senescence of grafted plants. An efficient antioxidant system that reduces oxidative damage plays a key role in enhancing salt tolerance of grafted plants. In addition, induction of hormones may also enable grafted plants to adapt to salinity more efficiently. The above aspects could be involved in the tolerance of grafted plants to salinity at the leaf and/or root level (Table 3). The rootstock-mediated enhancement of salt tolerance undoubtedly provides an additional motivation for vegetable grafting in modern horticulture.

The physiological processes implicated in the salt tolerance of grafted plants have received much attention, but the molecular processes involved remain relatively unknown. Grafting restricts the transport of Na<sup>+</sup> to the shoot. However, the genes governing Na<sup>+</sup> transport are unknown.

Root-to-shoot signaling requires further studies. Plant adaptation to salt can occur in two timely distinct phases. In the first phase, the osmotic phase, adaptation mechanisms are activated immediately after the salt concentration in the root reaches to the threshold level, this results in a decrease in the rate of shoot growth. Determining how the salt-sensitive scion gets the message when the salt tolerant rootstock is exposed to salinity during this stage (not ionic message) is necessary.

Many studies on the effectiveness and mechanisms underlying enhancement of plant tolerance to NaCl by grafting have been conducted. However, limited research has been done on responses of grafted plants to other types of salinity (mixed or single-salt compositions). Thus, the identification of compatible rootstocks with tolerance to other types of salinity is a basic requirement for the continued success of grafting.

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