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Role of grafting in horticultural plants under stress conditions

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Abstract

The cultivation of grafted plants have gradually increased in the last years. As the use of this technique spread, the aims also expanded until today when grafting serves a spectrum of purposes: (1) to boost plant growth and development; (2) to control wilt caused by pathogens; (3) to reduce viral, fungal and bacterial infection; (4) to strengthen tolerance to thermal or saline stress; (5) to increase nutrient and mineral uptake to the shoot, etc. Throughout this review, we have examined the advantages of grafting plants for current agriculture, these being: resistance to evermore frequent soil diseases; tolerance of low temperatures characteristic of many latitudes of the world where intensive cultivation is economically important; tolerance to the growing problem of salinity from abuse of chemical fertilizers and desertification in many agricultural zones; and enhanced water and inorganic-nutrient uptake. All these advantages provide motivation for grafting in present-day world agriculture.

***Key words**: Grafting, soil pathogens, salt stress, thermal stress, mineral nutrition.*

Introduction

The cultivation of grafted horticultural plants began in Korea and Japan at the end of 1920 on grafting watermelon plants to squash rootstocks[1]. After the first experiments, the cultivation of grafted plants gradually increased in these countries, and currently most watermelon, cucumber and various Solanaceae crops are grafted before being transplanted in the greenhouse or in the field[2] . Thus, this technique is widely used in many parts of Korea and Japan, and throughout Asia and Europe for intensive crop systems[3], reaching 81% of the cultivation in Korea and 54% in Japan. Initially, the cultivation of grafted plants was intended to diminish damage by soil pathogens, primarily *Fusarium oxysporum*. However, as the use of this technique spread, the aims also expanded until today when grafting serves a spectrum of purposes: (1) to boost plant growth and development; (2) to control wilt caused by pathogens; (3) to reduce viral, fungal and bacterial infection; (4) to strengthen tolerance to thermal or saline stress; (5) to increase nutrient and mineral uptake to the shoot, etc.

The cultivation of grafted plants has expanded greatly in recent years due primarily to the discovery that the same variety can be grafted to different rootstocks, depending on the aim. Such crops as watermelon, melon, cucumber, tomato and eggplant are commonly grafted onto different rootstocks prior to being transplanted in the field or, predominantly, in the greenhouse. In this review, we seek to summarize the current role of grafted plants in horticulture and its responses to stress, such as soil pathogens, thermal stress, salinity and nutritional stress.

Response of Grafted Plants to Stress

Resistance to soil pathogens: Most horticultural crops are often exposed to a broad spectrum of adverse environmental factors, both biotic and abiotic. Some of the most dangerous and common biotic factors that most crops currently face are soil diseases caused by viruses, fungi and bacteria, as well as nematodes[4,6]. The main injuries to roots caused by these soil pathogens, which are becoming more and more numerous and threatening in greenhouse cultivation, are smaller foliar size, as well as thin weak stems, wilt, depressed flowering, and poorer fruit quality in short, a reduced life span of the plant[4,5]. The primary problem confronting farmers is that by the time the plants begin to present visual symptoms, the crop can already be lost. As the pathogens attack the roots, the first symptoms usually appear in the leaves when the plant is completely infected. The only feasible option for the farmer is to take preventive measures, involving soil treatments for the following crop season. Plant resistance offers another possibility, and, in this sense, the development and use of rootstocks resistant to different soil pathogens could offer one of the most promising advantages of grafted plants in present-day horticulture[7,8]. There is no doubt that a strong and vigorous rootstock has better tolerance against diseases caused by fungi such as *Verticillium* or *Fusarium*, by bacteria such as *Pseudomonas*, by viruses such as TYLCV (tomato yellow leaf curl virus, transmitted by *Bemisia tabaci*), although the degree of tolerance varies considerably from one plant to another, depending on the genotype of the rootstock[9]. Despite its importance, this mechanism of resistance or tolerance has not been intensely investigated[10]. Tolerance to these diseases in grafted plants may be due to the resistance of the rootstocks, as it is accepted that the root system synthesizes substances resistant to pathogen attack, and these are transported to the shoot through the xylem[11]. The activity of these substances, related to disease resistance, can vary during the development stages of grafted plants[12,13]. One of the points to be studied in this sense, having received little or no research, is that rootstocks are resistant or tolerant to pathogen attack, since no work to date concludes whether the reduction of damage by these agents in grafted plants is due to the greater resistance to diseases for the rootstock selected. It is accepted that the characteristics of disease susceptibility of the shoot are not translocated to the rootstock. This implies that the rootstocks are govern the degree of infection of a disease[10]. On the other hand, chemical soil fumigation, being strongly limited by different governments for reasons of environmental pollution, has sharply declined. Also, given the economic expense involved, this practice offer little solution to diseases that attack plants in infected soils[9]. Thus, the selection of rootstocks resistant to soil pathogens implies an advantage in terms of reduced use of chemical agents. Nevertheless, as indicated above, more research is needed in this regard to identify the mechanisms controlling disease tolerance.

***Resistance to low root temperatures**:* Injuries inflicted by low temperatures are defined as the damage caused by physiological and biochemical alterations induced by temperatures above the freezing point but below 12ºC.[14] Many of the most economically important crops, such as corn, tomato, squash, cucumber, watermelon and cotton are highly sensitive to cold temperatures during their vegetative development and reproduction[15,16]. In addition, seed germination and seedling development are two critical stages in the survival of a temperature-sensitive crops. Low soil temperature is one of the major factors affecting this survival, inflicting heavy economic losses in yield[17,18], by reducing plant growth and development, causing wilt and necrosis, and retarding fruit ripening[19,20]. All this results from a limitation in the uptake of water and essential mineral nutrients[20], bringing about a serious fall in root conductance[21] and an extrusion of endogenous solutes triggered by degraded membrane integrity[22]. On the other hand, because soil temperature tends to vary more slowly than aerial temperature, the roots can suffer consequences of cold over longer periods than does the shoot. It is well known that some rootstocks are more resistant to low temperatures, implying an adaptive advantage of certain crops. However, the reason why these rootstocks offer more resistance than do others is still not clearly understood. Exudation of xylem sap has been proposed[23], as has high oxygen consumption, as possible mechanisms of resistance to low temperatures. In addition, Tachibana[24] demonstrated that the roots of squash plants respond to the low temperatures by stimulating meristem activity and photosynthate translocation. This resistance could be explained by the mechanisms described above, although they have received little attention and their effect on the shoot is completely unknown[20]. However, different species have been studied at low temperatures in order to select the most resistant rootstocks for use in grafted crops. For example, the cucumber (*Cucumis sativus* L.) is often grafted onto *Cucurbita ficifolia* rootstocks as well as different genotypes of *Sicyos angulatus* which are resistant to low temperatures, boosting growth and yield in the cucumber[25-27]. Criteria for selecting rootstocks tolerant to low temperatures are based on lipid differences in membranes[28,29]. The desired profile includes an increase in the total of lipids per gram of fresh weight, an increase in the ratio fatty acid/total lipid, a high degree of unsaturation of fatty acids, and finally a reduction of the ratio esterol/total lipids[30-33]. Horvath et al.[34] demonstrated that the ratio esterol/phospholipids was the main indicator of low-temperature tolerance, since they found an inverse relationship between the ratio esterol/phospholipids and resistance to cold in the leaves of cereals. A high value of this ratio corresponds to a more cold-sensitive plasma membrane, prompting a strong esterol-esterol interaction in the lipid bilayer, this in turn causing disruptions in the membrane. These effects were also noted in membranes of roots subjected to low temperatures[32]. Studies on cucumber by Horvath et al.[31] and Bulder et al.[32] demonstrated that some of the effects caused in roots by tolerance to low temperatures were found in the leaves of sensitive species, and thus the presence of these effects in the leaves is not indicative of low-temperature tolerance in the roots, since the foliar lipid composition differs from the lipid composition of the roots. These are four examples that show that the use of grafted plants onto rootstocks tolerant of low soil temperatures would assure good development and optimal production of the crop with little or no economic loss from low environmental temperatures.

***Resistance to salinity**:* In the past, stress caused by high concentrations of salts in the environment had little importance because these situations arose only in areas near the coast or in particular environments with evaporation of salt-rich waters. However, the development of agricultural techniques in recent years has made salt stress one of the chief problems in agriculture today. The indiscriminate use of heavy quantities of chemical fertilizers and the overexploitation of aquifers has dramatically multiplied the surface area affected by salinity[35]. Currently, a third of all irrigated lands in the world are affected to a greater or lesser degree by salinity[36]. A heavy environmental concentration of salts unleashes various types of physical and chemical stress in plants, provoking complex responses that involve changes in plant morphology, physiology and metabolism[37,38]. It is commonly accepted that growth inhibition by salt stress is associated with alterations in the water relationships within the plant, caused by osmotic effects with specific ionic consequences (excesses or deficits) or energy availability related to carbohydrate concentrations[39]. Prior research on the possible mechanisms of growth inhibition and salt tolerance are often based on the comparative study of tolerant and sensitive lines. However, as with most types of environmental stress, the assessment of the tolerance level of the different processes of developing salt stress is a complex task, though it is fundamental to establish criteria for action in such situations. For example, growth and reproduction can be altered in different ways in the same plant, as the shoot is usually more salt sensitive than the root[40]. Salt stress has two components that negatively affect plant growth: the osmotic component and the ionic component. A heavy salt concentration lowers the water potential in the soil, inducing water stress in plants. This is known as the osmotic component of salinity. On the other hand, certain ions are toxic for glycophytes (the immense majority of cultivated plants)[35], and this represents the ionic component. Among the most abundant toxic ions are Cl^- and Na^+, although other ions can also cause problems, such as NO_3^-, SO_4^{2-} and NH_4^+ [41]. Damage from salinity has been attributed principally to an excess of Cl^- and Na^+ accumulation in the leaves,[42] provoking a nutritional imbalance, as these ions reduce the concentration of Ca, Mg and K [43,44]. The high concentration of Cl^- in the aerial parts of citrus can be prime cause of physiological disturbance and eventual visible damage to the foliage[45]. The high foliar concentration of Na^+ interferes with photosynthesis and transpiration[46]. Some of these adverse effects of salinity have been attributed to a K^+ deficiency, due to antagonistic action by Na^+ [47].

With reference specifically to the behaviour of the root system, plants that tolerate salinity can be grouped into ion-exclusive and ion-inclusive plants[41]. Ion-exclusive plants have diverse adaptive mechanisms to restrict salt from reaching the aerial parts except in very small quantities. These mechanisms include the efficient uptake selectivity by the roots with respect to certain ions, accumulation of Cl^- and Na^+ in the roots, and exclusion of ions from entering the roots from the exterior. On the contrary, inclusive plants take up salt in great quantities and store it in the stems and leaves. In this case, the main adaptations are based on the elimination of Cl^- and Na^+ from the cytosol by storage in the vacuoles or from the cell itself[35].

If the ions Cl^- and Na^+ damage the plant at high concentrations in the leaves, the selection of exclusive rootstocks (salt tolerant) could increase resistance to salinity in grafted plants[48,49]. This has promoted research on growth and yield with new salt-tolerant rootstocks[50]. In grafted citrus, Cooper[42] demonstrated that the foliar Cl^- concentration was the most useful value to assess the damage caused by salinity and to classify salt tolerance. Later, Zekri and Parsons[51] observed that the accumulation of heavy foliar concentrations of Cl^- caused leaf burn, notably reduced growth and upset water relationships. Meanwhile, no injury was noted in plants that accumulated Na^+ in the leaf, and neither growth nor the water relationship were not severely affected. Zekri[52] reported that the reduction in the foliar chlorophyll content was due more to Cl than Na^+ accumulation. Behboudian et al.[46] observed that the aerial parts of citrus grafted to the rootstock 'Cleopatra mandarin' (*Citrus reshni* Hort. ex Tan.) accumulated less Cl^- in its stems and leaves than did the aerial parts of citrus grafted to the rootstock 'rough lemon' (*Citrus jambhiri* Lush), evident in the more severe injury in the aerial parts of the latter. Walker[53] demonstrated that the rootstock 'Cleopatra mandarin' excludes Cl^- but not Na^+. This confirms the data reported by Sykes[54] identifying grafted fruit trees with the capacity of excluding Cl^-; however, these trees were incapable of excluding Na^+ or including it. This suggests that the ability to exclude these two ions stems from different mechanisms[54]. Picchioni et al.[55] studying the effect of salinity on grafted *Pistacia* spp., found higher Cl^- concentrations in the roots and rootstock than in the aerial parts. This same study on *Pistacia* reported five-fold greater storage capacity of Na^+ in the roots than in the leaves. With respect to the salt-tolerance mechanisms among inclusive plants, Zekri and Parsons[44] determined that in citrus grafted onto sour orange (*Citrus aurantium* (L.) Cl^- was not excluded, but instead was accumulated in the aerial part, where no effects or severe injury was evident; therefore, the conclusion was that the leaves of the aerial part must have the capacity of partially excluding Cl^- from the cytoplasm towards the vacuoles, where it could exert a certain influence on metabolic functions. One method of ascertaining whether the rootstock presents exclusive salt tolerance is to determine the proline in the leaves, since, as reported by Sánchez-Diaz and Aguirreolea[56], when the salts do not accumulate in leaves, the plants utilize organic substances to lower the osmotic potential of the cytoplasm and the vacuole and thereby lower the foliar water potential. Among these organic compounds that do not interfere in the cell metabolism at high concentrations is proline. The quantity of carbon used for the synthesis of these organic solutes can be high. Nevertheless, when ions are taken up by the leaves and accumulated in the vacuoles, the cell osmotic potential increases without damaging the salt-sensitive enzymes of the cytoplasm. In these leaves, the water balance is maintained between the cytoplasm and the vacuole, accumulating organic compounds such as proline in the cytoplasm. Because the volume of the cytoplasm in a adult vacuolated cell is small compared with the volume of the vacuole, the quantity of organic compounds synthesized is lower. Finally, Romero et al.[57] have shown that melon grafted plants exhibited differences in leaf content of Na^+ and especially Cl^- in comparison with ungrafted plants. It is assumed that grafted plants developed various mechanism to avoid physiological damage caused by the excessive accumulation of these ions in leaf, including the exclusion of Cl^- ion and/or decrease in Cl^- absorption by the roots and the replacement or substitution of total K^+ by total Na^+ in foliar parts. All the above leads to the conclusion that the selection of rootstocks that are exclusive or inclusive of ions could strengthen resistance to high salt concentrations in the soil.

Nutritional status in grafted plants: The fact that certain rootstocks show stronger resistance to soil pathogens[9,58], greater tolerance of low soil temperatures[19,20] as well as of salt stress[38,59] has been well documented in the past. Nevertheless, few works demonstrate the effect that the rootstock exerts on the foliar content in nutrients. Thus, the selection of rootstocks is rarely based on characteristics related to nutrient uptake, but rather almost always on resistance to environmental stress[60]. Knowledge of the rootstock/scion nutritional relationship could be decisive in choosing rootstocks tolerant or resistant to soils that are deficient or toxic in one or more nutrients, as well as in preparing fertilization programmes after the grafted plant is transplanted to the field or greenhouse[61]. Initially, Chaplin and Westwood[61], working with fruit trees grafted to different rootstocks found no clear evidence that the rootstock engendered a different nutritional composition in the leaves of those trees, concluding that the phenotype of the aerial part appeared to be more determinant of the foliar content in nutrients than was the rootstock. Later, Tagliavani et al.[62], in a similar study, suggested that the differences in the uptake and translocation of nutrients depended on the vigour of the aerial part, and that the concentrations of the different nutrients in the xylem appeared to be more indicative of the vigour derived from the combination of the rootstock and the scion. Later, Brown et al.[63], investigating grafted *Pistacia* spp., found that a change in the rootstock brought about variations in the foliar content of several essential nutrients of the plants. Ruiz et al.[60] suggested that in melon plants grafted to different rootstocks the foliar contents of N, Na and K were determined by the rootstock genotype, and also that the foliar content in N and Na found in these plants led to differences in yield. In an earlier work by Ruiz et al.[64] on grafted melon plants, the rootstock was found to have a positive effect on the foliar levels of total P, reflected by the greater shoot vigour in these plants as well as a higher carbohydrate content (glucose, sucrose, fructose and starch). These authors concluded that with good P uptake by the roots the concentration in carbohydrates falls, these components being transported from the root to the shoot, thereby increasing the vigour of the aerial part of the plant[10,64]. In addition, Pulgar et al.,[65] studying the concentration of different micronutrients in the leaves of watermelon grafted to different rootstocks, found that the free-Zn content was lower in grafted plants but presented greater foliar biomass than did the same species without grafting. Because Zn is directly involved in the synthesis of nitrogenous compounds of high molecular weight,[66] Pulgar et al.[65] concluded that the free-Zn levels were lower in grafted plants because of greater transport of this metal to the aerial part and higher efficiency in integrating this element into nitrogenous compounds that form chelates with Zn, thereby also explaining the greater foliar biomass found in these plants. In short, there is no doubt that in grafted plants the uptake of water and mineral nutrients is greater, giving rise to variations in the foliar concentration of these plants with respect to ungrafted plants. The first and basic consequence is more vigorous development of the plant and a proportional reduction in the susceptibility to different types of environmental stress.

Conclusions and Future Prospects

Throughout this review, we have examined the advantages of grafting plants for current agriculture, these being: resistance to evermore frequent soil diseases; tolerance of low temperatures characteristic of many latitudes of the world where intensive cultivation is economically important; tolerance to the growing problem of salinity from abuse of chemical fertilizers and desertification in many agricultural zones; and enhanced water and inorganic-nutrient uptake. All these advantages provide motivation for grafting in present-day world agriculture. That one rootstock can be more resistant than another against certain factors of biotic or abiotic stress is unquestionable. However, the mechanisms of such resistance has not yet been thoroughly investigated. Although grafting at times appears to be a mysterious surgical procedure accessible only to highly specialized professionals, only basic instructions (although of vital importance) are needed for most people to learn successful grafting[67]. It should be emphasized that grafting today is performed manually in most countries. In addition, the costs of the automated chambers to control the conditions of light, temperature and humidity, plus the price of the seeds selected for the graft, entail a substantial economic expense. The simple fact that the cut made in the hypocotyl is today made manually by specialized people using specially designed knives implies salaries that steadily rise. At present, semi-automatic and fully automatic grafting machines are being developed.[68] Because of the costs involved in grafting, the use of advanced technology is becoming more attractive, as automation could raise production by 150%[68]. Finally, with notable advances in molecular biology during the last decade, transgenic plants capable of resisting a great number of adverse factors represent competition against grafted plants. However, the many complications in finding and introducing genes for resistance to various environmental stress factors has until now conferred an advantage of grafting over genetic engineering in plants.

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