



Review

WATER AND SALINE STRESS ON CITRUS. STRATEGIES FOR REDUCING PLANT DAMAGES

Revisión bibliográfica

Estrés hídrico y salino en cítricos. Estrategias para la reducción de daños

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ABSTRACT. Water and saline stress affect markedly plant growth and yield. It is hoped that these stresses are intensified a cause of global climate change. Citrus, a perennial crop with a long horticultural life and a world importance are susceptible species to these kinds of stresses. For this reason, the objective of this review was to analyze the effects that water (drought and flooding) and saline stress cause on citrus crop and describing some of strategies proposed at present, to reduce plant damaged induced by them.

RESUMEN. El estrés hídrico y el estrés salino afectan sensiblemente el crecimiento y el rendimiento de las plantas. Se espera que estos estreses se intensifiquen cada vez más debido al cambio climático que se está produciendo a nivel global. Los cítricos, un cultivo perenne con una larga vida hortícola y gran importancia a nivel mundial, son especies sensibles a estos tipos de estrés. Por tal motivo, el propósito de la presente revisión fue analizar los efectos que tanto el estrés hídrico, por defecto y por exceso, como el estrés salino causan en el cultivo de los cítricos y describir algunas de las estrategias que actualmente se proponen para reducir los daños a las plantas provocados por los mismos.

Key words: Citrus, abiotic stress, tolerance

Palabras clave: Citrus, estrés abiótico, tolerancia

INTRODUCTION

Climate change has had a significant impact on agriculture (1), so it is expected, in addition, a direct or indirect impact on food production. The increase in average temperature, changes in precipitation patterns, the increasing variability in temperature and precipitation patterns, changes in water

availability, the frequency and intensity of 'extreme events', the increase in sea level and salinization will have profound impacts on agriculture, livestock and fisheries (2).

Hydric and saline stress will be, as described above, two of the stresses that are impacting agriculture, hence the importance of controlling the adverse effects they cause on the growth and yield of crops; as well as the strategies to be followed to counteract them.

Drought is considered one of the environmental factors that most limits the yield and development of crops and significantly affects photosynthesis (3-5). It must be considered that this stress

is growing strongly in size and severity in many regions of the world (6).

On the other hand, in the 90s it was estimated that the proportion of soils affected by salinity was around 10 % of the world total and that between 25 and 50 % of the irrigated areas were salinized. At present, there is no reference to the levels of areas affected by this factor, but it is clear that this situation is becoming increasingly acute in the areas cultivated worldwide, as a result of the lack of environmental awareness and exploitation of water resources irrationally, in addition to other edaphoclimatic factors that directly influence the salinity of soils (7).

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Citrus fruits, a perennial crop with a long horticultural life, are restricted in their vegetative growth and in their yield by drought stress (8), besides this stress affects the quality of the fruit and causes great economic losses to the producers. On the other hand, citrus fruits are considered sensitive to both flood stress (9) and salinity (10).

For all the above, this review presents the advances on the effects that water stress (both by default and excess) and saline cause on the production and quality of citrus fruits, as well as the strategies proposed to mitigate the adverse effects that they cause in this crop.

EFFECTS OF WATER STRESS ON CITRUS CULTIVATION

From all the resources necessary for the growth and development of plants, water is the most important and limiting. Water is the majority component of the plants, since it constitutes 90 % of the fresh mass in the herbaceous species and more than 50 % in the woody ones. Plants absorb water continuously through the roots and lose it through the leaves; however, the absorption occurs while the water potential of the plant is more negative than the water potential of the soil; since when the internal water potential is equaled to the external one, the absorption of water ceases and the plants become dehydrated.

Plant productivity is closely related to the amount of water available and the efficiency of its use. A plant that is capable of acquiring more water or that has a superior efficiency of its use will better withstand drought. It should be noted that some plants have adaptations, such as plants C_4 and CAM, which have modes of photosynthesis

that allow better exploitation of arid environments and have acclimation mechanisms that are activated in response to water stress (11).

On the other hand, many species are sensitive to a greater or lesser extent of stress due to excess water or flood stress and to survive these conditions have developed a wide variety of physiological, biochemical and molecular responses, many of which guide changes morphological and anatomical (12). Below we will analyze some of the results reported, internationally, on the effects caused by water stress, both by default and by excess, in the plants of different citrus species; as well as some strategies that have been used to mitigate the adverse effects of stress and to achieve a more efficient use of water.

STRESS DUE TO FLOOD

The physiological and metabolic effects of flooding in plants are mainly derived from the decomposition of mitochondrial aerobic respiration of the roots and the subsequent decrease of oxygen, which implies reductions in the water flow from the roots followed by alterations in the use of this, nutrient consumption and partition of the dry mass (12,13). This can bring changes in the partition of nutrients and endogenous concentrations of micro and macro elements, with multiple deficiencies (14).

On the other hand, at leaf level, there is a decrease in stomatal conductance, to avoid water losses, together with a decrease in photosynthetic activity, which constitutes the first defense barrier against stress.

Citrus fruits respond to flood by decreasing stomatal conductance and gas exchange (9, 5, 16).

In addition, it has been detected, also, that this stress causes an increase in the content of abscisic acid in the leaves and a reduction in the hydraulic conductivity of the roots (17), so that a prolonged period of stress can affect the growth and cause leaf damage such as chlorosis and wilting (18,19).

On the other hand, the effect of flooding on citrange 'Carrizo' postures was studied (20) and it was shown that a 36-day treatment significantly reduced the nitrogen content of the roots and leaves of the postures, in addition to caused important changes in the distribution of this element inside the plants. The concentration of sucrose increased significantly in the roots and leaves, while the starch was reduced, which indicates that flood stress alters the nitrogen and carbon contents and the partition of them in the cultivation of citrus fruits. Previously, other authors had reported (21), in one-year-old postures of the same cultivar, that the flood for 35 days had no effect on the water potential or the relative water content of the leaves; however, it reduced the hydraulic conductivity in the roots of the postures; which was related to the sub-regulation of the expression of aquaporins.

Inoculation with arbuscular mycorrhizal fungi has become one of the strategies that have been evaluated to reduce the damage that the flood causes in citrus fruits. Thus, the inoculation of the species *Diversispora spurca* in *Citrus junos* subjected to 37 days of flooding showed that although the flood significantly restricted the mycorrhizal colonization, the mycorrhizal postures exhibited stimulation in the growth, in the concentration of soluble proteins and in the activity of the catalase enzyme, causing less oxidative damage (22).

STRESS DUE TO WATER DEFICIT

The water deficit is associated with environments with low rainfall or with irregular distribution of precipitation and can be defined as any water content of a tissue or cell that is below the highest water content exhibited in the most hydrated state. The water deficit has several effects on growth, one of which is the limitation of foliar expansion and it is known that the leaf area is important, since photosynthesis is proportional to it (11).

Many authors have reported that the response of citrus trees to water deficit depends, mainly, on the phenology of the crop and the effects that have been observed are closely related to the timing, duration, and physiological state of the crop, water quality of irrigation, the genotype and the degree of stress imposed on the crop (23).

However, the negative impact can be mitigated by an improvement in fruit quality as has been demonstrated by several authors in several citrus species (24-26).

It cannot ignore the role that patterns play in the tolerance of citrus to water deficit. Thus, the behavior of the lime patterns 'Rangpur' and citrumelo 'Swingle' in 'Valencia' orange trees grown in water deficit conditions was studied (27) and it was found that stress reduced the leaf water potential and caused limitation in the diffusion of photosynthesis in both patterns. However, the trees grafted on the 'Rangpur' lime pattern presented an accelerated radical growth, maintenance of the "pool" of total carbohydrates and a large displacement in the partition of the carbohydrates, with the roots accumulating carbohydrates in conditions of water deficit.

Despite the greater sensitivity of the citrus pattern 'Swingle' to the water deficit compared to the 'Rangpur' file, it has been shown that plants transformed from this one with the P5CSF129A gene that codes for the key enzyme of the proline synthesis in conditions of water deficit, they were able to escape from water deficit better than non-transformed plants, since the high endogenous level of proline acted not only in favor of osmotic adjustment but also contributed to improve the indicators of gas exchange and to improve the damaging effects of stress oxidative induced by drought (28).

In addition, it has been suggested that the MYB-R2R3 type gene, stress response in trifoliolate orange (*Poncirus trifoliata* (L.) Raf.), designated as PtsrMYB, plays a positive role in tolerance to dehydration (29) and this may be due, in part, to the modulation of polyamine synthesis by the regulation of the arginine decarboxylase (ADC) gene.

Inoculation with arbuscular mycorrhizal fungi increases the tolerance of plants to water deficits, including citrus fruits (30).

Research on the effects of mycorrhization on citrus plants under water stress began more than 30 years ago, when the influence of AMF on stomatal conductance, photosynthesis and proline content of 'Rugoso' lemon (*Citrus jambhiri* L.) seedlings was reported during the development and recovery of a water deficit in the soil (31).

As of that moment, many interesting results have been reported, both from experiments carried out in semi-controlled conditions and in field conditions (32).

It is important to note that the response of mycorrhizal colonization to water deficit depends on the severity and periodicity of the deficit (33). In *C. sinensis* L. Osbeck grafted on *Poncirus trifoliata* L. Raf,

it was observed that there was no involvement of mycorrhizal colonization with *Glomus versiforme*, when the plants were exposed to a water deficit for up to six days (34).

However, once the deficit extended to 12 days, colonization declined from 40,7 to 8,3 %. This led to the idea that the amount of water in the soil that is optimal for the plant's growth can also be used for the development and sporulation of the mycorrhiza (30).

The tolerance to water deficit in mycorrhized citrus plants has been associated with an extra-radical hyphal growth that facilitates the absorption of water and nutrients, especially phosphorus nutrition. On the other hand, the spatial configuration of the radical system is modified, the concentration of polyamine spermine is increased, there is an osmotic adjustment through non-structural carbohydrates, K⁺, Ca²⁺ and Mg²⁺, and reactive oxygen species decrease (32).

Another aspect that can increase tolerance to the water deficit of citrus trees is the management of nitrogen fertilization. In this sense, it was demonstrated that foliar spraying of two-month-old *C. macrophylla* seedlings with KNO₃ 2 % accelerated tree tolerance to water deficit, increasing osmotic adjustment processes (35).

The results presented so far demonstrate that, when there is water limitations in the soil, the selection of the appropriate rootstock, the possible inoculation thereof with an efficient AMF strain and the application of nitrogen fertilization become a crop management that can mitigate the adverse effect caused by water deficit in citrus plants.

It is interesting to know that in recent years, due to growing demands for water from agriculture,

systematic drought events and the difficulty of adopting unconventional water sources for irrigation (36), the paradigm of water management in fruit trees, from full supply to partial water needs of the crop (37). One of the most promising techniques to achieve this objective is the use of deficit irrigation (DI), a water supply strategy proposed to improve water productivity and reduce the application of irrigation (38).

In citrus, results have been reported in several species associated with the implementation of this irrigation strategy. Thus, for example, some authors (39) showed that it is possible to grow 11-year-old orange trees 'Navelina' (*Citrus sinensis* L. Osb.), grafted on citrange 'Carrizo' pattern (*C. sinensis* L. Osb. x *Poncirus trifoliata* L. Osb.), with limited water resources in the Mediterranean area without causing severe reductions in yield. The results guided to that the hydric deficit diminished the yield between a 10 -12 % but the productivity of the water increased in a 24 % in relation to the control treatment completely irrigated. In addition, the importance of the phenological stage in the response of plants to water deficit was confirmed.

These same authors, in addition, evaluated the influence of three deficit irrigation treatments on the yield and quality of the fruit of the 'Salustiano' orange tree, aged 12 years old, and reported that regulated deficit irrigation has a significant and important effect on the quality of the fruits; however, its effect was not so clear on yield, to such an extent that irrigation treatment at 50 % of crop evapotranspiration did not significantly reduce this indicator, despite having practically reduced it by almost 10 % (40).

In Italy, in a young orange tree plantation, the deficit irrigation and a partial drought of the root zone were studied, through water supply according to different percentages of crop evapotranspiration, and it was found that the composition of the fruit was favored with the water restrictions imposed (41).

In Central India, it was found that in mandarin trees (*Citrus reticulata* Blanco) cv. 'Nagpur' grafted on 'Rugoso' lemon pattern, drip irrigation treatments on alternate days corresponding to 80 % of ETc stimulated the growth and yield of the plants and saved 29 % of the irrigation water, compared to the treatment control (42). Subsequently, the use of this deficit irrigation strategy was suggested for citrus orchards growing in hot and sub-humid climate of Central India (43).

The application of this strategy for a longer period of time (five years) was investigated in Valencia, Spain (44).

They showed that the restriction of the water supply (40 and 60 % of the control treatment) during the initial phase of cellular lengthening of the fruits of orange trees 'Navelina', did not negatively affect the quantity and quality of the yield, provided that the water potential of the trunk at noon (Ψ_{st}) does not exceed the value of -2,0 MPa.

The application moment importance of the deficit irrigation in the quality of the grapefruit fruits (*Citrus paradisi* Macf.) was verified when the trees were irrigated to 50 % of the ETc in the phases I, II and III of growth of the fruits. The results showed that the treatment in phase I only delayed the external maturation, while the one carried out in phase II delayed the ripening of the fruit, increased the acidity and reduced the concentration of sugars. Treatment in phase III advanced internal maturation (45).

Previously, the influence of the application of deficit irrigation (reduction of 40 and 29 % of the water applied in the control treatment), during the growth of the fruits, in the quality of the mandarin 'Fortuna' (*Citrus clementina* Hort ex. Tanaka x *C. reticulata* Blanco) had been reported. Both treatments of deficit irrigation improved the quality of the fruit in the harvest due to an increase in the TSS and the proline in the juice, maintaining the fruit its quality more time during the storage, in comparison with the control treatment. On the other hand, at the end of storage, the fruits from the deficit irrigation treatments showed a thicker crust and less damage from cold damage (46).

In Cuba, in the climatic conditions of the Isle of Youth, the obtaining of early harvests, with the consequent advance of the ripening of the grapefruit fruits, was determined by the humidity of the soil, induced by the precipitation, in the period included between the 3rd tenth of June and the 1st of July (beginning of phase III of fruit growth), so that when this is equal to or greater than 85 % of the field capacity allowed the harvest of up to 11 and 43 % of fruits in the 3rd tenth of July and 1st of August, respectively (47).

A study conducted in another location (Ceiba del Agua, Artemisa province), evaluated the influence of water deficit on the growth of grapefruit fruit from the dynamics of the equatorial diameter during phases I and II of growth during two years; and it was proven that deficits occurred from 30 at to 90 days of age of the fruit, markedly affected the growth of the same, prolonged in time the phase II of linear growth, and this extended with respect to the first year in 40 days more, consequently the fruits

at the time of harvest reached a smaller final size. As a result, the fruits of the first year at 110 days, had obtained 90 % of the final size, while those of the second reached around 150 days (48).

These results acquire a great connotation, at present, due to the global need to take care of water resources and the importance of water for all living beings is well known. For this reason, it has been investigated in areas of various citrus-growing countries such as Spain, Italy, India, among others. There is no doubt that the implementation of an irrigation system in the cultivation of citrus fruits that saves water without significantly affecting the yield and the quality of the fruits, becomes an option of great economic and environmental impact. In addition, in citrus areas, which do not have irrigation and can be affected by water stress (both excess and defect), it is necessary to establish strategies that contribute to the mitigation of the adverse effects caused by this stress. Among them, plays an important role the appropriate selection of the rootstock, the possible inoculation with strains of efficient arbuscular mycorrhizal fungi, the adequate supply of nitrogen nutrition, among others.

Effects of salt stress in the cultivation of citrus fruits

Salinity is among the environmental factors that cause considerable losses in agricultural production worldwide and it is one of the most serious problems facing sustainable agriculture in irrigation production systems in arid and semi-arid regions (49).

Around 20 % of the cultivated area in the world and almost half of the irrigated lands are affected by this stress (50). This is a critical problem, especially in citrus fruits,

as they are one of the most important horticultural crops worldwide, considered sensitive to salinity (51).

Salinity causes severe damage to citrus fruits, such as tissue burns, loss of yield, foliar abscission and finally death of the plant (10). This environmental stress has three components: an ionic one linked to the accumulation to toxic levels of the Cl⁻ and Na⁺ ions in the cytoplasm, leading to an ionic imbalance; an osmotic component due to the compartmentalization of this toxic ion in the vacuole that causes the water potential of the cytosol to decrease in order to balance the low external water potential and ensure the entry of water into the plant cell and avoid damage to the macromolecule (52). In addition, from the toxic and osmotic effects of salinity, the high cellular concentration of NaCl causes accelerated formation of reactive oxygen species (53). These species can cause alteration in normal metabolism through oxidative damage to lipids, proteins and nucleic acids (54).

The accumulation of other ions, such as boron can often exist simultaneously and may have synergistic effects on plant responses to stress by NaCl (55). In citrus, it has been found that the accumulation of Cl⁻, B³⁺ and in some cases, Na⁺, in the foliar tissues can be toxic; however, it is difficult to quantify the contribution that both the osmotic or toxic effect causes in the decrease in growth induced by salinity, although researchers have found a decrease in growth without observing symptoms of damage.

Therefore, it is thought that osmotic effects are dominant in the effect of decreasing growth, although if stress remains, ion toxicity can become the dominant stress (56).

On the other hand, the ability of plants to withstand salt stress rests on the root system and it is based on the ability to control the consumption of ions by the radical cells, the load of the xylem and the removal of salt from the xylem and the upper tissues (57). The ability of citrus fruits to restrict the transport of Cl⁻ from the roots to the branches is directly dependent on the genotype of the rootstock in question (58).

The physiological effects of salinity depend on the duration of stress, the genotype and the age of the plants (59). Some studies have shown that salt stress induces a decrease in net photosynthesis and stomatal conductance, affecting the availability of CO₂ for carboxylation (60).

It is also known that stomata play a fundamental role in the regulation of transpiration based on their density on the leaf surface and a mechanism of closure, enabling the plant to control water losses in environmental stress conditions. In fact, it has recently been reported that low stomatal density and reduced transpiration are critical factors that determine stress tolerance and may allow plants to adapt more easily to salinity (61).

To evade the effects of salinity, plants regulate their osmotic potential and compartmentalize toxic ions. The regulation of the osmotic potential to maintain the turgor pressure includes several processes, such as the consumption of K⁺, the compartmentalization of Na⁺ and Cl⁻ in the vacuole and the synthesis of compatible solutes such as proline, glycinebetaine, sugars, polyols, among others. (62).

At the molecular level, the mechanisms involved with Na⁺ compartmentation are well documented in *Arabidopsis thaliana* and many genes

encoding co-transporters and Na⁺ regulators have been characterized (eg, NHX1, SOS1, SOS2 and SOS3) (63).

In citrus, recently, associations were reported between the expression levels of candidate Na⁺ transporter genes (SOS1, NHX1, HKT1) and the Na⁺ tolerance of two citrus patterns (mandarin 'Cleopatra' and trifoliolate orange) they differ in their ability to exclude Na⁺ under saline conditions (64). They suggested that the higher concentration of Na⁺ in the trifoliolate orange genotype and therefore, the low concentration of this ion in the stems, is the result of the accelerated recovery of Na⁺ from the xylem current and a poor translocation to the tissues of the aerial part, probably as a consequence of the over-expression of SOS1 in roots and of HKT1 in roots and aerial part.

However, the above, in the case of citrus fruits, the damage caused by salinity is generally associated with the accumulation of Cl⁻ and not with the accumulation of Na⁺ (65). For this reason, citrus patterns tolerant to salinity are those capable of excluding Cl⁻ ions, hence the importance of identifying the most tolerant patterns for salinity affected areas (66).

The lime 'Rangpur' (*Citrus limonia* Osbeck), the tangerine Sunki (*Citrus sunki* Hort ex Tan) and the mandarin 'Cleopatra' (*Citrus reshni* Hort ex Tan) are considered tolerant patterns, while the trifoliolate orange (*Poncirus trifoliata* (L.) Raf.), and their hybrids such as, the citrange 'Carrizo' [*Citrus sinensis* (L.), Osbeck x *P. trifoliata* (L.) Raf.], are considered to be sensitive to salt (67). However, the over-expression of the betaine aldehyde dehydrogenase (AhBADH) gene in trifoliolate orange trees accelerated tolerance to

salt stress and this may be correlated with the low levels of lipid peroxidation, the protection of the photosynthetic machinery and the increase in the consumption of K⁺ ions (68).

In this sense, tolerance to salinity of 14 mandarin accessions, representative of the diversity in that group was studied and it was revealed that salt tolerance was mainly related to the limitation in the transport of Cl⁻ ions of the roots to the stems and with the processes of detoxification of this ion in the leaves (69). Previously, it had been suggested that the low Cl⁻ content could be used as an indicator of tolerance to salt stress in citrus genotypes and that the exploitation of this indicator would enable the improved evaluation of citrus genetic resources and should guide the identification of new sources of tolerance for the improvement of patterns (66).

The duplication of the genome in citrus fruits makes the plants acquire differentiated capacities to absorb and transport mineral elements. To provide information in this regard, seedlings of *Citrus macrophylla* (CM) 2x and 4x grew in moderate salinity (40 mM NaCl) and high (80 mM NaCl) for 30 days and the results revealed that the duplication of the genome improves tolerance to saline toxicity in CM, due to the lower accumulation of Cl⁻ in the leaves which retards the damage (70).

On the other hand, the overexpression of the CBF3/DREB1A gene of *Arabidopsis thaliana* in *Citrus macrophylla* plants increased the tolerance to salt stress, showing the transgenic lines a greater growth, similar accumulation of Cl⁻ and Na⁺ in the leaves and a better stomatic conductance compared to wild plants (71).

The use of arbuscular mycorrhizal fungi has been one of the strategies used to improve the salt tolerance of

citrus patterns. In this way, trifoliolate orange 61 days old with or without AMF (*Funneliformis mosseae*) was subjected to 45 days of stress by 100 mM NaCl. The mycorrhization significantly increased plant growth, the relative water content and the uptake of K⁺ in the tissue and decreased Na⁺ absorption under stress or non-stress conditions. Thus, the AMF significantly increased the K⁺/Na⁺ ratio in leaves, roots and complete plant in conditions or not of stress. It was suggested that the increase of selective uptake of K⁺ over Na⁺ stimulated by mycorrhizae accelerated the tolerance of plants to stress by NaCl, thus conferring a higher relative water content and growth to the mycorrhized citrus positions (72).

Subsequently, it was found that the response to mycorrhization depends on the sensitivity of the rootstock to stress by NaCl (73). In this way, mandarin positions 'Cleopatra' (*Citrus reshni* Hort ex Tan) and 'Alemow' (*Citrus macrophylla* Wester) were inoculated with a mixture of AMF (*Rhizophagus irregularis* and *Funneliformis mosseae*) and subjected to stress by NaCl. Three months later it was found that the fungal inoculation significantly increased the growth of the stressed plants in the case of mandarin 'Cleopatra' postures; however, the inoculation in 'Alemow' did not attenuate the negative effect of salinity.

The beneficial effect of mycorrhization was not related to the protection against the consumption of Na⁺ or Cl⁻, but this response was associated with the nutritional status of the plants, since it was demonstrated that AMF altered the response to salt stress, improving more the Phosphoric, potassium, ferric and cupric nutrition in mandarin plants 'Cleopatra' than in 'Alemow'.

In addition, mycorrhization increased the concentration of Mg²⁺ in the roots, but this was higher in mandarin 'Cleopatra' than in 'Alemow'; which explained why mycorrhizal fungi did not fully recover the chlorophyll concentrations in 'Alemow'.

Another strategy that has been evaluated is nutrition with NH₄⁺. Thus, it was shown that nutrition with NH₄⁺ in citrange 'Carrizo' plants acts as an inducer of resistance against salinity conditions. NH₄⁺ confers resistance by stimulation of abscisic acid and polyamines, especially putrescine and increasing the basal H₂O₂ and proline content; in addition to the reduction of Cl⁻ ion consumption after salt stress (74).

Subsequently, it was reported that the application of KNO₃ in three lemon cultivars counteracted the harmful effect of stress by NaCl, so it is highly recommended for use by growers with problems of this type of salt (75).

The applications of phytoalexin resveratrol and α -tocopherol (76), as well as ascorbic acid and melatonin (77) have been other strategies that have been used to mitigate the harmful effects of salt stress. In the first case, it was found that the combination of resveratrol and α -tocopherol reduced the damage of the membranes induced by NaCl, the degradation of pigments, the accumulation of H₂O₂ in the leaves and restored the reduction of photosynthesis induced by the salt. In addition, this application reduced the translocation of Na⁺ and Cl⁻ towards the leaves.

On the other hand, the application of ascorbic acid and melatonin to Citrus aurantium seedlings showed that this treatment differentially modulated the carbohydrates, proline, phenols, glutathione and the total antioxidant strength of the tissues, compared with the treatment of NaCl alone. This combination was

able to regulate the expression of the genes CaMIPS, CaSLAH1 and CaMYB73 and, therefore, to accelerate the metabolism of sugars, the homeostasis of ions and the regulation of transcription.

All these results reveal that there are several strategies to reduce the damage that salt stress causes in the cultivation of citrus fruits and therefore, reduce the losses induced in the yield and the quality of the fruits. However, it should not be forgotten that, under natural conditions, citrus trees often experience multiple stresses at the same time; therefore, there are direct and indirect interactions between salinity and almost all physical abiotic stresses that include flood, drought, nutrient deficiency, high irradiation, high temperature and high atmospheric evaporative demand. In addition, salinity stress has direct effects on the roots, predisposing trees to biotic environmental stresses including attack by root rot, nematodes and bacterial diseases (76).

CONCLUSIONS

The results presented in this review provide the possibility of controlling the adverse effects of both water and salt stress on citrus fruits and also provide an updated view of some of the strategies that have been adopted to reduce the damage caused by these stresses of the plants. The importance of the selection of the rootstock as one of the key elements is emphasized; it is proposed the inoculation with adequate strains of arbuscular mycorrhizal fungi, which contributes to the tolerance to both hydric and saline stress; as well as the application of some chemical agents.

Of great relevance and economic and environmental importance are the investigations carried out for the implantation of deficit irrigation in several citrus-growing countries, because this technology allows a considerable saving of water without appreciably affecting the yield or the quality of the fruits.

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