Parvaiz Ahmad · Mohd Rafiq Wani
Mohamed Mahgoub Azooz
Lam-Son Phan Tran *Editors*

Improvement of Crops in the Era of Climatic Changes

Volume 1

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Preface

Increasing global population and climate change are the two robust forces that collectively challenge scientists to devise such result-oriented techniques which ensure better crop productivity to meet up the world's ever-increasing food demand. The plant development and productivity are detrimentally affected by diverse environmental stress factors such as heat, cold, drought and salinity which limit agricultural crop production worldwide. Stressed climatic conditions are the prime causes for diminishing the overall yield of major crops by more than 50 %, which causes huge financial losses worth hundreds of millions of dollars each year. Consequently, to nosh the global population under such adverse environment remains a major challenge for all nations. On such situation, molecular breeding and genetic engineering have significantly contributed to expand the fundamental knowledge of cellular mechanisms involved in stress response, thus suggesting novel strategies to augment stress tolerance. If productivity, all over the world, is not increased in the context of constantly varying climatic conditions, food insecurity may foster major economic and political uncertainty. A major constraint for recuperating yield under abiotic stress is our limited understanding of the diverse genes that underline stress tolerance, as well as the hitches faced by breeders and biotechnologists, who are in quest of combining favourable alleles to create desired stress-adapted high-yielding genotypes. Consequently, a better understanding of gene function in plant stress adaptation and means to exploit these genes to augment crop performance are essentially needed, if we have to comprehend the full potential of our efforts in crop improvement. In this context, the book *Improvement of Crops in the Era of Climatic Changes Volume 1* will serve as avant-garde resource for researchers and students who are engrossed in developing improved crop cultivars and management methods. Written by a varied group of internationally distinguished experts, *Improvement of Crops in the Era of Climatic Changes Volume 1* is a concise yet comprehensive resource for researchers, students and others seeking advancements in this burning area of research and will lead to new commands and pondering on the subject of climate change and crop improvement.

In this book, we present a collection of 13 chapters written by 48 reputed experts in the field of plant abiotic stress tolerance and crop improvement. It is a well-timed contribution to a topic that is of vast eminence. The chapters provide a state-of-the-art account of the information available on abiotic stress tolerance and crop improvement. Chapter 1 throws light on citrus rootstocks for improving the horticultural performance and physiological responses under constraining environments. The chapter reveals the horticultural benefits due to the use of citrus rootstocks for alleviating the deleterious consequences of abiotic stresses. Chapter 2 deals with role of silicon in enrichment of plant nutrients and protection from biotic and abiotic stresses. This chapter is aimed to cover all the aspects regarding the valuable performance of silicon for survival of plants. Chapter 3 addresses the transgenic approaches for phytoextraction of heavy metals. Here, the authors scrupulously reviewed various approaches used to develop transgenic plants having increased phytoextraction competence for effective remediation of heavy metal contaminated soils. Chapter 4 is about using an allometric model for the accumulation of mineral nutrients in crops under saline–water stress: a field experience in fertigation. In this chapter, the authors described the theoretical background and analysed the field experience on crops fertigation, following stages of model development and discussing the growth restrictions imposed by saline and water stress to the nonrestricted forecast.

Chapter 5 deals with control of biotic and abiotic stresses in cultivated plants by the use of biostimulant microorganisms. In this chapter, the authors gave an up-to-date overview on the recent breakthroughs in the use of biostimulant microorganisms on plants for improving crop vigour, yield and quality and for increasing plant tolerance against biotic and abiotic stresses. Chapter 6 describes cyclic nucleotides and nucleotide cyclases in plants under stress, wherein the authors have shown that cyclic nucleotides such as cAMP and cGMP are involved in signal transduction in response to various environmental stresses. Chapter 7 deals with breeding and transgenic approaches for development of abiotic stress tolerance in rice. This chapter summarizes the recent advancement in breeding and transgenic approaches for the improvement of abiotic stress tolerance in rice using paradigm from the research targeted at drought, salinity and temperature stresses. Chapter 8 describes mineral bioavailability through mutation breeding in pulse crops: a review. In this chapter, the authors have made an endeavour to divert the attention of think tanks of countries like India and their policy holders, agriculturists and decisive bodies to look upon the collaborative work with the associations actively working on mutation breeding. In a strategic development for curbing the malnutrition and food insecurity problems, the work on the neglected crops like pulses has to be straightaway enhanced, and the same has been critically highlighted in the chapter. Chapter 9 is about abiotic stress and control of yield in cereals. Here, the authors examined the physiological processes impacted by abiotic stresses leading to reduced grain yield. In addition, the chapter is themed around the challenge of finding ways to improve cereal grain yield under such stresses.

Chapter 10 is about improvement of crop production under saline stress by a biohydraulic approach. In this chapter, the authors reviewed the strategies by which plants can be enabled to grow on saline soils. Chapter 11 deals with induced mutagenesis for the improvement of pulse crops with special reference to mung bean: a review update. In this review, the authors revealed various aspects of contemporary knowledge of pulse crop improvement programmes through induced mutations, biotechnological approaches, molecular advances and new parameters of selection. They concluded that cultivars with improved efficiency vis-à-vis yield, early maturity, uptake of micronutrients, tolerance to abiotic stresses like drought, cold and salinity and resistance to biotic stresses like disease and insect pests can be easily developed by using mutation breeding and marker-assisted selection. Chapter 12 describes crop improvement through tissue culture. This chapter presents an overview of in vitro propagation and regeneration via meristems, cell, tissue and organ cultures, organogenesis and somatic embryogenesis. Additionally, new methods and developments in protoplast isolation and culture, hairy root culture and transfer of genes in transgenic plants are covered. These technologies could significantly simplify breeding programmes and overcome some important agronomic and environmental traits that would not be achievable through conventional breeding and propagation. Chapter 13 deals with agricultural pollution: an emerging issue. In this chapter, the authors proposed that the current issues of agricultural pollution can be resolved by practices like agricultural waste management, pest management and manure recycling. In addition, the chapter recommended that proper planning and unprejudiced decisions at government level are essentially required to unravel this perilous issue.

We wish to express abstemious appreciation to our well-versed contributors, who readily accepted our invitation to write their chapters. Moreover, we would like to thank Springer Science+Business Media, LLC, New York, particularly Eric Stannard (Editor Botany, Springer), Kevin Wright (Developmental Editor, Springer), Andy Kwan (Assistant Editor, Springer), Flora Kim (Developmental Editor, Springer) and all the other staff members of Springer, New York, who were directly or indirectly associated with us in the current project for their steady support and efforts in bringing out the timely publication of this volume.

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2. Dr. Mohd Rafiq Wani (Co-editor)

Dr. Mohd Rafiq Wani is currently Assistant Professor in Botany at Government Degree College (Boys), Anantnag, University of Kashmir, India. Dr. Wani did his Masters in Botany in 2003 with specialization in “Genetics and Plant Breeding” from Aligarh Muslim University (AMU), Aligarh, UP, India. After obtaining a Doctorate degree in 2008 for his research work on “Chemical Mutagenesis in Mung bean” from the same University, he joined the Department of Higher Education, Government of Jammu and Kashmir in 2009. He teaches a range of bioscience-related subjects at undergraduate/postgraduate levels. At present, his research interests are mainly focused on the improvement of pulses through induced mutations and exploring the physiological and biochemical responses of crop plants to a range of biotic and abiotic stresses. As a part of his research endeavour, Dr. Wani has extensively researched and written on the issues of induced chemo-mutagenesis among the food crops, with special reference to pulses. He has around thirty (30) research publications to his credit, published in various international and national journals of repute. Moreover, he has also submitted several book chapters to various research-oriented volumes. Dr. Wani, while constantly working for his academic and research interests, is currently in the process of editing many volumes of books on the subjects of plant stress physiology and induced plant mutagenesis with reputed international publishers like Springer New York, USA, and Wageningen Academic Publishers, Netherlands. In addition, he is an Editorial Member and Reviewer of few online journals pertaining to plant sciences, besides being the life member of various scientific societies like Indian Society of Pulses Research and Development (ISPRD) and Indian Society of Genetics and Plant Breeding (ISGPB).

3. Prof. Dr. Mohamed Mahgoub Azooz (Co-editor)

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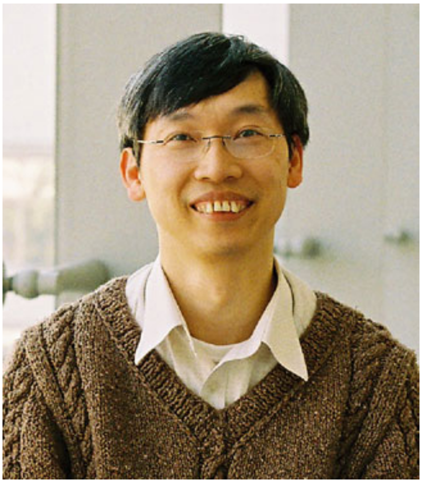
4. Dr. Lam-Son Phan Tran (Co-editor)



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Chapter 1
Citrus Rootstocks for Improving the Horticultural Performance and Physiological Responses Under Constraining Environments

Rafael V. Ribeiro, Erick Espinoza-Núñez, Jorgino Pompeu Junior, Francisco A.A. Mourão Filho, and Eduardo C. Machado

1 Introduction

Citrus trees are grown from latitude 40°N to 40°S, flowering and fruiting in climates ranging from tropical to temperate (Davies and Albrigo 1994). In those areas, fruit yield and tree development may be restricted due to environmental stresses, such as drought, salinity, flooding, and chilling/freezing and high temperature. To avoid the negative impact of environmental stresses, we may combine the best scion and rootstock to each condition, and this choice must consider the fruit yield and its sustainability in long term as citrus trees are perennial plants and production costs are not low.

We know that the sensitivity to environmental stresses is markedly affected by the rootstocks through modifications in the supply of water, carbon, and mineral nutrients to shoots (Syvertsen and Lloyd 1994). In fact, rootstocks are able to

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modify the citrus response to a range of environmental stresses, affecting citrus growth, flowering, and fruiting even under non-limiting conditions (Davies and Albrigo 1994; Murkute et al. 2005).

This chapter has an aim to present our current understanding about how citrus trees respond to environmental changes with especial emphasis to the role of rootstocks in alleviating the stresses caused by water deficit, flooding, salinity, chilling/freezing, and high temperature. The recent advances for explaining stress resistance of citrus plants are also considered. To accomplish this task, only literature directly related to citrus rootstock was considered herein. Before dealing with this, we present an overview about the rootstocks and their importance for fruit production and citrus growth.

2 Benefits to Crop Yield and Plant Growth Due to Citrus Rootstocks: An Overview

The first use of rootstocks in citriculture was in 1842 to control root rot caused by *Phytophthora* in Azores Islands through the use of resistant rootstocks (Chapot 1975). Since that time, most commercial orchards, except in some Asian countries, have been formed by combining citrus scion and rootstock as an attempt to join the best characteristics of each species. The use of rootstocks allows the reduction of juvenility, unproductive initial period, and the cultivation of citrus in areas initially considered unsuitable due to soil characteristics, diseases, pests, and environmental stresses (Castle et al. 1993; Castle 2010). The rootstock is responsible for physical support, absorption of water and nutrients, biosynthesis of plant growth regulators like abscisic acid and cytokinins, and physicochemical interaction with surrounding soil. The physiology of the whole tree is affected by rootstock, including traits of economic relevance such as fruit yield, fruit size, juice quality, tree vigor, and resistance against biotic and abiotic stresses (Castle et al. 1993; Medina et al. 2005). Fruit maturation, fruit holding on tree, and postharvest preservation are also affected by rootstock (Hodgson 1967). The scion influence on rootstock is less studied, but it affects root growth and the resistance to cold, drought, pests, and diseases (Castle 1987).

There is no ideal rootstock for all soil and climate conditions; thus, it is essential to identify the most suitable species for each growing area, considering climate, soil, crop management, scion, pests, diseases, and fruit destination. In general, citrus have to overcome constraints imposed by abiotic (drought, cold, salinity, alkalinity) and biotic factors. For instance, sour orange (*Citrus aurantium* L.) is resistant to root rot, citrus blight disease, water deficit, and cold, inducing high yield and high fruit quality. However, sour orange is susceptible to citrus tristeza virus (CTV), and it cannot be used as rootstock in countries where the virus is present (Castle et al. 1993).

Rangpur lime (*C. limonia* [L.] Osb.), volkamer lemon (*C. volkameriana* V. Ten. & Pasq.), and rough lemon (*C. jambhiri* Lush.) confer resistance to drought and induce high fruit yield. These rootstocks, however, induce low fruit quality as compared to fruits obtained on sour orange, Cleopatra mandarin (*C. reshni* hort. ex Tanaka), Sunki mandarin (*C. sunki* [Hayata] hort. ex Tanaka), Trifoliate (*Poncirus trifoliata* Raf.), and their hybrids (Pompeu Junior 2005). They are susceptible to citrus blight, citrus sudden death (CSD) (Rodriguez et al. 1979; Bassanezi et al. 2003), and nematodes *Tylenchulus semipenetrans*, *Platylenchus jaheni*, and *Radopholus citrophilus* (Calzavara et al. 2007). Rangpur lime has replaced sour oranges due to the occurrence of CTV. However, Rangpur lime is susceptible to CSD, which increased the use of Swingle citrumelo as rootstock in Brazilian citriculture in the last years (Pompeu Junior and Blumer 2008a). In fact, Swingle citrumelo (*C. paradisi* Macf. Bhp. Duncan × *P. trifoliata* Raf.) has become the main citrus rootstock in Florida (USA) and the second most planted in Brazil (Castle 2010). Scions grafted on Swingle citrumelo have good fruit yield in sandy and clay soils, but it does not have good performance in alkaline and poorly drained soils. In addition, Swingle citrumelo is moderately sensitive to water deficit and cold conditions (Wutscher 1979), requiring irrigation for high fruit yield. The Swingle citrumelo is incompatible with Pera sweet orange (*C. sinensis* [L.] Osb.) and Murcott tangor (*C. sinensis* [L.] Osb. × *C. reticulata* Blanco), requiring an interstock (Pompeu Junior 1991).

Due to the reduction of agricultural areas close to the major consuming centers and high production costs for orchard management, high-density plantations are an alternative for obtaining high yield and reduction of harvest costs. In this context, the selection of new rootstocks, dwarfing techniques, and the use of interstocks are necessary to obtain highly productive orchards (Castle 1978). Regardless of this trend, the use of a single rootstock for all kinds of scions, soils, and climates limits the potential yield of citrus trees and increases the vulnerability of citrus orchards. Scion and rootstock diversification is essential in a sustainable citriculture, less susceptible to unexpected biotic and abiotic stresses.

Although there are many reports dealing with the interaction of scion/rootstock, our current understanding about the physiological basis underlying the rootstock effect on entire tree is limited (Webster 2004; Jones 2012). Some studies have suggested the translocation of minerals, plant growth regulators, carbohydrates, and water (Castle 1995; Webster 1995). At the graft union, rootstock would modify the amount or proportion of growth regulators, sugars, amino acids, minerals, and water moving from roots to shoots and also from shoots to roots (Webster 1995). In general, rootstocks affect the citrus physiology and subsequently the plant growth and development. The physiological changes caused by rootstocks will be presented and discussed in the following sections of this chapter. There are several research works confirming the importance of the rootstock on tree growth and fruit production. For instance, Orlando tangelo (*C. tangerina* hort. ex Tanaka × *C. paradisi* Macf.) scions grafted on rough lemon, Palestine sweet lime (*C. limettioides* Tanaka), and Cleopatra mandarin exhibited higher vigor than on Rusk citrange (*P. trifoliata* [L.] Raf. × *C. sinensis* [L.] Osb. Bhp. Washington Navel) and trifoliate selections (Castle and Krezdorn 1973). Some field experiments in nonirrigated orchards with orange, mandarin, and lime trees revealed the significant effects of rootstocks on tree vigor and fruit yield and quality. Tangelos and lemons are invigorating rootstocks that induce higher tree height and fruit yield as compared to scions on trifoliate

(*P. trifoliata*) and its hybrids (Mourão Filho et al. 2007; Cantuarias-Avilés et al. 2011; Espinoza-Núñez et al. 2011).

The rootstocks have significant effects on citrus juice quality, causing large variations in soluble solids concentration (Wutscher 1988; Castle 1995). Gardner (1969) investigated the rootstock effect on fruit quality using reciprocal fruit grafts and showed that fruit harvested from Valencia sweet orange/rough lemon and grafted on Valencia sweet orange/sour orange and vice versa had the size and juice quality characteristic of the "adoptive mother tree." It was estimated that almost 40 % of the soluble solid variation in citrus juice is attributed to the rootstock. In a similar experiment, Rangpur lime and Butwal lemon (*Citrus limon* Burm. f.) fruits, differing in acidity, were reciprocally grafted. Fruits kept their natural acidity, demonstrating that organic acids are fruit-synthesized unlike sugars that are translocated from other organs.

Considering plant structure, citrus dwarf trees have advantages over larger trees. They produce more fruit per canopy volume and allow high planting density and increasing fruit production per area (Castle 1978). Smaller trees facilitate inspection and control of diseases and pests and then improve the orchard health. The use of dwarfing rootstocks is a method for obtaining small trees. Flying Dragon trifoliate is considered a dwarfing rootstock, allowing the formation of small mature trees in several climates and crop conditions (Donadio and Stuchi 2001). The use of interstock is another way to produce small trees, as discussed in the next section.

2.1 Combining Species: Scions, Rootstocks, and Interstocks

The grafting technique aims to create an association between two genetically different individuals. Eventually, a third individual called interstock can be inserted in order to prevent the occurrence of incompatibility or to induce dwarfing (Castle 1978; Pompeu Junior 2005). Recently, the use of two or more rootstocks has increased further the complexity of citrus trees (Setin et al. 2009).

Grafting promotes the contact of two plants with distinct anatomical, physiological, and biochemical traits, which may cause low affinity and even incompatibility between scions and rootstocks. At the first view, plants grow normally and after two or more years of grafting, they begin to present nutritional deficiencies, leaf abscision, drying of apical shoots, excessive sprouting in rootstock, and reduced fruit yield and finally die. Incompatibility is a premature senescence phenomenon caused by anatomical and biochemical processes, which are intensified under stressful conditions (Feucht 1988). There is no evidence of being associated with any known virus or pathogen, and the incompatibility may be classified as localized or translocated (Mosse 1962). It is considered translocated, when an interstock between scion and rootstock does not solve the incompatibility. It is noteworthy that a larger rootstock trunk diameter than the scion diameter or vice versa is not always an indicative of incompatibility. Several citrus species grafted on trifoliate and its hybrids have reasonable to high fruit yield and show differences in rootstock and in scion diameters without the occurrence of gum ring (Castle et al. 1993).

Bitters et al. (1982) have shown that interstock length had small effect on size and fruit yield. However, the height of interstock insertion affects tree size and fruit production. Sampaio (1993) reported that trifoliate interstock between Valencia sweet orange (*C. sinensis*) and Rangpur lime caused reduction in tree size and low fruit yield. The Flying Dragon trifoliate (*P. trifoliata* cv. monstrosa) interstock reduced, by 30–50 %, the size of orange and grapefruit trees, depending on the combination of scion/rootstock. In addition, the interstock improved the fruit production per canopy volume (Ashkenazi et al. 1994). Espinoza-Núñez et al. (2011) have found that the effect of Flying Dragon trifoliate as interstock depends on its interaction with the rootstock. This interstock reduced the tree size of Tahiti lime (*C. latifolia* [Yu. Tanaka] Tanaka) grafted on Catania 2 Volkamer lemon and increased tree size in plants grafted on Davis A trifoliate, when compared with trees without interstock. Similarly, Flying Dragon interstock increased fruit yield of Tahiti lime grafted on Swingle citrumelo and Davis A trifoliate, but reduced fruit yield on Morton citrange (*P. trifoliata* × *C. sinensis*). The use of interstock as "filters" of pathogens in disease control did not show positive results as the insertion of Cleopatra mandarin or Swingle citrumelo interstock did not prevent the citrus blight or CSD in susceptible combinations (Carlos 1996; Pompeu Junior and Blumer 2008b).

Inarching, or replacement of the rootstock, is used to save plants in which rodents, diseases, and mechanical or chemical agents have damaged the root system or trunk. The inarching technique was used to save the first Washington navel orange tree planted in California in 1877, whose rootstock was damaged by gummosis (Pompeu Junior 2005). Inarching with tolerant rootstocks may be used to control CTV and exocortis and also to overcome the incompatibility between scion and rootstock. Marcottage is the suppression of the rootstock by canopy rooting, and it is used when a disease affects only the rootstock. Among the limitations of this technique, the scion sensitivity to water deficit and root rot limits its use in commercial orchards. The simultaneous use of two rootstocks of different species in order to prevent diseases and increase drought resistance is a new technique with only preliminary results.

3 Improving Physiological Responses Under Constraining Conditions with Rootstocks

About the terminology, we will use the general terms resistant and resistance, in a broad sense, for genotypes that are able to withstand or support the stressful conditions. Stress resistance has two components, i.e., tolerance and avoidance (Fageria et al. 2006), and the component of resistance involved in stress acclimation and adaptation of citrus trees will not be specified along this chapter. Another point is that some research works deal with relative tolerance/resistance comparing citrus species under limiting conditions. Actually, one must consider the sensitivity/resistance of a given genotype by comparing the plant performance between non-stressed (control) and stressed individuals.

3.1 Water Deficit

Water scarcity is the main factor limiting crop productivity (Boyer 1982), and the frequency and severity of drought events are expected to increase (IPCC 2007). As an evergreen species, citrus trees are subjected to the seasonal variation of water availability in several growing areas. Besides the use of irrigation, one of the most effective strategies to deal with water shortage is the choice of an appropriate scion/rootstock combination.

Reductions in stomatal and mesophyll conductance, transpiration, and net CO_2 assimilation are found in citrus trees under water deficit (Medina and Machado 1998; Arbona et al. 2005a; García-Sánchez et al. 2007; Magalhães Filho et al. 2008; Melgar et al. 2010), which affects growth, flowering, and fruit yield in citrus orchards (Shrestha et al. 1996; Botia 2008; Pérez-Pérez et al. 2010). Decreases in stomatal and mesophyll conductances are key regulatory mechanisms in citrus trees under moderate water deficit (Erismann et al. 2008). Stomatal closure due to water deficit is not always dependent on leaf turgor pressure, suggesting the participation of chemical signals from roots to shoots (Forner-Giner et al. 2011b).

In Valencia sweet orange trees grafted on Rangpur lime and Carrizo citrange, leaf gas exchange rates decreased progressively under water deficit. On the other hand, ABA concentrations in roots, leaves, and xylem sap increased between three and seven times (Gomes et al. 2003, 2004; Melgar et al. 2010; Forner-Giner et al. 2011b). These data suggest ABA may play a role as a chemical signal regulating stomatal function in citrus trees. In fact, Rangpur lime tetraploid trees with increased production of ABA by roots have enhanced resistance against water deficit (Allario et al. 2013). In Carrizo citrange, Forner-Giner et al. (2011b) observed increases in pH of xylem sap, with plants showing stomatal closure and decrease of transpiration. These authors suggested the modulation of ABA action through pH changes in xylem sap.

Besides the diffusional limitation due to mesophyll and stomatal resistances, photosynthetic activity may be affected by biochemical and photochemical limitations. However, the quantum efficiency of photosystem II of Rangpur lime, Swingle citrumelo, and Sunki mandarin trees was not affected by moderate water deficit, indicating that primary photochemistry is resistant to water shortage. Increases in the ratio between apparent electron transport rate and photosynthesis have suggested increases in electron flow to alternative electron sinks, such as photorespiration and Mehler reaction (Erismann et al. 2008). Water deficit causes significant reduction in the carboxylation rate and concentration of ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBisCO) in Valencia sweet orange trees, being a significant limitation to citrus photosynthesis under drought (Vu and Yelenosky 1988).

Under severe water deficit, the impairment of photosynthesis will cause excessive energy pressure on photochemistry, with probable generation of reactive oxygen species. In fact, some authors have investigated the influence of water deficit on antioxidative metabolism of citrus trees (Campos et al. 2011; Pérez-Clemente et al. 2012; Carvalho et al. 2013). In addition, the interaction between citrus trees and mycorrhizal fungus caused reductions in lipid peroxidation and in reactive oxygen species production under water deficit, increasing the activities of superoxide dismutase (SOD), catalase (CAT), ascorbate (APX), and guaiacol peroxidases (G-POD) (Wu et al. 2006, 2007). However, those research works did not involve any rootstock comparison. Although the enzymatic and nonenzymatic antioxidant systems are responsible for the neutralization of harmful effects of reactive oxygen species (Mittler 2002), there are few comparative studies about the influence of citrus rootstocks on antioxidant responses in both leaves and roots under water deficit.

As an overall consequence of water deficit on citrus physiology, plants have reduced growth and fruit yield (Hilgeman and Sharp 1970; Davies and Albrigo 1994; Davies and Bower 1994; Shrestha et al. 1996; Pérez-Pérez et al. 2010), with severity depending on water deficit intensity and also on the phenological phase affected by drought (Ginestar and Castle 1996; Camargo et al. 1999; Pérez-Pérez et al. 2010; Carr 2012). In general, citrus rootstocks have differences related to distribution and depth of root system, uptake of nutrients and water, anatomy of vascular system, production of phytohormones, and the regulation of water status and carbon assimilation, changing the sensitivity of the scion to water deficit (Castle and Krezdorn 1977; Vasconcellos and Castle 1994; Medina et al. 1998; Magalhães Filho et al. 2008; Rodríguez-Gamir et al. 2010; Jover et al. 2012). Root hydraulic conductivity, aquaporin expression, and osmotic adjustment determine the ability of rootstocks to provide water and nutrients to the scion and then maintain leaf gas exchange (Sinclair and Allen 1982; Syvertsen and Graham 1985; Rieger 1995; Medina et al. 1998; Molinari et al. 2004; Boscariol-Camargo et al. 2007; Rodríguez-Gamir et al. 2010).

Soil matrix is the main limiting factor to water uptake under low soil water availability, whereas the root hydraulic conductivity may represent up to two-third of the total limitation under well-watered conditions (Huang and Eissenstat 2000). Root hydraulic conductivity has been positively correlated to shoot growth rate. Citrus trees on invigorating rootstocks (rough lemon, Rangpur lime, and Carrizo citrange) have higher root hydraulic conductivity, stomatal conductance, and transpiration rates than trees on non-invigorating rootstocks such as Cleopatra mandarin and sour orange (Syvertsen 1981; Syvertsen and Graham 1985; Medina et al. 1998). Likewise, high root hydraulic conductivity is observed in rootstocks with high specific root length, with plants showing high photosynthesis, high water and mineral transport capacities, and fast root turnover (Huang and Eissenstat 2000). As invigorating rootstocks exhibit higher density and diameter of xylem vessels than non-invigorating rootstocks (Vasconcellos and Castle 1994), xylem characteristics appear to determine hydraulic conductivity and govern tree growth (Rodríguez-Gamir et al. 2010). Rootstocks with high hydraulic conductivity probably keep leaves more hydrated throughout the day with longer periods of stomatal opening and photosynthesis (Medina and Machado 1998; Medina et al. 1998).

Under water deficit, water tension inside xylem vessels increases and may reach a species-specific tension threshold, when little air bubbles may cause interruption of water supply to tree canopy. This phenomenon is called cavitation and the susceptibility to cavitation is a key characteristic to understand the resistance to water deficit (Tyree and Sperry 1989; Brodribb 2009; Nardini et al. 2011).

In Clementine mandarin (*C. clementina*) grafted on Carrizo citrange and trifoliate orange, cavitation occurs in leaf water potential below –1.0 MPa, triggering decreases in stomatal conductance and transpiration (Poggi et al. 2007).

3.1.1 Mechanisms of Resistance

Anatomically, each rootstock shows peculiar features (Castle and Youtsey 1977; Eissenstat and Achor 1999). Drought resistance could be attributed to fibrous root distribution and quantity, the horizontal and vertical extent of root system development, and water uptake and transport efficiency (Castle et al. 1993). For instance, rough lemon and Rangpur lime are rootstocks that confer high drought resistance and high fruit yield due to their spread, well-distributed, and deep root systems that occupy large soil volume and access more efficiently the soil nutrients and water (Syvertsen 1981). Citrus ability to transport water and nutrient is a physiological characteristic largely affected by rootstocks (Kriedemann and Barrs 1981; Syvertsen and Graham 1985; Medina et al. 1999). Scions on rough lemon and *P. trifoliata* have higher transpiration rates than on Cleopatra mandarin and sour orange. Those differences in transpiration were associated to the root hydraulic conductivity (Sinclair 1984).

Osmotic adjustment and water transport intrinsic proteins—aquaporins—may be additional mechanisms of drought resistance in citrus trees. In fact, in silico analysis of ESTs from roots of Rangpur lime under water stress revealed that several proteins often associated with water deficit were induced, such as proline-related synthase, aquaporins, and dehydrins (Boscariol-Camargo et al. 2007). The Cl^- inclusion mechanism in Rangpur lime rootstock may represent another physiological trait to avoid water deficit, enabling plants to accumulate Cl^- in leaves and then adjust osmotically (Brumós et al. 2010). As consequence, leaf turgor is maintained and citrus growth is less impaired by water deficit. Thus, the good performance of Rangpur lime under drought is probably related to its root capacity to absorb water and maintain shoot water status.

Solute accumulation through osmotic adjustment decreases the leaf osmotic potential while maintains water potential gradient to support water uptake and stomatal aperture (Molinari et al. 2004; García-Sánchez et al. 2007; Campos et al. 2011). Osmotic adjustment was observed in several rootstocks such as Carrizo citrange and Cleopatra mandarin (García-Sánchez et al. 2007), Swingle citrumelo (Molinari et al. 2004; Campos et al. 2011), F-A 5 hybrid, and trifoliate trees (Rodríguez-Gamir et al. 2010). Even fruits are able to adjust osmotically under water deficit (Yakushiji et al. 1996).

Rodríguez-Gamir et al. (2010) reported that F-A 5 rootstock was more resistant to water deficit than its parentals Cleopatra mandarin and *P. trifoliata*, which was associated with osmotic adjustment, causing higher relative water content, higher leaf turgor, and improved gas exchange as compared with other rootstocks. These same physiological traits caused the higher resistance of Cleopatra mandarin, when compared with Carrizo citrange under water deficit (García-Sánchez et al. 2007). Interestingly, reduction in plant hydraulic conductivity may affect the effectiveness of osmotic adjustment in maintaining shoot water status (Rieger 1995).

3.1.2 Improving Plant Performance Under Water Deficit

Swingle citrumelo plants transformed with genes that encode key enzymes of proline synthesis (*P5CSF129A*) have increased the constitutive proline concentration. Under water deficit, those transformed plants had turgid leaves and higher stomatal conductance and photosynthesis as compared to non-transformed ones (Molinari et al. 2004; Campos et al. 2011). Proline is also involved in protective mechanisms against oxidative damage, and its accumulation in transformed Swingle citrumelo plants determined low lipid peroxidation and maintenance of photosynthesis under water deficit (Campos et al. 2011). In addition, Carvalho et al. (2013) found that proline acts as a regulatory/signaling molecule, altering gene transcription levels related to the antioxidant metabolism.

Under low soil water availability, sweet oranges and mandarins scions budded on Cleopatra mandarin have higher water uptake, shoot water status, and leaf gas exchange than scions on Carrizo citrange (Romero et al. 2006; Pérez-Pérez et al. 2008). Comparing the root mass densities, Cleopatra mandarin has higher values and also higher plasticity than rough lemon, throughout the year (Syvertsen and Lloyd 1994). These results lead to the following question (Jones 2012): What governs the tree water relations, the tree vigor, or a direct effect of rootstock? Apparently, invigorating rootstocks are better than non-invigorating rootstocks for crop production under seasonal water deficit conditions. Although invigorating rootstock uptakes more water and causes rapid soil drying, its larger root system is able to explore more efficiently the soil resources when there is available water (Espinoza-Núñez et al. 2011).

Another interesting aspect is the symbiotic relationship between vesicular–arbuscular mycorrhizal fungus and citrus roots. Volkamer lemon in symbiosis with mycorrhizal fungus (*Glomus*) shows improvements in root growth and transpiration under both well-watered and moderate water deficit conditions. Under severe water deficit, the symbiosis caused fast recovery of transpiration in Volkamer lemon seedlings after soil rehydration (Fidelibus et al. 2001). Satsuma mandarin (*C. unshiu* Marc.) grafted on trifoliate rootstocks with the inoculation of mycorrhizal fungus developed large root system, which improved plant performance under water deficit (Shrestha et al. 1996). The association between citrus and mycorrhizal fungus also improved the antioxidant metabolism of citrus trees (Wu et al. 2006, 2007).

3.2 Flooding

Among the environmental stresses, the effects of low oxygen availability and soil chemical disturbance caused by flooding are relatively less studied as compared to water deficit, salinity, and temperature. Flooding is an important agricultural factor in citrus-growing regions at low altitudes, where the water table is relatively high or the irrigation is not properly used. Excessive rainfall is another seasonal cause of soil flooding. In general, citrus species are sensitive to low oxygenation caused by flooding (Syvertsen and Lloyd 1994), with sensitivity depending on scion/rootstock combination (Syvertsen and Levy 2005).

Leaf wilting, senescence, and abscision are among the main plant responses to flooding. However, the intensity of those symptoms depends on the rootstock (Vu and Yelenosky 1991; Arbona et al. 2008). For instance, Hamlin sweet orange grafted on sour orange died after 30 days of flooding, whereas only 20 % of the plants of this same scion cultivar on rough lemon did not survive after 60 days under the same stress condition (Vu and Yelenosky 1991). The occurrence of flooding with saline water changes the volatile composition from lemon trees, which may affect pollination and crop production (Velikova et al. 2012).

Reductions in leaf water potential and leaf turgor due to increases in resistance to water flow were reported in lemon trees (*C. limon* [L.] Burm. f.) grafted on sour orange and on *C. macrophylla* subjected to flooding (Ruiz-Sánchez et al. 1996; Ortuño et al. 2007; Gimeno et al. 2012). Reduced vegetative growth is another consequence of flooding, with citrus trees showing reduced shoot length (Syvertsen et al. 1983; Ruiz-Sánchez et al. 1996). As consequence of growth impairment and reduced phloem transport, starch may accumulate in leaves of trees under flooding conditions (Vu and Yelenosky 1991), with increases in root starch concentration being also noticed (Gimeno et al. 2012).

As mentioned above, flooding causes impairment of citrus growth, and this is a consequence of physiological changes caused by low soil redox potential and low soil oxygen availability. The main plant responses include the reduction in root hydraulic conductivity and structural changes in fibrous roots (Syvertsen et al. 1983; Hartmond et al. 1987). The reduction in root hydraulic conductivity results from a downregulation of aquaporin (PIP1 and PIP2) expression, triggered by decreases in pH of root xylem sap (Rodríguez-Gamir et al. 2011).

Leaf CO_2 assimilation of citrus rootstocks is also reduced by flooding, which was associated with stomatal closure, low chlorophyll content, reduced activity of RuBisCO, low RuBP regeneration driven by electron transport rate, and photochemical damage at the PSII level (Hartmond et al. 1987; Schaffer 1991; Vu and Yelenosk 1991; García-Sánchez et al. 2007; Gimeno et al. 2012; Velikova et al. 2012). Although flooding has caused low stomatal conductance, the intercellular CO_2 concentration remained similar between control and stressed plants and was not a limiting factor to photosynthesis (Vu and Yelenosky 1991; Ruiz-Sánchez et al. 1996; García-Sánchez et al. 2007; Gimeno et al. 2012; Velikova et al. 2012). On the other hand, stomatal closure has an important role in preventing leaf dehydration and maintaining leaf water status once flooding consequences were similar to those of water deficit (García-Sánchez et al. 2007; Ortuño et al. 2007). Leaf water balance may be maintained by low stomatal conductance as it reduces leaf transpiration (demand) in plants that have reduced hydraulic conductivity (supplying capacity). As compared to water deficit, flooding is less restrictive to citrus plants in terms of photosynthesis and leaf water-use efficiency (García-Sánchez et al. 2007).

Although previously suggested by Arbona and Gómez-Cadenas (2008), the stomatal closure under flooding is not related to increases in leaf ABA concentration in Carrizo citrange during the first days of stress. Stomatal behavior and ABA were related to each other only at the latter stages of flooding, when an inverse relationship was found (Rodríguez-Gamir et al. 2011). In addition, the accumulated ABA was not driven from roots, and Rodríguez-Gamir et al. (2011) have suggested that old leaves have increased the ABA synthesis and transported it to young tissues. The recovery of stomatal aperture after flooding events is an important physiological trait determining citrus performance, which is affected by rootstock (Ruiz-Sánchez et al. 1996). In fact, the recovery capacity is an essential trait for plant survival and development after stressful events.

Osmotic adjustment is another citrus response to flooding found in Cleopatra mandarin, being related to the accumulation of osmotically active amino acids. Although proline accumulation has been found under flooding (García-Sánchez et al. 2007; Arbona et al. 2008), this molecule is suggested to be effective in protecting cellular function with nonsignificant role in osmotic adjustment (García-Sánchez et al. 2007). However, proline role in the detoxification of reactive oxygen species and in the protection of cell membranes was not confirmed under flooding (Arbona et al. 2008).

While leaf respiration was not affected by flooding, the respiration and total concentration of nonstructural carbohydrates were reduced in roots of sour orange and rough lemon (Vu and Yelenosky 1991). Velikova et al. (2012) have found increased leaf respiration in lemon trees subjected to flooding. Such discrepancy in relation to the data reported by Vu and Yelenosky (1991) may be due to water quality and experimental design as Velikova et al. (2012) evaluated the response of lemon trees to recurrent flooding with saline water.

Regarding the nutritional status, flooding decreased the root concentration of nitrogen and potassium due to soil leaching and reducing uptake, respectively (Gimeno et al. 2012). Citrus sensitivity to flooding is influenced by growth substrate type, with plants being more affected when waterlogging occurs in organic soils (Schaffer 1991). In soils with high organic matter, Tahiti limes grafted on *C. macrophylla* were more resistant to flooding when compared to *C. aurantium* and *C. paradisi* (Schaffer 1991).

As photosynthesis is almost abolished in plants under flooding and they continue to intercept light energy, the generation of reactive oxygen species is a probable consequence. Besides the generation of H_2O_2 through the Mehler reaction and photorespiration, the fermentative metabolism may be indirectly another source of H_2O_2. In such situation, the enzymatic and nonenzymatic antioxidant systems have pivotal function in the detoxification of plant tissues (Blokhina et al. 2003). The onset of lipid peroxidation (membrane damage) may play an important role in flooding sensitivity, because as fast as this specific oxidation occurs, the more sensitive is the rootstock to flooding (Arbona et al. 2008). The delay in membrane damage is caused by an active antioxidant system, which has increased activities of superoxide dismutase, ascorbate peroxidase, catalase, and glutathione reductase, as well as recycling of antioxidant metabolites.

3.2.1 Mechanisms of Resistance

Rough lemon is considered a rootstock resistant to flooding. Some of the specific traits of this rootstock may be related to its higher flooding resistance such as high root growth and root hydraulic conductivity, and high photosynthetic capacity and low leaf abscision (Syvertsen 1981; Vu and Yelenosky 1991). The ability to replace damaged roots under flooding is another factor causing better performance of rough lemon in these conditions (Syvertsen and Lloyd 1994; Hardy et al. 2012). The rootstocks F-A 5 and F-A 13 are also resistant to flooding. However, the morphophysiological basis of such resistance has not been identified (Forner et al. 2003).

Desired traits in flooding-resistant plants are rapid recovery of leaf water status and stomatal aperture and less sensitivity of carbon metabolism, with maintenance of photosynthesis and carbohydrate availability to resume growth after the stressful event. Apparently, those traits would be linked to rapid replacement of dying roots. In addition, an active antioxidant system is another physiological trait important under flooding. Although anatomical adaptations to flooding have not been observed in citrus rootstocks, studies comparing the root and leaf anatomy of citrus plants in such stressful condition were not found in literature. Also, another interesting characteristic would be the resistance against opportunistic diseases, such as those caused by *Phytophthora* (Hardy et al. 2012).

3.2.2 Improving Plant Performance Under Flooding

Some researches have been carried out with the aim of improving citrus performance under flooding, a difficult task due to our little understanding about the genotypic variation in relation to physiological and anatomical responses of citrus to this kind of environmental stress.

Inoculation of vesicular–arbuscular mycorrhizal fungus did not improve the performance of sweet orange, Carrizo citrange, and sour orange rootstocks under flooding (Hartmond et al. 1987). The use of interstock has not improved the performance of Verna lemon trees under flooding, with plants presenting higher physiological sensitivity as compared to plants without the interstock. The high sensitivity to flooding when using interstock was probably caused by high O_2 demand due to high root biomass (Gimeno et al. 2012). The interstock also affected the sugar translocation from shoot to root. Grafted plants without interstock showed an increase in root sugar concentration, whereas those with an interstock had reduced sugar concentration in the roots (Gimeno et al. 2012).

Transgenic Carrizo citrange expressing the Mybleu transcript factor has increased the resistance to flooding through enhancements in expression of genes of carbohydrate metabolism (alcohol dehydrogenase, pyruvate decarboxylase, and sucrose synthase) and antioxidant system (superoxide dismutase). Higher expression of class-1 hemoglobin proteins (*HB1*) was also noticed in transgenic plants as compared to the wild type (Caruso et al. 2012).

3.3 Salinity

Salinity is a well-known environmental stress, affecting plant growth and development, and it becomes an important constraint in semiarid and arid areas where irrigation is used as a common agricultural technique to improve crop production