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Towards a New Ecophysiological Approach to Understand Citrus Crop Yield Under Abiotic Stresses Mirroring in the Brazilian Savanna Genetic Resources

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1. Introduction

Under the threat of unavoidable global warming and its consequences, citrus production has important impacts on water consumption in (irrigated) orchards and nurseries. Knowledge of agriculture indicates that more than 60% of variability in crop productivity may be explained by fluctuations in climate. More than 55% of the causes of crop losses can be identified as soil water deficits. In this context, areas for citrus production in Brazil are located in São Paulo and Minas Gerais states, but the most productive regions are the northwestern and the northern regions of São Paulo state, where frequent and intense droughts, high air temperatures and vapor pressure deficits occur. In these regions there are more incidences of citrus diseases, such as citrus variegated chlorosis and citrus sudden death. These factors have induced some citrus growers to irrigate their orchards. Field experiments have shown that irrigation may increase citrus production by more than 50% on an area basis, compared to non-irrigated areas. Considering extensive land areas for citrus in Brazil, irrigation systems may become very expensive. Alternatively, citrus groves have migrated to the south of São Paulo state, where soil water deficits and air temperatures are low. However, high temperatures enhance citrus growth and fruit production. Thus, the southern region, with approximately 5.5 million new citrus plants, might be interesting for plant water balance and disease attenuation, but not for carbon gain, and consequently, production. In fact, the northwestern and the northern regions were still responsible for the largest production in 2007/2008. To support the citrus industry, with 190 million productive plants, greenhouse- and screenhouse-protected nurseries use drip fertirrigation to produce high quality varieties and cultivars of scions grafted on specific rootstocks; screenhouse-protected systems also prevent plants from diseases and their vectors. But there are indications of over irrigation in nurseries, suggesting waste of water. It has also been reported that water may not be a renewable natural resource, and that water consumption is increasing, as the human population enlarges. The original habitat of citrus species is believed to be shaded environments of forest understories in southeastern Asia. On the

other hand, citrus land areas in São Paulo state were originally occupied by the Brazilian savanna, or *Cerrado*. In this review, we re-visit and discuss the ecophysiology of sunlight and water use by citrus species, and present some aspects of the ecophysiological responses of native cerrado species, which could mirror, encourage or at least provoke physiological reflections on strategies to be used in citrus breeding programs of the 21st century.

2. General characteristics of the Brazilian savanna

The cerrado is a mosaic of biomes (Batalha, 2011) that occupies approximately 21% of the Brazilian territory (Figure 1). The cerrado is considered to be one of the last agricultural frontiers in the world (Borlaug, 2002). In the cerrado areas, a warm and rainy season is observed from October to March and a dry and cold season from April to September. It rains approximately 1500mm per year in the cerrado, and air temperatures may range between 22 and 27°C (Klink & Machado, 2005).



Fig. 1. Geographical distribution of the cerrado among Brazilian states.

From the native cerrado area (2 million Km²) almost 50% has been destroyed and transformed into agricultural land areas.

Amongst other areas intended for conservation in the world, the cerrado is one of the 25 critical hot spots because of its high biological diversity and an increasing human population pressure that the cerrado has recently undergone (MMA, 2002).

Changes in the cerrado also brought several environmental effects, such as habitat fragmentation, biodiversity extinction, presence of invasive species, soil erosion, changes in the fire regimes, unbalance in the carbon cycle and probably regional climate changes (Klink & Machado, 2005). In a short term perspective, this reduction in the cerrado biodiversity might directly or indirectly affect the functioning of the ecosystem (Chapin III et al., 2000).

3. Climate and genetic origin center of *citrus* and cerrado woody plants

The native habitat of citrus species is believed to be the shaded environments of forest understory in southeastern Asia (Davies & Albrigo, 1994) (Figure 2). Such information is the

backbone of discussions we intend to develop in the present text, since citrus plantations in São Paulo and Minas Gerais states in Brazil are currently occupying lands that were originally occupied by the native Brazilian savanna, or *Cerrado*. Consequently, the savanna vegetation, which is believed to have been selected and adapted in the early Cretaceous (Ratter et al., 1997) or in the Holocene (Ledru, 2002) is partially comprised of trees and shrubs showing physiological responses and plant development behavior that are considerably different from citrus plants.

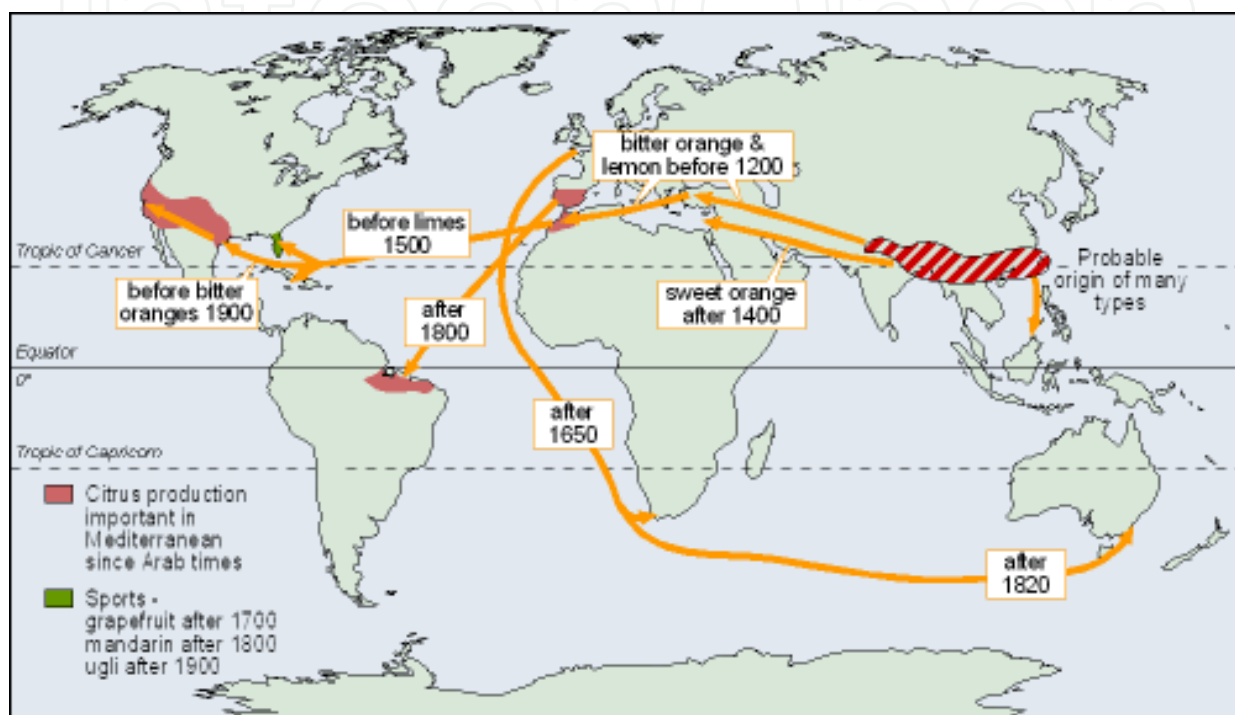


Fig. 2. Citrus origin center. Map adapted from information published by Davies & Albrigo (1994). Observation: This map was not originally drawn by the authors of this chapter

Despite their native shaded habitat in southeastern Asia, citrus plants are considered to be well acclimatized to tropical and subtropical sunny conditions (Ribeiro and Machado, 2007). Evidence suggests that citrus plants exhibit dynamic rather than chronic photoinhibition, given by the recovery of the maximum quantum efficiency of photosystem II, PSII, (F_v/F_m) at the end of the day, or when the photosynthetic photon flux density (PPFD) decreases (Ribeiro and Machado, 2007). Therefore, such reductions of F_v/F_m observed for citrus plants (Jifon and Syvertsen, 2003; Ribeiro and Machado, 2007) seem to be related to photoprotection, reducing the energy pressure on the PSII and avoiding injuries to the photosynthetic apparatus, which if not avoided would lead to photo oxidation.

However, a possible reason that citrus plants make use of the photoprotective mechanisms in tropical regions may be related to their native habitats in southeastern Asia, which suggests that the citrus plant is a shade species, or at least moderately adapted to shaded environments. Citrus leaves show photosynthetic responses that saturate at $600 \mu\text{mol m}^{-2} \text{s}^{-1}$ of PPFD (Vu et al., 1986; Habermann et al., 2003; Ribeiro and Machado, 2007), which can be considered a low-light saturation of photosynthesis, typical of shade species (Gvinish, 1988). Tropical and subtropical areas receive high solar radiation loads, and daily-integrated global solar radiation may reach values of $35 \text{ MJ m}^{-2} \text{ day}^{-1}$ or even higher values (Ribeiro and

Machado, 2007). Then, both citrus plants that are cultivated in tropical and subtropical areas and cerrado woody plants that are maintained as preserved sites in these regions have to cope with high irradiation loads, although cerrado woody plants are already adapted to such conditions. In fact, photochemical responses of cerrado woody plants are quite variable and dependent on species, because of the high plant diversity in cerrado ecosystems. Some case studies show that cerrado species have diurnal adjustments of non-photochemical energy dissipation in PSII to reduce the risk of photoinhibition when irradiances are high (Mattos, 1998; Lemos-Filho, 2000; Lemos-Filho et al., 2004; Franco et al., 2007). Therefore, photochemical adjustments in cerrado woody plants allow dynamic photoinhibitions, similar to daily adjustments in citrus plants. However, in citrus plants such balance between assimilative and non-assimilative processes occur mainly during the warm and wet season (October - March) of tropical regions, whereas for cerrado plants the correlation between the dry season (April - September) and photo damages to PSII is more frequent, although some results of dynamic photoinhibition in the wet season have already been described for these plants (Franco and Lüttge, 2002).

Therefore, differences between citrus and cerrado woody plants do not seem to be related to the way these plants cope with high irradiance loads. Then, one could argue that citrus plantations in São Paulo and Minas Gerais states, that occupy devastated areas previously occupied by the cerrado vegetation, would exhibit no contrasting biological performance in comparison with the cerrado vegetation, which does not produce any important economical crop. It would be easy to inaccurately justify devastation of cerrado areas to be used for citrus plantations. However, the cerrado vegetation is considered to have been selected under an important pressure of dry/wet seasons (Pinheiro and Monteiro, 2010). Consequently, the main constraint for cerrado woody species during the wet season is a nutritional stress, as soil nutrients are leached to soil beds after heavy rains, while in the dry season the lack of water availability to roots becomes the main concern. In fact, the dry season in such regions creates a remarkable pressure for the survival of cerrado species (Hao et al., 2008; Habermann et al., 2011a; Habermann and Bressan, 2011).

Under an ecological point of view, and considering the low-light saturation of citrus photosynthesis and its shallow root system, it can be said that citrus plants present a forest-like ecophysiological behavior. Moreover, only 20% of citrus leaves can be considered to be sun-exposed at the external canopy layer (Cohen and Fuchs, 1987), and only 10% of the total external PPFD can reach deep layers of a citrus canopy (Davies and Albrigo, 1994). Cerrado plant architectures, on the other hand, exhibit diverse strategies when it comes to sunlight penetration into the canopy. Despite the limited data concerning plant architecture in cerrado woody plants, their strategies range from vertical leaf orientation, which may not be related to leaf heat avoidance (Habermann et al., 2011b) to evergreen/deciduousness behaviors (Franco et al., 2005).

Although citrus and cerrado woody plants may show similar photochemical parameters, their overall ecophysiological strategies are quite distinct, which might represent hidden consequences for land use, which has not been studied so far.

4. Root system, water absorption/use strategies in citrus and cerrado plants

It has been long discovered by the citrus industry that the use of citrus rootstocks and scions is the best way to produce fruits in different tropical and subtropical regions from all over the world (Davies & Albrigo, 1994). Therefore, there are several species, varieties and

cultivars of citrus rootstocks indicated for specific regions, with specific climates, under particular disease and pest pressures.

By the middle of the 20th century, the Brazilian citrus industry was found to be under the threat of a new disease, called Citrus Tristeza Virus (CTV). Some observations made by Dr. Sylvio Moreira and Dr. Victória Rossetti suggested that orange plants that had been previously grafted on 'Rangpur' lime (*Citrus limonia* L.) rootstocks had escaped that disease, which was later confirmed, as evidenced by the 'Rangpur' lime resistance to CTV. Since then, 'Rangpur' lime has been a widely used citrus rootstock species for orange production in Brazil (Azevedo et al, 2006). But by the beginning of the year 2000, another threat, called citrus sudden death, was discovered to affect plants grafted on the 'Rangpur' lime rootstock. Aside from being a threat to 'Rangpur' lime-grafted orange plants, the citrus sudden death seems to be more prevalent among plants cultivated in warm regions, such as the northern and northwestern regions of São Paulo state (Jesus Junior & Bassanezi, 2004). Citrus Variegated Chlorosis (CVC), caused by the bacterium *Xylella fastidiosa* (Rossetti et al., 1990), is another important citrus disease and, although it does not limit the usage of any specific rootstock, it has influenced the migration of citrus groves to the south of São Paulo state. In this region, the incidence of CVC seems to be low due to mild environmental stresses that do not allow a fast bacterial spread within the plant xylem (Gomes et al., 2003; Habermann & Rodrigues, 2009).

The above description is a typical example of how horticulture, citrus breeding and phytopathological research programs intervene for the success of citrus industry. Therefore, the exploration of soil resources, mainly water (see next section for nutrients), by citrus plants has always depended on the "available" rootstocks species, cultivars and varieties as genetic resources. On the other hand, cerrado woody species have never undergone human intervention, except devastation and use of land for (citrus!) plantations. Cerrado plants have been facing biotic and abiotic stresses for millions of years, and adaptive pressures have always been applied to them (Pinheiro and Monteiro, 2010).

Interestingly, the 'Rangpur' lime is considered to be the best rootstock species for regions subjected to severe environmental stresses, such as the northern and northwestern regions of São Paulo state. Using one-year-old 'Valência' sweet orange plants, grafted on 'Rangpur' lime rootstock, it was observed that the 'Rangpur' lime's roots grow approximately 40 cm within 60 days (Magalhães Filho et al., 2008). On the other hand, using 40-day-old plants of a cerrado woody species (*Styrax ferrugineus*) it was observed that the main root reaches 60 cm in length within 75 days (Habermann & Bressan, 2011) (Figure 3). Therefore, the length root growth for both plants is very similar. However, the cerrado plants were only 40-days-old, whereas the citrus plants showed this root growth rate capacity in plants that had been cultivated for one year, as required by standard horticulture procedures. These representative case studies show that the long and deep root that was observed for *S. ferrugineus* is common for many cerrado species (Rawistscher 1948; Franco 1998), whereas for citrus plants such root behavior is only observed for the 'Rangpur' lime rootstock, in comparison with other citrus rootstocks (Magalhães Filho et al., 2008). Thus, in nature, cerrado species show a fast root growth rate to reach deep soil layers, allowing them to uptake water from deep water sources during the dry season (April-September).

Therefore, considering that disease limitations (CTV, CVC and citrus sudden death) and seasonal water deficit determine the specific rootstock to be used for citrus cultivations in the central, northern and northwestern regions of São Paulo state (Habermann & Rodrigues,

2009), and also that citrus plantations in São Paulo and (in the south of) Minas Gerais states are nowadays occupying lands that were previously occupied by the native cerrado vegetation, it would be valuable to investigate the plant biology, and to a further extent, the plant physiology of cerrado woody species. Indeed, Haridasan (2008) highlights the importance of understanding different aspects of plant biology of several species from the cerrado vegetation.



Fig. 3. Morphological details of the root system of plants of *Styrax ferrugineus* (on the left), *S. camporum* (in the middle), and *S. pohlii* (on the right) cultivated in rhizotrons (1 m long).

Since severe wet and dry seasonal events may have been one of the most important pressures for the new savanna vegetation that formed during the Tertiary and Quaternary geological eras (Pinheiro & Monteiro, 2010), it is expected that cerrado species present very good adaptations to cope with these pressures. In general, cerrado species present long and deep root systems (Rawistscher 1948; Franco 1998; Habermann & Bressan, 2011), low specific leaf areas (SLA) and thick leaves, especially in evergreen species (Franco et al., 2005). These characteristics make cerrado species very resilient to the seasonal water deficit, and some analysis (Prado et al., 2004) performed with data obtained from field observations demonstrated that there was no severe water stress during the dry season for 22 cerrado woody species.

Although efficient scion/rootstock combinations may increase the water use efficiency in citrus plants (Ribeiro & Machado, 2007), low stomatal conductance affects the CO₂ assimilation rates by decreasing carbon availability at the carboxylation sites. Such effects may be caused by the low values of soil temperatures (Magalhães Filho et al., 2009), soil water availability (Ribeiro & Machado, 2007) and also by high vapor pressure deficits

(Habermann et al., 2003) observed during the dry season in subtropical areas (Ribeiro & Machado, 2007; Habermann & Rodrigues, 2009). Significant reductions in the water use efficiency have been reported for irrigated field-grown citrus plants during the dry season (Ribeiro, 2006), which confirm that other factors, other than soil water availability, may affect the photosynthesis of citrus plants (Ribeiro & Machado, 2007). These effects may have significant consequences for fruit production, when considering different regions, with different micro-climates and different disease pressures and their physiological damages for plants (Habermann & Rodrigues, 2009).

Therefore, although cerrado woody species are (obviously) never studied under the plant production perspective, it is clear that such species are more suitable, or well adapted to deal with environmental stresses that occur in the areas that are currently cultivated with citrus plants in São Paulo and Minas Gerais states.

5. Soil fertility and aluminum “toxicity” for cerrado and citrus plants

Aluminum (Al^{3+}) is the third most abundant element on Earth, after oxygen (O_2) and silicon (Si^{4+}). Aluminum in the soil (Al^{3+}) constitutes a major limitation to crops (Rengel, 1992; Hartwig et al., 2007), mainly in tropical regions, causing imbalances in nitrogen, sulphur and carbon cycles (Bolan and Hedley, 2003; Tang and Rengel, 2003).

When the soil pH drops to values below 5, Al^{3+} becomes soluble in the soil solution and, if absorbed by plants, it inhibits the root growth, limiting water and nutrient uptakes (Kochian et al., 2004). It is well established that Al^{3+} inhibits the root cell expansion/elongation and cell divisions nearby (Kochian et al., 2004). Aluminum is mostly associated with the cell apoplast, but some associations between Al^{3+} and the symplastic cell environment have also been reported (Kochian et al., 2004). In addition, Al^{3+} is reported to disrupt the cytoskeletal dynamics, interacting with both microtubules and actin filaments, which may affect calcium (Ca^{2+}) homeostasis, playing an important role in toxicity (Kochian et al., 2004).

On the other hand, for cerrado species, Al^{3+} does not seem to negatively affect the absorption of other cations, such as Ca^{2+} , magnesium (Mg^{2+}) and potassium (K^+) (Haridasan, 1982; Medeiros and Haridasan, 1985). The reason for this lack of aluminum toxicity in cerrado plants is still unknown, and the metabolic pathways involved in this process are still unclear.

The cerrado areas present well drained and deep soils, with deep water tables, and these soils are rich in aluminum (Haridasan, 2008). When compared with soils that are used for agriculture, soils from cerrado areas are considered to be poor in nutrients (Table 1). However, cerrado plants are well adapted to these low fertile soils, and a high plant biodiversity is supported by these soils (Castro et al., 1999). In cerrado areas, one may find around 210 species per hectare, including trees, shrubs and grasses (Gardner, 2006).

Approximately 70% of citrus groves from São Paulo state occur in areas where root growth restrictions have been demonstrated due to high Al^{3+} contents in the soil (Pereira et al., 2003). Therefore, a high level of knowledge about mineral nutrition and the discovery of mechanisms involved in aluminum toxicity avoidance in cerrado species would be very important to figure out an alternative research strategy to “construct” transgenic plants of citrus rootstocks that could become insensitive to the toxic Al^{3+} in the soil.

Citrus plants absorb great amounts of Mg^{2+} and Ca^{2+} (Oliveira, 1986), and are very sensitive to Al^{3+} , which is highly available in acidic soils (Malavolta & Violante Neto, 1988; Table 1). In citrus leaves, aluminum affects photosystem II in thylakoid membranes, reducing the

photochemical performances of the photosynthetic apparatus, causing leaf chlorosis and also reducing the dry mass accumulation and plant development (Jiang et al., 2008). On the other hand, cerrado species show an opposite response pattern. A lack of Al^{3+} for the roots of cerrado species can reduce photosynthetic rates, causing leaf chlorosis and necrosis, and can even reduce the dry mass accumulation. Moreover, two aluminum hyperaccumulator cerrado species use chloroplasts as a sink for Al^{3+} , with no apparent signs of toxicity (Andrade et al., 2011).

Soil	pH	OM	P (resin)	Al^{3+}	H+Al	K ⁺	Ca ²⁺	Mg ²⁺	BS	V%
	(CaCl ₂)	(g dm ⁻³)	(mg dm ⁻³)	(mmolc dm ⁻³)						(%)
Unfertilized*	4.0	12.0	1.0	9.0	47.0	0.3	1.0	1.0	2.0	4.0
Fertilized**	5.2	14.3	65.7	0.0	17.7	2.6	36.7	14.0	53.3	74.3

OM - organic matter, BS - base saturation, V% - fertility rate

*adapted from Habermann & Bressan, 2011

**adapted from Corá et al., 2005

Table 1. Fertility parameters, and macro- and micronutrient contents in contrasting soils from different cerrado conditions (fertilized and non-fertilized soils) in São Paulo state, Brazil.

Aluminum hyperaccumulator plants are mainly woody species that absorb and maintain, in their (leaf) tissues, more than 1000 mg Kg⁻¹ of Al^{3+} , exceeding the Al^{3+} presence in the soil or in the non-accumulating species growing nearby (Haridasan, 1982, Jansen et al., 2002). In 1971 Professor Goodland suggested that cerrado plants accumulate aluminum (Haridasan, 2000), resulting in plants that exhibited what he called olygotrophyc schleromorphism. This author suggested that the scleromorphism in cerrado species could be caused by aluminum toxicity, since the symptoms of aluminum toxicity are similar to the deficiency caused by malnutrition (Haridasan 2000). Based on results reported by Hutchinson (1943), Chenery (1948 a, b) and Webb (1954), who had also identified aluminum accumulation syndromes in plants from the Australian and other savannas, Goodland suggested that the Vochysiaceae and Melastomataceae plant families from the cerrado could also be considered aluminum accumulators (Haridasan 2000).

Currently, it is known that the most important hyperaccumulator species in the cerrado are: *Miconia ferruginata*, *M. burchellii*, *M. albicans*, *M. fallax*, *M. pohliana* (Melastomataceae); *Symplocos platyphylla* (Symplocaceae); *Palicourea rigida*, *P. squarrosa*, *Coussarea* spp., *Faramea cyanea*, *Rudgea viburnioides* (Rubiaceae); *Vochysia thyrsoidea*, *V. rufa*, *V. haenhiiana*, *V. elliptica*, *V. tucanorum*, *V. divergens*, *Qualea dichotoma*, *Q. Grandiflora*, *Q. Multiflora*, *Q. parviflora*, *Calisthene major*, *Salvertia convalhariadora* (Vochysiaceae) (Haridasan, 1982, 1987, 1988; Haridasan & Araújo, 1987).

Vochysia thyrsoidea and *Miconia fallax* cultivated without Al^{3+} in the soil show chlorotic and necrotic leaves, and severe reduction in the growth rate (Haridasan, 1988; Haridasan, 2000; Haridasan, 2008) (Figure 4 and 5) and *Styrax camporum* shows reductions in the root development [(Habermann, G. 2010, unpublished data) Figure 6]; however, when these species are transplanted to an Al^{3+} -rich soil, or Al^{3+} -rich nutritive solution, the plants recover well, suggesting that some cerrado species are incapable of surviving in calcareous soil, because aluminum might be an essential nutrient for these plants.



Fig. 4. Seedlings of *Vochysia thyrsoidea* growing in an acid and Al^{3+} -rich soil, showing healthy green leaves (top); and in a calcareous soil, showing chlorotic leaves (bottom) (pictures originally published by Haridasan, M. in Braz. J. Plant Physiol, v. 20, p. 183-195, 2008).



Fig. 5. Seedlings of *Miconia albicans*, growing in acid cerrado soil (left) (healthy green leaves) and alkaline calcareous soil (right) (chlorotic leaves and stunted growth) (picture originally published by Haridasan, M. in Braz. J. Plant Physiol, v. 20, p. 183-195, 2008).



Fig. 6. Seedlings of *Styrox camporum* cultivated in a nutritive solution without aluminum showing dark necrotic roots (on the left) and with 20 mg L^{-1} of aluminum showing normal development of roots (on the right) (Habermann, G. 2010).

Not only does toxic Al^{3+} in the soil negatively affect citrus crop production, but also a low soil pH may provoke serious problems to the nutritional plant balance. Most citrus groves in São Paulo and Minas Gerais states show soil pH around 5.0 (Table 1). Correcting soil pH can enhance production from 46 to 61 kg per 'Valência' sweet-orange tree (Anderson, 1987). Notwithstanding, soil pH corrections are very expensive and yearly-mandatory.

6. Conclusions

We tried to show that many studies about the plant biology and ecophysiology of cerrado species have been and are still being conducted, but a few, if any, are investigating native plants and their use as genetic resources for citrus plants. In addition, it was highlighted that since cerrado plants are adapted to the natural stresses that occur in the areas that are nowadays occupied by citrus plantations, they may show several (adapted) responses to deal with such environmental stresses. Thus, it is about time that citrus research and plant breeding biotechnology start looking at the plant biology of cerrado woody plants. As far as we know, this research strategy is practically neglected, not only for citrus plants, but for many other crops.

In the future, under global warming effects, it will be too late to overcome the consequences of not having used native plants as genetic resources. Irrigation, which is extremely expensive, will be the last and only option for orchards. Brazil, which is the largest producer of citrus fruit, may lose its productive capacity by not having researched its native genetic resources, which have been and are being destroyed even before we begin to understand and make good use of them.

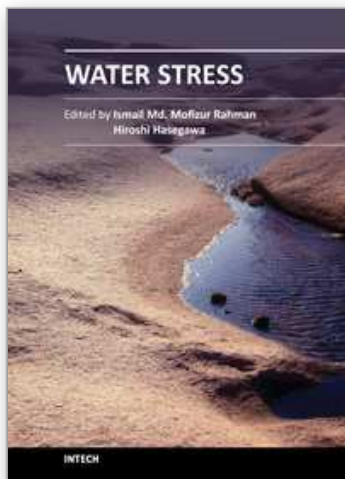
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Water Stress

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Plants experience water stress either when the water supply to their roots becomes limiting, or when the transpiration rate becomes intense. Water stress is primarily caused by a water deficit, such as a drought or high soil salinity. Each year, water stress on arable plants in different parts of the world disrupts agriculture and food supply with the final consequence: famine. Hence, the ability to withstand such stress is of immense economic importance. Plants try to adapt to the stress conditions with an array of biochemical and physiological interventions. This multi-authored edited compilation puts forth an all-inclusive picture on the mechanism and adaptation aspects of water stress. The prime objective of the book is to deliver a thoughtful mixture of viewpoints which will be useful to workers in all areas of plant sciences. We trust that the material covered in this book will be valuable in building strategies to counter water stress in plants.

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