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EDITORIAL

Insights into rootstock biology under low oxygen

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INTRODUCTION

The use of rootstocks by the fruit industry is essential nowadays because of their ability to effectively improve yield, induce tolerance to abiotic and biotic stresses, increase water and mineral use efficiency, modify plant growth and canopy architecture, and facilitate renewal of old plantations. Rootstocks are also important to increase mechanization and reduce labor costs in modern fruit orchards and help growers cope with the effects of global climate change. This last aspect is becoming an important issue in cultivated areas where environmental stresses such as frost, drought, and flooding are unpredictable.

Changes in temperature and rainfall regimes are also obliging growers to look for new plantation areas. This also implies the use of new types of soils which generate different edaphic conditions for the roots. In Chile, temperature increases have caused the boundary of fruit production to move south where volcanic soils prevail. The edaphic conditions of these soils are different from those of traditional fruit cultivation areas located in the central and northern parts of the country.

All of the above aspects increase the interest for new rootstocks better adapted to new climatic and soil conditions. This represents a new challenge for breeders (Gainza et al., 2015a) who need to obtain rootstocks with increased tolerance to biotic stresses (pests and diseases) and environmental stresses such as drought, frost, salinity, high temperature, and flooding. In this special issue, stress caused by low oxygen concentration at the root level, referred to as hypoxia, will be analyzed. Hypoxia is common in heavy soils and is exacerbated by soil compaction and excess water, which are important in the new areas being incorporated for new plantations in southern Chile.

Hypoxia stress

Excess water produces oxygen depletion in soils because it dramatically reduces the diffusion coefficient of gases in soil pores. Gas diffusion is also greatly influenced by soil physical characteristics such as texture, structure, pore size, and tortuosity. Neira et al. (2015) state that compaction and water saturation are the main barriers for oxygen diffusion in soils; water is the most effective barrier. Gas diffusion in water, including oxygen, is slower than its diffusion value in air by a factor of 10^4. Gas diffusion can also be affected by organic matter because it reduces soil compaction by increasing aggregate stability and produces changes in pore size distribution in the soil. However, after Neira et al. (2015), the effect of organic matter on oxygen diffusion has not been clearly stated, and more research is needed on this aspect.

Hypoxia and hormones

A decrease in soil oxygen diffusion induces anatomical, physiological, and molecular changes in roots and aerial parts of a plant. This affects processes such as nutrient and water uptake, and particularly root respiration (Toro and Pinto, 2015). Salazar et al. (2015) analyze changes in gene expression associated with pathways that are not present under normal oxygen supply. For example, under excess of water, increases in abscisic acid (ABA) have been reported in several species such as alfalfa, tobacco, pea, tomato, and *Malus* spp. However, the ABA response to hypoxia may depend on the plant species and flooding duration. Some species are more responsive to hypoxia than others which show a large accumulation of ABA in their leaves and roots. Ethylene accumulation is also a response to hypoxia. Salazar (2015) states that under flooding the expression of ethylene receptor genes is up-regulated by low oxygen and excess ethylene induces senescence in leaves and aerenchyma formation in the roots and stems. This is believed to facilitate oxygen transport from the upper part of the plant to the roots.

Other plant responses under flooding conditions have been linked to hormone-induced signals. Under low oxygen, there is an accumulation of 1-aminocyclopropane-1-carboxylic acid (ACC) in the roots, which is transported to the stems. Once this compound reaches the aerial parts in the presence of oxygen, it is converted into ethylene by the ACC oxidase enzyme, and triggers responses such as epinasty or leaf senescence. Under prolonged flooding conditions, Salazar indicates that ethylene may down-

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regulate ABA synthesis and activate the expression of genes related to the biosynthesis of gibberellins, which results in shoot elongation and formation of adventitious roots. Both effects are related to morphological modifications intended for better oxygen use under hypoxia conditions.

Plant hemoglobins and hypoxia

Other genes that are up-regulated under low oxygen are those related to hemoglobin biosynthesis. Information reported by Riquelme and Hinrichsen (2015) indicates that the expression of these proteins in plants correlates well with plant development and its tolerance to hypoxia. Although the function of plant hemoglobins is not yet well known, their overexpression in leaves and roots caused by a low root oxygen levels indicates that they can participate in the capture and transport of oxygen in plants, and in this way contribute in maintaining the energy charge in the root cells. Research on plant hemoglobins is still at a very early stage, although information generated in recent years indicates that they can play an important role in hypoxia-tolerant rootstocks and allow fruit trees to cope better under low oxygen conditions.

Respiration and hypoxia

The major physiological responses to hypoxia stress conditions are mainly associated with reduced root respiration. This is analyzed by Toro and Pinto (2015), who describe the characteristics of the plant respiratory process, particularly under stress. Reduced respiration means low availability of metabolic energy (ATP) and carbon chains for growth processes (new compound biosynthesis). That is why plants immediately stop to grow when oxygen decreases in the soil. However, under low oxygen, maintenance processes are normally actively repairing damage caused in the cell machinery, especially protein reparation. It is costly to maintain protein turnover at a convenient rate; however, it is necessary for plants because damage caused by oxidative stresses would be permanent. Changes in the proportion of respiration components (growth and maintenance) have been reported in plants subjected to oxygen deficiency. This allows the authors to postulate that plants with a high capacity for repair can better tolerate abiotic stresses than plants with low capacity. This can be the case for rootstocks tolerant to hypoxia where the maintenance component of respiration can be more important than in the case of sensitive rootstocks.

The importance of rootstock/scion compatibility

In addition to the traits described above, a new generation of rootstocks must have good compatibility with the scions of different species or cultivars of the same species. This is a very desirable trait because it is well known that the limiting factor for the widespread use of rootstocks for new cherry, almond, apricot, and peach plantations is their lack of an appropriate range of compatibility with different cultivars of these species. In general, good compatibility occurs between closely-related cultivars or species, but it is exceptional between individuals from different genera even if they are related to some degree. Incompatibility has been associated with both anatomical and biochemical alterations the graft interface, in where both induce blockage of carbohydrate transport in the scion above the graft union. Nevertheless, incompatibility symptoms might not occur at early stages but years later when anatomical irregularities in the rootstock/scion union breaks vascular and cambial continuity. This can produce the death of adult trees and result in major economic loss for the growers. The physiological and metabolic mechanisms by which incompatibility is expressed years later remain unclear. Several hypotheses are analyzed by Gainza et al. (2015b) in this special issue. Improvements in the knowledge about the physiological and metabolic control of the establishment of the graft union in *Prunus* spp. can help to develop new rootstock material. For this, physiological and molecular markers are important in assisting rootstock breeding programs. These aspects are analyzed by Morales-Olmedo et al. (2015) and Guajardo et al. (2015), respectively.

Assisted selection in rootstocks

There is currently not much available information to assist in selecting *Prunus* spp. rootstocks with a wide range of compatibility and tolerance to different stresses. Using information from genetic maps, a high level of synteny has been demonstrated among *Prunus* species, and this suggests that they all share a similar genomic structure. Applying methods to identify regions of the genome involved in the expression of important traits, Guajardo et al. (2015) show that it is possible to identify genetic determinants involved in tolerance to abiotic stresses and other traits in *Prunus* rootstocks. In her article, Guajardo provides insights on the advances in the development of molecular markers for use in marker-assisted selection (MAS) in *Prunus* species. This with the aim to provide a general approach to identify the genetic determinants of stress tolerance in *Prunus* rootstocks.

Final remarks

Root biology is an important field of research that is producing results that can have important uses in agriculture in the future. This is particularly true for cultivated perennial plants such as fruit trees and grapevines where the use of rootstocks in commercial plantations is for many reasons essential. Therefore, it is crucial to obtain new rootstocks better adapted to the new conditions imposed by global change as well as the generation of new knowledge about root behavior under different soil conditions. The reviews of this special issue focus on these topics.

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