

Grapevine roots: the dark side

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Abstract

Since the second half of the XIXth century, grapevine has been grown grafted worldwide to cope with Phylloxera. Consequently, the cultivated grapevine is a chimeric plant made from two genotypes which interact together. The result of this interaction must ensure a balanced functioning dedicated to fruit production in terms of quantity and quality. The rootstock acts as an interface between the edaphic environment and the scion, and is an important component of adaptation to environment. The rootstock is responsible for the uptake of water and minerals from the soil, feeding the aerial parts in exchange for a supply of carbon that is stored as reserves, or used to produce nutrients and growth regulators. Many signaling and regulating molecules, such as hormones and nucleic acids, are also exchanged between the two partners. Despite its importance, little is known about the root system and the grafting zone (rootstock-scion interface) in grapevine. Until recently the study of rootstocks received little attention from growers and the scientific community. New challenges, such as climate change, environmental issues, and yield limitations, have brought new light on the “dark side” of the grapevine. This paper reviews the main physiological processes involved in the functioning of roots and the graft interface. Key, challenging scientific issues as well as applied perspectives for the industry will be discussed.

Keywords: grapevine, rootstock, *Vitis*, root system, interaction, mineral nutrition, water

INTRODUCTION

Since the XIXth century, the grapevine species *Vitis vinifera* has been grafted in most vineyards in the world to cope with the soil-born aphid *Daktulosphaira vitifoliae* [Fitch]. Rootstocks are cultivars or hybrids of American *Vitis* species naturally resistant to phylloxera. In addition to solving biotic problems such as phylloxera or nematodes, rootstocks have varying tolerances to adverse environmental conditions. From an applied point of view, the rootstock plays the role of interface between the edaphic component of the environment and the *V. vinifera* scion that bears the fruit. Consequently, it is a key component in mediating environmental effects and influencing fruit qualities.

Introduction of rootstocks has created a new source of genetic diversity. In association with the large number of scion cultivars, rootstocks generate a very high number of combinations increasing variability and adaptation. However, grafting is not a neutral practice. The grafted grapevine is a chimera between two genotypes and the resulting phenotype depends on 2 genotypes interacting with the environment. The functioning of the grafted plant is more the result of an interaction, than an additive process (Tandonnet et al., 2010; Lefort and Léglise, 1977). Replacing the root system not only modifies the root properties but also has profound effects on scion development, biomass accumulation and allocation, fruit composition and plant response to abiotic stresses. These effects appear as soon as the graft is established and may evolve as the plant ages.

At the whole plant level, rootstock effects have been widely described, but the underlying physiological mechanisms have poorly been studied. This is mainly due to difficulties accessing roots and the lack of methodologies allowing the assessment of the

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complexity of the grafted system and long distance signaling. This article will provide an overview of the recent knowledge collected on grapevine root growth and development, mineral nutrition, water relations, and rootstock-scion interactions which together contribute to the rootstock effect on fruit composition.

ROOTSTOCK EFFECTS ON FRUIT COMPOSITION

The rootstock effect on wine quality may be estimated with tasting experiments comparing wines produced from fruit of vines grafted on different rootstocks in the same plot to limit other sources of variability (Ollat et al., 2003b). Most of these effects can be explained by yield variation or modification of the leaf/fruit ratio (Tandonnet et al., 2011). The differences picked by the wine tasters are often related to a modified balance between primary and secondary metabolite compounds. Rootstocks may affect the accumulation of primary metabolites, and especially sugars. This effect may, or may not, be yield dependent (Figure 1).

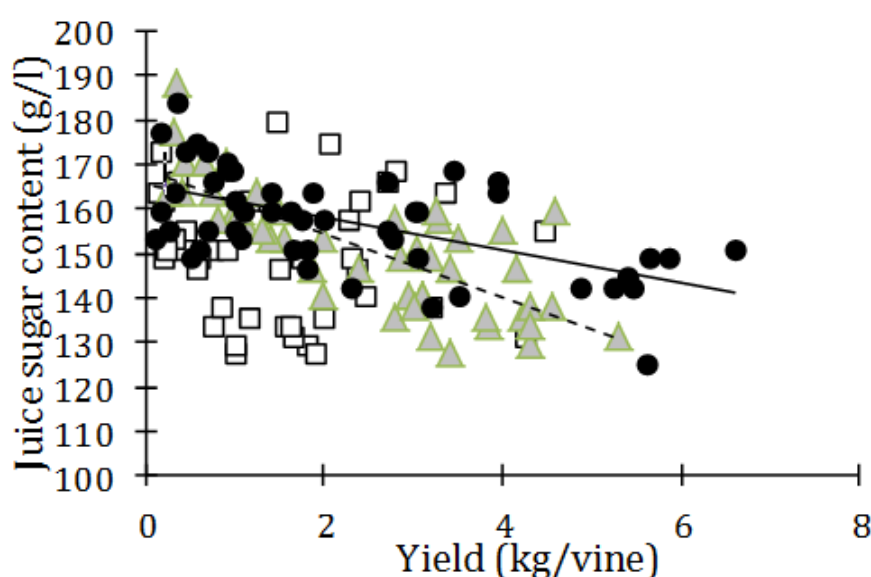


Figure 1. Relationship between single vine yield and sugar content of the fruit at harvest of 'Cabernet Sauvignon' grapevines grafted onto 3 rootstocks ('Riparia Gloire de Montpellier': black open squares, SO4: gray triangles, 'Gravesac': black dots). Lines represent significant linear regressions for SO4 (dashed line) and 'Gravesac' (full line). The regression was not significant for 'Riparia Gloire de Montpellier'.

Figure 1 illustrates changes in sugar content in berries as yield increases for three rootstocks, 'Riparia Gloire de Montpellier' (RGM), SO4 and 'Gravesac'. It shows also that sugar content can be low even at low yield (for RGM) and that the slope of the regression is higher for SO4 than 'Gravesac', indicating a larger reduction of sugar content as yield increases for the former rootstock. Differences in leaf to fruit ratio or in allocation of sugars between vegetative growth and fruit may explain these effects.

Rootstocks also affect amino acids and polyphenolic concentrations in the fruit (Habran et al., 2016; Berdeja et al., 2014).

On a large metabolomics data set, specific data analyses (i.e., supervised OPLS) allow the identification of compounds more associated to one variable. When this type of analysis was carried out on CS grafted onto either 110R or RGM the results showed that fruit of CS-110R was characterized by more anthocyanins and acylated anthocyanin, flavonoids and stilbenes. The most affected anthocyanins were cyanidin, delphinidin, and petunidin O glucoside and their corresponding acetylated forms (Figure 2). It was also shown that the

expression of genes related to phenylpropanoid and general secondary metabolism monitored in berries during ripening differed between two scion-rootstock combinations, especially under drought conditions (Berdeja et al., 2015).

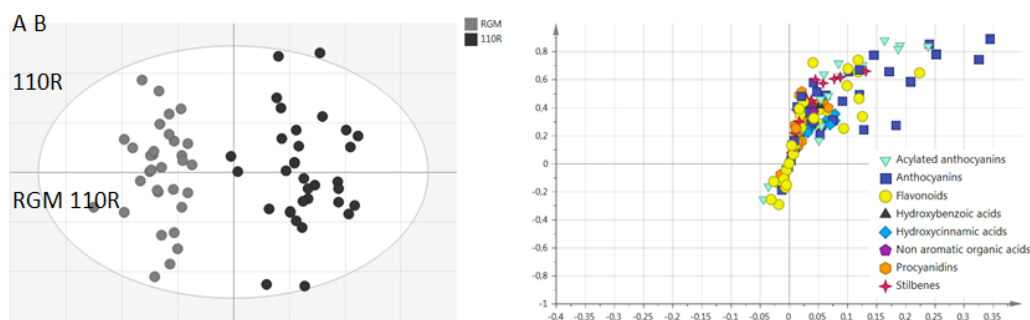


Figure 2. OPLS analyses of LC-MS data for secondary metabolites in grape berry skin of 'Cabernet Sauvignon' grafted onto 'Riparia Gloire de Montpellier' and 110R. A: Individual score plots after data normalization. B: S plot of factorial weights for CS-RGM and CS-110R. Colors indicate the different secondary metabolites compounds which characterized specifically one or the other rootstock (Habran et al., 2016).

To further explain the effects of rootstock on fruit composition and berry metabolism, deeper investigations should be performed at the root level to analyze how rootstocks modify root development, mineral nutrition and water relations. Rootstock-scion interactions should also be taken into account, starting from the earliest steps of the grafting process.

ROOT GROWTH AND DEVELOPMENT

Rooting ability at early stage

The root system of grapevine is made from adventitious roots which developed from stem parts after grafting during the first growth cycle. Adventitious roots emerge from cambial or other meristematic cells (Legué et al., 2014) and neighboring vascular tissues (Bellini et al., 2014). *Vitis* species show a large variability in the formation of adventitious roots (Pongracz, 1983). As an example *V. berlandieri* is known to be recalcitrant to rooting while *V. riparia* and *V. vinifera* having no difficulties (Ollat et al., under press). Rooting ability was recently shown to have a medium heritability and good rooting individuals can be found within the progeny between poor rooting parents (Smith et al., 2013). Genetic architecture data for this trait, or other parameters linked to early root development or root morphology, are lacking despite the applied interest for rootstock breeding.

Root system development

Grapevine is a perennial plant with a root system expanding mainly during the first 7 to 8 years after planting (Branas, 1974; Champagnol, 1984). Later, soil colonization improves mainly through ramification. Root system development is competing for carbohydrates with the other sinks of the plant, especially the fruit. This competition can strongly affect the roots during the first years of production, because roots are a weaker sink than fruits (Williams, 1996).

At adult stage, root system architecture and rooting depth depend mainly on soil type, training system, and cultural practices (Smart et al., 2006). Rootstock has a major effect on the rooting density and the ratio between fine and coarse roots (Southey and Archer, 1988; Morano and Kliever, 1994; De Herralde et al., 2010). It was also shown that rootstock genotypes differ in rooting angles at early stages (Branas and Vergne, 1957). Differences tend to disappear as the plant gets older in the vineyard and most roots are localized in the

40-60cm top layer. However some genotypes as 140Ru show a better ability than the others to grow in compacted layers of soil (Southey and Archer, 1988).

Even if correlations between young and field grown plants are poor, some characteristics of rootstock genotypes, such as ramification and root diameter, could be evaluated at early stages using special devices designed to have better access to roots (e.g., rhizotrons) (De Herralde et al., 2010). Figure 3 illustrates the root development of two rootstocks, 110R and 'Riparia Gloire de Montpellier' (RGM), after 29 days of growth in 30×40 cm rhizotrons. 110R displayed a more vertical root system with few ramification and RGM a more horizontal with a high ratio between fine and coarse roots.

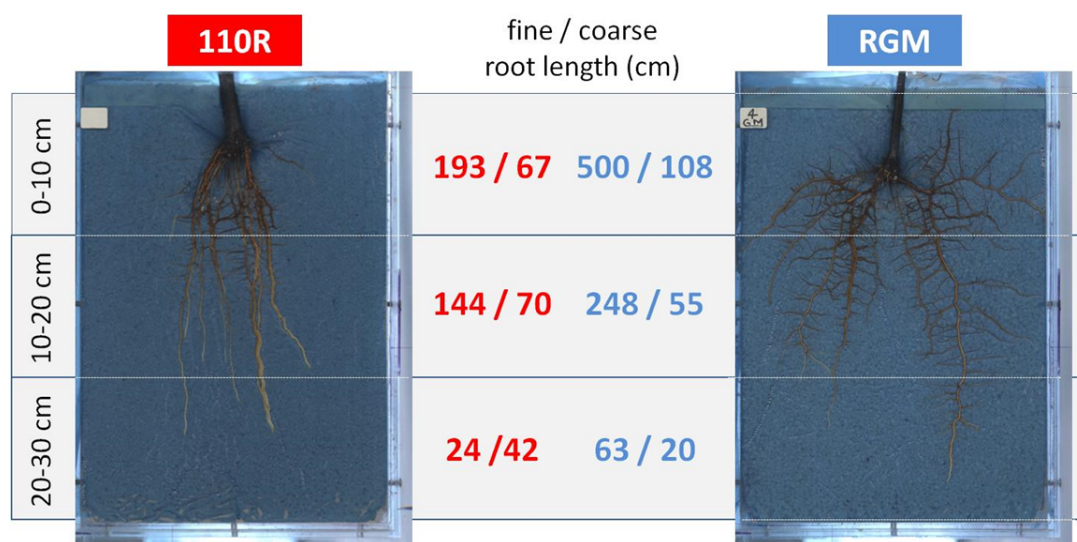


Figure 3. Rhizotron devices used for root systems studies with two different rootstocks: left 110R (left panel); right RGM 'Riparia Gloire de Montpellier' (right panel). Numbers indicate the total length of fine and coarse roots for each rootstock evaluated with WinRhizo software (Dumont et al., 2016).

More than root architecture, grapevine root growth plasticity in response to environment conditions determines when and where roots capture resources and are likely an important component of adaptation (Comas et al., 2010). Only few data have been reported about root growth plasticity (Comas et al., 2005). Root growth dynamics were studied for field grown *V. vinifera* 'Merlot' grafted onto 1103P and 101-14 MGt, that confer high and low vigour to the shoot, and high and low tolerance to water stress, respectively (Bauerle et al., 2008). It was observed that 1103P has a greater ability to develop roots in the summer during localized wetting events implying better competition for ephemeral resources in a patchy environment. In contrast 101-14 MGt seemed to use a long-term strategy consisting of the growth of a large root system, and root growth that occurs mainly during the wet period of winter. Whether this ability is associated to conferred vigour and adaptation to limiting growing conditions needs to be verified (Zhang et al., 2016).

MINERAL NUTRITION

As mineral uptake and first steps of their assimilation occur in roots, mineral nutrition is a key process in explaining the soil and rootstock effects on fruit composition. For example nitrogen may interfere with polyphenolic metabolism, phosphorus with sugar metabolism and energy production, and potassium with the control of acidity. In addition, toxicities and deficiencies are fully linked to mineral uptake properties by roots. Although the response of grapevine to mineral nutrition is well documented in terms of vegetative growth, yield, and fruit composition, evidence for the physiological mechanisms underlying these traits specifically related to uptake by roots in grapevine is still very scarce (Keller, 2015). Few

studies are related to iron (Varanini and Maggioni, 1982), potassium (Pinton et al., 1990), nitrate (Pii et al., 2014) and chloride uptake (Henderson et al., 2015), as well as ATPase activity supporting proton exchanges at root levels (Pinton et al., 1990; Pii et al., 2014).

Nitrogen uptake and allocation

Nitrogen is considered as one of the main parameters controlling plant growth, and in grapevine fertilization is managed to ensure optimal yield and fruit composition (Lecourt et al., 2015). While this parameter is very important, rootstocks are not well characterized for their ability to take up nitrogen and translocate it to the aerial parts. Studying the effect of nitrogen supply on two scion-rootstocks combinations with one year old plants, Lecourt et al. (2015) observed that the rootstock affects N concentration in roots, but not in leaves, while the level of N supply modified N concentration in leaves, but not in roots. It was suggested that rootstocks may differ in their perception of N satiety and threshold transport of N to the shoot. When analyzing the other nutrients, P content in leaves was only affected by the N x rootstock interaction, suggesting that P translocation to aerial parts could be affected by rootstocks, as previously reported (Grant and Matthews, 1996). In addition, it was shown that rootstock genotype affected the elemental concentration ratio between the leaves and the roots, CS/1103P having a higher concentration in leaves than CS/RGM (Figure 4). With the objective to identify the molecular components underlying these rootstock effects, transcriptomic analyses were performed and preliminary results provide interesting information suggesting what root transcriptome is differentially reprogrammed in the two rootstock genotypes and that these changes are associated with differences in hormone levels (Cochetel et al., 2014).

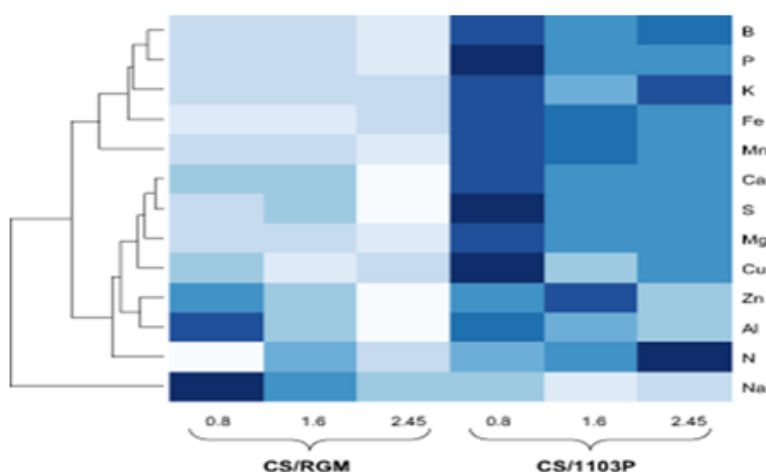


Figure 4. Heatmap of normalized element concentration ratio between the leaves and roots of 'Cabernet Sauvignon'/'Riparia Gloire de Montpellier' (CS/RGM) and CS/1103Paulsen (CS/1103P) grown under three nitrogen treatments (0.6, 1.6 and 2.45 mmol KNO₃) measured 60 days post-treatment, *n*=5. The intensity of color indicates the ratio level: light, lower ratio, and dark, higher ratio (Lecourt et al., 2015).

Responses to deficiency or toxicity

The variability existing among rootstocks allows the cultivation of grapevine in many limited environments. In some vineyards, limestone chlorosis and salinity are two major problems and the different abilities of rootstocks to cope with these limitations are well described (Keller, 2015; Ollat et al., 2016a). As these traits are important for rootstock breeding, their physiological and genetic determinisms have been analyzed with the objective of identifying molecular markers for selection.

High uptake and root-to-shoot transport of chloride resulted in its excessive accumulation in leaf tissues, causing impaired leaf function and damage under salinity (Downton et al., 1990; Walker et al., 1997). Chloride exclusion by roots may prevent chloride accumulation in leaves, thus contributing to salt tolerance (Stevens and Walker, 2002). Indeed, a much lower chloride concentration was found in xylem sap and shoot tissue of potted grape vines when they are grafted onto a salt-tolerant (140 Ru) rather than a salt sensitive rootstock (K51-40) (Tregeagle et al., 2010). The uptake capacities did not differ between the two genotypes, but chloride concentration was much higher in 140 Ru roots, indicating a lower capacity to transport chloride from parenchyma cells, to xylem, and eventually, to the aerial parts (Gong et al., 2011). It was suggested that there is a single dominant gene for chloride exclusion in *V. berlandieri* (Newman and Antcliff, 1984). Studying a progeny with complex genetic background showed a continuous variation in chloride accumulation in both laminae and petioles, suggesting that different species may carry different genes that combine in complex hybrids (Gong et al., 2011). Some candidate genes encoding ion transporters, such as *VviNHX1*, *VviSLAH3*, *VviALMT1* and members of the NRT1 family, were shown to be differently expressed between rootstocks with various excluding capacities (Upadhyay et al., 2012; Henderson et al., 2014). However, cation-chloride cotransport is not likely involved in salt tolerance (Henderson et al., 2015).

Limestone chlorosis affects shoot growth and laminae chlorophyll content, with necrotic symptoms under severe situations. These symptoms are due to difficulties in the uptake of iron in soils with high pH. Plants have developed different strategies to cope with this problem. Most dicotyledonous plants, including grapevine, utilize "Strategy I", which means increased reducing activity and release of protons in the root apoplast. Other morphological and physiological changes in grapevine roots have been reported, including the accumulation of organic acids (especially citrate), shifts in the redox state of the cytoplasm, and increases in the activity of several key enzymes (Ollat et al., 2003a; Jiménez et al., 2007; Covarrubias and Rombola, 2013). Differences between *Vitis* species and among rootstocks have been reported for their ability to cope with limestone and induce Strategy I responses (Bavaresco et al., 1991, 1993; Brancadoro et al., 1995; Jiménez et al., 2007). In order to analyze the genetic determinism of the limestone chlorosis response, a QTL mapping approach was conducted recently, using a *V. vinifera* × *V. riparia* progeny (Bert et al., 2013). Although several QTLs were detected for leaf chlorophyll content indicating a polygenic control, no identified QTLs were associated with candidate genes.

The role of mycorrhizas

It is well known that grapevines form symbiotic associations in their roots with arbuscular mycorrhizal fungi (AMF). The interaction is based on biotrophic nutrient exchanges between partners. The host plant provides carbon to the fungal partner which in turn improves water and nutrient uptake from the soil (Schreiner, 2005; Trouvelot et al., 2015). The fungus may receive 4 to 20% of the carbon photosynthetically fixed by the host plant, which can result in a depressive effect on plant growth during the first week of colonization. However, positive effects on growth were already observed in grapevine a few weeks after inoculation, and varied according to rootstocks and fungi species (Linderman and Davis, 2001). AMF contribute to supply minerals with low mobility, and especially phosphorus. Extension of the exploitable soil volume by the external mycelium network is the primary cause of enhanced nutrient uptake. It was shown that P concentration increases in grapevine roots and leaves in presence of mycorrhizas and important reprogramming of host genes have been reported (Cangahuala-Inocente et al., 2011). Other effects of AMF on mineral nutrition of grapevine are highly complex and have been reviewed recently (Trouvelot et al., 2015). AMF were also shown to improve plant water relations and photosynthesis of young transplanted plants (van Rooyen et al., 2004), probably in relation with their ability to improve plant performances in dry situations (Trouvelot et al., 2015). Inoculation also alleviates iron chlorosis symptoms in lime-susceptible grafted combinations (Bavaresco et al., 2010), and has a beneficial role in improving grapevine salt tolerance (Khalil, 2013).

These few findings show that the control of mineral nutrition is a very complex trait. More energy should be invested to improve our understanding of this important component of root physiology.

WATER RELATIONS

Within the plant, water flow is under the control of the water potential gradient between the soil and the atmosphere. The plant may be considered as a pipe where the flow is slowed down by multiple resistances along the pathway. These resistances are linked to the structural and physiological properties of the different tissues. In grapevine, the major resistances to water flow are located at the leaf and root levels (Tramontini and Lovisolo, 2016). The grafting point contributes to a significant part of trunk resistance, but it is still much lower than resistance at the root level (de Herralde et al., 2006). At tissue and cellular levels, water flows in cell walls and through cell membranes, respectively through the apoplastic and symplastic pathways. Water flow through the symplastic pathway is facilitated by the abundance and activity of membrane proteins called aquaporins. Aquaporins are highly regulated at transcriptomic and post-translational level.

The genetic diversity existing between rootstocks for their response to drought have been reported by several authors (Carbonneau, 1985; Fregoni et al., 1978; Serra et al., 2014; Ollat et al., 2016b). The mechanisms involved may be summarized as follows: first rootstocks can affect water uptake capacities through root morphology, growth properties and functioning, as well as their extraction capacities; rootstocks can also modify the transport of water from the roots to the shoots through the hydraulic properties of roots, trunk and grafting union; finally they may regulate water losses by the canopy by their effects on canopy development and by the regulation of leaf gas exchange mediated by root born chemical or hydraulic signals (Ollat et al., 2016b; Serra et al., 2014).

At the root level

The plasticity of root growth in response to soil water content has been mentioned previously and genetic variability for this trait should be further explored. In addition, several authors suggested that water extraction capacities by roots could be affected by rootstocks and explain rootstock effects on plant transpiration (Carbonneau, 1985; Soar et al., 2006). Genetic control of rootstock on this complex trait was demonstrated using a quantitative genetic approach. Inter-annual steady QTLs could be identified explaining up to 21% of the phenotypic variance (Marguerit et al., 2012). Transcriptomic analyses performed on roots of different rootstocks submitted to water deficit showed that the expression of genes involved in cell wall structure and biosynthesis, and membrane and secondary metabolism, are differentially affected by rootstocks (Peccoux, 2011; Corso et al., 2015). These results support the idea that, depending on the rootstock, structural properties of the roots can be modified by water conditions and affect the conducting properties at tissue level in roots. It was shown recently that there is a differential development of suberized apoplastic barriers in roots between drought sensitive and tolerant rootstocks (Barrios-Masias et al., 2015).

Water conduction

The transport of water from the roots to the aerial parts may also be a key component of the rootstock control of plant water status and response to water supply. Differences in hydraulic properties between rootstocks at the root or trunk levels have been reported (Peterlunger, 1990; de Herralde et al., 2006; Peccoux, 2011; Tramontini et al., 2013). It was also shown that the proportion of root conductance under metabolic control differs between rootstocks (Lovisolo et al., 2008; Tramontini et al., 2013). As a molecular component of symplastic water flow, differences between rootstocks were detected for the abundance of aquaporin transcripts under well-watered conditions (Gambetta et al., 2012) and under water stress conditions (Rossdeutsch et al., 2016). Embolism by breakage of water columns is also a major process that drastically reduces hydraulic conductance. In grapevine, petioles and roots are more vulnerable to xylem cavitation than shoots (Tramontini and Lovisolo,

2016). Differences between *Vitis* species have been recorded for their sensitivity to embolism in stems (Knipfer et al., 2015). How stem properties reflect differences in roots or in trunks of different rootstocks should be tested.

Control of aerial gas exchanges

The role of rootstocks on leaf gas exchange has been reported by many authors (Düring, 1994; Soar et al., 2006; Tramontini et al., 2013; Marguerit et al., 2012). Data should be interpreted with caution because the differences could be linked to rootstock effect on canopy development and leaf area. Different transpiring leaf areas could modify soil water status. In that case, the response is a response to water status, not a direct rootstock effect on gas exchange regulation (Jones, 2012). Using adapted phenotyping platforms to control substrate water content regardless of leaf area (Sadok et al., 2007), Marguerit et al. (2012) was able to demonstrate on a large progeny that rootstocks have a direct effect on gas exchange inducing reduction of transpiration for different levels of water status. Gas exchange is under the control of chemical and hydraulic signals which relate the root water status to the other parts of the plant, especially the leaves. While exploring the variability among rootstocks for their ability to generate such signals under water stress, it was shown that rootstocks differ in their ability to produce ABA in the regulation of the molecular components of ABA signal transduction (Rossdeutsch et al., 2016). These components allow the sorting of rootstocks according to their genetic background and their reported adaptation to drought. Finally, it was shown that rootstocks may affect intrinsic water use efficiency (Iacono et al., 1998) and QTLs were identified for this trait both under control and water stress conditions (Marguerit et al., 2012).

ROOTSTOCK-SCION INTERACTIONS AND GRAFTING PROCESS

As stated in the introduction, the phenotype of a grafted plant is the result of interactions between the genotypes of scion and rootstock. Few studies have focused on these interactions (Lefort and Légise, 1977; Tandonnet et al., 2010). Analyzing all the possible combinations between 3 genotypes, Tandonnet et al., (2010) reported that scion and scion/rootstock interaction effects explained a larger part of variance than the rootstock effect alone for the biomass of the different plant compartments, including the root system. Working on a larger population with a genetic approach confirms the importance of interactions (Tandonnet, personal communication). Focusing on drought responses on 8 scion × rootstock combinations (4×2), Tramontini et al. (2013) observed that the rootstock effect was related to water supply to the leaves, and scion effect was related to the control of transpiration. Both rootstock and scion contributed to the hydraulic properties of each compartment. This complexity was further characterized for 7 rootstocks associated with 2 scion genotypes (Rossdeutsch, 2015).

The earliest steps of grafting are most probably determinant in explaining the interactions between scion and rootstock genotypes, but few data deal with the physiological and molecular mechanisms underlying the graft formation. Successful grafting is a complex biochemical and structural process that begins with the adhesion of the grafted partners, followed by callus formation and the establishment of a functional vascular system (Pina and Errea, 2005). For grapevine, vascular connection takes place fairly quickly and dye application shows that the continuity between both partners has already been restored 2 months after grafting (including 4 weeks for callusing). Differences between rootstock-scion combinations in the rate of restoring continuity were not obvious (Figure 5).

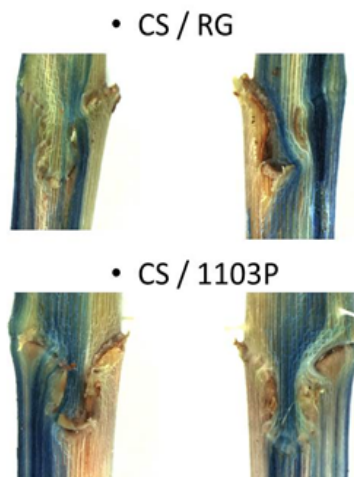


Figure 5. Toluidine blue infiltration in a young grafted plant 8 weeks after grafting (Cookson et al., 2013).

At the molecular level, graft union formation presumably requires considerable re-programming of gene expression, protein translation, and metabolism, but the sequence of events underlying graft union formation remains largely uncharacterized. Many genes associated with cell wall synthesis, secondary metabolism, and signaling were up-regulated in the graft interface tissue of an autograft in comparison to the rootstock tissue during the early stages during the first 4 weeks after grafting (Cookson et al., 2013). In addition, transcriptional re-programming of genes involved cell wall synthesis, and phloem and xylem development categories. When comparing heterograft's to autografts, it was shown that many genes related to stress response were up-regulated, suggesting that cells at the graft interface can detect the presence of a non-self-grafting partner (Cookson et al., 2014). Finally, transcriptome modification was analyzed 4 months after grafting in the shoot apical meristem of combinations of rootstocks with the same scion. Globally, hetero-grafting induces an up-regulation of many genes in the shoot apex however there was no difference between the two hetero-grafting combinations. Genes from the categories DNA, chromatin structure, histones, flavonoids and leucine rich repeat containing receptor kinases were the most up-regulated (Cookson and Ollat, 2013). All together these results support the idea that cross-talk between genomes should be further investigated in order to improve our understanding of grafting and rootstock effects. The most modern approaches should be used to analyze how two genomes can interact and what kind of regulation is involved. The contribution of mi-RNA and/or epigenetic regulation should be investigated.

CONCLUSIONS

This report presents a brief overview of some of the most recent knowledge about rootstock-scion interactions and the underlying physiological mechanisms. Considering that roots are a key component in facing the agricultural challenges of the XXIst century, i.e., reducing inputs and climate change, it is clear that much more energy should be focused on studying this part in grapevine. Mineral nutrition, in interaction with water uptake, should be a major topic of interest. Knowledge of grafting physiology is also a big issue and may help in designing more efficient grafting technics and understanding the decay observed in the vineyards for some rootstock-scion combinations. Root phenotyping is an important issue and grapevine researchers should collaborate with laboratories working on other perennials using modern phenotyping facilities to develop adapted tools. In the first decade of the XXIst century, a lot of efforts were made to sequence *V. vinifera* genome allowing for the integration of this genome information into breeding programs. Additionally, there has

been a lot of progress in understanding fruit physiology. All these efforts should grow to include wild *Vitis* species and rootstocks. These well integrated approaches that exploit the natural diversity across *Vitis* species will help to answer important questions in understanding rootstock effects at the whole plant level related to soil and environmental effects on fruit physiology.

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