MINI REVIEW

Grapevine rootstock effects on abiotic stress tolerance

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Abstract

Amongst 60 species within the *Vitis* genus, *Vitis vinifera* L. is the mostly used species for the production of wine and distilled liquors. Before the devastation of European viticulture caused by the introduction of phylloxera from North America, varieties of *V. vinifera* used commercially for wine production in Europe were traditionally grown on their own roots. Subsequently, the use of rootstocks from the pest's origin was introduced to provide resistance to this and other deleterious diseases and to save the fate of European viticulture. Rootstocks have been bred from a number of *Vitis* species and are known, in addition to the enhanced resistance to phylloxera and other pathogens, confer tolerance to abiotic stresses (*e.g.* drought, high salinity and Fe-deficiency) and to alter specific aspects of harvest/postharvest fruit quality of a scion. This review summarizes recent data related to the responses of grapevine rootstocks to abiotic stresses, with particular attention to drought, salinity and iron chlorosis.

Keywords: *Vitis*; grafting; drought; salinity; iron chlorosis; vigour.

Introduction

Grafting is a technique extensively used in the cultivation of several horticultural species such as grapevine, apple and peach. Grafting technique involves the aerial part of

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one variety or species, called scion, which is grafted onto the basal portion of other variety or species, called rootstock, to form a plant with new characteristics (Arrigo and Arnold, 2007; Lee *et al.*, 2010). Grafting success depends on several parameters: physiological compatibility between bionts, observance of polarity, climate/period and the genetic affinity between scion/rootstock combinations (Fregoni, 2005; Gregory *et al.*, 2013). Indeed, to obtain a successful grafting the vascular cambium, responsible for cell division, of both scion and rootstock has to be in contact in order to connect xylem and phloem (Marguerit, Brendel, Lebon, Van Leeuwen, & Ollat, 2012; Cookson *et al.*, 2014).

Practice of grafting was already widespread in ancient times but the principal reason for its use in viticulture was the *Daktulosphaira vitifoliae* (phylloxera) epidemic. Phylloxera, native to North America, was introduced into Europe at the end of the nineteenth century and destroyed around four million of vineyard hectares. There are some evidences that a Bordeaux grower called Leo Laliman was the first to advise grafting European grapevines, *V. vinifera*, onto rootstocks from *Vitis* species originate from North America. The higher resistance to this pest observed in the American species is related to their co-evolution with phylloxera, which leads to the development of resistance mechanisms that still are not completely understood. Proper sanitation may reduce the risk of phylloxera infestation, but it is no guarantee against its spread. The potential economic loss from phylloxera infestation is so great that planting on resistant rootstocks is recommended even in regions where phylloxera is not yet present (Arrigo and Arnold, 2007).

The growth of many plants in cultivated systems is profoundly affected by selection of appropriate rootstocks, which have been bred from a number of *Vitis* species, especially *V. berlandieri*, *V. riparia*, and *V. rupestris*. In addition to the enhanced resistance to phylloxera, grapevine rootstocks are known to confer resistance to various pathogens and tolerance to abiotic stresses (e.g. drought, high salinity and Fe^{2+} deficiency). Moreover,

rootstocks were found to regulate the size of the scion, to affect fruit development/ripening, to contribute to fruit quality and further they can alter specific aspects of postharvest fruit quality of a scion (Arrigo and Arnold, 2007; Fisarakis, Chartzoulakis, & Stavrakas, 2001; Grant and Matthews, 1996; Gregory *et al.*, 2013; Lee *et al.*, 2010; Marguerit *et al.*, 2012; Walker, Blackmore, Clingeleffer, & Correll, 2002, 2004).

Influence of rootstocks on grapevine tolerance to drought, high salinity and iron deficiency

In addition to their ability to help scion to cope with biotic stresses, rootstocks can confer also tolerance to a large range of abiotic stresses. Among these, drought and high salinity have an enormous impact on crop production; indeed, they are one of the major factors limiting plant productivity and cause a severe yield reduction (Cramer *et al.*, 2007; Tsago, Andargie, & Takele, 2014). Therefore, breeding of crop varieties that use water more efficiently is a key strategy for the improvement of agro systems (Marguerit *et al.*, 2012). Based on the global climate models which predict an increase in the aridity in the next future (Dai, 2013), water deficit may become the major limiting factor. In this context, rootstocks may play an important role in limiting crop loss by improving water use efficiency, potential for survival, growth capacity and scion adaptability to stress conditions (Marguerit *et al.*, 2012; Meggio *et al.*, 2014; Serra, Strever, Myburgh, & Deloire, 2014).

Rootstocks exhibit differential degrees of tolerance in response to drought, for example 101-14 and Schwarzmann are considered less tolerant, while Lider 116-60, Ramsey, 1103 Paulsen, 140 Ruggeri, Kober 5BB and Richter 110 confer to scion higher drought tolerance (Flexas *et al.*, 2009).

The ability of these rootstocks to confer high tolerance to water stress depend on several factors, of which vigour is one of the most important. For some perennial crop species, altered scion vigour has been linked to differences in hydraulic parameters of the root system. Gambetta *et al.* (2012) suggested a pivotal role of aquaporins proteins in relation to grapevine rootstocks vigour and control of water use during drought. In the above-cited experiment they showed that VvPIPs expression was consistently higher in high-vigour rootstock and demonstrate their role in control of rootstocks vigour.

Furthermore, Galmés *et al.* (2007) demonstrate that the expression of the aquaporin genes in 110 Richter was different between leaves and roots; in particular, they showed that aquaporins expression upon water stress was low in leaves, in order to limit transpiration, and increased in the roots to enhance water uptake.

The hydraulic capacity of a root system to deliver water

scion is related to the increase in Lpr (per root surface area or per biomass), and/or whole-root-system surface area. Indeed, Alsina *et al.* (2011) found that grapevines grafted onto 1103P rootstock (high vigour) exhibited greater whole-root-system hydraulic conductance compared to 101-14 (low vigour) resulting from continued growth at greater depth during the warmer and drier summer months.

Stomata have another important role in regulating water loss during water stress (Marguerit *et al.*, 2012), and stomatal closure is one of the earliest responses to water deficit (Damour, Simonneau, Cochard, & Urban, 2010). Stomatal closure is driven by several factors, including phytohormones accumulation. Abscisic acid (ABA) is one of the most studied water stress responsive hormones in plants and its synthesis is one of the fastest plant responses to abiotic stresses. Its accumulation in leaves is related to stomatal closure to reduce water loss and eventually limiting cellular growth (Hochberg *et al.*, 2013; Serra *et al.*, 2014).

Grapevine rootstocks that increased the efficiency of stomatal closure by chemical (e.g. ABA) and hydraulic (e.g. aquaporins) signalling, induced also a major tolerance to water stress.

Recently, a molecular (Corso *et al.*, unpublished data), biochemical and physiological (Meggio *et al.*, 2014) study of novel candidate genotype to be used as rootstock in grapevine was performed. This genotype, designed as M4 [(*V. vinifera* x *V. berlandieri*) x *V. berlandieri* x *cv* Resseguier n.1] and established from 1985 by the Agricultural and Environmental Sciences - Production, Landscape, Agroenergy research group operating at the Milan University, was selected for its high tolerance to osmotic stresses. In comparison with the 101.14 commercial genotype, M4 ungrafted plants subjected to water and salt stress showed a greater capacity to tolerate water stress maintaining photosynthetic activity also under severe stress conditions and accumulating, especially at the root level, sugars, amino acids and potassium. In particular, Meggio *et al.* (2014) observed a concurrent decrease of stomatal conductance (gs) and net assimilation (An) in both genotypes in the early stages of WS, but at later time points, a different physiological response to water stress took place between the two genotypes. Indeed, an almost complete inhibition of both assimilation and transpiration rates was observed in 101.14 as stomatal conductance drop to values of 5% with respect to its control. On the contrary M4, maintaining gs values of 20% with respect to its control, allowed higher transpiration rates (24%) partially recovered An to values of approximately 60% compared to control (Meggio *et al.*, 2014; Corso *et al.*, unpublished data). All these data indicates that, after a concurrent decrease of all physiological parameters observed in both genotypes in the early stages of drought,

as stress conditions became severe, M4 was able to maintain higher transpiration and net assimilation rates demonstrating a much better ability to acclimatize in comparison to the susceptible genotype.

Salt stress is another environmental perturbation that negatively affects grapevine growth and yield. High salinity cause severe problems in water uptake and availability of micronutrients, increasing toxic-ion concentration and degradation of soil structure (Ismail *et al.*, 2013). *V. vinifera* is moderately sensitive to high salinity in the soil and damages caused by this stress are primary related to the chloride ions. The inhibition of grapevine growth and CO_2 assimilation in relation to high salinity is mainly due to changes in stomatal conductance (similarly to what observed for water stress), electron transport rate, leaf water potential, chlorophyll, fluorescence, osmotic potential, and leaf ion concentrations (Cramer *et al.*, 2007). Together with these physiological problems, salt stress causes, at molecular level, formation of reactive oxygen species (ROS), membrane disorganization, metabolic toxicity and reduced nutrient acquisition, as well as induction of several genes related to plant hormones (e.g. abscisic acid and jasmonates) (Cramer *et al.*, 2007; Ismail, Riemann, & Nick, 2012). Grapevine responses to salinity depend on several factors, such as soil type, rootstock–scion combination, irrigation system and climate. Grapevines are more sensitive to Cl^- toxicity than Na^+ toxicity (Cramer 2007). Rootstocks obtained from wild *Vitis* species differ widely in their ability to exclude Cl^- (in reducing order *V. rupestris*, *V. cinerea*, *V. champini* and *V. berlandieri*), and consequently in their capability to higher tolerate salinity. Therefore, response efficiency of the scion in presence of salt soils vary in relation to the comparative exclusion of sodium versus chloride by the genotype of the root system (Fisarakis *et al.*, 2001). Fisarakis *et al.* (2001) showed that there is a great variability in the uptake and accumulation of Na^+ and Cl^- among rootstocks. Specifically, they demonstrate that *V. berlandieri* species had a great ability for Cl^- and/or Na^+ exclusion, although this ability is reduced in hybrids having *V. vinifera* as parent. This explains the reduced ability for Cl^- exclusion of some rootstocks, such as 41B (*V. berlandieri* × *V. vinifera*), compared to the others. Salinity, as well as water stress, negatively affects grapevine yield; in this context Walker *et al.* (2002) showed a strong influence of rootstock on scion production upon salt stress. In particular they observed that rootstocks imparting most vigour at high salinity (e.g. Ramsey, 1103 Paulsen and R2), determined by the weight of one-year-old pruning wood in each year also produced a higher number of bunches per vine at both the medium and high salinity treatments.

Iron (Fe) chlorosis is further physiopathology that affects grapevine grown on calcareous soil. Iron Chlorosis resulted from iron deficiency, associated with high levels of soil bicarbonate is one of the main nutritional disorders observed in sensitive grapevine genotypes. Fe deficiency causes a reduction of grapevine longevity and productivity, affecting growth and reducing yield (Covarrubias and Rombolà, 2013). Grapevines upon iron deficiency stress enhance the activity of Fe-reductase enzyme and increase the release of protons and organic compounds in roots. This result in a lower pH and higher solubility of Fe (III) and is known as strategy I (Jiménez, Gogorcena, Hévin, Rombolà, & Ollat, 2007). In this context bicarbonate concentration is particularly important, indeed bicarbonate is one of the main factors causing Fe chlorosis in strategy I plants but mechanisms of its involvement in this stress are still not clear (Covarrubias and Rombolà, 2013). Several *V. vinifera* cultivars are subjected to stress induced by calcareous soils, however the use of selected rootstocks can solve this problem. For example, Bavaresco and Lovisolo (2000) showed that different scion/rootstock combinations among three Pinot blanc cultivars and two rootstocks (SO_4 and 3309C) lead up to different results in response to iron chlorosis, strongly related to the chlorophyll content and vegetative growth which were correlated with specific conductivity in scion/rootstock surface. In another work, Bavaresco, Fraschini, & Perino (1993) compared the response of 140 Ruggeri and 101-14 rootstocks to iron chlorosis showing that the iron-efficient rootstock (140 Ruggeri) did not induce chlorosis when growing on the calcareous soil, while the opposite occurred with the iron-inefficient rootstock (101-14). Ksouri, M'rah, Gharsalli, & Lachaâl (2006) found that the high tolerance of 140 Ruggeri to Fe-chlorosis is partially due to its high root Fe(III)-reductase activity and the ability of this rootstock to release phenolic compounds in the medium (Ksouri *et al.*, 2006). Currently this rootstock is largely employed in south Mediterranean and North Africa viticulture areas, characterized by lime soils and dry environmental conditions.

A heat map with the degree of tolerance to abiotic stresses of grapevine rootstocks is showed in Fig 1.

Rootstocks widely used in viticulture and characterization of new genotypes with OMICS techniques

Widely used grapevine rootstocks are individuals derived from crosses of two or more species belonging to the genus *Vitis*. In particular, the majority of commercial rootstocks used in viticulture belong to *V. riparia*, *V. berlandieri* and *V. ruprestris* hybrids (Arrigo and Arnold, 2007), leading to a narrow genetic variability. Indeed, 90% of cultivated vines are grafted onto less than ten rootstocks (Serra *et al.*, 2014). This situation may cause several risks, such as the onset of pathogens, nematodes and insects mutations, which leads these species to overcome resistance of the root system. An example is the AxR1 Californian rootstock (*V. vinifera* x *V. rupestris*), which is no longer used for effectiveness loss (Grant and
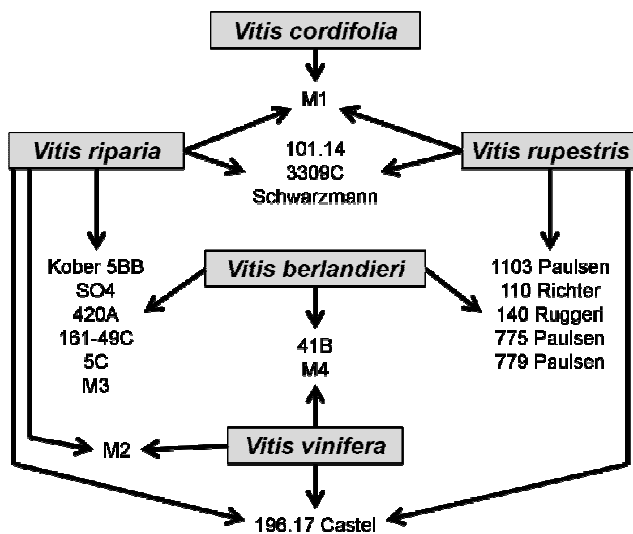
Matthews, 1996).

Currently, non-*vinifera* rootstocks, which exhibit a higher tolerance to phylloxera and nematode infestation, in comparison to *V. vinifera*, confer more resistance to the plant to these pests, but they cannot prevent the proliferation of the aphid. A scheme of the widely used rootstocks and their parental is reported in Fig 2.

Fig 1. Grapevine rootstocks and their response to abiotic stresses. Low (L), medium (M) and high (H) vigour of rootstocks are reported (Scion vigour). Degree of tolerance to phylloxera, drought, salinity and iron chlorosis is also reported.

Fig 2. Grapevine rootstocks and their parents

The development of new rootstocks able to confer tolerance to biotic and abiotic stresses, and contribute to grape quality and ripening/development, is an important step for the future of viticulture.

In the last years, significant efforts have been done for the selection of the optimal rootstock/scion combinations to satisfy specific grape growing needs (Hamdan and Basheer-Salimia, 2010; Komar, Vigne, Demangeat, Lemaire, & Fuchs, 2010; Koundouras *et al.*, 2009; Meggio *et al.*, 2014). The selection of new rootstocks was initially carried out by phenotypic and genetic techniques. In order to better characterize new rootstocks and give insights into the mechanisms that allow them to have the desired characteristics, we need more accurate information than the phenotypical one. Actually, the development of the "omics" sciences, such as transcriptomic, proteomic and metabolomic approaches became essential to functionally characterize the selected rootstocks and to understand the effect of these rootstocks on the scion (Deluc *et al.*, 2009; Grimplet *et al.*, 2009a; Grimplet *et al.*, 2009b; Rodríguez-Celma *et al.*, 2013; Wang, Gerstein, & Snyder, 2009). Improving the knowledge about the molecular, biochemical and physiological bases of stress resistance is an absolute requirement for the selection of genotypes able to cope with stress conditions without any negative consequences on the vegetative growth and production of high quality grape. The eco-physiological techniques of analysis, together with omics approaches may give a valuable contribution to the understanding of the syndrome kinetics, as well as the progressive deterioration of plant performances paralleling the onset of the stress.

Concluding remarks

Viticulture and winemaking are influenced by a large number of factors, among which climate, soils, and grown varieties/genotypes are the most important (Fraga, Malheiro, Moutinho-Pereira, & Santos, 2012). Grapevine physiological changes, together with grape berry development and ripening, are high related to the clime and other factor, such as plant hormones levels (Grimplet *et al.,* 2009b; Marguerit *et al.,* 2012; Ziliotto *et al.,* 2012). The duration of the growing season of a particular cultivar is affected, together with the climate that strongly influences the yield and wine quality, also by the combination of these factors: soil moisture, air temperature, and crop-management practices (Webb *et al.*, 2012). Breeding of new grapevine genotypes, which can better deal with the environmental changes, is essential for Italian and European viticulture. Indeed, development of new grapevine rootstocks with a higher tolerance to environmental stresses, drought in particular, should be a successful strategy to overcome climate limitations (Hannah *et al.*, 2013) and maintain the traditional Mediterranean grapevine growing area. This strategy have several advantages compared to the breeding programs

associate to grape cultivar, mainly related to the handiness to confer desired characteristics (*e.g.* drought tolerance) to the vine. In addition to their capability to overcome climate limitations, grapevine rootstocks greatly influenced grapevine reproductive performances (Koundouras, Tsialtas, Zioziou, & Nikolaou, 2008; Kidman, Dry, McCarthy, & Collins, 2013), fruit development, ripening and quality (Walker *et al.*, 2002, 2004). So, together with the induction of an higher tolerance to environmental disturbance to the scion, viticulture need new rootstocks which did not alter quality of grape berry and wine or, better, which increase their qualitative characteristics.

So, considering new scenario for the European and Italian vine growing and the climate changes which can alter quality of grape berries and wine on a global scale, development of new rootstocks with desirable traits it will be one of the main goal of the future viticulture.

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