















Challenges of viticulture adaptation to global change: tackling the issue from the roots

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Abstract

Viticulture is facing emerging challenges not only because of the effect of climate change on yield and composition of grapes, but also of a social demand for environmental-friendly agricultural management. Adaptation to these challenges is essential to guarantee the sustainability of viticulture. The aim of this review is to present adaptation possibilities from the soil-hidden, and often disregarded, part of the grapevine, the roots. The complexity of soil–root interactions makes necessary a comprehensive approach taking into account physiology, pathology and genetics, in order to outline strategies to improve viticulture adaptation to current and future threats. Rootstocks are the link between soil and scion in grafted crops, and they have played an essential role in viticulture since the introduction of phylloxera into Europe at the end of the 19th century. This review outlines current and future challenges that are threatening the sustainability of the wine sector and the relevant role that rootstocks can play to face these threats. We describe how rootstocks along with soil management can be exploited as an essential tool to deal with the effects of climate change and of emerging soil-borne pests and pathogens. Moreover, we discuss the possibilities and limitations of diverse genetic strategies for rootstock breeding.

Keywords: climate change, genetics, rootstock, sustainability, Vitis

Introduction

Changes in climate have impacted viticulture in almost all wine regions in the last decades, mainly as a consequence of temperature rise, changes in precipitation patterns and an increase in the frequency of extreme events (Intergovernmental Panel on Climate Change 2014, Cramer et al. 2019), thus influencing yield and quality in grape production. Drought, soil erosion and salinity are some of the most important indirect effects of climate change that restrict productivity and affect composition of grapes (Santos et al. 2020). Adaptation and mitigation are complementary strategies for reducing and managing those impacts. Although potential mitigation activities have been identified recently, it is necessary to develop new adaptation strategies to deal with climate change. In addition, vineyards also face the

need for an effective and environmentally respectful control of disease and pests. Finally, maintaining yield, quality standards and typicality are also a challenge of viticulture worldwide (Fraga et al. 2012), with increasingly competitive markets related to globalisation. Such need for adaptation may be the greatest challenge for viticulture since the late 19th century, when the aphid-like phylloxera insect (*Daktulosphaira vitifoliae* Fitch), accidentally introduced from North America to Europe, became a pest that devastated most of the European vineyards.

Grafting woody plants to rootstocks is a common agricultural practice, used from the second millennia BCE, and has allowed the clonal propagation and domestication of woody species that do not easily root from cuttings (Mudge et al. 2009). *Vitis vinifera* L. was domesticated, however,

several thousands of years before (Zohary and Spiegel-Roy 1975) without need of grafting, as this species shows a high rooting capacity. Grafting susceptible *V. vinifera* scions onto wild North American *Vitis* spp. (which roots display different tolerance levels and resistance to phylloxera feeding) allowed cultivation of the original scion cultivars and, in consequence, saved the European wine industry (Warschefsky et al. 2016). Since that time, grapevine grafting has been routine in more than the 80% of vineyards worldwide (Ollat et al. 2016), mainly in regions where phylloxera is present.

The wild American species *V. riparia* and *V. rupestris* were initially selected as grafting rootstocks for their resistance and their capacity to self-root. In contrast to own-rooted *V. vinifera*, these two species have poor tolerance to calcareous soils, which are characteristic of many traditional viticultural regions. Hence, *V. berlandieri* (synonym *V. cinerea* cv. Helleri) was used as a combined source of phylloxera resistance and tolerance to high-pH soils in the same rootstock. To combine these favourable traits, inter-specific hybridisation was carried out and recent molecular studies showed that only three accessions, one from each of the three mentioned species (*V. berlandieri* cv. Rösséguiet 2, *V. rupestris* cv. du Lot and *V. riparia* cv. Gloire de Montpellier), can represent about 40% of the inter-specific parentage in current widely used rootstocks (Riaz et al. 2019).

These accessions, along with selections of *V. aestivalis* and *V. vinifera*, were indeed the main parentages used in the first waves of rootstock breeding (Cousins 2005a, Reisch et al. 2012, Riaz et al. 2019) (Table 1). Subsequently, different breeding programs involving interspecific hybridisation have generated a set of commercial rootstocks that gather resistance to threatening pests and diseases and are tolerant to different soil and abiotic stress conditions (Figure 1). It is still difficult, however, to pyramid all the many desired traits in single accessions (Cousins 2005a, Ollat et al. 2016).

Again, rootstocks can play a relevant role in facing future challenges. Rootstock cultivar choice has already been identified as a mid-term strategic and anticipatory tool to adapt viticulture to climate change (Neethling et al. 2017, van Leeuwen et al. 2019). The use of a given rootstock can modify crop characteristics through changes in vigour, fertility, budburst and harvest earliness and in fruit composition (May 1994), with no additional cost for the grower when establishing a vineyard, except on those phylloxera-free areas where own-rooted vines can be several times cheaper than those grafted, for example three times in Australia according to Martin (2014). Finally, although it would be obviously unrealistic to claim that growers can tackle this issue solely from the roots, rootstocks do play a considerable role to innocuously defend the vineyard from some of its main foes: phylloxera, nematodes and soil-borne fungal

Table 1. Main parentages used in the first wave of rootstock breeding.

Common name [†]	Breeder [‡]	Breeding year [‡]	Parentage
Rupestris du Lot	Initially noticed by R. Sijas	1879	<i>V. rupestris</i> Scheele selection ^{††,§§}
Riparia Gloire de Montpellier	L. Violla and R. Michel	1880	<i>V. riparia</i> Michaux selection ^{††,§§}
3309 Couderc	Georges Couderc	1881	<i>V. riparia</i> cv. Tomenteux × <i>V. rupestris</i> ^{††,§§,¶¶}
101-14	Alexis Millardet and Charles de Grasset	1882	<i>V. riparia</i> × <i>V. rupestris</i> ^{††,§§,¶¶,a}
41 B	Alexis Millardet and Charles de Grasset	1882	<i>V. vinifera</i> cv. Chasselas Blanc × <i>V. berlandieri</i> ^{††,§§}
333 EM	Gustave Foëx	1883	<i>V. vinifera</i> cv. Cabernet Sauvignon × <i>V. berlandieri</i> ^{§§}
420 A	Alexis Millardet and Charles de Grasset	1887	<i>V. berlandieri</i> × <i>V. riparia</i> ^{§§,¶¶,a}
161-49 Couderc	Georges Couderc	1888	<i>V. berlandieri</i> × <i>V. riparia</i> G. de M. ^{¶¶,b}
Schwarzmann	F. Schwarzmann	1891 ^{††}	<i>V. riparia</i> × <i>V. rupestris</i> ^{††,c}
140 Ruggeri	Antonino Ruggeri	1894	<i>V. berlandieri</i> cv. Boutin B × <i>V. rupestris</i> cv. du Lot ^{¶¶}
1103 Paulsen	Federico Paulsen	1896	<i>V. berlandieri</i> cv. Rösséguiet 2 × <i>V. rupestris</i> cv. du Lot ^{¶¶}
SO4	Sigmund Teleki and Heinrich Fuhr	1896	<i>V. berlandieri</i> cv. Rösséguiet 2 × <i>V. riparia</i> G. de M. ^{¶¶}
5 BB Kober	Sigmund Teleki and Franz Kober	1896	<i>V. berlandieri</i> cv. Rösséguiet 2 × <i>V. riparia</i> G. de M. ^{¶¶}
5 C Teleki	Alexandre Teleki and Heinrich Birk	1896	<i>V. berlandieri</i> cv. Rösséguiet 2 × <i>V. riparia</i> G. de M. ^{¶¶}
125 AA	Sigmund Teleki and Franz Kober	1896	<i>V. berlandieri</i> cv. Rösséguiet 2 × <i>V. riparia</i> G. de M. ^{¶¶}
Ramsey	Thomas Munson [§]	1900 [§]	Natural selection of <i>V. Champinii</i> Planchon ^{§,††}
110 Richter	Franz Richter	1902	<i>V. berlandieri</i> cv. Boutin B × <i>V. rupestris</i> cv. du Lot ^{¶¶}
196-17 Castel Börner	Pierre Castel	1906	1203 C × <i>V. riparia</i> G. de M. ^{§§,c}
Freedom	Carl Bomer ^{¶¶}	1936 ^{¶¶}	<i>V. riparia</i> × <i>V. cinerea</i> cv. Arnold ^{¶¶}
Fercal	California State University ^{††}	1956 ^{††}	1613-59 × Dog Ridge 5 ^{††,‡‡}
	Institut Nacional de la Recherche Agronomique (INRA)	1959	B.C n° 1B (<i>V. berlandieri</i> × <i>V. vinifera</i>) × 31 R (<i>V. berlandieri</i> × <i>V. longii</i>) ^{§§,d}
Gravesac	INRA	1962	161-49 Couderc × 3309 Couderc (complex hybrid) ^{§§}

[†]Common name according to Dry (2007) first or to Maul et al. (2020) if absent; [‡]breeder and breeding year according mainly to Pl@nt Grape (2020); ^{††}Maul et al. (2020); ^{‡‡}Garris et al. (2009); ^{§§}Pl@nt Grape (2020); ^{¶¶}Riaz et al. (2019); [§]Teubes (2014); [¶]Rühl (1996); ^ade Andrés et al. (2007); ^b*V. riparia* Gloire de Montpellier written as *V. riparia* G. de M.; ^cLin and Walker (1998); ^dLaucou et al. (2008).

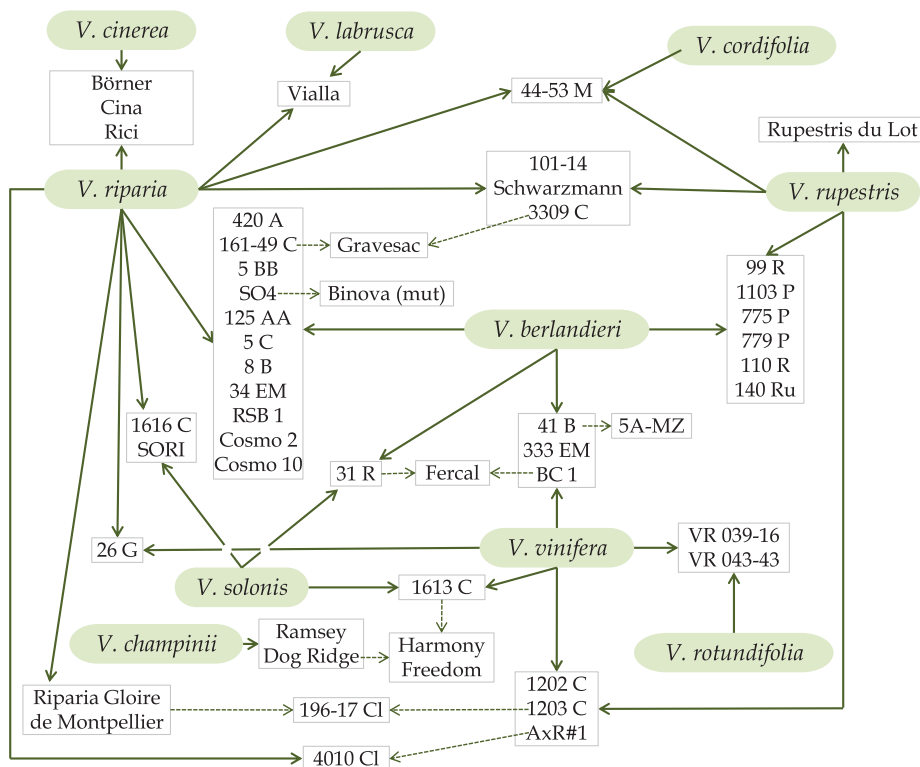


Figure 1. Main rootstocks used worldwide and their parental species (own elaboration based on Shaffer et al. (2004)).

pathogens (Gramaje and Armengol 2011, McKenry and Bettiga 2013, Powell et al. 2013).

In this review, we present relevant reasons to maintain attention on the roots—and on the rootstock—in order to help global viticulture combat some of its major challenges, including the role genetics can play to assist rootstock improvement.

Challenges related to abiotic stresses

Water stress, increasing soil salt concentration and high temperature represent the major threats of abiotic origin to viticulture, having been identified as the most common abiotic constraints that exert a negative impact on Mediterranean vineyards (Jones et al. 2005, Schultz and Stoll 2010). These problems will be exacerbated in the near future according to climate change projections (Intergovernmental Panel on Climate Change 2014). In addition, the pressure of increasing population, industry and agriculture on water resources has led to the search for alternative sources of irrigation water, which usually contain a high salt concentration (Costa et al. 2016). Therefore, grapevine roots and rootstocks will need to cope with a future environment in which increasing water scarcity and salinity will restrain their growth and function, constraining the performance of the whole plant and, consequently, the sustainability of the vineyard. This section presents an overview on how rootstocks can contribute to tackle these challenges.

Water stress

Water stress is becoming a key question to improve vineyard sustainability, as about two-thirds of the major viticulture areas of the world have an annual precipitation below 700 mm (Flexas et al. 2010), and it is projected that in the near future water availability will be the limiting factor in regions where it is not (Santos et al. 2020). A more efficient use of water is possible by modulating water availability

through regulated deficit irrigation (RDI), but the role of the rootstock to improve water use efficiency (WUE) plays a central role, because a more efficient, extensive and deeper root system provides access to a potential greater water supply to take profit of the rain water or irrigation, thus enhancing plant WUE (Medrano et al. 2015). Additionally, rootstocks can also provide another tool to reduce water stress through the reduction of scion vigour, as a decreased leaf area implies lower total transpiration (Clingeffer et al. 2011). These characteristics, along with soil improvement to increase soil water storage capacity, are the two main ways to secure the environmental sustainability of vineyards.

The physiology of grapevine roots under water deficit conditions has been studied in recent decades, comprising the implications of water stress from both the molecular and physiological points of view (Walker et al. 2010, Corso and Bonghi 2014, Meggio et al. 2014, Serra et al. 2014, Ollat et al. 2016, Zhang et al. 2016, Yildirim et al. 2018). The complexity of the characters related to WUE and drought response makes the detection of quantitative trait loci (QTL) related to those specific traits difficult. The choice of more water-use-efficient and drought-tolerant rootstocks has been proposed as a measure of adaptation to climate change in viticulture (Fraga et al. 2012, Berdeja et al. 2015, Bianchi et al. 2018, Romero et al. 2018, Sabir and Sahin 2018). The rootstock chosen can modify vineyard adaptation to drought conditions through several physiological mechanisms, as detailed below.

Ability to uptake and transport soil water. Grapevine root system structure and development is dependent on both environmental and genetic factors. Root system development is affected by soil physical and chemical properties and rootstock genotypes, together with different rootstock–scion combinations (Kocsis et al. 2016).

Change of root system density and distribution under water limitation depends on rootstock genotypes and appears to be related to transcriptomic regulations that could promote sugar and protein transport, osmotic adjustment or suberin and wax production in roots (Yıldırım et al. 2018). Root hydraulic architecture affects the volume of soil explored mainly through greater branching of the fibrous roots and a greater number of root tips (Gullo et al. 2018), accessing to more water resources. The genotype mainly appears to modify the root density, whereas root distribution is mainly dictated by soil properties (Smart et al. 2006, Keller 2010). For example, the drought-tolerant rootstock 1103 Paulsen (*V. rupestris* × *V. berlandieri*) produces a large proportion of its root biomass in the first months after planting and during summertime. Conversely, the less vigorous rootstock 101-14 (*V. rupestris* × *V. riparia*) grows roots more gradually, and shows much lower growth plasticity to soil moisture level or depth compared to 1103 Paulsen (Alsina et al. 2011). The intrinsic capacity of roots to uptake water is also related to the expression of aquaporins, either genetically and environmentally determined, whose contribution to the root hydraulic conductance ranges from 4 to 40% (Lovisolo et al. 2016). This trait could be explored as a breeding target to improve rootstock response to water deficit.

Concerning soil water movement through the roots, drought-tolerant rootstocks usually show higher hydraulic conductance of their root system, as they usually display longer root vessels, higher cross-sectional area of first order roots and larger trunk diameter than drought-sensitive rootstocks (Alsina et al. 2011). There is also a difference in the extent of embolisation between rootstock genotypes, probably not related to minor embolism formation, but rather to a higher efficiency on embolism repair (Lovisolo et al. 2008). Those differences in xylem embolism formation and repair, however, were negligible when a common scion was grafted on different rootstocks (Barrios-Masias et al. 2019). Additionally, root structural changes (earlier and greater root suberisation in the less drought-resistant genotypes) under drought conditions could potentially lead to a more enduring decrease in root hydraulic conductivity (Barrios-Masias et al. 2015), that could increase the sensitivity of plant water status to changes in the vapour pressure deficit (Maurel et al. 2010).

Scion water use regulation. Rootstocks play an important role in controlling scion transpiration rates under well-watered and water stress conditions (Marguerit et al. 2012, Peccoux et al. 2018).

The rootstock effect on the vigour conferred to the scion cultivar constitutes a major source of variation in water use regulation, as low-moderate vigour conferring rootstocks show reduced transpiration (Clingeffer et al. 2011). In contrast, the rootstock can modify the scion's stomatal sensitivity to water stress by shifting the level of stomatal closure towards lower (drought-resistant) or upper (drought-sensitive) leaf water potential (Ψ_{leaf}), independently of the scion's near-isohydric or near-anisohydric behaviour (Tramontini et al. 2013). The contribution of the rootstock to the control of scion transpiration under drought conditions involves a combination of hydraulic and hormonal root-to-shoot signalling (Koundouras et al. 2008, Marguerit et al. 2012, Rossdeutsch et al. 2016). Particularly, the concentration of abscisic acid (ABA) could

be genetically controlled by the rootstock although other chemical signals and their interaction (cytokinins, ethylene, pH) can come into play (Davies et al. 2005). Despite the well-known rootstock influence on gas exchange, the underlying physiological mechanisms (e.g. ABA signal, plant hydraulic conductance, root system characteristics) remain under discussion (Peccoux et al. 2018).

Water use efficiency of rootstocks and irrigation. Many field-based studies under different irrigation and edaphoclimatic conditions, involving different grapevine cultivars, have demonstrated that yield and productive WUE ($\text{WUE}_{\text{yield}}$, kg/m^3 water applied) can be increased by using rootstocks that will produce the same or more with less water (Soar et al. 2006, Williams 2010, Kidman et al. 2014, Chitarra et al. 2017). The values of $\text{WUE}_{\text{yield}}$ reported in field-grown irrigated grapevines vary widely depending on the rootstock: 2–11 kg/m^3 in Syrah vines in Australia (Stevens et al. 2010, Kidman et al. 2014) and 12–20 kg/m^3 in Syrah vines in Australia (Soar et al. 2006); 5–6.5 kg/m^3 in Chardonnay in Australia (Stevens et al. 2008); 2–4 kg/m^3 in Cabernet Sauvignon in Greece (Koundouras et al. 2009); 4–16 kg/m^3 in Cabernet Sauvignon in California (Williams 2010); 9–18 kg/m^3 in Monastrell vines in south-east Spain (Romero et al. 2018); and 9–29 kg/m^3 in Gaglioppo in Italy (Chitarra et al. 2017).

In general, the more restrictive the irrigation strategy (less volume of water applied) the more $\text{WUE}_{\text{yield}}$ increases, regardless of the rootstock (Soar et al. 2006, Stevens et al. 2008, Koundouras et al. 2009, Williams 2010, Kidman et al. 2014), indicating that the application of deficit irrigation techniques such as sustained deficit irrigation, RDI or partial root zone drying, in grapevine cultivars grafted on different rootstocks will increase grapevine $\text{WUE}_{\text{yield}}$ (Williams 2010, Romero et al. 2018).

Nevertheless, rootstocks do not affect productivity uniformly among studies, even being occasionally in contradiction, which suggests that specific rootstocks–scion interactions and different experimental/soil–climate conditions are also important for rootstock performance and $\text{WUE}_{\text{yield}}$ in grapevines (Zhang et al. 2016).

Role of rootstock on carbon balance. Rootstocks can significantly affect stomatal conductance and leaf photosynthesis of the scion under water stress conditions (Padgett-Johnson et al. 2000, Galbignani et al. 2016, Romero et al. 2018, Sabir and Sahin 2018). Corso et al. (2015) described the activation of 'primary and secondary mechanisms' of the detoxification of reactive oxygen species in a new drought-tolerant rootstock (Merli et al. 2016), and the possible implications for drought tolerance by promoting higher water uptake capacity, active plant growth and carbon assimilation. The respiratory activity of roots expends a significant proportion of the carbohydrates fixed by leaf photosynthesis (Escalona et al. 2012); however, studies of the implications of the rootstocks–scion interaction on the respiratory costs of the roots are still scarce (Franck et al. 2011, Hernández-Montes et al. 2017). Several studies contributed to better understand the effects of water availability on vine root growth, activity and distribution (Van Zyl 1984, Huang et al. 2005, Comas et al. 2010, Romero et al. 2012), and the relationship between root biomass, root respiration and carbon allocation has been reported (Comas et al. 2005, Schreiner 2005, Franck et al. 2011).

Numerous studies demonstrate the effect of rootstocks on scion vigour, mainly through changes in the xylem hydraulic function (Gambetta et al. 2012). Rootstocks conferring high vigour maintain greater water uptake capacity and increase resources accumulated in organs during the growing season (Romero et al. 2018). Low vigour rootstocks, however, presented a higher sink/source ratio, that could contribute to improve vineyard resilience to climate change, making this adaptation compatible with grape quality under semi-arid conditions (Romero et al. 2018).

Development of the whole root system has been studied in depth (Volder et al. 2005, Comas et al. 2010), as well as the evolution of roots with time (Morinaga et al. 2003, Eissenstat et al. 2006). Since root growth, life span and longevity vary among rootstocks, and those differences could affect the whole plant carbon balance, a better knowledge of the genetic variability of root growth and death and associated respiration rate may improve below-ground management of grapevines. The contribution of the root system to total plant carbon (C) storage can range from 9 to 26%, and total C storage in the vineyard can range from 5.7 to 7.2 t C/(ha/year) (Brunori et al. 2016). Thus, vineyard soils and root systems can positively contribute to the mitigation strategies to manage climate change by increasing soil carbon storage (Funes et al. 2019).

Salinity

The increased use of irrigation for grapevine growing, frequently associated with low-quality water because of scarcity of this resource (Costa et al. 2016, Hirzel et al. 2017), is making salinity an increasing problem in viticulture. In fact, predictions in some grapegrowing areas forecast surpassing the salinity threshold of grapevine tolerance at the end of the century (Phogat et al. 2018). Under high salt exposure, grapevine roots are exposed to osmotic stress which indeed decreases water availability to the plant. In addition, vines can exhibit specific phytotoxicities mainly because of the accumulation of Na^+ and Cl^- ions within plant tissues, which can disrupt cellular metabolism if the concentration reaches toxic thresholds (Munns and Tester 2008, Chaves et al. 2010). The symptoms of salt stress in grapevines include reduction in stomatal conductance and photosynthesis, and leaf burn, which are generally related to an increase in shoot Cl^- rather than in Na^+ concentration in plant tissues (Downton 1977, Walker et al. 1997), resulting in reduced vigour and yield (Walker et al. 2002, Zhang et al. 2002).

In grapevines, salt tolerance appears to be linked to the process of ion exclusion, namely the ability of some rootstocks to limit the accumulation of Cl^- and/or Na^+ in the leaves and other above-ground organs (Gong et al. 2011, Henderson et al. 2018). In this sense, the transport activities at the cell membrane level play a crucial role in several processes including root ion uptake and movement of these ions to the shoots, which mainly depend on transport from the symplast to the xylem apoplast (Munns and Tester 2008). In grapevines, the main mechanism underlying the capacity for ion exclusion occurs at the root parenchyma/xylem interface, where ions are actively retrieved from the xylem stream (Gong et al. 2011). Recent research, however, has proven the complexity of the mechanisms that induce adaptive responses to salt stress in grapevine (Fu et al. 2019, Haider et al. 2019). In this sense, several studies (Gong et al. 2011, Fort et al. 2015) evaluated the variation in Cl^- exclusion in different rootstock populations, concluding that the Cl^- exclusion trait is controlled by

multiple genes. Henderson et al. (2014) aimed at discerning the molecular identity of membrane proteins that control Cl^- exclusion in grapevine and concluded that transcriptional events contributing to the Cl^- exclusion mechanism in grapevine are not stress-inducible, but constitutively different between contrasting cultivars. In addition, Henderson et al. (2014) observed expression changes of nitrate transporter (*NRT1*) and chloride channel (*CLC*) family genes, known to have members with roles in anion transport in other plants, suggesting these genes as candidates for controlling anion homeostasis and Cl^- exclusion in *Vitis* species, although they were not able to identify obvious Cl^- transporters. In a subsequent study, Henderson et al. (2018), successfully mapped a QTL that controls Na^+ exclusion in rootstocks and identified the causal gene (*VisHTK1;1*) underlying that trait; these findings may assist with breeding Na^+ tolerant grapevine rootstocks. Recently, Prinsi et al. (2020) characterised the root-level response to salt stress of two grapevine rootstocks (M4 and 101-14), indicating that M4 had a greater capability to maintain and adapt energy metabolism and to sustain the activation of salt-protective mechanisms, while, in 101-14, the energy metabolism was deeply affected and an evident induction of the enzymatic antioxidant system occurred. Overall, the information provided by this group of studies constitutes the basis for further research on the performance of different graft combinations against salt stress.

In addition, long-term studies showed that the rootstock employed exerts a great influence on grapevine response to salinity, although scion presents also a relative tolerance (Walker et al. 2014). This might be because of the abovementioned ion exclusion ability of some rootstocks that provides root system integrity and functionality (Gong et al. 2011, Meggio et al. 2014, Henderson et al. 2018, Walker et al. 2018).

Therefore, the selection of new rootstocks could be an interesting solution to overcome some of the risks associated with salinity, such as preventing excess of Cl^- and Na^+ in leaves and bunches, and the subsequent negative effect on yield and fruit composition, and should rely on the research efforts mentioned in this section (Gong et al. 2014, Henderson et al. 2018, Prinsi et al. 2020), despite these being restricted to only three genotypes. In this context, a recent survey (Heinitz et al. 2020) identified promising Cl^- -excluding accessions within a collection of *Vitis* species native to south-western USA and northern Mexico. This survey reported that ion exclusion was not associated with any particular species or geographic region, although the authors pointed out that *V. girdiana* from southern Nevada took up less than half the concentration of Cl^- in roots as compared to 140 Ruggeri, a known salt excluder. Moreover, the observed prevalence of the Cl^- exclusion trait across multiple genetic backgrounds suggested that the surveyed collection may host multiple sources for Cl^- exclusion in grapevines (Heinitz et al. 2020).

In combination with the proper choice of the genetic material, agronomic practices should be adapted to the plant material in order to minimise the impacts that salinity may exert on vine root distribution and functioning (Schultz and Stoll 2010). These include the irrigation regime to be applied, both in terms of the leaching fraction and the frequency of irrigation (Aragüés et al. 2015). Because some salts are added through fertilisers or as components (or contaminants) of other soil additives, soil fertility testing is warranted to refine nutrient management programs

(Bravdo 2012). Moreover, soil management practices could be specifically employed to minimise soil evaporation and therefore reduce the risk of concentration of soil salts (Aragüés et al. 2014).

Challenges related to biotic stresses

Grapevine rootstocks contribute to control pest-related problems in vineyards, being critical for their long-term sustainability. They have been an essential component in the vast majority of grapegrowing regions, where phylloxera is present (Ollat et al. 2016). The use of rootstocks for the management of phylloxera has been clearly successful and well-based during a long period of time, although some reports have cited the presence of high infestation rates on the leaves in some parts of the world (Granett et al. 2001, Fahrentrapp et al. 2015). Due to the complexity, however, of this phenomenon and the recent reviews on this topic (Granett et al. 2001, Yin et al. 2019) in this review, we have focused on other soil-borne pest and diseases.

Nematodes have been traditionally considered relevant damaging agents of grapevines, which are primarily managed in some areas of the world by using tolerant or resistant rootstocks. Nevertheless, nematode communities in vineyard soils are complex and the build-up of virulent populations or the description of new species can compromise rootstock performance (McKenry and Bettiga 2013). Grapevine rootstocks are also exposed to soil-borne fungi, which can affect the root system causing a diverse range of symptoms, including root necrosis, root mass reduction and root rot. Little attention has been devoted to the relationships between phytopathogenic fungi and grapevine rootstocks but, in recent years, soil-borne fungal pathogens have emerged as a threat for grapevine production worldwide, causing substantial economic losses to the wine industry (Gramaje and Armengol 2011). Both, nematodes and soil-borne fungi are currently among the most important challenging biotic factors in viticulture, with important implications for grapevine rootstocks, so they are discussed here accordingly.

Nematodes

Many plant-parasitic nematode (PPN) species have been found on grapevines (Teliz et al. 2007). Some have been recognised as causing significant damage to grapes: root-knot (*Meloidogyne* spp.), dagger (*Xiphinema index*), root-lesion (*Pratylenchus* spp.), citrus (*Tylenchulus semipenetrans*) and ring (*Criconemoides xenoplax*) nematodes. Plants affected by PPNs show an unspecific symptomatology that includes yellowing, poor growth, early ripening of grapes, stunting and usually forming aggregations of symptomatic plants that may follow or not the vine rows. Their damage is related to their population density, but differences in climate, soil characteristics and grape cultivar/rootstock could change the susceptibility of grapevine (Nicol et al. 1999). Nematodes damage plants by direct feeding on the roots or, in the case of some species, by vectoring viruses (e.g. *X. index* as vector of fanleaf virus) (Brown et al. 1993).

Meloidogyne spp. are sedentary endoparasites, establishing a permanent feeding site by inducing the formation of giant cells and the gall in the root. The most important species are the tropical *M. arenaria*, *M. incognita* and *M. javanica*, and the temperate *M. hapla* (Moens et al. 2009). Other species (*M. ethiopica*, *M. nataliei* and *M. hispanica*), however, have been found affecting grapevines in some regions, and they constitute a challenge to breeding programs (Bird et al. 1994, Carneiro et al. 2004, Castillo et al. 2009).

Xiphinema index has a worldwide distribution. This nematode feeds ectoparasitically on root tips (Nicol et al. 1999) retarding root extension, causing swelling and root tip gall formation. *Xiphinema index* is the vector of grapevine fanleaf virus (GFLV). Other species from Longidoridae could be virus vectors for grapevine (Brown et al. 1993). *Xiphinema index* may persist in the soil for long periods of time (up to 10 years), feeding on root fragments (Raski et al. 1965) or up to 4 years if the host is absent (Demangeat et al. 2005, Esmenjaud et al. 2010). The prevalence of virus particles may last for more than 4 years (Demangeat et al. 2005), and the depth where they are frequently found (40–110 cm) (Villate et al. 2012) hinders field management.

Replanting is the most susceptible period to nematode infection, when plants are young and the amount of inoculum may be high if the previous crop was also grapevine. In this case, additionally to other agronomical measures, the most efficient and economic method to control PPNs is the use of resistant rootstocks. Some of them have produced interesting results in the control of some *Meloidogyne* spp. (i.e. Harmony and Freedom rootstocks), but the resistance has been overcome by virulent populations of *M. incognita* and *M. arenaria* (Esmenjaud and Bouquet 2009). Resistance against some specific nematodes has been found in several sources, mainly *Vitis* spp. but also in other related genera (Esmenjaud and Bouquet 2009). In this sense, several rootstock lines with a different degree of resistance to *M. arenaria*, *M. incognita*, *X. index*, *P. vulnus*, *M. xenoplax* and *T. semipenetrans* from diverse resistance sources (*V. rupestris*, *M. rotundifolia*, *V. rufotomentosa*, *V. champinii*, *V. riparia*) have been developed in California (Ferris et al. 2012). These rootstocks maintained their resistance even when they were challenged with different combinations and population levels of nematodes and high temperature (Ferris et al. 2012, 2013).

The resistance against *X. index* and GFLV is challenging because GFLV can be acquired from infected plants and inoculated to recipient plants within 1–10 min (Wyss 2014). In this sense, only transgenic plants expressing the coat protein delayed the viral infection (Vigne et al. 2004), artificial miRNAs targeting the coat protein gene (Jelly et al. 2012) and nanobody-mediated resistance (Hemmer et al. 2018) appear promising to control GFLV in the future. Nematex Alain Bouquet rootstock, developed by Institut National de la Recherche Agronomique (France), delays the appearance of GFLV in infested vineyards (Ollat et al. 2011). More research is needed, however, because some of these *Muscadinia* hybrids have a poor performance in calcareous or dry soil conditions (Ollat et al. 2016).

Resistance to nematodes in rootstocks is usually characterised by the presence of major genes associated with the expression of a hypersensitive resistance reaction preventing the feeding and reproduction of nematodes (Staudt and Weischer 1992, Esmenjaud and Bouquet 2009). Several genes and/or regions have been found to confer resistance to *Meloidogyne* (*N. Mur1*, *MJR1*...) [reviewed by Saucet et al. (2016), Smith et al. (2018b)] and for *X. index* (locus *XiR1*) from *V. arizonica* (Hwang et al. 2010). Recently, resistance to *X. index* in *M. rotundifolia* has been found in three QTLs (*XiR2*, *XiR3* and *XiR4*) (Rubio et al. 2020).

Soil-borne fungi

The main soil-borne fungal diseases affecting grapevines are: Armillaria root rot, Phytophthora crown and root rot, black-foot disease, Verticillium wilt and Petri disease

(Bettiga 2013). In general, these are well-known diseases, but more recently black-foot and Petri diseases, which belong to the complex of fungal trunk pathogens of grapevines (Gramaje et al. 2018), have received special attention because of their implication on the young grapevine decline syndrome (Gramaje and Armengol 2011). Black-foot is caused by *Cylindrocarpon*-like asexual morphs, including species belonging to the genera: *Campylocarpon* Halleen, Schroers & Crous; *Cylindrocladiella* Boesew; *Dactylonectria* L. Lombard & Crous; *Ilyonectria* P. Chaverri & C. Salgado; *Neonectria* Wollenw; *Pleioacarpon* L. Lombard & D. Aiello; and *Theλονectria* P. Chaverri & C. Salgado. These pathogens affect the root system or the crown area of the rootstocks, and then move into the trunk, which they can rot quickly after infection (Hallen et al. 2006, Agustí-Brisach and Armengol 2013, Lombard et al. 2014, Carlucci et al. 2017, Aigoun et al. 2019). Although Petri disease pathogens [*Cadophora luteo-olivacea* (J.F.H. Beyma) T.C. Harr. & McNew, species of *Phaeoacremonium* W. Gams, Crous & M.J. Wingf. and *Phaeoniella chlamydospora* (W. Gams, Crous, M.J. Wingf. & Mugnai) Crous & W. Gams] are not strict soil-borne fungi, they can colonise the plant vascular system through roots or via wounds such as the non-callused part of the lower trunk (Gramaje et al. 2011, 2015). The general above-ground symptoms associated with infection by black-foot and Petri diseases are reduced growth, shortened internodes, delayed budburst, wilting of the foliage and plant death (Gramaje and Armengol 2011, Agustí-Brisach and Armengol 2013, Gramaje et al. 2018). Nevertheless, these symptoms resemble those associated with abiotic disorders, such as spring frost, winter damage, nutrient deficiency and/or water stress (Gramaje et al. 2018), so their diagnostics are not always easy.

Inoculum of these fungal pathogens is present in diseased plants and can be incorporated into the soil by infected roots and/or pruning debris, surviving in the soil for extended periods of time (Gramaje and Armengol 2011, Agustí-Brisach et al. 2013, 2014). Moreover, simultaneous infections from different species sometimes result in a disease complex that can further damage the crop. Thus, the prevention of infections in the nursery and in the vineyard is critical for the management of black-foot and Petri diseases (Gramaje and Armengol 2011).

A general, practical and cost-efficient approach for the management of these soil-borne fungi might be the identification and the use of rootstocks tolerant to black-foot and Petri diseases. The pathogenic variation of the target fungi can compromise the efficiency of host resistance. We currently have a good knowledge about the biology of the pathogens and of their genetic and virulence diversity, although most investigations conducted so far have shown that there is no clear association between genetic groups and pathogenic variation (Tegli et al. 2000, Cottral et al. 2001, Borie et al. 2002, Alaniz et al. 2009, Comont et al. 2010, Chaverri et al. 2011, Cabral et al. 2012, Gramaje et al. 2013, 2014, Martín et al. 2014).

The existing artificial inoculation assays for black-foot and Petri disease pathogens have indicated that grapevine rootstocks might show varying levels of susceptibility to pathogen infection, but no evidence of qualitative resistance to these fungi has been found (Eskalen et al. 2001, Alaniz et al. 2010, Gramaje et al. 2010, Brown et al. 2013). Eskalen et al. (2001) evaluated the susceptibility of 20 rootstocks originating from crosses of North American *Vitis* spp. to Petri disease pathogens, but none of them were resistant to

fungal infection under controlled conditions. Gramaje et al. (2010) found 161-49 Couderc to be the least susceptible among five grapevine rootstocks previously inoculated with Petri disease pathogens under field conditions in Spain. In contrast, rootstocks 140 Ruggeri and 110 Richter (both crosses of *V. berlandieri* × *V. rupestris*) were greatly affected by the fungi. On the north coast of California, large-scale replanting of grapevine rootstock crosses of *V. berlandieri* × *V. riparia* by new rootstock crosses of *V. riparia* × *V. rupestris* and *V. berlandieri* × *V. rupestris* resulted in increased incidence of young vine decline and subsequent plant death from the early 1990s (Gubler et al. 2004). Petri disease pathogens were later isolated from these affected vines. This information and the results published by Gramaje et al. (2010) suggested that grapevine rootstock crosses of *V. riparia* × *V. berlandieri* could be the least susceptible to Petri disease pathogens.

The dominant grapevine rootstock in Spain, 110 Richter, was found to be the most susceptible to black-foot fungi among five common grapevine rootstocks in potted experiments (Alaniz et al. 2010). In similar experimental conditions carried out in New Zealand, Brown et al. (2013) assessed the susceptibility of four rootstocks to the black-foot species *Cylindrocladiella parva* and concluded that *V. riparia* cv. Gloire de Montpellier was the most susceptible and 101-14 the least. All this information will be of a great value for plant pathologists, grapevine breeders and viticulturists for future screening of grape germplasm collections and breeding programs.

Little is known about the mechanisms of rootstock resistance to black-foot and Petri diseases. Previous studies with *V. vinifera* cultivars highlighted the role of phenolic substances production as a possible plant defence mechanism against Botryosphaeriaceae spp., another important group of fungal trunk pathogens of grapevine which infect the plants through pruning wounds (Lambert et al. 2012). Relatively high lignin content and composition in cell walls has been associated with woody tissues of *V. vinifera* cultivars, having more tolerance to the fungal trunk disease Eutypa dieback (Rolshausen et al. 2008). Recent reports also suggested that *V. vinifera* susceptibility is positively correlated to xylem vessel diameter for *P. chlamydospora* (Pouzoulet et al. 2017). These findings warrant further research as such traits may be useful markers when selecting for tolerant rootstocks or new genotypes. In the short term, rootstocks found to be more tolerant to black-foot and Petri diseases could also be recommended for future plantings, which will contribute to vineyard longevity.

Challenges related to conferred vigour, yield and grape composition management

Maintaining yield and composition standards is also a challenge for viticulture worldwide (Fraga et al. 2012), and rootstocks can also play a great role in this regard. When choosing the rootstock for establishing a new vineyard, it is necessary to consider first the factors that limit or greatly condition correct vineyard performance (i.e. those mentioned in previous sections) discarding then unsuitable rootstocks (May 1994). Once the unsuitable rootstocks have been discarded, it is necessary to choose one among the potentially well-suited ones, which is usually done attempting to fulfil requirements in terms of yield and grape composition. This section focuses on fruit quality attributes related to winegrapes, acknowledging that the requirements

and implications of rootstock use on table grapes, raisins or grape juice may be different.

The rootstock effects on vine yield and winegrape composition have been widely evaluated since the introduction of rootstocks at the end of the 19th century, under a broad range of soil and climatic conditions for all major cultivars [aggregated information can be found, for instance in May (1994), Cordeau (1998), Fregoni (1998), Galet and Smith (1998), Hidalgo (1999), Morris et al. (2007), Pulko et al. (2012), Miele and Rizzon (2017) and Marín et al. (2019)]. Nevertheless, considering that the performance of scions grafted to different rootstocks is not consistent, as scion \times rootstock interactions occur (Clingleffer et al. 2019), and that site-specific effects can be observed because of variation in climate and soil (Walker et al. 2019), it is necessary to specifically evaluate each scion cultivar and growing conditions.

The evaluation of the agronomic implications of using certain rootstock needs to consider that direct and indirect effects coalesce. The effect of rootstocks on yield and fruit composition are related, and therefore some of the gains in composition that some rootstocks confer are associated with a decrease in yield. For instance, a trial with cv. Shiraz during four consecutive seasons, where five rootstocks and two levels of water availability were compared (Stevens et al. 2016), showed that variations in yield accounted for 25% of the differences in anthocyanin concentration when data were pooled across the four seasons. More clearly, in an experiment where the performance of cv. Tempranillo grafted on ten rootstocks was evaluated during three consecutive seasons (Albuquerque et al. 2010), changes in yield explained 62% of the variation observed in phenolic substances. Similar results have been reported in other experiments (Koundouras et al. 2009, Ozden et al. 2010, Renouf et al. 2010, Loureiro et al. 2016). Similarly, differences in yield usually correlate positively with changes in the vigour conferred, improved composition generally associated to lower vigour (Renouf et al. 2010, Romero et al. 2018, Marín et al. 2019), especially when there are no differences in yield associated to the rootstock chosen (Wooldridge et al. 2010).

The challenge of developing new rootstocks is neither to improve fruit composition through yield reduction, nor to increase yield and thus not improve composition, but to improve at least one of them with no undesirable changes in the other. Although there are differences among currently used rootstocks, this effect is not so well-known, since differences are frequently subtle and difficult to evaluate. In the next paragraphs, we describe four relevant aspects through which a proper choice of the rootstocks could improve vineyard performance and that need to be considered in the development of new ones.

Direct effect on the synthesis of phenolic substances

Apart from the indirect mechanisms associated with lower yield and vigour that lead to some rootstocks producing berries with a higher concentration of phenolic substances, the rootstock could also exert some direct effects that, to date, are relatively unexplored. Jogaiah et al. (2014), in an experiment aimed at understanding how rootstocks affected earliness in budburst, observed differences in the concentration of bud phenolic substances at budburst depending on the rootstock. Sap phenolic substances have also been reported to be affected by the rootstock (Wallis et al. 2013). In another recent experiment (Degu et al. 2015), a metabolic effect largely attributed to the rootstock was identified in some Muscat clones, implying changes in the concentration of quercetin 3-*O*-glucoside, resveratrol, and procyanidin

dimer B1. Similarly, Németh et al. (2017) reported changes in scion cane resveratrol depending on the rootstock. Apart from those specific effects, it can be assumed that part of the genetic machinery regulating the response of rootstocks to drought can also cause a difference in the synthesis of phenolic substances. In particular, rootstocks have been observed to affect ABA regulation in vines when coping with water stress (Marguerit et al. 2012, Serra et al. 2014, Rossedeutsch et al. 2016), and this will affect the synthesis of phenolic substances, a process related to ABA signalling in the berry (Wheeler 2006, Castellarin et al. 2007, He et al. 2010).

Synchrony of sugar accumulation and phenolic ripening

Recently, most of the world's highest quality wine-producing regions have shown a trend to warming during the growing season (Jones et al. 2005). This change has led to an advancement in phenology that has resulted in earlier harvest dates, and an uncoupling between sugar accumulation and phenolic ripening that leads to undesirable high sugar concentration when adequate phenolic maturity is reached (Mira de Orduña 2010, van Leeuwen and Darriet 2016). Moreover, advanced phenology indirectly implies that physiological ripening processes are occurring at times of the season with higher temperature that, in warm areas, can have a negative impact on grape composition. In this regard, anthocyanin biosynthesis is reduced, and organic acid metabolism in the berry hastened, leading to the production of wines with altered sensory profiles, poor colour and unbalanced alcohol concentration (Keller 2010, Carbonell-Bejerano et al. 2013, Teixeira et al. 2013, Bonada et al. 2015). Rootstocks are known to modify phenology (van Leeuwen and Destrac-Irvine 2017); *V. rupestris* and *V. berlandieri* \times *V. rupestris* usually delay ripening (Cordeau 1998, Hidalgo 1999), and can therefore be used to mitigate to some extent this negative consequence of climate change. Unfortunately, to our knowledge, the mechanisms causing this delay have not been well explored, and could constitute a target in rootstock breeding programs.

Potassium absorption and translocation

Soil pH is one of the most important factors that affect grape composition, and it is closely related to K concentration (Boulton 1980, Kodur et al. 2013). Vineyards grown in warm areas tend to produce grapes with excessive K concentration, which leads to a high juice pH (>3.8) and, in consequence, to less stable wines of reduced colour and flavour (Ribéreau-Gayon et al. 2006, Martins et al. 2012) that can require acidity adjustment during winemaking (Gómez et al. 2015). Rootstocks differ in their ability for K absorption (Rühl 2000, Kodur et al. 2009, 2013), which has an impact on berry and juice pH (Harbertson and Keller 2012). In general terms, high pH and potassium uptake are related to higher vigour (Rühl 1989, Clingleffer et al. 2011), the changes observed for organic acids being smaller. As reported for other grape characteristics, the significance of such effects may change with scion cultivar and site (Walker and Clingleffer 2009, Walker et al. 2019). As a result, growers should consider rootstock selection as part of their strategy to maintain pH low in warm areas.

Dwarfing rootstocks

Finally, regarding vigour control, there is a major issue that remains mostly unexplored: dwarfing rootstocks. In spite of their differences in vigour, none of the rootstocks available

has a true dwarfing character, which contrasts with the ubiquity of dwarfing rootstocks in other deciduous fruit crops (Cummins and Aldwinckle 1995, Webster et al. 2001, Cousins 2005b). That fact is quite surprising, since modern viticulture is frequently oriented to mid-to-medium-high planting densities that require rootstocks capable of reducing vine vigour (Intrieri et al. 2016). To our knowledge, only Bologna University's breeding program, initiated in 1990 through self-pollination of commercial rootstocks, has been focused towards that goal, having obtained satisfactory results for the rootstocks named 'Star 50' and 'Star 74' (Intrieri et al. 2016). Obtaining dwarfing rootstocks could significantly change the way we grow grapes, allowing a higher density or easing vineyard management in soils and climates where high vigour is problematic.

Genetic tools to assist rootstock breeding to overcome current and future challenges in viticulture

Characteristics of grapevine rootstock breeding

Because of grafting, most cultivated grapevine plants are genetic chimeras with two different genotypes facing the aerial and the soil environments, respectively. This chimerism provides the opportunity of independently breeding root traits without markedly altering the cultivar-characteristic fruit traits. At the same time, given the existent interactions between both genotypes, selection of appropriate rootstocks can help modulating specific scion phenotypes (Albacete et al. 2015, Ollat et al. 2016, Warschewsky et al. 2016). In terms of the germplasm that can be used, rootstock improvement is much less restricted than grapevine scion selection, which is conditioned by the convenience of preserving traditional cultivars that winegrowers and consumers can associate to their characteristic grape and wine products. Classical rootstock breeding can take advantage of a broad range of distant species in the Vitaceae family, which are cross-fertile and grafting-compatible with *V. vinifera* scions, to introduce genetic determinants of beneficial root features through hybridisation. Different grapevine wild relatives are naturally distributed across a high diversity of soils and environments and coexist with different pathogens (Cousins 2005a). Overall, they represent a wide source of genetic determinants for resistance and tolerance adaptive traits (Padgett-Johnson et al. 2003, Keller 2010, Reisch et al. 2012, Ollat et al. 2016). Still, this genetic diversity has considerable potential for further exploitation when considering that less than ten rootstock genotypes, some of them already generated in the 19th century, are used to graft about 90% of the current vineyards in spite of the diversity of soil environments that comprise the totality of vineyards worldwide (Keller 2010). In fact, only four species (*V. berlandieri*, *V. rupestris*, *V. riparia* and *V. vinifera*), and only a handful of accessions in each case, represent about 90% of the parentage of the most important rootstocks (Riaz et al. 2019). A bottleneck for the progress of rootstock breeding to face new challenges is that, while resistance to phylloxera is still an essential target trait that must be pursued, true resistance to this pest is mostly limited to *V. cinerea* (syn. *V. berlandieri* cv. Helleri), which on the other hand displays poor rooting capacity (Mullins et al. 1992).

In addition to non-trivial root performance phenotyping, rootstock breeding particularly requires characterising interactions with scion genotypes upon grafting (Clingleffer et al. 2019). These interactions range from grafting

compatibility, scion vigour and hydraulic conductivity to fruit quality and production features (Ollat et al. 2016). Another level of complexity that requires consideration is the performance of rootstocks under different soils, which depends not only on abiotic composition and structure but also on biotic factors such as the soil microbiome that have been less characterised so far. Altogether, long and laborious phenotyping processes constrain the success of classical rootstock breeding, which becomes apparent since only about 20 new rootstocks have been successfully developed worldwide and included in the nursery offer during the 21st century (Table 2). These time lapses can be reduced by means of high-throughput phenotyping approaches assisting root phenotyping (de Herralde et al. 2010, Bianchi et al. 2018). These techniques, however, are not always easily applicable on grapevine rootstocks because of root accessibility and soil space restrictions. Moreover, root traits observed in young plants or at ex situ small scale are not always reproduced by adult vines in vineyard soils. Genetic selection based on the detection of molecular polymorphisms associated to the desired phenotypes can be an alternative to phenotypic selection for those traits that do not show strong genetic-environmental interactions.

Molecular advances to assist future rootstock breeding

Molecular markers can be exploited to reduce expensive and time-consuming phenotyping tasks of complex physiological traits targeted by grapevine rootstock breeding. Currently, genome-wide markers can be identified at affordable cost by next-generation sequencing techniques including whole-genome re-sequencing or partial genotyping-by-sequencing (GBS) (Hyma et al. 2015, Liang et al. 2019). Nevertheless, rootstock breeding often involves gathering together traits from highly diverse *Vitis* species comprising genome structural variation that is only being elucidated recently (Zhou et al. 2019). Genome assembly has been useful to develop specific markers for resistance to downy mildew (*Plasmopara viticola*) in 'Börner', a hybrid of *V. riparia* Gm183 × *V. cinerea* Arnold rootstock cultivar (Holtgräwe et al. 2020), while another assembly is available for the ancestral pure rootstock selection *V. riparia* cv. Gloire de Montpellier (Girollet et al. 2019). Amplicon sequencing (AmpSeq) is an approach that proved useful for the development of *Vitis* inter-specific marker panels (Zou et al. 2020), a convenient feature for the transferability of core genome markers to inter-specific germplasm and hybrids that rootstock breeding has to deal with. Irrespective of how markers are identified, they are basic to the identification of genetic loci controlling traits of interest by genetic approaches such as QTL mapping or genome-wide association studies (Delrot et al. 2020). Still, their success is limited in grapevine rootstocks because of methodological difficulties in studying below-ground processes in large germplasm populations. Furthermore, characterisation of relevant root traits has often shown to be complex and polygenic and to interact with the genetic background and the environment (Delrot et al. 2020). Consequently, the availability of robust genetic markers for marker-assisted selection (MAS) boosting rootstock breeding is still scarce.

Rootstock improvement through genetic engineering—possibilities and limitations

Alleles determining potentially interesting root traits are usually dispersed across different *Vitis* species, which slows

Table 2. Breeding data of new rootstocks released in the 21st century.

Common name	Country	Breeder	Breeding year	Released year	Parentage
RS-3	USA	Michael McKenry & David Ramming (USDA)	1991 [†]	2003 ^{‡,§}	Ramsey [¶] × Schwarzmann ^{†,¶,††}
Merbein 5489	Australia	CSIRO	1967 ^{‡‡}	2005 ^{‡‡}	Complex hybrid from <i>V. berlandieri</i> ^{§§}
Merbein 5512					Complex hybrid from <i>V. cinerea</i>
Merbein 6262					5 BB Kober ^{¶¶} × <i>V. vinifera</i> ^{¶¶}
Georgikon 28	Hungary	Georgikon faculty	–	2005 ^{¶¶}	<i>V. rupestris</i> cv. A. de Serres × <i>M. rotundifolia</i> cv. Cowart ^{a,b}
UCD GRN-1	USA	Andy Walker (University of California Davis)	–	2008 ^{a,b}	[<i>V. rupestris</i> × (<i>V. champinii</i> cv. Dog Ridge × <i>V. riparia</i> G. de M. ^c) × <i>V. riparia</i> G. de M. ^{a,b}
UCD GRN-2					[<i>V. rupestris</i> × (<i>V. champinii</i> cv. Dog Ridge × <i>V. riparia</i> G. de M. ^c) × <i>V. champinii</i> cv. c9038 ^{a,b}
UCD GRN-3					[<i>V. rupestris</i> × (<i>V. champinii</i> cv. Dog Ridge × <i>V. riparia</i> G. de M. ^c) × <i>V. champinii</i> cv. c9038 ^{a,b}
UCD GRN-4					[<i>V. rupestris</i> × (<i>V. champinii</i> cv. Dog Ridge × <i>V. riparia</i> G. de M. ^c) × <i>V. champinii</i> cv. c9021 ^{a,b}
UCD GRN-5					L6-1 (Ramsey ^{¶¶} × <i>V. riparia</i> G. de M. ^c) × <i>V. champinii</i> cv. c9021 ^{a,b}
Matador	USA	Peter Cousins (USDA)	2000 ^d	2010 ^{d,e}	101-14 ^{¶¶} × 3-1A (<i>V. mustangensis</i> × <i>V. rupestris</i>) ^c
Minotaur					4-12A (<i>V. champinii</i> cv. Dog Ridge × <i>V. rupestris</i>) × <i>V. riparia</i> ^c
Kingfisher					(<i>M. rotundifolia</i> × <i>V. vinifera</i>) × 140 Ruggeri ^{¶,†}
Nemadex Alain Bouquet	France	INRA	1987 ^f	2011 ^g	106/8 [<i>V. riparia</i> × (<i>V. cordofolia</i> × <i>V. rupestris</i>)] × <i>V. berlandieri</i> cv. Ressayguier 1 ^{h,i}
M1	Italy	University of Milan	Ends of 1980s ^h	2014 ^h	8 B (<i>V. berlandieri</i> × <i>V. riparia</i>) × 333 EM ^{¶,h,i,j}
M2					R 27 (<i>V. berlandieri</i> × <i>V. riparia</i>) × 5 C Teleki ^{¶,h,i,j}
M3					41 B [¶] × <i>V. berlandieri</i> cv. Ressayguier 1 ^{h,i}
M4					Self-pollination of 'Binova' (SO4 [¶] mutation) ^{h,k}
Star 50	Italy	Cesare Intrieri (Bologna University)	1990 ^{h,k}	2014 ^h	41 B [¶] × 110 Richter ^{¶,l}
Star 74					
RG8	Spain	Rafael García (Vitis Navarra nursery)	1997 ^l	AP ^l	
RG9					
RG10					

[†]McKenry (2001); [‡]Foundation Plant Services (2020); [§]Foundation Plant Services (2003); [¶]parentage of Ramsey, Schwarzmann, 5 BB Kober, 101-14, 140 Ruggeri, 333 EM, 5 C Teleki, 41 B, SO4 and 110 Richter are specified in Table 1; ^{††}Anwar and McKenry (2002); ^{‡‡}Australian Government (2008); ^{§§}Jones et al. (2009); ^{¶¶}Hajdu (2015); ^aClark and Finn (2010); ^bFerris et al. (2012); ^c*V. riparia* Gloire de Montpellier written as *V. riparia* G. de M.; ^dGWRDC (2012); ^eCousins (2011); ^fPl@nt Grape (2020); ^gOllat et al. (2011) ^hBavaresco et al. (2015); ⁱTergeo (2015); ^jPorro et al. (2013); ^kIntrieri et al. (2016). ^lPersonal communication; AP, In authorisation process in Spain. CSIRO, Commonwealth Scientific and Industrial Research Organization; INRA, Institut National de la Recherche Agronomique; USDA, United States Department of Agriculture.

down the performance of grapevine rootstock breeding through classical crosses. Genetic engineering could be an alternative shortcut to introduce additional favourable traits into already superior rootstock genotypes. Genetic transformation has been attempted for grapevine rootstock improvement, for instance to increase rooting capability (Geier et al. 2008) or resistance to root-knot nematodes (*Meloidogyne* spp.) (Yang et al. 2013). Concerning abiotic stress, drought tolerance is increased in transgenic grapevine plants over-expressing an ABA biosynthesis gene from *V. amurensis*, although it was associated to other pleiotropic effects (He et al. 2018). Taking advantage of the transport of molecules, such as mRNA, miRNA, peptides and hormones, from the rootstock to the scion parts of grafted plants, transgenic rootstocks could also be used to confer scions with resistance to airborne pathogens or to alter other scion phenotype traits such as vigour (Vigne et al. 2004, Agüero et al. 2005, Haywood et al. 2005, Dutt et al. 2007). Nonetheless, despite that grafting (use of wild-type scion on genetically modified rootstocks) does not involve the genetic transformation of the edible part of vines, limiting genetically modified organism (GMO) legislation, even for genome-edited plants, along with concerns on biosafety,

product labelling and acceptance by consumers might still be an issue.

***Vitis* genetic diversity available to cope with upcoming root challenges**

While the application of MAS or genome editing on grapevine rootstock improvement requires knowledge on the genetic control of relevant root traits, genetic loci and the underlying causal polymorphisms have been identified in only a handful of cases mostly related to resistance to the major soil pests.

Resistance to phylloxera remains the first evaluation step of any grapevine rootstock breeding program as grafting is the only sustainable practice currently available to face this pest (Reisch et al. 2012). There is genetic variation for the level of tolerance/resistance to phylloxera and the *RDV1* locus located in linkage group (LG) 13 was identified as a major QTL derived from *V. cinerea* determining the high resistance in the hybrid rootstock 'Börner' (Zhang et al. 2009). Another phylloxera resistance locus, *RDV2* located on LG 14, has recently been described together with linked molecular markers that can be used to select for

phylloxera resistance in breeds derived from the *V. cinerea* 'C2-50' donor accession (Smith et al. 2018a). Phylloxera resistance loci derived from *M. rotundifolia* have also been identified in a backcross population from the cross between VRH8771 (*V. vinifera* × *M. rotundifolia*) and *V. vinifera* cv. Cabernet Sauvignon, which included *RDV6*, a major QTL located on LG 7 that explained >70% of the variation for nodosity and number of larvae (Rubio et al. 2020). This QTL, however, might show low transferability because, as compared to *Vitis* species, LG 7 is split into LGs 7 and 20 in muscadines. In addition, muscadine hybrids need to be further backcrossed to introgress desired traits such as rooting capacity and tolerance to mineral deficiencies.

Concerning nematode resistance, *XiR1* is a major QTL derived from *V. arizonica* controlling resistance to *X. index* (Xu et al. 2008). This locus has been mapped to LG 19, co-localising with a cluster of putative nucleotide binding/leucine-rich repeat (NB-LRR) genes (Hwang et al. 2010). More recently, muscadine-derived resistance to *X. index* was also mapped in a VRH8771 × Cabernet Sauvignon backcross, including *XiR2* and *XiR3* QTLs located on LGs 9 and 10, respectively (Rubio et al. 2020). For root-knot nematodes, the *MJR1* locus conferring resistance to *M. javanica* has been mapped to another NB-LRR gene cluster on LG 18 and markers are also available to select for this resistance in descendants from the *V. cinerea* 'C2-50' donor (Smith et al. 2018b).

Although grapevine germplasm comprises a large diversity to be exploited, the genetic information available on rootstock abiotic stress tolerance is limited to a few reports. For salinity tolerance, a major QTL, the Na⁺ exclusion (*NaE*) locus at LG 11, and the likely responsible gene, *VisHKT1;1* encoding a high-affinity potassium family transporter, were identified after GBS analyses in a population derived from a cross between K51-40 (*V. champinii* × *V. riparia*) and 140 Ruggeri (*V. berlandieri* × *V. rupestris*) rootstocks (Henderson et al. 2018). This population exhibited high variation in leaf Na⁺ concentration (Gong et al. 2014) and the study by Henderson et al. (2018) identified that the *NaE* locus explained up to 72% of this variation. While *V. berlandieri*, *V. riparia* and *V. vinifera* species appear to carry dominant alleles for strong Na⁺ exclusion at the *NaE* locus, two functional missense Single Nucleotide Polymorphisms (SNPs) in these alleles of *VisHKT1;1* could serve as markers to trace salt tolerance in rootstock breeding when these species are hybridised to other genetic backgrounds such as *V. champinii* or *V. rupestris* that carry alleles leading to Na⁺ accumulation and low salt tolerance.

Relative to drought tolerance, several QTLs, each of them explaining a low variation proportion, were detected for the control of rootstock-dependent scion acclimation of transpiration rate to water deficit when Cabernet Sauvignon scion was grafted onto a Cabernet Sauvignon × *V. riparia* cv. Gloire de Montpellier cross progeny (Marguerit et al. 2012). In another quantitative genetics study using the same rootstock cross population and scion combination, a major QTL involved in the control of tolerance to lime-induced iron deficiency was detected in LG 13 (Bert et al. 2013). Rooting capacity of dormant canes has proven to have moderate heritability and could be improved in a few generations (Smith et al. 2013). This relevant trait should be also pursued in rootstock breeding, and genetic loci controlling this trait have been reported in the same Cabernet Sauvignon × *V. riparia* cv. Gloire de Montpellier genetic background (Tandonnet et al. 2018). This work

identified four main QTLs mapping on LGs 1, 2, 5 and 9 explaining each 10–20% of the total variance in root biomass and root number traits. The study also showed that rootstock-dependent scion growth is mostly controlled by genetic loci other than these related with rootstock root growth, detecting a QTL on LG 3 explaining 11% of the variance in scion biomass. This QTL might be useful for rootstock control of scion vigour. For other relevant root traits such as resistance to soil-borne pathogenic fungi, no QTL analysis has been described so far. Further germplasm screening and research efforts in genetics and genomics are required to identify genetic variations responsible for improved root traits to face new threats in viticulture. Nonetheless, phenotyping of rootstock-related traits to map interesting loci and pyramiding the many desired traits together in single rootstock accessions still remain challenging itself.

Conclusions

Winegrowers are already facing the challenge of keeping up with global change. Maximising quality while maintaining yields is not and will not be easy with an increasing market and social demand for a more sustainable viticulture under climate change. Almost a century and a half after growers started using rootstocks as a solution to phylloxera, roots and the rhizosphere are far from being as studied as the above-ground parts of grapevine. Improved knowledge of the structure and function of grapevine roots and rhizosphere in different soils, climates and under diverse agronomical practices may provide a wider range of solutions to cope with the challenges associated to global change. In this regard, the genetic diversity hosted in *Vitis* ssp. can provide new functional abilities, whereas the advent of new molecular and genome editing tools has the potential to make breeding processes much more efficient.

Water scarcity and salinity, along with high temperature will impose more frequent and severe drought and stress events. Under this perspective, water management in the wider sense will play a major role. Irrigation in the areas with sufficient water and energy available will be a good adaptation tool, provided care is taken to avoid eventual salinity problems. In areas with water scarcity, more efficient rootstocks and scions will be the best option, always combined with appropriate soil and canopy management. Pest and disease control using more environmental respectful practices is also a challenge. Soil-borne fungi and nematodes are currently the most important pathogens at the soil level, for which rootstocks can be an innocuous and relatively inexpensive solution, as they have already been a remedy for phylloxera from the late 19th century.

Apart from affecting vigour and yield, rootstocks also play a role in grape composition. They have direct effects on grape composition and on the response of phenolic substances to water stress, and can serve to indirectly avoid the decoupling of the accumulation of sugar and phenolic substances during fruit ripening by means of delaying the phenology. Because rootstock accessions differ in K absorption, they can potentially be used to help control berry pH in warm areas. Genetic engineering tools provide a better understanding of molecular mechanisms underlying resistance and improved traits that are targeted in rootstock breeding programs. Marker-assisted selection is also a valuable tool for a more precise and faster development of new rootstocks.

Finally, the complexity of soil–root interactions, and of those between rootstock and scion, makes necessary a

multidisciplinary approach, since physiology, pathology, ecology, genetics and even sociology need to be considered when outlining the strategies to improve grapevine adaptation to current and future challenges.

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