



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

D. MARÍN<sup>1</sup> , J. ARMENGOL<sup>2</sup> , P. CARBONELL-BEJERANO<sup>3\*</sup> , J.M. ESCALONA<sup>4</sup> , D. GRAMAJE<sup>3</sup> , E. HERNÁNDEZ-MONTES<sup>4†</sup> , D.S. INTRIGLIOLO<sup>5</sup> , J.M. MARTÍNEZ-ZAPATER<sup>3</sup> , H. MEDRANO<sup>4</sup> , J.M. MIRÁS-AVALOS<sup>6</sup> , J.E. PALOMARES-RIUS<sup>7</sup> , P. ROMERO-AZORÍN<sup>8</sup> , R. SAVÉ<sup>9</sup> , L.G. SANTESTEBAN<sup>1</sup> and F. DE HERRALDE<sup>9</sup>

<sup>1</sup> Department of Agricultural Engineering, Biotechnology and Food, Public University of Navarre, Pamplona 31006, Spain;

<sup>2</sup> Instituto Agroforestal Mediterráneo, Universitat Politècnica de València, Valencia, 46022, Spain; <sup>3</sup> Institute of Grapevine and Wine Sciences (ICVV), National Research Council (CSIC), University of La Rioja and Government of La Rioja, Logroño 26007, Spain; <sup>4</sup> Agro-Environmental and Water Economics Institute (INAGEA), University of Balearic Islands (UIB), Palma 07122, Spain; <sup>5</sup> Irrigation Department, Applied Biology and Soil Sciences Center (CEBAS), Spanish National Research Council (CSIC), Campus Universitario de Espinardo, Murcia 30100, Spain; <sup>6</sup> Department of Soil and Irrigation (associated to EEAD-CSIC), Agrifood Research and Technology Centre of Aragon (CITA), Zaragoza 50059, Spain;

<sup>7</sup> Institute for Sustainable Agriculture (IAS), Spanish National Research Council (CSIC), Campus Alameda del Obispo, Córdoba 14004, Spain; <sup>8</sup> Department of Viticulture, Instituto Murciano de Investigación y Desarrollo Agrario y Alimentario (IMIDA), Murcia 30150, Spain; <sup>9</sup> Fruit Production Programme, Institute of Agrifood Research and Technology (IRTA), Barcelona 08140, Spain

\*Department of Molecular Biology, Max-Planck-Institute for Developmental Biology, Tübingen 72076, Germany

†Department of Horticulture, Irrigated Agriculture Research and Extension Center, Washington State University Prosser WA, 99350, USA

Corresponding author: Dr Felicidad de Herralde, email felicidad.deherralde@irta.cat

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

<sup>†</sup>Common name according to Dry (2007) first or to Maul et al. (2020) if absent; <sup>‡</sup>breeder and breeding year according mainly to Pl@nt Grape (2020); <sup>††</sup>Maul et al. (2020); <sup>‡‡</sup>Garris et al. (2009); <sup>§§</sup>Pl@nt Grape (2020); <sup>¶¶</sup>Riaz et al. (2019); <sup>§</sup>Teubes (2014); <sup>¶</sup>Rühl (1996); <sup>a</sup>de Andrés et al. (2007); <sup>b</sup>*V. riparia* Gloire de Montpellier written as *V. riparia* G. de M.; <sup>c</sup>Lin and Walker (1998); <sup>d</sup>Laucou et al. (2008).

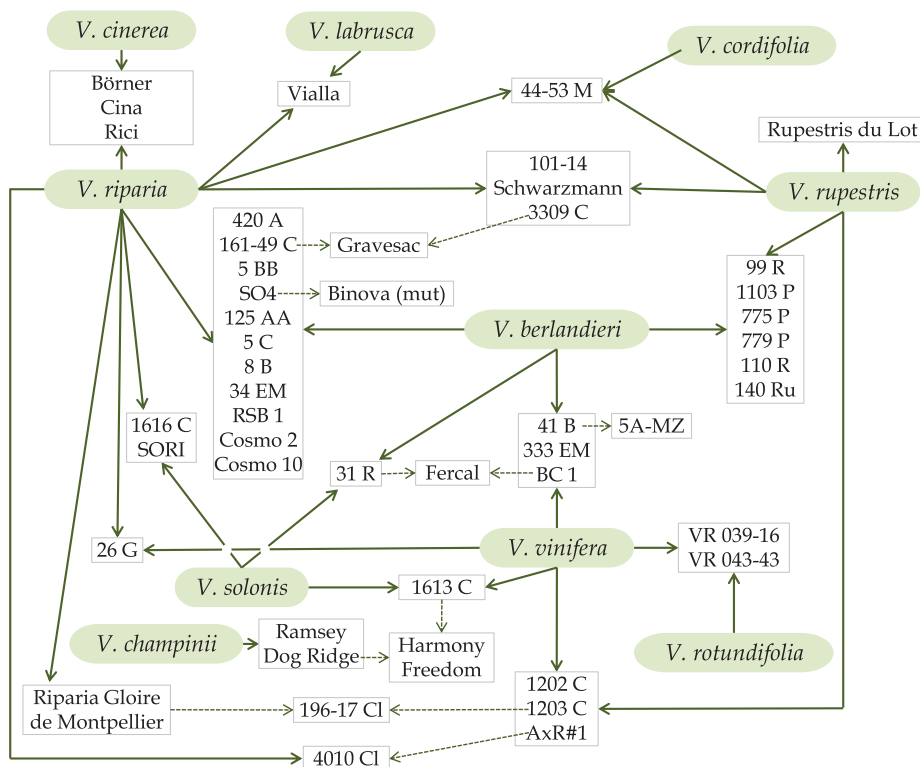


Figure 1. Main rootstocks used worldwide and their parental species (own elaboration based on Shaffer et al. (2004)).

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, Yıldırım 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 (Yildirim 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 ( $\Psi_{\text{leaf}}$ ), 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 ( $\text{WUE}_{\text{yield}}$ ,  $\text{kg/m}^3$  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  $\text{kg/m}^3$  in Syrah vines in Australia (Stevens et al. 2010, Kidman et al. 2014) and 12–20  $\text{kg/m}^3$  in Syrah vines in Australia (Soar et al. 2006); 5–6.5  $\text{kg/m}^3$  in Chardonnay in Australia (Stevens et al. 2008); 2–4  $\text{kg/m}^3$  in Cabernet Sauvignon in Greece (Koundouras et al. 2009); 4–16  $\text{kg/m}^3$  in Cabernet Sauvignon in California (Williams 2010); 9–18  $\text{kg/m}^3$  in Monastrell vines in south-east Spain (Romero et al. 2018); and 9–29  $\text{kg/m}^3$  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<sup>+</sup> and Cl<sup>-</sup> 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<sup>-</sup> rather than in Na<sup>+</sup> 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<sup>-</sup> and/or Na<sup>+</sup> 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<sup>-</sup> exclusion in different rootstock populations, concluding that the Cl<sup>-</sup> exclusion trait is controlled by

multiple genes. Henderson et al. (2014) aimed at discerning the molecular identity of membrane proteins that control Cl<sup>-</sup> exclusion in grapevine and concluded that transcriptional events contributing to the Cl<sup>-</sup> 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<sup>-</sup> exclusion in *Vitis* species, although they were not able to identify obvious Cl<sup>-</sup> transporters. In a subsequent study, Henderson et al. (2018), successfully mapped a QTL that controls Na<sup>+</sup> exclusion in rootstocks and identified the causal gene (*VisHTK1;1*) underlying that trait; these findings may assist with breeding Na<sup>+</sup> 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<sup>-</sup> and Na<sup>+</sup> 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<sup>-</sup>-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<sup>-</sup> in roots as compared to 140 Ruggeri, a known salt excluder. Moreover, the observed prevalence of the Cl<sup>-</sup> exclusion trait across multiple genetic backgrounds suggested that the surveyed collection may host multiple sources for Cl<sup>-</sup> 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 <sup>†</sup>	2003 <sup>‡,§</sup>	Ramsey <sup>¶</sup> × Schwarzmann <sup>†,¶,††</sup>
Merbein 5489	Australia	CSIRO	1967 <sup>‡‡</sup>	2005 <sup>‡‡</sup>	Complex hybrid from <i>V. berlandieri</i> <sup>§§</sup>
Merbein 5512					Complex hybrid from <i>V. cinerea</i>
Merbein 6262					5 BB Kober <sup>¶¶</sup> × <i>V. vinifera</i> <sup>¶¶</sup>
Georgikon 28	Hungary	Georgikon faculty	–	2005 <sup>¶¶</sup>	<i>V. rupestris</i> cv. A. de Serres × <i>M. rotundifolia</i> cv. Cowart <sup>a,b</sup>
UCD GRN-1	USA	Andy Walker (University of California Davis)	–	2008 <sup>a,b</sup>	[ <i>V. rupestris</i> × ( <i>V. champinii</i> cv. Dog Ridge × <i>V. riparia</i> G. de M. <sup>c</sup> ) × <i>V. riparia</i> G. de M. <sup>a,b</sup>
UCD GRN-2					[ <i>V. rupestris</i> × ( <i>V. champinii</i> cv. Dog Ridge × <i>V. riparia</i> G. de M. <sup>c</sup> ) × <i>V. champinii</i> cv. c9038 <sup>a,b</sup>
UCD GRN-3					[ <i>V. rupestris</i> × ( <i>V. champinii</i> cv. Dog Ridge × <i>V. riparia</i> G. de M. <sup>c</sup> ) × <i>V. champinii</i> cv. c9038 <sup>a,b</sup>
UCD GRN-4					[ <i>V. rupestris</i> × ( <i>V. champinii</i> cv. Dog Ridge × <i>V. riparia</i> G. de M. <sup>c</sup> ) × <i>V. champinii</i> cv. c9021 <sup>a,b</sup>
UCD GRN-5					L6-1 (Ramsey <sup>¶¶</sup> × <i>V. riparia</i> G. de M. <sup>c</sup> ) × <i>V. champinii</i> cv. c9021 <sup>a,b</sup>
Matador	USA	Peter Cousins (USDA)	2000 <sup>d</sup>	2010 <sup>d,e</sup>	101-14 <sup>¶¶</sup> × 3-1A ( <i>V. mustangensis</i> × <i>V. rupestris</i> ) <sup>c</sup>
Minotaur					4-12A ( <i>V. champinii</i> cv. Dog Ridge × <i>V. rupestris</i> ) × <i>V. riparia</i> <sup>c</sup>
Kingfisher					( <i>M. rotundifolia</i> × <i>V. vinifera</i> ) × 140 Ruggeri <sup>¶,†</sup>
Nemadex Alain Bouquet	France	INRA	1987 <sup>f</sup>	2011 <sup>g</sup>	106/8 [ <i>V. riparia</i> × ( <i>V. cordofolia</i> × <i>V. rupestris</i> )] × <i>V. berlandieri</i> cv. Ressayguier 1 <sup>h,i</sup>
M1	Italy	University of Milan	Ends of 1980s <sup>h</sup>	2014 <sup>h</sup>	8 B ( <i>V. berlandieri</i> × <i>V. riparia</i> ) × 333 EM <sup>¶,h,i,j</sup>
M2					R 27 ( <i>V. berlandieri</i> × <i>V. riparia</i> ) × 5 C Teleki <sup>¶,h,i,j</sup>
M3					41 B <sup>¶</sup> × <i>V. berlandieri</i> cv. Ressayguier 1 <sup>h,i</sup>
M4					Self-pollination of 'Binova' (SO4 <sup>¶</sup> mutation) <sup>h,k</sup>
Star 50	Italy	Cesare Intrieri (Bologna University)	1990 <sup>h,k</sup>	2014 <sup>h</sup>	41 B <sup>¶</sup> × 110 Richter <sup>¶,l</sup>
Star 74					
RG8	Spain	Rafael García (Vitis Navarra nursery)	1997 <sup>l</sup>	AP <sup>l</sup>	
RG9					
RG10					

<sup>†</sup>McKenry (2001); <sup>‡</sup>Foundation Plant Services (2020); <sup>§</sup>Foundation Plant Services (2003); <sup>¶</sup>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; <sup>††</sup>Anwar and McKenry (2002); <sup>‡‡</sup>Australian Government (2008); <sup>§§</sup>Jones et al. (2009); <sup>¶¶</sup>Hajdu (2015); <sup>a</sup>Clark and Finn (2010); <sup>b</sup>Ferris et al. (2012); <sup>c</sup>*V. riparia* Gloire de Montpellier written as *V. riparia* G. de M.; <sup>d</sup>GWRDC (2012); <sup>e</sup>Cousins (2011); <sup>f</sup>Pl@nt Grape (2020); <sup>g</sup>Ollat et al. (2011) <sup>h</sup>Bavaresco et al. (2015); <sup>i</sup>Tergeo (2015); <sup>j</sup>Porro et al. (2013); <sup>k</sup>Intrieri et al. (2016). <sup>l</sup>Personal 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<sup>+</sup> 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<sup>+</sup> 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<sup>+</sup> 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<sup>+</sup> 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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### References

- Agüero, C.B., Uratsu, S.L., Greve, C., Powell, A.L.T., Labavitch, J. M., Meredith, C.P. and Dandekar, A.M. (2005) Evaluation of tolerance to Pierce's disease and *Botrytis* in transgenic plants of *Vitis vinifera* L. expressing the pear GIP gene. *Molecular Plant Pathology* **6**, 43–51.
- Agustí-Brisach, C. and Armengol, J. (2013) Black-foot disease of grapevine: an update on taxonomy, epidemiology and management strategies. *Phytopathologia Mediterranea* **52**, 245–261.
- Agustí-Brisach, C., Mostert, L. and Armengol, J. (2014) Detection and quantification of *Ilyonectria* spp. associated with black-foot disease of grapevine in nursery soils using multiplex nested PCR and quantitative PCR. *Plant Pathology* **63**, 316–322.
- Agustí-Brisach, C., Gramaje, D., García-Jiménez, J. and Armengol, J. (2013) Detection of black-foot disease pathogens in the grapevine nursery propagation process in Spain. *European Journal of Plant Pathology* **137**, 103–112.
- Aigoun, W., Elena Jimenez, G., Cabral, A., Leon, M., Sabaou, N., Armengol, J., Chaouia, C., Mahamedi, A.E. and Berraf-Tebbal, A. (2019) Characterization and pathogenicity of *Cylindrocarpon*-like asexual morphs associated with black foot disease in Algerian grapevine nurseries, with the description of *Pleioacarpon algeriense* sp. nov. *European Journal of Plant Pathology* **154**, 1–15.
- Alaniz, S., García-Jiménez, J., Abad-Campos, P. and Armengol, J. (2010) Susceptibility of grapevine rootstocks to *Cylindrocarpon liriodendri* and *C. macrodidymum*. *Scientia Horticulturae* **125**, 305–308.
- Alaniz, S., Armengol, J., León, M., García-Jiménez, J. and Abad-Campos, P. (2009) Analysis of genetic and virulence diversity of *Cylindrocarpon liriodendri* and *C. macrodidymum* associated with black foot disease of grapevine. *Mycological Research* **113**, 16–23.
- Albacete, A., Martínez-Andujar, C., Martínez-Perez, A., Thompson, A.J., Dodd, I.C. and Perez-Alfocea, F. (2015) Unravelling rootstock × scion interactions to improve food security. *Journal of Experimental Botany* **66**, 2211–2226.
- Albuquerque, M.V., Castaño, F.J. and Yuste, J. (2010) Influencia de diez portainjertos sobre el comportamiento de la variedad Tempranillo. *Vida Rural* **305**, 52–56.
- Alsina, M.M., Smart, D.R., Bauerle, T., de Herralde, F., Biel, C., Stockert, C., Negron, C. and Save, R. (2011) Seasonal changes of whole root system conductance by a drought-tolerant grape root system. *Journal of Experimental Botany* **62**, 99–109.
- Anwar, S.A. and McKenry, M. (2002) Developmental response of a resistance-breaking population of *Meloidogyne arenaria* on *Vitis* spp. *Journal of Nematology* **34**, 28–33.
- Aragüés, R., Medina, E.T. and Clavería, I. (2014) Effectiveness of inorganic and organic mulching for soil salinity and sodicity control in a grapevine orchard drip-irrigated with moderately saline waters. *Spanish Journal of Agricultural Research* **12**, 501.
- Aragüés, R., Pueyo, E.T., Zribi, W., Clavería, I., Álvaro-Fuentes, J. and Faci, J. (2015) Soil salinization as a threat to the sustainability of deficit irrigation under present and expected climate change scenarios. *Irrigation Science* **33**, 67–79.
- Australian Government (2008) Sweet Mountain Grape (*Vitis berlandieri*). *Plant Varieties Journal* **21**, 148–152.
- Barrios-Masias, F.H., Knipfer, T. and McElrone, A.J. (2015) Differential responses of grapevine rootstocks to water stress are associated with adjustments in fine root hydraulic physiology and suberization. *Journal of Experimental Botany* **66**, 6069–6078.
- Barrios-Masias, F.H., Knipfer, T., Walker, M.A. and McElrone, A.J. (2019) Differences in hydraulic traits of grapevine rootstocks are not conferred to a common *Vitis vinifera* scion. *Functional Plant Biology* **46**, 228–235.
- Bavaresco, L., Gardiman, M., Brancadoro, L., Espen, L., Failla, O., Scienza, A., Vezzulli, S., Zulini, L., Velasco, R., Stefanini, M., Gaspero, G. and Testolin, R. (2015) Grapevine breeding programs in Italy. Reynolds, A., ed. *Grapevine breeding programs for the wine industry* (Woodhead Publishing: Cambridge, England) pp. 135–157.
- Berdeja, M., Nicolas, P., Kappel, C., Dai, Z.W., Hilbert, G., Peccoux, A., Lafontaine, M., Ollat, N., Gomes, E. and Delrot, S. (2015) Water limitation and rootstock genotype interact to alter grape berry metabolism through transcriptome reprogramming. *Horticulture Research* **2**, 15012.
- Bert, P.-F., Bordenave, L., Donnart, M., Hévin, C., Ollat, N. and Decroocq, S. (2013) Mapping genetic loci for tolerance to lime-induced iron deficiency chlorosis in grapevine rootstocks (*Vitis* sp.). *Theoretical and Applied Genetics* **126**, 451–473.
- Bettiga, L.J. (2013) *Grape pest management*, 3rd ed. (University of California: Berkeley, CA, USA).
- Bianchi, D., Grossi, D., Tincani, D., Lorenzo, G., Brancadoro, L. and Rustioni, L. (2018) Multi-parameter characterization of water stress tolerance in *Vitis* hybrids for new rootstock selection. *Plant Physiology and Biochemistry* **132**, 333–340.
- Bird, G., Diamond, C., Warner, F. and Davenport, J. (1994) Distribution and regulation of *Meloidogyne nataliei*. *Journal of Nematology* **26**, 727–730.
- Bonada, M., Jeffery, D.W., Petrie, P.R., Moran, M.A. and Sadras, V. O. (2015) Impact of elevated temperature and water deficit on the chemical and sensory profiles of Barossa Shiraz grapes and wines: temperature and water effects on grapes and wines. *Australian Journal of Grape and Wine Research* **21**, 240–253.
- Borie, B., Jacquiot, L., Jamaux-Despreaux, I., Larignon, P. and Peros, J.P. (2002) Genetic diversity in populations of the fungi *Phaemoniella chlamydospora* and *Phaeacremonium aleophilum* on grapevine in France. *Plant Pathology* **51**, 85–96.
- Boulton, R.B. (1980) The general relationship between potassium, sodium and pH in grape juice and wine. *American Journal of Enology and Viticulture* **31**, 182–186.
- Bravdo, B. (2012) Effects of salinity and irrigation with desalinated effluent and sea water on production and fruit quality of grapevines (review and update). *Acta Horticulturae* (**931**), 245–258. <https://doi.org/10.17660/ActaHortic.2012.931.27>
- Brown, D.J.F., Dalmasso, A. and Trudgill, D.L. (1993) Nematode pests of soft fruits and vines. *Plant parasitic nematodes in temperate agriculture* (CAB International: Wallingford, England) pp. 427–462.
- Brown, D.S., Jaspers, M.V., Ridgway, H.J., Barclay, C.J. and Jones, E.E. (2013) Susceptibility of four grapevine rootstocks to *Cylindrocladiella parva*. *New Zealand Plant Protection* **66**, 249–253.
- Brunori, E., Farina, R. and Biasi, R. (2016) Sustainable viticulture: the carbon-sink function of the vineyard agro-ecosystem. *Agriculture, Ecosystems & Environment* **223**, 10–21.
- Cabral, A., Rego, C., Nascimento, T., Oliveira, H., Groenewald, J.Z. and Crous, P. (2012) Multi-gene analysis and morphology reveal novel *Ilyonectria* species associated with black foot disease of grapevines. *Fungal Biology* **116**, 62–80.
- Carbonell-Bejerano, P., Santa María, E., Torres-Pérez, R., Royo, C., Lijavetzky, D., Bravo, G., Aguirreolea, J., Sánchez-Díaz, M., Antolín, M.C. and Martínez-Zapater, J.M. (2013) Thermotolerance responses in ripening berries of *Vitis vinifera* L. cv Muscat Hamburg. *Plant and Cell Physiology* **54**, 1200–1216.
- Carluci, A., Lops, F., Mostert, L., Halleen, F. and Raimondo, M. (2017) Occurrence fungi causing black foot on young grapevines and nursery rootstock plants in Italy. *Phytopathologia Mediterranea* **56**, 10–39.
- Carneiro, R., Randig, O., Maria Ritta, A. and Ana Cristina, G. (2004) Additional information on *Meloidogyne ethiopica* Whitehead, 1968 (Tylenchida: Meloidogynidae), a root-knot nematode parasitising kiwi fruit and grapevine from Brazil and Chile. *Nematology* **6**, 109–123.
- Castellarin, S.D., Matthews, M.A., Di Gaspero, G. and Gambetta, G. A. (2007) Water deficits accelerate ripening and induce changes in gene expression regulating flavonoid biosynthesis in grape berries. *Planta* **227**, 101–112.

- Castillo, P., Gutierrez, C., Palomares-Rius, J., Navarrete, C. and Landa, B. (2009) First report of root-knot nematode *Meloidogyne hispanica* infecting grapevines in southern Spain. *Plant Disease* **93**, 1353–1353.
- Chaverri, P., Salgado, C., Hirooka, Y., Rossman, A.Y. and Samuels, G.J. (2011) Delimitation of *Neonectria* and *Cylindrocarpon* (Nectriaceae, Hypocreales, Ascomycota) and related genera with *Cylindrocarpon*-like anamorphs. *Studies in Mycology* **68**, 57–78.
- Chaves, M.M., Zarrouk, O., Francisco, R., Costa, J.M., Santos, T., Regalado, A.P., Rodrigues, M.L. and Lopes, C.M. (2010) Grapevine under deficit irrigation: hints from physiological and molecular data. *Annals of Botany* **105**, 661–676.
- Chitarra, W., Perrone, I., Avanzato, C.G., Minio, A., Boccacci, P., Santini, D., Gilardi, G., Siciliano, I., Gullino, M.L., Delledonne, M., Mannini, F. and Gambino, G. (2017) Grapevine grafting: scion transcript profiling and defense-related metabolites induced by rootstocks. *Frontiers in Plant Science* **8**, 654.
- Clark, J.R. and Finn, C.E. (2010) Register of new fruit and nut cultivars list 45. *HortScience* **45**, 41.
- Clingeffer, P., Morales, N., Davis, H. and Smith, H. (2019) The significance of scion × rootstock interactions. *OENO One* **53**, 335–346.
- Clingeffer, P.R., Smith, B., Edwards, E., Collins, M., Morales, N. and Walker, R.R. (2011) Rootstocks, a tool to manipulate vine growth characteristics, fruit composition and wine quality attributes, water use efficiency and drought tolerance. Novello, V., Bovio, M. and Cavalletto, S., eds. *Proceedings of the 17th GiESCO: 29 August–2 September 2011; Asti-Alba, Italy* (Publications & Actualités Vitivinicoles: Montpellier, France) p. 454.
- Comas, L.H., Bauerle, T.L. and Eissenstat, D.M. (2010) Biological and environmental factors controlling root dynamics and function: effects of root ageing and soil moisture. *Australian Journal of Grape and Wine Research* **16**, 131–137.
- Comas, L.H., Anderson, L.J., Dunst, R.M., Lakso, A.N. and Eissenstat, D.M. (2005) Canopy and environmental control of root dynamics in a long-term study of Concord grape. *New Phytologist* **167**, 829–840.
- Comont, G., Marie-France, C., Larignon, P. and Delmotte, F. (2010) AFLP markers reveal two genetic groups in the French population of the grapevine fungal pathogen *Phaeoaniella chlamydospora*. *European Journal of Plant Pathology* **127**, 451–464.
- Cordeau, J. (1998) Création d'un vignoble: greffage de la vigne et porte-greffes, élimination des maladies à virus (Editions Féret: Bordeaux, France).
- Corso, M. and Bonghi, C. (2014) Grapevine rootstock effects on abiotic stress tolerance. *Plant Science Today* **1**, 108–113.
- Corso, M., Vannozzi, A., Maza, E., Vitulo, N., Meggio, F., Piacco, A., Telatin, A., D'Angelo, M., Feltrin, E., Simone Negri, A., Prinsi, B., Valle, G., Ramina, A., Bouzayen, M., Bonghi, C. and Lucchin, M. (2015) Comprehensive transcript profiling of two grapevine rootstock genotypes contrasting in drought susceptibility links the phenylpropanoid pathway to enhanced tolerance. *Journal of Experimental Botany* **66**, 5739–5752.
- Costa, M., Vaz, M., Escalona, J., Egipto, R., Lopes, C., Medrano, H. and Chaves, M. (2016) Modern viticulture in southern Europe: vulnerabilities and strategies for adaptation to water scarcity. *Agricultural Water Management* **164**, 5–18.
- Cottral, E., Ridgway, H., Pascoe, I., Edwards, J. and Taylor, P. (2001) UP-PCR analysis of Australian isolates of *Phaeoaniella chlamydospora* and *Phaeoacremonium aleophilum*. *Phytopathologia Mediterranea* **40**, S479–S486.
- Cousins, P. (2005a) Evolution, genetics, and breeding: viticultural applications of the origins of our rootstocks. Cousins, P. and Striegler, R.K., eds. *Grapevine rootstocks: current use, research, and application. Proceedings of the 2005 rootstock symposium; 5 February 2005; Osage Beach, MI, USA* (Mid-America Viticulture and Enology Center: Mountain Grove, MO, USA) pp. 1–7.
- Cousins, P. (2005b) Rootstock breeding: an analysis of intractability. *HortScience* **40**, 1945–1946.
- Cousins, P. (2011) Three root-knot nematode resistant rootstocks released by USDA Agricultural Research Service. FPS grape program newsletter 1 (United States Department of Agriculture: Washington, DC, USA).
- Cramer, W., Guiot, J. and Marini, K. (2019) MedECC booklet: risks associated to climate and environmental changes in the Mediterranean region. A preliminary assessment by the MedECC Network Science-policy interface. [https://www.medecc.org/wp-content/uploads/2018/12/MedECC-Booklet\\_EN\\_WEB.pdf](https://www.medecc.org/wp-content/uploads/2018/12/MedECC-Booklet_EN_WEB.pdf)
- Cummins, J.N. and Aldwinckle, H.S. (1995) Breeding rootstocks for tree fruit crops. *New Zealand Journal of Crop and Horticultural Science* **23**, 395–402.
- Davies, W.J., Kudoyarova, G. and Hartung, W. (2005) Long-distance ABA signaling and its relation to other signaling pathways in the detection of soil drying and the mediation of the plant's response to drought. *Journal of Plant Growth Regulation* **24**, 285–295.
- de Andrés, M.T., Cabezas, J.A., Cervera, M.T., Borrego, J., Martínez-Zapater, J.M. and Jouve, N. (2007) Molecular characterization of grapevine rootstocks maintained in germplasm collections. *American Journal of Enology and Viticulture* **58**, 75–86.
- Degu, A., Morcia, C., Tumino, G., Hochberg, U., Toubiana, D., Mattivi, F., Schneider, A., Bosca, P., Cattivelli, L., Terzi, V. and Fait, A. (2015) Metabolite profiling elucidates communalities and differences in the polyphenol biosynthetic pathways of red and white Muscat genotypes. *Plant Physiology and Biochemistry* **86**, 24–33.
- Delrot, S., Grimplet, J., Carbonell-Bejerano, P., Schwandner, A., Bert, P.-F., Bavaresco, L., Dalla Costa, L., Gaspero, G., Duchêne, E., Hausmann, L., Malnoy, M., Morgante, M., Ollat, N., Pecile, M. and Vezzulli, S. (2020) Genetic and genomic approaches for adaptation of grapevine to climate change. Kole, C., ed. *Genomic designing of climate-smart fruit crops* (Springer: Cham, Switzerland) pp. 157–270.
- Demangeat, G., Voisin, R., Minot, J.-C., Bosselut, N., Fuchs, M. and Esmenjaud, D. (2005) Survival of *Xiphinema index* in vineyard soil and retention of grapevine fanleaf virus over extended time in the absence of host plants. *Phytopathology* **95**, 1151–1156.
- Downton, W. (1977) Photosynthesis in salt-stressed grapevines. *Functional Plant Biology* **4**, 183.
- Dry, N. (2007) *Grapevine rootstocks. Selection and management for South Australian vineyards* (Lythrum Press: Adelaide, SA, Australia).
- Dutt, M., Li, Z.T., Kelley, S.A., Dhekney, S., Van Aman, M., Tattersall, J. and Gray, D.J. (2007) Transgenic rootstock protein transmission in grapevines. *Acta Horticulturae* **738**, 749–754.
- Eissenstat, D., Bauerle, T., Comas, L., Lakso, A.N., Neilsen, D., Neilsen, G.H. and Smart, D. (2006) Seasonal patterns of root growth in relation to shoot phenology in grape and apple. *Proceedings of the Vth international symposium on mineral nutrition of fruit plants; 16–21 January 2005; Talca, Chile. Acta Horticulturae* **721**, 21–26.
- Escalona, J.M., Tomàs, M., Martorell, S., Medrano, H., Ribas-Carbo, M. and Flexas, J. (2012) Carbon balance in grapevines under different soil water supply: importance of whole plant respiration. *Australian Journal of Grape and Wine Research* **18**, 308–318.
- Eskalen, A., Gubler, W.D. and Khan, A. (2001) Rootstock susceptibility to *Phaeoaniella chlamydospora* and *Phaeoacremonium* spp. *Phytopathologia Mediterranea* **40**, S433–S438.
- Esmenjaud, D. and Bouquet, A. (2009) Selection and application of resistant germplasm for grapevine nematodes management. Ciancio, A. and Mukerji, K.G., eds. *Integrated management of fruit crops nematodes* (Springer Netherlands: Dordrecht, The Netherlands) pp. 195–214.
- Esmenjaud, D., Decroocq, S., Bouquet, A. and Ollat, N. (2010) Host suitability of *Vitis* and *Vitis-Muscadinia* material to the nematode *Xiphinema index* over one to four years. *American Journal of Enology and Viticulture* **61**, 96–101.
- Fahrentrapp, J., Müller, L. and Schumacher, P. (2015) Is there need for leaf-galling grape phylloxera control? Presence and distribution of *Daktulosphaira vitifoliae* in Swiss vineyards. *International Journal of Pest Management* **61**, 340–345.
- Ferris, H., Zheng, L. and Walker, M.A. (2012) Resistance of grape rootstocks to plant-parasitic nematodes. *Journal of Nematology* **44**, 377–386.
- Ferris, H., Zheng, L. and Walker, M.A. (2013) Soil temperature effects on the interaction of grape rootstocks and plant-parasitic nematodes. *Journal of Nematology* **45**, 49–57.
- Flexas, J., Galmés, J., Gallé, A., Guliás, J., Pou, A., Ribas-Carbo, M., Tomàs, M. and Medrano, H. (2010) Improving water use efficiency in grapevines: potential physiological targets for biotechnological improvement. *Australian Journal of Grape and Wine Research* **16**, 106–121.
- Fort, K.P., Heinitz, C.C. and Walker, M.A. (2015) Chloride exclusion patterns in six grapevine populations. *Australian Journal of Grape and Wine Research* **21**, 147–155.

- Foundation Plant Services (2003) Release of UC patented nematode-resistant rootstocks. FPS Grape Program Newsletter (Foundation Plant Material Services: Davis, CA, USA).
- Foundation Plant Services (2020) Grape Variety: RS-2. Grape program at Foundation Plant Services. <https://fps.ucdavis.edu/>
- Fraga, H., Malheiro, A.C., Moutinho-Pereira, J. and Santos, J.A. (2012) An overview of climate change impacts on European viticulture. *Food and Energy Security* **1**, 94–110.
- Franck, N., Morales, J.P., Arancibia-Avenida, D., García de Cortázar, V., Perez-Quezada, J.F., Zurita-Silva, A. and Pastenes, C. (2011) Seasonal fluctuations in *Vitis vinifera* root respiration in the field. *New Phytologist* **192**, 939–951.
- Fregoni, M. (1998) *Viticoltura di qualità*, 1st ed. (L'Informatore Agrario: Verona, Italy).
- Fu, Q., Tan, Y., Zhai, H. and Du, Y. (2019) Evaluation of salt resistance mechanisms of grapevine hybrid rootstocks. *Scientia Horticulturae* **243**, 148–158.
- Funes, I., Savé, R., Rovira, P., Molowny-Horas, R., Alcañiz, J.M., Ascaso, E., Herms, L., Herrero, C., Boixadera, J. and Vayreda, J. (2019) Agricultural soil organic carbon stocks in the north-eastern Iberian Peninsula: drivers and spatial variability. *Science of the Total Environment* **668**, 283–294.
- Galbignani, M., Merli, M.C., Magnanini, E., Bernizzoni, F., Talaverano, I., Gatti, M., Tombesi, S., Palliotti, A. and Poni, S. (2016) Gas exchange and water-use efficiency of cv. Sangiovese grafted to rootstocks of varying water-deficit tolerance. *Irrigation Science* **34**, 105–116.
- Galet, P. and Smith, J. (1998) Grape varieties and rootstock varieties. *Collection Avenir oenologie* (Oenoplurimedia: Chaintré, France).
- Gambetta, G.A., Manuck, C.M., Drucker, S.T., Shaghasi, T., Fort, K., Matthews, M.A., Walker, M.A. and McElrone, A.J. (2012) The relationship between root hydraulics and scion vigour across *Vitis* rootstocks: what role do root aquaporins play? *Journal of Experimental Botany* **63**, 6445–6455.
- Garris, A., Cousins, P., Ramming, D. and Bald, A. (2009) Parentage analysis of freedom rootstock. *Research note. American Journal of Enology and Viticulture* **60**, 357–361.
- Geier, T., Eimert, K., Scherer, R. and Nickel, C. (2008) Production and rooting behaviour of rolB-transgenic plants of grape rootstock 'Richter 110' (*Vitis berlandieri* × *V. rupestris*). *Plant Cell, Tissue and Organ Culture* **94**, 269–280.
- Giollet, N., Rubio, B., Lopez-Roques, C., Valière, S., Ollat, N. and Bert, P.-F. (2019) De novo phased assembly of the *Vitis riparia* grape genome. *Scientific Data* **6**, 127.
- Gómez, J., Lasanta, C., Palacios-Santander, J.M. and Cubillana-Aguilera, L.M. (2015) Chemical modeling for pH prediction of acidified musts with gypsum and tartaric acid in warm regions. *Food Chemistry* **168**, 218–224.
- Gong, H.J., Blackmore, D., Clingeleffer, P.R., Sykes, S.R. and Walker, R.R. (2014) Variation for potassium and sodium accumulation in a family from a cross between grapevine rootstocks K 51-40 and 140 Ruggeri. *Vitis* **53**, 65–72.
- Gong, H., Blackmore, D., Clingeleffer, P.R., Sykes, S., Jha, D., Tester, M. and Walker, R.R. (2011) Contrast in chloride exclusion between two grapevine genotypes and its variation in their hybrid progeny. *Journal of Experimental Botany* **62**, 989–999.
- Gramaje, D. and Armengol, J. (2011) Fungal trunk pathogens in the grapevine propagation process: potential inoculum sources, detection, identification, and management strategies. *Plant Disease* **95**, 1040–1055.
- Gramaje, D., Armengol, J. and Ridgway, H. (2013) Genetic and virulence diversity, and mating type distribution of *Togninia minima* causing grapevine trunk diseases in Spain. *European Journal of Plant Pathology* **135**, 727–743.
- Gramaje, D., García-Jiménez, J. and Armengol, J. (2010) Field evaluation of grapevine rootstocks inoculated with fungi associated with Petri disease and Esca. *American Journal of Enology and Viticulture* **61**, 512–520.
- Gramaje, D., Mostert, L. and Armengol, J. (2011) Characterization of *Cadophora luteo-olivacea* and *C. melinii* isolates obtained from grapevines and environmental samples from grapevine nurseries in Spain. *Phytopathologia Mediterranea* **50** (Supplement), S112–S126.
- Gramaje, D., Úrbez-Torres, J.R. and Sosnowski, M.R. (2018) Managing grapevine trunk diseases with respect to etiology and epidemiology: current strategies and future prospects. *Plant Disease* **102**, 12–39.
- Gramaje, D., Mostert, L., Groenewald, J.Z. and Crous, P. (2015) *Phaeoacremonium*: from esca disease to phaeoohyphomycosis. *Fungal Biology* **119**, 759–783.
- Gramaje, D., Leon, M., Santana, M., Crous, P. and Armengol, J. (2014) Multilocus ISSR markers reveal two major genetic groups in Spanish and South African populations of the grapevine fungal pathogen *Cadophora luteo-olivacea*. *PLoS One* **9**, e110417.
- Granett, J., Walker, M.A., Kocsis, L. and Omer, A.D. (2001) Biology and management of grape phylloxera. *Annual Review of Entomology* **46**, 387–412.
- Gubler, W.D., Baumgartner, K., Browne, G.T., Eskalen, A., Latham, S.R., Petit, E. and Bayramian, L.A. (2004) Root diseases of grapevines in California and their control. *Australasian Plant Pathology* **33**, 157.
- Gullo, G., Dattola, A., Vonella, V. and Zappia, R. (2018) Evaluation of water relation parameters in *Vitis* rootstocks with different drought tolerance and their effects on growth of a grafted cultivar. *Journal of Plant Physiology* **226**, 172–178.
- Grape and Wine Research and Development Corporation (2012) Rootstock breeding and associated R&D in the viticulture and wine industry (Grape and Wine Research and Development Corporation: Adelaide, SA, Australia).
- Haider, M.S., Jogaiah, S., Pervaiz, T., Yanxue, Z., Khan, N. and Fang, J. (2019) Physiological and transcriptional variations inducing complex adaptive mechanisms in grapevine by salt stress. *Environmental and Experimental Botany* **162**, 455–467.
- Hajdu, E. (2015) Grapevine breeding in Hungary. Reynolds, A., ed. *Grapevine breeding programs for the wine industry: traditional and molecular techniques* (Woodhead Publishing: Cambridge, England) pp. 103–134.
- Hallen, F., Fourie, P.H. and Crous, P.W. (2006) A review of black foot disease of grapevine. *Phytopathologia Mediterranea* **45**, S55–S67.
- Harbertson, J.F. and Keller, M. (2012) Rootstock effects on deficit-irrigated winegrapes in a dry climate: grape and wine composition. *American Journal of Enology and Viticulture* **63**, 40–48.
- Haywood, V., Yu, T.-S., Huang, N.-C. and Lucas, W.J. (2005) Phloem long-distance trafficking of gibberellic acid-insensitive RNA regulates leaf development: phloem delivery of RNA regulates leaf development. *The Plant Journal* **42**, 49–68.
- He, F., Mu, L., Yan, G.L., Liang, N.N., Pan, Q.H., Wang, J., Reeves, M.J. and Duan, C.Q. (2010) Biosynthesis of anthocyanins and their regulation in colored grapes. *Molecules* **15**, 9057–9091.
- He, R., Zhuang, Y., Cai, Y., Agüero, C., Liu, S., Wu, J., Shuhan, D., Walker, M.A., Lu, J. and Zhang, Y. (2018) Overexpression of 9-cis-epoxycarotenoid dioxygenase cisgene in grapevine increases drought tolerance and results in pleiotropic effects. *Frontiers in Plant Science* **9**, 970.
- Heinitz, C.C., Riaz, S., Tenschler, A.C., Romero, N. and Walker, M.A. (2020) Survey of chloride exclusion in grape germplasm from the southwestern United States and Mexico. *Crop Science* **60**, 1946–1956.
- Hemmer, C., Djennane, S., Ackerer, L., Hleibieh, K., Marmonier, A., Gersch, S., Garcia, S., Vigne, E., Komar, V., Perrin, M., Gertz, C., Belval, L., Berthold, F., Monsion, B., Schmitt-Keichinger, C., Lemaire, O., Lorber, B., Gutiérrez, C., Muyldermans, S., Demangeat, G. and Ritzenthaler, C. (2018) Nanobody-mediated resistance to grapevine fanleaf virus in plants. *Plant Biotechnology Journal* **16**, 660–671.
- Henderson, S.W., Baumann, U., Blackmore, D.H., Walker, A.R., Walker, R.R. and Gilliam, M. (2014) Shoot chloride exclusion and salt tolerance in grapevine is associated with differential ion transporter expression in roots. *BMC Plant Biology* **14**, 273.
- Henderson, S.W., Dunlevy, J.D., Wu, Y., Blackmore, D.H., Walker, R.R., Edwards, E.J., Gilliam, M. and Walker, A.R. (2018) Functional differences in transport properties of natural HKT1;1 variants influence shoot Na<sup>+</sup> exclusion in grapevine rootstocks. *New Phytologist* **217**, 1113–1127.
- Hernández-Montes, E., Escalona, J., Tomàs, M. and Medrano, H. (2017) Influence of water availability and grapevine phenological stage on the spatial variation in soil respiration. *Australian Journal of Grape and Wine Research* **23**, 273–279.
- de Herralde, F., Savé, R., Aranda, J. and Biel, C. (2010) Grapevine roots and soil environment: growth, distribution and function. Delrot, S., Medrano, H., Or, E., Bavaresco, L. and Grandi, S., eds. *Methodologies and results in grapevine research* (Springer Netherlands: Dordrecht, The Netherlands) pp. 1–20.
- Hidalgo, L. (1999) *Tratado de viticultura* (Mundi Prensa: Madrid, Spain).

- Hirzel, D.R., Steenwerth, K., Parikh, S.J. and Oberholster, A. (2017) Impact of winery wastewater irrigation on soil, grape and wine composition. *Agricultural Water Management* **180**, 178–189.
- Holtgräwe, D., Rosleff Soerensen, T., Hausmann, L., Pucker, B., Viehöver, P., Töpfer, R. and Weisshaar, B. (2020) A partially phase-separated genome sequence assembly of the *Vitis* rootstock 'Börner' (*Vitis riparia* × *Vitis cinerea*) and its exploitation for arker development and targeted mapping. *Frontiers in Plant Science* **11**, 156.
- Huang, X., Lakso, A.N. and Eissenstat, D.M. (2005) Interactive effects of soil temperature and moisture on Concord grape root respiration. *Journal of Experimental Botany* **56**, 2651–2660.
- Hwang, C.F., Xu, K., Hu, R., Zhou, R., Riaz, S. and Walker, M.A. (2010) Cloning and characterization of XiR1, a locus responsible for dagger nematode resistance in grape. *Theoretische und Angewandte Genetik* **121**, 789–799.
- Hyma, K., Barba, P., Wang, M., Londo, J., Acharya, C., Mitchell, S., Sun, Q., Reisch, B. and Cadle-Davidson, L. (2015) Heterozygous mapping strategy (HetMappS) for high resolution genotyping-by-sequencing markers: a case study in grapevine. *PLoS One* **10**, e0134880.
- Intergovernmental Panel on Climate Change (2014) . Core writing team, Pachauri, R.K. and Meyer, L.A., eds. *Climate change 2014: synthesis report. Contribution of working groups I, II and III to the fifth assessment report of the Intergovernmental Panel on Climate Change* (Intergovernmental Panel on Climate Change: Geneva, Switzerland).
- Intrieri, C., Filippetti, I., Allegro, G., Valentini, G. and Pastore, C. (2016) 'Star 50' and 'Star 74': new dwarfing grape rootstocks. *Acta Horticulturae* **1136**, 23–26.
- Jelly, N., Schellenbaum, P., Walter, B. and Maillot, P. (2012) Transient expression of artificial microRNAs targeting grapevine fanleaf virus and evidence for RNA silencing in grapevine somatic embryos. *Transgenic Research* **21**, 1319–1327.
- Jogaiah, S., Maske, S.R. and Upadhyay, A. (2014) Rootstock induced changes in enzymes activity and biochemical constituents during budbreak in 'Thompson Seedless' grapevine. *Vitis* **53**, 57–64.
- Jones, G.V., White, M.A., Cooper, O.R. and Storchmann, K. (2005) Climate change and global wine quality. *Climatic Change* **73**, 319–343.
- Jones, T.H., Cullis, B.R., Clingeleffer, P.R. and Rühl, E.H. (2009) Effects of novel hybrid and traditional rootstocks on vigour and yield components of Shiraz grapevines. *Australian Journal of Grape and Wine Research* **15**, 284–292.
- Keller, M. (2010) Managing grapevines to optimise fruit development in a challenging environment: a climate change primer for viticulturists. *Australian Journal of Grape and Wine Research* **16**, 56–69.
- Kidman, C.M., Olarte Mantilla, S., Dry, P.R., McCarthy, M.G. and Collins, C. (2014) Effect of water stress on the reproductive performance of Shiraz (*Vitis vinifera* L.) grafted to rootstocks. *American Journal of Enology and Viticulture* **65**, 96–108.
- Kocsis, L., Tarczal, E. and Molnár Kocsisné, G. (2016) Grape rootstock-scion interaction on root system development. *Acta Horticulturae* **1136**, 27–32.
- Kodur, S., Tisdall, J.M., Clingeleffer, P.R. and Walker, R.R. (2013) Regulation of berry quality parameters in "Shiraz" grapevines through rootstocks (*Vitis*). *Vitis* **52**, 125–128.
- Kodur, S., Tisdall, J.M., Tang, C. and Walker, R.R. (2009) Accumulation of potassium in grapevine rootstocks (*Vitis*) as affected by dry matter partitioning, root traits and transpiration. *Australian Journal of Grape and Wine Research* **16**, 273–282.
- Koundouras, S., Tsialtas, I.T., Zioziou, E. and Nikolaou, N. (2008) Rootstock effects on the adaptive strategies of grapevine (*Vitis vinifera* L. cv. Cabernet-Sauvignon) under contrasting water status: leaf physiological and structural responses. *Agriculture, Ecosystems & Environment* **128**, 86–96.
- Koundouras, S., Hatzidimitriou, E., Karamolegkou, M., Dimopoulou, E., Kallithraka, S., Tsialtas, J.T., Zioziou, E., Nikolaou, N. and Kotseridis, Y. (2009) Irrigation and rootstock effects on the phenolic concentration and aroma potential of *Vitis vinifera* L. cv. Cabernet Sauvignon grapes. *Journal of Agricultural and Food Chemistry* **57**, 7805–7813.
- Lambert, C., Bisson, J., Waffo-Téguo, P., Papastamoulis, Y., Richard, T., Corio-Costet, M.-F., Mérillon, J.-M. and Cluzet, S. (2012) Phenolics and their antifungal role in grapevine wood decay: focus on the Botryosphaeriaceae family. *Journal of Agricultural and Food Chemistry* **60**, 11859–11868.
- Laucou, V., Boursiquot, J.-M., Lacombe, T., Bordenave, L., Decroocq, S. and Ollat, N. (2008) Parentage of grapevine rootstock 'Fercal' finally elucidated. *Vitis* **47**, 163–167.
- Liang, Z., Duan, S., Sheng, J., Zhu, S., Ni, X., Shao, J., Liu, C., Nick, P., Du, F., Fan, P., Mao, R., Zhu, Y., Deng, W., Yang, M., Huang, H., Liu, Y., Ding, Y., Liu, X., Jiang, J., Zhu, Y., Li, S., He, X., Chen, W. and Dong, Y. (2019) Whole-genome resequencing of 472 *Vitis* accessions for grapevine diversity and demographic history analyses. *Nature Communications* **10**, 1190.
- Lin, H. and Walker, M.A. (1998) Identifying grape rootstocks with simple sequence repeat (SSR) DNA markers. *American Journal of Enology and Viticulture* **49**, 403–407.
- Lombard, L., van der Merwe, N., Groenewald, J.Z. and Crous, P. (2014) Lineages in Nectriaceae: re-evaluating the generic status of *Ilyonectria* and allied genera. *Phytopathologia Mediterranea* **53**, 340–357.
- Loureiro, M.D., Moreno-Sanz, P., García, A., Fernández, O., Fernández, N. and Suárez, B. (2016) Influence of rootstock on the performance of the Albarín Negro minority grapevine cultivar. *Scientia Horticulturae* **201**, 145–152.
- Lovisola, C., Lavoie-Lamoureux, A., Tramontini, S. and Ferrandino, A. (2016) Grapevine adaptations to water stress: new perspectives about soil/plant interactions. *Theoretical and Experimental Plant Physiology* **28**, 53–66.
- Lovisola, C., Tramontini, S., Flexas, J. and Schubert, A. (2008) Mercurial inhibition of root hydraulic conductance in *Vitis* spp. rootstocks under water stress. *Environmental and Experimental Botany* **63**, 178–182.
- Marguerit, E., Brendel, O., Lebon, E., van Leeuwen, C. and Ollat, N. (2012) Rootstock control of scion transpiration and its acclimation to water deficit are controlled by different genes. *New Phytologist* **194**, 416–429.
- Marín, D., García, R., Eraso, J., Urrestarazu, J., Miranda, C., Royo, J.B., Abad, F.J. and Santesteban, L.G. (2019) Evaluation of the agronomic performance of 'Syrah' and 'Tempranillo' when grafted on 12 rootstocks. *Vitis* **58** (Special Issue), 111–118.
- Martin, G. (2014) Cost benefit analysis of winegrape rootstock research, development and extension. Final report to Australian Grape and Wine Authority (Australian Grape and Wine Authority: Adelaide, SA, Australia).
- Martín, L., Sáenz de Miera, L. and Martín, M. (2014) AFLP and RAPD characterization of *Phaeoacremonium aleophilum* associated with *Vitis vinifera* decline in Spain. *Journal of Phytopathology* **162**, 245–257.
- Martins, V., Cunha, A., Gerós, H., Hanana, M. and Blumwald, E. (2012) Mineral compounds in the grape berry. Gerós, H., Chaves, M.M. and Delrot, S., eds. *The biochemistry of the grape berry* (Bentham Science Publishers: Sharjah, United Arab Emirates) pp. 23–43.
- Maul, E., Röckel, F. and Töpfer, R. (2020) Wiederentdeckte traditionelle Rebsorten und die Einordnung ihrer geographischen und zeitlichen Entstehung. *Deutsches Weinbau-Jahrbuch* **71**, 137–147.
- Maurel, C., Simonneau, T. and Sutka, M. (2010) The significance of roots as hydraulic rheostats. *Journal of Experimental Botany* **61**, 3191–3198.
- May, P. (1994) *Using grapevine rootstocks: the Australian perspective*, 1st ed. (Winetitles: Adelaide, SA, Australia).
- McKenry, M. (2001) Three new grape rootstocks with broad nematode resistance. *FPMS Grape Program Newsletter* **7** (Foundation Plant Material Services: Davis, CA, USA).
- McKenry, M.V. and Bettiga, L.J. (2013) *Nematodes*. Bettiga, L.J., ed. *Grape pest management* (University of California: Berkeley, CA, USA) pp. 449–470.
- Medrano, H., Tomás, M., Martorell, S., Escalona, J.-M., Pou, A., Fuentes, S., Flexas, J. and Bota, J. (2015) Improving water use efficiency of vineyards in semi-arid regions. A review. *Agronomy for Sustainable Development* **35**, 499–517.
- Meggio, F., Prinsi, B., Negri, A.S., Simone Di Lorenzo, G., Lucchini, G., Pitacco, A., Failla, O., Scienza, A., Cocucci, M. and Espen, L. (2014) Biochemical and physiological responses of two grapevine rootstock genotypes to drought and salt treatments. *Australian Journal of Grape and Wine Research* **20**, 310–323.
- Merli, M.C., Magnanini, E., Gatti, M., Pirez, F.J., Buesa Pueyo, I., Intrigliolo, D.S. and Poni, S. (2016) Water stress improves whole-canopy water use efficiency and berry composition of cv. Sangiovese (*Vitis vinifera* L.) grapevines grafted on the new drought-tolerant rootstock M4. *Agricultural Water Management* **169**, 106–114.

- Miele, A. and Rizzon, L.A. (2017) Rootstock-scion interaction 2: effect on the composition of Cabernet Sauvignon grape must. *Revista Brasileira de Fruticultura* **39**, e-434.
- Mira de Orduña, R. (2010) Climate change associated effects on grape and wine quality and production. *Food Research International* **43**, 1844–1855.
- Moens, M., Perry, R.N. and Starr, J.L. (2009) Meloidogyne species—a diverse group of novel and important plant parasites. Perry, R.N., Moens, M. and Starr, J.L., eds. *Root-knot nematodes* (Centre for Agricultural Bioscience International: Wallingford, England) pp. 1–17.
- Morinaga, K., Imai, S., Yakushiji, H. and Koshita, Y. (2003) Effects of fruit load on partitioning of 15N and 13C, respiration, and growth of grapevine roots at different fruit stages. *Scientia Horticulturae* **97**, 239–253.
- Morris, J.R., Main, G.L. and Striegler, R.K. (2007) Rootstock and training system affect 'Sunbelt' grape productivity and fruit composition. *Journal of the American Pomological Society* **61**, 71–77.
- Mudge, K., Janick, J., Scofield, S. and Goldschmidt, E.E. (2009) A history of grafting. Janick, J., ed. *Horticultural reviews* (John Wiley: Hoboken, NJ, USA) pp. 437–493.
- Mullins, M.G., Bouquet, A. and Williams, L.E. (1992) *Biology of the grapevine* (Cambridge University Press: Cambridge, England).
- Munns, R. and Tester, M. (2008) Mechanisms of salinity tolerance. *Annual Review of Plant Biology* **59**, 651–681.
- Neethling, E., Petitjean, T., Quéno, H. and Barbeau, G. (2017) Assessing local climate vulnerability and winegrowers' adaptive processes in the context of climate change. *Mitigation and Adaptation Strategies for Global Change* **22**, 777–803.
- Németh, G., Molnár, Z., Podmaniczky, P., Sárdy, D.N., Kállay, M., Dunai, A. and Kocsis, L. (2017) Trans-resveratrol content in grape cane and root of different scion-rootstock combinations. *Mitteilungen Klosterneuburg* **67**, 256–264.
- Nicol, J.M., Stirling, G.R., Rose, B.J., May, P. and Heeswijck, R.V. (1999) Impact of nematodes on grapevine growth and productivity: current knowledge and future directions, with special reference to Australian viticulture. *Australian Journal of Grape and Wine Research* **5**, 109–127.
- Ollat, N., Esmenjaud, D., Demangeat, G., Lemaire, O. and Van Helden, M. (2011) Un porte-greffe pour lutter contre le court-noué: le Némadex Alain Bouquet, du nom de son créateur, retarde la contamination des vignes. *Phytoma* **649**, 29–33.
- Ollat, N., Peccoux, A., Papura, D., Esmenjaud, D., Marguerit, E., Tandonnet, J.-P., Bordenave, L., Cookson, S.J., Barrieu, F., Rossedeutsch, L., Lecourt, J., Lauvergeat, V., Vivin, P., Bert, P.-F. and Delrot, S. (2016) Rootstocks as a component of adaptation to environment. Gerós, H., Chaves, M.M., Gil, H.M. and Delrot, S., eds. *Grapevine in a changing environment* (John Wiley: Chichester, England) pp. 68–108.
- Ozden, M., Vardin, H., Simsek, M. and Karaaslan, M. (2010) Effects of rootstocks and irrigation levels on grape quality of *Vitis vinifera* L. cv. Shiraz. *African Journal of Biotechnology* **9**, 3801–3807.
- Padgett-Johnson, M., Williams, L.E. and Walker, M.A. (2000) The influence of *Vitis riparia* rootstock on water relations and gas exchange of *Vitis vinifera* cv. Carignane scion under non-irrigated conditions. *American Journal of Enology and Viticulture* **51**, 137–143.
- Padgett-Johnson, M., Williams, L.E. and Walker, M.A. (2003) Vine water relations, gas exchange, and vegetative growth of seventeen *Vitis* species grown under irrigated and nonirrigated conditions in California. *Journal of the American Society for Horticultural Science* **128**, 269–276.
- Peccoux, A., Loveys, B., Zhu, J., Gambetta, G.A., Delrot, S., Vivin, P., Schultz, H.R., Ollat, N. and Dai, Z. (2018) Dissecting the rootstock control of scion transpiration using model-assisted analyses in grapevine. *Tree Physiology* **38**, 1026–1040.
- Phogat, V., Cox, J.W. and Šimunek, J. (2018) Identifying the future water and salinity risks to irrigated viticulture in the Murray-Darling Basin, South Australia. *Agricultural Water Management* **201**, 107–117.
- Pl@ntGrape (2020) Catalogue of vines cultivated in France, IFV—INRAE—l'Institut Agro, Montpellier SupAgro, 2009–2020. <http://plantgrape.plantnet-project.org/en/>
- Porro, D., Pedò, S., Bertoldi, D., Bortolotti, L., Failla, O. and Zamboni, M. (2013) Evaluation of new rootstocks for grapevine: nutritional aspects. *Acta Horticulturae* **984**, 109–115.
- Pouzoulet, J., Scudiero, E., Schiavon, M. and Rolshausen, P.E. (2017) Xylem vessel diameter affects the compartmentalization of the vascular pathogen *Phaeoemoniella chlamydospora* in grapevine. *Frontiers in Plant Science* **8**, 1442.
- Powell, K.S., Cooper, P.D. and Forneck, A. (2013) The biology, physiology and host-plant interactions of grape phylloxera *Daktulosphaira vitifoliae*. Johnson, S.N., Hiltbold, I. and Turlings, T. D.J., eds. *Advances in insect physiology*, Vol. 45 (Elsevier: London, England) pp. 159–218.
- Prinsi, B., Failla, O., Scienza, A. and Espen, L. (2020) Root proteomic analysis of two grapevine rootstock genotypes showing different susceptibility to salt stress. *International Journal of Molecular Sciences* **21**, 1076.
- Pulko, B., Vrščič, S. and Valdhuber, J. (2012) Influence of various rootstocks on the yield and grape composition of Sauvignon Blanc. *Czech Journal of Food Sciences* **30**, 467–473.
- Raski, D.J., Hewitt, W.B., Goheen, C.E., Taylor, C.E. and Taylor, R. H. (1965) Survival of *Xiphinema index* and reservoirs of fanleaf virus in fallowed vineyard soil. *Nematologica* **11**, 349–352.
- Reisch, B., Owens, C. and Cousins, P. (2012) *Grape*. Badesbees, M.L. and Byrne, D., eds. *Fruit breeding* (Springer: New York, NY, USA) pp. 225–262.
- Renouf, V., Tregouat, O., Roby, J.P. and Van Leeuwen, C. (2010) Soils, rootstocks and grapevine varieties in prestigious Bordeaux vineyards and their impact on yield and quality. *Journal International des Sciences de la Vigne et du Vin* **44**, 127–134.
- Riaz, S., Pap, D., Uretsky, J., Laucou, V., Boursiquot, J.-M., Kocsis, L. and Walker, M.A. (2019) Genetic diversity and parentage analysis of grape rootstocks. *Theoretical and Applied Genetics* **132**, 1847–1860.
- Ribéreau-Gayon, P., Dubourdieu, D. and Donèche, B. (2006) *Handbook of enology*. Volume I. The microbiology of wine and vinifications, 2d edn (John Wiley: Chichester, England).
- Rolshausen, P.E., Greve, L.C., Labavitch, J.M., Mahoney, N.E., Molyneux, R.J. and Gubler, W.D. (2008) Pathogenesis of *Eutypa lata* in grapevine: identification of virulence factors and biochemical characterization of cordon dieback. *Phytopathology* **98**, 222–229.
- Romero, P., Botía, P. and Navarro, J.M. (2018) Selecting rootstocks to improve vine performance and vineyard sustainability in deficit irrigated Monastrell grapevines under semiarid conditions. *Agricultural Water Management* **209**, 73–93.
- Romero, P., Dodd, I.C. and Martínez-Cutillas, A. (2012) Contrasting physiological effects of partial root zone drying in field-grown grapevine (*Vitis vinifera* L. cv. Monastrell) according to total soil water availability. *Journal of Experimental Botany* **63**, 4071–4083.
- Rossedeutsch, L., Edwards, E., Cookson, S.J., Barrieu, F., Gambetta, G.A., Delrot, S. and Ollat, N. (2016) ABA-mediated responses to water deficit separate grapevine genotypes by their genetic background. *BMC Plant Biology* **16**, 91.
- Rubio, B., Lalanne-Tisné, G., Voisin, R., Tandonnet, J.-P., Portier, U., Van Ghelder, C., Lafargue, M., Petit, J.-P., Donnart, M., Joubard, B., Bert, P.-F., Papura, D., Le Cunff, L., Ollat, N. and Esmenjaud, D. (2020) Characterization of genetic determinants of the resistance to phylloxera, *Daktulosphaira vitifoliae*, and the dagger nematode *Xiphinema index* from muscadine background. *BMC Plant Biology* **20**, 213.
- Rühl, E.H. (1989) Uptake and distribution of potassium by grapevine rootstocks and its implication for grape juice pH of scion varieties. *Australian Journal of Experimental Agriculture* **29**, 707–712.
- Rühl, E.H. (1996) 'Borner' rootstock grape. US Patent: Plant 9575.
- Rühl, E.H. (2000) Effect of rootstocks and K+ supply on pH and acidity of grape juice. *Acta Horticulturae* **512**, 31–37.
- Sabir, A. and Sahin, Z. (2018) The response of soilless grown 'Michele Palieri' (*Vitis vinifera* L.) grapevine cultivar to deficit irrigation under the effects of different rootstocks. *Erwerbs-obstbau* **60**, S21–S27.
- Santos, J.A., Fraga, H., Malheiro, A.C., Moutinho-Pereira, J., Dinis, L.-T., Correia, C., Moriondo, M., Leolini, L., Dibari, C., Costafreda-Aumedes, S., Kartschall, T., Menz, C., Molitor, D., Junk, J., Beyer, M. and Schultz, H.R. (2020) A review of the potential climate change impacts and adaptation options for European viticulture. *Applied Sciences* **10**, 3092.
- Saucet, S.B., Van Ghelder, C., Abad, P., Duval, H. and Esmenjaud, D. (2016) Resistance to root-knot nematodes *Meloidogyne* spp. in woody plants. *New Phytologist* **211**, 41–56.
- Schreiner, R.P. (2005) Spatial and temporal variation of roots, arbuscular mycorrhizal fungi, and plant and soil nutrients in a mature Pinot Noir (*Vitis vinifera* L.) vineyard in Oregon, USA. *Plant and Soil* **276**, 219–234.



- Schultz, H. and Stoll, M. (2010) Some critical issues in environmental physiology of grapevines: future challenges and current limitations. *Australian Journal of Grape and Wine Research* **16**, 4–24.
- Serra, L., Strever, A., Myburgh, P.A. and Deloire, A. (2014) Review: the interaction between rootstocks and cultivars (*Vitis vinifera* L.) to enhance drought tolerance in grapevine. *Australian Journal of Grape and Wine Research* **20**, 1–14.
- Shaffer, R., Sampaio, T.L., Pinkerton, J. and Vasconcelos, M.C. (2004) Grapevine rootstock for Oregon vineyards (Oregon State University, Oregon State University Extension Service: Corvallis, OR, USA).
- Smart, D.R., Schwass, E., Lakso, A. and Morano, L. (2006) Grapevine rooting patterns: a comprehensive analysis and a review. *American Journal of Enology and Viticulture* **57**, 89–104.
- Smith, B.P., Wheal, M.S., Jones, T.H., Morales, N.B. and Clingeleffer, P.R. (2013) Heritability of adventitious rooting of grapevine dormant canes. *Tree Genetics and Genomes* **9**, 467–474.
- Smith, H.M., Smith, B.P., Morales, N.B., Moskwa, S., Clingeleffer, P.R. and Thomas, M.R. (2018b) SNP markers tightly linked to root knot nematode resistance in grapevine (*Vitis cinerea*) identified by a genotyping-by-sequencing approach followed by Sequenom MassARRAY validation. *PLoS One* **13**, e0193121.
- Smith, H.M., Clarke, C.W., Smith, B.P., Carmody, B.M., Thomas, M.R., Clingeleffer, P.R. and Powell, K.S. (2018a) Genetic identification of SNP markers linked to a new grape phylloxera resistant locus in *Vitis cinerea* for marker-assisted selection. *BMC Plant Biology* **18**, 360.
- Soar, C.J., Dry, P.R. and Loveys, B.R. (2006) Scion photosynthesis and leaf gas exchange in *Vitis vinifera* L. cv. Shiraz: mediation of rootstock effects via xylem sap ABA. *Australian Journal of Grape and Wine Research* **12**, 82–96.
- Staudt, G. and Weischer, B. (1992) Resistance to transmission of grapevine fanleaf virus by *Xiphinema index* in *Vitis rotundifolia* and *Vitis munsoniana*. *Viticultural and Enological Sciences* **47**, 56–61.
- Stevens, R.M., Pech, J.M., Gibberd, M.R., Walker, R.R. and Nicholas, P.R. (2010) Reduced irrigation and rootstock effects on vegetative growth, yield and its components, and leaf physiological responses of Shiraz: reduced irrigation and rootstock effects on Shiraz. *Australian Journal of Grape and Wine Research* **16**, 413–425.
- Stevens, R.M., Pech, J.M., Taylor, J., Clingeleffer, P.R., Walker, R.R. and Nicholas, P.R. (2016) Effects of irrigation and rootstock on *Vitis vinifera* (L.) cv. Shiraz berry composition and shrivel, and wine composition and wine score: irrigation and rootstock effects on Shiraz quality. *Australian Journal of Grape and Wine Research* **22**, 124–136.
- Stevens, R.M., Pech, J.M., Gibberd, M.R., Walker, R.R., Jones, J.A., Taylor, J. and Nicholas, P.R. (2008) Effect of reduced irrigation on growth, yield, ripening rates and water relations of Chardonnay vines grafted to five rootstocks. *Australian Journal of Grape and Wine Research* **14**, 177–189.
- Tandonnet, J.-P., Marguerit, E., Cookson, S.J. and Ollat, N. (2018) Genetic architecture of aerial and root traits in field-grown grafted grapevines is largely independent. *Theoretical and Applied Genetics* **131**, 903–915.
- Tegli, S., Santilli, E., Bertelli, E. and Surico, G. (2000) Genetic variation within *Phaeoacremonium aleophilum* and *P. chlamydosporum* in Italy. *Phytopathologia Mediterranea* **39**, 125–133.
- Teixeira, A., Eiras-Dias, J., Castellarin, S.D. and Gerós, H. (2013) Berry phenolics of grapevine under challenging environments. *International Journal of Molecular Sciences* **14**, 18711–18739.
- Teliz, D., Landa, B., Rapoport, H., Pérez Camacho, F., Jiménez-Díaz, R. and Castillo, P. (2007) Plant-parasitic nematodes infecting grapevine in southern Spain and susceptible reaction to root-knot nematodes of rootstocks reported as moderately resistant. *Plant Disease* **91**, 1147–1154.
- Tergeo (2015) I nuovi portinnesti M. *Il Corriere Vinicolo* **31**, 17.
- Teubes, A. (2014) History of rootstocks in South Africa (part 5). *Wineland Magazine*. <https://www.wineland.co.za/history-of-rootstocks-in-south-africa-part-5/>
- Tramontini, S., Vitali, M., Centioni, L., Schubert, A. and Lovisolò, C. (2013) Rootstock control of scion response to water stress in grapevine. *Environmental and Experimental Botany* **93**, 20–26.
- van Leeuwen, C. and Darriet, P. (2016) The impact of climate change on viticulture and wine quality. *Journal of Wine Economics* **11**, 150–167.
- van Leeuwen, C. and Destrac-Irvine, A. (2017) Modified grape composition under climate change conditions requires adaptations in the vineyard. *OENO One* **51**, 147–154.
- van Leeuwen, C., Destrac-Irvine, A., Dubernet, M., Duchêne, E., Gowdy, M., Marguerit, E., Pieri, P., Parker, A., de Rességuier, L. and Ollat, N. (2019) An update on the impact of climate change in viticulture and potential adaptations. *Agronomy* **9**, 514.
- Van Zyl, J.L. (1984) Response of Colombar grapevines to irrigation as regards quality aspects and growth. *South African Journal of Enology and Viticulture* **5**, 19–28.
- Vigne, E., Komar, V. and Fuchs, M. (2004) Field safety assessment of recombination in transgenic grapevines expressing the coat protein gene of grapevine fanleaf virus. *Transgenic Research* **13**, 165–179.
- Villate, L., Morin, E., Demangeat, G., Helden, M. and Esmenjaud, D. (2012) Control of *Xiphinema index* populations by fallow plants under greenhouse and field conditions. *Phytopathology* **102**, 627–634.
- Volder, A., Smart, D., Bloom, A. and Eissenstat, D. (2005) Rapid decline in nitrate uptake and respiration with age in fine lateral roots of grape: implications for root efficiency and competitive effectiveness. *The New Phytologist* **165**, 493–501.
- Walker, R.R. and Clingeleffer, P.R. (2009) Rootstock attributes and selection for Australian conditions. *Australian Viticulture* **13**, 70–76.
- Walker, R.R., Blackmore, D.H. and Clingeleffer, P.R. (2010) Impact of rootstock on yield and ion concentrations in petioles, juice and wine of Shiraz and Chardonnay in different viticultural environments with different irrigation water salinity. *Australian Journal of Grape and Wine Research* **16**, 243–257.
- Walker, R.R., Blackmore, D.H., Clingeleffer, P.R. and Correll, R.L. (2002) Rootstock effects on salt tolerance of irrigated field-grown grapevines (*Vitis vinifera* L. cv. Sultana). 1. Yield and vigour inter-relationships. *Australian Journal of Grape and Wine Research* **8**, 3–14.
- Walker, R.R., Blackmore, D.H., Clingeleffer, P.R. and Emanuelli, D. (2014) Rootstock type determines tolerance of Chardonnay and Shiraz to long-term saline irrigation: grapevine response to long-term salinity. *Australian Journal of Grape and Wine Research* **20**, 496–506.
- Walker, R.R., Blackmore, D.H., Clingeleffer, P.R. and Iacono, F. (1997) Effect of salinity and Ramsey rootstock on ion concentrations and carbon dioxide assimilation in leaves of drip-irrigated, field-grown grapevines (*Vitis vinifera* L. cv. Sultana). *Australian Journal of Grape and Wine Research* **3**, 66–74.
- Walker, R.R., Blackmore, D.H., Clingeleffer, P.R., Holt, H., Pearson, W. and Francis, I.L. (2019) Effect of rootstock on yield, grape composition and wine sensory attributes of Shiraz grown in a moderately saline environment. *Australian Journal of Grape and Wine Research* **25**, 414–429.
- Walker, R.R., Blackmore, D.H., Gong, H., Henderson, S.W., Gilliam, M. and Walker, A.R. (2018) Analysis of the salt exclusion phenotype in rooted leaves of grapevine (*Vitis* spp.): salt exclusion in rooted leaves of grapevine. *Australian Journal of Grape and Wine Research* **24**, 317–326.
- Wallis, C.M., Wallingford, A.K. and Chen, J. (2013) Grapevine rootstock effects on scion sap phenolic levels, resistance to *Xylella fastidiosa* infection, and progression of Pierce's disease. *Frontiers in Plant Science* **4**, 502.
- Warschafsky, E.J., Klein, L.L., Frank, M.H., Chitwood, D.H., Londo, J.P., von Wettberg, E.J.B. and Miller, A.J. (2016) Rootstocks: diversity, domestication, and impacts on shoot phenotypes. *Trends in Plant Science* **21**, 418–437.
- Webster, A.D., Malling, W. and Me, K. (2001) Rootstocks for temperate fruit crops: current uses, future potential and alternative strategies. *Acta Horticulturae* **557**, 25–34.
- Wheeler, S.F. (2006) The role of abscisic acid in grape berry development. PhD Thesis, School of Agriculture and Wine Discipline of Horticulture, Viticulture and Oenology in collaboration with CSIRO Plant Industry Horticulture Unit, The University of Adelaide, Adelaide, SA, Australia. <https://digital.library.adelaide.edu.au/dspace/bitstream/2440/57767/8/02whole.pdf>
- Williams, L.E. (2010) Interaction of rootstock and applied water amounts at various fractions of estimated evapotranspiration (ETc) on productivity of Cabernet Sauvignon: effects of rootstock and water amounts on yield. *Australian Journal of Grape and Wine Research* **16**, 434–444.
- Wooldridge, J., Louw, P.J.E. and Conradie, W.J. (2010) Effects of rootstock on grapevine performance, petiole and must composition,

- and overall wine score of *Vitis vinifera* cv. Chardonnay and Pinot noir. *South African Journal of Enology and Viticulture* **31**, 45–48.
- Wyss, U. (2014) *Xiphinema index*, maintenance and feeding in monoxenic cultures. Maramorosch, K. and Mahmood, F., eds. *Rearing animal and plant pathogen vectors* (CRC Press: Boca Raton, FL, USA) pp. 235–267.
- Xu, K., Riaz, S., Roncoroni, N., Jin, Y., Hu, R., Zhou, R. and Walker, M.A. (2008) Genetic and QTL analysis of resistance to *Xiphinema index* in a grapevine cross. *Theoretical and Applied Genetics* **116**, 305–311.
- Yang, Y., Jittayasothorn, Y., Chronis, D., Wang, X., Cousins, P. and Zhong, G.-Y. (2013) Molecular characteristics and efficacy of 16D10 siRNAs in inhibiting root-knot nematode infection in transgenic grape hairy roots. *PLoS One* **8**, e69463.
- Yin, L., Clark, M.D., Burkness, E.C. and Hutchison, W.D. (2019) Grape phylloxera (Hemiptera: Phylloxeridae), on cold-hardy hybrid wine grapes (*Vitis* spp.): a review of pest biology, damage, and management practices. *Journal of Integrated Pest Management* **10**, 1–9.
- Yıldırım, K., Yağcı, A., Sucu, S. and Tunç, S. (2018) Responses of grapevine rootstocks to drought through altered root system architecture and root transcriptomic regulations. *Plant Physiology and Biochemistry* **127**, 256–268.
- Zhang, J., Hausmann, L., Eibach, R., Welter, L.J., Töpfer, R. and Zyprian, E.M. (2009) A framework map from grapevine V3125 (*Vitis vinifera* ‘Schiava grossa’ × ‘Riesling’) × rootstock cultivar ‘Börner’ (*Vitis riparia* × *Vitis cinerea*) to localize genetic determinants of phylloxera root resistance. *Theoretical and Applied Genetics* **119**, 1039–1051.
- Zhang, L., Marguerit, E., Rossdeutsch, L., Ollat, N. and Gambetta, G. A. (2016) The influence of grapevine rootstocks on scion growth and drought resistance. *Theoretical and Experimental Plant Physiology* **28**, 143–157.
- Zhang, X., Walker, R.R., Stevens, R.M. and Prior, L.D. (2002) Yield-salinity relationships of different grapevine (*Vitis vinifera* L.) scion-rootstock combinations. *Australian Journal of Grape and Wine Research* **8**, 150–156.
- Zhou, Y., Minio, A., Massonnet, M., Solares, E., Lv, Y., Beridze, T., Cantu, D. and Gaut, B.S. (2019) The population genetics of structural variants in grapevine domestication. *Nature Plants* **5**, 965–979.
- Zohary, D. and Spiegel-Roy, P. (1975) Beginnings of fruit growing in the Old World. *Science* **187**, 319–327.
- Zou, C., Karn, A., Reisch, B., Nguyen, A., Sun, Y., Bao, Y., Campbell, M.S., Church, D., Williams, S., Xu, X., Ledbetter, C.A., Patel, S., Fennell, A., Glaubitz, J.C., Clark, M., Ware, D., Londo, J.P., Sun, Q. and Cadle-Davidson, L. (2020) Haplotyping the *Vitis* collinear core genome with rhAmpSeq improves marker transferability in a diverse genus. *Nature Communications* **11**, 413.

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