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SPECIAL ISSUE

From soil to canopy: the diversity of adaptation strategies to drought in grapevine

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ABSTRACT

One of the main consequences of climate change is the increase in frequency and severity of abiotic stresses, which mostly occur in combination. Grapevine, which grows under a wide variety of pedo-climatic conditions, has acquired different adaptive mechanisms during its evolution. Harnessing the genetic diversity of these mechanisms is key to the future adaptation of viticulture to climate change in many traditional wine growing areas. The interactions between scion and rootstock through grafting represent an additional level of diversity and adaptive potential to be explored.

At the physiological level, these mechanisms are related to processes such as root system development and function (water and nutrient uptake, transport and storage), gas exchange regulation, hydraulic properties along the soil-plant-atmosphere continuum, reserve storage, short- and long-distance signalling mechanisms and plasticity. At the molecular level, hormonal, osmotic and oxidative metabolisms are involved. Interactions with microorganisms also contribute to the adaptive potential of the plant. As a whole, adaptation to any constraint appears to be the result of the complex interactions of these processes.

Based on a literature review of studies on grapevine and other plants, and on investigations performed in our own laboratory, the present overview explores the diversity of adaptive responses to drought, how these responses characterise different adaptation strategies, and how these strategies can be leveraged for the selection of new genotypes for the future growing conditions.

KEYWORDS: grapevine, *Vitis* spp., hydraulic traits, microbiome, roots, stress memory, Open GPB 2024

INTRODUCTION

Climate change has now become a reality and is affecting all aspects of life on Earth (IPCC, 2023). Its impact on agriculture is of particular concern, as humans rely on it for food production and it is also critical for the sustainability of many regions worldwide (Smith *et al.,* 2014). While climate changes (such as increasing temperature, higher risks of drought, extreme events and combinations of deleterious environmental conditions) and their uncertainties have been predicted at the world level (IPCC, 2023), their impacts on the agricultural sector, involving complex interactions between biological, socioeconomic and political aspects, are difficult to assess and predict (Ruane & Rosenzweig, 2018). Similar to other crops, the suitability of growing wine grapes may evolve significantly across different regions. Given that the profitability of viticulture relies majorly on the link between the quality of wines and the pedo-climatic conditions of grape growing sites, the socioeconomic impact of climate change could be even higher for wine grapes than for other crops. In their review, van Leeuwen *et al.* (2024) report that most traditional areas of the coastal parts and lowland regions of southern Europe and Southern California may lose their suitability for producing high quality wines with economically sustainable yields. Meanwhile, other regions in the north of Europe and at higher latitudes in North and South America may become more suitable for profitable wine production. Globally, the increases in suitability are mainly related to the rise in average temperature, while the loss of suitability is linked to increased drought risks combined with extreme temperature events. In most traditional winegrowing areas of Europe, grapevines are predominantly grown rain-fed in environments with poor soils, which is considered a highly sustainable way of economical land development. In these locations, poor access to water resources limits the possibility of irrigation, increasing the vulnerability of grapevine to other biotic and abiotic stresses in severe drought. In order to maintain the suitability of these regions for winegrowing, understanding the physiological responses of grapevine to drought and the mechanisms of adaptation/tolerance should be a top priority.

THEORETICAL FRAMEWORKS FOR ADDRESSING DROUGHT ADAPTATION

In response to stress, plants have developed complex processes which support reproduction or survival and are controlled by sophisticated molecular regulatory mechanisms which can be specific or generalist. The response of a plant to a combination of stresses can be unique, and it can be much more complex than a response to a single stress (Ollat *et al.,* 2023; Martínez-Lüscher *et al.,* 2024). Simonneau *et al.* (2017), Gambetta *et al.* (2020) and Gambetta *et al.* (2024) described the diversity of the responses of grapevine to drought depending on the stage, duration and intensity of stress application, thus corroborating the assumption that adaptation can rarely be linked to a single type of process. As stated previously (Ollat *et al.,* 2019; Ollat *et al.,* 2023), the adaptation of a crop such as grapevine can be defined as the ability to maintain an optimal trade-off between yield, berry composition and the longevity of the perennial structures. From a general point of view, adaptation means either a process across generations leading to a new combination of favourable alleles or a status "to be adapted" which corresponds to a given combination of alleles (Cooper & Hammer, 1996). The resulting phenotype is constitutively adapted to, or changes with, environmental pressure. This ability to change is defined as plasticity (Bradshaw, 1965), which does not always result in a more adapted phenotype. Acclimation is defined as the ability of a plant to withstand abiotic and biotic stresses through modifications (Mickelbart *et al.,* 2015). As in other species, there are numerous studies on the identification of genes involved in the responses of grapevine to abiotic stresses through transcriptomic approaches, corroborating the assumption that the mechanisms involved are complex (as reviewed in Delrot *et al.,* 2020; Gomès *et al.,* 2021; Martínez-Lüscher *et al.,* 2024). However, only very few genes identified in grapevine, such as *VaHsfC1* (Jiao *et al.,* 2022), *VvGST40* (Nerva *et al.,* 2022), and *VvEPLF9.1* (Clemens *et al.,* 2022) have been functionally validated (as reported by Ollat *et al.,* 2023), and their effects on whole plant performance in relation to adaptation have not been clearly demonstrated thus far.

To address these different levels of complexity and to apply them to crop improvement, Munns and Miller (2023) suggest that plant responses to abiotic stresses should be analysed in terms of capacities, thus providing a simplified framework for understanding successful adaptation strategies. When considering an abiotic stress as an external force applied to an object (in our case a plant), and not as the response itself, the authors defined a constraint as the effect of the stress on apparent change in volume, shape or length of the object, depending on its capacity to respond; for example, the effect of applying a certain amount of pressure (stress) to a wooden ball by squeezing it in your hand will not be the same as for a rubber ball. Like a wooden ball, adapted plants show little evidence of constraint or perception of stress; however, they adopt a strategy to manage the consequences, such as changing their shape or composition. Conversely, like a rubber ball, non-adapted plants respond directly to the constraint; for example, they may grow very slowly and barely survive in response to the same pressure or stress. By analysing the responses of the plants in terms of capacities, it may be possible to determine which processes need to be targeted in order to limit or overcome the impact of stresses. This may help prioritise traits and underlying genes for efficient plant improvement. Munns and Miller (2023) defined seven capacities which can be divided into three categories (Table 1) and showed how they are relevant to several stress responses.

As reported by Munns and Miller (2023), plants not only respond to drought by dropping leaves and thus decreasing their leaf area (asset management), but they also modify their leaf shape or inclination and their

TABLE 1. Seven plant capacities critical for adaptation to abiotic stress according to Munns and Miller (2023) and grouped according to stress tolerance strategy (first column).

Strategies	Capacities	Description
Change yourself	Asset management	Manage structural assets (leaves and roots) under changed circumstances
	Shape shifting	Shape shift through development to be efficient (organ shape, phenological phase)
Move whatever you can	Supply chain management	Take up resources, and store and supply them to plant parts (carbon, water and minerals)
	Exclusion	Selective ion uptake capacity and compartmentalisation
Use whatever you have	Energy production	Generate energy required for cellular functions (ATP and NAD(P)H)
	Repair	Conduct repairs to maintain plant tissues (polymer replacement, ROS scavenging)
	Communication	Communicate between plant parts at both cellular and long-distance levels

root-to-shoot ratio (shape shifting). While photosynthesis is reduced, affecting growth, carbohydrate pools can still be maintained, thus providing energy for cell division and maintenance (supply chain and energy production). Osmotic adjustment occurs, as does the repair of oxidised macromolecules (supply chain and repair). The regulation of water uptake (together with mineral nutrients) and water losses, and its efficiency in terms of biomass production are also fundamental (supply chain and exclusion). Interactions with soil microorganisms, such as arbuscular mycorrhizal fungi (AMF), contribute to these capacities. Long distance signalling regulates stomatal opening (also regulated at leaf level by short distance signals) and ensures a balance between shoot and root growth (communication), roots and shoots both playing a major role in the adjustment of plant water status (uptake *versus* transpiration). This may involve various strategies of adaptation, such as saving water *versus* increasing the explored volume of soil for water resources.

Moving from a conceptual framework to a real case, Gambetta *et al.* (2020) and Gambetta *et al.* (2024) described the complex responses of grapevine to drought. They highlighted the traits or processes that may be the most relevant for identifying adapted cultivars, taking into consideration the fact that relevant traits or processes can vary depending on the intensity and timing of the water deficit (Figure 1). Under increasing water deficit, the capacity of grapevines to grow and produce fruit (supply chain, asset management and shape shifting) is progressively affected. When water deficit is moderate, the effects on berry quality can be positive, in particular in red cultivars grown to produce red wines. Under severe levels of water deficit, the capacity to control gas exchanges through hydraulic and biochemical signals becomes key (communication, supply chain and asset management). Meanwhile, under extreme drought conditions, there is a risk of mortality (asset management, repair and exclusion). At any level of water availability, above and belowground plant traits will contribute to the responses of the whole plant.

When water availability is unlimited, canopy area, maximal transpiration, stomatal conductance and root system size are the main drivers of water uptake (Lobet *et al.,* 2014; Gambetta *et al.,* 2020). When water becomes scarce, another set of relevant traits is required in order to regulate water losses through stomatal regulation and to maintain water uptake from the soil via appropriate root development and hydraulic architecture. Photosynthetic machinery appears to be very tolerant to mild water deficit, and varieties differ in their strategy to cope with photoinhibition (Medrano *et al.,* 2003; Flexas *et al.,* 2004). The accumulation of different kinds of osmo-protectants, in particular in leaves, allows turgor pressure to be maintained as plant water potential decreases (Gambetta *et al.,* 2020). Finally, when drought becomes severe, the capacity to maintain the hydraulic conductance across the soil-plant-atmosphere continuum appears to be essential. Grapevines are hydraulically segmented and appear to operate most of the time within a 'safe' margin of water potentials (Charrier *et al.,* 2018; Lamarque *et al.,* 2023). Stem cavitation is extremely rare, while basal leaves and petioles are more vulnerable (Schultz, 2003; Tombesi *et al.,* 2014; Gambetta *et al.,* 2020). Basal leaf drop is a prominent symptom of drought in grapevine (Figure 2), and the variations in sensitivity of petiole or leaf conductivity under

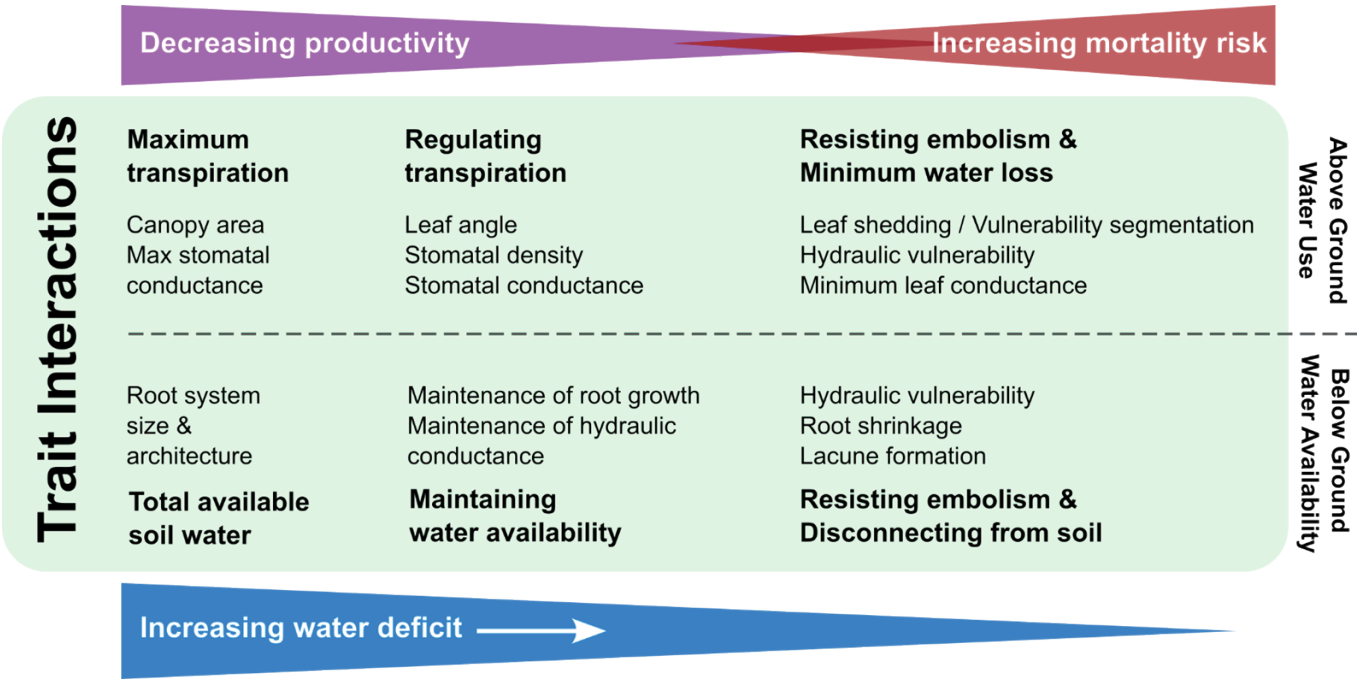


FIGURE 1. Numerous traits involved in the responses of grapevine to increasing intensity of water deficit (Gambetta *et al.,* 2024).



FIGURE 2. Leaf shedding symptoms of Tempranillo vines under drought situation in Cariñena (Spain), © Laure de Rességuier (Bordeaux Sciences Agro).

water stress has been reported to be intraspecific across *Vitis vinifera* (Tombesi *et al.,* 2014; Martorell *et al.,* 2015; Dayer *et al.,* 2020). The perennial features of grapevines and the impacts of pluriannual drought are nevertheless rarely studied (Shtein *et al.,* 2021). Cavitation fatigue (*i.e.*, a decrease in resistance to cavitation after multiple cycles of cavitation and refilling; Hacke *et al.,* 2001; Gambetta *et al.,* 2020) should be considered, as well as season-to-season carry-over effects on bud fertility and stress memory mechanisms. If droughts should occur repeatedly, the resulting effects of a decline in carbon assimilation (lower gas exchange) and storage reserve replenishment – especially in roots – on vineyard lifespan should be investigated.

As a result of their general analysis, Gambetta *et al.* (2020) were able to define drought tolerance as a combination of four traits: maximal transpiration rate (E_{max}), stomatal regulation expressed as the Gs/Ψ_{leaf} curve, turgor loss point (Ψ_{TLP}) and the volume of soil explored by the root system. This combination defines a "grapevine's stress distance" and could quantify (with a unit of time) how long a vine can function without water, under given environmental conditions, before reaching its critical water potential threshold.

Ongoing research aims to identify the most relevant traits and those that are the easiest to characterise, as well as to explore the variability that exists across available genetic resources, the physiological and genetic control mechanisms, and how the performance of ideotypes under future climatic conditions can be simulated. Some examples of this research is described in the following sections.

UNRAVELLING LEAF AND CANOPY HYDRAULIC TRAIT COMBINATIONS THAT CONFER DROUGHT TOLERANCE

Dayer *et al.* (2022) characterised several hydraulic traits (E_{max} and plant stomatal conductance G_{Smax}, stomatal closure Gs90, extent of osmotic adjustment $\Psi_{TLP,}$ leaf vulnerability to embolism (P50 leaf), the hydraulic safety margin (*i.e.*, the difference between stomatal closure and 50 % loss of conductivity (PLC) due to embolism)) across nine genotypes (five *Vitis vinifera* cultivars and four *Vitis* accessions). These authors showed that all nine genotypes closed their stomata before leaf embolism development ($HSM_{P50} > 0$), and that the variability of all the considered traits was greater among *V. vinifera* cultivars than among *Vitis* accessions. Using the soil-plant water transport model SurEau (Cochard *et al.,* 2021) and based on the previously evaluated traits, the time taken for a mature grapevine to reach full leaf conductivity loss without water was calculated. It was shown that Grenache and Vidadillo (a minor Spanish variety) could last up to 150 days, followed by the *Vitis labrusca* accession (125 days). The shortest time (75-80 days) was estimated for *Vitis candicans* and *V. vinifera* cv. Yiannoudi (a Cypriot variety). Using a simulated library comprising more than 50,000 random trait combinations (eight hydraulic traits were considered: Gc_{max}, Gc_{90}, G_{night}, G_{min}, π_0, leaf modulus of elasticity, $P50_{leaf}$ and PLC_{slope}), ideotypes that performed better than Grenache were identified (2.2 % of the simulations), and the 200 best-performing combinations (0.3 %) were called "Elites". These Elite ideotypes were characterised by an average time to reach 100 % PLC of 173 days, linked mainly to lower Gc_{max} and G_{min}, a less negative Gc_{90}, a more negative $P50_{leaf}$, and a larger HSM_{P12}. Elite status was not associated to any specific single trait, confirming that drought tolerance estimated with the "grapevine's stress distance" parameter depends on a trait syndrome (*i.e.*, a combination of traits). When including belowground traits, such as rooting volume, in the modelling approach, it was possible to identify Super Elite ideotypes, which were characterised by an average time of 234 days for 100 % PLC. Finally, when the performance of the current Elite and Super Elite ideotypes were simulated under the most pessimistic future climatic scenario up to the end of the 21st century for six currently existing wines regions (that do not use irrigation), all the genotypes were projected to perform well in Bordeaux and Champagne up to 2070. In these regions, Grenache and Vidadillo are predicted to be unaffected until the end of the century, but to experience some leaf conductivity loss after 2050 in drier and warmer regions. Elites and some Super Elites may suffer only after 2070, especially in very hot and dry regions, such as the Napa Valley and Paso Robles in California. This study shows that, based on drought tolerant trait syndromes that prevent hydraulic failure, significant genetic improvement in terms of drought tolerance can be expected in grapevine, even within intra *V. vinifera* crosses. Other traits not included in this work, such as components related to carbon assimilation and root system characteristics, should also be investigated.

DROUGHT TOLERANCE FROM THE PERSPECTIVE OF SOIL

Despite processes at the soil-root interface being central to the control of plant water status (Javaux *et al.,* 2021), belowground studies are rare, in particular in grapevine. Delval *et al.* (2024) showed that transpiration is controlled by a decrease in belowground hydraulic conductance (*i.e.*, soil and root hydraulics) rather than by xylem cavitation in the trunk. Roots are a key component of plant adaptation to drought, in which a combination of structural and hydraulic properties can act across different time and spatial scales, and which is related to a whole spectrum of previously described capacities (Lynch, 2022; Ollat *et al.,* 2016; Fichtl *et al.,* 2023; Bernardo *et al.,* 2025). According to Bernardo *et al.* (2025), the root system is still considered as the 'dark side' of a perennial plant: its structure and physiology have been little investigated, and identifying the combination of root traits that could maximise drought tolerance remains a significant challenge. Flor *et al.* (2025) have suggested that several rootstock properties related to xylem anatomy, hydraulic segmentation sensitivity, root growth and the control of the minimal conductance of the scion may interact to affect whole grapevine drought tolerance. This multi-level complexity of root systems (structural, architectural and functional, as well as the plasticity of these properties) and their inaccessibility limit our understanding of the most relevant traits associated with drought tolerance. Nevertheless, with modern phenotyping techniques and modelling approaches, advances are being made in the field.

1. Root phenotyping and modelling

Many techniques, with distinct advantages and limitations, are now available for analysing a large set of root traits (de Herralde *et al.,* 2010; Dumont *et al.,* 2016; Archer & Saayman, 2018; Fichtl *et al.,* 2023; Fichtl *et al.,* 2024). These techniques include field-grown grapevines to more controlled systems, such as plants grown in pots of various size and

shapes, rhizotrons and hydroponics, as well as labour-intensive handwritten records to image-based phenotyping tools (Figure 3). Root traits describe the spatial distribution and morphology of both the root system and individual roots. While anatomical and physiological characteristics, as well as the plasticity of traits in response to drought, may be central to drought adaptation (Simonneau *et al.,* 2017), they remain difficult to assess.

As already mentioned, our quantitative understanding of the role of root system architecture (RSA) in the uptake of soil water remains extremely limited, which is mainly due to the inherent complexity of the soil-plant continuum. Quantitative models that couple the hydraulic behaviour of soil and roots in an explicit 3D framework can be used to quantify the contribution of root traits (anatomical and structural) to root water uptake and drought tolerance, thus increasing our understanding of genotype (rootstock × scion) × environment × management interactions and simulate the performances of rootstock ideotypes under various conditions (Fichtl *et al.,* 2024; Bernardo *et al.,* 2025). As shown above for canopy hydraulic traits, modelling supports the identification of the most relevant root traits to be included in breeding programmes. For instance, ArchiSimple (Pagès *et al.,* 2014) is a model that describes the 3D organisation of roots within a soil-based root system. The model is built on simple relationships and parameters that have a significant biological meaning. Most of these relationships describe the links between root elongation, branching and root tip diameters. While ArchiSimple was initially used for annual plants, it has more recently been adapted to studying young grapevine root systems (Larrey *et al.,* 2024). It has been parameterised for several well-known rootstock genotypes (Larrey *et al.,* 2025), as well as the parents of a bi-parental rootstock progeny , and all individuals of the same progeny grown as cuttings (Tandonnet *et al.,* 2021). The model has been used to virtually design root systems with high accuracy (Figure 4). Other generic root models, such as CRootBox/CPlantBox (Schnepf *et al.,* 2018; Zhou *et al.,* 2020; Fichtl *et al.,* 2024), OpenSimRoot (Postma *et al.,* 2017), RootTyp (Pagès *et al.,* 2004) and DigR (Barczi *et al.,* 2018), can also be used to predict the architecture of mature vines based on phenotyping data.

2. Genetic architecture of root developmental traits

The ability to breed new genotypes that have improved characteristics depends on the heritability and genetic architecture of the relevant traits. Given the difficulties associated with phenotyping belowground properties of large populations, very few studies have analysed the genetic architecture of root traits for field grown grapevine. Some studies have assessed the rooting ability of cuttings. Alahakoon and Fennell (2023) phenotyped a *Vitis riparia* × Seyval blanc (complex genetic background) progeny after 35 days of development in perlite: QTLs were identified for several rooting traits with hot spots on the linkage groups (LGs) 1, 9, 13 and 19. In this work, all QTLs explained a percentage of variance below 10 %. Other studies performed on cuttings for different *Vitis* progenies and various phenotyping approaches are in progress (Thapa, 2022; Schmitz, 2023).

Grafting with a scion affects root system development (Tandonnet *et al.,* 2010). Consequently, it is essential to work on grafted plant material to assess the genetic architecture of rootstock traits in real growing conditions. Tandonnet *et al.* (2018) were the first authors to study the genetic architecture of grapevine root system traits in grafted plants grown in field nursery conditions and using a bi-parental progeny of 138 individuals (*V. vinifera* × *V. riparia*; Marguerit *et al.,* 2009). Traits such as root number (total and per class of diameter), root biomass (total and per class of diameter) and root diameter were recorded. Heritability for these traits varied between 0.55 (for root number with a diameter above 4 mm) and 0.70 (for total root number). Significant QTLs were identified on the LGs 1, 5 and 9, some of them explaining approximately 20 % of phenotyping variance.

More recently, Blois *et al.* (2023) studied the genetic architecture of root traits using a Genome Wide Association Study approach on a population of *Vitis berlandieri* of



FIGURE 3. Pictures illustrating various growing systems and phenotyping approaches, from vineyards to greenhouses, used for characterising root traits. Root number and diameter distribution in trench wall (A), root diameter and number after root system excavation (B), root diameter, root elongation, root length and root length in soil tube (C), rhizotron (D), rhizoponics (E) and hydroponics (F).

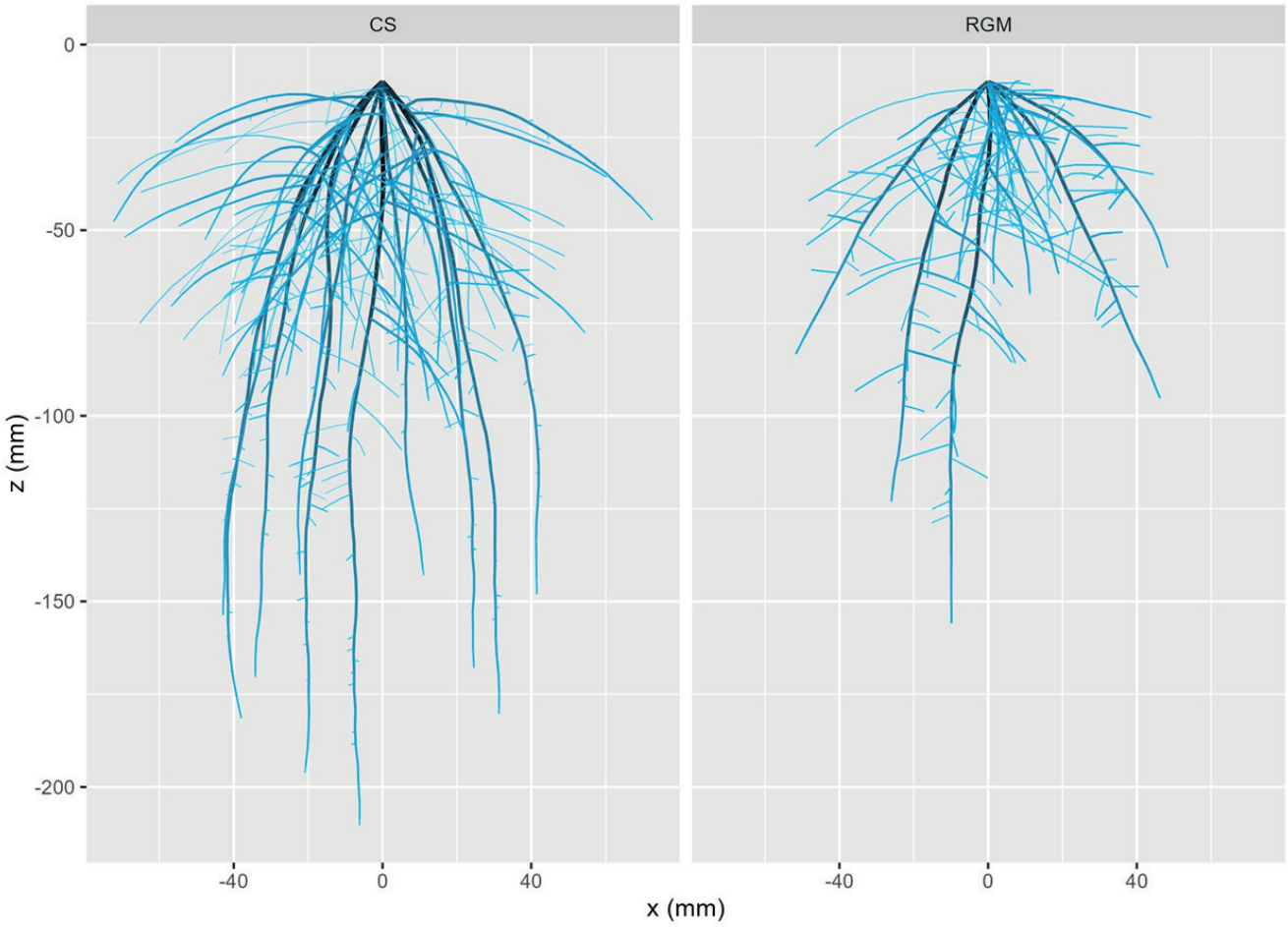


FIGURE 4. 2D vertical projections of 3D root systems simulated with the ArchiSimple model for two CS and RGM cuttings after 60 days. Darker segments indicate larger root diameters. From Larrey *et al.* (2023).

219 individuals. The plants had been grown grafted with the population in the rootstock position for one year in pots. In this study, heritability ranged from 0.44 (percentage of medium diameter root number) to 0.80 (total root number). The most significant associations found in these three studies are summarised in Table 2.

Hence, these studies show that there may be some hotspots in the *Vitis* genome for the control of root development, but systematic meta-analyses of QTLs should be performed to confirm this hypothesis. Interestingly, the genes involved in the control of root development in model species have been identified within the confidence intervals of some of QTLs or linked to relevant SNP markers. Candidate genes regulating root development in grapevine include transcription factors, genes involved in organ development, and genes involved in hormonal (especially auxin) and mineral status regulation (Akalahoon & Fennell, 2023; Blois *et al.,* 2023; Tandonnet *et al.,* 2018). However, none of these genes have been functionally validated for grapevine. Moreover, the low levels of variance explained by associated SNP markers (Table 2), could result from polygenic genetic architecture. Under a polygenic scenario, the use of multi-locus methods (*i.e.*, methods that allow a simultaneous estimation of all-marker effects; Flutre *et al.,* 2022; Vikas *et al.,* 2022) to detect low-effect variants shows promise, and it could provide a more comprehensive knowledge of the genetic architecture of root system development. Ultimately, this knowledge could be useful to develop genomic/phenomic predictions for rootstock breeding (Bernardo *et al.,* 2025).

3. Analyses of root trait syndromes for drought responses and their genetic control

In addition to structural properties, functional traits linked to water use capacity of roots could contribute to drought tolerance; for example, cell hydraulic adjustment, aquaporin regulation, root growth rate, secondary growth, growth maintenance, lacuna formation, cavitation resistance, root turnover and seasonal timing of growth (Bernardo *et al.,* 2025). Plasticity of both structural and hydraulic traits in response to drought is also a key feature for adaptation. Plastic and non-reversible responses include development patterns, vascular anatomy, suberin deposition, formation of cortical lacunae and hydraulic fusing. Elastic and reversible responses are related to osmotic adjustment and aquaporin regulation (Barrios-Masias *et al.,* 2015; Bartlett *et al.,* 2021; Gambetta *et al.,* 2012).

TABLE 2. QTLs identified by Blois *et al.* (2023) based on a Genome Wide Association approach, and QTLS of the same traits identified by Tandonnet *et al.* (2018) and Alahakoon and Fennell (2023). NA means not calculated.

Traits	QTLs (Linkage group number and the position/SRR marker)	% of explained variance	H^2	Reference
Average root diameter	CHR8_3,205,879	1.7	0.47	Blois *et al.* (2023)
	CHR10_24,863,208	25.1		
	CHR17_4,986,873	0.9		
	CHR18_13,881,469	1.8		
	CHR1_1,785,738	5.5	NA	Alahakoon and Fennell (2023)
	CHR9_3,741,936	6.0		
	CHR12_9,587,096	4.1		
	CHR17_5,893,163	6.2		
	CHR18_2,451,088	4.6		
	CHR1_VVC19	17.3	0.64	Tandonnet *et al.* (2018)
	CHR5_VMC16D4	18.9		
Total number of roots	CHR5_19,758,975	0.4	0.82	Blois *et al.* (2023)
	CHR9_VMC3G8	20.7	0.70	Tandonnet *et al.* (2018)
Number of small roots	CHR1_2,250,037	1.4	0.61	Blois *et al.* (2023)
	CHR9_18,214,759	0.6		
	CHR13_8,270,412	1.0		
	CHR17_4,296,526	8.5		
	CHR9_VMC3G8	17.8	0.65	Tandonnet *et al.* (2018)
Number of medium roots	CHR5_19,758,975	4.3	0.79	Blois *et al.* (2023)
	CHR14_21,295,561	6.0		
	CHR2_VVIO55	4.3	0.52	Tandonnet *et al.* (2018)

Diversity panel studies and pangenomic approaches have already demonstrated their potential for identifying key genes that control responses to abiotic factors like salinity (Cochetel *et al.,* 2023). In the case of adaptation to drought, analyses have been carried out to identify genetic variation in the drought response strategies of roots among and within a wide range of *Vitis* species available in European germplasm collections; the ultimate goal was to link genotypes to phenotypes and identify the most relevant traits related to adaptation and their genetic control (de Miguel *et al.,* 2023; Patin *et al.,* 2023). Following the identification of such traits for breeding drought-adapted rootstocks, molecular proxies, or intermediate traits of these complex root traits, can be investigated. Intermediate phenotypes, such as metabolites, are easier to characterise and could be useful for bridging the gap between genotypes and phenotypes (Patin *et al.,* 2024). Molecular proxies are mechanism-related manifestations of complex phenotypes with a potential for high-throughput phenotyping, huge genetic diversity, high heritability and simpler genetic architectures (Christ *et al.,* 2018). Together with the characterisation of the genetic diversity of a broad range of species and accessions using pangenomic approaches, it will be possibly to use the generated knowledge to implement multi-locus GWAS and to calibrate genomic/phenomic prediction models. For this purpose, both cuttings and grafted plants of 50 accessions from 12 *Vitis* species (Figure 5) have been phenotyped under control and water deficit conditions. The morphological, anatomical, functional and molecular (*i.e.*, metabolomic and transcriptomic) traits of roots were evaluated. The preliminary results showed a large among- and within-species variability, in most parameters, including functional traits such as osmotic adjustment in roots. Transcriptomic and un-targeted metabolomic analyses of root tissues confirmed this large variability among accessions within species (Patin *et al.,* 2024). Multivariate correlations between root structural traits and drought responses that have significant heritability have been identified, with promising perspectives for the development of hi rootstock breeding programmes (Patin *et al.,* 2025).

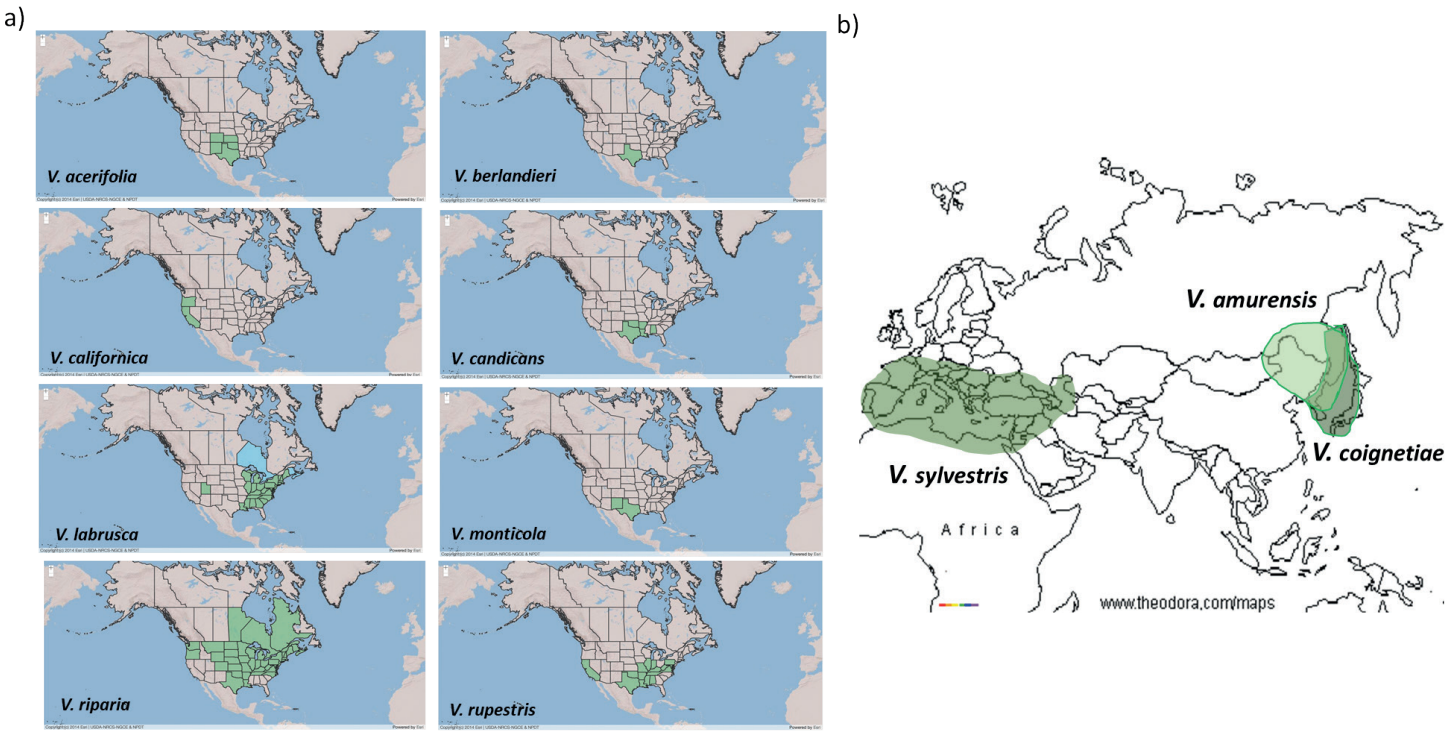


FIGURE 5. Distribution of a wide range of wild *Vitis* spp. phenotyped for root drought responses in Patin *et al.* (2023). a) Current presence per state (coloured in pale blue) of eight out of nine *Vitis* spp. according to USDA Plant database (https://plants.sc.egov.usda.gov/). No data is available for *Vitis* × *doaniana*. b) Approximative distribution of *Vitis sylvestris* based on Petitpierre *et al.* (2023), and *Vitis amurensis* and *Vitis coignetiae* based on Jürges *et al.* (2009).

4. Mineral homeostasis and interactions with microorganisms could contribute to drought adaptation

In addition to root characteristics directly related to water uptake and transport, other processes may contribute to adaptive responses. According to Gambetta *et al.* (2020), little is known about the compounds contributing to osmoregulation in grapevine, but several types of osmolytes, such as amino acids, calcium and potassium, may be involved. Therefore, mineral uptake by the root system and translocation to the aerial parts could be a component of drought responses, depending on "supply chain" capacity. Morel *et al.* (2024) analysed rootstock and scion effects on the mineral composition of the aerial parts of grapevine (petioles) in the GreffAdapt experimental vineyard containing 55 rootstocks combined with five scion varieties (Marguerit *et al.,* 2019). This comprehensive dataset confirmed that rootstock genotype significantly affects the mineral composition of the aerial parts of grapevine, specifically certain nutrients involved in osmoregulation. Scion and interaction effects were also highly significant (Figure 6). As shown for many other adaptive traits, combining two genotypes by grafting increases the complexity of the responses (Tandonnet *et al.,* 2010; Ollat *et al.,* 2024; Bernardo *et al.,* 2025).

The plant-associated microbiome is also known to be involved in tolerance to abiotic stress, especially to drought (Darriaut *et al.,* 2022). Among diverse beneficial microorganisms, arbuscular mycorrhizal fungi (AMF) have been shown to improve grapevine water status and drought stress tolerance (Nicolás *et al.,* 2015; Kozinova *et al.,* 2024). External AMF application appeared to enhance growth, water status and photosynthesis activity more efficiently under reduced irrigation (Torres *et al.,* 2021). Extreme deficit irrigation conditions have also been shown to enhance root colonisation by AMF at any stage across the season, compensating for a lower density of fine roots (Schreiner *et al.,* 2007). Ye *et al.* (2023) reported that AMF colonisation enhances osmotic regulation and oxidative responses, as well as the expression of genes of the abscisic acid biosynthesis pathway and encoding aquaporins in leaves. Rootstocks significantly affect AMF communities recruited by roots (Lailheugue *et al.,* 2024; Noceto *et al.,* 2024), and microbial richness and mycorrhization frequency have been reported to be negatively correlated with the water deficit indicator $\delta^{13}C$ in berry juice (Lailheugue *et al.,* 2024). In addition, differences between two grapevine rootstocks grown under nitrogen deficiency conditions have been identified in terms of their biosynthesis and exudation of strigolactones, compounds known to be involved in the establishment of AMF symbiosis in the rhizosphere (Lailheugue *et al.,* 2023). Strigolactone application on leaves has also been shown to alleviate the drought stress responses of grapevine (Min *et al.,* 2019). It therefore appears to be crucial to determine the factors that regulate the ability of various rootstocks to recruit beneficial microorganisms, and how this affects water uptake. The genetic architecture of such properties also needs to be characterised.

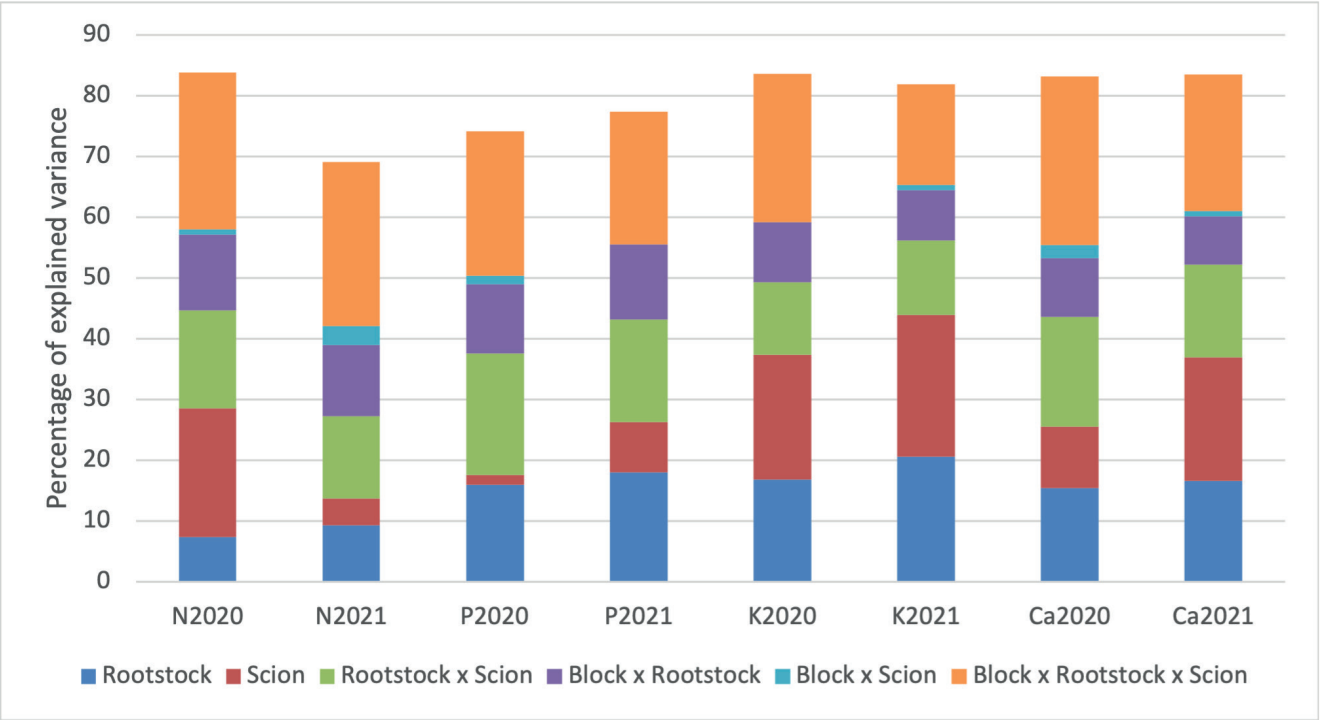


FIGURE 6. Percentage of variance of petiole mineral contents measured in 2020 and 2021 (N = nitrogen, P = phosphorus, K = potassium, Ca = calcium) explained by rootstock, scion and specified interactions. Adapted from Morel *et al.* (2024).

EPIGENETIC REGULATION AND MEMORIES OF DROUGHT RESPONSES

Most adaptive responses are genetically regulated, meaning that breeding new cultivars for both scions and rootstocks is a powerful tool for adaptation to drought in the context of climate change; however, the contribution of epigenetic processes to mitigating the environmental effects must also be considered, especially in the case of a clonally propagated plant such as grapevine (Fortes & Gallusci, 2017; Berger *et al.,* 2023).

Studies on the epigenetic mechanisms involved in grapevine development and stress response have been reviewed by Berger *et al.* (2023) and Venios *et al.* (2024). Among others, epigenetic regulation plays a role in stress memory and in the priming process. Plant priming describes the capacity of plants to modify their responses to biotic and abiotic stresses after initial exposure to mild stress or to eliciting molecules (Gallusci *et al.,* 2023). In grapevine, stress memory has not been clearly demonstrated thus far. Nevertheless, Marfil *et al.* (2019) have observed that a combination of drought and UV-B during one season affects the epigenetic landscape over at least two seasons. In addition, it appears that vegetative progenies of grapevines initially grown in the field with different levels of water availability retain the ability to respond to water deficit depending on the phenotype of their mother plant (Paggay *et al.,* 2022; de Deus *et al.,* 2023). When exposed to a combination of heat and drought, primed plants showed changes in expression of the genes linked to epigenetic modifications, even after stress removal. Transcriptional responses have also been found to be modified the year after the application of the stress, with a general increase in DNA methylation for primed plants; however, the epigenetic control of memory seemed to be preferentially related to post-transcriptional regulation and histone modifications (Tan *et al.,* 2024). First year analyses performed on Cabernet-Sauvignon cuttings showed that priming affects the survival capacities of plants regardless of plant size. There is now an urgent need for studying the consequences of priming on the intensity of stress symptoms across two or more stress cycles at metabolomic, transcriptomic and epigenetic levels.

CONCLUSIONS

This overview explores plant adaptation to drought from soil to atmosphere. Grapevine has been shown to develop many different strategies – especially as a grafted plant – for coping with a threat of future decreasing water availability. Adaptation to even a single stress event depends on many plant-related factors, such as their maximal transpiration and root hydraulic components. Thus, it is critical for scientists and growers to consider the plant as a whole, and across its entire lifespan. Different syndromes of traits could also be better adapted to specific drought scenarios and stress memory should been taken into account. The analysis of agricultural systems using a conceptual framework is highly recommended to help simplify the underlying complexity of responses and adaptive capacities. Modelling is potentially useful as an integrative tool to address this complexity and integrate a wide combination of traits to anticipate responses

to future climatic conditions. Other integrative approaches can be implemented to link genotype to phenotype, taking into account epigenetic regulation and extended genotype, including interactions with microorganisms. Regulation hubs or the groups of processes related to whole plant hydraulicity, which contribute to building up the plant's capacity to produce and survive, should be taken into account when identifying key traits and genes for the breeding of more adapted genotypes of both scions and rootstocks. In addition, it is important to take into account trait plasticity in various water availability conditions that are influenced by soil properties, climatic hazards and growing practices when studying the interactions between genotypes, environment and practices. Together, these approaches could help to provide systemic solutions to drought that leverage both breeding and management practices.

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