



Response and Recovery of Grapevine to Water Deficit: From Genes to Physiology

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Abstract

Grapevine is a crop of global economic importance which is often cultivated in dry Mediterranean climates. In the context of climatic change, periods of drought could increase and become more intense. Growers will face increasing pressure to increase irrigation efficiently and/or adopt new grapevine varieties with increased drought resistance and water use efficiency. Adapting viticulture to these challenges requires an improved understanding of how grapevines behave under drought to enable sustainable

management strategies and develop new varieties and rootstocks. This chapter summarizes our current understanding of the changes in physiology, signaling, metabolism, and gene expression that mediate grapevine's response and adaptation to drought.

11.1 Introduction

Water scarcity, which occurs when demands exceed supplies, threatens crop production in dry growing regions across the globe. Changing climatic conditions could exacerbate this situation, as more intense and prolonged drought events are predicted for many regions (IPCC 2014). Grapevines are a high-value crop in many parts of the world and are commonly grown in Mediterranean-like regions with long, dry summers making them prone to extended periods of drought. Unusually prolonged droughts (even considered mega-droughts) have recently wreaked havoc on grape growers in Australia, California, and Chile (Thrupp et al. 2008; Abare 2008; Garreaud et al. 2017). With warmer winters, regions in the western USA are also dealing with less snowpack accumulation in mountain ranges, which provide surface runoff that supplies irrigation water (Mote et al. 2008). Growers in regions that rely on irrigation have recently faced restricted water allocations as they compete with demands from urban, industrial, and

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conservation sectors. Given that agriculture water use dominates total water use in these regions (i.e., ~80% of the total in some regions), growers will face increasing pressure to use water more efficiently. This requires an improved understanding of grapevine behavior under drought to enable growers to manage deficit irrigation strategies while respecting the vine's stress thresholds.

Wine grapes in many parts of the world are traditionally grown without supplemental irrigation. This tradition still holds in many regions (e.g., France, Spain, Italy), while many other growing regions (and other grape commodities, e.g., table grapes, juice, and raisins) rely on irrigation to improve vine yields and avoid drought-induced vine mortality. Even under conditions where irrigation is applied, growers often deliberately impose a water deficit particularly for premium wine grape production and to facilitate earlier harvests and time to market for table grapes. This is often accomplished using regulated deficit irrigation, where less water is applied than that needed to match the evapotranspiration demands of the vineyard. This results in soil water depletion over time and increased water stress in the vines particularly if the deficit coincides with increased atmospheric demand during the hottest portion of the growing season. Deficit irrigation applied at the right time and right intensity helps to control vegetative growth, reduce humidity, and allow adequate light penetration in the fruiting zone (Keller 2015). Maximizing water use efficiency in vineyards requires adequate understanding of the physiological constraints imposed by water deficits so stress thresholds can be approached without long-lasting detrimental effects that prevent fruit ripening or bud fruitfulness in future growing seasons.

The vast majority (>95%) of water absorbed by grapevine root systems is transported directly to the canopy and lost to the atmosphere via transpiration. Water exits the leaves through the stomata, where it is exchanged for CO₂ needed for photosynthesis. Water that remains within grapevines is used for maintaining cell turgor, building and expanding new cells, translocating

nutrients and sugars, providing evaporative cooling, and facilitating gas exchange (Keller 2015). Under drought, these physiological processes can be largely disrupted, but the timing and degree of these disruptions vary across these processes. Mild stress in grapevines occurs when leaf water potential (Ψ_{leaf}) ranges from approximately -0.8 MPa to -1.1 MPa, while moderate stress is often characterized when Ψ_{leaf} is -1.2 to -1.4 MPa. Severely stress grapevines exhibit Ψ_{leaf} below -1.6 MPa.

11.1.1 Overview of Grapevine Response to Drought: From Mild to Severe Stress

Growth and expansion of tissues are one of the most sensitive indicators of drought-induced water stress in grapevines. Non-stressed vines that are actively growing usually have long tendrils that extend past the shoot tip. Under mild water stress, turgor and relative water content start to decrease in grapevine cells, which results in reduced cell division and expansion. One of the earliest signals of drought stress is reduced shoot tip and tendril growth. At this same time, plants reduce cell wall synthesis and protein production needed to drive cellular metabolism (Hsiao 1973).

As soil water content continues to decrease and water stress increases, abscisic acid (ABA), a plant hormone and key water stress response signal, is produced and combines with turgor loss to initiate stomatal closure under mild-moderate drought stress. This leads to initial reductions in photosynthesis due to substrate limitation (i.e., CO₂). ABA production also impacts other key physiological processes at the molecular level including cellular osmotic adjustment, regulation of aquaporin activity, and antagonizing auxin to inhibit cell loosening/expansion.

As grapevines approach moderate water stress, shoot growth and leaf expansion cease completely (Schultz and Matthews 1988). Decreased canopy size and photosynthetic

capacity lead to less carbon export to sinks and thus depletion of reserves from storage sites in woody organs (Holzapfel et al. 2010). This process is likely associated with altered transport processes in the phloem.

Root growth decreases under water stress due to lost cell turgor and increases penetration resistance of drying soils (Bengough et al. 2011), but the reduction in root growth is generally less severe than that of the canopy (likely associated with higher expansin protein activity and osmotic regulation of root tips; During and Dry 1995), thus leading to higher root:shoot ratios under drought stress. Grapevine root respiration is known to decrease with soil water deficit, and a loss of membrane integrity leads to root dieback under severe drought stress. Both responses are likely associated with lacuna formation in the cortex of grapevine fine roots that also reduces the hydraulic conductivity and precedes root shrinkage and xylem embolism in these organs (Cuneo et al. 2016).

Under moderate to more severe stress shoot tips will dry up and fall off and reduce the apical dominance within the shoot. This response likely induces a hormonal signal down the shoot triggering responses in older leaves on the shoot. Leaves change angle and orient themselves parallel to the sun's rays, thus reducing incident radiation and heat load as evaporative cooling associated with transpiration is lost. Moderate to severe water stress limits photosynthesis via damage to various components integral to light harvesting, electron transport, and carbon fixation by photosynthetic enzymes. Delays in ripening, reduced bud fruitfulness, reduced winter hardiness, and even sudden vine collapse can eventually occur at this stage.

11.2 Regulating Water Use Under Drought

11.2.1 Stomatal Regulation

Leaf gas exchange in vascular plants is facilitated by stomata, tiny pores at the leaf surface each encompassed by a pair of adjacent guard cells. Changes in the turgor of the guard cells allow the

plant to open and close the stomata, regulating the trade-off between carbon uptake and water loss (Buckley and Mott 2002). Stomatal closure initiates during the early stages of drought stress. Plants close the stomata to avoid excessive water loss, and consequently, xylem tensions that could trigger cavitation. The physical mechanism by which g_s and water potential are coordinated is complex and poorly understood because the stomata are responding to a spectrum of factors at any moment, from intercellular signaling to a wide range of environmental factors (Hetherington and Woodward 2003). Stomatal regulation can result directly from hydraulic signals, i.e., changes in the local water status of (or around) the guard cells (Fig. 11.1). These changes in water status can result from osmotic changes within the guard cells themselves, and/or through changes in the water potential gradient resulting from the hydraulic conductance of the pathway. At the same time, biochemical factors (e.g., ABA discussed below) mediate stomatal response to water deficit and can trigger stomatal closure even in the absence of changes in leaf water potential (Christmann et al. 2007).

Hydraulic and chemical signals have been extensively studied, but their relative contribution to stomatal regulation remains under debate. In some species and experimental conditions, one signal may dominate (e.g., Comstock 2002; Ahmadi et al. 2009). Experiments assessing the stomatal response to ABA in basal lineages such as ferns and lycophytes indicated that these plants use only passive hydraulic mechanisms for stomatal regulation (Brodribb and McAdam 2011; McAdam and Brodribb 2012). Further examination of this response was studied by comparing the stomatal responses to vapor pressure deficit (VPD) under a wider group of phylogenetic representative species including ABA-sensitive stomata (angiosperms) and ABA-insensitive stomata (ferns and conifers, Brodribb and McAdam 2011; McAdam et al. 2016a, b). These studies observed that only angiosperms are able to rapidly increase foliar ABA levels during a VPD transition (from low to high levels) to regulate stomatal closure, while minimal changes in foliar ABA levels were

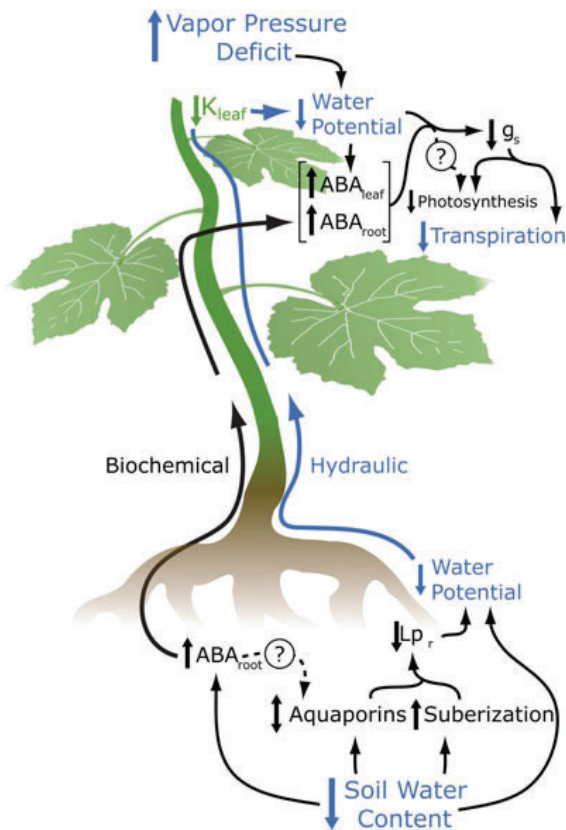


Fig. 11.1 Summary of grapevine whole plant integration under drought. The two pathways modulating stomatal conductance, transpiration, and photosynthesis are biochemical (black) and hydraulic (blue). Biochemical signaling results from the production and sensing of chemical signals (e.g., ABA), either locally in leaves and/or via the long-distance transport from roots to leaves. Hydraulic signals likely originate through the integration of decreases in root ($L_{p,r}$) and leaf (K_{leaf}) hydraulic conductance resulting in decreases in water potential that impact stomatal conductance (g_s)

observed for ferns and conifers (McAdam and Brodribb 2015, 2016). Recent studies in grapevine showed that the hydraulic control was dominant during the early phases of water stress, while chemical signals seemed to have an additive effect involved in the long-term maintenance of stomatal closure under prolonged water stress (Tombesi et al. 2015). Thus, in grapevine an integrated system that includes both types of signals seems to be more likely than a control based on either chemical or hydraulic signaling alone (Fig. 11.1) (Tardieu and Davies 1993; Peccoux et al. 2017).

At a molecular level, many proteins that regulate stomatal responses to the environment have been identified. The ERECTA transcription factor family, putative leucine-rich repeat receptor-like kinases have been related to the perception of water stress signals across the cell membranes in Arabidopsis (Masle et al. 2005). ERECTA coordinates transpiration and photosynthesis, and as such is regarded as a transpiration efficiency gene (Reynolds and Tuberosa 2008). On the other hand, several proteins located in the plasma membrane and tonoplast of guard cells, including channels and carriers, are also known to be involved in the regulation of stomatal movements (Chaves et al. 2011; Costa et al. 2015). For instance, aquaporins (membrane water channels) play an important role in stomatal regulation by facilitating the exchange of water across membranes (Chaumont and Tyerman 2014). Experiments on grapevine showed that the leaf hydraulic conductance decreased by about 30% under water stress concomitantly with a decrease of expression of some aquaporin isoforms (Pou et al. 2013). In that study, positive correlations were observed between stomatal conductance (g_s), leaf hydraulic conductance, and leaf aquaporin expression and activity, suggesting a contribution of aquaporins in regulating vine water use at the leaf level. Similarly, experiments on field-grown Chasselas grapevines growing under different radiation and irrigation regimes revealed that short-term changes in the hydraulic conductivity of the petioles were explained largely by changes in the leaf g_s and the expression of aquaporins (Dayer et al. 2017a).

11.2.2 ABA as a Key Regulator of Stomatal Conductance

ABA is a plant growth regulator involved in various physiological processes that include positive or negative roles depending on the plant conditions. For example, when ABA is at low concentration under non-stressful conditions, it

has been shown to be essential for vegetative growth in several organs (e.g., primary root growth) (Sharp et al. 2000), but when ABA accumulates under drought it reduces growth and inhibits stomatal opening. ABA can be synthesized in all cells and organs, including guard cells, and thus plays an important role in regulating gas exchange via stomatal closure as water stress increases (Munns and Cramer 1996; Boursiac et al. 2013). The 9-*cis*-epoxycarotenoid dioxygenase (NCED) genes catalyze the first step in ABA biosynthesis and represent the rate-limiting step in Arabidopsis and presumably many other plant species (Endo et al. 2008). In *V. vinifera*, the *VviNCED1* and *VviNCED2* genes are linked to ABA synthesis and were shown to be up-regulated during water deficit (Speirs et al. 2013; Rossdeutsch et al. 2016). The expression of other genes in the NCED family (*VviNCED3*, *VviNCED5*, and *VviNCED6*) varies across three different genotypes of *Vitis*; although the relative contributions of these different isogenes in the control of ABA biosynthesis, it is not entirely clear (Hopper et al. 2016).

Under water deficit roots and shoots synthesize ABA and there have been conflicting views on the relative contribution of root and leaf derived ABA in stomatal regulation (Davies and Zhang 1991; Tardieu and Simonneau 1998; Dodd 2005). ABA content in roots is well correlated with both soil moisture and root-relative water content in many plant species. At the molecular level, Speirs et al. (2013) reported that the expression of the ABA biosynthesis genes *VviNCED1* and *VviNCED2* were activated in roots, but not in leaves, in response to water deficit, suggesting that roots could link stomatal response to soil moisture status. On the other hand, leaf cells are known to synthesize ABA (Cutler and Krochko 1999) when their water status is affected by local environmental conditions such as high VPD so one would expect that the same would be true for changes in water status brought about by soil water deficits (via hydraulic signals). In fact, there is an increasing number of studies that suggest leaf derived ABA is the dominant regulator of stomata. Reciprocal

grafting studies in tomato showed that changes in apoplastic ABA levels in leaves were responsible for stomatal closure, and that ABA production by roots was not required to trigger the response (Holbrook et al. 2002). In Arabidopsis, Christmann et al. (2007) demonstrated that changes in turgor pressure of leaf mesophyll cells occurred within minutes of root-induced osmotic stress and elicited activation of ABA biosynthesis in shoots, putatively signaling stomatal closure. In grapevine, the source of xylem sap ABA was suggested to originate from the leaf rather than the roots due to the abundance of leaf ABA and the increased expression of *VviNCED1* and another ABA biosynthetic gene *VviZEP* in the leaves during the day (Soar et al. 2006). Interestingly, shoot derived ABA likely influences root physiology as well. In angiosperms, ABA levels in the roots, as well as root growth, were influenced by ABA synthesized in the leaves rather than sourced from the roots (McAdam et al. 2016a). Although the importance and role of root-sourced ABA are still controversial some of the conflicting observations may be due to differences in the intensity and speed of the development of water deficit under experimental conditions.

ABA biosynthesis and its subsequent regulation of stomata are complex. In Arabidopsis, the ABA biosynthesis core signal network involves at least 138 proteins and over 500 interactions (Lumba et al. 2014). In the absence of ABA, the central ABA signaling 2C protein phosphatases (PP2C) inhibit the activity of serine/threonine protein kinases (SnRKs) and downstream ABA signaling (Fig. 11.2). When ABA is present, the PYR/PYL/RCAR protein family of ABA receptors (Ma et al. 2009; Park et al. 2009) bind ABA increasing their interaction with the PP2Cs. This interaction disrupts the PP2C–SnRK interaction, thus liberating the SnRKs to activate downstream ABA responses. In grapevine, studies have characterized how the expression of some of these signaling components changes in response to drought. The PP2Cs, *VviHAIL* and *VviAHG3*, and the SnRK, *VviOST1* (ortholog of OST1 from rice), increase in *Vitis* leaves under water

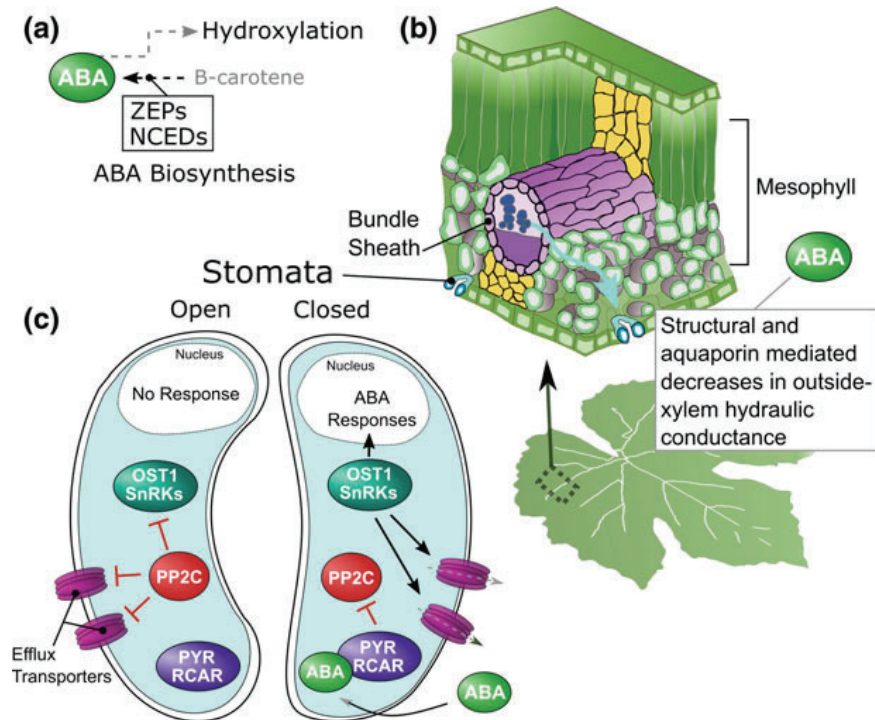


Fig. 11.2 On overview of ABA biosynthesis, signaling, and its role in mediating changes in leaf hydraulic conductance and stomatal regulation during drought. **a** ABA is biosynthesized from B-carotene (*not all steps are shown*) with the zeaxanthin epoxidase (ZEP) and 9-*cis*-epoxycarotenoid dioxygenase (NCED) proteins catalyzing the rate-limiting steps. ABA is catabolized via hydroxylation. **b** In response to drought, ABA is thought to mediate decreases in outside-xylem hydraulic

conductance in the leaf lamina. **c** In the stomatal guard cells, ABA signaling mediates stomatal closure. Under well-watered conditions, the 2C protein phosphatases (PP2C) inhibit the activity of serine/threonine-protein kinases (SnRKs) and downstream ABA responses. When ABA is present, it binds to the PYR/PYL/RCAR receptors which disrupt the PP2C-SnRK interaction, thus liberating the SnRKs to activate downstream ABA responses

deficit (Hopper et al. 2016). In addition, the abundance of *VviABI5* and *VviABF2*, ABA-responsive transcription factors which are targeted by *VviOST1*, also increases during water deficit (Haider et al. 2017). Two receptors involved in ABA perception, *VviRCAR5* and *VviRCAR6*, were downregulated in leaves and roots. Both genes are putative negative regulators of *VviPP2C4* and *VviPP2C9* and showed higher expression under water deficit (Boneh et al. 2012; Rossdeutsch et al. 2016).

Recent studies have identified the role of protein phosphorylation in ABA-induced stomatal closure that involves kinases and phosphatases (Zhang et al. 2014). However, more effort should be focused on revealing the protein

abundance and phosphorylation status of these proteins to complete our understanding in the plant response to stress.

Changes in the pH of xylem sap commonly observed under drought stress can be an important component of root-to-shoot signaling and may act synergistically with ABA. The potential effects of pH have been outlined elsewhere (Wilkinson 1999) and include (1) changes in ABA metabolism resulting in increased leaf ABA concentration; (2) direct effects on leaf water status that could alter guard cell turgor or sensitivity to leaf ABA concentrations; (3) direct effects on ion fluxes through the guard cell plasma membrane; and (4) an increase of ABA concentration in the apoplast surrounding guard cells.

11.2.3 The Influence of Root and Leaf Hydraulic Conductance on Plant Water Use

In addition to stomatal regulation, the hydraulic conductance of leaves and roots also contributes to the regulation of plant water use. Under water deficit, hydraulic conductance decreases sharply in fine roots and leaves. This drop-in hydraulic conductance plays an important role in protecting grapevines from more severe levels of water stress that can result in embolism and mortality (see Sect. 11.4).

While water deficit tends to decrease root hydraulic conductance (Vandeleur et al. 2009) contrasting results have been obtained for ABA applications (Gambetta et al. 2017). An increase in the root hydraulic conductance regulated by aquaporins was observed in maize mutants overexpressing ABA (Parent et al. 2009). In contrast, other studies have observed only a transient increase in root hydraulic conductance (Hose et al. 2000), or even no effect (Wan and Zwiazek 2001; Aroca et al. 2003), in response to ABA applications. The increase in root hydraulic conductance by ABA has been interpreted as a mechanism to improve the water supply to the shoot, decreasing the water potential gradient along the flow pathway under soil or atmospheric water stress (Kudoyarova et al. 2011; Pantin et al. 2013).

Diurnal changes in root hydraulic conductance have also been observed under well-watered conditions concomitantly with changes in shoot transpiration (Vandeleur et al. 2009). In general, these variations correlate with the transcript abundance of aquaporins in roots suggesting that aquaporins facilitate water transport across roots to meet the transpirational demand of the shoots (Sakurai-Ishikawa et al. 2011; Laur and Hacke 2013; Vandeleur et al. 2014). Gene expression studies in various plant species have reported contrasting responses of aquaporin expression to water stress. Experiments using mercuric chloride demonstrated a decrease in aquaporin activity in water-stressed desert plants and *Populus* sp. seedlings (Martre et al. 2001; Siemens and Zwiazek 2003; North

et al. 2004). In grapevine, Gambetta et al. (2012) observed differences in root hydraulic conductance between low and high vigor conferring rootstocks that corresponded to differences in the expression and activity of aquaporins.

On the other hand, a great variation in the apparent sensitivity of leaf hydraulic conductance to xylem ABA concentration has been reported (Correia et al. 1995). For instance, a large variability in leaf hydraulic conductance sensitivity to exogenous ABA was observed between different grapevine genotypes (Coupel-Ledru et al. 2017). Those authors found that ABA accumulation in the xylem sap of intact grapevine plants was highly dependent on the genotype, suggesting variability in ABA biosynthesis capacity or catabolism. This observation was further confirmed in nine grapevine genotypes where ABA-mediated responses to water deficit separate the genotypes by their genetic background (Rossdeutsch et al. 2016). Thus, stomatal regulation likely results from the complex integration of guard cell osmotic pressure, leaf water status and hydraulic conductance, and root-to-shoot controls.

Under water deficit, the increase in ABA concentration in roots and leaves is coincident with decreases in hydraulic conductance. In leaves, studies showed that xylem fed-ABA decreases the leaf hydraulic conductivity by decreasing water permeability in the vascular bundle sheath cells (Shatil-Cohen et al. 2011). Pantin et al. (2013) further demonstrated that vascular ABA decreased the leaf hydraulic conductance putatively by inactivating bundle sheath aquaporins, indicating that ABA indirectly impacts guard cell water relations through these changes in leaf hydraulics. These results led the authors to suggest that ABA regulates stomata via an additional indirect mechanism, whereby reduced water permeability within leaf vascular tissues results in local changes in water potential that are sensed by guard cells (Fig. 11.2) (Pantin et al. 2013). These decreases in the hydraulic conductance in the pathway between the xylem and the stomata (i.e., the outside-xylem pathway) occur across species and contribute to stomatal closure and protection from more severe stress

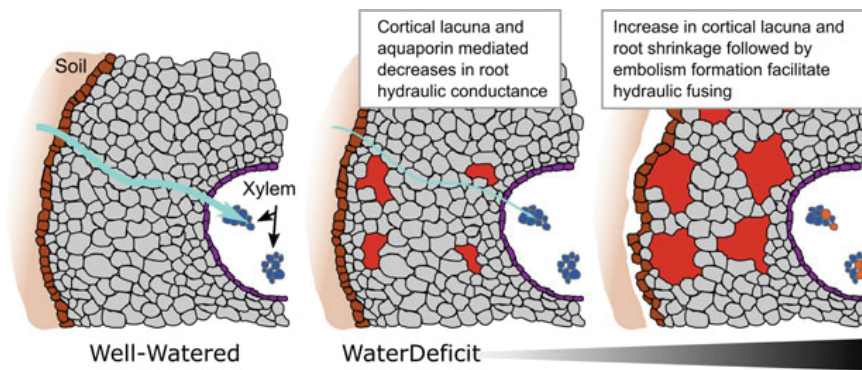


Fig. 11.3 Responses of grapevine fine roots to drought. Water transport (light blue arrow) from the soil across the root cortex (gray) into the xylem decreases under water deficit. This decrease in water uptake is first mediated by decreases in hydraulic conductance which occurs as a result of structural changes (e.g., lacuna formation in red)

and aquaporin mediated decreases. As stress increase, the lacunas expand and the root shrinks largely disconnecting the root from the soil, a process referred to as hydraulic fusing. Eventually, if the stress becomes severe, enough xylem vessels embolize (orange vessels)

levels (Scoffoni et al. 2017a, b); similar findings have been found recently in grapevine leaves (Albuquerque et al. unpublished data). The same is true in fine roots where water deficit leads to sharp decreases in hydraulic conductance which occurs as a result of structural changes (Cuneo et al. 2016) and aquaporin mediated decreases (Fig. 11.3).

11.2.4 Cultivar Sensitivity to ABA: The Iso/Aniso Debate

In some species, g_s appears to regulate plant water status so tightly that leaf water potential does not vary significantly (Tardieu and Davies 1993; Saliendra et al. 1995). Plants that present this conservative response under drought have been classified as “isohydric”. In contrast, plants that have a less strict stomatal control, exhibiting more negative water potentials under drought have been classified as “anisohydric” (Tardieu and Simonneau 1998; Soar et al. 2006). This broad classification assumes that genotype fixes a plant’s behavior somewhere in between these two theoretical extremes; however, it is widely recognized that this is not always the case (Chaves et al. 2010; Domec and Johnson 2012). For instance, contrasting studies are plentiful in the literature demonstrating the same grapevine

variety can exhibit different behaviors depending on the growing conditions (e.g., field grown versus potted plants; Medrano et al. 2003; Sousa et al. 2006; Lovisolo et al. 2010; Charrier et al. 2018). This classification has also been used to describe the underlying mechanisms of drought-induced changes in plant physiology such as root and leaf hydraulic conductance (Schultz 2003; Vandeleur et al. 2009), nighttime g_s (Cirelli et al. 2015), vulnerability to cavitation (Hukin et al. 2005), and plant mortality (McDowell et al. 2008). For instance, the degree of iso/anisohydric behavior has been explained by the differential expression of root aquaporins in two grapevine genotypes (Grenache and Syrah; Vandeleur et al. 2009). In that study, both varieties show increased root suberization under water stress, thus reducing the total hydraulic conductance of the root system, but only cv. Chardonnay (the more drought-sensitive, anisohydric) seemed to partially compensate for this decrease through increased expression of the grape aquaporin *VvPIP1;1*.

Differences in stomatal response to drought might be partially determined by genetic differences in the capacity to produce ABA. Only part of this variation is under heritable control since leaf developmental stage and environmental preconditioning exert a large influence on the stomatal response to drought (Chaves et al.

2010). In grapevine, different *Vitis* genotypes exhibiting different levels of drought adaptation differ in key steps involved in ABA metabolism and signaling; both under well-watered conditions and in response to water deficit (Ross-deutsch et al. 2016).

11.2.5 Other Hormone Pathways: Ethylene, GABA

Even though ABA signaling is seen as the main pathway for stomatal regulation, chemical signals other than ABA have been proposed (Christmann et al. 2007; Wilkinson et al. 2007) including the nonprotein amino acid γ -aminobutyric acid (GABA; Serraj et al. 1998). Rapid accumulation of GABA was identified in plant tissues upon exposure to drought (Serraj et al. 1998). In water deficit studies in Arabidopsis, GABA accumulation was observed to be stress-specific and its accumulation induced stomatal closure (Mekonnen et al. 2016). In addition, other studies have identified specific plant transporter proteins (e.g., aluminum-activated malate transporter) that are modulated by GABA and affect diverse aspects of the drought response (Ramesh et al. 2015).

Ethylene could be another important factor under water deficit. A precursor of ethylene 1-aminocyclopropane-1-carboxylic acid (ACC) that moves in the xylem from root to shoots has been observed to increase in water-stressed grapevines (Haider et al. 2017). A role for ethylene under drought was demonstrated by the use of ACC oxidase (ACO, which catalyzes the conversion of ACC into ethylene) antisense lines in tomato (Sobeih et al. 2004). In these plants, ethylene evolution was much lower than normal under both well-watered and drought conditions. Under water deficit, the stomatal response in the ACO antisense plants was the same as the wild type, but a decrease in leaf growth was measured in wild type, but not ACO antisense plants. ACC synthase (ACS) is the rate-limiting enzyme in the biosynthesis of ethylene and dehydrated leaves of Cabernet Sauvignon exhibited increases in the

expression of *VviACS7*, *VviACS4*, and *VviACS8*-like (Hopper et al. 2016).

In Arabidopsis, the ethylene response factors (ERFs) are considered integrators of hormone pathways, and ERF5 and ERF6 play a crucial role in leaf growth as response to dehydration (Dubois et al. 2013). Hopper et al. (2016) observed an increase in *VviERF6*-like in *Vitis vinifera* cv. Cabernet Sauvignon leaves under water stress. Equally, the ethylene receptors *VviETR2*, *VviERS2*, and *VviERS1* are all increased under water deficit. The WRKY gene family is also known to affect the ethylene signaling. In Arabidopsis, *AtWRKY40* is regulated by members of the APETALA 2/ethylene-responsive element binding factor (AP2/ERF) transcription factor family (Koyama et al. 2013), and in some grape genotypes the grape orthologue, *VviWRKY40*, is up-regulated under water deficit along with AP2/ERF transcription factors (Hopper et al. 2016). Genes from the ERF family, *VviERF9*, *VviERF055*, *VviERF022*, and *VviERF128* showed increased expression under water deficit (Hopper et al. 2016). *VviERF055* is homologous to an ERF transcription factor in *Arabidopsis*, the translucent green (TG), which is thought to increase drought tolerance by binding to aquaporin promoters. These coordinated changes in gene expression suggest a role for ethylene and ethylene signaling in the drought response, but more research on this topic is needed.

Stomata play a key role in plant adaptation to the environment, as they regulate the trade-off between water and CO₂ and modeling is an effective tool to investigate the integration, simulation, and prediction of environmental effects on stomatal regulation (Zhu et al. 2017, 2018). However, models could be improved by incorporating a more nuanced understanding of additional chemical signals. For example, hydrogen peroxide is an important reactive oxygen species (ROS) molecule involved in guard cell functioning and more specifically in the guard cell ABA-signaling network (Schroeder et al. 2001). Including the concentration of hydrogen peroxide in plant, models may provide an essential and

complementary link between g_s , photosynthesis, and ABA (Damour et al. 2010).

11.3 Photosynthesis and the Effect of Drought

Decreases in carbon fixation observed in grapevines subjected to water stress is initially due to stomatal closure (see above; Chaves 1991; Flexas et al. 2004) as evidenced by a close correlation between g_s and photosynthesis (Naor and Wample 1994; Flexas et al. 2002), by full recovery of photosynthesis when exposing the leaves to saturating amounts of CO_2 (Cornic 2000), and by increasing instantaneous water use efficiency (i.e., the ratio of photosynthesis to transpiration) under these conditions (Cornic and Fresneau 2002). Further decreases in photosynthetic carbon assimilation under water stress are associated with other biochemical processes such as photophosphorylation and reduced activity of RuBisCO (Tezara et al. 1999). Significant disruption of the photosynthetic machinery occurs under severe stress that can often coincide with high light and high-temperature conditions that exacerbate the damage.

11.3.1 Diffusive Versus Metabolic Limitations to Photosynthesis

This diffusive limitation to CO_2 is not only imposed by the stomata but also by the pathway from the substomatal cavity into mesophyll cells and sites of carboxylation in the chloroplasts (Perez-Martin et al. 2009). Conductance of CO_2 into mesophyll cells (g_m) can impose a significant limitation on photosynthesis (Centritto et al. 2003; Flexas et al. 2007). It was proposed that aquaporins and carbonic anhydrase play an important role in regulating g_m (Flexas et al. 2006; Kawase et al. 2013), and recent work showed that most of the variations observed in g_s and g_m in olive leaves was explained by two leaf aquaporins and the expression of carbonic

anhydrase had a significant effect on g_m under water-stressed conditions (Perez-Martin et al. 2014).

When water stress becomes severe alterations of photosynthetic metabolism occur, such as decreases in ATP production, ribulose-1,5-biphosphate RuBP regeneration, and RuBisCO activity (Chaves 1991; Cornic 2000; Flexas et al. 2004). Primary events of photosynthesis such as the electron transport rate are very resilient to drought, and changes in the efficiency of photosystem II (PSII) do not occur until photosynthesis becomes very low (g_s below $0.05 \text{ mol H}_2\text{O m}^{-2} \text{ s}^{-1}$; Flexas et al. 2002, 2004; Medrano et al. 2002). At this level of severe water stress photosynthesis does not recover upon re-watering (Quick et al. 1992), indicating that non-stomatal inhibition is dominant. As g_s decreases, further RuBisCO activity steeply declines (Bota et al. 2002, 2004; Flexas et al. 2002; Maroco et al. 2002). Thus, RuBisCO has been proved to be highly stable and resistant to water stress.

Similar to RuBisCO, the key carbon and nitrogen metabolic enzymes sucrose-phosphate synthase and nitrate reductase are also highly stable under water stress (Flexas et al. 2004). By contrast, less attention has been paid to other enzymes involved in the regeneration of RuBP in the Calvin cycle, and there is still lack of knowledge regarding their regulation under drought, particularly for grapevine.

11.3.2 Sugar Signaling Metabolism and Osmotic Adjustment

Carbohydrates have different roles in the plant, from energy storage compounds to metabolic signaling molecules. There is evidence that an increase of sugars in the guard cells under water stress may determine the stomatal sensitivity to ABA (Wilkinson and Davies 2002). In general, soluble sugars tend to be maintained or even increased under water stress despite a lower carbon assimilation rate. This is possible mainly because other processes such as growth and

sucrose transport to sink tissues are inhibited. In contrast, the concentration of starch decreases under drought (Chaves 1991; Dayer et al. 2016). In addition, sugars seem to favor the expression of genes related to biosynthesis and storage of reserves (e.g., starch) and repress those associated with photosynthesis and remobilization of sugars (Ho 2001). Some evidence has been provided that water deficit and other related abiotic stresses affect the expression of sugar transporter genes. For instance, in *Arabidopsis* transcript accumulation of the tonoplast monosaccharide transporters was increased in response to drought treatment (Wormit et al. 2006). In grapevine, water stress increased the gene expression for sucrose transporters known to code for mesophyll cell proteins in leaves without affecting the transcript abundance for the phloem loading protein (Pastenes et al. 2014). In addition, water stress may inhibit important functions of vacuolar invertase-mediated sucrose hydrolysis and osmotic potential modulation (Andersen 2002). Studies in grapevine observed that water stress induction of *VvGIN2* gene encoding a putative vacuolar invertase may contribute to the increase of cell osmotic potential in response to water deficit that helps maintain basic metabolic functions (Medici et al. 2014).

Grapevines have the ability to support growth and productivity under water deficit through osmotic adjustment (Schultz and Matthews 1993; Patakas and Nortsakis 1999). The accumulation of osmolytes in leaves is attributable to a variety of small molecules with both metabolomic and transcriptomic studies highlighting the accumulation of sugar and amino acids (Hochberg et al. 2013; Medici et al. 2014; Haider et al. 2017). For instance, Patakas et al. (2002) demonstrated the importance of organic solute and ion accumulation under water stress in grapevines. Proline metabolism is a common osmoprotectant across plant species and is among the three most responsive amino acids that change in response to water deficit, increasing as much as two to three times in *V. vinifera* leaves (Cramer et al. 2007). Haider et al. (2017) reported an increase in proline levels during water deficit as well.

Increase in proline results from an increase in delta 1-pyrroline-5-carboxylate synthetase (P5CS) abundance, a biosynthetic enzyme that initiates the proline pathway (Cramer et al. 2007). Another important enzyme in proline metabolism is proline dehydrogenase (PDH) whose expression also increases as a result of water deficit (Peng et al. 1996). In *Vitis*, *PDH*, *P5CS*, and other genes involved in proline metabolism were up-regulated under water deficit (Haider et al. 2017). This osmotic adjustment may have long-term effects on grapevine performance under drought. For example, vines that have undergone successive water deficits are able to maintain slightly higher levels of g_s , which are thought to result in part from osmotic adjustment (Hochberg et al. 2017a). Two rootstocks (M4 and 101-14) that differ in their drought resistance exhibited differences in their ability to osmotically adjust with the more drought-resistant rootstock (M4) accumulating greater concentrations of sugars, amino acids, and osmotin like-proteins in response to drought (Prinsi et al. 2018).

Some transcript factors are involved in osmoprotection change in response to abiotic stress. For example, fructose biphosphate aldolase and galactinol synthase experienced an increase in transcript abundance at an early stage of water deficit in grapevines (Cramer et al. 2007). In *Poplar*, genes encoding sucrose synthase, galactinol synthase, and raffinose synthase were all increased under water deficits (Shatil-Cohen et al. 2011). Similarly, genes encoding galactinol and raffinose synthases were similarly up-regulated in loblolly pine under drought stress (Lorenz et al. 2011).

11.3.3 Photosynthetic Pigments and Antioxidant Defense

Water stress reduces the tissue concentration of photosynthetic pigments such as chlorophylls and carotenoids (Poormohammad Kiani et al. 2008), primarily through the production of reactive oxygen species in the thylakoids (Niyogi 1999; Reddy et al. 2004). Carotenoids, in

addition to their function as accessory pigments, play an important function as antioxidants protecting and sustaining photochemical processes (Havaux 1998). Carotenoids form a key part of the plant antioxidant defense system but are very susceptible to oxidative destruction. β -Carotene, presents in the chloroplasts of all green plants, is exclusively bound to the core complexes of PSI and PSII (Havaux 1998). A major protective role of β -carotene in photosynthetic tissue may be through direct quenching of triplet chlorophyll, which prevents the generation of singlet oxygen and protects from oxidative damage (Farooq et al. 2009), which becomes increasingly important under severe water stress conditions.

11.3.4 Photoinhibition and Oxidative Stress

Under field conditions, plants are normally exposed to different stresses simultaneously, such as water deficit, high temperatures and radiation regimes, and high VPD. Under well-watered conditions, most of the light absorbed by the leaves is used for photosynthesis and photorespiration processes. However, in situations where stomata close (e.g., water deficit) the combination of high irradiance with low CO_2 availability cause the plant to absorb an excess of radiant energy that has the potential to damage the photosynthetic apparatus. Under these conditions, the leaves experience a transient decrease of the photochemical efficiency of PSII in a process called photoinhibition, which is a form of non-photochemical quenching (Gamon and Pearcy 1990; Baker 2008). Photoinhibition is most commonly equated with photodamage, a long-term depression of quantum efficiency due to damage to the photosynthetic apparatus as a result of excess photosynthetic photon flux density (Walters and Horton 1993). Chronic photoinhibition may be considered as a depression of photosynthetic efficiency from which the plant does not recover after 3–4 days in shade (Greer and Laing 1992). To avoid this damage, plants can prevent this excess of light absorption by either adjusting their leaf angles to the sun, losing

the chlorophyll content, or diverting the absorbed light to different processes such as thermal dissipation (Demmig-Adams and Adams 2006). Thermal dissipation is a very important non-radiative process that can dissipate >75% of the light energy absorbed by the leaves (Niyogi 1999). The xanthophyll cycle plays a primordial role in the thermal dissipation process (Demmig-Adams and Adams 2006) and also a direct action as antioxidant by increasing the tolerance of the thylakoid membrane to lipid peroxidation (Niyogi 1999).

When the leaf cannot keep pace between the light energy absorbed and thermal dissipation of this energy, the production of highly reactive molecules is exacerbated. These molecules are referred to as reactive oxygen species (ROS) and are generated mainly in the chloroplast and may lead to an oxidative damage (e.g., photooxidation) of the photosynthetic apparatus if the plant is not efficient in scavenging these molecules (Niyogi 1999). Some of the ROS molecules reported in the literature include hydrogen peroxide (H_2O_2), superoxide and hydroxyl radicals and singlet oxygen (O_2^-). Reactive oxygen species are also essential signaling molecules that mediate ABA-induced stomatal closure and ABA-induced inhibition of stomatal opening (Yan et al. 2007). Among all ROS, hydrogen peroxide emerges as one of the most important considering its role in guard cell functioning and more specifically in the guard cell ABA-signaling network (Schroeder et al. 2001; Wang and Song 2008). In addition, Gunes et al. (2006) showed that grapevine leaves can generate O_2^- and H_2O_2 in response to boron excess, which may happen under water deficit as well.

The balance between ROS synthesis and scavenging depends on the rate and duration of the water stress (Lawlor and Tezara 2009). For example, when the water stress develops rapidly over days under high light, ROS damage is observed (Demmig-Adams and Adams 2006). Detoxification mechanisms consume reducing power and form water and include reactions with reduced compounds such as ascorbate and glutathione (Mittler 2002; Asada 2006). Interestingly, increased ROS production along with the

high redox state of the electron membrane chain under water stress, induce the expression of genes coding for components of energy-dissipating and regulation systems in the chloroplasts, allowing acclimation to stress conditions (Pfannschmidt et al. 2003). In *Vitis*, genes associated with ROS increased when exposed to water deficit (Cramer et al. 2013). Genes involved in ROS detoxification such as phospholipid hydroperoxide glutathione peroxidase (TC45235, O48646), gamma-glutamylcysteine synthetase, and NADPH glutathione reductase showed increases in their gene expression under water deficit (Cramer et al. 2007). Photorespiratory enzymes of the glyoxysome/peroxisome participate in water stress signal and in oxygen free-radical metabolism (Corpas et al. 2001; Moreno et al. 2005). Cramer et al. (2007) showed that several of these enzymes increased their transcript abundance in grapevines during water deficit. GABA transaminase subunit isozyme 1 is an enzyme in the “GABA shunt” pathway, which is known for its role in defense against ROS (Bouché et al. 2003; Fiorani et al. 2005; Umbach et al. 2005). Cramer et al. (2007) showed an increase in grapevine GABA transaminase transcript abundance in response to water deficit.

11.3.5 Membrane Stability

Cell and organelle membranes are one of the first receptors of stress, and they can protect the cell through modifications affecting both stress perception and rigidity of the cell structure. Quantitative changes in the membrane lipids, such as unsaturation level of phospholipids and glycolipids, affect membrane fluidity and as a consequence the activity of membrane-bound proteins (Quartacci et al. 2002). Drought causes alterations in membrane fluidity, and membrane stability is commonly used as a physiological index for the evaluation of resistance to drought tolerance (Premachandra et al. 1990). In addition, cell membranes are susceptible to damage from ROS produced via the metabolism of the cell, and/or as a result of stress (Koca et al. 2006), and the interaction between ROS and cell membranes

produces lipid peroxides that can be used as a stress indicator. Because ROS species are produced in the chloroplasts, chloroplast membranes are particularly susceptible to oxidative stress.

A decrease in cellular volume caused by membrane disruption increases the cytoplasmic compounds, and the chances of molecular interactions that can cause protein denaturation and membrane fusion (Farooq et al. 2009). A broad range of compounds has been identified that can prevent such adverse molecular interactions. Some of these include proline, glutamate, glycine betaine, mannitol, sorbitol, polyols, trehalose, sucrose, fructans, macromolecules (Hoekstra et al. 2001). Such responses have not been addressed in grapevines.

11.4 Extreme Drought and Long-Term Productivity

11.4.1 Hydraulic Fusing and Embolism

Under severe water deficits, grapevines have more drastic responses such as petiole embolism, leaf shedding, and in severe cases stem embolism. However, the vulnerability of grapevine organs to embolism is not equal with grapevine petioles and leaves being significantly more vulnerable to embolism than stems (Hochberg et al. 2016, 2017b; Charrier et al. 2016). This phenomenon is referred to as “vulnerability segmentation” or “hydraulic fusing”. First put forth by Zimmermann (1983), segmentation (or fusing) results when an increased vulnerability to embolism in distal organs such as petioles, leaves, and/or fine roots prevents embolism in perennial organs such as stems and trunks. Studies suggest that grapevine leaves and petioles have a P_{50} (i.e., the pressure at which there is 50% loss of hydraulic conductance via embolism) ranging from -1.0 to -2.0 MPa (Hochberg et al. 2016, 2017b; Charrier et al. 2016) while stems have a P_{50} ranging from approximately -2.0 to -3.0 MPa (Choat et al. 2010; Brodersen et al. 2013; Charrier et al. 2018). Grapevine stems become less and less vulnerable through

the season and this likely increases the segmentation between leaves/petioles and stems (Charrier et al. 2018).

Equally, roots could also be more vulnerable to embolism to protect the vine against more negative water potentials (Lovisolo and Schubert 2006; Lovisolo et al. 2008). More recent results using noninvasive methods corroborated these results and demonstrated that xylem of grapevine fine roots had a P_{50} similar to that of leaves (-1.8 MPa) (Cuneo et al. 2016). It was also recently discovered that grapevine fine roots subjected to drought stress form lacuna prior to root shrinkage and embolism formation. Together, these responses likely result in fine roots becoming hydraulically disconnected from the drying soil (Cuneo et al. 2016).

Hydraulic fusing in grapevine leads to premature leaf senescence and leaf shedding (Hochberg et al. 2017b), and the progression of leaf mortality mirrors increases in leaf and petiole embolism (Charrier et al. 2018). Together with other mechanisms (e.g., in roots), these responses appear to isolate drought-induced damage of the xylem systems to expendable plant parts other than stems and trunks (Charrier et al. 2018). Stem embolism is extremely detrimental to the plant, and significant levels are typically fatal (from 50 to 90% loss of conductivity depending on species; Brodribb and Cochard 2009; Urli et al. 2013; Li et al. 2015) so its prevention and/or repair (discussed below) are likely critical. In general, leaf shedding represents a move toward dormancy helping deciduous plants such as grapevine escape severe levels of water deficit (Zhao et al. 2017; Volaire 2018). Although this “abandon the current season and wait it out” strategy may be effective for long-term survival, it would have severely negative effects on current season productivity in an agricultural setting.

11.4.2 Recovery and Repair

Drought stress responses such as reduced growth and/or stomatal closure are largely reversible over a short time frame. Stomatal conductance

recovers rapidly when grapevines are re-watered while under moderate levels of water deficit (Hochberg et al. 2017a; Dayer et al. 2017b). However, this recovery time lengthens as the severity of the stress experienced by the vine increases (Charrier et al. 2018). Other responses such as leaf shedding can only be reversed over longer time frames. The repair (i.e., refilling) of embolized xylem vessels can take place over both short (hours to days) and long (over winter) time frames (Brodersen and McElrone 2013). Although embolism repair has been the subject of debate because of methodological artifacts leading to false conclusions (Torres-Ruiz et al. 2015), the increasing use of noninvasive imaging, especially X-ray microCT, now provides a much more robust means to examine embolism repair in situ (Brodersen et al. 2010; Knipfer et al. 2016; Hochberg et al. 2017b). Studies using these technologies confirm that grapevines are not as susceptible to embolism as previously thought and thus routine cycles of embolism formation and repair do not appear to occur on a daily basis during the growing season.

The mechanisms involved in embolism repair are still largely based on speculation. Root pressure has traditionally been invoked as a cornerstone mechanism in xylem repair across many species including grapevine (Sperry 1993; Tibbetts and Ewers 2000; Isnard and Silk 2009). MicroCT studies have associated grapevine embolism repair with root pressure (Knipfer et al. 2015; Charrier et al. 2016), and *Vitis* species differing in their ability to produce root pressure under drought exhibited corresponding abilities to refill embolized xylem vessels (Knipfer et al. 2015). Certainly overwintering in grapevine, with the significant amount of root pressure produced in spring, should facilitate significant embolism repair.

In the absence of root pressure, embolism repair is thought to involve solute loading into embolized vessels from adjacent living xylem parenchyma thus creating an osmotic driving force to facilitate vessel refilling (Brodersen and McElrone 2013). Using microCT, Brodersen et al. (2010) illustrated that vessel refilling in grapevine was achieved by water influx from the

xylem parenchyma manifesting as droplets that expand until the vessels is filled. The orientation of this refilling was most often associated with ray tissues suggesting a possible role for carbohydrates in the process. Studies in other species also invoke the role of carbohydrates in the production of the osmotic gradients that could potentially drive the refilling process (Salleo et al. 2009; Nardini et al. 2011). However, it should be pointed out that refiling has only been observed in potted grapevines where soil is uniformly saturated when re-watered, a case that is almost always absent under field conditions.

There are currently no functional studies that unequivocally identify any molecular mechanism involved in embolism repair; however, numerous attempts have been made to correlate changes in gene expression with drought recovery in xylem associated tissues. Transcriptomic studies in Poplar during recovery from water deficit highlight an induction of genes involved in transport, including aquaporins and ion transporters, and carbon metabolism (Secchi and Zwieniecki 2010; Secchi et al. 2011). These findings correspond with the hypothesized mechanisms discussed above. In grapevine, a study by Chitarra et al. (2014) revealed similar changes in targeted drought, aquaporin, and carbon-related genes. Studies that combine function analyses of putative proteins involved in the repair process with noninvasive, real-time visualization of refilling are required to make firm conclusions regarding the molecular mechanisms involved in embolism repair.

11.4.3 Carry Over Effects

Since water deficits are commonly applied in viticulture, there are questions regarding their effects on crop performance over the long-term; to what extent do repeated seasonal water deficits have carry over effects on growth and/or yield, and to what extent can grapevines recover from both moderate and more severe water deficits? Some drought stress responses such as reduced growth and/or stomatal closure are largely reversible over a short time frame (i.e., within

season) while others such as leaf shedding can only be reversed by overwintering.

Water deficits clearly decrease vigor and yields in the current season and sometimes can lead to carry over effects that reduce yields in the following season through negatively impacting bud fertility (Buttrose 1974; Williams and Matthews 1990). However, this appears to be dependent on the crop load (Dayer et al. 2013) suggesting an important impact of source–sink relationships and carbohydrate reserves. Several recent leaf removal studies effects on grape berry composition and starch reserves were only observed in treatments that severely reduced the source–sink ratio suggesting grapevines largely compensate for these changes (Bobeica et al. 2015; Silva et al. 2017). The compensatory capacity of grape berries to maintain normal ripening (i.e., sugar accumulation) seems especially high (Pellegrino et al. 2014). At the molecular level, Silva et al. (2017) demonstrated compensatory changes in woody tissues that increased sink strength via the upregulation of *VvSusy*, a key regulator of starch synthesis, and an increase in acid invertase activity when the source was limiting. Similar changes may be expected under water deficit where stomatal closure and decreased photosynthesis equally limit source production (discussed below).

11.5 Conclusions

Recent advances in grapevine have demonstrated that a large number of genes are involved in plant drought responses. There is strong evidence that ABA plays a key role in various aspects of metabolism in the overall response. The identification of genes that lead to the stress-induced production of ABA and the perception of this signal are important in understanding stomatal regulation under mild water deficit. However, further work is required to fully elucidate the signal transduction and transcriptional regulation of these genes under stress conditions, especially at the protein level.

Further studies are essential to determine the molecular basis of altered carbon assimilation

and transport of sugars within the plant. For instance, there is still lack of knowledge about the enzymes involved in the regeneration of RuBP in the Calvin cycle and their regulation under drought, particularly for grapevine. Dormancy and the redistribution of carbon stores from season to season are also poorly understood although they likely have a cornerstone role in growth and productivity over the lifespan of a vineyard.

Often drought is accompanied by other environmental stresses such as high temperatures and high VPD that also result in oxidative stress. And like drought, scavenging of the reactive oxygen species, cell membrane stability, expression of aquaporins, and osmotic adjustment are some of the protective mechanisms that allow plants to cope with these stresses as well. Research has advanced in the identification of redox signals (e.g., hydrogen peroxide) that may regulate the energy balance of the leaf involving the expression of several genes that are linked to photosynthesis and other metabolic pathways. It is critical to understand how these different stress response pathways are integrated in grapevine and other plants.

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