Research Paper

Hydraulics and gas exchange recover more rapidly from severe drought stress in small pot-grown grapevines than in field-grown plants

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ABSTRACT

Modifications of plant hydraulics and shoot resistances (R_{shoot}) induced by water withholding followed by rewatering, and their relationships with plant water status, leaf gas exchange and water use efficiency at the leaf level, were investigated in pot-grown and field-grown, own-rooted Syrah grapevines in an arid climate. Water stress induced anisohydric behavior, gradually reducing stomatal conductance (g_s) and leaf photosynthesis (A) in response to decreasing midday stem water potential (Ψ_s). Water stress also rapidly increased intrinsic water-use efficiency (A/g_s); this effect persisted for many days after rewatering. Whole-plant (K_{plant}), canopy (K_{canopy}), shoot (K_{shoot}) and leaf (K_{leaf}) hydraulic conductances decreased during water stress, in tune with the gradual decrease in Ψ_s, leaf gas exchange and whole plant water use. Water-stressed vines also had a lower Ψ gradient between stem and leaf ($\Delta\Psi_l$), which was correlated with lower leaf transpiration rate (E). E and $\Delta\Psi_l$ increased with increasing vapour pressure deficit (VPD) in non-stressed control vines but not in stressed vines. Perfusion of xylem-mobile dye showed that water flow to petioles and leaves was substantially reduced or even stopped under moderate and severe drought stress. Leaf blade hydraulic resistance accounted for most of the total shoot resistance. However, hydraulic conductance of the whole root system (K_{root}) was not significantly reduced until water stress became very severe in pot-grown vines. Significant correlations between K_{plant}, K_{canopy} and Ψ_s, K_{canopy} and leaf gas exchange, K_{leaf} and Ψ_s, and K_{leaf} and A support a link between water supply, leaf water status and gas exchange. Upon re-watering, Ψ_s recovered faster than gas exchange and leaf-shoot hydraulics. A gradual recovery of hydraulic functionality of plant organs was also observed, the leaves being the last to recover after rewatering. In pot-grown vines, K_{canopy} recovered rather quickly following restoration of Ψ_s, although gas exchange recovery did not directly depend on recovery of K_{canopy}. In field-grown vines, recovery of water status, gas exchange and hydraulic functionality was slower than in pot-grown plants, and low g_s after rewatering was related to sustained decreased K_{plant}, K_{canopy} and K_{shoot} and lower water transport to leaves. These results suggest that caution should be exercised when scaling up conclusions from experiments with small pot-grown plants to field conditions.

1. Introduction

Plants control the amount of water lost via transpiration by regulating their stomatal aperture to avoid levels of water stress that could compromise their growth and survival. This stomatal control has been identified as an early event in plant response to water deficit (Chaves et al., 2010). The regulation of stomatal closure is a complex feature, involving chemical signals (e.g. ABA) and hydraulic signals (e.g. water flow, cavitation) (Schultz, 2003; Lovisolo and Schubert, 1998; Lovisolo et al., 2008; Torres-Ruiz et al., 2015, Tombesi et al., 2015).

Plants have been broadly characterized as isohydric or anisohydric depending on their water potential (Ψ) and stomatal conductance (g_s) responses to water stress (Tardieu and Simonneau, 1998). Isohydric plants have greater stomatal control and a minimum Ψ that remains relatively high and more or less constant as soil dries. Anisohydric plants, by contrast, exhibit less stomatal control and substantial depression of Ψ during drought. Some grapevine varieties (e.g. Grenache) are classified as isohydric, while others (e.g. Syrah and Chardonnay) display more anisohydric characteristics (Schultz, 2003). However, this classification into two categories is controversial and imprecise, and consequently, is not always applicable (Chaves et al.,

2010; Bota et al., 2016). Furthermore, it has been reported that the same cultivar may behave iso- or anisohydrically depending on growing and experimental conditions (Schultz, 2003; Pou et al., 2012; Bota et al., 2016). More recent analyses show that a continuum exists in the range of stomatal sensitivities to water stress in *V. vinifera*, rather than an isohydric–anisohydric dichotomy, that is further enriched by the diversity of scion-rootstock combinations and their interaction with different soils (Lavoie-Lamoureux et al., 2017). Besides, across species, a tight regulation of Ψ_L is not necessarily associated with greater stomatal control or with more constrained assimilation during drought. Therefore, iso/anisohydric defined in terms of Ψ_L regulation cannot be used as an indicator of a specific mechanism of drought-induced mortality or as a proxy for overall plant vulnerability to drought (Martínez-Vilalta and García-Forner, 2017).

There is evidence in vines that ABA plays an important role in linking the stomatal response to the soil moisture status, allowing optimization of gas exchange in relation to the prevailing environmental conditions in field-grown vines (Speirs et al., 2013) and in pot-grown vines (Lovisolo et al., 2008), although this is not conclusive. In this regard, Tombesi et al. (2015) reported an increase in the foliar ABA concentration in pot-grown vines only after the onset of stomatal closure and severe water stress, and not in the early phases of drought stress. Besides, it has been reported that an ABA-related reduction in transpiration promotes gradual embolism repair in rehydrated grapevines after drought (Lovisolo et al., 2008; Tombesi et al., 2015).

It has been also suggested that isohydric and anisohydric behavior may be regulated by plant hydraulics (Schultz, 2003), and some studies have confirmed a strong interdependence between plant hydraulic conductance and stomatal response under water stress and recovery in different species (Salleo et al., 2000; Brodribb and Holbrook, 2003; Pou et al., 2008; Vandeleur et al., 2009; Lovisolo et al., 2010; Torres-Ruiz et al., 2015). For instance, in grapevine an "optimistic" cultivar with anisohydric behavior was associated with a minor reduction in root hydraulic conductance and lower vulnerability to embolism formation compared to a more "pessimistic" isohydric cultivar (Vandeleur et al., 2009).

The loss of hydraulic functioning by the plant and the reduced water-conducting capacity under drought constitutes a signal involved in stomatal regulation (Lovisolo and Schubert, 1998; Schultz, 2003). Xylem embolism produced by cavitation and reduction in vessel diameter (of newly formed vessels) reduces plant water transport capacity, and both mechanisms have been reported in water-stressed grapevines (Lovisolo and Schubert, 1998). However, the vulnerability to cavitation varies among plant organs, a phenomenon that has been termed hydraulic segmentation (i.e. more distal organs such as leaves and petioles will be at greater risk to embolism than more basal organs such as the trunk or shoots; Tyree and Zimmermann, 2002). Some of the hydraulic modifications and gas exchange responses reported in grapevine genotypes with varying stomatal sensitivity under water stress and recovery, such as lower root and whole-plant hydraulic conductance and lower diameter of newly formed xylem vessels (Vandeleur et al., 2009; Lovisolo and Schubert, 1998), an increase in intrinsic water use efficiency (WUEi) (Poni et al., 2007), and faster recovery of photosynthetic capacity upon re-watering (Pou et al., 2012) have been proposed as important features of adaptation to dry environments. In addition, the capacity of roots and shoots to recover hydraulic functionality following drought stress is also a crucial aspect of plant adaptation to seasonality in water availability (Lo Gullo et al., 1998).

This study evaluated how own-rooted Syrah grapevines (classified variously as isohydric or anisohydric) responded to moderate and severe water stress followed by a period of recovery after rewatering under different growing and experimental conditions (pot-grown vs. field-grown conditions). We studied the degree of temporal coordination between plant hydraulics, water transport in different organs, stomatal function and plant water use. In addition, we focused on potential differences in physiological behavior between potted and field-grown vines under water stress and recovery.

2. Material and methods

2.1. Pot experiment

2.1.1. Plant material and irrigation treatments

Forty plants of three-year-old, own-rooted *Vitis vinifera* L. cv. Syrah were grown outdoors at Washington State University's Irrigated Agriculture Research and Extension Center (46°17′N; 119°44′W; 270 m a.s.l.) in 14.6 L pots filled with a mixture of 50% sandy loam soil, 25% peat moss, 25% pumice, and 30 g/L dolomite, with a volumetric soil water content (Θ_v) of ~34% at field capacity. The plants were irrigated daily to saturation. At the beginning of the experiment (8 August, 2011), 12 plants were maintained as controls, while irrigation was stopped in the other 28 plants (water stress or WS treatment). In the control pots water was replaced daily according to the amount of water consumed, as determined by weighing. In 22 of the WS pots water deficit was imposed by withholding water during 7 days, followed by a recovery period with daily irrigation to field capacity for 7 days. Six additional plants were left unirrigated for 12 and 15 days to impose very severe water deficit. The soil in all pots was covered with aluminum foil to prevent evaporation from the soil surface.

2.1.2. Soil water content and stem and leaf water potential measurements

In each pot, Θ_v in the root zone was measured in the early morning every day or every two days with a TDR probe (model Hydrosense CS620, Campbell Scientific, Logan, UT, USA). Midday stem (Ψ_s) water potential was determined every day or every two days with a pressure chamber (model 600, PMS Instrument Co., Albany, OR, USA). Three to four replicate measurements per treatment (1 per plant) were obtained on each sampling date. Measurements were performed on young, fully expanded, fully sun-exposed leaves.

2.1.3. Leaf gas exchange and plant water use measurements

Leaf gas exchange was measured between 09:00 and 10:00 h and also at midday (12:00–13:00) every day or every two days. Measurements were made on healthy, fully-expanded leaves exposed to the sun (two leaves on each of 3 or 4 vines per treatment). Leaf photosynthesis rate (A), stomatal conductance (g_s), transpiration rate (E), leaf temperature (T_{leaf}) and intercellular CO_2 concentration (Ci) were measured with a portable photosynthesis measurement system (model LCpro+, ADC Bioscientific, Hoddesdon, U.K.). During measurements, the leaf chamber temperature was maintained between 25 and 32 °C. The air flow rate was 250 μmol mol^{-1}. All measurements were taken at ambient CO_2 concentration (380–390 μmol mol^{-1}) and at saturating photosynthetic photon flux of 1500 μmol m^{-2} s^{-1}. Continuous changes in whole-plant transpiration (E_{plant}) were measured by placing the pots on digital scales (model Benchmark BM1212, Rice Lake Weighing Systems, Rice Lake, WI, USA) connected to a data logger (model CK10X, Campbell Scientific, Logan, UT, USA) that recorded data every 15 min.

2.1.4. Hydraulic conductance measurements

Quasi-steady state measurements of hydraulic conductance of the root system (K_{root}) and the aboveground plant portion (K_{canopy}) were made using a high pressure flow meter (HPFM, Dynamax, Houston, TX, USA). The root system (which included the belowground stem portion) was separated from the aboveground organs by cutting the stem near the soil surface. Immediately after cutting, the HPFM was connected first to the base of the aboveground plant portion, and then the root system. Intact root systems in the pots, without removing the roots from the substrate, were connected to the HPFM (Bogeat-Triboulot et al., 2002). Filtered, degassed, distilled water was forced to flow through each plant portion under constant pressure (P = 0.3 MPa), and the hydraulic conductance (K) was calculated from the slope of the plot