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Short communication

Water deficit severity during berry development alters timing of dormancy transitions in wine grape cultivar Malbec

Krista Shellie[a,*], Alisson P. Kovaleski[b], Jason P. Londo[c]

[a] U.S. Department of Agriculture, Agricultural Research Service, Horticultural Crops Research Unit-Parma ID worksite, 29603 University of Idaho Lane, Parma, ID 83660 USA

[b] Cornell University, School of Integrative Plant Science, Section of Horticulture, 630 W. North Street Geneva, NY 14456 USA

[c] U.S. Department of Agriculture, Agricultural Research Service, Grape Genetics Research Unit, 630 W. North Street, Geneva, NY 14456 USA

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ABSTRACT

The objective of this study was to test the hypothesis that vine water stress during the growing season can lengthen the dormancy cycle by inducing earlier transition into endodormancy. A bud forcing assay was used to compare the dormancy transitions of field-grown 'Malbec' grapevines that had been deficit-irrigated for seven consecutive growing seasons to supply 35 or 70% of estimated water demand to that of fully-watered vines. Canes were field-sampled from deficit-irrigated and fully-watered plots at multiple time points over a span of 100 days, beginning 30 days prior to harvest. Buds at nodes two through eight were cut into single-node segments, held under bud-forcing conditions for 60 days, and evaluated daily for the occurrence of bud break. Contrary to our initial hypothesis, water stress shortened the dormancy cycle by delaying the onset of endodormancy, decreasing the amount of chilling required for release from endodormancy and increasing the readiness to resume growth during ecodormancy. Results support the idea that drought stress-induced regulatory networks 'cross-talk' with environmental and hormonal regulatory signals that modulate the activity-dormancy cycle. Understanding the underlying mechanisms by which drought stress alters the activity-dormancy cycle may be critical for sustaining vine productivity in a changing climate.

1. Introduction

Grapevine (*Vitis vinifera* L.) is a deciduous woody perennial that is widely grown in arid climates within the temperate zone. Approximately 16% of global commercial wine grape acreage is located in semi-arid regions where monthly average temperature is below 0 °C for at least one month of the year (Jones et al., 2012). Grapevines, like many other temperate crops, undergo an annual activity-dormancy cycle to avoid injury when environmental conditions are unfavorable for growth (Lavee and May, 1997). Synchronization of active and dormant states with seasonal changes in the environment is critical for sustained productivity. Dormancy is a dynamic state of growth suspension that progresses through stages distinguished by use of the prefix 'para', 'endo' or 'eco', according to the origin of the regulating source of growth inhibition (Lang, 1987; Lavee and May, 1997; Kalberer et al., 2006). During para- and endodormancy, the source of growth inhibition is endogenous. During paradormancy, the location of the source of growth inhibition is within the plant but external to the affected meristematic tissue. During endodormancy, the source of growth inhibition is located within the affected tissue. The transition from endo- to ecodormancy signals the end of endogenous growth inhibition and the ability of meristematic tissue to resume growth under favorable environmental conditions. The signaling and regulatory mechanisms that underlie dormancy transitions are complex and poorly understood. Environmental signals, such as day length and air temperature, and tissue abscisic acid (ABA) concentration appear to play a role in the induction of endodormancy (Lavee and May, 1997; Rohde and Bhalerao, 2007; Zheng et al., 2015; Vergara et al., 2017). The transition from endo- to ecodormancy requires prior exposure to chilling temperatures or some other type of artificial dormancy release treatment (Dokoozlian et al., 1995; Pérez et al., 2009; Vergara and Pérez, 2010; Halaly et al., 2011; Londo and Johnson, 2014).

Wine grapes are often exposed to drought during their active growth cycle and some severity of vine water stress is considered desirable for wine quality. Deficit irrigation strategies are common production tools in arid regions used to manage yield, canopy size, and cluster

Abbreviations: ET_r, reference crop evapotranspiration; ET_c, estimated crop water demand; Ψ_{ml}, leaf water potential; δ^{13}, ratio of carbon^{13} to carbon^{12}; ABA, abscisic acid; BB_{50}, 50% bud break; ROS, reactive oxygen species

* Corresponding author.
E-mail addresses: Krista.Shellie@ars.usda.gov (K. Shellie), ap874@cornell.edu (A.P. Kovaleski), Jason.Londo@ARS.USDA.GOV (J.P. Londo).

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microclimate (Keller et al., 2016). The drought-induced metabolic rearrangements and regulatory networks have been shown to 'cross-talk' with environmental and hormonal regulatory signals that modulate the activity-dormancy cycle (Druart et al., 2007; Krasensky and Jonak, 2012). For example, an increase in ABA occurs in vines under drought stress (Stoll et al., 2000) and during induction of endodormancy (Zheng et al., 2015; Vergara et al., 2017). The increased concentration of ABA induced by water stress could induce earlier onset of endodormancy; however, the relationship between drought stress during the growing season and the timing of transition from para- to endodormancy has not been evaluated. The objective of this study was to test the hypothesis that vine water stress during the growing season lengthens the dormancy cycle by inducing an earlier transition into endodormancy.

2. Material and methods

2.1. Trial site and irrigation treatments

The material used in this study was obtained from own-rooted vines of the wine grape cultivar Malbec that were planted in 2007 as part of an irrigation field trial at the University of Idaho Parma Research and Extension Center in Parma, ID (lat. 43°37′7.9716N, long. 116°12′54.1W, 750 m asl). The above ground drip irrigation system at the trial site was designed to independently supply different amounts of water to plots of vines in a randomized block design with six replicate blocks. Each replicate plot was comprised of three adjacent vine rows with six vines per row. The trial perimeter contained a two-vine deep border which also had independent water supply. The vines used in this study were located in plots that had been deficit-irrigated at 35 or 70% of estimated water demand (ET_c) for seven consecutive growing seasons (2011–2016) and in the trial perimeter that had been fully-irrigated for four consecutive growing seasons (2013–2016). Each year, the soil in the entire vineyard was irrigated to field capacity prior to bud break and at the end of the growing season. Differential irrigation treatments were initiated when berries were ~7 mm in diameter and vines were at growth stage 31 of the modified E-L grapevine growth stage system (Coombe, 1995). Deficit-irrigated plots were irrigated weekly and well-watered vines were irrigated more frequently. Vine water demand was estimated weekly by multiplying reference crop evapotranspiration (ET_r), acquired from a weather station located within 3 km of the study site (http://www.usbr.gov/pn/agrimet/wxdata.html), by a crop coefficient that varied from 0.3 during canopy establishment to 0.8 (Allen et al., 1998; Keller et al., 2016). The vines were planted in north to south oriented rows with 2.4 m between rows and 1.8 m between vines. Shoots were vertically positioned, cordon trained, and spur-pruned annually to ~16 buds/m of cordon. Disease, weed and pest control were managed according to local commercial practices. Additional details about previous year's irrigation treatment amounts and deficit severities were reported in Shellie (2017) and King and Shellie (2016).

The air temperature in the vineyard was measured at ~2 m above the cordon wire at 15-min intervals and recorded on a data logger as hourly averages (HMP50 temperature and humidity probe and CR1000 Campbell, Scientific).

2.2. Vine water status, yield and berry maturity

For the 2016 growing season, water stress severity was quantified weekly by measuring midday leaf water potential (Ψ_{ml}) with a pressure chamber and seasonally by determining the ratio of carbon^{13} to carbon^{12} (δ^{13}) in the juice at harvest following the method described by Shellie (2017). All irrigation treatments were harvested on the same date and harvest date was based upon the soluble solids concentration and titratable acidity of a composite cluster sample as described by Shellie (2017). Yield components and berry maturity were measured at harvest following the methods described by Shellie (2017).

2.3. Bud-forcing conditions and dormancy transitions

Canes were field-sampled from deficit-irrigated and fully-watered plots on 10 sampling dates over a span of 100 days, beginning 30 days prior to harvest. Canes were sampled on 17, 25 Aug; 7 Sept; 3, 17, 27 Oct; and 3, 6, 17, 28 Nov 2016. On the morning of each sampling date, a cane located on a retained spur position with developed periderm was excised from the vine between the second and third basal node and trimmed to contain only basal nodes three through eight. The presence of periderm was deemed a necessary sampling criterion after we observed that single-node segments without periderm decayed prior to bud break during the forcing bio-assay (data not shown). Canes sampled from replicate field plots were combined, transported immediately to the laboratory, and then cut to yield 24 replicate, single-node segments of uniform diameter. The replicate single-node cuttings from each irrigation treatment were placed into separate wet floral blocks located inside a stainless steel tray containing reverse osmosis water. The trays were stored at a constant temperature of 25 °C with a 24 h photoperiod, as described by Londo and Johnson (2014). Each single-node segment was evaluated daily for the presence of bud break [E-L stage 4 (Coombe, 1995)] for up to a maximum of 60 days and was then discarded after bud break was recorded. Cuttings which had not broken bud after 60 days were dissected and visually assessed for viability based on the presence or absence of green tissue. Sample size was adjusted for non-viable buds. When 50% of viable buds did not reach E-L stage 4 within 60 days under forcing conditions, the buds were considered endodormant. Buds collected on field-sampling dates after endodormancy were considered ecodormant if > 50% of viable buds had completed bud break within 60 days under forcing conditions. The potential influence of cluster removal on dormancy transition was evaluated by not removing the clusters from a sub-sample of vines in each irrigation treatment and separately field-sampling these vines in tandem with the harvested vines on each of the six sampling dates after harvest.

2.4. Statistical analysis

2.4.1. Bud break percentage, synchronicity and rate

Bud break data were analyzed as cumulative bud break, using log logistic curves. The curves were created using the drc library (Ritz et al., 2015) on R (ver. 3.3.0, R Foundation for Statistical Computing, Vienna, Austria). Only data collected from viable buds were used. The data were fit into a log logistic curve with three parameters using equation 1:

$$\%Budbreak = 100 \times \frac{d}{1 + e^{[-b \times (\ln t - q)]}} \quad (1)$$

where d is the maximum proportion of bud break reached within 60 days under bud-forcing conditions and ranges from 0 to 1 (resulting in a percent bud break between 0 and 100); t is time in days; q is the inflection point of the log logistic curve, or the time to reach half of the maximum bud break at a given collection date; and b is the slope of the linear combination associated with the logistic curve. Parameters d and b were compared for the irrigation treatments within each collection date based on the more robust standard errors calculated using the sandwich library, as suggested in the drc library (Ritz et al., 2015), with which t tests were performed using the function compParm() and p-values corrected for multiple comparisons using Bonferroni's method. While the influence of parameter d is very clear (% bud break), b represents a synchronicity of bud break, with greater magnitudes meaning less time between the first and last buds to break. In the comparisons, b was scaled to the percent bud break at any given sampling date. To compare timing of bud break, the estimated dose of days to reach 50% bud break (BB_{50}) was calculated. If BB_{50} was not reached within 60 days under forcing conditions (end of data collection period), the estimated time to BB_{50} was plotted as ≥ 60 days, since prediction was not possible. BB_{50} was compared using the function EDcomp() in