



# Carbohydrate distribution during berry ripening of potted grapevines: Impact of water availability and leaf-to-fruit ratio



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## ABSTRACT

Insufficient leaf photoassimilation could allow mobilized carbohydrate reserves to contribute to berry sugar accumulation. However, the extent of this contribution during rapid and slow berry sugar accumulation is undefined. The potential effect of leaf-to-fruit ratio and water availability on carbohydrate reserve distribution in potted Tempranillo grapevines was examined during berry maturation. Within each leaf-to-fruit ratio treatment (full and 50% leaves), vines were grown under full or 50% reduced irrigation regimes. Dry biomass development, and the starch and soluble sugar concentrations were determined in the roots, trunks, stems and leaves. Berry sugar and anthocyanin accumulation were also assessed. Under full irrigation, no starch remobilization from roots was observed, regardless of the leaf-to-fruit ratio. Under reduced water supply, starch remobilization from roots was concurrent with rapid berry sugar accumulation, especially in grapevines with low leaf-to-fruit ratio. Soluble sugar accumulation coincided with starch depletion in the roots of grapevines under reduced water availability. When berry sugar accumulation slowed, an increase in carbohydrates was observed in the roots. Sustained water constraints during rapid berry sugar accumulation resulted in a forced reliance on stored carbohydrates to support berry sugar accumulation, but did not significantly alter the tempo of berry sugar and anthocyanin accumulation. A reduced leaf-to-fruit ratio intensified the reliance of fruit sugar accumulation on stored carbohydrates. Besides the importance of post-harvest carbohydrate reserve replenishment when root carbohydrate reserves are depleted during berry maturation, the reserves are also refilled during maturation when berry sugar accumulation slows. This study showed distinctly that root carbohydrate replenishment could already start a few weeks before harvest, and this replenishment could be important when the post-harvest carbon assimilation period is ineffective.

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## 1. Introduction

Leaf-to-fruit ratio and vine water status are parameters likely to influence vine carbon balance during berry maturation (i.e. the berry sugar accumulation phase). Abiotic factors such as temperature, light intensity, and water could limit vine carbon assimilation by restricting leaf photoassimilation (Escalona et al., 1999), while reduced leaf-to-fruit ratios, up to a point, could result in an increase

of leaf photosynthetic activity (Candolfi-Vasconcelos and Koblet, 1991). However, the importance of the contribution of root carbohydrate reserves to support berry sugar accumulation under differing leaf-to-fruit ratios and grapevine water status is still a research question.

Carbohydrates are synthesized by plants through leaf photosynthesis and the effect of the abiotic factors in association with the vine internal competition for carbon, can affect the dynamics of non-structural carbohydrate reserve storage within the grapevine (Holzapfel and Smith 2012). These reserves are distributed to the different plant organs, and the concentration and partitioning within different organs vary throughout the growing season. The distribution of carbohydrates could be affected by soil water availability (soil depth, root implementation and functioning) and soil

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temperature (Dayer et al., 2013; Field et al., 2009; Rogiers et al., 2011a).

Studies have shown that grapevines with higher crop load, and those subjected to elevated water constraint, exhibit reduced carbohydrate reserve concentrations at budburst the following season. Water constraints during the growing season (pre-dawn leaf water potential values below  $-0.6$  MPa), and high crop loads (leaf-to-fruit ratios below  $8 \text{ cm}^2$  leaf area per gram of fruit), have been reported to cause reduced starch concentrations in grapevine trunks during the dormancy period (Dayer et al., 2013). Furthermore, defruiting at the onset of fruit ripening increases total non-structural carbohydrate (TNC) concentration in the roots in subsequent seasons, while a complete defoliation at harvest reduces it (Smith and Holzapfel 2009). No previous studies, to the best of our knowledge, have however investigated the potential effect of the interaction between water availability and leaf-to-fruit ratio on the distribution of non-structural carbohydrate content between the different grapevine organs, during the berry sugar accumulation phase.

Non-structural carbohydrates provide energy and carbon for grapevine growth, and/or are stored as reserves in perennial plant organs. The stored carbohydrates are used for early season vegetative growth until leaf photosynthesis becomes the primary source of carbon, generally around flowering for the grapevine (Zapata et al., 2004). Carbohydrate reserves are also utilized towards the reproductive development, including supporting berry sugar accumulation, as confirmed by  $^{14}\text{C}$  tracing studies (Candolfi-Vasconcelos et al., 1994). Woody tissues, especially perennial roots, also start to accumulate carbohydrates from anthesis, and the crop load influences the continuation of the perennial reserve accumulation during grape maturation (Holzapfel et al., 2010). Due to the involvement of carbohydrate reserves in these various functions, strong competition is expected to exist between the different sinks from véraison (berry softening) and the end of berry sugar accumulation (Davies and Robinson 1996; Wang et al., 2003a).

Carbohydrates are mainly stored as starch in grapevine roots, and this starch can be hydrolyzed to form soluble sugars. During dry conditions, the activity of starch-degrading enzymes, such as  $\alpha$ -amylase, is often found to increase in plant tissues, resulting in starch breakdown, and an increase in soluble sugar concentrations (Jacobsen et al., 1986; Li and Li 2005). The ratio of starch to soluble sugars has been reported to decrease in grapevine perennial organs during water constraints (Rogiers et al., 2011b), as well as following early (Bennett et al., 2005) or late season (Smith and Holzapfel 2009) defoliation.

Similar to sugar accumulation, fruit anthocyanin accumulation also commences at véraison, and normally continues throughout berry maturation (Boss et al., 1996). The accumulation of anthocyanins in the berries is an important contributor to the quality of the fruit from a wine quality perspective. The grapevine water status is one of the major factors known to affect sugar (Wang et al., 2003b) and anthocyanin (Ojeda et al., 2002) accumulation in ripening berries.

The aim of this study was to investigate the interactive effects of leaf-to-fruit ratio and vine water status during the berry sugar accumulation stage on carbohydrate partitioning in perennial and annual grapevine organs. Although starch and/or soluble sugar concentrations at certain stages of the annual grapevine growth cycle (mainly at dormancy, budburst or harvest) have been predominantly reported for the roots and trunks, the kinetic of whole-vine TNC content distribution during the berry sugar accumulation phase is still a research question. The first goal was to determine the combined effect of water constraint and limited leaf-to-fruit ratio on the TNC allocation to perennial and vegetative organs during the berry sugar accumulation phase. The second goal was to quantify the contribution of remobilized starch reserves towards berry sugar content when whole vine leaf photoassimilation becomes

insufficient for sink demands during berry maturation. The last goal was to investigate how the accumulation of fruit sugar and anthocyanins responds when a greater reliance is placed on the starch reserves to support berry sugar accumulation. Experiments were conducted on grapevines grown in large pots, allowing the analysis of whole grapevines and individual organ biomass, including the whole root systems, where carbohydrate distribution was determined as affected by the different treatments (leaf-to-fruit ratio and water availability).

## 2. Materials and methods

### 2.1. Experimental design and treatments

Forty own-rooted *Vitis vinifera* L. cv Tempranillo (clone D8V12) grapevines were used in the 2013/2014 growing season, planted in commercial potting mix soil in 50 L pots. The grapevines were grown in an outside bird proof cage in the warm to very warm climate of the Riverina region (Wagga Wagga, New South Wales, Australia). The three-year-old grapevines were spur pruned to four two-bud spurs in the winter, left with eight primary shoots each, and distributed in four rows of ten vines each, with a three-wire trellis system installed to support the vegetative growth. At fruit set, the total amount of bunches and berries per vine were counted, and vines were crop thinned just after fruit set so that all grapevines were left with six to seven bunches, totaling 400 berries per vine. Prior to the application of the treatments at the onset of véraison (very first sign of berry softening), four randomly selected vines, one per row, were destructively harvested in order to represent  $T_0$  for the population of grapevines. After removal of the four initial vines through destructive harvesting, the nine remaining vines per row were evenly spaced out in the row, resulting in a four row by nine column array, containing three treatment replicates. Two irrigation treatments, two defoliation treatments, and three destructive harvest dates were randomized in the block design. Pressure compensated drip emitters (4 L/hr each) were used for irrigation during the experiment. Rainfall, atmospheric temperature, and relative humidity were recorded and collected from an on-site weather station and vapor pressure deficit (VPD) was calculated. Environmental conditions were summarized for three fortnightly intervals during the experiment, referred to as intervals 1, 2 and 3.

In order to study the interaction between either low or high leaf-to-fruit ratios, and either low or high water availability throughout the berry sugar accumulation phase, four distinct treatments were applied, i.e., low leaf-to-fruit ratio and low water availability (LowL/F:50%); low leaf-to-fruit ratio and high water availability (LowL/F:100%); high leaf-to-fruit ratio and low water availability (HighL/F:50%); high leaf-to-fruit ratio and high water availability (HighL/F:100%). Vines with a low leaf-to-fruit ratio were left with 50% less leaves than those with a high ratio (40 vs 80 leaves). Every second leaf from the base of each shoot was removed until each vine had the desirable amount of leaves. Vines were irrigated three times a day (0730, 1400 and 1800 h), with equal water volume applied each time of the day, ranging between 12 and 20 min of irrigation application time per irrigation event. The higher water availability treatment was conducted with the aim of watering pots each day just to the point of first visual free draining during the midday irrigation, via two irrigation emitters located to the left and right of a vine near the middle of each pot. In the lower water availability treatment, 50% of the water was delivered over the same period, through one irrigation emitter in the middle of the pot. Vines of both leaf-to-fruit ratio treatments received the same water volume within each irrigation treatment. Secondary shoots (laterals), and any newly formed leaves from primary shoots during the course of

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