



Carbon partitioning to berries in water stressed grapevines: The role of active transport in leaves and fruits



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ARTICLE INFO

Article history:

Received 11 April 2014

Received in revised form 4 June 2014

Accepted 7 June 2014

Available online 27 June 2014

Keywords:

Grapevine

Grape berry

Carbon partitioning

Phloem loading

Phloem unloading

Water stress

ABSTRACT

Although imposed water stress is a common agricultural practice worldwide, the physiological and molecular responses of grapevine leaves and fruits, and their interactions, in relation to carbon partitioning remain unknown. We have assessed, in field grown grapevines, the effect of four deficit irrigation regimes, from veraison through to the end of the season, on daily and seasonal non-structural carbon stocks and assimilation in leaves and sugar content in berries, along with the transcript profile for sugar transport proteins in leaves and berries. Average midday xylem water potentials along the season ranged from mild to severe water stress, i.e., -0.7 MPa to -1.05 MPa, respectively. In all the treatments, berries reached equal sugar concentration 20–35 days after veraison because of a proportional effect on berry volume and sugar content per berry. In berries, mild water stress accelerated the sugar accumulation increasing the abundance of *VvSUC27*, *VvHT3* and *VvHT5*, only strictly around veraison. Transcripts abundance in berries did not match sugar uptake rate since, *VvSUC11*, *VvSUC12*, *VvHT5*, as well as the cell wall invertase *VvCWI*, kept rising after berries were filled. In leaves, when berries reached maximal sugar content, export was transiently reduced resulting in starch accumulation. 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. The latter suggests that mild water stress triggers active sugar transport in the source tissues as a means for supporting the sugar accumulation in berries under depressed carbon assimilation by leaves.

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1. Introduction

Carbon partitioning, the process by which reduced carbon is distributed from photosynthesizing leaves to heterotrophic plant organs and tissues, strongly determines plant growth and development, as well as crop yield (Genard et al., 2008). Carbohydrates resulting from the carbon fixation in leaf mesophyll cells are funneled to the various plant organs incapable of complete autotrophy, through the phloem vasculature. Regulatory mechanisms have been described along the carbon partitioning pathways, enabling the coordination in the growth and development of the various plant parts, as well as allowing the interaction between sink and source organs.

The first step in the process of energy delivery, right after photosynthesis, is phloem carbon loading where either active or passive mechanisms have been described. Among the former, one

consist of sucrose and/or polyols channeling to the apoplast, from where they are actively taken by means of proton gradient mediated symporter proteins (Lalonde et al., 2004; Noiraud et al., 2001) and, the other, relies on the build up of carbon polymers from sucrose, incapable of returning back to mesophyll cells but to move forward to the sieve elements (Rennie and Turgeon, 2009). The passive, or so called downstream phloem loading, considered to be a more primitive mechanism, is achieved by the maintenance of high solute concentration in the mesophyll cells so that photosynthates diffuse through plasmodesmata to the sieve elements, and has been described mainly in tree species (Rennie and Turgeon, 2009; Turgeon, 2010). It has been observed that the capacity to adapt to environmental changes, particularly those increasing the potential for carbon supply, as it occurs upon increases in the light availability, is more readily accomplished in apoplastic phloem loader species (Amiard et al., 2005). Such observation suggests that the plasticity of the species to adapt the carbon partitioning to environmental cues might be limited in those relaying solely in anatomical pathways, as it occurs in passive symplastic phloem loaders (Fu et al., 2011). In fact, plasmodesmata

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density is already set in early developmental stages in leaves (Slewisinski and Braun, 2010). Transcription of the sucrose symporter proteins (SUC) in leaves of apoplastic loaders has been proposed as a powerful mechanism to adapt not only to increasing potential for sucrose export, such as that observed upon increases in the light availability but, also, in the opposite, when sink demand decreases. The former, by increasing the transcript levels and the latter by reducing them, both mediated by sucrose as a signal molecule (Ransom-Hodgkins et al., 2003). It has to be stressed, however, that this hypothesis has been experimentally supported by work on apoplastic phloem loading species only (Ainsworth and Bush, 2011).

At the other end, in sink organs, plants have also evolved mechanisms for maintaining the proper carbon supply. The Munch theory explains that carbon delivery occurs by mass flow (Münch, 1930), which depends on the proper pressure gradient along the sugar transit pathway. This means that, besides the need to move sugars into the phloem in leaves, there has to be a capacity to unload it at the sink end, for the gradient to be sustained. Similar to that described in the source phloem side, active and passive strategies have developed in sink tissues and they occur irrespective of the one for phloem loading (Fisher and Oparka, 1996; Patrick, 1997). Besides, one plant organ may switch from one mechanism to other (Godt and Roitsch, 2006; Roitsch, 1999). Precisely, the “sink strength”, interpreted as the capacity of a plant part to predominately attract sugars (Minchin and Thorpe, 1996), often results because of a transition from passive to active phloem carbon unloading. Such change, observed in some fruits, involves the increase in the abundance of transport proteins and H⁺/ATPases in cell membranes, which strongly drops the solute concentration at the phloem end and favors a convenient hydrostatic pressure gradient between the source and the sink. Very importantly, this transitions from passive to active unloading have also been observed upon environmental constraints (Roitsch, 1999; Zhang et al., 2006), conforming a potential mechanism to favor the sugar filling of plant parts, relevant for the species dispersion.

A better knowledge about the mechanisms of adaptation to changes in sink to source ratio is relevant since many environmental factors strongly determine, on one hand the photosynthetic capacity at the canopy level and, on the other, the magnitude of the sink strength, both influencing crop yield and quality (i.e., sugar concentration in fruits). One such complex environmental condition is water stress. Its complexity lies in the fact that it concomitantly reduces photosynthesis and, up to same extent, the size of sink organs. Comparison of results from various reports on water stress effects on carbon partitioning in some species has been difficult due to variations in the time point, duration, and severity of the applied water stress (Roitsch, 1999). Also, most studies on water stress have been made on potted plants in controlled environments with light intensities far below that of ambient or have been focused on partial processes, mechanisms and/or plant parts, leading to hypothesis based on fragmentary obtained data.

Grapevines are of great economical importance, and imposed water stress is a worldwide common agronomical practice because of its convenient effect on red wine quality. Even though grapevines, depending on the variety, are known as water stress resistant plants, according to Flexas et al. (2002), a decline in photosynthesis due to either regulation or damage is observed under different water stress levels. Effects range from simple declines in stomatal conductance to non-reversible effects upon re-watering of plants (Flexas et al., 1999). Therefore, the extent of the water restriction will strongly determine the source to sink relation of plants during grape berry ripening. At the leaf level, despite being a species candidate for symplastic phloem loading,

transcripts of genes coding for sucrose transport have been identified and thought to act as phloem carbon loaders (Davies et al., 1999). At the fruit level, grapevines are a well-characterized model species in terms of the strength of the berries as sugar sinks (Lemoine et al., 2013) where sucrose and hexose transporters, as well as cell wall invertases, have been identified (Afoufa-Bastien et al., 2010; Hayes et al., 2007). Berry growth follows a double-sigmoid curve with three distinct phases: (a) a first rapid growth phase where cell division occurs; (b) a lag phase with little change in berry size in which seed size and fresh weight reaches its maximum and; (c) a second rapid growth phase, whose transition from the lag phase is known as veraison, characterized by changes in colour, flesh softening, acidity and, most importantly, sugar accumulation, mainly as fructose and glucose (Coombe, 1992; Coombe and McCarthy, 2000). In grapes, a shift from a symplastic to an apoplastic phloem unloading pathway is known to occur around veraison leading to a massive import of hexoses (Zhang et al., 2006). In the present study, treatments of water stress were imposed right around veraison in order to restrict source and sink activities mainly to leaves and berries respectively.

Here we report on the water stress effect on carbon partitioning in field grown grapevines, simultaneously assessing carbon assimilation, storage and exportation at the leaf level, grape berry sugar filling kinetics and the transcript profile for sugar transporter proteins in leaves and fruits. Results are discussed in terms of the possible adaptations in both, sink and source organs, as well as their interaction.

2. Materials and methods

2.1. Plant material and experimental design

The experiment was carried out on 12 years old, own rooted, *Vitis vinifera* plants cv. Carmenere, in a commercial vineyard grown under a Mediterranean climate (with no summer rains) in the Maipo Valley in central Chile (33° 42'S, 70° 35'W), during the 2011–2012 growing season. Grapevines were trained to a vertical system with a Guyot double pruning method with nearly north–south oriented rows and a planting density of 5000 plants ha⁻¹. The vineyard was irrigated by conventional drip irrigation.

There were five blocks, one per row, and each containing all the treatments. In each, row four separated groups of five homogenous vines were selected. Each group of plants corresponded to one treatment, in which every plant of the group was irrigated with the same combination of drip emitters. No rain occurred throughout the experiment.

2.2. Leaf water status and gas exchange measurements

Four irrigation treatments were established by means of using a combination of drip emitters with different water volumes, resulting in T1: 1 mm h⁻¹; T2: 2 mm h⁻¹; T3: 4 mm h⁻¹; T4: 6 mm h⁻¹. Irrigation regimes were applied from few days before veraison through the end of the season, twice a week, with water volumes corresponding to 15% (T1), 30% (T2), 60% (T3) and 90% (T4) of the ETc, respectively, and resulting in a seasonal average midday stem water potential ranging from –1.1 MPa to –0.7 MPa for the extreme treatments T1 and T4, respectively. Irrigation of the vineyard, before the beginning of the experiment, was scheduled to maintain midday stem water potential values of –0.9 MPa. Plant water status was monitored weekly by measuring midday stem water potential of fully mature leaves bagged with a plastic sheet and covered with aluminum foil for at least 2 h before measurements (Fulton et al., 2001).

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