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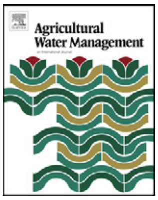

Responses of leaf night transpiration to drought stress in *Vitis vinifera* L.

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ABSTRACT

Night-time transpiration (E_{night}) is potentially an important factor affecting whole-plant water balance and, thus, water use efficiency. The aims of the present study were: to evaluate night-time changes of stomatal conductance (g_{night}) and transpiration under different soil water availability conditions for seven grapevine cultivars and to compare leaf-level estimates of night-time water losses with more realistic whole-plant estimates in plants growing outdoors. Two experiments were conducted on seven grapevine cultivars (*Vitis vinifera* L.) growing in pots maintained at field capacity and drought stress conditions. Night transpiration was evaluated by leaf gas exchange and plant mass measurements. Results showed that E_{night} and g_{night} were far above cuticular values, suggesting sustained stomatal aperture during night-time which was reduced under drought stress. Differences between cultivars were found in the extent of drought stress-induced reduction of E_{night} (from a 36% reduction in Escursac to 82% in Malvasia). However, transpiration losses calculated on the basis of leaf gas exchange measurements often over-estimated the actual whole plant water loss, suggesting the presence of some water inputs to pots/plants during the night, presumably due to dew deposition. Significant stomatal opening persists during the night in irrigated grapevines, leading to substantial water losses by transpiration. Those water losses are significantly reduced under drought stress. It is remarkable that night-time plant water losses can be partially or fully compensated by dew deposition. Therefore, instantaneous leaf gas exchange measurements can result in an over-estimation of the night water losses. The present study shows for the first time that night transpiration due to partially open stomata can be compensated by dew deposition.

1. Introduction

Water scarcity is one of the major limitations for current agriculture (Araus, 2004; Morison et al., 2008) and viticulture production worldwide (Chaves et al., 2007). Climate change predictions suggest that drought will become an even greater problem during the next 50 years (IPPC, 2007; European Environmental Agency, 2010). For instance, Schultz (2000) predicted for the European viticultural area that a two-fold increase in atmospheric CO_2 levels would result in reductions of soil water availability ranging from 20% in Central Europe to 70% in the Iberian Peninsula and the Balearic Islands. According to this scenario, reducing water use for irrigation and increasing water use efficiency (WUE, as the yield to water consumption ratio) has become a major priority in agricultural and viticultural research (Morison et al., 2008).

In grapevines, many studies have focused on WUE responses to different degrees of drought stress (Bota et al., 2001; Flexas et al., 2002; Souza et al., 2003; Pou et al., 2008; Zsófi et al., 2009), intercultivar differences in WUE (Bota et al., 2001; Gibberd et al., 2001; Gaudillère et al., 2002; Tomás et al., 2012) and the effects of rootstock on WUE (Satisha et al., 2006). Most of these studies have been undertaken at the leaf scale, during daytime and using indicators of the leaf intrinsic WUE (e.g., the ratio of net photosynthesis to stomatal conductance, A_N/g_s, or the ^{13}C isotopic ratio in leaf dry matter, $\delta^{13}C$). However, as Schultz and Stoll (2010) recently pointed out, intrinsic WUE does not always relate to instantaneous real WUE (i.e., the ratio of net photosynthesis to transpiration, A_N/E), due to complex interactions of stomatal closure with leaf temperature and vapor-pressure deficit. Most importantly, leaf-scale A_N/E often does not reflect the whole-plant WUE (WUE_{plant}), i.e. the ratio of yield biomass to water consumption (Flexas et al., 2010; Schultz and Stoll, 2010). Accordingly, we have shown that, although leaf-level WUE increases under drought stress in many cultivars,

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Abbreviations: Ψ_{PD}, predawn leaf water potential; Ψ_{MD}, midday leaf water potential; Ψ_{stem}, midday stem water potential; g_s, stomatal conductance; A_N, leaf net photosynthesis; E, leaf transpiration rate; g_{cut}, cuticular conductance; E_{cut}, cuticular transpiration; g_{night}, night stomatal conductance; E_{night}, night transpiration; T_{leaf}, leaf temperature; SWC, soil water content; A_N/g_s, intrinsic water use efficiency; A_N/E, instantaneous water use efficiency; WUE_{leaf}, leaf water use efficiency; WUE_{plant}, plant water use efficiency; $VPD_{ambient}$, air vapour-pressure deficit; $T_{ambient}$, ambient temperature; C_i, internal CO_2 concentration.

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WUE_{plant} may increase only slightly, remain the same or even decrease (Tomás et al., 2012). This is counterintuitive, since day-time photosynthesis constitutes the only source of plant carbon gain, and day-time transpiration the largest source of water losses. Therefore, discrepancies between WUE_{leaf} and WUE_{plant} may arise from night-time water losses and from daily carbon losses, (i.e. plant respiration), the latter occurring not only in leaves but in all plant organs. The effects of drought stress on WUE_{plant} are further complicated by the fact that plant growth and fruit development are also distinctly affected by soil water availability (Medrano et al., 2003). Despite the potential importance of night-time transpiration and respiration for the whole plant carbon balance and WUE_{plant} under drought stress, these night fluxes have been scarcely studied in grapevines. (Flexas et al., 2010; Schultz and Stoll, 2010; Escalona et al., 2012).

Regarding night-time water losses, water transpired through the cuticle could contribute to total water losses, which certainly would lower whole day-scaled WUE_{leaf} given the fact that cuticles are almost impermeable to CO_2 diffusion (Boyer et al., 1997). This would mean that water is lost without any gain in photosynthesis. Nevertheless, cuticular conductance to water vapor is generally very low ($5\,mmol\,H_2O\,m^{-2}\,s^{-1}$ or less) in *Vitis* (Boyer et al., 1997; Flexas et al., 2009). However, contrary to previous thoughts, stomatal conductance can be maintained during night-time when no photosynthesis occurs, constituting a significant source of water loss and hence reducing WUE in many species (Caird et al., 2007a,b). According to several reports, nocturnal transpiration due to partial stomatal opening at night-time can constitute a significant source of water loss and reduced WUE in many species, including crop (Caird et al., 2007b; Easlon and Richards, 2009; Rogiers et al., 2009) and non-crop species (Barbour and Buckley, 2007; Cavender-Bares et al., 2007; Dawson et al., 2007; Kavanagh et al., 2007; Marks and Lechowicz, 2007; Moore et al., 2008; Howard and Donovan, 2009). Although the physiological basis of g_{night} is poorly understood, it is known that g_{night} responds to similar internal and external factors as daytime g_s, including CO_2 levels, abscisic acid (ABA), wind speed, drought stress and vapor pressure deficit (Leymarie et al., 1998; Caird et al., 2007b; Kavanagh et al., 2007; Chu et al., 2009; Easlon and Richards, 2009; Flexas et al., 2010; Zeppel et al., 2012). For grapevines, data of g_{night} and night transpiration (E_{night}) are scarce. Rogiers et al. (2009), showed g_{night} values of $15–25\,mmol\,H_2O\,m^{-2}\,s^{-1}$ in anisohydric cultivars such as Semillon and Chardonnay (E_{night} values of $22–32\,mmol\,H_2O\,m^{-2}\,s^{-1}$). In the same study, much lower values close to cuticular conductance (g_{night} ca. $50\,mmol\,H_2O\,m^{-2}\,s^{-1}$) were reported for isohydric cultivars as Grenache (E_{night} values of $<10\,mmol\,H_2O\,m^{-2}\,s^{-1}$). Flexas et al. (2010), showed somewhat higher g_{night} values in irrigated Tempranillo and Manto Negro (both isohydric cultivars), ranging from $33\,mmol\,H_2O\,m^{-2}\,s^{-1}$ in Manto Negro (a drought-tolerant cultivar) to $107\,mmol\,H_2O\,m^{-2}\,s^{-1}$ in Tempranillo (less drought-tolerant). Under moderate drought stress, g_{night} values were significantly reduced to 9 and $19\,mmol\,H_2O\,m^{-2}\,s^{-1}$ for Manto Negro and Tempranillo, respectively. Under well-irrigated conditions, values for E_{night} ranged from 0.3 to $1.2\,mmol\,H_2O\,m^{-2}\,s^{-1}$, representing a substantial loss of water at night-time. By scaling up from these values, a typical individual grapevine plant with $6\,m^2$ of leaf area would lose from 1 to 4 L of water during a 9-h night. It is important to note that, with the exception of the study by Caird et al. (2007b), in field-grown *Lycoperscon esculentum* and preliminary data presented by Flexas et al. (2010), on *Vitis vinifera*, most of these reports were based on studies with potted plants in growth chambers. Since the conditions in growth chambers often include low relative humidity of air due to drying air by the thermoregulatory system, night-time transpiration rates may have been exacerbated as compared with field conditions, where air humidity can be high at night and dew is often deposited on leaves.

Therefore, preliminary data of grapevines and other species provide evidence that night-time transpiration can be an important component of whole-plant water balance (i.e., WUE), particularly under drought stress conditions. Nevertheless, similarly as for WUE, estimates of E_{night}, at leaf-scale may not necessarily correlate with whole-plant water losses. Total plant water balance is relatively easy to determine in potted plants by weighing them over time (mini-lysimeters).

The specific aims of the present study were to: (i) evaluate night-time changes in stomatal conductance and transpiration associated with changes in environmental conditions and soil water availability; (ii) to elucidate differences in these parameters among grapevine cultivars under irrigation and drought; and (iii) to compare leaf-level estimates of night water losses with more realistic whole-plant measurements in plants growing outdoors, in order to envisage the importance of night time transpiration for daily water losses in grapevines under environmental conditions in the field.

2. Materials and methods

Two main experiments were conducted: the first was designed to test how general is the occurrence of g_{night} and E_{night} and their relevance under drought stress in different grapevine cultivars, and thee second was aimed to obtain a more detailed study of the nocturnal dynamics of g_{night} and E_{night}, according to drought stress levels, and to compare the leaf level and whole-plant level estimates of night-time water balance.

2.1. Experiment 1

2.1.1. Plant material and treatments

The experiment was carried out in the summer of 2010 at the experimental site of the University of Balearic Islands (Spain) (39°38′14.73″N lat., 2°38′51.21″E long.). Environmental conditions were typical of Mediterranean areas.

Seven cultivars of *V. vinifera* L. were used: Cabernet Sauvignon, Pinot Noir, Tempranillo, Malvasía, Grenache, and two local cultivars, Manto Negro and Escursac. We used own-rooted material to avoid any effect of the rootstock on cultivar-specific differences on leaf gas exchange. Ungrafted plants were rooted in the greenhouse as follows: 50 shoot portions per cultivar with two buds were immersed in an Indolbutiric solution ($2\,g\,L^{-1}$ dissolved in ethanol:H_2O 50:50, Panreac) for 30 s. All material was previously disinfected with a Captan solution for 3 h and hydrated for 24 h. Rooted plants were placed in horticultural substrate Prohumin (Projar SA, Valencia, Spain), heated at 27–30 °C, and maintained at fixed ambient conditions (80% relative humidity, and 25 °C of air temperature). Shoots were transplanted into 16 L pots containing a mix of horticulture substrate and perlite (3:1), and placed outside in the experimental field of UIB (Mallorca) in April 2010. Plants were maintained outdoors during the growing season, the experiment was performed in the month of July. Only plants with high and uniform stem vigour were selected for the experiment for a total of ten plants per treatment per cultivar. At the beginning of the experiment, total leaf area was homogenized by elimination of some basal leaves in specific plants, all plants presented one main shoot 1.5 m length with 20–22 mature leaves and 5 young developing leaves.

Two soil water level treatments were imposed: (i) Field capacity, in which plants were watered every day to saturation; and (ii) moderate drought stress, where irrigation was stopped at the beginning of the experiment until the maximum g_s reached $75\,mmol\,H_2O\,m^{-2}\,s^{-1}$ as described by Medrano et al. (2002). Once this drought stress level was reached, it was kept constant for 30 days by replenishing the same amount of water lost by the plants the previous day (as monitored every day of the experiment