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Variability of water use efficiency in grapevines

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ABSTRACT

Predictions of climate change indicate an increase in water scarcity in Mediterranean areas. Therefore, improving water use efficiency (*WUE*) becomes crucial for sustainable viticulture in the Mediterranean for both grapevine growth and fruit productivity. Variability of *WUE* between cultivars presents an opportunity to select the most appropriate cultivars in viticultural areas with increasing aridity. In this review, an update on the variability of *WUE* in different grapevine cultivars and environmental conditions is presented.

Most studies on *WUE* are focused at the leaf level and frequently used to estimate whole-plant *WUE*. However, there are large discrepancies when scaling-up *WUE* from leaf to whole-plant level. There are several structural and physiological processes, not included in leaf *WUE* measurements, considered as possible factors to solve the gap between leaf and whole-plant *WUE*. Canopy structure and plant respiration are described as the most important components involved in whole-plant *WUE* regulation, and proposed as potential targets for its improvement.

1. Introduction

Grapevine is one of the most widespread crops worldwide (7.59 Mha in 2011; OIV, 2011). Europe presents the largest vineyard area in the world (around 38%), mostly located in Mediterranean areas (Fraga et al., 2013; Mullins et al., 1992). With more than 10.000 cropped varieties, it is reputed for its large genetic variability and adaptation to a wide range of climatic conditions, from temperate to semi-arid and tropical (Kliewer and Gates, 1987; Mullins et al., 1992). Along its range of cropping environmental conditions, soil water availability has also been described as one of the most important constrains limiting grape growth production and fruit quality (Williams and Matthews, 1990).

According to climate change models, an expected twofold increase of the current CO_2 atmospheric levels would lead to an increase in temperature leading to a decrease of water availability, especially in Mediterranean areas (IPCC, 2007; Schultz, 2000). Moreover, the combined effect of drought with periods of high air temperature and high evaporative demand during the grapevine growing season could have a negative effect not only to its productivity but also to its berries and wine quality when environmental conditions are limiting (Chaves et al., 2007; Costa et al., 2007; Escalona et al., 1999). It has been widely reported that the effect of these stress promote dramatic reductions in plant carbon assimilation due to a severe decline of photosynthesis, as well as to a partial loss of canopy leaf area (Chaves et al., 2003, 2007; Flexas et al., 1998, 2002; Maroco et al., 2002; Santos et al., 2007). Consequently, irrigation practices have been progressively implemented especially in the "New World" of viticulture and are becoming more common in Mediterranean areas where grapevine was classically a rain fed crop. Irrigation entails an increasing demand of water which could become environmentally unsustainable in the near future. As a consequence, the evaluation and improvement of water use efficiency (*WUE*) is an important research subject for grapevine crop (Chaves et al., 2007; Flexas et al., 2010; Tomás et al., 2012).

The term *WUE* reflects the balance between production (kg of biomass produced or moles of CO_2 assimilated) and water costs (m^3 of water used or moles of water transpired). This balance can be measured at different space levels from leaves to whole-plant or crop; or at different time scales, from minutes (instantaneous exchange of water vapor for carbon dioxide) to months (i.e., biomass accumulation or yield) (Flexas et al., 2010; Medrano et al., 2010; Morison et al., 2008). At the leaf level, *WUE* can be determined by gas exchange measurements or carbon isotope ratio of leaf dry matter. In the shorter term, it is common to use instantaneous leaf gas exchange measurements, relating net CO_2 assimilation rate (A_N) either to stomatal conductance

Abbreviations: A_N/g_s, intrinsic water use efficiency; A_N/E, instantaneous water use efficiency; $\delta^{13}C$, carbon isotope composition; *WUE*, water use efficiency; WUE_l, leaf water use efficiency; WUE_{WP}, whole-plant water use efficiency.

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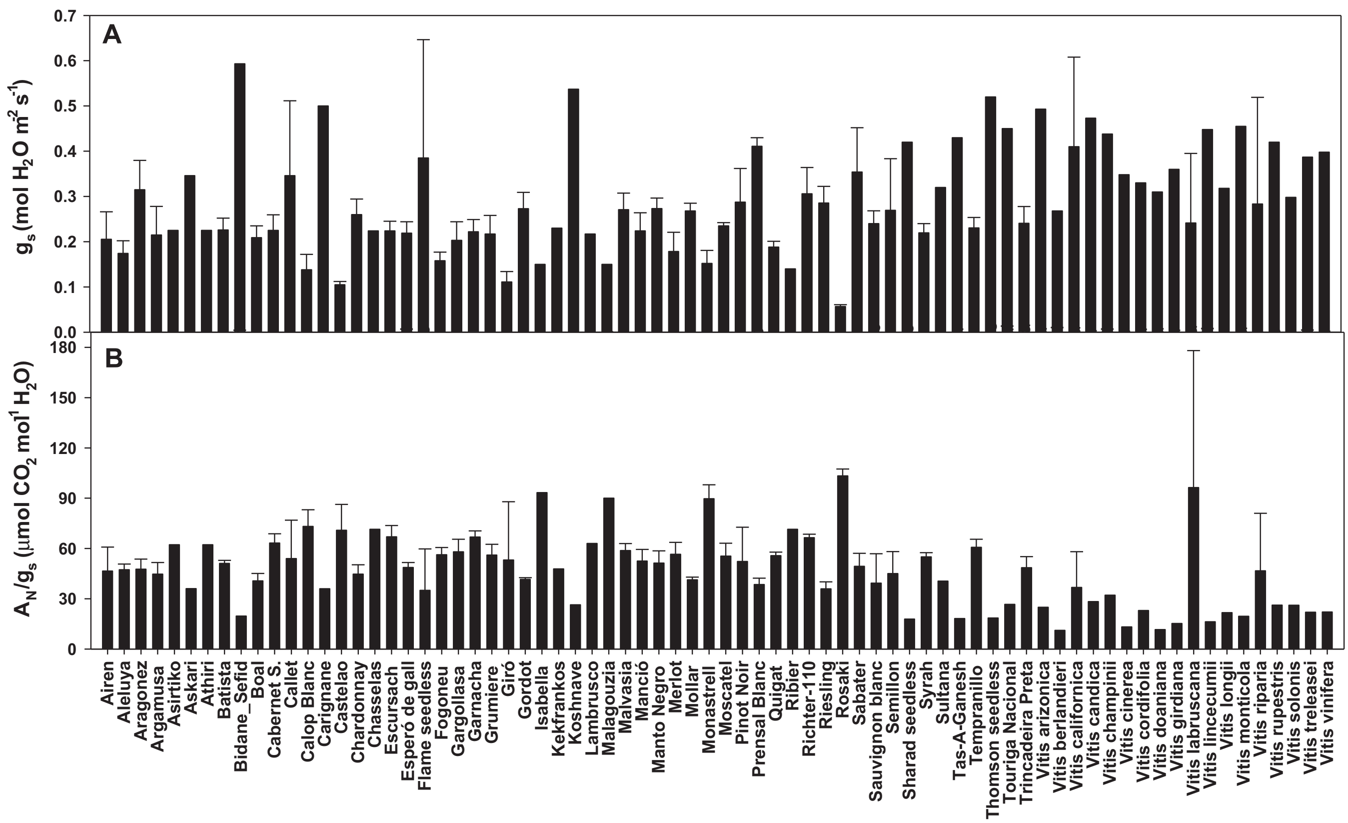

Fig. 1. Average ± SE values for (A) stomatal conductance (g_s) and (B) intrinsic water use efficiency (A_N/g_s) (B) in different grapevine cultivars under irrigation. Bars are average ± SE of published results. Data have been compiled from the following references: Baigorri et al. (2001), Bota et al. (2001), Chaves et al. (2007, 2010), Correia et al. (1995), Costa et al. (2012), De la Hera et al. (2007), Dobrowsky et al. (2005), Downton et al. (1987), Escalona et al. (1999, 2003), Flexas et al. (1999, 2009), Ghaderi et al. (2011), Gómez-del-Campo et al. (2002, 2004, 2007), Liu et al. (1978), Maroco et al. (2002), Moutinho-Pereira et al. (2004), Naor and Wample (1994b), Naor et al. (1994a), Padgett-Johnson et al. (2000, 2003), Patakas et al. (2003a,b, 2005), Poni et al. (1993, 2009), Pou et al. (2008, 2012), Quick et al. (1992), Rodrigues et al. (1993), Rogiers et al. (2009, 2011), Rogiers and Simon (2013), Romero et al. (2012), Santesteban et al. (2009), Satisha et al. (2006), Schultz (2003), Schultz and Stoll (2010), Sivilotti et al. (2005), Souza et al. (2005), Tomás et al. (2012), Winkel and Rambal (1993), Zsófi et al. (2009), and Zufferey et al. (2000).

(g_s) – i.e., the so-called intrinsic water use efficiency (WUE_i), or to leaf transpiration rate (E) – defined as instantaneous water use efficiency (WUE_{inst}) (Fischer and Turner, 1978). These two parameters, A_N/g_s and A_N/E, are mostly used to characterize genetic and environmental effects, respectively (Chaves and Oliveira, 2004; Flexas et al., 2004; Galmés et al., 2007; Morison et al., 2008). The carbon isotope ratio of leaf dry matter ($\delta^{13}C$) is used to assess long-term variations in leaf *WUE* (WUE_l) (Condon et al., 2004; Morison et al., 2008) and it is also commonly used to assess differences between genotypes (Chaves et al., 2007; Gibberd et al., 2001; Tomás et al., 2012). At the whole-plant level, WUE_{WP} is defined as the balance between the plant's dry matter production and its water consumption. For grapevines in particular, this term is much less studied than WUE_l parameters or the carbon isotope ratio of berry dry matter ($\delta^{13}C$) (Chaves et al., 2007; Souza et al., 2005). However, scarce studies have tested the validity of leaf level parameters as reliable indicators of WUE_{WP}.

Within this context, the aim of the present review is to summarize the current knowledge on variations of grapevine *WUE* in response to different environmental conditions and genotypes. Particular emphasis is pointed to the advances and difficulties for scaling up from instantaneous leaf level estimates to larger whole-plant WUE_{WP} parameters.

2. Genetic variability of water use efficiency at leaf level

Large intra-specific variability of WUE_l has been described in grapevines (Fig. 1) (Bota et al., 2001; Costa et al., 2012; Gaudillère et al., 2002; Gómez-Alonso and García-Romero, 2010; Koundouras et al., 2008; Pou et al., 2008; Prieto et al., 2010; Rogiers et al., 2011; Schultz, 2003; Souza et al., 2005; Tomás et al., 2012; Zsófi et al., 2009). This variability can be inferred from the different responses of leaf gas exchange parameters, A_N and g_s, involved in carbon and water economy, respectively. In grapevines, a non-linear relationship between A_N and g_s has been reported suggesting that the diversity of WUE_l is mostly related to variations in g_s (Chaves et al., 2007; Escalona et al., 1999; Flexas et al., 2002, 2010; Medrano et al., 2012). In fact, this is further confirmed from the observation of genetic variability of A_N/g_s and its two individual components (Fig. 2). A general trend is observed in Fig. 2A consisting of a negative correlation between g_s and A_N/g_s when pooling numerous

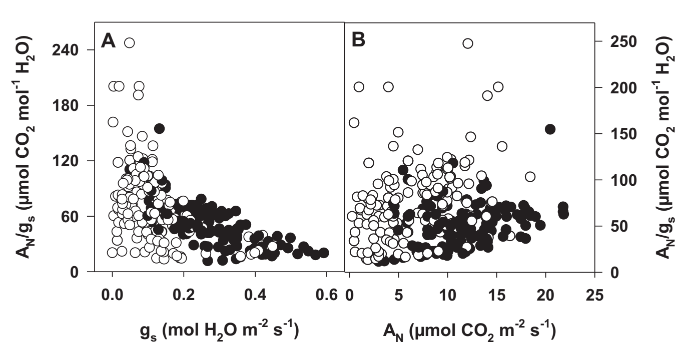

Fig. 2. The relationship between intrinsic water use efficiency (A_N/g_s) and (A) stomatal conductance (g_s) and (B) net CO_2 assimilation (A_N). Data are pooled for different grapevine cultivars under irrigation (filled symbols) or water stress (open symbols). Data have been compiled from references of Fig. 1.