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Commentary

# Does homeostasis or disturbance of homeostasis in minimum leaf water potential explain the isohydric versus anisohydric behavior of *Vitis vinifera* L. cultivars?

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Due to the diurnal and seasonal fluctuations in leaf-to-air vapor pressure deficit ($D$), one of the key regulatory roles played by stomata is to limit transpiration-induced leaf water deficit. Different types of plants are known to vary in the sensitivity of stomatal conductance ($g_s$) to $D$ with important consequences for their survival and growth. Plants that minimize any increase in transpiration with increasing $D$ have a tight stomatal regulation of a constant minimum leaf water potential ($\Psi_{leaf}$); these plants are termed as 'isohydric' (Stocker 1956). Plants that have less control of $\Psi_{leaf}$ have been termed as 'anisohydric' (Tardieu and Simonneau 1998). Isohydric plants maintain a constant $\Psi_{leaf}$ by reducing $g_s$ and transpiration under drought stress. Therefore, as drought pushes soil water potential ($\Psi_{soil}$) below this $\Psi_{leaf}$ set point, the plant can no longer extract water for gas exchange. Anisohydric plants allow $\Psi_{leaf}$ to decrease with rising $D$, reaching a much lower $\Psi_{leaf}$ in droughted plants relative to well-watered plants (Tardieu and Simonneau 1998), so this strategy produces a gradient between $\Psi_{soil}$ and $\Psi_{leaf}$ that allows gas exchange to continue over a greater decline in $\Psi_{soil}$. Thus, anisohydric plants sustain longer periods of transpiration and photosynthesis, even under large soil water deficit, and are thought to be more drought tolerant than isohydric species (McDowell 2011).

In practice, the distinctions between isohydric and anisohydric strategies are often not clear (Franks et al. 2007), even among different cultivars of the same species. For example, cultivars of poplar (Hinckley et al. 1994) and grapevine (Schultz 2003, Lovisolo et al. 2010) have been shown to exhibit both contrasting hydraulic behaviors. A third mode of behavior was also suggested by Franks et al. (2007), in which the difference between soil and midday water potential ($\Psi_{soil} - \Psi_{leaf}$) is maintained seasonally constant but $\Psi_{leaf}$ fluctuates in synchrony with soil water availability (isohydrodynamic behavior). The lack of a clear distinction between these two strategies and the complex and variable responses of stomata to $D$ under high and low soil moisture is depicted in two papers in this issue (Rogiers et al. 2012 and Zhang et al. 2012), showing that even typically anisohydric grape (*Vitis vinifera* L.) cultivars (Semillon and Merlot, respectively) may constrain $g_s$ during periods of extremely low $\Psi_{soil}$. The same individuals can switch from an isohydric-like behavior when transpiration is low to an anisohydric-like behavior with increasing water demand. Interestingly, both studies indicated that classifying species as either isohydric or anisohydric is a simplistic view of stomatal functioning and does not represent well the complex stomatal behavior under drying soil, and Zhang et al. (2012) also reported an isohydrodynamic behavior. Both studies suggested that when soil water is limited, $g_s$ is aimed at protecting the integrity of the hydraulic system, whereas as soil water content increases, stomata regulate transpiration less. The results of Zhang et al. (2012) indicated that under limited soil moisture the decrease in $g_s$ with increasing $D$ was proportional to reference $g_s$ ($g_s$ at $D = 1$ kPa); which is in agreement with the stomata-sensitivity model developed by Oren et al. (1999) for isohydric species (see xeric line in Figure 1A). However, a significant departure from this theoretical model was observed under high soil moisture (see wet and mesic lines in Figure 1B). Similarly, in this issue Rogiers et al. (2012) showed that under

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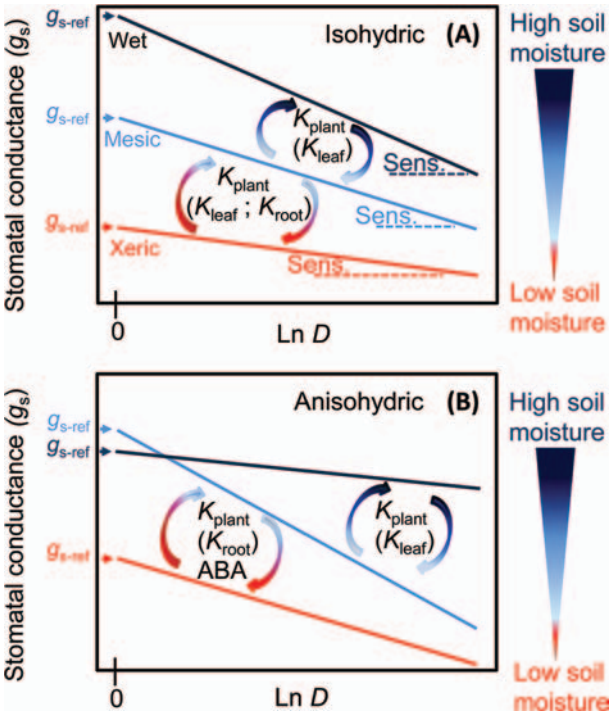


Figure 1. Responses of light-saturated stomatal conductance ($g_s$) to water vapor pressure deficit ($D$) as a function of soil moisture (wet, mesic, xeric) in (A) isohydric and (B) anisohydric species as depicted in two papers in this issue (Rogiers et al. 2012 and Zhang et al. 2012). For isohydric species and under saturated light, Oren et al. (1999) showed that the decrease in $g_s$ with increasing $D$ is proportional to $g_s$ at low $D$. Therefore, the sensitivity (*Sens.*) of the stomatal response to $D$ can be determined by fitting the data to the functional form: $g_s = g_{s-ref}$ - *Sens.* × ln($D$) where $g_{s-ref}$ (designated as reference stomatal conductance) is $g_s$ at $D = 1$ kPa (ln$D = 0$), and *Sens.* is the rate of stomatal closure and reflects the sensitivity of $g_s$ to $D$ [$-dg_s/d\ln D$, in mmol m$^{-2}$ s$^{-1}$ ln(kPa)$^{-1}$]. The slope, -*Sens.* is proportional to $g_{s-ref}$ with the proportionality averaging 0.60 across a wide range of species (Oren et al. 1999). For isohydric species (A), it has been shown that $g_{s-ref}$ and *Sens.* are both a function of soil moisture and whole-plant hydraulic conductance ($K_{plant}$) (Domec et al. 2009). For anisohydric species (B), $g_{s-ref}$ and stomatal sensitivity to $D$ can decrease as soil moisture increases and that the same individuals can switch from an anisohydric-like behavior when soil water moisture content is high to an isohydric-like behavior when soil water is low (Rogiers et al. 2012, Zhang et al. (2012). In this issue, Zhang et al. (2012) attributed the departure from an anisohydric to isohydric behavior to whole-plant hydraulic conductance $K_{plant}$ and Rogiers et al. (2012) to the combined effect of $K_{plant}$ and hormonal signaling on $g_s$ by suggesting that the limited soil moisture induced an increase in endogenous ABA, which in turn triggered the increase in stomatal responsiveness to $D$. To go further, we propose that $K_{plant}$ is driven by change in leaf hydraulic conductance ($K_{leaf}$) when soil moisture is high, and by root hydraulic conductance ($K_{root}$) when soil moisture is low and that based on the results from Rogiers et al. (2012), the $K_{root}$-induced decline in $K_{plant}$ in dry soil acted in concert with ABA production to close stomata.

natural conditions, stomatal sensitivity to $D$ increased under dry soil conditions and that, as in Zhang et al. (2012), stomatal sensitivity to $D$ was proportional to reference $g_s$. Specifically, Rogiers et al. (2012) demonstrated that reference $g_s$ decreased in most treatments with increasing soil moisture, meaning that vines exhibited a high stomatal sensitivity to $D$ in very dry soils but not in wet soils (see xeric, mesic and wet lines in Figure 1B). Although Rogiers et al. (2012) also showed that stomatal sensitivity to $D$ increased with reference $g_s$, their slope was higher than the previously reported generic value of –0.6 based on the Oren et al. (1999) hydraulic model. Rogiers et al. (2012) attributed this departure to the combined effect of leaf hydraulic and hormonal signaling on $g_s$ (Figure 1B). Their results suggested that the limited soil moisture induced an increase in endogenous abscisic acid (ABA), which in turn triggered the increase in stomatal responsiveness to $D$. The stomatal closure in both studies likely occurred in response to a decrease in leaf or stem hydraulic conductance, but other factors cannot be excluded. Feed-forward behavior of stomata with respect to regulation of $\Psi_{leaf}$ has been attributed to the presence of chemical signals brought to the leaf in the transpiration stream (Davies et al. 1994). Thus, a combination of hydraulic and hormonal signal in some species could be a mechanism allowing some species to switch from an isohydric to anisohydric behavior.

The existence of both isohydric and anisohydric behaviors raises the question of what the costs are for species that operate at more negative $\Psi_{leaf}$ under drought. Compared with isohydric species, anisohydric species maintain carbon assimilation at higher rates as drought intensifies, but this strategy may put anisohydric plants at greater risk of xylem dysfunction if drought is sufficiently intense to push $\Psi_{soil}$ below water potentials that would induce hydraulic failure (Hoffmann et al. 2011, McDowell 2011). Potential drawbacks associated with lower $\Psi_{leaf}$ include a decrease in xylem conductivity due to embolism and a requirement for increased lignin investment in both xylem and leaf structure to resist tension-induced xylem collapse (see Hacke et al. 2001, Blackman et al. 2010). It makes sense that some plants have the potential to switch from an isohydric to anisohydric behavior in order to maximize carbon gain when soil moisture is available and limit plant desiccation when soil moisture is low. Recently, another grape variety, Shiraz, which has been traditionally classified as anisohydric, exhibited isohydric stomatal behavior in dry soils (Collins et al. 2010). These studies raise questions concerning the nature of the mechanisms involved in both stomatal strategies and how the same individuals can switch from one to the other. We can also wonder if such behavior is typical of cultivated grapevines or if it can be extended to lianas in general and perhaps to other plant species.

The underlying mechanism of the so-called 'humidity response', where stomatal conductance decreases with increasing $D$, remains unknown (Jones 1998, Meinzer 2002). Most of the mechanisms used to explain isohydric behavior are based on stomatal sensitivity to changes in $D$ or soil moisture. However, there are several other potential mechanisms that can help in maintaining seasonal constancy of

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plant water status, including the utilization of stored water or the changes in transpiring surface area as shown in Zhang et al. (2012), where increases in whole-plant leaf-specific hydraulic conductance ($K_{plant}$) were, at least partially, explained by a reduction in the leaf surface during the dry season. Stomata react to prevent embolism at different levels of $\Psi_{leaf}$, and so the mechanisms controlling stomatal closure also involve differences in hydraulic architecture in the leaves: the onset of leaf vein cavitation makes $\Psi_{leaf}$ drop sharply to maintain the same transpiration rate and thus acts as a signal for stomatal closure (Brodribb and Jordan 2008, Johnson et al. 2009). Evidence that stomata are able to sense and respond rapidly to xylem cavitation, or to changes in $K_{plant}$ associated with dynamics of embolism (Cochard et al. 2002, Domec et al. 2006), implies that embolism in certain plant organs and species, including grapevine, may play a rather different role than was originally believed (Zwieniecki et al. 2000). Chouzouri and Schultz (2005) and more recently, Zufferey et al. (2011) showed that there was a good correlation between drought resistance and vulnerability to embolism in several grapevine cultivars of different geographic origin, and that the decrease in $g_s$ occurred concomitantly with an increase in cavitation events for all varieties, as soil water availability became restricted. Therefore, isohydric and anisohydric behavior under well-watered and water-stressed conditions may be explained by differences in $K_{plant}$ on both a seasonal basis, as soil water varies in time, and on a diurnal basis, as $D$ varies while soil water availability remains nearly constant (Domec et al. 2009). While differences in stomatal behavior in these two strategies may be best explained at the whole-plant level, $K_{plant}$ reflects the conductance of various plant organs (leaves, stems and roots), which can be investigated individually to search for the mechanistic basis of isohydric versus anisohydric behavior (Figure 1A and B). Because of the crucial importance of leaf hydraulic conductance ($K_{leaf}$) in determining $g_s$ and its sensitivity to water potential (Brodribb and Jordan 2008), variation in leaf hydraulics and its components in response to water availability should receive greater attention in studies aimed at understanding isohydric versus anisohydric behavior (Figure 1A and B). It seems that leaf cavitation plays an important role as a 'hydraulic fuse', thereby limiting leaf transpiration and the propagation of embolism and preserving the integrity of other organs (Chen et al. 2010, Johnson et al. 2011). For example, can we predict that species with a hydraulic design limited by $K_{leaf}$ should be better suited to supply water evenly to the leaf, which should increase stomatal sensitivity to environmental changes (Figure 1A)? Although vine species are characterized by a very efficient water transport system, those species also seem to have developed mechanisms allowing them to refill and repair damaged vessels (Zufferey et al. 2011). As suggested by McDowell (2011), and in this issue by Rogiers et al. (2012) and Zhang et al. (2012), anisohydric species may be more susceptible than isohydric species to drought-related mortality induced by hydraulic failure. However, it has been reported that in general, anisohydric plants are better adapted to drier environments because of their more cavitation-resistant xylem (McDowell 2011, Hoffmann et al. 2011), or maybe by some (still) unknown refilling mechanisms (Lovisolo et al. 2008). Can we therefore identify xylem structural features that confer morphological advantages, allowing $\Psi_{leaf}$ to approach leaf vein cavitation thresholds without incurring damage from xylem hydraulic failure? To answer such questions, an empirical approach combined with a stomatal hydro-mechanical model is essential (Schultz 2003, Franks et al. 2007). This will provide a better understanding of the complex signals (both chemical and hydraulic) underlying the multi-sensory behavior of stomata.

As suggested by the results of Rogiers et al. (2012), the isohydric and anisohydric stomatal behaviors of grapevine varieties in response to slowly developing water stress imply very different strategies in terms of water use. In countries (mostly in Europe) where irrigation is prohibited when grapes are grown for wine making, varieties that cannot switch from an anisohydric to isohydric behavior may be at risk. Under future climates with potential reductions in precipitation and an increase in the intensity of summer drought, irrigation may play an essential, even if controversial, role in viticulture (Lovisolo et al. 2010), to maintain cultivation of some grapevine varieties for wine production.

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## Conflict of interest

None declared.

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