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REVIEWS

Opinion

Iso/Anisohydry: A Plant–Environment Interaction Rather Than a Simple Hydraulic Trait

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Plants are frequently classified as isohydric or anisohydric in an attempt to portray their water relations strategy or ecological niche. However, despite the popularity of the iso/anisohydric classification, the underlying biology remains unclear. We use here a simple hydraulic model and the extensive literature on grapevine hydraulics to illustrate that the iso/anisohydric classification of a plant depends on the definition used and the environment in which it is grown, rather than describing an intrinsic property of the plant itself. We argue that abandoning the iso/anisohydric terminology and returning to a more fundamental hydraulic framework would provide a stronger foundation for species comparisons and ecological predictions.

Trends

In recent years there have been a growing number of studies that use the terminology isohydric or anisohydric to portray plant hydraulic strategies.

These classifications are considered to derive from genetic differences and are thus used for species comparison and modeling.

There is more than one definition of isohydrocity, and the different definitions are not always in agreement.

The Iso/Anisohydric Terminology – More Than One Meaning

The iso/anisohydric terminology was introduced by Berger Landefeldt [1] to describe the daily patterns of water relations (Figure 1A), distinguishing plant species based on their ability to decouple their leaf water potential (Ψ_l) (see Glossary) from atmospheric demand. The terminology was rarely mentioned in the 60 years that followed its creation, but was reintroduced in the 1990s [2,3] when isohydric was used to describe plants that maintain a constant daily minimal leaf water potential (Ψ_{min}) regardless of the pre-dawn soil water potential (Ψ_{soil}), and anisohydric to describe plants that exhibit progressively lower Ψ_{min} as a function of lower Ψ_{soil}. Thus, the modern use of the iso/anisohydric terminology normally refers to water management under long-term drought (Figure 1B).

Originally it was presumed that species could be classified as either isohydric or anisohydric and that understanding the classification of a species would allow us to deduce underlying physiological characteristics, much like the difference between cold- and warm-blooded animals. For example, Tardieu and Simonneau [3] proposed that qualitative differences in abscisic acid signaling of stomatal closure could be the source of the difference between isohydric and anisohydric plants. That idea was first called into question when plants belonging to the same species (*Vitis vinifera*) showed large differences in their isohydrocity [4]. Later, multispecies comparisons showed that species are ordered on a continuum rather than a dichotomy, and also that very few species – if any at all – conform strictly to definitions of isohydric or anisohydric [5,6]. Nonetheless, the wish to frame Ψ_l and transpiration (E) dynamics into a unified concept that could be used for species comparison across studies and predictions of ecological patterns continues to motivate the use of the terminology, with over 50 publications referencing iso/anisohydric in 2015 alone (Figure 2).

However, survey of this literature reveals that a diversity of interpretations lies under the umbrella of the iso/anisohydric concept (Table 1). The definition of Tardieu and Simonneau

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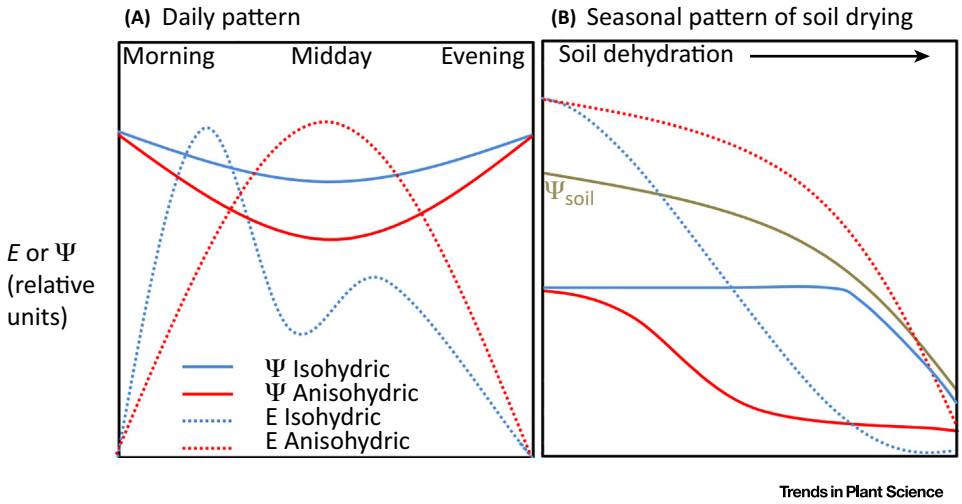

Figure 1. The Iso/Anisohydric Concept (A) as Described in Berger Lendelfeldt (1936) [1] and (B) as Commonly Described Today (Tardieu and Simmoneau, 1998 [3]). Berger Lendelfeldt made use of the terms to distinguish between the daily patterns of transpiration (*E*) and water potential (Ψ). In its modern use the terminology normally refers to the relationship between the soil water potential (Ψ_{soil}) and the minimal daily leaf water potential (Ψ_{min}) in datasets collected over long periods.

Glossary

Ψ: water potential.
Ψ_l: leaf water potential.
Ψ_{crit}: the critical leaf water potential the plant is avoiding, evident through stomatal closure.
Ψ_{min}: minimum daily leaf water potential.
Ψ_{soil}: soil water potential.
Ψ_{PD}: pre-dawn leaf water potential – a common proxy for Ψ_{soil}.
Ψ_{TLP}: the leaf water potential at turgor loss point.
$\Delta\Psi$: the difference between Ψ_{min} and Ψ_{PD}.
σ: slope of the $\Psi_{min} \sim \Psi_{soil}$ regression.
A_{max}: maximal assimilation.
E_{max}: maximal transpiration.
g_s: stomatal conductance.
***k*:** hydraulic conductance of the soil to leaf flow pathway.
***k*(Ψ_{soil}):** the response function of *k* to Ψ_{soil}.
k_{plant}: plant hydraulic conductance.

[3] is still the most common, but some studies have resurrected the original definition of Berger Landefeldt [1], using the g_s (stomatal conductance) response to vapor pressure deficit (VPD; e.g., [7]). In addition, following the notion that g_s is the major regulator of Ψ_l, the range of phenomena referenced by this terminology has grown to include g_s response to Ψ_l or Ψ_{soil} (where isohydric are characterized by tighter stomatal closure; e.g., [8,9]). Furthermore, the goal of comparing species behavior collected from various studies led to the development of quantitative (and continuous) measures of the iso/anisohydric degree [5,6] as opposed to the initial qualitative definition by Tardieu and Simonneau [3]. For the evaluation of the isohydrocity of a species, Klein [5] focused on daily fluctuation in Ψ_l, using either the difference of

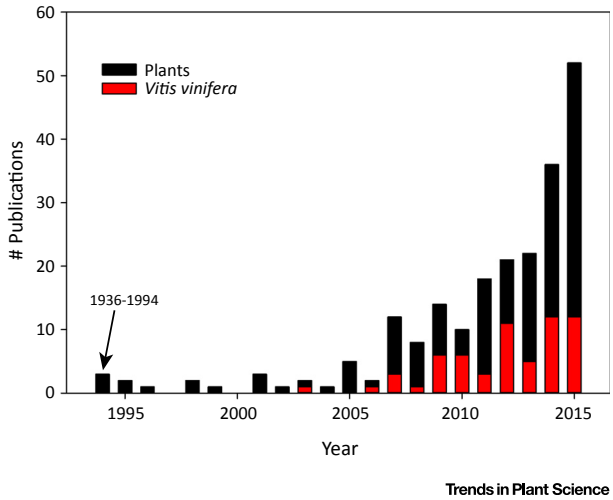

Figure 2. Number of Publications Dealing with Iso/Anisohydric Phenomenon in the Past 80 Years for All Species (Black) and Grapevines (*Vitis vinifera*; Red). Data were collected from the Web of Science database (https://clarivate.com/products/web-of-science/) using the 'collect citation report' function as described in the supplementary methods (see Methods in the supplemental information online). *The 1994 column represents the three publications between 1936 and 1994.

Table 1. The Variability of the Iso/Anisohydric Terminology with Notable Mentions

Definition	Isohydric	Anisohydric	Refs
Daily fluctuation in leaf water content or water potential in response to VPD	'Small' fluctuations	'Large' fluctuation	[1]
The ability (or its lack) to maintain constant Ψ_{MD} when Ψ_{soil} declines	Constant Ψ_{MD} in response to decreasing Ψ_{soil}	Decreasing Ψ_{MD} in response to decreasing Ψ_{soil}	[2,3]
Daily $\Delta\Psi = \Psi_{PD} - \Psi_{MD}$	'Small' $\Delta\Psi$	'Large' $\Delta\Psi$	[5]
Analysis of the regression of g_s versus Ψ_{min} or Ψ_{soil}	Stomatal closure at low $\Psi_{min/soil}$	Stomatal closure at high $\Psi_{min/soil}$	[9]
σ (the slope of Ψ_{MD} vs Ψ_{PD})	$\sigma < 1$	$\sigma > 1$	[6]
Hydroscape area: area of triangle bounded by the regression line, *y* axis, and 1:1 line in a plot of Ψ_{MD} versus Ψ_{MD}	'Small' hydroscape area	'Large' hydroscape area	[25]

$\Psi_{PD} - \Psi_{min}$ in a given day ($\Delta\Psi$; MPa) or the Ψ_l leading to 25% of maximal stomatal conductance ($\Psi g_s 25$). Martínez-Vilalta *et al*. [6] focused on long-term drought, using the slope (σ; MPa MPa^{-1}) of the $\Psi_{min} \sim \Psi_{soil}$ regression. It is important to mention that most studies, including the above, use predawn water potential (Ψ_{PD}) and midday water potential as a proxy for Ψ_{soil} and Ψ_{min}.

Both Klein [5] and Martinez-Vilalta *et al*. [6] used the literature to test the iso/anisohydric concept over dozens of species, ordering them according to an iso/anisohydric continuum. In some cases the different approaches led to a difference in the isohydrocity assigned to a given species. For example, the average $\Delta\Psi$ of grapevines (0.84 MPa) suggest that they are more isohydric than other woody species (trees) that, on average, exhibit $\Delta\Psi$ = 1.63 MPa (Figure 3A) [5]. However, their σ (=0.73 MPa MPa^{-1}) suggests that their degree of isohydrocity is similar to the average of other species (Figure 3B) [6]. Accordingly, when Martínez-Vilalta and Garcia Forner [10] classified 102 species based on these different metrics they resulted in very different species rankings across the iso/anisohydric continuum depending on the classification parameter that was used.

Furthermore, although most definitions assume that iso- versus anisohydric behavior arises from differences in the 'tightness' of stomatal regulation of transpiration, the meta-analysis of Martínez-Vilalta and Garcia Forner [10] containing many species found low correlation between g_s and several different isohydrocity definitions. Additionally, Coupel-Ledru *et al*. [11] showed that, in a Syrah × Grenache progeny of 186 genotypes, there was no significant correlation between *E* and $\Delta\Psi$ or Ψ_{min}, highlighting the existence of a large variability in hydraulic conductance (***k***) within the progeny. It therefore appears that variability in hydraulic factors other than stomatal regulation (e.g., *k* and *E*), could lead to disagreement between different definitions, and that for a comprehensive description of the plant hydraulic properties we need to include $\Delta\Psi$, *E*, and also *k*.

The discrepancies between classifications arrived at by different definitions is not surprising when viewed through the lens of a minimal hydraulic model (Box 1, Figure 4, and Figure S1 in the supplemental information online). In the case where $\boldsymbol{E_{max}}$ and *k* are conserved between plants, and only variation in Ψ_{crit} occurs, the different definitions of iso/anisohydric yield consistent classifications (shown in Figure 4A). To explore the case where Ψ_{crit}, E_{max}, and *k* can vary, we plot the behavior of five simulated plants (numbered P1 to P5 in Figure 4B) across which these variables are systematically varied, and consider the rankings that result from different definitions. Based on σ (as in Martínez-Vilalta *et al*. [6]; with σ values calculated for $-0.5 < \Psi_{soil} < 0$), the isohydrocity degree of the five simulated plants is P5 > P1 = P2 = P3 = P4, the largest being the most

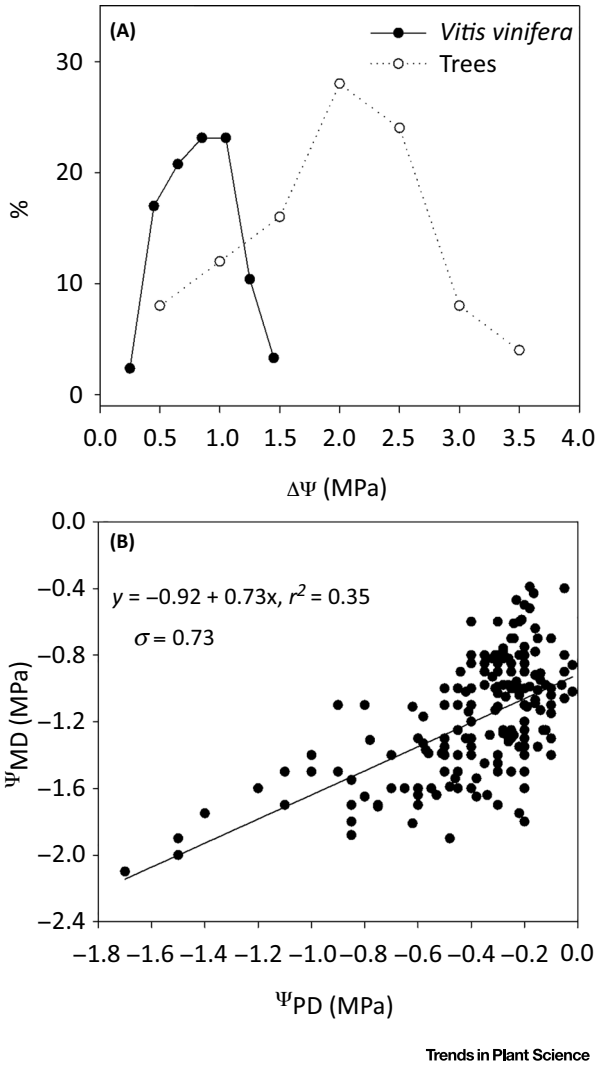

Figure 3. Comparing the Isohydrocity of Grapevines Using (A) the Frequency (%) of the Difference between Midday Water Potential and Predawn Water Potential ($\Delta\Psi$; as in [5]), and (B) the Slope of the Relationship between the Midday ~ Predawn Water Potentials (σ; as in [10]). *Vitis vinifera* appears to be very isohydric compared to 25 species of trees according to $\Delta\Psi$, but not according to σ. The trees database was taken from [5] and that of *Vitis vinifera* from the *Vitis vinifera* hydraulic database (see Methods in the supplemental information online).

isohydric. However, the isohydrocity of the same plants could also be ranked P3 > P1 = P4 > P2 = P5 based on $\Delta\Psi$ ($\Delta\Psi$ values were taken for $\Psi_{soil} = 0$), or P5 > P2 > P1 = P4 > P3 based on $\Psi g_s 25$ (as in Klein [5]). In addition, Figure 4B shows that σ and $\Delta\Psi$ vary with Ψ_{soil}, reflecting the dependence of these parameters and the environment. Thus, even if we were to agree on a single definition (as suggested by Martínez-Vilalta and Garcia-Forner [10]), there is still the issue that hydraulic parameters related to the iso/anisohydric terminology are not solely determined by the genotype, but also by the environment.

Plant Water Relations Largely Depend on the Environment: Evidence from Grapevine Hydraulic Data

One of the challenges in comparing data from multiple studies is that they contain both environmental and genotypic variability that are difficult to separate from one another. One solution would be to look for studies on the same genotype conducted over a range of environmental conditions.

Box 1. A Model of the Relationship between Ψ_{soil}, Ψ_l, and E_{max}

We present a minimal model based on Darcy's law to describe the dynamics of plant water potential and the relationship between water potential and transpiration. Our goal is to encompass the diversity of plant water relations with a minimum of input parameters. The central assumptions of the model are (i) no out-of-phase terms (i.e., no storage), and (ii) E is regulated to prevent Ψ_l from falling below a critical water potential (Ψ_{crit}). Assumption ii is based on the model of Sperry *et al*. [35] that assumes stomata are regulated to avoid the Ψ_{crit} that results in turgor loss or catastrophic cavitation. In support, many studies have linked stomatal closure with these physiological characteristics (e.g., [36]), highlighting the existence of Ψ_{crit}. The inputs to the model are the maximum transpiration (E_{max}), the soil-to-canopy hydraulic conductance (k), Ψ_{crit}, and Ψ_{soil}.

The model calculates the minimum Ψ_l during a day (Ψ_{min}) based on the maximum daily transpiration (E_{max}), which is the maximum E subject to the constraint of maintaining $\Psi_{min} \geq \Psi_{crit}$:

$$\Psi_{min} = \Psi_{soil} - \frac{E_{max}}{k(\Psi_{soil})} \quad \text{[Equation I]}$$

To incorporate the effects of soil drying on soil hydraulic conductance, the hydraulic conductance function was empirically fitted from Simonin *et al*. [37] and defined as:

$$k(\Psi_{soil}) = \frac{1}{\Psi_{soil}^2 + 0.5} \quad \text{[Equation II]}$$

The model shows that all four parameters have a major effect on the daily drop in water potential ($\Delta\Psi$). Ψ_{soil} and Ψ_{crit} are the upper and lower thresholds that define the maximal daily $\Delta\Psi$, whereas k is the slope that determines how far E will drive the daily decline of Ψ_l. The combination of $\Delta\Psi$, k, and E determines if Ψ_{crit} will be reached (Figure 4). Results from the model using different combinations of the output parameters show a variety of possible patterns of behavior that highlight environmental effects and expose discrepancies between the different iso/anisohydric definitions (Figure 4; discussed in the main text).

Grapevine (*Vitis vinifera* L.) is ideally suited for such an analysis because it is one of the best-studied species owing to its high economic value and the known effect of irrigation on berry quality [12,13]. In addition, the growing demand for wine has resulted in the propagation of popular wine cultivars in very different environments, creating an excellent opportunity for studying the effect of factors such as environment, rootstock, and season on plant hydraulics [9].

Variability in the regulation of g_s and Ψ_l between environments and cultivars of grapevine has been measured and discussed for almost half a century [14], but the iso/anisohydric terminology was relatively recently introduced into grapevine research [4] to distinguish between the hydraulics of Grenach and Shiraz (=Syrah). Since then over 60 publications have used the terminology in grape research (Figure 2), mostly to compare cultivars (e.g., [15–17]). Usage of the terminology has evolved to a stage where specific cultivars are routinely described as being iso/anisohydric even when Ψ_l is not measured [8,18]. An implicit assumption of this classification is that plant hydraulic behavior is determined solely by the genotype.

However, of the four inputs to our simple hydraulic model (Box 1), only Ψ_{crit} is entirely a physiological parameter. The other three are either pure environmental factors (Ψ_{soil}) or contain major environmental components (for k and E_{max}, soil conductance and VPD, respectively). Thus, it is not surprising that $\Delta\Psi$ histograms of Grenach and Shiraz sampled over different environments overlap (Figure 5). This does not undermine the findings of several authors that showed significant hydraulic differences between these cultivars under similar conditions [4,7], but instead demonstrates that the environment plays a dominant role compared to the genotype. In a similar manner, Cabernet Sauvignon was shown to have a constant Ψ_{min} under deteriorating Ψ_{soil} in one experiment [16], but a gradually lower Ψ_{min} in another [19], probably due to differences in E_{max} or k. This was further supported by Tramontini *et al.* [20] who showed that the water relations of Shiraz and Cabernet Sauvignon varied significantly depending on the hydraulic properties of the soil in which they were grown, with the soil effect being as significant as that presented by the cultivar. In addition, Merli *et al*. [21] showed that water relations in Sangiovese change according to the rootstock on which it is grafted.

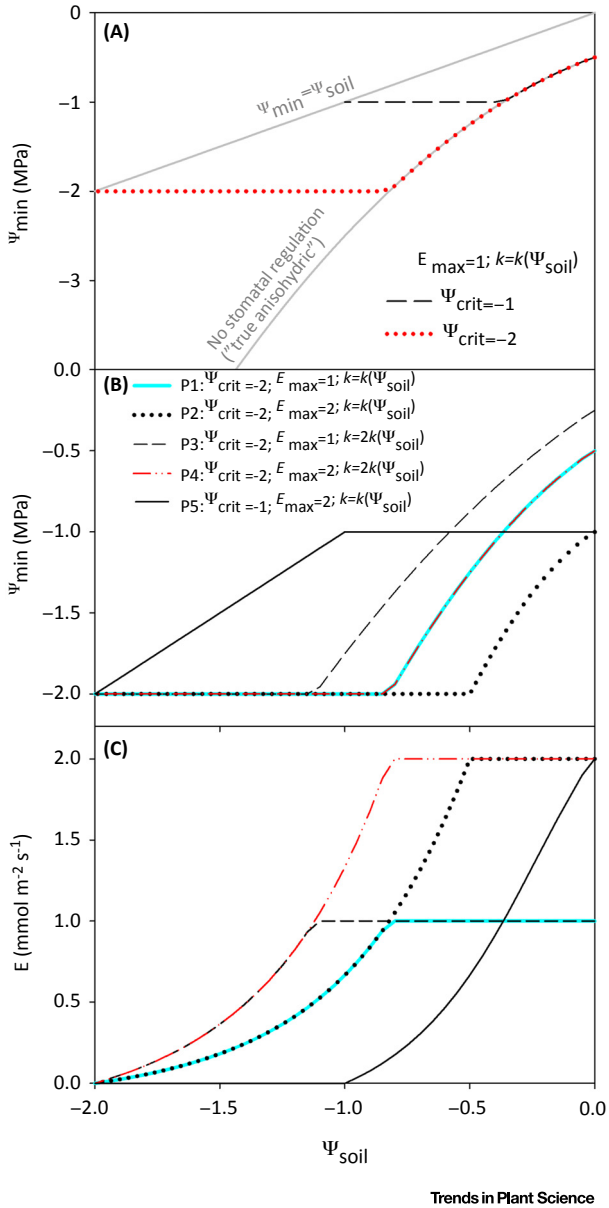

Figure 4. Model (see Box 1) Calculation of the Minimal Daily Water Potential (Ψ_{min}; A,B) and the Maximal Transpiration (E_{max}; C) as a Function of Ψ_{soil}. The model illustrates (A) scenarios where Ψ_{crit} is different, but E_{max} and the soil–canopy conductance function $\boldsymbol{k(\Psi_{soil})}$ are the same; (B,C) scenarios where $k(\Psi_{soil})$ and E_{max} are different but Ψ_{crit} is the same. E_{max} was calculated to satisfy $\Psi_{min} \geq \Psi_{crit}$. The grey lines in A present the upper ($\Psi_{min} = \Psi_{soil}$) and lower (no regulation of E_{max}) boundaries for Ψ_{min}. The model calculation for each Ψ_{soil} is presented in Figure S1. The calculated values when $\Psi_{crit} = 1$ or $\Psi_{crit} = 2$ appear as blue lines in Figure S1. The initial E_{max} values ($E_{max} = 1$ or $E_{max} = 2$) appear as green lines in Figure S1. An example for the calculation of a plant bearing $\Psi_{crit} = -2$ MPa, $E_{max} = 1$, and $k = k(\Psi_{soil})$ (cyan) is presented in Figure S1 as cyan squares.

The major effect of the environment is evident in the model (Box 1 and Figures 4 and S1), which shows how variation in Ψ_{soil} leads to significantly different hydraulic behavior. Specifically, under well-watered conditions (i.e., $\Psi_{min} > \Psi_{crit}$), plants will be anisohydric following most definitions. According to the model parameters, when Ψ_{soil} is above −0.5 MPa, plants exhibit high daily $\Delta\Psi$, high σ (Figure 4A,B), and unregulated transpiration (Figure 4C). Conversely, when Ψ_{soil} is below −0.5 MPa, low daily $\Delta\Psi$, low σ, and downregulation of transpiration are expected.

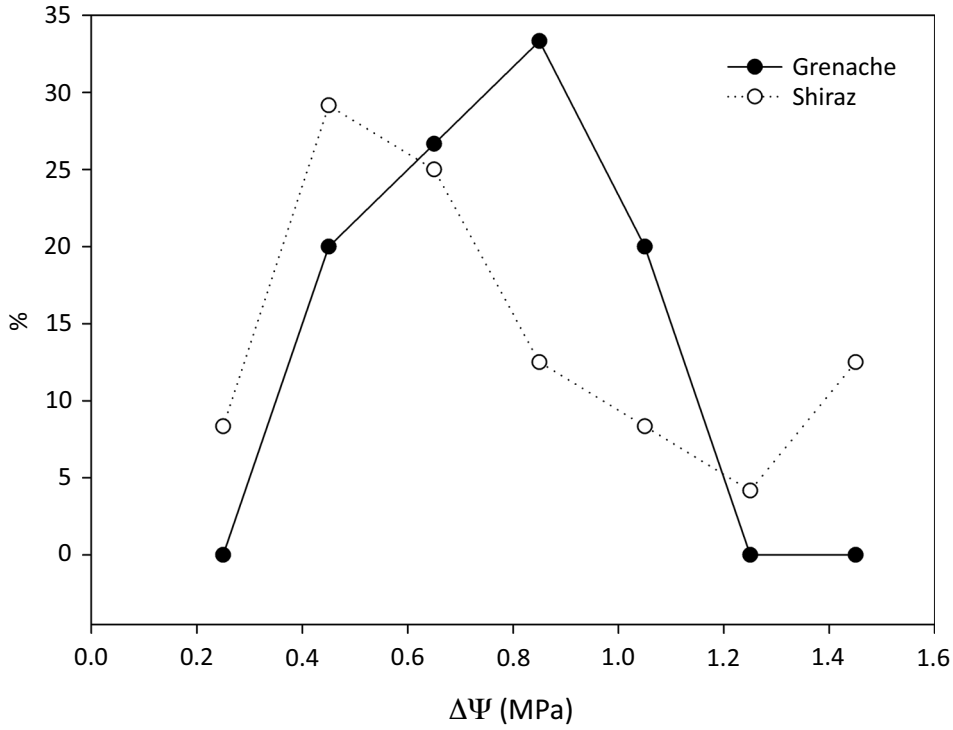

Figure 5. Comparison of the $\Delta\Psi$ Frequency (%) between Grenache and Shiraz. Data taken from the *Vitis vinifera* hydraulic database (Table S1 and Methods in the supplemental information online).

Vineyard measurements support this prediction: grapevines downregulate their transpiration in response to high VPD under water deficit, but not under well-watered conditions [22,23]. In addition, Poni *et al*. [24] have shown that Sangiovese had a very anisohydric σ (>1) when $\Psi_{PD} > -0.6$ MPa, but a very isohydric σ (~0) when Ψ_{PD} was between −0.6 MPa and −1.1 MPa. Similar results for eight different species were obtained by Meinzer *et al*. [25], who showed that σ is significantly larger under high Ψ_{PD} (compared to low Ψ_{PD}). These findings suggest that plants shift from anisohydric to isohydric depending on Ψ_{soil} [26], and that increasing the size of a dataset (i.e., across a wider range of Ψ_{soil}) might lead to a change in classification. Considering the large effect of the environment it appears that, for proper characterization of the genotypic effect, basic physiological characteristics should be studied rather than the degree of water potential homeostasis (or its lacking) observed under specific conditions.

Back to the Future: Reconnecting with the Basic Concepts of Plant Hydraulics

Twenty years into the iso/anisohydric discussion, it is still unclear which term (isohydric or anisohydric) represents species that favor wet versus dry environments, underscoring both the difficulty of reducing plant hydraulics to a single axis of variation and the artificiality of the iso/anisohydric spectrum. In general, we expect that more detailed characterization of plant hydraulic function will be necessary to understand the ability of a plant to cope with water limitation. Nevertheless, identifying what constitutes a minimal set of water relations parameters that enable meaningful comparison of multiple species, and that could potentially be used to model plant behavior, remains an important goal. One possibility might be to reshape iso/anisohydric into a more biologically robust concept – as recently proposed [10,25].

To this end, Meinzer *et al*. [25] investigated the $\Psi_{PD} \sim \Psi_{MD}$ relationship of eight species in controlled environmental conditions (pots in greenhouse), allowing minimal environmental effects and comparison of genotypic differences. To assure the complete relevant range of Ψ_{PD} the authors dried the plants for ~40 days. They defined isohydrocity in relation to the area between the 1:1 line ($\Psi_{PD} = \Psi_{MD}$) and the slope of the regression only when Ψ_{PD} leads to stomatal closure and restriction of transpiration (with larger areas being associated with less stringent stomatal control of Ψ and thus more anisohydric behavior; Table 1). The analysis showed that there is a good correlation between this definition of isohydrocity and turgor loss point ($\boldsymbol{\Psi_{TLP}}$). Given the difficulty and time required for the experiments required by this definition, it would seem simpler and more robust to focus investigations into differences between plant hydraulic strategies on the physical parameters (e.g., Ψ_{TLP}) that contribute to, rather than the behaviors that derive from, plant–environment interactions. In the context of the minimal hydraulic model presented here, we should seek the biological components of Ψ_{crit}, E_{max}, and k.

For example, categorizing plant species based on their Ψ_{TLP} provides numeric evaluation of plant hydraulics using well-defined concepts. The acquisition of Ψ_{TLP} (or assuming negative turgor, the buckling point [27]) is much easier than the long dehydration experiments that are necessary for reliable $\Psi_{PD} \sim \Psi_{MD}$ relation analysis. More importantly, Ψ_{TLP} is known to define the operating range of many species [28] and is closely linked with stomatal regulation [29]. In fact, there is evidence that during dehydration the reduction in turgor pressure can define much of the down regulation in g_s [30,31], presenting Ψ_{TLP} as a promising candidate for Ψ_{crit}. Thus, for ecological predictions or modeling Ψ_{TLP} can be used as a good indicator for stomatal closure.

A combination of Ψ_{TLP} with xylem hydraulic characteristics [maximal hydraulic conductance ($\boldsymbol{k_{plant}}$) or xylem vulnerability to embolism] could better capture plant performance under water stress, although they require more complicated measurement protocols [32]. k_{plant} defines the ability of a plant to transpire while avoiding Ψ_{TLP}. Because there is a strong correlation between transpiration and assimilation (A), the combination of k_{plant} and Ψ_{TLP} could be used as an indicator for maximal productivity in water-abundant environments (when $\Psi_{soil} \sim 0$). Modifying Equation I in Box 1 to predict maximal assimilation ($\boldsymbol{A_{max}}$) based on maximal transpiration (E_{max}), assuming $\Psi_{crit} = \Psi_{TLP}$, can be expressed as:

$$A_{max} \approx E_{max} = \Psi_{TLP} \times k_{plant} \quad \text{[Equation 1]}$$

Alternatively, to understand species ability to survive prolonged droughts, Ψ_{TLP} could be combined with the xylem vulnerability curve to understand the margin between stomatal closure and mortality [33]: normally high xylem resistance to cavitation will lead to improved survival under water limitation [34]. It should be stressed that these represent minimal sets of parameters for addressing specific types of questions. Many other plant characteristics (e.g., chlorophyll content, carboxylation efficiency, hydraulic capacitance, etc.) may need to be evaluated to develop a deep understanding of the ability of species to cope with water limitation.

In conclusion, the discrepancy between different definitions of the iso/anisohydric classifications, together with the major effects that environmental factors have on water relations, suggest that the iso/anisohydric terminology should be abandoned. Discussing plant hydraulics in the frame of the suggested model (E_{max}, k, and Ψ_{crit}) rather than the iso/anisohydric terminology would clarify the similarities and differences between genotypes, leaving aside the environmental effect. We believe that defining a plant by its Ψ_{TLP}, or even better when combined with maximal k_{plant} or the xylem vulnerability, provides a richer and more objective perspective than phenomenological classifications such as 'near anisohydric' (see also Outstanding Questions).

Outstanding Questions

Among the different definitions of iso/anisohydric, which is the most useful?

Do these classifications represent biological factors, or are they dominated by the environment in which plants are growing?

Is the degree of water potential homeostasis observed over a time interval of interest (e.g., diurnal to seasonal) a meaningful trait for understanding plant hydraulic strategies?

Which hydraulic traits represent a minimal set for capturing species differences, and therefore may be useful for modeling or ecological predictions?

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Supplemental Information

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