Discrimination ability of leaf and stem water potential at different times of the day through a meta-analysis in grapevine (*Vitis vinifera* L.)

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Abstract

Water potential is considered to be the "gold-standard" measure for plant water status determination. However, there are some discrepancies on how and at what time of the day water potential measurements should be performed in order to obtain meaningful information. The aim of this work is to evaluate the discrimination ability of water potential measurements in grapevines depending on the time of the day and of the measurement procedure (leaf vs. stem). To do so, a meta-analysis was performed using >78,000 measurements of water potential data obtained in field irrigation experiments, provided by 13 research teams working in this subject in Spain. For each measurement day and experiment, Discrimination Ratio (DR) was calculated and used to determine the discrimination ability of each method, and then pooled for comparison. The measurement procedure with the greatest DR can be hypothesised to be the most suitable under the average working conditions. Leaf water potential showed lower DR mean values than predawn or stem water potential. The climatic conditions and the cultivar may affect to the discrimination ability, although the abovementioned trend was always maintained. Leaf water potential in vineyards should therefore be replaced, as a general rule, by either stem or predawn water potential readings, without a clear pre-eminence of the performance of predawn and stem water potential measurements. Building a common dataset and its subsequent meta-analysis has been proved to be an efficient and robust tool to compare plant measurements, and should be implemented for other species and/or measurement procedures.

1. Introduction

Water availability is the most limiting factor for vineyard productivity in arid and semi-arid areas, since water deficit results in (i) significant reductions in yield (Santesteban and Royo, 2006; Van Leeuwen et al., 2018), (ii) lower sugar accumulation (Matthews and Anderson, 1988; Salon et al., 2005; Santesteban and Royo, 2006) and, if severe stress occurs, (iii) impairs wine quality (Van Leeuwen et al., 2018). Even more, climate change has made that in some grape growing areas, where water scarcity was traditionally not considered to be a relevant issue, currently need to analyse its impact on grape ripening and on the quality of the resulting wine (Coipel et al., 2006; Van Leeuwen et al., 2009). Recent research suggests that grape production will increasingly depend on irrigation, as water stress conditions may intensify (Fraga et al., 2018, 2016) due to an increase in evapotranspiration (Fraga et al., 2013), more uneven rainfall patterns (Jones et al., 2005; Ramos et al., 2008), and to a significant drying trend expected over southern Europe (Santos et al., 2016). Therefore, anticipating irrigation requirements in the future is strategic to maintain wine regional identity and the sustainability of the wine industry (Bonada et al., 2018; Costa et al., 2016; Fraga et al., 2018).

In this context, irrigation management needs to rely on plant water status measurements that allow growers to make fast and effective decisions (Naor, 2006). Scholander pressure bomb provides a relatively quick, flexible and accurate estimation of plant water status through the measurement of water potential (Ψ), considered a reference measure for water status determination (Scholander et al., 1965). However, there are some discrepancies on how and at what time of the day these measurements should be performed in order to obtain meaningful information accurate for research and vineyard management.

Concerning the measurement procedure, two major approaches exist; either measuring leaf (Ψ_L) or stem (Ψ_S) water potential. The former procedure consists in measuring directly on readily detached leaves, only bagged at the moment of detachment, whereas the latter requires bagging leaves in opaque and hermetic bags 1-2 h prior to measurement. This way, in bagged leaves, leaf water potential reaches an equilibrium with stem xylem water potential (Begg and Turner, 1976). Although some researchers have used Ψ_L successfully (Girona et al., 2006; Sebastian et al., 2015; Williams and Baeza, 2007), there is an increasing trend to use Ψ_S (Cancela et al., 2016; Choné et al., 2001; Gálvez et al., 2014; Intrigliolo et al., 2015; Munitz et al., 2016; Olivo et al., 2009; Patakas et al., 2005; Salon et al., 2005; Santesteban et al., 2011a). Choné et al. (2001), in their study combining data from experiments performed in France and California, concluded that Ψ_S was a better indicator of water stress in grapevines than Ψ_L. Mirás-Avalos et al. (2014) observed that Ψ_L and Ψ_S performed similarly well, whereas Lanari et al. (2014) indicated that, despite Ψ_L and Ψ_S correlated equally well to soil water content, the former was more closely related to leaf net assimilation than the latter. Nevertheless, all those research works were based on relatively limited datasets in terms of climatic conditions and grape varieties. There is, therefore, a lack of global analysis that could lead to more generalizable conclusions.

Concerning the moment of measurement, there are two mainstream trends that rely on measuring water potential predawn (Ψ_{PD}) or at noon (Ψ_n). Before dawn, stomata are majorly closed, the plant has rehydrated at the maximum and, consequently all the leaves are considered to reach a relative equilibrium among them and with the wetter part of the soil. Under these conditions, it is generally assumed that leaf and stem water potential are the same. At noon, when the evaporative demand is usually maximum, and plants are subjected to the greatest water stress, discrepancies between studies evaluating the suitability of each procedure arise. For instance, Williams and Trout (2005), Choné et al. (2001) and Mirás-Avalos et al. (2014) outlined that, under their study conditions, Ψ_{PD} measurements could not distinguish among irrigation regimes, while stem water potential at noon (Ψ_{S-n}) did. On the contrary, Intrigliolo and Castel (2006) and Loveys et al. (2008) found that Ψ_{S-n} could not discriminate between irrigation treatments shown to be different according to Ψ_{PD}. Santesteban et al. (2011b) reported no differences in the discrimination ability of Ψ_{PD} and Ψ_{S-n}. Moreover, some authors claim that either early- or mid-morning (Ψ_{S-m}) can be a more suitable moment for taking measurements, as differences in water status become maximum and discrimination ability is between irrigation treatments is maximum (Cole and Pagay, 2015; Santesteban et al., 2011b). Last, some researchers argue that, since all the methods used to assess vineyard water status are highly correlated with one another, all of them can assess vine water status equally well (Williams, 2017, 2012), or that measuring Ψ_L in leaves of shaded shoots can be a suitable alternative (Williams, 2012).

Therefore, there is no consensus on how (leaf or stem) and at what time of the day grapevine water potential has to be measured. When discussing this issue, each researcher gives more or less weight to the pros and cons of each method and time of the day, based on his/her own experience and beliefs. This lack of agreement can be explained as some external factors are affecting to the suitability of each measurement modality and that, as suggested by some authors, climatic conditions, variety and vine water status may condition it. In this context, the aim of this work is to evaluate through a wide-scope meta-analysis the discrimination ability of water potential measurements in grapevines depending on the procedure of measurement (leaf vs. stem) and of the time of the day. The hypothesis underlying is that the measurement procedure with the greatest discrimination ability between irrigation treatments can be considered the most suitable under the average working conditions.

2. Material and Methods

2.1. Data acquisition

Within the activities of the RedVitis Network, 13 research teams working in grapevine water relations all over Spain were contacted in order to have access to complete datasets of grapevine water potential data from irrigation experiments. RedVitis is a research network, coordinated by the Public University of Navarra (UPNA), and funded by the Spanish Ministry of Economy and Competitiveness (MINECO), aimed at increasing the interaction among Spanish research teams in viticulture. Researchers were asked to provide the original data (individual leaf data) of water potential measurements, and data needed to fulfil several requirements: (i) to have been obtained in field experiments (not potted vines), (ii) to include at least two doses of irrigation strategies, and (iii) to provide at least five measurement days per year. When irrigation experiments had been performed within a factorial design (for instance, in combination with cluster thinning or leaf removal), only data from the control vines were included in the analysis. The data received for each experiment were subjected to an exploratory analysis using box-plots to remove potential outliers, and rearranged to fit a format that allowed later meta-analyses. Measurements performed before dawn were labelled as "pre-dawn", those between 8:00 and 10:30 solar time as "morning", and those between 11:00 and 13:00 solar time as "noon".

As a whole, leaf measures included in the meta-analysis amounted 78,854 and comprised data from 438 'experimental replicates', considering as such every experiment, year, variety and methodology of determining water potential for which irrigation doses had been compared. The location of the experiment sites is detailed in Figure 1a, whereas the total number of leaves measured at each region is indicated in Figure 1b. Table 1 provides a description of the experimental datasets included in this work, indicating the varieties, the measurement procedures and the number of leaves considered for each site location. In any case, it is necessary to highlight that the irrigation experiment vineyards included in this meta-analysis followed the standards of vineyard irrigation practices in Spain, and that irrigated vines receive less than 200 mm per year under rainfall regimes that very rarely exceed 300-400 mm during the growing season.

2.2. Data analysis

Data from each experiment replicate were used to estimate the discrimination ability of water potential measured following each procedure and time of the day through the calculation of its Discrimination Ratio (DR). This index has already been used to compare the discriminating ability of water potential measurements in grapevines (Cole and Pagay, 2015; Santesteban et al., 2011b), and follows the principles described in Levy et al. (1999) and Browning et al. (2004). Briefly, for each experiment replicate, the mean standard deviation (SD) of the measurements obtained from different leaves on the same day within an irrigation treatment (SD_w) and the SD of the mean values measured from different treatments throughout the season (SD_b) were calculated. Then, SD_b was corrected using SD_w to estimate the seasonal underlying SD (SD_u) as follows,

$$SD_u = \sqrt{SD_b^2 + \frac{SD_w^2}{k}} \qquad [1]$$

where SD_u represents an unbiased estimate of the SD, and k accounts for the number of leaves measured in each irrigation treatment each day.

Finally, DR was calculated as

$$DR = \frac{SD_u}{SD_w} \qquad [2]$$

Then, DR values calculated for each experimental replicate were pooled according to the water potential measurement procedure and time of the day, and compared (i) graphically using boxplots and (ii) by means of pairwise t-tests. In both cases the comparisons gave a weighted relevance to each experimental replicate depending on its contribution in terms of the number of leaves measured. The higher DR, the greater discrimination ability the measurement method has, as variation between the leaves measured within a treatment are smaller with respect to the variation in the whole experiment. It is necessary to underline that the fact that DR is greater for a given than for other is mainly due to the effective difference between the irrigation treatments compared, and does not have additional implications in terms of measurement method comparison. On the contrary, that fact that in this meta-analysis data from a wide dataset are considered altogether implies that the evidences that will arise will serve as a tool to compare discrimination ability and broad scale usefulness.

All calculations were performed using R v. 3.1.2 (R Core Team, 2014), whereas and ggplot2 (Wickham, 2009) and gridExtra (Auguie, 2016) packages were used for figure production, and weights package (Pasek, 2018) was used for producing t-tests comparing weighted data.

3. Results and discussion

3.1 Descriptive statistics

The range of water potential values observed for each measurement method was different (Figure 2). As expected, the highest (less negative) values were recorded at pre-dawn, followed by mid-morning and noon measurements. When the medians of leaf and stem water potential values were compared, the gap between them was ca. 0.08 MPa at mid-morning, and ca. 0.10 MPa at noon. This average difference is similar to that reported at noon by Mirás-Avalos et al. (2014) and Intrigliolo and Castel (2006) in two regions of Spain with very different soil and climate conditions (0.12 MPa), but smaller than those reported by Williams and Araujo (2002) and Williams (2012) in the Unites States (0.25 MPa), or by Shackel (2007) in the US (0.4 MPa). This fact is probably linked to the low irrigation rates applied usually in our vineyards despite the reduced water availability, resulting in reduced transpiration due to stomatal closure and, as a consequence to a smaller gradient between stem and leaf water potential in the average conditions in Spain.

Quite surprisingly, the distribution pattern of the values recorded for each measurement modality varied remarkably in the violin plot (Figure 2). Leaf water potential measurements showed the most disperse distribution pattern, particularly at mid-morning, whereas stem and pre-dawn measurements followed a sharper normal curve shape. This difference is probably a consequence of the fact that Ψ_L is more dependent on leaf exposure and environmental conditions than Ψ_S (Patakas et al., 2005), and it could be a hint of the dependency of leaf water potential measurement on the microclimatic conditions of the leaf where the measurements are made.

Concerning the evolution of the values recorded along the season (Figure 3), all the measurement modalities provided the lowest values at the central part of the measuring campaign, matching the typical seasonal pattern of water deficit under Mediterranean climates (Flexas et al., 2002; Intrigliolo and Castel, 2008; Santesteban et al., 2011a). The period with the lowest water availability for the vines was located between DOY 210 and 240 (corresponding to August in the Northern hemisphere) for all the measurement modalities except for Ψ_{L-m} . In this case, this period was anticipated approximately one month to DOY 180-210. This advancement can be due to the fact that the time -window selected to determine water potential in the morning is usually established by researchers using noon as reference (e.g.: between 2.5 and 3.5 h before noon), and significant differences occur in the time lapse between sunrise and the measurement time depending on the calendar date. Therefore, in order to get more easily comparable results, it would be advisable to fix the morning measurement period as referred to sunrise time, and not to noon. The fact this advancement was not observed for Ψ_{S-m} is a consequence of the lesser dependence of Ψ_S on atmospheric conditions, but does not imply that the aforementioned consideration for morning measurements should not be taken into account when measuring Ψ_{S-m}.

3.2 Discrimination ability

The discrimination ability of the five water potential measurement procedures compared was evaluated through the calculation of their Discrimination Ratio (DR). Despite there were remarkable differences between the DR values observed between experiments, a clear trend arose: Ψ_L had much lower discriminating ability than either Ψ_{PD}-or Ψ_S (Figure 4). Therefore, the meta-analysis of our complete dataset stresses the limitations of leaf water potential measurement, supporting the concerns manifested in earlier research (Choné et al., 2001; Cole and Pagay, 2015; Intrigliolo and Castel, 2006; Patakas et al., 2005). Although part of the poorer performance of Ψ_L could be blamed to be due to leaf transpiration during measurement (Williams, 2017), the authors supplying data bagged the leaves just before severing the petiole to avoid this error source.

When the DR obtained for Ψ_{PD}, Ψ_{S-m} and Ψ_{S-n} were compared, the differences observed were much smaller and not significant according to the p-values (Figure 4), Although Ψ_{S-m} provided the highest median DR value, followed by Ψ_{PD} and Ψ_{S-n}, it was not possible to identify a significant superiority for any of the three modalities. This result agrees with Santesteban et al. (2011b), where Ψ_{S-m} slightly outperformed Ψ_{PD} and Ψ_{S-n}, but without great differences. Cole and Pagay (2015), using a more limited dataset, similarly found that Ψ_{S-m} displayed the highest DR values. The two elements considered for DR calculation [Eq. 2] played a relevant role in the differences observed between measurement methods (Figure 5). The low DR ratio of Ψ_{L-m} appears to be mainly caused by a high variability between the measurements within each treatment, as its CV values are high, whereas in Ψ_{S-n}., the mean variability between treatments decreases, as its CV is the lowest.

As the morning advances, the differences between treatments tend to be smaller under the majority of the conditions considered (Figure 5b). This trend had already been outlined by several authors (Cole and Pagay, 2015; Intrigliolo and Castel, 2006; Santesteban et al., 2011b), who observed that water potential differences between irrigation treatments diminish over the day, making more difficult to find differences between irrigation treatments at noon. Therefore, from that point of view, the earlier in the day we measure, the clearer the difference in water status appears. However, Ψ_{PD} measurement showed an increased within-treatment variability that makes its DR to be similar to that of Ψ_{S-m} and Ψ_{S-n}. This increased variability probably arises from the greater impact associated to the error of the measuring process, as resolution of most chambers is 0.02 MPa, and a certain degree of subjectivity can exist in the water potential readings (Goldhamer and Fereres, 2001). This increased CV for Ψ_{PD} measures was also observed by Centeno et al. (2010), though no additional comments were made therein. Some authors have pointed out that Ψ_{PD}, alleged to be a surrogate measure of water potential in the rhizosphere, has some inconveniences, as it may come into equilibrium only with the wettest portion of the soil profile (Ameglio et al., 1997), and can be overestimating the amount of water available if the irrigation bulbs are small.

Taking all the above into consideration, it can be concluded that, for the majority of the conditions in Mediterranean-like areas, it is better to use either Ψ_S or Ψ_{PD} to discern vineyard water status, and that, for the latter, an increased sample size could yield the best discrimination results. However, as outlined in the introduction, there are some external factors that affect the performance of the measurement methods, so no categorical statements on which one performs best should be carelessly made, as every method can be most suitable under certain agronomic or operational conditions. In the next section, two of the factors (climate and variety) that can affect discrimination ability are examined using this dataset.

3.3 Factors affecting discrimination ability

a. Influence of climatic conditions

Environmental conditions are frequently mentioned as a factor conditioning the suitability of water potential measurement modalities (Cole and Pagay, 2015; Santesteban et al., 2011b). In order to analyze that factor with this dataset, the experimental sites were classified according to their mean temperature (T) of the growing season (April to October), and labelled as COOL (T<18 ºC), MILD (18-20ºC) and WARM (>20ºC). As the number of sites with growing season T < 18ºC was low, only MILD and WARM sites were considered for comparison (Figure 6). The major effect of site climatic conditions on DR was observed in $\Psi_{S\text{-}m}$, for which a change for the worse occurred at mid-morning in WARM sites. This poorer performance can be hypothesized to be caused by a greater impact of the rapidly changing conditions during the morning on water status in warmer climates, making measurements less reliable. Therefore, caution should be taken if $\Psi_{S\text{-}m}$ is measured in the warmer climates and, according to our dataset, Ψ_{PD} and $\Psi_{S\text{-}n}$ should be preferred in those areas.

b. Influence of the cultivar

Grapevine varieties respond very distinctly to water deficit (Chaves et al., 2010), to an extent that lead researchers to classify them as isohydric and anisohydric (Medrano et al., 2003; Santesteban et al., 2009; Schultz, 2003; Soar et al., 2006). Although later research demonstrated that this classification may prove inappropriate, and that variety response can range (at least) from near-isohydric to near-anisohydric depending on the circumstances (Chaves et al., 2010; Lovisolo et al., 2010; Pou et al., 2012), there is still a consensus on the differential response of grapevine cultivars facing water deficit. These differences probably arise out of centuries of human-mediated selection of cultivars to make them fit to very diverse growing environments. In order to investigate the implication of the cultivar on the DR of water potential measurement methods, the 23 varieties included in our dataset were classified as native from relatively COOL or WARM grape growing regions (10 and 7 varieties, respectively). The remaining six varieties were classified as NEUTRAL, since no clear origin could be assigned, or that they came from regions with intermediate climatic conditions, and were not used for comparison.

When DR values depending on the origin of the variety are compared (Figure 7), a significantly differential pattern can be observed for $\Psi_{S\text{-}m}$ and $\Psi_{S\text{-}n}$. Stem water potential measurements in varieties native from WARM areas were much more discriminant at noon than at mid-morning, whereas the opposite behaviour can be observed for those native from COOL areas. It is not easy to set a sound hypothesis on the reasons behind that behaviour; however, this could be linked to differences in their diurnal patterns of transpiration or water use (Bota et al., 2001; Escalona et al., 1999; Schultz, 2003; Soar et al., 2006).

4. Conclusions

Building a common dataset and its subsequent meta-analysis can be a very efficient and robust tool to discern the suitability of the most commonly used procedures for assessing grapevine water status. Under growing conditions similar to those considered in this work, the measures of leaf water potential in vineyards should be replaced, as a general rule, by either stem or predawn water potential readings, since the former has been proved to be much less discriminant than the two latter, and only operational limitations that restrict their implementation could justify its use. Among the three other measurement procedures evaluated, a preference towards mid-morning stem water potential appeared could be concluded, although the discriminating abilities of the three procedures were relatively similar. The main limitation of predawn water potential is linked to higher internal variability of the measurements, so if sample size is increased, it would lead to the most discriminant information. Climatic conditions and variety seem to affect the discriminating ability of stem water potential measurements at different times of the day, mid-morning measures being more discriminant in milder climates and for varieties original from cooler areas.

Finally, the authors would like to highlight that it would be very advisable to perform meta-analyses for other crops and/or measurement procedures commonly used in order to increase the certainty on the appropriateness of measured variables or procedures. This approach provides a robustness that can hardly obtained by the analysis of individual experiments.

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Table

Table 1. Description of the experiment datasets included in the meta-analysis, including locations, varieties, number of individual leaves and measurement procedures

Region	Location	Varieties [1]	No. of leaves	Ψ_{PD}	$\Psi_{L\text{-}m}$	$\Psi_{S\text{-}m}$	$\Psi_{L\text{-}n}$	$\Psi_{S\text{-}n}$
Andalucia	El Ejido	CR, FL	1,776					X
C. Madrid	Colm. de Oreja	CS	1,596	X	X		X	X
C. Valenciana	Mogente	CS	648					X
	Requena	BO	336					X
	Requena	BO	1,680	X		X		X
	Requena	BO	3,312		X	X	X	X
	Requena	TE	14,104	X	X	X	X	X
Castilla La Mancha	Albacete	CS, MA, TE	2,332					X
	Albacete	AI, CS, CH, MA, TE	1,408				X	
	Argam. de Alba	MR	2,200	X				
	Fuente Álamo	MO	168					X
	Malpica del Tajo	SY	743	X	X		X	X
	Tomelloso	CA, MA, TE	756	X				X
Castilla y León	Medina del Campo	VE	912	X	X		X	X
	Valladolid	CS	1,184		X			X
	Vill. del Bierzo	ME	936				X	X
Cataluña	C. de Mont	GA	660	X	X		X	
Extremadura	Guadajira	DB, TE	9,300			X		X
	La Albuera	MA	384					X
Galicia	A Rua	GO	1,314		X		X	X
	Leiro	AL, BR, GO, SO, TR	3,738				X	X
	O Rosal	AL	2,880		X		X	X
Islas Baleares	Palma	GA, TE	432	X				X
	Consell	MN, TE	648	X	X		X	
	Consell	MN, TE	360	X	X		X	
Murcia	Jumilla	MO	6,977	X	X		X	X
Navarra	Cascante	TE	882	X				
	Corella	TE	3,072	X	X		X	
	Traibuenas	TE	3,508	X				
	Traibuenas	CS, GR, TE	14,316	X		X		X

[1] AI: Airén; AL: Albariño; BR: Brancelao; CA: Cariñena; CH: Chardonnay; CR: Crimson Seedless; CS: Cabernet Sauvignon; DB: Doña Blanca; FL: Flame Seedless; GA: Garnacha (syn. Grenache); GO: Godello; GR: Graciano; MA: Macabeo; ME: Mencía; MN: Manto Negro; MR: Merlot; MO: Monastrell; SO: Sousón; SY: Syrah; TE: Tempranillo; TR: Treixadura; VE: Verdejo. Ψ_{PD}, predawn water potential, $\Psi_{L\text{-}m}$, mid-morning leaf water potential, $\Psi_{S\text{-}m}$, mid-morning stem water potential, $\Psi_{L\text{-}n}$, noon leaf water potential, $\Psi_{S\text{-}n}$, noon stem water potential

Figure captions

Figure 1.-Geographical distribution of the experiments included in the study, indicating (a) experiment site location and (b) number of leaves per measurement method at each region. In (a), site location is plotted over the Huglin Index map provided in Honorio et al. (2018). PD, Predawn; LM, leaf mid-morning; SM, stem mid-morning; LN, leaf noon; SN, stem noon.

Figure 2.-Violin plot of the daily mean water potential values recorded for each water potential measurement procedure. Water potential for the different measurement modes and moments are presented as boxplots, indicating the median and quartiles with whiskers reaching up to 1.5 times the interquartile range. The violin plot outlines illustrate kernel probability density, i.e. the width of the violin area represents the proportion of the data located there.

Figure 3. Seasonal evolution of (a) predawn, (b) mid-morning and (c) noon water potentials. Box upper and lower limits correspond to percentiles 25 and 75 for each measurement period, the central line to the median, and box width is proportional to the number of data considered.

Figure 4. Boxplot of the Discrimination Ratios (DR) obtained for each measurement method. Point size and darkness are proportional to the number of leaves of each experiment, whereas box width is proportional to the number of experiments available for each measurement procedure. X-axis has been cut in DR = 5 to improve visualization, as just a small proportion of experiments showed DR > 5. Letters above the boxes indicate significant differences between methods ($p<0.05$) according to *p*-values from pairwise weighted *t*-tests indicated in the inserted table. Ψ_{PD}, predawn water potential, Ψ_{L-m}, mid-morning leaf water potential, Ψ_{S-m}, mid-morning stem water potential, Ψ_{L-n}, noon leaf water potential, Ψ_{S-n}, noon stem water potential.

Figure 5. Boxplot for the coefficients of variation (CV) of each measurement procedure: (a) variability in water potential between the leaves measured in one treatment each day of experiment; (b) underlying variability in water potential between the leaves (CVb) measured each day of experiment between treatments.

Figure 6. Effect of climate on Discrimination Ratios (DR). Boxplot of DR obtained for each measurement method in MILD and WARM climate areas. Point size and darkness are proportional to the number of leaves of each experiment, whereas box width is proportional to the number of experiments available for each measurement procedure. X-axis has been cut in DR = 5 to improve visualization, as just a small proportion of experiments showed DR > 5. *p*-values in the figure represent the significance between climate areas according to weighted *t*-tests.

Figure 7. Effect of variety on Discrimination Ratios (DR). Boxplot of DR obtained for each measurement method in varieties native to COOL and WARM climate areas. Point size and darkness are proportional to the number of leaves of each experiment, whereas box width is proportional to the number of experiments available for each measurement procedure. X-axis has been cut in DR = 5 to improve visualization, as just a small proportion of experiments showed DR > 5. *p*-values in the figure represent the significance between varieties according to weighted *t*-tests.