Water relations of woody perennial plant species

Régime hydrique chez les espèces pérennes ligneuses

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Abstract: Field irrigation experiments were performed on young « Nonpareil » almond trees, mature « Bartlett » pear trees and mature « Pinot Noir » grapevines, to determine the relation of a number of alternative measures of plant water status (predawn and midday stem and leaf water potential), to a number of indices of plant physiological activity (leaf conductance, vegetative growth and fruit growth and composition). Almonds were exposed to three levels of irrigation over three years, and midday stem water potential (SWP) and leaf conductance, collected at approximately weekly intervals, is reported for the third year of the study. A strong linear increase in both leaf conductance and trunk growth occurred with increasing SWP, and this relation was consistent both within and between treatments. A similarly positive linear relation was found between SWP and fruit size in pear, with a negative relation between SWP and fruit soluble solids and fruit color. In grapevine, SWP was found to be uniform across all lower canopy positions tested (trunk, cordon and near the base of current year shoots) and positively correlated to early season shoot growth even before irrigation treatments were applied. Midday SWP was found to be more sensitive than midday leaf water potential (LWP) for detecting treatment differences over the course of the season, but both were well correlated to average seasonal leaf conductance within and between irrigation treatments. Predawn SWP and LWP were not as well correlated to average seasonal leaf conductance, but the most important factor determining midday leaf conductance was wind speed, indicating that grape leaf stomatal responses are quite sensitive to this environmental factor.

Key words: Stem water potential, SWP, leaf water potential, LWP, predawn, midday, leaf conductance, fruit growth, fruit quality

Introduction

Understanding the physiological responses of plants to water limited conditions is of general importance in biology, as well as of particular importance to agricultural science, and as such, this topic has been the subject of much research and many excellent reviews (e.g., Bradford and Hsiao, 1982; Jones and Tardieu, 1998). It is clear that many, perhaps most, plants are designed to function over a range of water availability, and that a number of short and long term responses, often called « stress responses » are exhibited by plants over this range. For the purpose of this paper, I will use the approach suggested by Levett (1980), with « stress » referring to an environmental condition, which may be internal or external to the plant, and « strain » as the impact of this condition on the biological process of interest. I should admit at the outset however, that I regard these and other related definitions as provisional, since a clear and scientifically-based terminology for describing the occurrence and consequences of water stress in plants requires a thorough understanding of the biological processes involved, and for many of these processes our current understanding is quite rudimentary. At the whole-organism level, water is obtained from the soil by roots to re-supply water lost from the leaves, and hence the term « water availability » can typically be regarded as referring to soil water availability, and « water limited conditions » as referring to as any decrease in water availability that causes a strain (i.e., change in biological activity) in the plant. In their review, Bradford and Hsiao (1982) present a general picture of the many plant stress responses that are known to occur as water availability is decreased, with some responses (i.e., reduction in growth rates) occurring first, and others (stomatal closure, reduced photosynthesis) occurring later, but one key question, and a focus of the present paper, is the question of how we quantify the decrease in water availability in the first place.
Many contrasting measures of plant water availability have been suggested, each focusing at a different point along the soil-plant-atmosphere-continuum. The usefulness of any particular measure however, will depend on the objective in making the measurement on the one hand, and on the relation between the point being measured and the desired plant response on the other. For instance, many current irrigation practices are based on direct measures of soil moisture, or indirect estimates of soil available water through an estimation

of atmospheric evaporative demand (Ferreres and Goldhamer, 1990). These approaches assume, among other things, that the soil serves as a reservoir, and that replacing the water lost from this reservoir is equivalent to maintaining a non-limiting water supply to the plant, and hence maintaining the plants under non-stressed conditions. In the case of wine grapes and other fruits however, moderate levels of water stress (e.g., the practice of Regulated Deficit Irrigation, RDI) may be desirable for optimum horticultural/economic productivity (e.g. Lampinen *et al*., 1995, Shackel *et al*., 2000), and hence the assumption of maintaining plants under non-stressed conditions would not apply. Since the ultimate purpose of any management practice designed to influence water availability (irrigation, planting density, cover crop, etc.) is to obtain optimum horticultural/economic productivity, I will propose that a key property of any measure of plant water availability must be that it is closely related to the plant responses that determine horticultural/economic productivity. The plant is a complex system, and fruit yield and quality are a final result from the interaction of environmental conditions with many physiological processes, such as vegetative growth patterns, stomatal opening, photosynthetic rates, root nutrient uptake, etc. Hence, as a first approximation, any proposed measure of plant water availability should be closely related to these processes. Since for any given experimental system (field site, greenhouse, etc.) the points along the soil-plant-atmosphere-continuum will be physically interdependent, it is expected that any particular measure of plant water availability within a site (soil-based, plant-based, atmosphere-based) will probably be related to any other measure of plant water availability at the same site. Hence, if one of these measures is correlated to any given plant physiological process or horticultural characteristic, then we may expect that the other measures may also have some correlation. The advantages of soil- and/or atmosphere-based measures are generally related to their practical usefulness in irrigation scheduling (e.g. automation), but it is reasonable to assume that an appropriate plant-based measure of water availability should be more directly related to plant physiological responses than soil- or atmosphere-based measures. A key physiological measure of water availability within the plant is water potential, and although some researchers have questioned the general relevance of this measure to plant function (Sinclair and Ludlow, 1985) a few early studies in woody perennial crop species (Garnier and Berger, 1985, McCutchan and Shackel, 1992) reported a close relation of water potential to both irrigation regime and plant physiological activity, and currently there are three alternative measures that have been suggested: predawn water potential (PWP), midday stem water potential (SWP) and midday leaf water potential (LWP). A number of recent studies have determined the relation of one or more these alternatives to various physiological or horticultural characteristics, and/or compared the sensitivity of these alternatives to various irrigation practices. The sensitivity of a measure in response to a change in irrigation practice is important if the method is to be used for irrigation management, even if the method detects differences prior to any apparent difference in physiological responses. Presumably the most sensitive method for irrigation scheduling would also be the most useful measure of plant water availability. In review of the recent studies in deciduous orchard crops, Naor (2006) concluded that LWP was not as closely related to plant physiological processes as was PWP or SWP, and that other indirect plant-based measures of water availability, such as diurnal stem diameter changes, also showed promise as practical tools for irrigation scheduling. The following paper will present evidence in deciduous trees and grapevine that the plant-based measure of midday stem water potential (SWP) is closely related to many important physiological processes, as well as key aspects of fruit quality.

Materials and analytical and experimental methods

Physiological Measurements: Values of water potential were measured with the pressure chamber technique on leaves that were either enclosed for more than 10 minutes to prevent transpiration and allow equilibration with stem water potential (SWP, Fulton *et al.*, 2001), or leaves that were only enclosed immediately before excision to prevent post-excision desiccation (Turner and Long, 1980) to give leaf water potential (LWP). In some cases, measurements were made pre-dawn, also using both approaches. Unless otherwise specified, LWP was measured on upper canopy, fully exposed recently mature leaves, and SWP was measured on lower canopy mature leaves that were attached to stems that were close to the trunk or a main scaffold. Stomatal conductance was measured on the abaxial (lower) surface of upper canopy, recently mature sunlit leaves with a steady-state porometer (Model 1600, LICOR, Lincoln, NB), with minimal disturbance to the natural position of the leaf. Trunk circumference was measured with a steel tape, and converted to the equivalent cross-sectional area of a circle as a relative measure of overall plant size. When fruit was harvested, the number of fruits were counted and the total fresh weight obtained to estimate average fruit size, and other measures of fruit quality (color, soluble solids) were measured on a sub sample using standard laboratory techniques (colorimeter, refractometer).

Plant Material and Experimental Design: Almond trees of the « Nonpareil » and « Carmel » varieties were planted and grown in an experimental orchard in Winters, CA, under three contrasting irrigation regimes (WET, MEDUIM, DRY) for three years (1991 - 1993). Irrigation was supplied by under-tree low-volume microsprinklers at twice-weekly intervals for the wet treatment and weekly or less often for the medium and dry treatment. Irrigation amounts and timing were based on maintaining contrasting levels of midday stem water potential (SWP). A >50 year old commercial pear orchard having trees of the « Bartlett » variety was irrigated with under-tree impact sprinklers designed to give approximately 100% (WET), 60% (MEDIUM) and 30% (DRY1, DRY2) of tree water requirements for a period of three years (1992 - 1994). For the final year of this study, the start of irrigation on one of the two blocks of dry trees was delayed (DRY2), based on the observation that trees in this block required a longer period to deplete soil moisture reserves. The field site for the grapevine study was located on the campus of the University of California, Davis. The plant material was own-rooted sixteen-year-old Pinot Noir vines trained using a bilateral « T » trellis system with four cordons per trunk. Vines were planted on 2.4 m spacing in East-West rows 3.7 m apart. Bud break occurred on 15 March 2001 and flowering was on 26 April 2001. Two irrigation treatments were applied in two large blocks using in-line drip irrigation beginning 22 May 2001 and continued through 24 August 2001: non-irrigated and weekly irrigation to cumulative ETc levels. ETc was calculated using the Kc values from Hanson *et al.* (1999).

Results and discussion

One practical advantage that has been reported for midday SWP is the consistency of the measurement at different positions within the plant. Presumably, this is due to the fact that the xylem tissue is a very low resistance pathway for water flow, and hence, for the rates of water transport that are typically found during plant transpiration, the gradient in SWP is not large within the stem portion of the plant. For Pinot Noir grapevine, we studied the effect of position on SWP for positions near the trunk, which should have the highest SWP, and for various positions along the cordon and on primary and secondary shoots (fig. 1A). The correlation for SWP measured at any two contrasting positions along the water flow pathway across a wide range of SWP values was very strong (fig. 1B), with a mean difference of about +0.01MPa (fig. 1C). The random measurement error calculated from these data (SD = 0.08MPa) is comparable to that reported in other woody perennial species (SD = 0.05 - 0.07MPa, Fulton *et al.*, 2001). The comparisons shown in figure 1B are always for an upstream (X axis) versus downstream (Y axis) position along the water flow pathway, and hence it is expected that the average difference would be slightly negative, since the SWP should always decrease from upstream to downstream. The fact that the difference was slightly positive (+0.01MPa) presumably indicates that there is no measurable SWP gradient within the

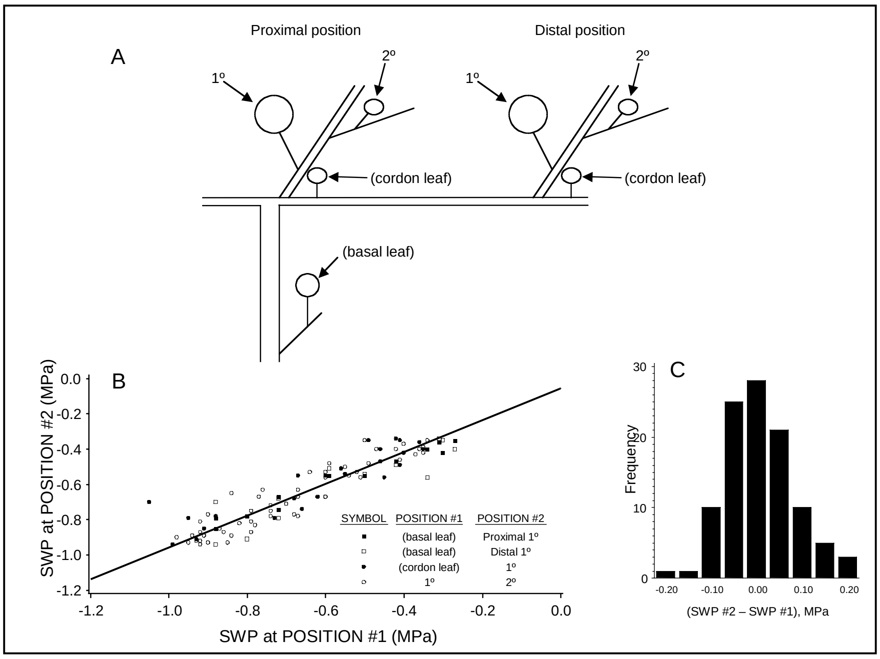


*Figure 1. (A) Diagram of the contrasting positions in cordon-trained grapevines that were used to evaluate the size of within-plant differences that may occur in midday stem water potential (SWP) as a result of the water potential gradients caused by transpiration. (B) Relation of SWP measured at a point upstream in the water flow pathway to a point downstream in the pathway. Line shown is the first principal component axis fit to the data (Y = 0.90*X - 0.054). (C) Histogram of the difference between the X and Y values for each point shown in B. The overall mean ∀SD of this difference was +0.0082∀0.081MPa.*

accuracy of these measurements. These data demonstrate a very important practical advantage of SWP, namely that that the measurement is essentially independent of the choice of leaf on the major scaffold branches of the plant. This result has also been found in a number of other woody perennial species (data not shown).

Over the course of a three year study in almonds, clear differences in SWP were exhibited for the three irrigation treatments for most of the season in all years (fig. 2A shows the 1993 season), and there were corresponding differences in leaf conductance from about mid-July onward in 1993 (fig. 2B). For SWP, the tree-to-tree variation was generally larger in the medium and dry treatment compared to the wet treatment (note error bars in fig. 2 A), but the ranking of trees within a treatment, particularly the medium and dry treatments, was consistent across dates and highly significant (ANOVA not shown). Presumably, this indicated that there were individual trees with more access to stored soil moisture reserves than other trees in the same treatment. Since environmental factors known to influence leaf conductance (air temperature, light, etc.) changed from date to date, a seasonal average leaf conductance value was calculated for each individual tree, and this showed a strong and positive correlation to the corresponding individual tree seasonal average SWP (fig. 3A). There was a similarly strong correlation between the 3-year average SWP of individual trees and tree size, as measured by the trunk cross sectional area at the end of the 3-year study (fig. 3B). These data strongly support the hypothesis that water deficits, as measured by SWP, are a key determinant of plant physiological responses both at the leaf level (conductance), and at the whole plant (growth) level. Further, these data suggest that the dependence of these responses is linear with SWP to a good approximation. This contrasts with the widely held view that one or both of these responses should exhibit a threshold response to water deficits.

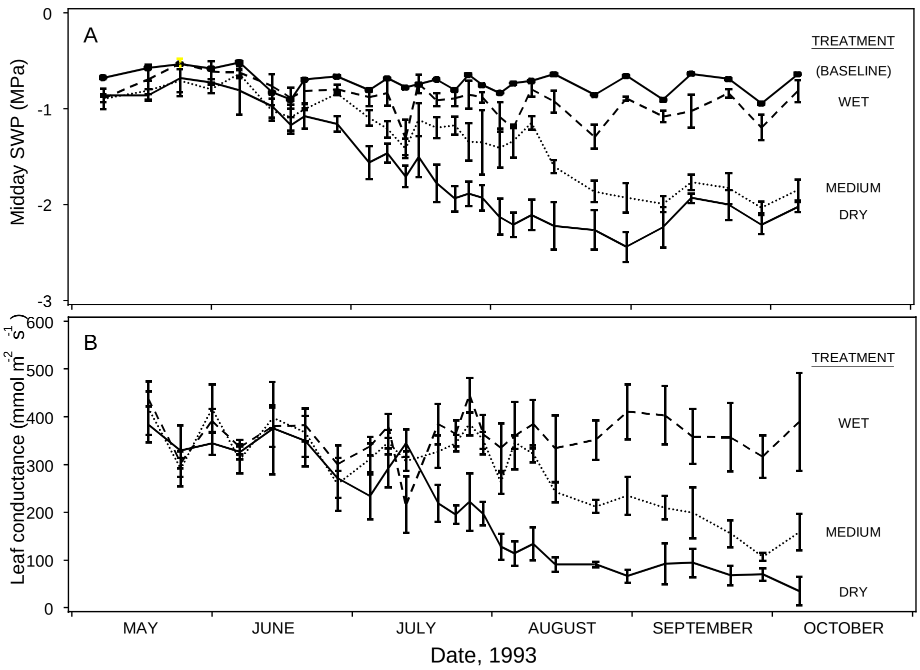


Figure 2. Midday stem water potential (SWP, A) and leaf conductance (B) during the 1993 growing season in almonds under three contrasting levels of irrigation. Also shown for reference (A) is the value of SWP expected for fully irrigated almonds under the same midday conditions of air temperature and relative humidity (baseline).

Similarly to young almond trees, well established pear trees also showed a straightforward decline in SWP with decreased irrigation and progressive separation between treatments over time (fig. 4). As also found in almond, significant tree-to-tree variation was found, particularly within the dry treatments, and there was a very strong correlation between seasonal average SWP and many measures of fruit quality. Lower SWP was associated with smaller fruit size (fig. 5), higher soluble solids (fig. 6) and more advanced coloration (yellow color, fig. 7). The effects of individual tree differences in SWP were particularly clear for fruit size (fig. 5), and showed that there were some trees in the most severe dry treatment (DRY 2) which had both SWP and fruit size values that were comparable to some of the trees in the WET treatment. Overall tree growth, as measured by pruning weight, was also highly and positively correlated to SWP (data not shown). Hence it is clear that, as in almonds, reductions in SWP had profound effects on many physiological responses in pear trees, including a number of important aspects of harvested fruit quality.

Figure 3. (A) Relation of tree averaged leaf conductance to tree averaged SWP in 1993 (data from figure 2). (B) Relation of trunk cross-sectional area after 3 years of growth (1991 - 1993) to tree averaged SWP over the same time period for almonds under the three irrigation regimes shown in figure 2.

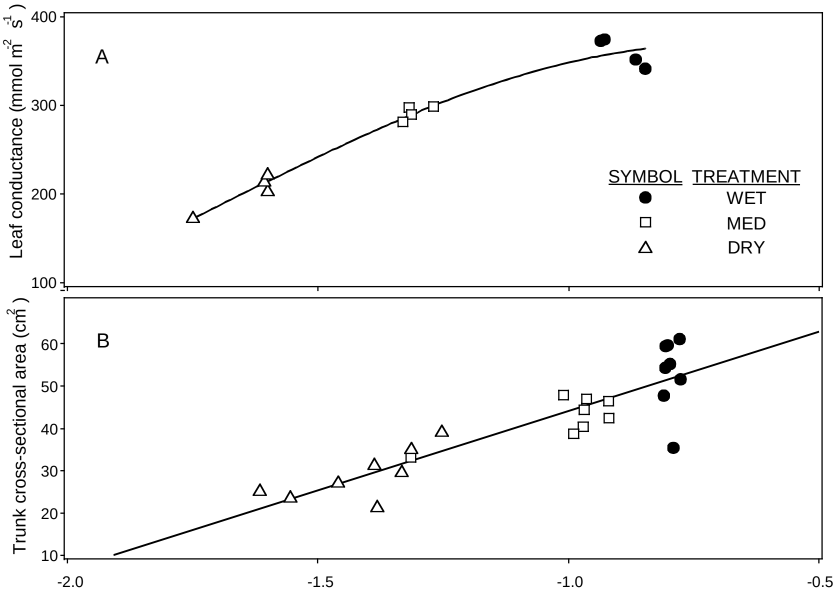


Figure 4. Midday stem water potential (SWP) during the 1994 growing season in pears under four contrasting levels of irrigation.

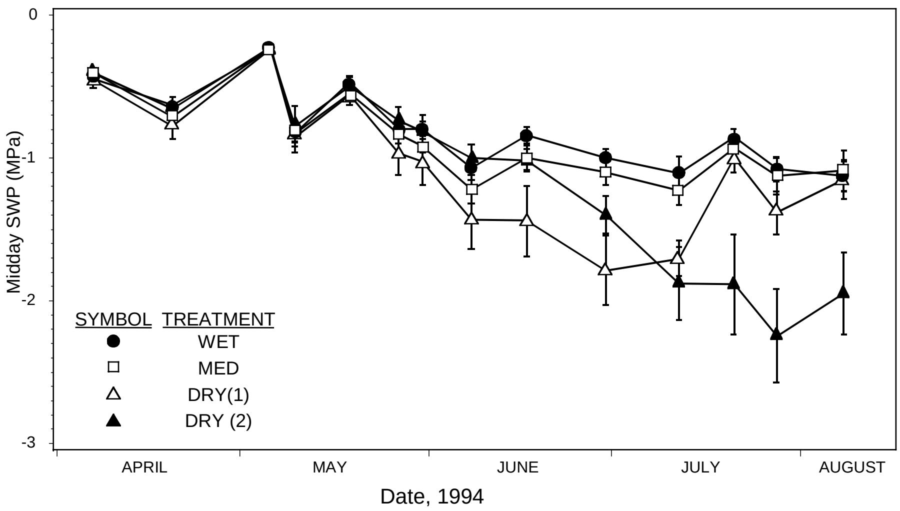
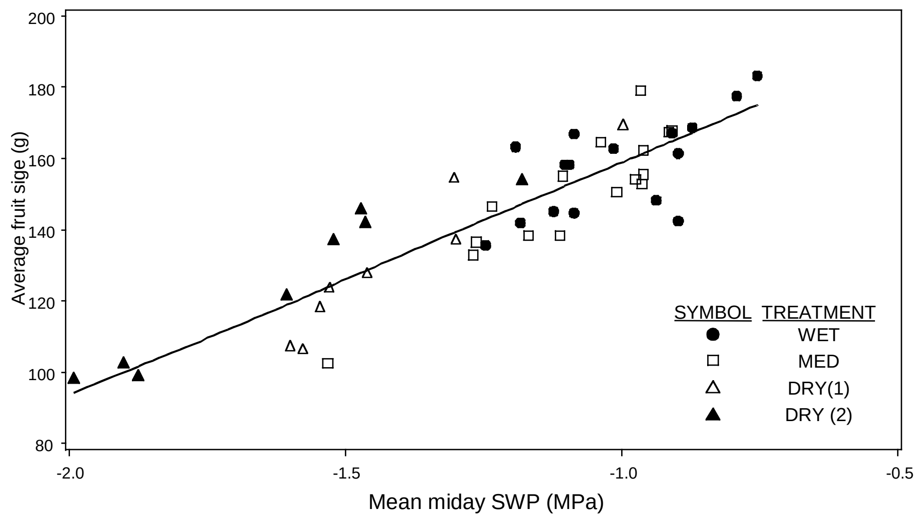


Figure 5. Relation of pear fruit size at harvest to tree averaged midday stem water potential (SWP) during the main fruit growth period (June - August) in 1994



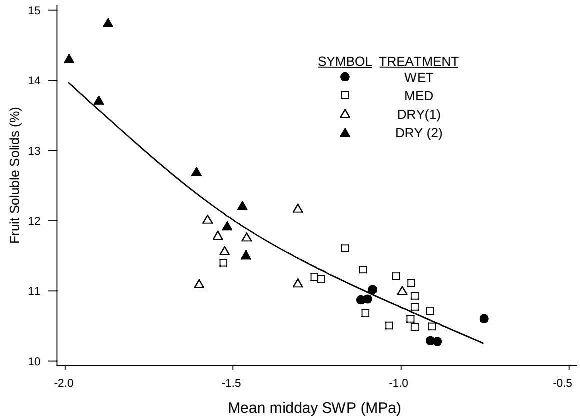


Figure 6. Relation of pear fruit soluble solids at harvest to tree averaged midday stem water potential (SWP) during the main fruit growth period (June - August) in 1994, as in figure 5.

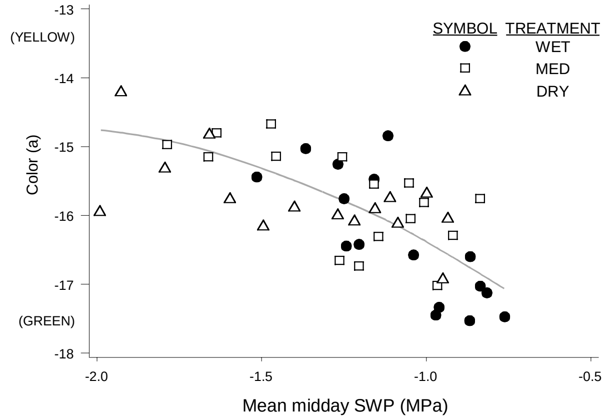


Figure 7. Relation of pear fruit skin color (a value of the l. a. b. scale) at harvest to tree averaged midday stem water potential (SWP) for the period when SWP was measured (July - August) in 1993.

In May, prior to the application of any irrigation to a block of Pinot Noir grapevines, a survey indicated that there were clear vine-to-vine differences in SWP, in some cases with adjacent vines exhibiting differences on the order of 0.5 MPa (Fig. 8). Differences in vine vigor were also apparent in this block, and the length of randomly selected shoots on each vine by the end of May had a significant positive correlation to vine SWP (fig. 9). Statistically significant differences in SWP between irrigated and non-irrigated vines began to appear in early June, and although the irrigation treatment effect on LWP was of the same magnitude, LWP values were more variable, and hence did not show statistically significant differences until late July (fig. 10). The daily pattern in LWP, SWP and leaf conductance was followed on 6 occasions in 2001, and both LWP and SWP showed a similar daily pattern, with minimum values consistently occurring in the afternoon period (2:00 - 3:00, fig. 11). As expected, there was also a progressive increase in separation between irrigated and non-irrigated vines as the season progressed in both SWP and LWP, but the differences due to irrigation were more apparent in the afternoon period than at other times of day, particularly pre-dawn (fig. 11). On any given day, the daily pattern in stomatal conductance was similar for irrigated and non-irrigated vines, and also showed a progressive increase in separation between treatments as the season progressed, but the daily pattern itself was not consistent over the season. On some days there were relatively constant values of conductance from mid morning to late afternoon (fig. 11, 9:00 - 17:00, June 12) whereas on other days a clear maximum value occurred, although the time of maximal leaf conductance varied from late- morning on some days (11:00, July 20 and August 17) to late afternoon on others (18:00, June 13).

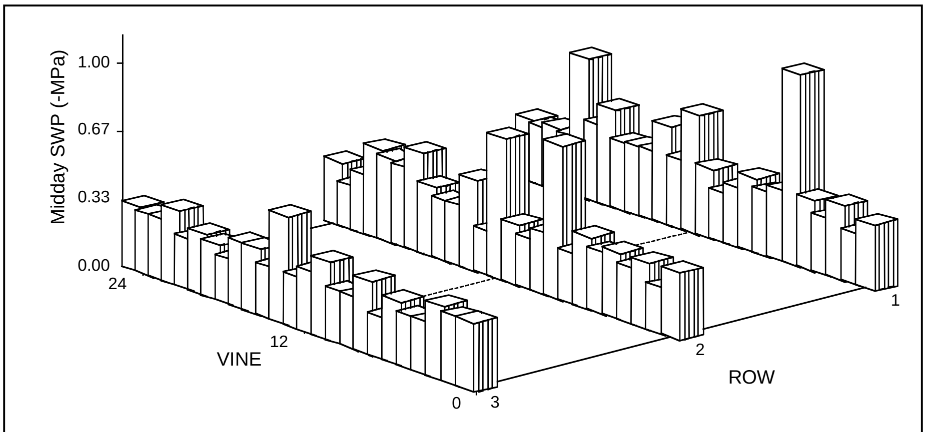


Figure 8. Spatial distribution of the midday stem water potential (SWP) measured on individual vines in May before any irrigation was applied. For clarity, the SWP values are plotted as positive quantities.

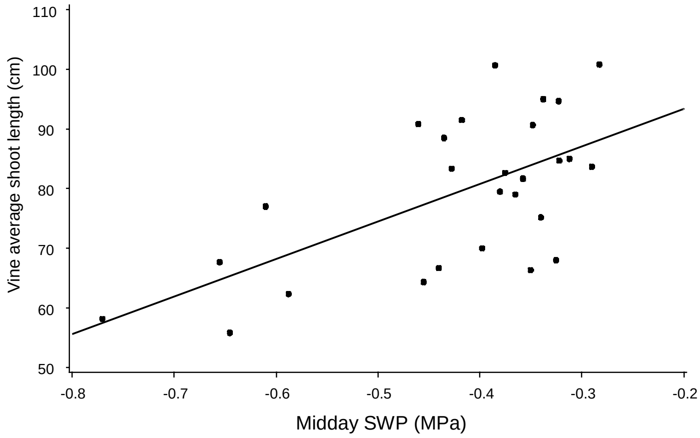


Figure 9. Relation of shoot length at the end of May to vine averaged midday stem water potential (SWP) observed during May, prior to any irrigation, for a subset of the vines shown in figure 8. Line is the linear regression through the data (r-square = 0.38).

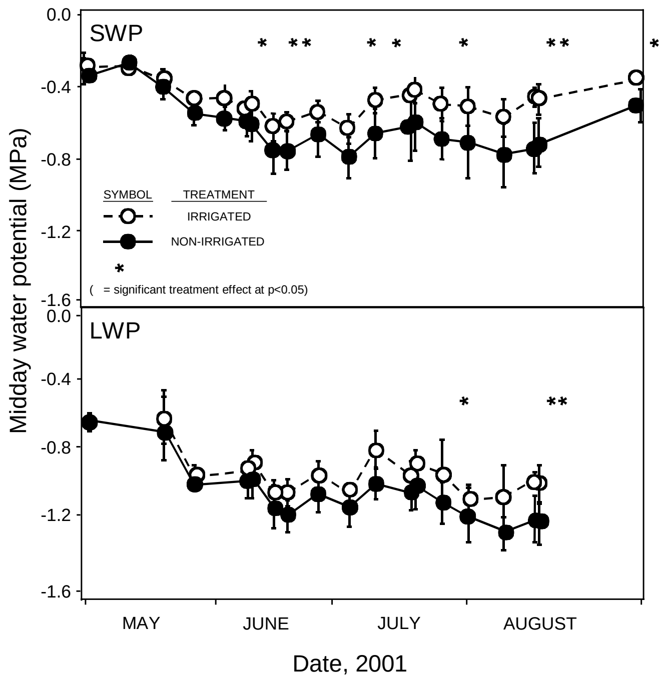


Figure 10. Midday stem water potential (SWP, top) and leaf water potential (LWP, bottom) over the 2001 growing season for Pinot Noir under irrigated and non-irrigated conditions. Each point is the mean of 6 vines, and error bars are ∀ 2SE, which for this sample size is an approximate 95% confidence interval. Asterisks indicate a statistical difference between irrigated and non-irrigated vines.

These data suggest that grapevine leaf conductance is highly sensitive to environmental factors as well as plant water status. A stepwise linear regression was performed for midday leaf conductance as the dependent variable and environmental factors of radiation, temperature, vapor pressure deficit (VPD) and wind speed, as well as SWP and LWP as independent variables, and this analysis showed wind speed as the most important factor, followed by temperature, SWP and radiation, all with a similar influence (table 1).

Table 1. Results of stepwise regression analysis for midday leaf conductance. Values for conductance were averaged by vine, SWP values were not averaged before analysis. Data uses vines from all treatments taken on nine dates from June 12 through August 17, 2001.

Factor	Partial R^2	F value	P > F
Wind (m s^{-1})	0.41	133.9	<0.0001
Temperature (^oC)	0.14	131.2	<0.0001
SWP (MPa)	0.13	52.4	<0.0001
Radiation (W m^{-2})	0.12	66.2	<0.0001
VPD (KPa)	0.01	10.33	0.0009
LWP (MPa)	N/A	N/A	ns at .015

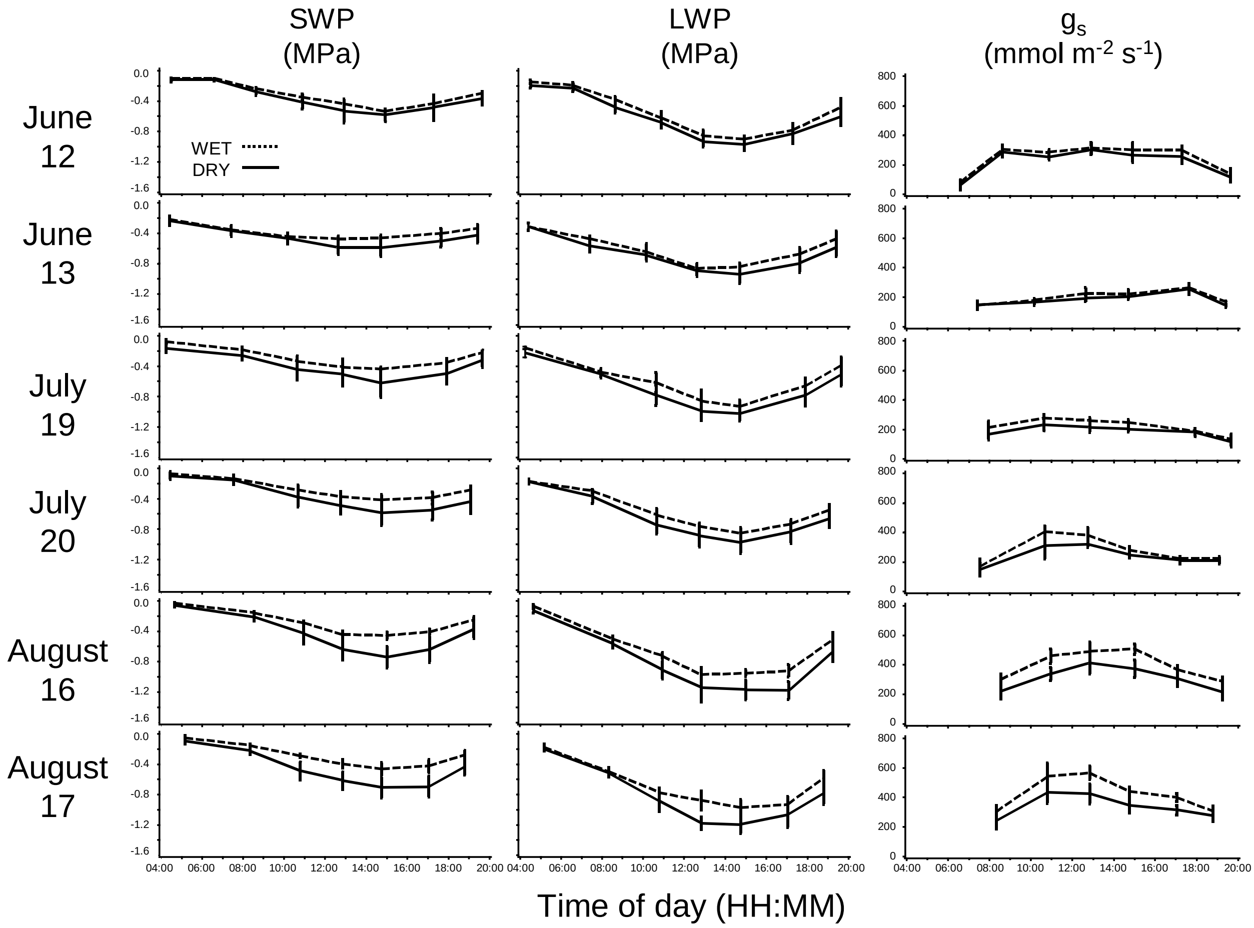


Figure 11. Daily course of stem water potential (SWP), leaf water potential (LWP) and leaf conductance in Pinot Noir vines for a number of dates in the 2001 growing season under irrigated and non-irrigated conditions. Each point is the mean of 6 vines, and error bars are ∀2SE, which for this sample size is an approximate 95% confidence interval.

The relationship between SWP and conductance was clearly influenced by wind, with windy days (wind speeds > 3.5 m s^{-1}) having generally low leaf conductance and a lower regression slope of conductance on SWP than low wind days (wind speeds < 2.8 m s^{-1}, fig. 12). On low wind days, the average leaf conductance was 428.4 mmol m^{-2} s^{-1}, compared to high wind days with an average leaf conductance of 230.0 mmol m^{-2} s^{-1}. In order to compare the sensitivity of the alternative measures of plant water deficits used in this study, an average water potential and leaf conductance was calculated for each vine over all the dates and conditions shown in figure 11. Since all vines were represented at each time point, a comparison among these average values of leaf conductance will represent a comparison among vines, averaged across a wide range of environmental effects. For these data there was a significant and essentially linear relation between leaf conductance and all of the alternative measures of plant water status, but the correlation coefficient of conductance to LWP and SWP was higher than that to predawn LWP or SWP (fig. 13). It is interesting to note that there was a systematic difference between LWP and SWP of about 0.1 MPa, even at predawn,

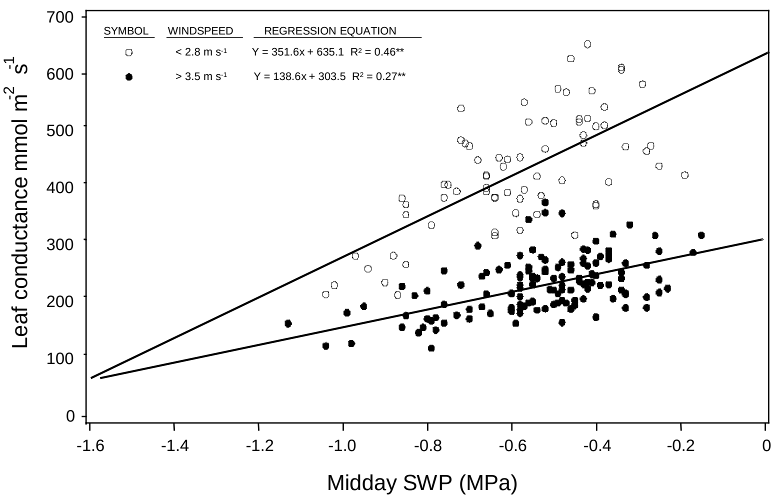


Figure 12. Relation of midday leaf conductance to midday stem water potential (SWP) for the Pinot Noir vines shown in figure 11, divided into environmental conditions of high and low wind speed. Each point is the mean of 3 - 5 values of conductance (fully exposed leaves) and one value of SWP per vine.

presumably indicating that leaf, and hence plant, transpiration may not be negligible at this time, as is normally assumed.

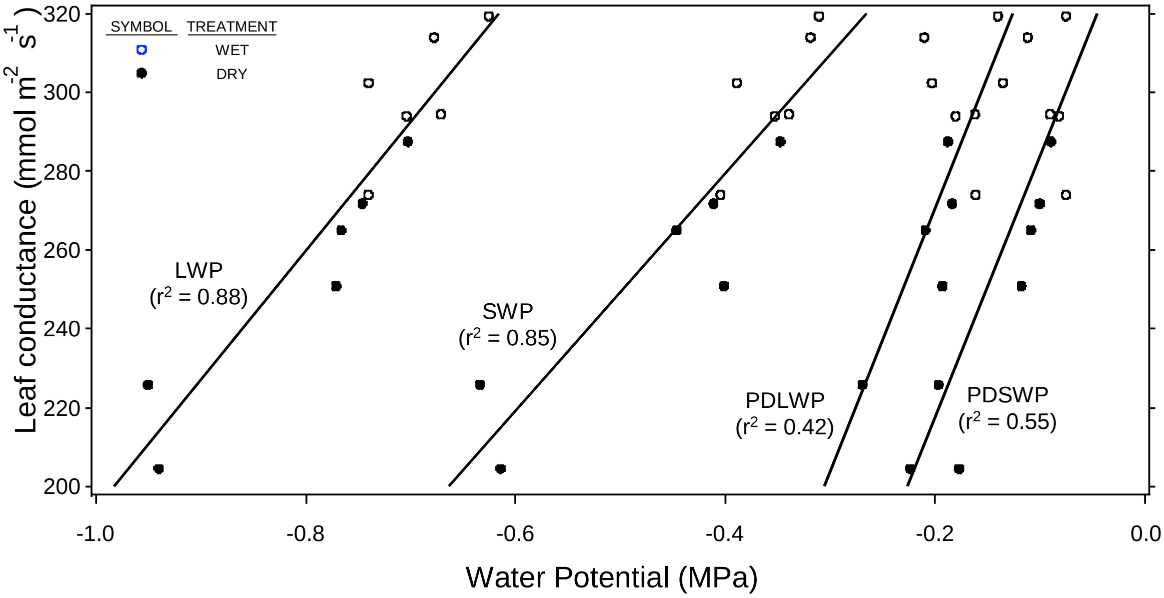


Figure 13. Relation of vine average leaf conductance to vine average leaf or stem water potential during the daytime (LWP, SWP) or at predawn (PDLWP, PDSWP), with averages taken over all days and times shown in figure 1. Each point is the vine average value, and the lines are the regression lines for each alternative measure of plant water status (r-square value for each line is also indicated).

Conclusion

In a wide variety of woody crop species we have found midday stem water potential (SWP) to be a valuable tool for quantifying the degree of water stress experienced by the plant, and for understanding the physiological responses of the plant to water limited conditions. The primary criterion for any proposed measure of water stress in plants should be that it is correlated with the well known short- and long-term responses of plants to water limited conditions, such as reductions in leaf conductance and reductions in plant growth. For both of these responses we have found very strong and essentially linear relations with SWP in a number of crops, including grapevine, and hence we suggest that SWP is a good candidate as a standard measure of water stress in woody perennial plants. We have also reported strong and essentially linear relations of fruit quality attributes (size, soluble solids and color) to SWP in pear, and hence propose that SWP should be a useful tool to predict, and possibly manage, fruit development in a wide range of woody perennial crop plants.

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