

Stem-water Potential as a Sensitive Indicator of Water Stress in Prune Trees (*Prunus domestica* L. cv. French)

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Additional index words. evapotranspiration, leaf-water potential, soil water, stomatal conductance

Abstract. The relative sensitivity of plant- and soil-based measures of water availability were compared for prune trees subjected to a range of irrigation regimes under field conditions. Over the growing season, leaf- and stem-water potentials (ψ) measured at midday exhibited clear differences between frequently irrigated trees and unirrigated trees that were growing on stored soil moisture. Stem ψ was less variable than leaf ψ , and the daily variability in stem ψ was closely related to daily variability in evaporative demands, as measured by vapor pressure deficit (VPD). As a result of lower variability, stem ψ reflected the small stress effect of a moderate, 50% soil moisture depletion irrigation interval, whereas leaf ψ did not. The relation between soil water content and estimated orchard evapotranspiration (ET) was influenced by local differences in soil texture within the experimental plot. The relation between stem ψ and ET, however, was not influenced by soil texture and, in addition, was very similar to the relation between stem ψ and leaf stomatal conductance. Both relationships indicated that a 50% reduction in leaf and canopy level water loss characteristics was associated with relatively small reductions (0.5 to 0.6 MPa) in stem ψ . Stem ψ appears to be a sensitive and reliable plant-based measure of water stress in prune and maybe a useful tool for experimental work and irrigation scheduling.

Plant water stress under dry soil conditions is associated with various physiological responses, such as growth reductions and stomatal closure, which can reduce plant water use and can also limit overall plant productivity (Bradford and Hsiao, 1982). Irrigation to avoid plant water stress is a common practice, and the need for irrigation is often based on a soil-water balance approach, using estimates of environmental water demand [e.g., reference crop evapotranspiration (ET_0), Burman, 1980] and/or measures of soil-water status (Campbell and Campbell, 1982). The value of both of these measures, however, is limited, because they are not directly related to the occurrence of plant water stress and hence may not be directly related to the symptoms that ultimately reduce plant productivity. For instance, Denmead and Shaw (1962) found that under high ET_0 conditions (6 to 7 mm·day⁻¹), a relatively wet soil (soil matric potential greater than -0.03 MPa) was required to support maximum plant transpiration. Under lower ET_0 conditions, however (1.4 mm·day⁻¹), maximum plant transpiration could be maintained to a much drier level of soil moisture (-1.2 MPa). This difference indicates that the need for irrigation was not simply related to a given level of supply or demand, as measured by soil moisture or ET_0 , respectively, but rather to an integrated effect of both factors. Soil-based measurements can also exhibit substantial spatial variability, leading to unreliable estimates of soil-water thresholds for irrigation (Warrick and Nielsen, 1980).

A plant-based measurement, such as water potential (ψ), should be the most straightforward indicator of plant water stress and, hence, of the need for irrigation (e.g., Peretz et al., 1984), because it measures the integrated effect of soil, plant, and atmospheric conditions on water availability within the plant itself. In most studies, the ψ of sun-exposed (transpiring) leaves has been used for this purpose, but in many cases this leaf ψ

strongly depends on local environmental conditions and hence is highly variable. Variability associated with changing environmental conditions can be reduced by the use of predawn ψ measurements (Meyer and Green, 1980); however, these measurements indicate the degree of overnight recovery in ψ , rather than the ψ experienced under midday conditions of typically maximal photosynthetic rates and water demand. In many cases, leaf ψ has not been clearly related to symptoms of plant water stress, and its value for quantifying stress has been questioned (Sinclair and Ludlow, 1985). CowPea [*Vigna unguiculata* (L.) Walp.] grown under severely water-limited field conditions exhibited a similar leaf ψ to that of well-irrigated control plants, while leaf conductance was substantially reduced (Bates and Hall, 1981). Bramley apples (*Malus domestica* Borkh.) grown under water-limited conditions exhibited symptoms of premature leaf senescence compared with well-irrigated trees, while both had similar ψ (Jones, 1985; Jones et al., 1983).

The relation of leaf ψ to leaf conductance in transpiring leaves may be obscured by the occurrence of a within-leaf ψ gradient, which is positively associated with the rate of leaf transpiration (Shackel and Brinckmann, 1985). If this gradient is large, then different tissues within a transpiring leaf will be at substantially different ψ s, and the average leaf ψ (Tyree and Hammel, 1972) may not be directly related to the physiological response of interest. Post-excision errors in leaf ψ (Turner and Long, 1980) have a similar obscuring effect on the relation between leaf ψ and leaf conductance, since excised leaves with a high conductance would desiccate and hence decline more rapidly in ψ than leaves with a low conductance.

Excision artifacts and within-leaf ψ gradients can be eliminated by stopping leaf transpiration with a plastic bag before leaf ψ is measured (Begg and Turner, 1970; Garnier and Berger, 1985; Meyer and Green, 1981; Olien and Lakso, 1986). When bagged leaves remain attached to the plant for ≈ 1 h, leaf ψ would be expected to equilibrate with the ψ of the stem, and, therefore, would be a measure of stem ψ . Stem ψ is less

Received for publication 8 Oct. 1991. Accepted for publication 24 Feb. 1992. This work supported in part by a grant from the California Prune Board. The cost of publishing this paper was defrayed in part by the payment of page charges. Under postal regulations, this paper therefore must be hereby marked advertisement solely to indicate this fact.

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Abbreviations: ET, evapotranspiration; ψ , water potential; VPD, vapor pressure deficit.

influenced by short-term environmental variability than is transpiring leaf ψ (Meyer and Green, 1981) and, under some conditions, has been found to be more clearly related to soil-water conditions. Stem ψ of peach (*Prunus persica* L. Batsch) trees irrigated at 50% actual evapotranspiration (AET) was substantially lower than the stem ψ of 100% AET trees, whereas there was little difference in transpiring leaf ψ between these two treatments (Gamier and Berger, 1985).

In this study, soil and plant measures of water availability were compared on French prunes to determine the consistency and relative sensitivity of these measurements with respect to plant performance under several irrigation regimes.

Materials and Methods

This research was conducted at the Univ. of California (UC) Davis pomology experimental orchards during the 1988 and 1989 growing seasons. Prune trees on Marianna 2624 rootstock had been planted in 1982 with 4.6-m spacing between rows and three within-row spacings of 1.5 m (high density), 2.3 m (medium density), and 4.6 m (low density) on a Reiff loam soil. Trees in the various densities had been pruned differently so that canopy cover was similar in all densities. The experimental plot (46 × 23 m) was divided into three irrigation regimes: wet, medium, and dry. The wet plots were irrigated daily to maintain a soil matric potential of -10.0 to -20.0 kPa as measured by tensiometers (see below) for the upper meter of soil. The medium plots were irrigated when the moisture content of the soil within the root zone dropped to 50% of the value between field capacity (FC) and permanent wilting point (PWP), as determined with a neutron probe (see below). Water was applied to the dry plots when PWP was reached throughout the majority of the monitored soil depths (30 to 180 cm). The orchard floor was drip-irrigated with biwall tubing, having emitters every 30 cm. The tubing was placed on the soil surface at 30-cm intervals, allowing the entire orchard floor to be uniformly irrigated at a precipitation rate of $\approx 7 \text{ mm}\cdot\text{h}^{-1}$. Volumetric soil water content was measured periodically at 30-cm intervals from 30 to 180 cm within the soil profile with a neutron probe (Campbell Pacific Nuclear, Pacheco, Calif.). Field capacity at these same positions was determined 3 to 5 days after irrigation from a saturated 6 × 6-m bare soil plot covered with a reflective tarp (Hillel et al., 1972) and ranged from 0.29 to 0.39 $\text{cm}^3\cdot\text{cm}^{-3}$. Six neutron access sites in the medium plots and nine (four in the high density, five in the low density) in the dry plots were used to monitor soil moisture. Access sites were located both within and between tree rows.

In 1988, the water content corresponding to PWP (moisture content at -1.5 MPa soil matric potential) at each depth was obtained from a local soil survey and ranged from 0.09 to 0.12 $\text{cm}^3\cdot\text{cm}^{-3}$ (Huntington et al., 1981). Together with observed FC, these values determined the 50% depletion point used for irrigation scheduling in the medium plot. The values of PWP were revised slightly in 1989, based on the minimum soil water contents observed in the dry plots in 1988 (0.08 to 0.14 $\text{cm}^3\cdot\text{cm}^{-3}$). During each season, the pattern of water depletion at each depth was used to determine the effective root zone in the medium plot (Wilcox, 1959). In 1988, most water uptake occurred in the top meter of soil (McCutchan, 1990), and the 50% depletion point in the medium plot corresponded to an average moisture content of 0.15 $\text{cm}^3\cdot\text{cm}^{-3}$ throughout this upper meter of soil. In 1989, soil moisture depletion patterns indicated that significant water uptake occurred to 150 cm (McCutchan, 1990), and the 50% depletion point correspond to

an average moisture content of 0.21 $\text{cm}^3\cdot\text{cm}^{-3}$ throughout this 150-cm depth.

For medium and dry plots, the difference between consecutive measurements of soil moisture (typically, 7-day intervals), was used to estimate crop evapotranspiration (ET) over that time interval. Water depletion at each neutron access site was weighted by the soil surface area represented by that site. Drainage of water below the root zone appeared to be minor, but could not be accurately determined (McCutchan, 1990), and no correction for drainage was made. Hence, values of crop water use, which ranged from 1 to 5 $\text{mm}\cdot\text{day}^{-1}$ over the course of the season in the medium plots, may have been slightly overestimated. Based on the overall lack of difference in ψ and other physiological measurements between the trees in the wet and those in the medium plots, we assumed that ET_{MED} could be used as an estimate for reference (nonlimiting) crop ET. Thus, to account for site effects and also for seasonal differences in evaporative demand, water use in the dry plots was expressed relative to the water use in the medium plots as a ratio ($\text{ET}_{\text{DRY}} : \text{ET}_{\text{MED}}$).

Soil moisture in the wet plots was monitored by tensiometers (six replications per depth), sealed with a rubber sleeve stopper and measured with a pressure transducer (Burger and Paul, 1987). The tensiometers were placed at four depths (30, 45, 60, and 90 cm) and located both within and between tree rows. All tensiometers were measured at 3- to 4-day intervals. The timing and duration of daily irrigations were adjusted as necessary to maintain the upper meter of soil at -10.0 to -20.0 kPa. Meteorological data for reference crop ET_0 and vapor pressure deficit (VPD) were obtained from a nearby weather station (California Irrigation Management Information System, CIMIS, Station no. 6, Davis, Calif.).

Tree water potential and leaf conductance. Leaf and stem ψ were measured on mature leaves with a pressure chamber (Soil Moisture Equipment Corp., Santa Barbara, Calif.). Sun-exposed (transpiring) leaf ψ was measured on leaves from the outer canopy, which had remained sunlit for at least 2 h before measurement. Two to three leaves per tree were selected from three trees in each treatment at midday (1200 to 1500 HR). Leaves were placed inside a plastic bag just before excision to avoid post-excision water loss (Turner and Long, 1980).

Stem ψ was determined by measuring the ψ of leaves located near the trunk or a main scaffold branch, which had been enclosed overnight in a black plastic bag covered with aluminum foil (Begg and Turner, 1970). Leaf conductance was measured with a steady state porometer (LI-1600, LI-COR, Lincoln, Neb.) on about five leaves per tree that had a similar exposure as those used for leaf ψ . For seasonal comparisons with crop ET and leaf conductance, the stem ψ for the medium and dry treatments was expressed relative to the stem ψ for the wet treatment as a difference ($\psi_{\text{DRY}} - \psi_{\text{WET}}$). This procedure is preferable to a ratio (as used for ET) because drought increases the magnitude of ψ relative to the control with no theoretical limit, whereas drought reduces both ET and conductance toward a theoretical limit of 0. Additional stem ψ and leaf conductance measurements were made in 1990 on prune trees from an irrigation trial in a commercial orchard, $\approx 65 \text{ km}$ north of Davis (Gridley, Calif.).

Results

Plant-water status. A more complete seasonal pattern of soil- and plant-based measurements was obtained in 1989 than 1988 (McCutchan, 1990), and, since overall patterns were similar, only data for 1989 will be presented. The effect of the dry

treatment was evident in stem and leaf ψ (Fig. 1 A, B). Trees from the dry plots exhibited a substantially lower ψ than the trees from the medium and wet plots from early May to early August. When the dry plots were irrigated in early August, stem and leaf ψ recovered and reached values that were similar to those for the wet and medium treatments. Stem and leaf ψ were similar for the wet and medium treatments over the season (Fig. 1 A,B). On the days before irrigation of the medium plots, however, stem ψ was significantly lower for medium than wet plots, whereas leaf ψ was not (Table 1). Following irrigation, neither stem nor leaf ψ showed any significant difference between wet and medium plots.

In the wet plots, day-to-day fluctuations in midday stem ψ were associated with parallel variations in midday VPD (Fig. 2A). There was a strong correlation ($R^2 = 0.81$) between stem

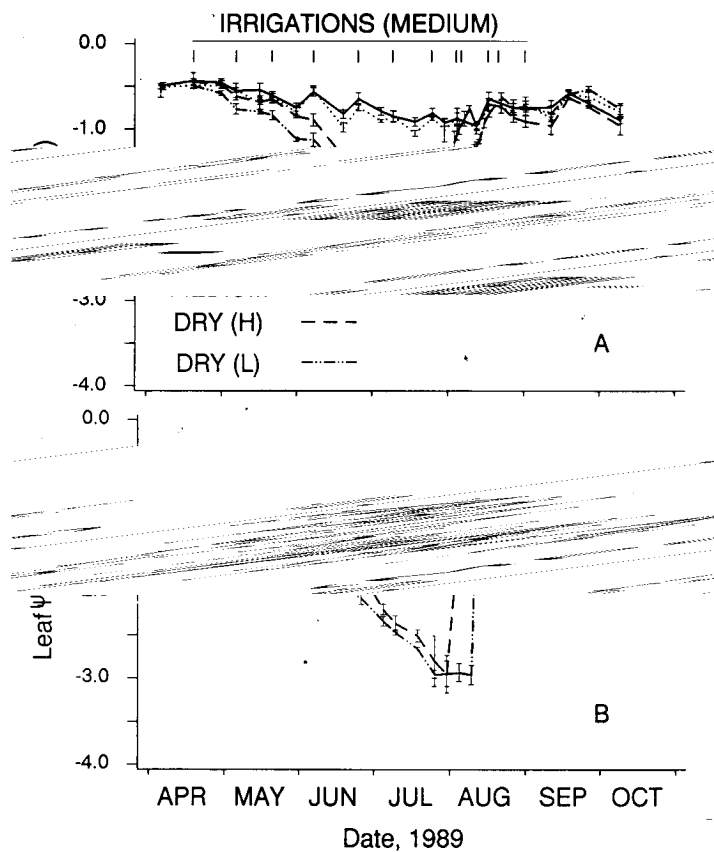


Fig. 1. Seasonal pattern of stem ψ (A) and leaf ψ (B) at midday (1200-1500 HR) for wet, medium, and dry plots in 1989, the latter for high (H) and low (L) planting densities. Means are shown \pm 2 SE, and the dates when the medium plots were irrigated are indicated.

Table 1. Comparison of mean leaf and stem ψ measurements for the wet and medium plots for days before or just following irrigation in the medium treatment (N = 10 days).

Measure	Treatment	Before irrigation	Following irrigation
Stem Ψ	Wet	-0.74 b ²	-0.67 a
	Medium	-0.79 c	-0.69 ab
	Difference	-0.05	-0.02
Leaf Ψ	Wet	-1.30 b	-1.19 a
	Medium	-1.36 b	-1.22 a
	Difference	-0.06	-0.03

²Mean separation within the same measure category by Duncan's multiple range test, $P = 0.05$.

ψ and VPD for all data, with the exception of those from early in the season (7 Apr.-7 May), one period during the middle of the season (26 July-5 Aug.), and the last measurement date (10 Oct.) (Fig. 2B). Leaf ψ had a lower correlation ($R^2 = 0.70$) with VPD than stem ψ . No other single midday environmental factor, such as relative humidity, solar radiation, air temperature, or windspeed, was as strongly correlated with stem ψ as VPD. This was also the case for ET_c , which integrates these and other environmental factors (data not shown).

Relation of crop water use to soil and plant measures of water availability. Soil moisture was progressively depleted in the dry plots (early May through early August) and the rate of crop water use also declined. Compared with water use in the medium plots, the dry plots exhibited a linear decline in water use with decreasing soil water content (Fig. 3A), whether planted at low or high density. However, trees at the high density exhibited higher water use at all soil water contents than trees at the low density. Stem ψ in the dry plots also declined with decreasing soil water content (Fig. 3B). Trees in the high-density plot, however, exhibited higher stem ψ than trees in the low-density plot for soil water contents $< 25 \text{ cm}^3 \cdot \text{cm}^{-3}$. These differences between the high- and low-density trees were associated with localized differences in soil texture. Soil samples

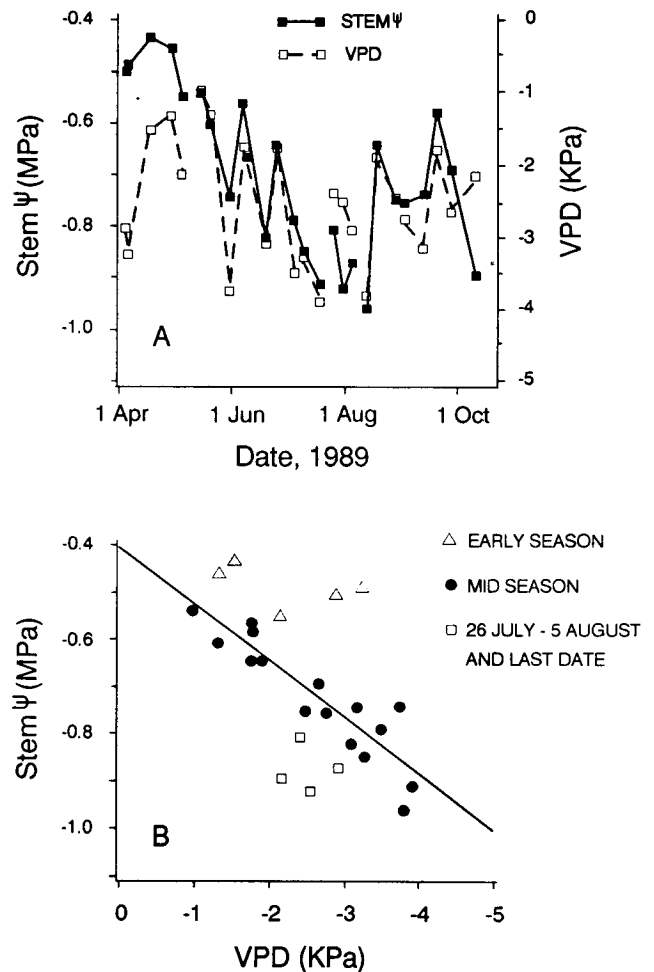


Fig. 2. (A) Seasonal pattern of midday stem ψ in the wet plots, as in Fig. 1, and the corresponding midday VPD in 1989. (B) The relation of stem ψ to VPD, with a linear regression ($\psi = -0.12 \cdot \text{VPD} - 0.41$, $R^2 = 0.81$) through the points corresponding to midseason values of stem ψ and VPD.

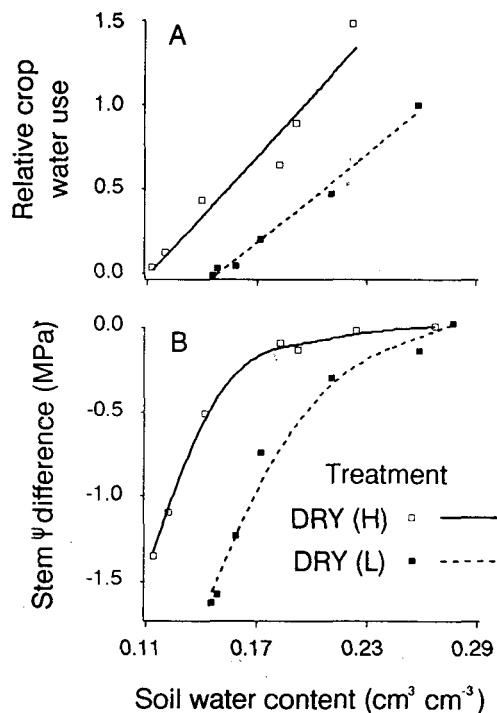


Fig. 3. (A) The relation of crop water use in the high (H) and low (L) density plots of the dry treatment, expressed as a fraction of the water use in the medium plots ($ET_{\text{DRY}}/ET_{\text{MED}}$) over the same period, to average soil water content in each of the dry treatments, respectively. (B) The relation of stem ψ in the dry plots, expressed as a difference from the stem ψ in the wet treatment ($\psi_{\text{DRY}} - \psi_{\text{WET}}$) over the same period, to average soil water content for the two planting densities, as in (A).

from the low-density plot contained less sand and retained more water at the same matric potential than samples from the high-density plot, as determined by moisture-release characteristics of undisturbed soil cores from depths of 45 and 90 cm (McCutchan, 1990).

Despite the spatial variability of soil texture within the dry plots and apparent differences in water relations between the trees in the high- and the low-density plantings, there was a uniform relation of crop water use to stem ψ independent of planting density (Fig. 4A). This relationship indicated that substantial reductions in crop water use were associated with relatively small initial reductions from control levels in stem ψ and that crop water use was progressively less sensitive to further reductions in stem ψ . A very similar relation was found between leaf conductance and stem ψ , when the data were pooled from the trees of this study (UC Davis site) and the trees in a commercial French prune orchard (Gridley site, Fig. 4B). For the UC Davis site, these data represent individual tree means for all treatments on two sampling dates in 1989 (31 July, just before irrigation in the high-density dry treatment, and 5 Aug., just before irrigation in the low-density dry treatment). Data for the Gridley site are also individual tree means collected from a range of irrigation treatments on 24 July 1990. As was the case for crop water use, the largest reductions in leaf conductance occurred at values of stem ψ that were close to the well-irrigated controls, with progressively less sensitivity of leaf conductance to further reductions in stem ψ . A 50% reduction from the control in both crop water use and leaf conductance corresponded to a difference of 0.5 to 0.6 MPa from control levels in stem ψ (Fig. 4 A, B).

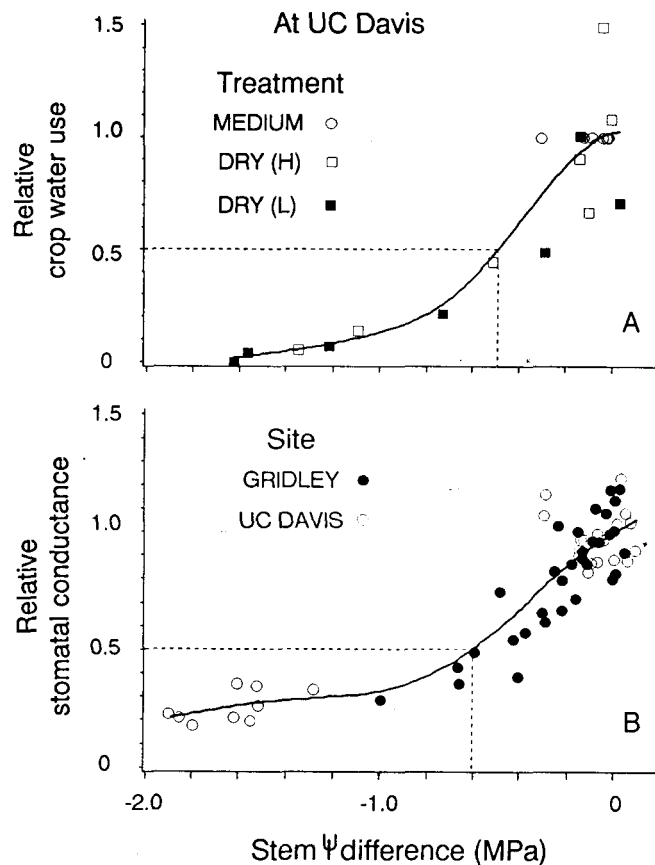


Fig. 4. (A) Crop water use (as in Fig. 3A) as a function of stem ψ (as in Fig. 3B) for medium and dry plots. Stem ψ for the medium plots is expressed as a difference from the stem ψ in the wet treatment, as in Fig. 3, but since the medium plots were used as a basis for calculating crop water use, all points for this treatment have a crop water use value of 1. Curved line is a smoothed spline fit to all data, and dashed line indicates the stem ψ corresponding to a 50% reduction in crop water use. (B) Stomatal conductance for medium and dry plots at Univ. of California (UC) Davis, and a range of treatments in a commercial orchard (Gridley), expressed relative to the stomatal conductance for the wet plots at each site, as a function of stem ψ , with a smoothed spline fit and 50% reduction point indicated, as in A.

Discussion

Measured at midday, both stem and leaf ψ showed the progressive development of substantial plant water deficits in the nonirrigated trees of this study, as well as the recovery of these trees to the levels exhibited by continuously irrigated control trees following irrigation of the former (Fig. 1 A,B). Stem ψ was generally less variable than leaf ψ , but for comparison of the dry with the control (wet) treatment, both measures were similar. Lower variability in stem ψ , however, improved the ability of this measure, compared with leaf ψ , to detect a small (0.05 MPa) but statistically significant difference between control trees and trees under an irrigation regime of mild soil moisture depletion (Table 1). In addition to its sensitivity and its relative predictability with respect to environmental VPD (Fig. 2B), stem ψ was also closely related to crop water use and stomatal conductance (Fig. 4 A,B). The steepness of these relations at high ψ indicates that prune trees may be responsive to water limitations at relatively small reductions (0.5 to 0.6 MPa) in ψ from control levels. Clearly, the ability to detect a progressive change in water status in advance of the occurrence

of any stress responses, such as stomatal closure, is a useful characteristic for any plant-based measure of water stress. Physiological responsiveness to water stress, however, may not lead to reductions in tree productivity, and in some cases benefits to deficit-irrigation strategies have been reported (e.g., Chalmers et al., 1986). Further studies will be needed to determine the overall impact of these responses on productivity in French prune trees.

In this study, a small difference (0.05 to 0.06 MPa) related to irrigation regime was detected in stem and leaf ψ measured at midday (Table 1) but was only statistically significant for stem ψ . However, the ability of midday stem ψ to reflect tree water relations differences, in the absence of apparent differences in leaf ψ , has been reported in other studies. Garnier and Berger (1985) found no difference in the leaf ψ of stressed vs. control peach trees, whereas there was a large (0.5 MPa) and significant difference in stem ψ . Olien and Lakso (1986) found a consistent rootstock effect related to dwarfing of ≈ 0.3 MPa on stem ψ in apple, whereas the difference in leaf ψ was much smaller (0.08 MPa) and not significant. Hence, stem and leaf ψ , even though both measure the same thermodynamic property, apparently may not be equivalent measures of plant water status. This distinction may be relevant to the question of whether ψ is mechanistically involved in plant water stress responses (e.g., Sinclair and Ludlow, 1985), since the absence of any measurable change in leaf ψ when plants respond to stress is often understood as indicating a lack of ψ involvement in the stress response.

The influence of stomatal conductance and leaf transpiration on the ψ gradient between the stem and the leaf is one factor that may account for the differential response of stem and leaf ψ to plant water stress. During transpiration, leaf ψ must be lower than stem ψ , and the difference will represent a ψ gradient. A large portion of this gradient may exist within the leaf itself (Shackel and Brinckmann, 1985), but, more importantly, the size of this gradient will be proportional to the rate of leaf transpiration. Hence, even if the measurement of leaf ψ is made under equilibrium conditions (Tyree and Hammel, 1972), the ψ of a previously transpiring leaf is equal to the sum of stem ψ plus a transpirationally induced ψ gradient. If this ψ gradient is large, then stomatal responses could theoretically cause any reduction in stem ψ to be offset by a reduction in transpiration and the size of the ψ gradient. In the case where both reductions were equivalent, there could be a clear reduction in stomatal conductance with decreases in stem ψ (Fig. 4B) but no change in leaf ψ . Depending on the size of the gradient, compared with the change in stem ψ under water stress conditions, an increase in leaf ψ during stress-induced stomatal closure is also possible. To evaluate these possibilities, the magnitude of the ψ gradient compared with the change stem ψ that may occur under stress conditions has to be determined. In this study, the stem-leaf ψ gradient was typically 0.5 MPa (Fig. 1), but other studies have shown gradients >1.0 MPa (Garnier and Berger, 1985). Our study has further indicated that conductance and whole orchard transpiration were reduced on the order of 50% with a reduction in stem ψ of 0.5 to 0.6 MPa (Fig. 4). Hence, the ψ gradient itself clearly may be similar in size to the reduction in stem ψ that occurs as soil moisture is depleted and stomatal conductance is reduced. This similarity may account for the differential response of stem and leaf ψ to plant water stress and may further

justify the use of stem ψ as the more appropriate measure of plant water status.

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