

Field evaluation of water transport in grape berries during water deficits

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The net flow in vascular and transpirational components of the grape berry water budget was evaluated during water deficits imposed at different stages of fruit development. Diurnal fluctuations in berry diameter were measured on field-grown grapevines (*Vitis vinifera* L. cv. Cabernet Sauvignon) by using electronic displacement transducers. Water deficits were imposed by withholding irrigation, and water potentials of mid-shoot leaves, basal stem xylem and clusters were determined with a pressure chamber. The relative net flows through pedicel xylem and phloem and through berry transpiration were estimated pre-veraison and post-veraison. The xylem functioned nearly exclusively in providing net inflow pre-veraison, while the phloem was clearly dominant post-veraison. Accordingly, the amplitude of diurnal contraction was markedly smaller post-veraison than pre-veraison. The amplitude of diurnal contraction increased dramatically with decreasing plant water status post-veraison, yet exhibited little sensitivity to low vine water status post-veraison. Measurements of the difference in water potential between clusters and source stems did not provide evidence of a gradient that would elicit significant water movement from the cluster to the stem at any time of the day. This was true for both irrigated and non-irrigated vines, although the non-irrigated vines exhibited a smaller gradient favoring inflow throughout much of the day. The gradient for xylem water transport to the cluster was considerably smaller post-veraison than pre-veraison. The results showed that berry transpiration functioned as the primary pathway for water loss both pre- and post-veraison.

Key words – Fruit ripening, fruit transpiration, grape, phloem, *Vitis vinifera*, water potential, xylem.

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Introduction

Water relations of developing fruit play an important role in determining fruit growth and composition. In addition to inhibiting berry growth in grape, water deficits alter several aspects of fruit ripening and composition (Hardie and Considine 1976, Matthews and Anderson 1988, Williams and Matthews 1990) and sensory properties of the subsequent wines (Matthews et al. 1990). Unlike the sigmoid pattern of enlargement in most plant organs, growth of some fleshy fruit, including *Prunus* sp.

and *Vitis* sp., exhibit a double sigmoid pattern (Coombe 1976) in which there are two periods of growth separated by a lag phase. In grape, the transition from the lag phase (Stage II) to the second growth phase (Stage III) is rapid, occurring over 1 or 2 days (Matthews et al. 1987b). The regulation of the resumption of growth in Stage III (i.e. veraison) is not understood, although it is clear that the onset of Stage III growth coincides approximately with increases in sugars (Coombe and Bishop 1980) and with increased plastic extensibility of the berry dermal tissue (Matthews et al. 1987b).

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Within the long-term growth habit, the developing grape berry undergoes diurnal changes in volume that are the consequence of its water balance. Such variations are not uncommon in stems (e.g. Schroeder and Wieland 1956, Klepper et al. 1971) and fleshy fruit (Elfving and Kaufmann 1972) of plants exposed to significant evaporative demand. The usual interpretation of this behavior is that the stem or fruit serves as a capacitor in the plant water balance, with stored water flowing from the stem or fruit through the stem xylem to transpiring leaves during periods of high evaporative demand (Kozlowski 1968, 1972, Jarvis 1975). However, we recently found that in potted vines grown in growth chambers, diurnal contraction abruptly diminished at the onset of veraison (Greenspan et al. 1994). Furthermore, experiments designed to test the diurnal flows in the berry water budget produced little evidence of net backflow to the parent vine in irrigated vines.

The present study was conducted with field-grown vines to test whether the phenomena observed in our earlier work were an artifact of potted vines or controlled environmental conditions, to evaluate the role of xylem conduits in supplying water to and retrieving water from the developing fruit, and to investigate the role of berry transpiration in the fruit water balance. The cluster-stem and leaf-stem water potential gradients were measured diurnally before and after veraison to determine if apoplastic backflow could occur under irrigated or non-irrigated conditions.

Abbreviations – Ψ , Water potential; $\Delta\Psi$, water potential "gradient"; the difference in water potential between two specified tissues.

Materials and methods

Plant material and treatments

Seven-year-old grape vines (*Vitis vinifera* L. cv. Cabernet Sauvignon) grown in a commercial vineyard in northern San Joaquin County, CA, USA, were investigated during the 1990 and 1991 growing seasons. The soil at this location is a Redding Gravely Loam with a depth of 1 m (Weir 1952). Vines were spaced at 1.8 × 3.0 m and were trained to a bilateral cordon using a single-wire trellis. The vineyard was drip irrigated with emitters located midway between the vines. Irrigation was applied three times per week in 1990, but was increased to six times per week in 1991 in order to decrease day-to-day variation in soil water content. These regimes applied 84 l vine⁻¹ week⁻¹, except following veraison in 1991 when 120 l vine⁻¹ week⁻¹ were applied. Water deficits were imposed at both pre- and post-veraison stages on some vines either by withholding irrigation or by reducing irrigation to once per week at a rate of 16 l vine⁻¹ week⁻¹.

Measurement of berry diameter

The diameters of several berries were continuously measured by linear variable differential transformers (Schae-

vits Engineering, Pennsauken, NJ, USA) or with resistive displacement transducers (Duncan Electronics, Costa Mesa, CA, USA) mounted in a custom frame (Greenspan et al. 1994). A datalogger (Campbell Scientific, Logan, UT, USA) recorded the transducer output once per minute, and the mean of each 15-min period was logged to obtain the complete diurnal record of berry diameter. The transducers were moved to new berries at least once per week to avoid artifacts caused by prolonged contact. Berry volume was estimated from a regression of volume on diameter from a random sample of pre- and post-veraison berries as previously described (Greenspan et al. 1994). For the calibration, berry volume was measured by water displacement, and diameter was measured by micrometer calipers.

Diurnal measurement of water potential gradients

To relate the dynamics of berry volume and water potential gradients ($\Delta\Psi$) within the shoot, the pressure chamber technique (Scholander et al. 1965, Turner 1981, Matthews et al. 1987a) was used for diurnal measurements of xylem tension of the cluster, stem and mid-shoot leaf on the same shoot. Sampled shoots were representative of exposed shoots and usually carried two clusters. When two clusters were present, the basal cluster was sampled. The mid-shoot leaf was selected as the leaf having an equal number of basipetal and acropetal leaves. Leaves and clusters were enclosed in polyethylene film, excised, and placed immediately into a humidified pressure chamber for measurement. For stem xylem measurement, a healthy basal leaf (as close as possible to the cluster) was enclosed in polyethylene film and covered with aluminum foil on the day preceding measurement (Begg and Turner 1970, Schultz and Matthews 1993).

Effects of water deficit on diurnal contraction

Berry diameter was measured simultaneously on both irrigated and non-irrigated vines. The amplitude of berry contraction was calculated as the difference between the morning maximum diameter and diurnal minimum diameter. This was expressed as a percentage of the morning maximum berry diameter to normalize differences in the size of measured berries. Midday leaf water potential (Ψ_{leaf}) measurements were made periodically during the period from 30–53 days post-anthesis (27–4 days pre-veraison) for pre-veraison measurements and 75–94 days post-anthesis (18–37 days post-veraison) for post-veraison measurements.

Berry water budget analysis

The xylem, phloem and berry transpiration components of fruit water balance were estimated pre- and post-veraison by using methods similar to those of Lang and Thorpe (1989) and those described in detail in Greenspan et al. (1994). Briefly, three treatments were imposed on

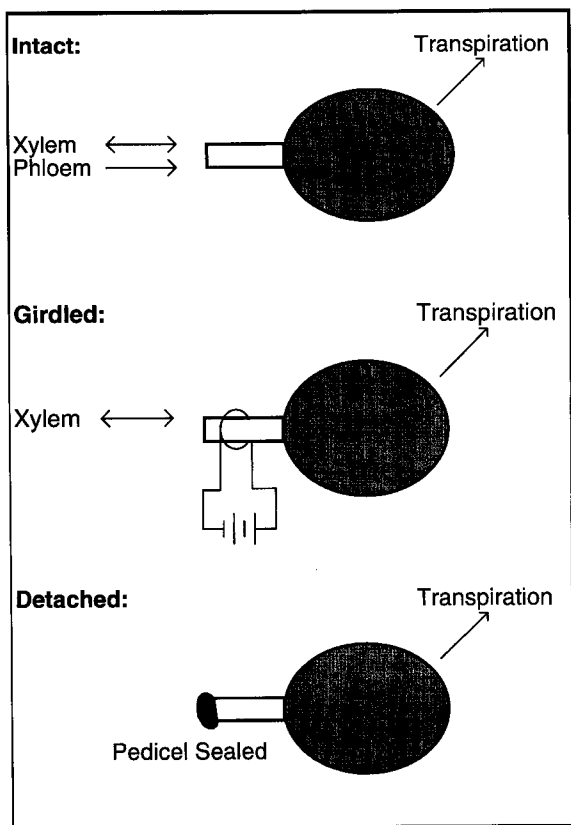


Fig. 1. Diagram of the treatments (intact, girdled, detached) used to evaluate water flows into and out of the berry.

separate berries (Fig. 1) and their diameters were measured for one diurnal cycle. The three treatments were (1) berry and all flows intact, (2) pedicel heat girdled and phloem flow eliminated, and (3) pedicel cut eliminating xylem and phloem flows. From these three treatments, the net flows of water to and from the berry via the xylem (plus non-vascular apoplast) and phloem in addition to water leaving the fruit through berry transpiration were estimated. Treatments were imposed in the morning, and

berries were used for a single diurnal measurement only. Handling of each berry was minimized to prevent disruption of the integrity of the surface wax platelets. The experiments were conducted both pre-veraison (ca 36 days post-anthesis, 36 days pre-veraison) and post-veraison (ca 91 days post-anthesis, 19 days post-veraison) on irrigated vines and on vines subjected to water deficit by the withholding of irrigation for several days.

Results

Pre-veraison berries of both irrigated (Fig. 2A) and non-irrigated (Fig. 2B) vines exhibited a pronounced contraction during the afternoon followed by a nighttime expansion. Both the magnitude and duration of the contraction were greater for non-irrigated vines than for irrigated vines. Contraction began later and ceased earlier in the irrigated fruit, suggesting that the water balance of non-irrigated fruit was more sensitive to diurnal changes in evaporative demand. Net berry growth, which occurred when nighttime expansion exceeded daytime contraction, was consistently greater in the irrigated vines than in the non-irrigated vines.

Post-veraison berries did not exhibit the pronounced contractions observed in pre-veraison fruit (Fig. 2A,B). For example, mean contraction of irrigated post-veraison fruit was $1.0 \pm 0.1\%$ of berry diameter ($n=31$) compared to a mean pre-veraison contraction of $5.9 \pm 0.4\%$ of diameter ($n=49$). The diurnal onset of both expansion and contraction was delayed post-veraison compared to pre-veraison.

Response of diurnal contraction to water deficits

The amplitude of the pre-veraison contractions increased substantially as low vine Ψ developed (Fig. 3). For midday Ψ_{leaf} that decreased from -1.1 to -1.4 MPa, diurnal contractions increased from a low of 4 to a high of 13% of initial diameter. Berries of vines that had not been irrigated were visibly shriveled during the afternoon. In contrast, post-veraison contractions ranged from only 1 to 3% of berry diameter over a midday Ψ_{leaf} range of -1.1 to

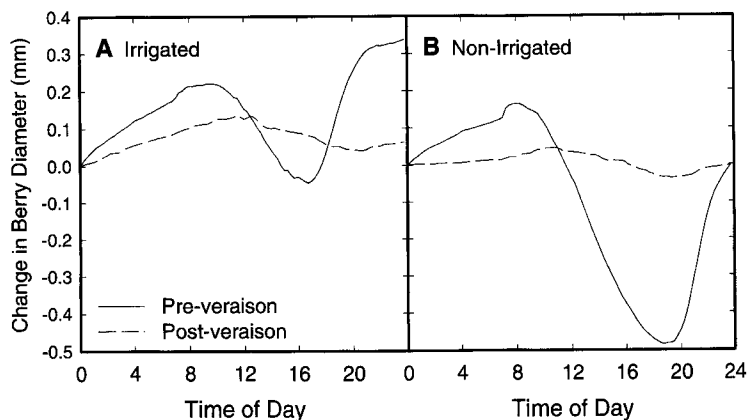


Fig. 2. Typical diurnal pattern of berry diameter change for pre-veraison and post-veraison berries of (A) irrigated and (B) non-irrigated vines. Mean initial diameters were 8.0 and 11.4 mm for pre- and post-veraison berries, respectively.

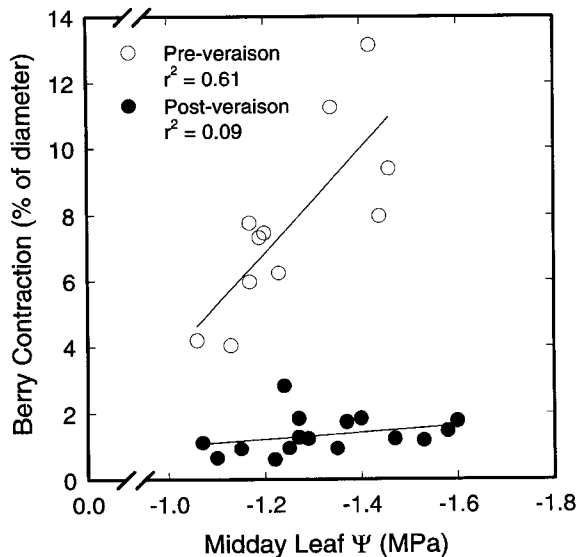


Fig. 3. Amplitude of diurnal berry contraction at various midday Ψ_{leaf} for pre- and post-veraison berries. Pre-veraison correlation is significant for $P < 0.01$; post-veraison correlation is not significant.

-1.6 MPa, and afternoon shriveling was not observed. Contraction was significantly correlated with midday Ψ_{leaf} pre-veraison ($P < 0.01$) but not post-veraison. Although the post-veraison contractions were smaller at any water deficit, they were not as recoverable as pre-veraison contractions; i.e. berry growth was inhibited by both pre- and post-veraison water deficits.

Components of the berry water budget

The diurnal water budget of the berry was assumed to be comprised of three components: xylem flow, phloem flow and berry transpiration. Net flow through each component was estimated from a series of experiments in which one or more pathways were eliminated. Daily water loss was primarily via berry transpiration, approximately $160 \pm 33 \text{ mm}^3$ per berry pre-veraison and $90 \pm 25 \text{ mm}^3$ per berry post-veraison (Fig. 4). This was largely balanced by water uptake through the vasculature, primarily through the xylem pre-veraison and through the phloem post-veraison. During pre-veraison, net flow through the phloem was very small. Similarly, net post-veraison flow through the xylem was small, and sometimes negative (from fruit to parent plant).

The net diurnal flow rates indicate that during pre-veraison (Fig. 5A), maximum xylem uptake lagged maximum transpiration by about 4 h. The transpiration rate exhibited a pattern of gradual increase and decline during the daylight hours while the net xylem inflow rate showed a sharp peak during the afternoon hours. This lag was not apparent in the post-veraison fruit (Fig. 5B) in which net vascular inflow (via phloem) closely followed, in time, the water lost via transpiration. Thus,

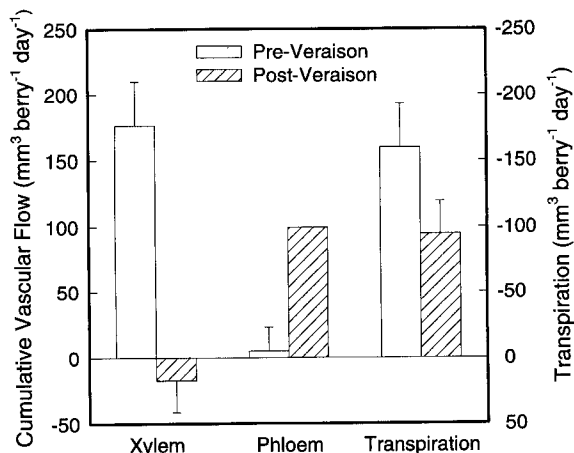


Fig. 4. Calculated cumulative daily vascular flow and transpiration for pre- and post-veraison berries of irrigated vines. Water flow was estimated from a linear combination of cumulative diurnal volume changes in intact, excised and girdled berries (see Materials and methods for details). Error bars indicate SE ($n=3$ pre-veraison and $n=2$ post-veraison).

significant phloem flow occurred over a longer daytime period but the maximum flow rate was only one-third of the maximum xylem flow rate observed pre-veraison.

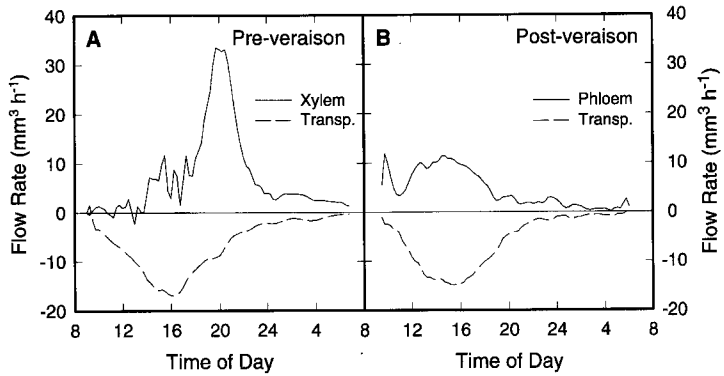
Diurnal water potential measurements

Diurnal measurements of Ψ_{xylem} for leaves, stems and clusters were performed during pre- and post-veraison to estimate $\Delta\Psi$ in the xylem for comparison with observed flow patterns. Diurnal excursions in Ψ were less for the stem than for leaves or clusters throughout the season (Figs 6A,B and 7A,B).

Pre-veraison, predawn Ψ_{leaf} was about 0.2 MPa higher in the irrigated vines than in the non-irrigated vines (Fig. 6A and B, respectively). Time at low Ψ was also greater in the non-irrigated vines, where Ψ of all organs declined more rapidly in the morning and recovered more slowly in the evening. In both irrigated and non-irrigated vines, Ψ_{leaf} approached equilibrium with Ψ_{stem} more rapidly than did Ψ_{cluster} . The minimum in $\Delta\Psi_{\text{cluster-stem}}$ during the afternoon (Fig. 6C) corresponded well in time to the observed maximum net inflow rate (Fig. 5A).

Xylem backflow (from cluster to shoot) requires a reversed, or positive, $\Delta\Psi_{\text{cluster-stem}}$. During pre-veraison, positive $\Delta\Psi_{\text{cluster-stem}}$ was observed infrequently and only in the early morning measurement on the non-irrigated vines (Fig. 6D). Positive $\Delta\Psi_{\text{cluster-stem}}$ did not coincide with times when berry contraction occurred, indicating that contraction was not due to reversed vascular water flow. However, the enhanced berry contraction that arose from pre-veraison water deficit (Figs 2A and 3) can be explained by smaller (less negative) midday $\Delta\Psi_{\text{cluster-stem}}$ in the non-irrigated vines supplying water at an insufficient rate to balance transpiration. The smaller gradient was, presumably, due to a lower Ψ_{stem} in the non-irrigated

Fig. 5. Calculated flow rates of transpiration (Transp) and to the vascular pathways (Xylem, Phloem) for (A) pre-veraison and (B) post-veraison berries. Flow rates were computed using a second-order central difference algorithm on diurnal measurements of cumulative volume change.



vines as well as to a slower recovery of Ψ_{stem} during the evening (Fig. 6B).

Midday Ψ_{leaf} of the post-veraison, irrigated vines (Fig. 7) had decreased compared to pre-veraison Ψ_{leaf} (Fig. 6), a phenomenon that has been observed in well-irrigated field-grown vines (Matthews et al. 1987a) and other crops (Acevedo et al. 1979). Ψ was considerably lower in the non-irrigated vines than in the irrigated vines after veraison, with predawn Ψ_{leaf} being about 0.8 MPa below that of the irrigated vines (Fig. 7A,B). Post-veraison daytime $\Delta\Psi_{leaf-stem}$ showed a pattern similar to that of pre-veraison $\Delta\Psi_{leaf-stem}$ for the irrigated vines, becoming more negative throughout the day and rapidly approaching equilibrium with the stem in the evening (Fig. 7C). The $\Delta\Psi_{leaf-stem}$ did not approach zero by early evening, however, in the non-irrigated vines (Fig. 7D).

Unlike the pre-veraison measurements, post-veraison $\Delta\Psi_{cluster-stem}$ did not become very negative as the day pro-

gressed (Fig. 7C,D), which agrees with the observation of reduced net xylem flow at this stage (Fig. 4). The $\Delta\Psi_{cluster-stem}$ was about zero throughout most of the day in the non-irrigated vines, but became negative by early evening (Fig. 7D). In the irrigated vines, $\Delta\Psi_{cluster-stem}$ was zero to slightly positive during the early part of the day, in agreement with our measurements of a scant xylem backflow from cluster to shoot at this stage (Fig. 4). This gradient became negative later in the day and returned to zero by early evening (Fig. 7C).

Discussion

The results confirm our earlier observations in controlled environments showing dramatic changes in the water relations of the grape berry at the transition to ripening (Greenspan et al. 1994). Significant berry transpiration was observed. The water potential of the cluster

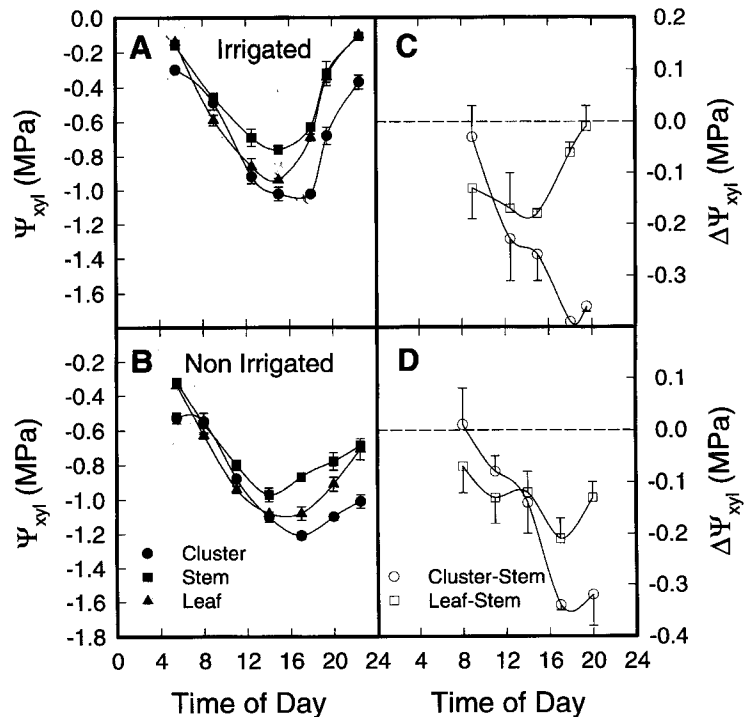


Fig. 6. (A,B) Diurnal xylem water potential (Ψ_{xyl}) of cluster, stem and leaf, and (C,D) diurnal water potential gradients ($\Delta\Psi_{xyl}$) of cluster-stem and leaf-stem from (A,C) irrigated and (B,D) non-irrigated pre-veraison vines. Water potential data are means of three measurements per organ and gradient data are means of gradients measured on the same three shoots used for organ water potentials. Measurements were made 21 days before veraison. Error bars indicate SE.

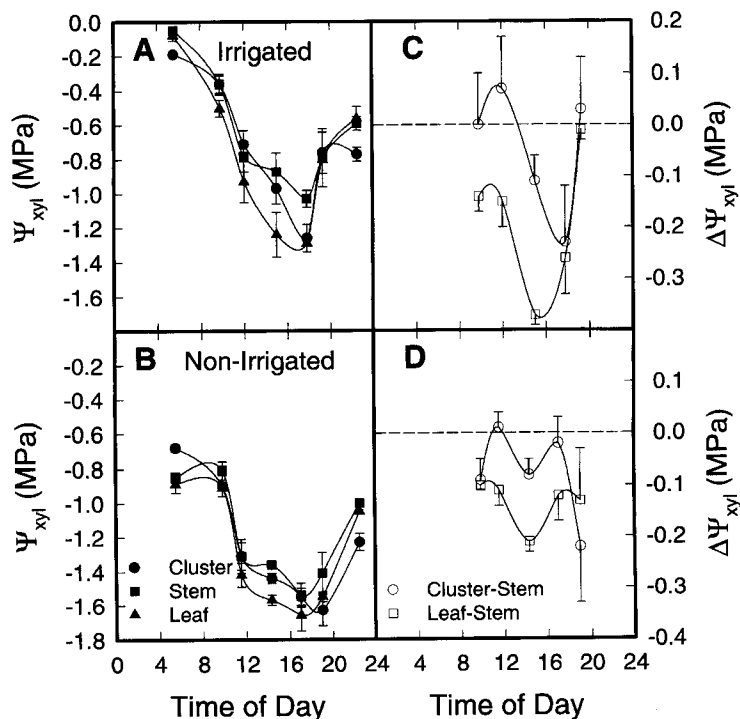


Fig. 7. (A,B) Diurnal xylem water potential (Ψ_{xyl}) measurements of cluster, stem and leaf, and (C,D) diurnal water potential gradients ($\Delta\Psi_{xyl}$) of cluster-stem and leaf-stem from (A,C) irrigated and (B,D) non-irrigated post-veraison vines. Water potential data are means of three measurements per organ and gradient data are means of gradients measured on the same three shoots used for organ water potentials. Measurements were made 8 days after veraison. Error bars indicate SE.

exhibited large diurnal swings common for transpiring tissues and was seldom more positive than the water potential of its water source, the basal stem xylem. These results and those from the independent analysis of berry water budget components show that there is little recycling of water from the berry back to the parent plant.

Environmental control of contraction

Diurnal contraction of pre-veraison berries under irrigated conditions in the field (about 6% of diameter) was many times greater than diurnal contraction during similar experiments in controlled environments (about 0.5% of diameter, Greenspan et al. 1994). Berry size was similar, as was the photoperiod during which contraction took place in both studies. We attribute the differences in degree of contraction to the lower evaporative demand in the growth chamber, where the light intensity was about 50% of full sunlight, and the vapor pressure deficit was about 2.7 kPa compared to about 4.4 kPa in the field. First, the rate of berry transpiration was greater in the field, resulting in a daily loss of about $135 \text{ mm}^3 \text{ day}^{-1}$ compared to about $90 \text{ mm}^3 \text{ day}^{-1}$ in the growth chamber. Second, the greater rate of leaf transpiration lowered leaf and stem water potential (Shackel and Brinckmann 1985). Midday Ψ_{leaf} of irrigated vines before veraison was typically -1.1 MPa in the field and -0.8 MPa in the growth chamber. This decreased the availability of water for berry uptake by diminishing $\Delta\Psi_{\text{cluster-stem}}$ during much of the day.

The diurnal transitions in water relations probably developed more rapidly in the growth chamber despite

some ramping of the dark-to-light transitions, because the changes in temperature and humidity occur over several hours in the field. Accordingly, berry growth occurred almost exclusively during dark periods in controlled environments, but continued well past dawn in field-grown vines. In both environments, net xylem inflow rate increased considerably during the evening, allowing the fruit to recover volume lost during the day (pre-veraison).

Xylem distribution of water to berries before veraison – a shift to phloem after veraison

Before veraison, the fruit are components of a well-connected hydraulic system that utilizes the xylem conduits. Factors that diminish Ψ (pressure potential) in the stem xylem also decrease water uptake by berries and, hence, increase berry contraction during the day. The amplitude of diurnal fruit contraction has been well correlated with decreasing leaf water potential in a number of fruits (Elfvig and Kaufmann 1972, Maotani et al. 1977, Tromp 1984) as it was here for pre-veraison grape berries grown in the field. When stem water deficits were diminished by restricting leaf transpiration, berry contraction was almost eliminated (Greenspan et al. 1994). Thus, the responses of berry contraction to soil water deficits and manipulation of shoot transpiration are also consistent with a hydraulically intact system distributing water via the xylem.

Pre-veraison, there was a continually positive net xylem flow into the berry that was the primary pathway for water flow (Figs 4 and 5). Post-veraison, the phloem fulfilled this role. In both cases, the complementary vascular

pathway played a relatively insignificant role in the overall berry water budget, regardless of the water status of the vine. Post-veraison net inflow (via phloem) was similar in both field and growth chamber experiments (typically $100 \text{ mm}^3 \text{ day}^{-1}$ in each environment). An increased reliance on phloem transport for water uptake during ripening, due in part to partial hydraulic isolation (Düring et al. 1987, Findlay et al. 1987) may contribute to drought tolerance in fruit by the avoidance of net water loss during the day. A dramatic decrease in the magnitude of daily contraction of berries at the transition from Stage II to Stage III was recently reported for Cabernet Sauvignon and Zinfandel grown in controlled environments (Greenspan et al. 1994), and was observed again in these experiments with Cabernet Sauvignon in the field. Contraction was about 6% of diameter each day before veraison, and about 1% of diameter after veraison. Thus, the phenomenon is not an artifact of root-bound, potted vines or other growth conditions peculiar to controlled environments.

Most water loss is by berry transpiration, not recycling to plant

The increased contraction of berries during pre-veraison soil water deficits may occur from either a reduced net vascular inflow or from backflow through the vasculature. This raises the question of whether fleshy fruit act as capacitors in whole plant water relations, as occurs in stems (Schroeder and Wieland 1956, Klepper et al 1971, Jarvis 1975). Backflow of vascular water from fruit to transpiring leaves has been suggested from diurnal measurements in which $\Psi_{\text{leaf}} < \Psi_{\text{fruit}}$ during midday for various crops (Klepper 1968, Tyvergyak and Richardson 1979, Syvertsen and Albrigo 1980, Yamamoto 1983), including grape (van Zyl 1987). However, for this to occur water should follow a negative water potential gradient from fruit to leaf. Therefore, a measurement of Ψ_{shoot} at the point of cluster attachment is necessary to determine if water movement from cluster to shoot occurs during the day. Liu et al. (1978) reported a negative midday $\Delta\Psi_{\text{cluster-shoot}}$ for grape, but shoot water potential was estimated as the average of base and tip measurements.

Several lines of evidence argue against significant backflow to the parent plant. First, in experiments specifically designed to test for backflow by disrupting other pathways, we found little evidence for net xylem flow from the berry to the parent plant in this field study. Second, our estimates of fruit transpiration were sufficient to account for the water loss associated with each case of fruit contraction. The daytime transpiration rates calculated from the field experiments were 0.31 ± 0.05 ($n=6$) and 0.16 ± 0.01 ($n=4$) $\text{mmol cm}^{-2} \text{ h}^{-1}$ for pre- and post-veraison berries, respectively. Third, low fruit water potentials tend to maintain gradients for water transport in the direction of the fruit. Measurements of the water potentials of stem and cluster indicated gradients that were almost exclusively in the direction of the cluster, the only exception being a slight gradient towards the

stem in the late morning for some shoots on non-irrigated vines. Similarly, Yamamoto (1983) did not detect gradients favoring water loss from pear fruit to parent plant. Finally, based on similar diurnal kinetics of water relations in peach, Berger and Selles (1993) formulated a model of the peach fruit water budget, and from it concluded that water did not flow from fruit to parent plant.

We do not argue that no backflow occurs. Indeed, the data in Fig. 6 indicate that a favorable gradient for backflow existed during a brief period in the pre-veraison, non-irrigated vines. Some backflow was reported in the grape variety Italia berry (Lang and Thorpe 1989) and in apple (Lang 1990). Since in apple there were varieties that did and did not exhibit backflow, there may be similar differences among grape varieties.

However, the significance of the berries as a water reservoir for the shoot is limited. Shoot transpiration of 610 g day^{-1} was estimated from pre-veraison measurements of leaf transpiration along whole shoots in the same vineyard (H. R. Schultz and M. D. Greenspan, unpublished data). Our pre-veraison measurements of berry contraction imply that the net loss by the fruit during contraction (assuming 100 berries cluster⁻¹ and 2 clusters shoot⁻¹) amounts to 11.0 g day^{-1} . Even if all of this water was recycled to the parent shoot, it represents less than 2% of shoot transpiration.

Conclusions

Under field cultivation the grape berry undergoes significant diurnal expansion and contraction. Both the amplitude of contraction and the sensitivity of contraction to vine water status diminish after veraison. There is a concomitant change from xylem-dominated to phloem-dominated water supply as the berry enters the ripening stage. With the exception of the small quantity of water retained for fruit growth, mass balance dictates that the water delivered by the vasculature must be removed from the fruit. It appears that this is accomplished primarily via berry transpiration and not by xylem backflow throughout fruit development. The dependence of berry water relations on transpiration indicates that the water status of the berry is highly dependent on canopy microclimate. Furthermore, the shift in water supply appears to convey a drought tolerance to the fruit during ripening, implying that water deficits imposed on the vine during this stage will have limited short-term impact on berry size.

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