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Resistance to Water Transport in Shoots of *Vitis vinifera* L.[1]

RELATION TO GROWTH AT LOW WATER POTENTIAL

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ABSTRACT

Apparent resistances to water transport in the liquid phase were determined from measurements of soil, root, basal shoot internode, shoot apex, and leaf water potentials and water flux in *Vitis vinifera* (cv White Riesling) during soil drying. Predawn water potential differences ($\Delta\Psi$) in the shoots accounted for 20% of the total $\Delta\Psi$ between the soil and the shoot apex when plants were well-watered but increased to about 90% when shoot growth ceased. The $\Delta\Psi$ from soil to root was essentially constant during this period. At low water potential, the $\Delta\Psi$ in the shoot was persistent when transpiration was low (predawn) or completely prevented (plant bagging). The apparent hydraulic resistance between the basal shoot internode and most rapidly expanding leaf (or shoot apex) increased several-fold when water was withheld. Leaf and internode expansion both exhibited high sensitivity to increasing hydraulic resistance. Measurements of pneumatic resistance to air flow through frozen internode segments indicated progressive vapor-filling of vessels as soil drying progressed. From these observations and others in the literature, it was suggested that embolization may be a common occurrence and play an important role in the inhibition of shoot growth at moderate water deficits.

Attempts to partition total resistance to water transport in the soil-plant system under a range of soil water contents have often found the major resistance in the plant (6). The resistance to radial water transport from soil to the stele increases under water (20 and nutrient (21) deficits, but it is not known whether axial resistance is similarly sensitive to environmental conditions. In most models the axial difference in water potential ($\Delta\Psi$) and resistance is assumed low and constant. There are, however, reports of considerable impedance to axial water movement in plant stems (16, 26) where the flow path is better defined than in roots and soil.

Early work in grape (23) and recent work in maize (27) suggested that stem xylem may cavitate under slight tension. If extensive, cavitation and subsequent embolization could lead to large apparent resistances to water transport and inhibited growth of apical organs. Therefore, measurements were made to determine whether stem resistance in grape was sensitive to water deficits in the range that is important to shoot growth.

MATERIALS AND METHODS

Growth Conditions. Grapevine (*Vitis vinifera* L. cv White Riesling) plants were grown from dormant rootings (Viticulture Field Station, University of California, Davis) in 8 L pots containing a soil:peat:perlite mixture (1:3:3) in a controlled environment (30/20 ± 1°C, 50/90 ± 10% RH, 13-h photoperiod with 550 to 1000 μmol photons m^{-2} s^{-1} PAR from cool-white fluorescent bulbs). One week after bud break (2–3 weeks after planting), plants were thinned to one or two shoots and inflorescences were removed. All plants were watered daily to saturation and fertilized with half-strength Hoagland solution 2 times per week. To ensure vertical growth, shoots were tied to stakes whenever necessary. Approximately 40 d after planting (shoot length and node number approximately 75 cm and 14, respectively), water was withheld from some plants. In experiments where soil water potential (Ψ_{soil}) was measured, the soil was covered with aluminum foil to prevent evaporation of soil water, to promote uniform soil water throughout the soil profile, and to minimize temperature gradients.

Growth of Shoots and Leaves. Growth of leaves and stems was measured with a hand-held micrometer every 24 h at the beginning of the photoperiod. The maximum rate of leaf expansion occurred at node 7 and 8, numbered basipetally from the shoot apex (24). The relationship between leaf length and leaf area was determined in order to nondestructively estimate leaf area/plant from measurements of leaf length. Two plants were grown under well-watered conditions until shoots reached about 75 cm in length (10–12 nodes with expanded leaves). Leaf length (for leaves ≥3.0 cm) was determined before excision from the shoot and leaf area measured immediately with a leaf area meter (r^2=0.92). This relationship did not vary significantly for plants which had water withheld until the leaves exhibited a 50% reduction of their initial growth rate, or until leaf growth ceased completely. Subsequently, this regression was used to estimate total leaf area from leaf length determinations in all experiments.

Plant and Soil Water Status. Soil and tissue water potential were determined by isopiestic thermocouple psychrometry (8) using sample chambers coated with melted and resolidified petrolatum and corrected for the heat of respiration. Solute potential was determined after freezing the sample (within the psychrometer cup) on dry ice for 10 min and allowing it to thaw for 35 min at room temperature on the laboratory bench in order to eliminate turgor.

Leaves were rinsed with distilled water to eliminate salts which may have accumulated on the surface, blotted dry with paper tissue, and allowed to dry for 30 min before beginning an experiment. Leaf discs (3.62 cm^2) were sampled and placed into the psychrometer cup with the adaxial surface facing up. For determination of shoot apex water potential (Ψ_{apex}), whole shoot apices (apical 2.5–3.0 cm) were detached from the plant and inserted into a psychrometer cup for the determination of tissue Ψ.

In order to obtain repeated root water potential (Ψ_{root}) measurements from the same plant without removing it from the growth medium, 10 × 10 cm ports were cut into the pot walls.

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The cut-out pieces were kept in the original position with plastic tape. Plastic bags (40 × 30 cm) were inserted into the pots, the soil mixture added, and the grapevine rooting planted. At time of sampling, the ports were removed, the clear plastic was cut open, and secondary roots, which had not been growing along the bag for more than 1 cm, were selected. This was done to ensure that the sample region was in good contact with the soil. Sampling was confined to 2 cm segments, taken 2.5 to 3.0 cm behind the root tip to avoid the root elongation zone. Adhering soil particles were then removed from the surface using fine paper tissue as a brush. Two to three sections from different roots were sealed into one psychrometer cup.

Soil samples were taken from the soil portion adjacent to the previously sampled roots and placed into another psychrometer cup. The hole left by the soil sample was refilled, the plastic bag retaped, and the port closed again. Each port was used only once. All samples were pressed gently onto the bottom of the cup to ensure good thermal contact.

In order to obtain the water potential gradient ($\Delta\Psi$) between the basal internode (Ψ_{base}) and the shoot apex (Ψ_{apex}), water potentials were determined by thermocouple psychrometry or the pressure chamber technique. An internode at the base of a shoot was rinsed with distilled water to eliminate surface accumulation of salts and blotted dry with paper tissue. After 30 min a section was cut from the internode with two razor blades mounted parallel to each other, 2.35 cm apart. Single sections were placed horizontally in a psychrometer cup and water and solute potential were determined as described. This method was used in experiments where only predawn Ψ was investigated and xylem tension was low. The technique has the obvious disadvantage of being destructive; however, it has the advantage that Ψ of both samples (*i.e.* basal shoot internode and shoot apex) was measured with the same method.

On all other occasions Ψ_{base} was determined from Ψ_{leaf} of a nongrowing and nontranspiring leaf subtending basal shoot internode. The leaf was wrapped in a clear polyethylene bag with moist paper towel in a corner of the bag and not in contact with the leaf. A second black polyethylene bag was wrapped around the first one and covered with aluminum foil. Precautions were taken so that the additional weight of bags and foil did not alter the position of the leaf. This technique assumes that the water potential of the bagged leaf equilibrates with the water potential of the shoot xylem which supplies the apical tissue sampled for water potential. At the time of sampling, the bagged leaf was detached from the shoot and its water potential determined with a previously humidified pressure chamber. Replicated measurements (n = 12) of Ψ_{base} using both methods produced the same mean, −0.32 MPa, and standard errors of less than 0.02 MPa.

Transpiration and Apparent Hydraulic Resistance. The rate of transpiration was estimated by two different techniques. A steady state diffusion porometer was used to determine the rate of single leaf transpiration of all leaves larger than 1.5 cm^2 on a shoot. The rates from all leaves were summed to obtain the rate of total plant transpiration which was used to calculate the instantaneous hydraulic resistance. Chamber air was stirred (2 m s^{-1}) which kept the boundary layer resistance at the leaf surface small. The rate of plant transpiration was also determined gravimetrically.

The driving force for this flux was estimated by water potential measurements of the basal stem xylem and of a leaf near the shoot apex. Diurnal measurements of leaf water status indicated that periods 4 h or more after dark/light or light/dark transitions were the only times in which the requirement for steady conditions was fulfilled. Preliminary measurements showed that water potentials were stable for approximately 2 h before samples were taken.

The apparent hydraulic resistance was calculated according to

$$Q = \frac{\Delta p}{R} \quad (1)$$

which is essentially Darcy's law governing water transport in soil. The primary difference in the two systems being the nonalignment of soil pores. Soil and shoot resistances were estimated using Eq. 1 from measurements of $\Delta\Psi$ and transpiration under steady conditions. In calculating R_{shoot}, it was assumed that all flux was to the apical leaf. For this and other reasons (see "Discussion") hydraulic resistances were termed apparent.

In order to estimate the presence of cavitated vessels, air flow through frozen stem segments was measured using the technique of Byrne *et al.* (9). Plants were sampled for basal leaf water potential near the end of the photoperiod at various times after withholding water. Intact stems were then plunged into an ethanol-dry ice bath to freeze xylem sap. Subsequent operations were performed at O°C in a walk-in cold room. Single internode segments (5 cm) were fractured with a razor and one end sealed to a micropotometer. A slight positive pressure (approximately 0.0025 MPa, determined with a manometer) was applied and the time required to pass a known volume of air was determined from the excursion of a meniscus in the potometer. The presence of vapor-filled vessels was indicated by increased air flow through frozen tissue. Results from more basipetal internodes than shown were equivocal due to frequent longitudinal splitting during freezing.

RESULTS

At high water status, predawn water potential differences ($\Delta\Psi$) between soil and roots and between soil and the shoot apex were approximately 0.2 and 0.4 MPa, respectively (Fig. 1). When water was withheld, the $\Delta\Psi$ between soil and roots remained stable at 0.20 to 0.30 MPa (Fig. 1) during the 12 d which were required to completely inhibit stem and leaf growth (24). Soil water potential declined from −0.02 MPa to approximately −0.45 MPa. During this period, the $\Delta\Psi$ between the soil and the shoot apex increased steadily from 0.40 to 0.95 MPa (Fig. 1). These observations, which indicate that spatial differences in water potential along the transport path from soil to apical shoot tissue occurred and were sensitive to the moderate water deficits that inhibit expansive growth, are the basis of the subsequent experiments.

Soil water and root water and osmotic potentials were determined diurnally to investigate whether water transport to roots was impaired significantly. Diurnal variation in soil water poten-

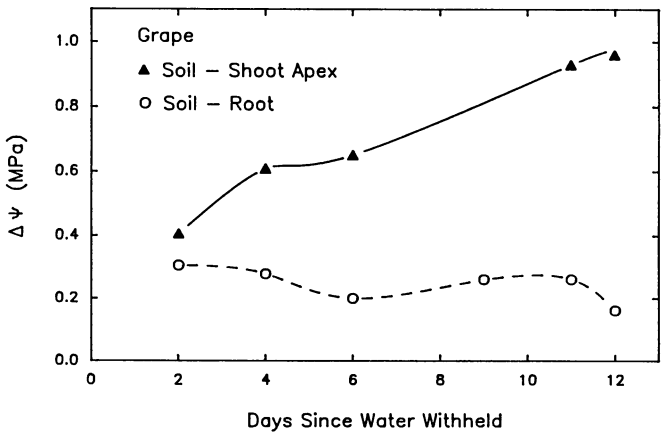

FIG. 1. Water potential differences ($\Delta\Psi$) at predawn between soil and roots, and between soil and shoot apex during the course of a drying cycle. Data are representative for a repeatedly obtained relationship for potted grapevine plants (*Vitis vinifera* L. cv White Riesling).

tial was not detectable at all soil water contents. At high water status, Ψ_{root} and Ψ_{soil} were about −0.30 and −0.02 MPa, respectively, which may indicate incomplete contact of the root surface with the soil solution (Fig. 2A). There were only slight diurnal changes in Ψ_{root} in well-watered soil (Fig. 2A). Nine d after water was withheld, Ψ_{root} and Ψ_{soil} had declined to approximately −0.45 and −0.16 MPa, respectively (Fig. 2B). Complete turgor maintenance was indicated by the coincident decline in root solute potential, Ψ_s (Fig. 2B). Again, only minor diurnal changes in water status were observed, although Ψ_{root} and root Ψ_s did decline precipitously following the dark-to-light transition (Fig. 2B). At this stage, leaf and shoot growth were 30% of the well-watered rate (24). Thirteen d after withholding water, Ψ_{soil} had declined to −0.59 MPa and stem and leaf growth had ceased completely. The diurnal fluctuations in Ψ_{root} and root Ψ_s were significant (Fig. 2C). Osmotic potential tracked water potential closely through day/night changes of 0.4 to 0.5 MPa (Fig. 2C). However, root turgor in the day was generally less than 0.2 MPa (Fig. 2C), whereas it was about 0.3 MPa at high soil water potential (Fig. 2A).

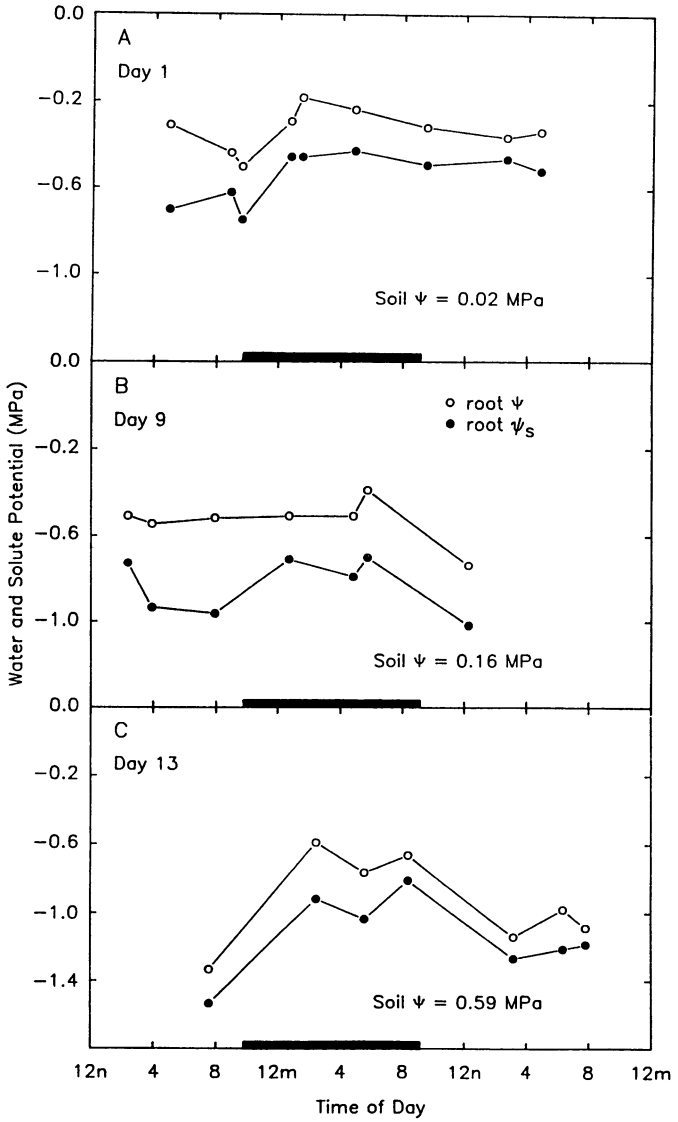

FIG. 2. Diurnal pattern of root water potential and root solute potential under A, well-watered conditions, and when water was withheld for B, 9 and C, 13 d. Each datum is a single determination of three root samples of the same plant enclosed in the same psychrometer cup. A different plant was sampled at each sampling time. Soil water potentials (Ψ_{soil}) are the means of 4 replications obtained by repeated sampling on the same day. Standard errors were less than 0.04 MPa.

Subsequently, the $\Delta\Psi$ within the stem was determined during a drying cycle since the gradients in water potential from soil to roots did not increase significantly (Figs. 1 and 2) and since the roots did not show signs of dehydrating (Fig. 2 A, B, and C). When water was again withheld for 12 d, the Ψ of the shoot apex decreased from −0.55 MPa to −1.20 MPa (Fig. 3). However, the Ψ of the basal internode remained relatively constant between −0.30 and −0.40 MPa. Thus, the $\Delta\Psi$ in the shoot increased from 0.25 to 0.80 MPa, due solely to the decreased Ψ of the shoot apex. The increased axial $\Delta\Psi$ in the shoot accounted completely for the change in $\Delta\Psi$ observed between the soil and shoot apex (*cf.* Fig. 1). No change in the $\Delta\Psi$ of the shoot was observed in well-watered controls during the 12-d experiment (Fig. 3).

The increased difference in water potential along the shoot under steady conditions suggested that the axial hydraulic resistance increased since water flux decreased as the soil dried and plant growth was inhibited. In order to estimate hydraulic resistance of the stem, water transport was determined by gravimetric measurements of mass lost from potted plants. In addition, parallel measurements of whole plant transpiration were obtained from porometer determinations of transpiration of each leaf on a shoot. Water loss during light and dark periods was determined by both methods 0, 9, and 13 d after withholding water. The methods produced similar estimates of water loss at both high and low flow rates. The mean difference (absolute value) in flow rate obtained by the two methods was 6.4 ± 2.3% (SE; n = 16) of the gravimetric value.

Under well-watered and high flow (light) conditions, the apparent resistance (R_{shoot}) was 0.02 × 10^3 MPa·s cm^{-3} (Fig. 4A). The R_{shoot} had increased significantly after 6 d without water to approximately 0.3 × 10^3 MPa·s cm^{-3} (Fig. 4A). R_{shoot} was stable thereafter until growth ceased when R_{shoot} increased to greater than 1 × 10^3 MPa·s cm^{-3}. Well-watered controls exhibited no change in R_{shoot} during this time (Fig. 4A). When transpiration was low (dark period), R_{shoot} was initially 0.16 × 10^3 MPa·s cm^{-3} at high water status (Fig. 4B). When water was withheld, R_{shoot} increased significantly within 2 d and was greater than 2.5 × 10^3 MPa·s cm^{-3} after 12 d without water (Fig. 4B). R_{shoot} of stressed plants was also greater than R_{shoot} of controls at all times of the diurnal cycle.

The estimates of R_{shoot} were obtained from rates of whole plant transpiration to facilitate comparison with earlier work (3, 4). These estimates assume a similar path length for each plant.

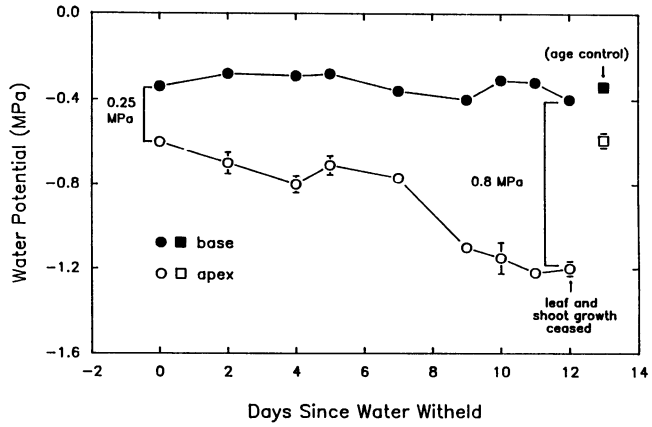

FIG. 3. Water potential of basal shoot internode (Ψ_{base}) and shoot apex (Ψ_{apex}) during a developing water deficit. Data are means ± SE (n = 3). Two well-watered control plants were grown for the same length of time (age control) as the stressed plants.

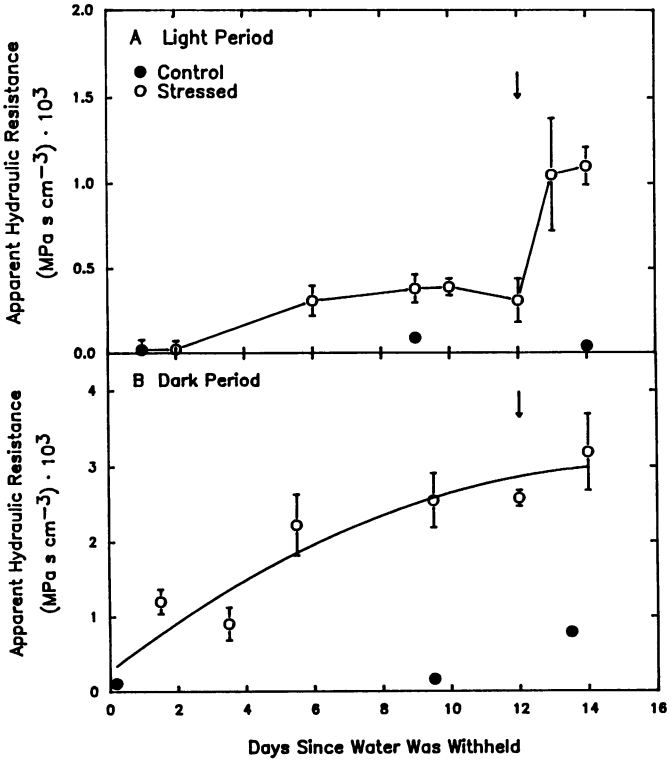

FIG. 4. Apparent hydraulic resistance between basal shoot internode and leaf 8 during a drying cycle of 14 d. Each datum is the mean ± SE (n = 8). Resistance calculations were based on gravimetric water flux measurements, psychrometric water potential measurements of leaf 8, and pressure chamber determinations of bagged basal leaves which were allowed to equilibrate with the stem xylem for 24 h. Arrows indicate the day on which shoot growth ceased.

Table I. *Apparent Hydraulic Resistance of Grape Shoots (R_{shoot}) Calculated for the Whole Plant and for a Unit Length of Shoot for Plants at High and Low Water Status*

The $\Delta\Psi$ was determined from shoot base to leaf 7 (from apex) and transpiration rates were obtained at predawn and in the light (data in parentheses). The R_{shoot} per unit shoot length was obtained from R_{shoot} and total shoot lengths assuming R_{shoot} was constant along the flow path. Predawn water potential of basal leaves (Ψ) indicates plant water status.

	Apparent R_{shoot}	
	Whole plant	Unit shoot
	MPa·s cm^{-3} 10^3	*MPa·s cm^{-4}*
Control		
Ψ = −0.47 MPa	0.7 (0.02)	15.6 (0.43)
Stressed		
Ψ = −0.77 MPa	5.8 (0.70)	94.2 (12.2)

When the whole plant resistances were expressed per unit shoot length, R_{shoot} during periods of high and low flux was several-fold greater at low than at high water status (Table I). The calculation of R_{shoot} using whole plant transpiration also underestimates the whole plant resistance since much of the flow does not reach the apical leaf sampled for water potential. However, R_{shoot} also was increased when R_{shoot} was estimated using the rate of transpiration of the individual leaf sampled for water potential. This overestimated R_{shoot} but also showed several-fold increases in R_{shoot} at high and low flow rates during a developing water deficit (data not shown). These large increases in R_{shoot} occurred when predawn Ψ_{leaf} decreased only 0.3 MPa (Table I).

Thus, leaf expansion declined rapidly with increasing R_{shoot} (Fig. 5) and internodes responded similarly to increasing R_{shoot} (Fig. 5, inset). Growth was inhibited by 50% in both organs at an apparent hydraulic resistance of 1.7 × 10^3 MPa·s cm^{-3} (Fig. 5). When growth was inhibited completely, R_{shoot} had increased 25-fold and the apparent hydraulic resistance from the basal internode to the shoot apex had increased 25-fold (Fig. 5, inset).

The data of Figures 1 and 3 indicate an increased gradient in stem water potential during moderate water deficits. The water potentials obtained at predawn may reflect persistent gradients required to generate sufficient sap flow for water lost by stomatal and cuticular transpiration and for cell growth and rehydration. In order to completely eliminate gradients induced by transpiration and to promote water potential equilibria, plants were enclosed in double black polyethylene bags for 24 h before samples were obtained from several positions along the root to shoot apex pathway. Under well-watered conditions, there was little difference in water potentials except for a significant decrease at the shoot apex (Fig. 6). However, the low water potentials developed by withholding water for 14 d were sustained under nontranspiring conditions. Root and shoot apex water potential had decreased from −0.15 to −0.85 MPa and from −0.39 to −1.60 MPa, respectively (Fig. 6). Thus, the root to shoot apex difference in water potential was 0.24 and 0.75 MPa in the control and stressed plant, respectively.

The failure of the large differences in water potential to be eliminated during periods of low transpiration suggested acute impediments to sap ascent in the shoot. The possibility that such impediments could arise from cavitations and subsequent loss of vessels for water transport was investigated by attempting to pass air through frozen internodes. If cavitation had occurred and vessels were emptied of sap, air should pass freely. The results showed an increasing gas permeability of frozen stem internodes as plant water status declined. At high midday water potential, low air flow (70–100 s to pass 500 μl air at 0.0025 MPa) was obtained through the 7th and 8th internode below the apex (Table II). At Ψ_{leaf} of −0.86 MPa, the time required to pass 500 μl air decreased to 16.5 and <2 s in internodes 7 and 8, respec-

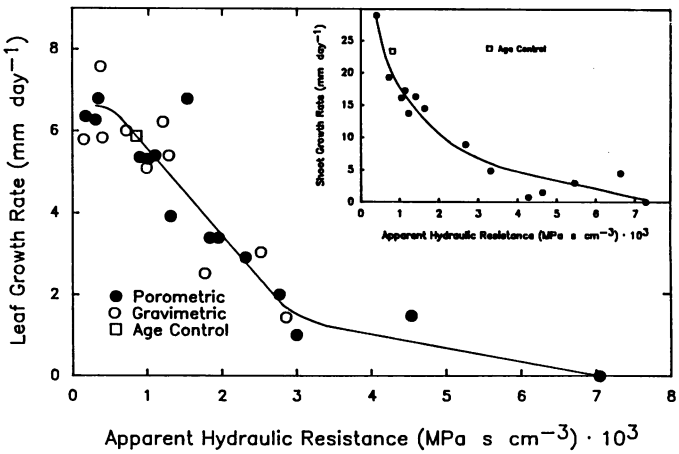

FIG. 5. Relationship of leaf and shoot (inset figure) growth to apparent hydraulic resistance in the stem when water was withheld for a period of 14 d. For leaf growth water flux was determined with a diffusion porometer at predawn or as the difference in pot weight between weighings at 0500 (4 h) before predawn and at 0900 (predawn). The $\Delta\Psi$ between leaf 7 and the basal shoot internode was calculated from psychrometric determinations (porometric experiment) or from pressure chamber measurements on previously bagged leaves (gravimetric experiment). For shoot growth (inset) water flux was determined with the porometer and $\Delta\Psi$ was determined psychrometrically. Each datum represents a single determination from a different plant. Age controls were continuously well-watered and sampled at d 14 of the drying cycle.

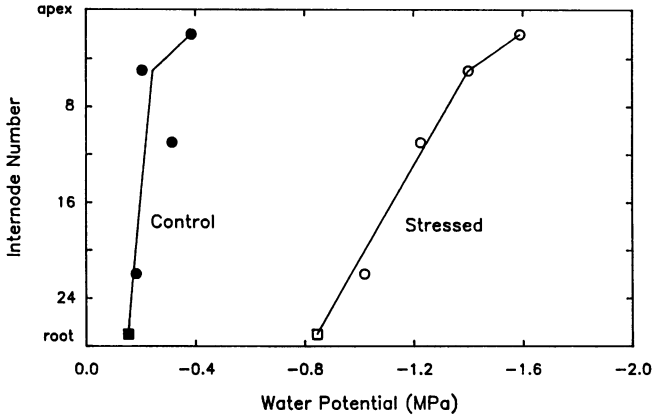

FIG. 6. Water potential of internodes located at different positions on the shoot of well-watered plants and plants from which water had been withheld until growth had ceased for 2 d. Plants were bagged in double black polyethylene bags to prevent transpiration for 24 h before sampling. Water potential was determined psychometrically.

Table II. *Time Required to Pass 500 μl Air at 0.0025 MPa Through Frozen 5 cm Internode Segments Which Were Taken from Plants at Different Water Statuses*

Midday Ψ_{leaf}	Internode (Basipetal from apex)	Elapsed Time ($\bar{X} \pm$ SE, $n = 4$)
MPA		*s*
−0.53	4–6	No flow
	7	70 ± 2
	8	98 ± 1
−0.86	4–6	No flow
	7	16.5 ± 1.0
	8	<2.0
−0.95	4, 5	No flow
	6	3.6 ± 0.5
	7	18.2 ± 0.3
	8	28.8 ± 0.3
	9	26.2 ± 1.2

tively (Table II). Permeability increased further at Ψ_{leaf} of −0.95 MPa and air flow was observed through more internodes than at higher water status. No evidence of cavitation was obtained in the youngest internodes tested (4 or 5) at any water potential (Table II).

DISCUSSION

The results showed that the $\Delta\Psi$ in the soil-plant system of grape plants increased significantly during the development of moderate water deficits. The predawn $\Delta\Psi$ from soil to apical leaf increased from approximately 0.40 MPa under well-watered conditions to >0.9 MPa at water deficits sufficient to completely inhibit shoot growth. The axial gradient within the grape stem also increased and at the cessation of growth accounted for 90% of the total increase in $\Delta\Psi$ in the soil-plant system. The increased $\Delta\Psi$ in the plant and the concomitant decline in water flux implicated large increases in the apparent hydraulic resistance within the plant.

A significant plant resistance is consistent with the bulk of the theoretical and experimental analyses which have shown a greater resistance in the plant than in the soil as soil water is depleted (6, 11, 20). The plant resistance generally included and was attributed to resistances encountered at the root-soil interface and across roots where, at high water status, the largest $\Delta\Psi$ usually occurs (28). The $\Delta\Psi$ between soil and root can increase further due to diminished soil hydraulic conductance (13) and to decreased contact of root with the soil solution caused by soil and root shrinkage (15).

However, $\Delta\Psi$ from soil to roots did not increase significantly throughout the present study. Measurements of root water and osmotic potential showed that the roots adjusted osmotically to remain turgid. Therefore, water transport to the root surface was not significantly impaired at the water deficits investigated. Water transport to the root/shoot transition was also not inhibited significantly since the water potential of the basal shoot internode decreased only slightly compared to apical tissues. Hence, resistance in the shoot was significant and variable.

An apparent dependence of whole plant resistance on flow rate, in which resistance increases as flow decreases over some range of flow rates such that $\Delta\Psi$ remains relatively constant, has been observed frequently (6). Blizzard and Boyer (3) found that the resistance in potted soybean was greater than and increased in parallel with soil resistance as soil water was depleted. The increased plant resistance was independent of any interfacial resistance since Ψ_{root} was measured directly. Although the increase in resistance in soybean was due solely to decreasing water flux ($\Delta\Psi$ remained constant), the variable plant resistance of grape and soybean is unlikely to be related to the putative flow-dependent resistance. The nonlinear relationship between $\Delta\Psi$ and whole plant transpiration is observed at high Ψ_{leaf} and low $\Delta\Psi$ and flow rates (6), and not under dry conditions. Furthermore, Passioura (21) recently presented evidence that the flow-dependent variable is not whole plant resistance, but is the minimum $\Delta\Psi$ required to observe flow and is dependent upon active solute transport in roots.

The theoretical and technical difficulties of determining root resistance were largely avoided since in grape large changes were observed in the shoot. The estimation of hydraulic resistance to water transport in the stem xylem is more straightforward and less susceptible to error than whole plant or root resistance. Water transport in the stem xylem does not involve phase changes or transmembrane flow. Thus, solute gradients are not a significant driving force for stem flow. The similarity of the psychrometric and pressure chamber measurements of stem xylem water potential indicate that there were low apoplastic solutes in the internodes. These considerations simplify the ascent of sap in stem xylem to essentially capillary hydraulics.

The increase in hydraulic resistance of the grape shoot when water was withheld was not dependent upon changes in flow rate since the $\Delta\Psi$ in the stem increased as soil water was depleted. R_{shoot} increased significantly whether $\Delta\Psi$ was obtained at low (dark) or high (light) flux rates, although resistance was greater at low than at high flow rates (5). Similarly, the apparent R_{shoot} increased significantly during water deficits whether resistance was determined on the basis of whole plant water loss or single leaf transpiration. Thus, the hydraulic resistance of the stem increased as water deficits developed regardless of any dependence of resistance on flow rate or branching of the pathway (22).

The increase in axial resistance was not due to errors caused by the flux for growth or by plant capacitance since the potential errors of these considerations were small. The volume flux for expansion of all leaves, internodes, and tendrils on the shoot was less than 0.03 and 0.9% of the flux for transpiration in the light and dark, respectively (24). Capacitance can create error due to overestimating flux through the entire path when apical tissue is dehydrating. Therefore, capacitance errors would lead to underestimates of R_{shoot} for the measurements made in the light. However, these estimates always showed that R_{shoot} increased when water was withheld. The time constants for flux responses to changing conditions in whole plants are typically 10 to 100 min. Boyer's work (4) showed that the time constant for rehydration from moderate water deficits was less than 60 min in sunflower and soybean. A similar time constant in grape would

result in errors of less than 5% since the measurements of water potential were made several hours after each change in growth chamber conditions.

The nature and significance of these large gradients and the apparent high resistances to water transport are unclear. Grape may not be unusual in this regard since large $\Delta\Psi$ within plant shoots are not uncommon, having been observed in hemlock (26), sitka spruce (14), tobacco (2), and *Vitis labrusca* (17). The presence of expanding cells which were not differentiated for water transport in the tissue sampled for apical water potential renders quantitative interpretation of our estimates of R_{shoot} under well-watered conditions difficult. Psychrometric determinations of the water potential of expanding tissues are subject to possible underestimates due to wall relaxation after excision (10). If present, this error would be greatest in rapidly expanding tissue and totally absent in nongrowing tissue (7). Thus, our estimates of the increase in R_{shoot} during soil drying were conservative since slightly lower resistances may have been present at high water status.

The increase in plant hydraulic resistance occurred early in the drying cycle and was coincident with the inhibition of leaf and shoot growth. During growth, the estimated resistance reflects some partitioning of flux for growth and for transpiration (5, 12). For example, when growth is high, the calculated resistance reflects more the resistance for growth transport at low transpiration (in dark) than at high transpiration (in light) due to the relative contribution of flux for growth in the dark and the light. Since the resistance increased under both conditions when water was withheld, the source of the increased resistance should be common to the pathways for transpiration and growth.

Analyses using $\Delta\Psi$ to a leaf or the stem apex showed the same large increases in hydraulic resistance. Under similar experimental conditions, there was no difference in the timing or degree of growth inhibition of leaves, internodes, and tendrils when water was withheld (24). These observations suggest that water transport for growth was impaired upstream of (*i.e.* basipetal to) the apical region of expansive growth in the shoot although the potential for significant and variable resistances in the petiole (2) or nonvascular tissue, *e.g.* leaf mesophyll (5), remains inadequately quantified.

Inhibition of axial transport in the stem xylem could result from formation of tyloses, constriction of xylem lumen, or cavitation and embolism in xylem water columns. There is no evidence of tylose development in functional xylem, particularly without premature weakening of vessel walls (*e.g.* by bacterial wounding, 30). Therefore, this possibility is discounted. Plant stems undergo regular excursions in diameter which, if due to changes in xylem dimensions, would lead to large effects on R_{shoot} since the frictional resistance of a capillary is inversely proportional to the fourth power of the radius. However, changes in stem diameter are more likely to reflect changes in water content of cells with low volumetric elastic moduli. Thus, parenchyma and other soft-walled cells are the sites of stem capacitance, whereas xylem vessels, whose walls incorporate secondary thickenings presumably to withstand considerable negative pressure, are unlikely to experience significant changes in geometry at the moderate water deficits encountered in this study.

The persistent $\Delta\Psi$ in stressed plants after extended periods under nontranspiring conditions indicated that the apical tissues were essentially hydraulically isolated from the soil, roots, and basal stem tissue. Westgate and Boyer (29) recently made similar observations in maize. These observations are consistent with the presence of vapor-blocked vessels. Embolism of xylem vessels and tracheids has been detected by pneumatic (9), hydraulic (25), and acoustic (18) techniques.

A comparison of the pneumatic and the hydraulic resistances in this study suggests that most vessels may become vapor-filled at low water status. The pneumatic (Table II) and hydraulic (Table I) resistances can be compared directly by converting the pneumatic data to hydraulic units per unit length from the lengths of stem segment and the ratio of viscosities of air and water (approximately 58.8; see Byrne *et al.* [9]). For example, the pneumatic resistance of internode 6 (about 2.7 cm) at low water potential was equivalent to approximately 0.392 MPa·s cm^{-4} (*cf.* the resistance per unit length at high water status in the light in Table I). The similarity of pneumatic resistance at low water status and hydraulic resistance at high water status suggests that most of the vessels in segments which rapidly passed air (less than 5 s) were vapor-filled, whereas a significant fraction of water-filled vessels remained in those internodes which required 16 to 20 s.

Our pneumatic data also indicate that some cavitation may occur in well-watered plants during periods of rapid transpiration and that a progressive failure of xylem vessels occurs as water deficits develop. Recently, Tyree *et al.* (27) provided ultrasonic evidence that a similar pattern exists in field-grown maize plants. Thus, some cavitation may be frequent under the moderate tensions in a normal diurnal cycle. Indeed, in an early investigation of axial water transport, Scholander *et al.* (23) argued against the cohesion theory of sap ascent on the basis of the high propensity for cavitation in the grapevine. These considerations suggest that the primary mechanism by which shoot growth is inhibited during water deficits may be via impaired water transport to the expanding organs at apical locations on the shoot.

Vapor blockage of vessels during the winter is a naturally occurring phenomenon in grape (25). The vessels in grape stems have large lumen (23) which may contribute to the propensity for cavitation (19). Root pressure may play a role by facilitating the dissolving of emboli or the refilling of vapor-filled vessels (19). It may not be coincidental that significant root pressures have been observed in grape (1). The pressure (or rate of exudation from a cut stem) was reduced 50% by a reduction in soil water content from 100 to 70% of field capacity (17). Hence, in addition to creating greater tension in the light (*i.e.* greater cavitation), declining soil water may also reduce the potential for refilling embolized vessels at night.

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