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Effects of water stress on vessel size and xylem hydraulic conductivity in *Vitis vinifera* L.

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Abstract

Modifications of vessel size and of shoot hydraulic conductivity induced by different water availability levels (ψ_{leaf} -0.35 MPa, -0.6 MPa and -0.8 MPa, respectively) were investigated in container-grown grapevine plants. Plant water loss, measured as xylem sap flow and as leaf transpiration, was lower in water-stressed plants. Morphometric measurements on xylem showed that vessels of water-stressed plants had lower transectional areas. Shoot hydraulic conductivity (k_h), shoot specific conductivity (k_s) and leaf specific conductivity (k_l) were lower in water-stressed plants. When conductivities were measured on shoot portions, differences between treatments were particularly high at the basal internodes. At the lower stress level no embolism was detected, and reduced conductivity could be explained by the reduction of vessel diameter, according to the Poiseuille equation. At the higher stress level k_h was further reduced by formation of vessel embolisms. The tension gradient along the shoot increased only at the higher stress level. Stomatal conductance was linearly correlated with k_l at low stress levels, suggesting a concerted regulation of water flow, while at higher stress levels stomatal conductance decreased with no changes of k_l. Reduced development of xylem vessels in grapevines subjected to moderate water stress may contribute to the control of water flow and to a reduction in vulnerability to xylem embolism.

Key words: Sap flow rate, transpiration, stomatal conductance, xylem vessel anatomy, vessel embolism.

Introduction

Xylem water transport in plants is the subject of intensive research because of its agronomical and ecological implications. On the one hand the aim of investigations focused on crop water management is to improve water use efficiency (Jones, 1990) whilst on the other hand, factors affecting water transport parameters are important determinants of drought tolerance and relative habitat preferences of native and cultivated species (Sperry and Tyree, 1990; Cochard *et al.*, 1994; Pockman *et al.*, 1995), and predictors of carbon and water balance in environmental models (Williams *et al.*, 1996).

Water movement from the roots to the atmosphere is controlled by the conductance of the components of the water pathway. Traditionally, stomatal conductance and root conductivity have been considered the main controlling factors of water flow in the plant (Jones, 1983). However, the efficiency of the water transport system (the xylem vessels in angiosperms) can also significantly affect water movement by imposing conductivity constraints (Tyree and Ewers, 1991) and perhaps by the regulation of delivery to the leaves of root chemical signals (Davies and Zhang, 1991; Davies *et al.*, 1994; Jackson, 1997). Xylem conductivity is determined by the structure and size of the vessels (Schultz and Matthews, 1993; Tyree and Ewers, 1991) and by their efficiency, which may be affected by the presence of embolisms (Tyree and Sperry, 1989).

When exposed to water stress, plants show modifications of water flow rate. Modifications of the conductivity components of the transpiration pathway (root, shoot and stomata) contribute to determine such changes. It has been reported that water stress affects shoot conductivity by inducing embolism in the xylem vessels (Schultz and Matthews, 1988; Tyree and Sperry, 1989; Tognetti *et al.*, 1996). However, very little information is available on the effects of water stress on shoot conductivity via modifications of vessel size. The experimental approach used here was to subject grapevine plants to water stress

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of different intensity, and to measure the size of xylem vessels, the presence of embolism and changes in shoot hydraulic conductivity. The grapevine was chosen as the experimental species because of its relatively wide vessels (Salleo *et al.*, 1985).

Materials and methods

Growing conditions and irrigation treatments

Two experiments were carried out in two subsequent years. In 1995, 20 × 4-year-old plants of *Vitis vinifera* cv. Freisa grafted on *Vitis riparia* × *berlandieri* 'Kober 5BB' were grown in a glasshouse. Each plant grew in a 25 l container filled with a substrate composed of a sandy-loam soil/expanded clay/peat mixture (4 : 2 : 1, by vol), fertilized once a month with 30 g of a complex (20–10–10) fertilizer. In January, plants were pruned to a single-bud spur. Average budbreak took place on 5 April. The single shoot of each plant was trained vertically by being tied to a stick. Plants were irrigated with a drip system delivering a programmed amount of water once a day (09.00 h). In the 85 d following budbreak, irrigation was managed to maintain the substrate in the containers at container capacity (Cassel and Nielsen, 1986). Container capacity was previously assessed allowing water to drip freely from the holes in the bottom of the container and it was daily checked in two reference containers (with one plant each) not included in the experiment. During the experiments, the surface of the plant containers was covered with gas-impermeable plastic film, to avoid water loss due to evaporation.

Eighty-five days after budbreak, two groups of 10 homogeneous replicate plants, grown to 21 internodes and randomly distributed in the glasshouse, were subjected to differential water treatment for 40 d. Thereafter for 35 d until the end of the growing season, water was again supplied to container capacity to all plants. During the differential water treatment, plants in the first group (IRR treatment) were watered to container capacity ($\psi_{soil} = -0.01$ MPa; soil volumetric water content = 22%; ψ_{leaf} at midday = -0.35 MPa). The plants of the second group were subjected to a water stress (WS1) treatment ($\psi_{soil} = -0.07$ MPa; soil volumetric water content = 15%; ψ_{leaf} at midday = -0.60 MPa), by irrigating with the same frequency, but for half the time. Just before the differential water treatment ψ_{leaf} at midday was in average -0.30 MPa without significant differences among all plants; 1 week after the end of the differential water treatment ψ_{leaf} at midday was on average -0.40 MPa and showed no significant differences between all of the plants.

In 1996 the same plants were used, and the growth conditions of 1995 were applied, with the exceptions described below. In this experiment plants were divided in three groups (7 replicates), each subjected to an irrigation treatment. Two treatments were as in 1995 (IRR and WS1 treatments). In the additional treatment (WS2), irrigation was withheld for 20 d (starting 20 d after the beginning of the differential water management in the WS1 treatment). At the end of this period ψ_{soil} was -0.20 MPa, soil volumetric water content was 11% and ψ_{leaf} at midday was -0.80 MPa.

Water movement throughout the plant and stomatal conductance

The amount of water flowing throughout the plant was estimated by the measurement of xylem sap flow and by gravimetric measurements. Measurements were taken at the end of the differential water management period on four consecutive days (total number of replicates = 4).

The stem heat balance (SHB) method (Sakuratani, 1981; Baker and van Bavel, 1987) adapted to woody plants was used to measure xylem sap flow. Gauges clamped to the stem, including heaters and sensors, were self-constructed according to the indications of Steinberg *et al.* (1989). A CR10 (Campbell Scientific Corporation, Logan, Utah, USA) datalogger was programmed to record measurements every 15 s and to average and store them every 15 min. Data were transferred to a personal computer for calculations of sap flow. Sheath conductance of the gauge was daily recalculated using minimum predawn values obtained after night calibration loops. A stem thermal conductance value of 0.54 W m^{-1} °C^{-1} was determined according to Sakuratani (1979).

Total plant transpiration was assessed at hourly intervals during the day on the same four plants using a scale.

Stomatal conductance and leaf transpiration were measured on seven leaves per plant (one every three nodes along the shoot) on the same plants where xylem sap flow was assessed. Leaf gas exchange measurements were taken at 11.00 h and 13.30 h using an open-system ADC-LCA3 infrared gas analyser equipped with a Parkinson Leaf Chamber (Analytical Development Company, Hoddesdon, UK). At 11.00 h and 13.30 h, temperature and relative humidity were, respectively, 31.9 °C and 35.7 °C, and 46.4% and 39.5%. Two minutes before measurement, leaves were oriented to a 90° angle with incident light (1200 μmol m^{-2} s^{-1}) to eliminate variations of stomatal conductance due to light intensity.

Plant growth

In order to assess leaf area an indirect method was used. In both years and for each treatment the width of all leaves of all plants was measured, and leaf area was calculated with reference to a regression equation obtained on 50 leaves per treatment (Schubert *et al.*, 1995). Shoot base diameters were measured with a hand vernier caliper, averaging the larger and the smaller diameter.

Shoot hydraulic conductivity (k_h)

k_h was assessed by two different methods. It was measured on cut shoot portions at the end of the season in both years, and it was estimated *in vivo* (on growing plants) in 1996.

At the end of the 1995 (15 September) growing season, shoots of the four plants used for sap flow and gas exchange determinations were cut at their base and divided in 0.2 m long portions, each including two nodes. Conductivity measurements were taken immediately after cutting. A controlled pressure system was used according to Schubert *et al.* (1995). After 2 min at 0.3 MPa m^{-1} to eliminate embolisms, and after a further 5 min at 0.1 MPa m^{-1} to allow stabilization, for each shoot segment two subsequent flow measurements for 2 min were made at a constant pressure gradient (0.1 MPa m^{-1}). Shoot hydraulic conductivity was calculated from pressure gradient and flow measurements. Shoot specific conductivity k_s and leaf specific conductivity k_l (Zimmermann, 1983) were calculated, respectively, dividing k_h by the xylem transectional area at the middle of the measured internode, and by the leaf area distal to the measured internode. The theoretical shoot conductivity was calculated using Poiseuille's equation, assuming a circular shape of the vessels, with the diameter measured as described below.

In order to measure hydraulic conductivity at different internodes along the shoot, in the 1995 experiment shoot portions were cut shorter than the majority of vessels (Sperry *et al.*, 1987). To verify the results on unsevered vessels, at the end of the 1996 growing season k_h measurements were made as in the previous year, but on longer shoot portions. In addition, in this experiment the formation of vessel embolisms were assessed. On each of the four plants per treatment, conductivity was first assessed on two 1.5 m long shoot segments at constant pressure gradient (0.1 MPa m^{-1}). The 1.5 m portions were then cut in 0.5 m segments. Conductivity was assessed on these segments at 0.1 MPa m^{-1}, before and after a high pressure water flush (0.4 MPa m^{-1} for 10 min) designed to eliminate shoot embolisms (Sperry *et al.*, 1987). The 1.5 m shoot portion length is higher than the average vessel length, and the 0.5 m length is higher than the average length of 82% of the vessels in *Vitis labrusca* and *V. riparia* (Sperry *et al.*, 1987).

In vivo k_h was calculated on the same four plants per treatment according to the water flux equation, as the ratio between water flow (F, kg s^{-1}) throughout the shoot and the water tension gradient from the base to the apex of the shoot ($d\psi/dx$, MPa m^{-1}) causing the flow. Water flow (F) was measured by the SHB method at the end of the differential water management period, as described above. The water tension gradient along the shoot ($d\psi/dx$) was assessed on the same plants immediately after the end of the flow measurements. On each plant three leaves at the base and three at the apex of the shoot were wrapped in the evening with a double layer, inside plastic and outside aluminium, bag according to Liu *et al.* (1978). The water potential of the bagged leaves was measured the following day with a pressure chamber (Soilmoisture Equipment Corp., Santa Barbara, CA, USA), and it was assumed to represent the water potential of the corresponding shoot xylem. Sap flow and water potential measurements were taken between 12.00 h and 14.00 h.

Water tension gradient

Water tension gradient along the shoot ($d\psi_{(\text{base-apex})}/dx$) was estimated in 1995 at seven node positions along the shoot, based on the ratio between the average transpiration from leaves distal to the node (calculated from the unit area transpiration multiplied by the leaf area), measured at the end of the differential water management period, and the k_l at the same node (Tyree and Ewers, 1991). In 1996, water tension gradient was directly measured by pressure chamber determinations as described in the previous section.

Morphometric measurements

Shoot and xylem transectional areas, and the areas of single vessel lumina were measured in 1995 at internodes 5, 11 and 17 on the same shoot portions used for conductivity measurements. Shoot sections about 0.5 mm thick were cut with a hand-held scalpel midway between the nodes. Sections were directly observed at a stereomicroscope (×100). Shoot, xylem and vessel areas were calculated from the average of two orthogonal measurements of shoot or vessel diameter, and of xylem thickness, respectively. Vessel transectional area was calculated from all the vessels observed inside three xylem wedges, 120° one to the other, per section. One section was cut and observed per each shoot portion and per plant.

Results

In 1995, plant growth at the end of the differential water management period was higher in irrigated plants than in water-stressed ones. In 1996, plant growth was again higher in irrigated plants than in both other treatments (Table 1).

As expected, water stress decreased the amount of water lost by the plant. Xylem sap flow measured throughout 24 h by the SHB method at the end of the differential water management period was about twice as high in irrigated than in water-stressed plants, in both experiments (Table 1). The relative differences in xylem sap flow were similar throughout the day (data not shown). Total plant transpiration was linearly correlated with sap flow throughout the shoot in both irrigated and stressed plants. The correlation coefficients (R^2) for measurements taken between 12.00 h and 14.00 h were, respectively, 0.964 and 0.951, and the sap flow/transpiration rate was 0.95.

Stomatal conductance (g_s) was measured in 1995 and it was in the average 35% higher in irrigated plants than in the water-stressed ones (Table 1).

The shoot, xylem and vessel transectional areas were measured in 1995. All were lower in water-stressed than in irrigated plants in all the shoot portions tested (Table 2). The ratio between xylem and shoot transectional areas was similar in irrigated and water-stressed plants at all internodes tested (66% and 67%, respectively). The summation of the transectional areas of vessel lumina (wall excluded) was in the average 11.3% of total xylem transectional area in both water-stressed and irrigated plants. The vessel diameters more frequently measured ranged between 60 and 80 μm for both irrigated and water-stressed plants; however, diameters larger than

Table 1. *Growth parameters (total leaf area, shoot length, basal shoot diameter), daily water loss, and stomatal conductance of grapevine plants subjected to different irrigation treatments in two following years (averages ±standard errors)*

All measurements were taken at the end of the differential water treatment (125 d after budbreak). IRR, irrigated to container capacity; WS1 and WS2, water stress treatments.

Year of experiment	1995		1996		
Water management treatment	IRR	WS1	IRR	WS1	WS2
Total leaf area (m^2)	0.489±0.04	0.418±0.03	0.499±0.04	0.401±0.04	0.396±0.03
Shoot length (m)	3.45±0.13	2.93±0.12	3.53±0.24	3.09±0.16	3.05±0.28
Basal shoot diameter (mm)	7.56±0.67	6.72±0.83	7.92±0.99	6.80±0.65	6.85±0.98
Daily water loss (kg m^{-2})	1.02±0.14	0.59±0.06	0.83±0.09	0.61±0.09	0.55±0.07
Stomatal conductance (mmol m^{-2} s^{-1})	208.6±18.2	152.9±16.8			

Table 2. *Shoot and xylem transectional areas measured in 1995 at internodes 5, 11 and 17 from the shoot base on grapevine plants subjected to two irrigation treatments (averages ± standard errors); IRR, irrigated; WS1, water-stressed*

Treatment	Internode	5	11	17
IRR	Shoot cross-sectional area (mm^2)	44.5±4.0	36.3±2.4	24.2±1.6
	Xylem cross-sectional area (mm^2)	28.6±2.6	24.8±1.4	15.9±1.6
WS1	Shoot cross-sectional area (mm^2)	35.5±4.4	30.1±2.9	20.3±1.0
	Xylem cross-sectional area (mm^2)	22.9±2.7	20.0±2.0	14.3±0.7

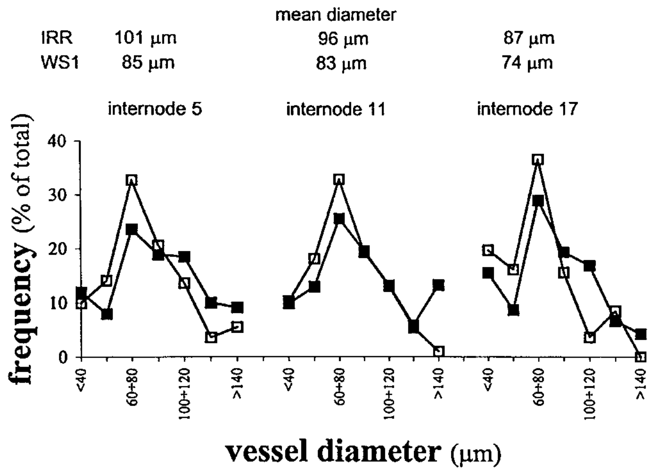

Fig. 1. Relative frequency of vessels of different diameter class of shoot sections at intenode 5, 11 and 17 in grapevine plants subjected to different irrigation treatments. Filled symbols, irrigated to container capacity (IRR); empty symbols, water-stressed (WS1).

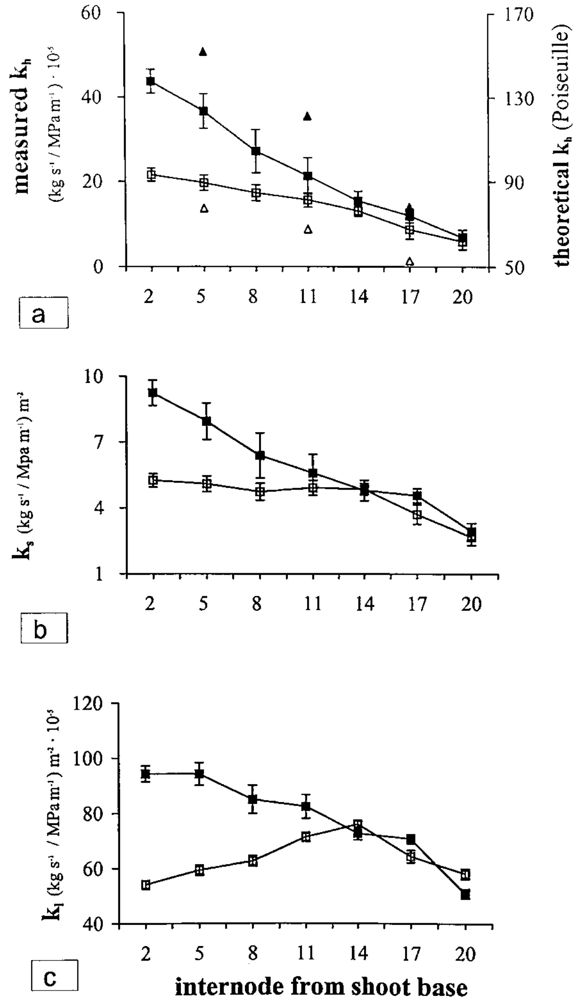

Fig. 2. Water conductivity measured in 1995 at different internodes along the shoot of grapevine plants subjected to different irrigation treatments (averages ± standard errors). Filled symbols, irrigated to container capacity (IRR); empty symbols, water-stressed (WS1). (a) Hydraulic conductivity per unit pressure gradient (k_h): measured data (squares) and calculated theoretical data (triangles), predicted by Poiseuille's equation. (b) Specific conductivity k_s ($=k_h$ per unit xylem transectional area). (c) Leaf specific conductivity (k_l), calculated as the rate between k_h and the leaf area distal to the node.

80 μm were always more frequently measured in irrigated plants (Fig. 1). As a consequence, average vessel transectional area was about 35% lower in water-stressed than in irrigated plants at all tested positions along the shoots.

In the 1995 experiment hydraulic conductivities were measured at different internodes. The shoot hydraulic conductivity (k_h) decreased from basal to apical segments in both irrigated and water-stressed plants. In irrigated plants, k_h was higher than in water-stressed ones; the differences were larger at the basal internodes (Fig. 2a). The calculated theoretical k_h predicted by Poiseuille's law, assuming xylem vessels to be capillaries, showed the same trend, although, as expected, absolute values were in the average 4 or 5 times higher than measured (Tyree and Zimmermann, 1971; Kramer, 1983).

The specific conductivity k_s ($=k_h$ per unit xylem transectional area) showed a similar pattern: it decreased from the base to the apex of the shoot in irrigated plants, while in stressed plants it was nearly constant and it was lower than in irrigated plants (Fig. 2b).

Leaf specific conductivity (k_l), calculated as the ratio of k_h and the surface of leaves distal to the internodes where conductivity was measured (Zimmermann, 1983), was also lower in water-stressed plants than in irrigated controls at the basal internodes, while smaller differences were observed at internodes 14–20 (Fig. 2c).

The average leaf specific conductivity (calculated from values measured in the different shoot portions) was correlated with stomatal conductance, but the relationship was different in irrigated and water-stressed plants: consistent variations of k_l corresponded to smaller variations in g_s in irrigated plants; in water-stressed plants g_s changes were not matched by k_l changes (Fig. 3).

In 1996, k_h was measured on shoot portions of two different lengths. It was in the average 23% higher in 0.5 m than in 1.5 m long shoot portions (Table 3), and the measurements taken on the 1.5 m shoot portions were

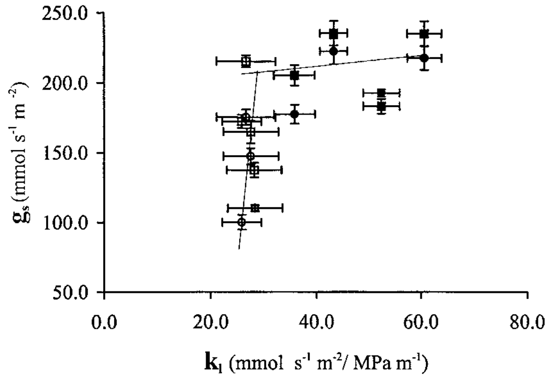

Fig. 3. Relationship between stomatal conductance (g_s) and leaf specific conductivity (k_l), measured in 1995. Filled symbols, irrigated plants (IRR); empty symbols, water-stressed plants (WS1). Squares are measurements taken at 11.00 h; circles are measurements taken at 13.30 h. Each symbol is the average ± standard errors of measurements taken on seven different nodes in a single plant.

significantly correlated with the average of the three measurements taken on the three 0.5 shoot portions obtained from the 1.5 portion ($R^2 = 0.71$). The differences between measurements taken on the shoot portions of different length can be explained by the reduced presence in shorter shoot portions of transverse cell walls (Schultz and Matthews, 1988), and the correlation between the two measurements shows that the subsequent measurements, taken on 0.5 m portions, are overestimated but representative of the true values.

In 1996, conductivity measurements were taken before and after elimination of embolisms in water-stressed plants. Conductivity was not affected by removing xylem embolisms in the IRR and in the WS1 treatments, while it increased about 24% after removing embolisms in the WS2 treatment (Table 3).

In 1996, the *in vivo* k_h was calculated, based on water flux and water tension gradient measured at the end of the differential water management period. The *in vivo* k_h was lower in both water stress treatments than in the irrigated treatment, and it was lower in the WS2 treatment than in the WS1 treatment (Table 3).

In 1995, the water tension gradient in the shoot increased from the base to the apex. The water tension gradient showed no significant differences at any node position between the irrigated and water-stressed treatments (Fig. 4). These results were confirmed in 1996, when no differences were found between the IRR and the WS1 treatments (corresponding to the treatments of 1995) that were 0.030 MPa m^{-1} and 0.031 MPa m^{-1}, respectively. However, the water tension gradient significantly increased in the WS2 treatment ($d\psi_{(\text{base-apex})}/dx$ on whole plant = 0.056 MPa m^{-1}).

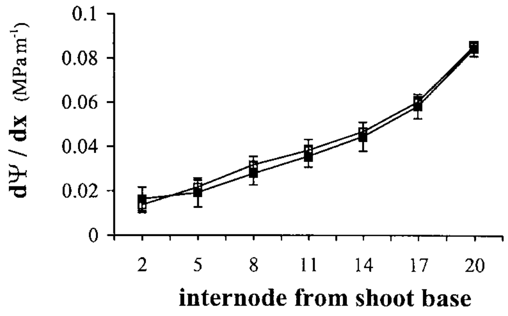

Fig. 4. Water tension gradient along the shoot ($d\psi/dx$) of grapevine plants subjected to different irrigation treatments (averages ± standard errors) calculated in 1995 as the transpiration rate/k_l ratio at different internodes in irrigated (IRR, filled symbols) and water-stressed (WS1, empty symbols) grapevines.

Discussion

Higher plants respond to water stress with a variety of physiological and molecular mechanisms. A common aspect of such responses is a decrease of the conductivity to water flow along the soil–plant–atmosphere water pathway (the so called bulk conductivity; Moreshet *et al.*, 1990), which can reduce water loss to the atmosphere. Stomatal resistance is a key component of bulk resistance to water flow (Meinzer *et al.*, 1996); however an increase of the resistance to water flow of other segments of the water pathway, such as the roots and the shoot, can be part of the plant response to water stress.

Shoot hydraulic conductivity decreases in response to water stress. Hydraulic conductivity can change as a result of (i) interruption of the water column in the vessels (embolism) or (ii) modifications of the size of the xylem vessels. Several reports have shown that water stress induces embolism and loss of function of the vessels (Schultz and Matthews, 1988; Sperry and Tyree, 1990; Hargrave *et al.*, 1994). The decrease of xylem conductivity due to vessel embolism can directly contribute to reduce water flow across the shoot (Schultz and Matthews, 1988)

Table 3. *Shoot hydraulic conductivity* k_h *(kg* s^{-1} *MPa* $m^{-1} \times 10^{-5}$*) measured in 1996 with different techniques on grapevine plants subjected to different irrigation treatments (averages ± standard errors); IRR, irrigated to container capacity; WS1 and WS2, water-stressed*

Treatment	IRR	WS1	WS2
Calculated *in vivo* k_h	38.3 ± 5.1	21.9 ± 3.2	10.7 ± 2.8
Measured k_h on 1.5 m cut shoot portions	30.4 ± 4.2	19.6 ± 2.1	8.5 ± 0.9
Measured k_h on 0.5 m cut shoot portions, before flushing	33.5 ± 3.2	21.8 ± 1.9	10.9 ± 0.4
Measured k_h on 0.5 m cut shoot portions, after flushing	32.8 ± 2.2	21.9 ± 2.1	13.5 ± 1.2

and at the same time it can induce stomatal closure, which in turn avoids further embolisms and limits transpiration (Sperry, 1986; Meinzer and Grantz, 1990; Sperry and Pockman, 1993).

The results of the 1995 experiment add a new component to this picture, showing that water stress induces a decrease in the average diameter of grapevine vessels and a decrease of xylem hydraulic conductivity. A negative effect of water stress on vessel size was hypothesized by Zimmermann and Milburn (1982) and is implied in the observation that in periods of drought, wood xylem rings develop less than when water is available. However, to our knowledge, no direct evidence of this effect has been reported until now. In this experiment no embolisms were detected in the xylem. Water-stressed plants had lower shoot growth and total transectional xylem area, which can both affect hydraulic conductivity, however, hydraulic conductivity was also lower when expressed per unit xylem cross-sectional area (k_s) and per unit leaf area (k_l). These results suggest that the decrease in vessel transectional area due to a diminished growth as a response to water stress was the main factor affecting conductivity. This conclusion is further supported by the observation that, as predicted by Poiseuille's law, although relative differences in vessel transectional areas (dependent on the square of the vessel radius) between irrigated and water-stressed plants were similar at all node positions tested, relative differences in k_h (dependent on the fourth power of the vessel radius) were larger in basal internodes, where vessel transectional areas are larger. Other factors, however, may contribute to conductivity changes: vessel diameter and length are positively correlated in Angiosperms (Zimmermann and Jeje, 1981), and so reduced vessel length may have co-operated with reduced vessel transectional area in decreasing xylem conductivity in water-stressed plants.

Conductivity was measured 35 d after the end of the water stress period, and the question may arise whether conductivity was also affected in growing plants at the end of the water stress period. To answer this question, in the 1996 experiment xylem conductivity was calculated from flow and pressure gradient measurements. This approach was followed as the sap flow/canopy transpiration rate was close to 1, showing that the plants used in this experiment had a very low or no capacitance at the time of the day when measurements were taken (between 12.00 h and 14.00 h) (Steinberg *et al.*, 1989; Lascano *et al.*, 1992). The results were close to conductivity values measured at the end of the growing season, and confirm that conductivity was negatively affected by water stress at the time stress was imposed on the plants.

The decrease of xylem hydraulic conductivity induced by water stress may contribute to reduce the bulk conductivity. However, other resistances affect flow across the plant. Previous reports showed that shoot conductivity is of similar magnitude as canopy conductivity, i.e. the conductivity of the water pathway from the shoot xylem to the substomatal chambers (Running, 1980; Moreshet *et al.*, 1990). It is difficult to compare liquid phase (e.g. xylem) and gas phase (e.g. stomatal) water conductivities, but an indication of their relative importance can be obtained comparing their changes as external conditions vary. Such relationships can be diverse: in some cases modifications of stomatal resistance have been shown to prevent a decrease in hydraulic conductivity due to xylem embolism (Sperry, 1986), while in other cases, stomatal conductance was found to vary in accordance to hydraulic conductivity (Meinzer and Grantz, 1990). In the present case the changes in water availability affected both stomatal conductance and hydraulic conductivity. As leaf specific conductivity decreased, stomatal conductance was initially linearly correlated with leaf specific conductivity, a situation similar to that described by Meinzer and Grantz (1990). However, an excessive decrease in hydraulic conductivity was avoided by stomatal closure, as reported by Sperry (1986). These results suggest that vessel size modifications contribute to regulate water flow throughout the plant at relatively low water stress levels, while at lower ψ_{leaf} the regulation of water flow is taken over by stomata.

Although the results of the 1995 experiment showed that moderately water-stressed vines (ψ_{leaf} -0.6 MPa) have smaller vessels, but no detectable embolisms, Schultz and Matthews (1988) reported that severe water stress (ψ_{leaf} down to -1.2 MPa) induced xylem embolism in the same plant. In that paper, reduction of ψ_{leaf} from -0.41 to -0.77 MPa decreased hydraulic conductivity about 96%. However, these authors did not measure vessel size. In order to assess the incidence of vessel size modification and of vessel embolism on hydraulic conductivity separately, a new experiment was conducted in 1996 with vines subjected to water stress treatments of different severity (ψ_{leaf} -0.6 and -0.8 MPa, respectively). In this experiment a ψ_{leaf} decrease from -0.35 to -0.8 MPa decreased hydraulic conductivity by 72%, in agreementh with the results of Schultz and Matthews (1988). In addition, it was found that at the higher stress level conductivity was about 24% lower before elimination of xylem emboli, implying partial embolism of the vessels. Correspondingly, in this treatment water tension along the shoot increased above the values measured in the IRR and WS1 treatments. In WS1 the plants adjusted to keep the pressure gradient equal to that of irrigated plants. This required lower g_s to compensate for the lower k_l in the stressed plants. When water stress was more severe, this balance was not maintained, presumably g_s was not reduced sufficiently to balance the ψ gradient, and embolism occurred. It was concluded from these results that grapevine shoots respond to water stress by two parallel mechanisms: modification of xylem vessel size, which is induced at moderate stress levels, and vessel embolism, which requires more severe water stress.

These two conductivity responses to water stress require different conditions and may play different roles. It was observed that a reduction of xylem size after 40 d of exposure to a moderate water stress as a growth decrease response. Moreover, the relationship between stomatal conductance and leaf specific conductivity suggests that reduction of xylem size affects shoot water flow at rather moderate water stress levels (WS1 treatment, see above). On the contrary, embolisms formed at higher stress levels in this experiment, which is the case in most angiosperms (Tyree and Ewers, 1991). Modification of vessel diameter and shoot embolism also differ in their capacity to be eliminated once the stress is over: in the first case again a slow growth process is needed, while embolisms can recover relatively quickly (Sperry, 1986; Sperry *et al.*, 1987; Yang and Tyree, 1992). Thus in a large-vessel species such as the grapevine, reduction of vessel size may be an adaptation to a persistent situation of moderate water stress, while embolism may be induced by a short and more severe water stress. Conditions of moderate water stress (-0.6 MPa in this experiment) in the grapevine are common even in humid temperate viticultural areas (Düring and Loveys, 1982). Thus modifications of vessel size are likely to be a common mechanism of response to water stress in this plant.

If reduction of vessel size and xylem embolisms are distinct mechanisms, they are not independent. The susceptibility of xylem vessels to embolism is linked to the size and structure of their pit pores, and, in general, smaller vessels, probably as they have less developed pores, are less susceptible to embolism (Salleo *et al.*, 1985; Sperry and Tyree, 1988; Hargrave *et al.*, 1994; Lo Gullo *et al.*, 1995). In *V. vinifera*, Salleo *et al.* (1985) interpreted the lower diameter of apical vessels mainly as a protection against embolism in the apical part of the shoot. In addition, another factor which can increase shoot embolism, water tension across the shoot, was not affected by the WS1 treatment, which induced changes in k_h due to modifications of vessel size. Thus the modification of vessel diameter at the basal internodes induced by moderate water stress may not only have the effect of reducing water loss from the plant, it may also help to avoid embolisms, which would impair functioning of the whole branch or tree. It is thus a passive mechanism, which may help the plant reducing water loss and preventing loss of function of the xylem at the cost of a lower water availability in the leaf.

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