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Downward shoot positioning affects water transport in field-grown grapevines

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Summary

Grape canopies (cv. Nebbiolo) were manipulated to obtain vines with alternatively upward and downward shoots on the same fruit-cane. Downward orientation reduced length and total leaf area of the shoot and water flow through the shoot, but did not modify shoot water potential. Shoot hydraulic conductivity, either evaluated on growing plants or on cut shoot portions, was lower in downward than in upward oriented shoots at all positions along the cane. This supports the hypothesis that downward shoot orientation causes a reduction of the hydraulic conductivity, which in turn reduces the availability of water and nutrients for the leaves growing downstream of the point of conductivity reduction. A mechanism which reduces growth in downward oriented shoots is proposed and practical consequences for viticulture, related to reduced water conductivity in downward-trained shoots, are discussed.

K e y w o r d s : hydraulic conductivity; shoot orientation; leaf transpiration; gas exchange; stem water potential.

Introduction

Positioning shoots on trellis systems is the base of all training systems in viticulture. It is well known that orientation affects shoot growth, the upward orientation inducing higher vigour than the downward (May 1966; Schubert *et al.* 1995). Bending of lignified grapevine shoots, normally associated with downward direction of the shoots, depresses shoot growth (Tassie and Freeman 1992); this effect is generally ascribed to mechanical damage to the vessels. In previous papers (Schubert *et al.* 1995, 1999) we analyzed the effects of shoot orientation on potted single-shoot grapevines, with their shoots tied to ascending or descending wires. It was shown that under these conditions the downward orientation decreased leaf gas exchange and xylem hydraulic conductivity. However, the application of these results to current grapevine management systems is limited by the fact that field-grown grapevines are multi- and not single-shooted; shoots grow upwards or downwards immediately after budbreak; only upward shoots are tied to wires, while downward shoots grow without support.

The aim of this experiment was to test the effects of shoot orientation in field-grown, multi-shooted vines in order to confirm under field conditions the effects observed with potted plants. To this end we designed a field system with downward and upward shoots on the same plants, minimizing the manipulations required to orient the shoots in either direction.

Material and Methods

Canopies of 12-year-old Nebbiolo vines, grafted on Kober 5 BB, were used. The vines were grown on a non-irrigated, flat sandy loam, located in Grugliasco (Piedmont, Italy). The trellis system was modified on 7 neighbouring plants in a N-S oriented row. The vines (1.5 m x 2.8 m between rows) were trained as a 2.5 m high simple canopy, each with one cane, bearing 10 buds. For each plant the 1st, the 3rd and the 5th shoot from the cane base were trained downwards, the 2nd, the 4th and the 6th upward, and the cane was cut above the 6th node (Fig. 1). Upward shoots were tied to a vertical wire when they reached a length of 0.3 m. The vertical wires were secured to a 6 m high trellis. Downward shoots were initially left untied, but were tied to wires when they were 0.5 m long. Budbreak took place on April, 15. Lateral shoots and clusters were removed immediately after the onset of growth.

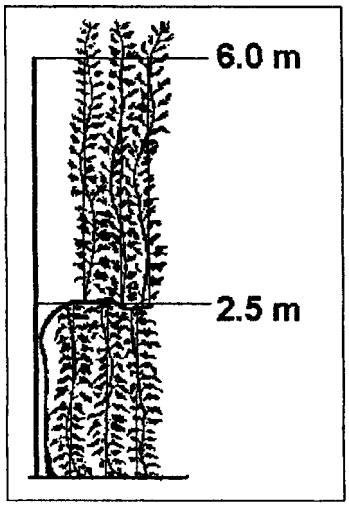

Fig. 1: Experimental manipulation of field-grown shoots of *Vitis vinifera* cv. Nebbiolo trained upward or downward.

Shoot length, shoot diameter and leaf area were measured 130 d after budbreak (DAB). To determine leaf area, the width of individual leaves was assessed on 14 shoots per treatment (two upward and two downward shoots per plant), and the leaf area was calculated referring to a stand-

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ard linear regression between leaf area and the square of leaf width, W^2:

Leaf area (cm^2) = (0.7121 * W^2) + 14.174

calculated from 100 leaves taken from similar plants outside of the experiment.

Shoot hydraulic conductivity (k_h) was assessed by evaluating vines 135 DAB (*in vivo*), and was directly measured on cut shoot portions immediately after leaf fall (190 DAB).

In vivo k_h was determined on 7 shoots per treatment (one upward and one downward shoot per plant in the experiment), as the ratio between water flow (F, $kg \cdot s^{-1}$) through the shoot and the water potential gradient per unit shoot length ($d\Psi_{shoot}/dx$, $MPa \cdot m^{-1}$) causing the flow (RICHTER 1973).

The amount of water flowing through each shoot (F) was estimated by measuring leaf transpiration. Previously LOVISOLO and SCHUBERT (1998) have shown that for grapevine in the late morning and early afternoon estimations of water flow obtained from leaf transpiration measurements are closely correlated with data from direct flow measurements obtained with the Heat Stem Balance method (BAKER and VAN BAVEL 1987). Gas exchange was measured at 10 leaves per upward shoot and 7 leaves per downward shoot (one out of 5 leaves at subsequent nodes on the shoot) between 10 and 14 h (solar time), using an open system (ADC-LCA3 infra-red gas analyzer) equipped with a Parkinson Leaf Chamber (Analytical Development Company, Hoddesdon, UK). Leaves were oriented to a 90° angle with incident light (1400 $\mu mol \cdot m^{-2} \cdot s^{-1}$), to eliminate variations of leaf gas exchanges due to light intensity.

Immediately after gas exchange measurements the water potential gradient along the shoot ($d\Psi_{shoot}/dx$) was assessed on the same shoots. Two leaves at the base and two at the apex of each shoot were wrapped with a double layer bag, inside plastic and outside aluminium, the evening before the measurement, according to LIU *et al.* (1978). The water potential of bagged leaves was measured using a Scholander-type pressure chamber (Soil Moisture Equipment Corp., Santa Barbara, CA, USA) and was assumed to represent the water potential of the corresponding shoot xylem (Ψ_{shoot}).

In order to directly measure shoot hydraulic conductivity, shoots were cut in 0.5 m long portions. This length was chosen to assess conductivity at three different positions along the shoot, since it has been reported that 87 % of the vessels of *V. labrusca* vines are not longer than 0.5 m (SPERRY *et al*. 1997). Moreover, we have shown previously (LOVISOLO and SCHUBERT 1998) that shoot portions shorter than the maximum vessel length leads to an overestimation of conductivity, but does not affect relative differences among treatments. The age of the shoot portions with 5-7 internodes was 100-115 d (basal), 55-70 d (medium), 15-30 d (apical).

Conductivity was measured immediately after cutting. An equipment with pressure control was used according to SCHUBERT *et al.* (1995). After 10 min at 0.4 $MPa \cdot m^{-1}$ to eliminate embolism and after subsequent 5 min at 0.1 $MPa \cdot m^{-1}$ to allow stabilization, for each shoot segment two subsequent flow measurements were made within 2 min with distilled water at a constant pressure gradient (0.1 $MPa \cdot m^{-1}$). Shoot hydraulic conductivity (k_h) was calculated from the ratio between the amount of water collected in 2 min ('flow', $kg \cdot s^{-1}$) and the pressure gradient causing the flow (0.1 $MPa \cdot m^{-1}$) which was kept constant by the equipment. Shoot specific conductivity (k_s) and leaf specific conductivity (k_l) (ZIMMERMANN 1983; TYREE and EWERS 1991) were calculated by dividing k_h by the xylem cross-sectional area at the middle of the 0.5 m shoot portion, and by the leaf area distal to the same portion. Xylem cross-sectional area was considered to be 8.75 % of the shoot trans-sectional area in upward shoots and 4.75 % in downward shoots, according to our previous results obtained with potted plants (SCHUBERT *et al.* 1999).

Data were submitted to the analysis of variance and the Duncan test.

Results

As expected, downward orientation reduced shoot growth. Shoot length, internode number, average internode formation rate ($nodes \cdot d^{-1}$), basal shoot diameter and total leaf area were higher in upward shoots (Tab. 1). The higher total leaf area in upward shoots was due to a higher number of leaves per shoot and to a greater area of leaves younger than 85 d; no differences in leaf area were observed between upward and downward shoots at the basal nodes (Fig. 2).

The shoot water potential (Tab. 2) and the water potential gradient along the whole shoot (Tab. 3) did not show significant differences between orientations.

In order to assess water flux to the leaves, the transpiration rate of each leaf (Fig. 3 a), measured by gas exchange

Table 1

Growth of upward and downward oriented shoots of field-grown grapevines. Averages with different letters are significantly different at the P=0.05 level

Shoot orientation	Shoot length (cm)	Number of internodes	Average internode formation rate ($nodes \cdot day^{-1}$)	Total leaf area (m^2)	Basal shoot diameter (mm)
Upward	405.1 a	49.2 a	0.42 a	0.866 a	11.38 a
Downward	288.2 b	36.3 b	0.31 b	0.506 b	7.79 b

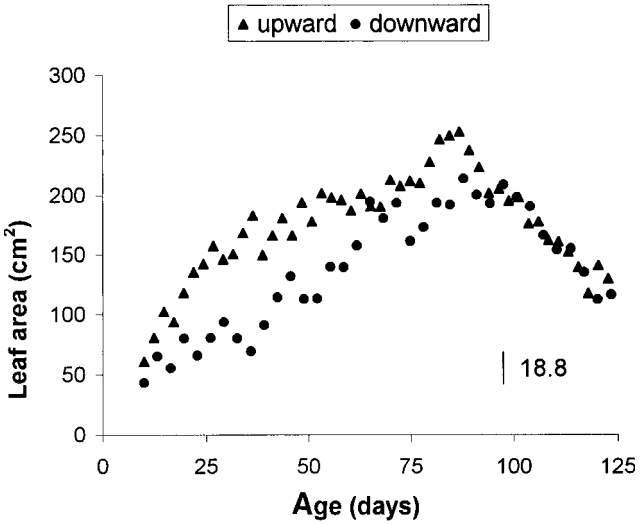

Fig. 2: Area of individual leaves of field-grown shoots of *Vitis vinifera* cv. Nebbiolo trained to different orientations. Bar represents the standard error of the mean (n=14).

Table 2

Shoot water potential (Ψ_{shoot}) at the shoot base (Ψ_{basal}) and at the shoot apex (Ψ_{apical}) of upward and downward oriented shoots (for details see Tab. 1)

Shoot orientation	Distance between the basal and apical measurements (m)	Ψ_{basal} (MPa)	Ψ_{apical} (MPa)
Upward	3.62 a	- 0.673 a	- 0.760 a
Downward	2.56 b	- 0.710 a	- 0.785 a

Table 3

Water potential gradient along the shoot ($\Delta\Psi_{shoot}/dx$), water flux (F) in the shoot and *in vivo* hydraulic conductivity (k_h) of upward and downward oriented shoots (for details see Tab. 1)

Shoot orientation	$\Delta\Psi_{shoot}/dx$ (MPa·m^{-1})	F g·h^{-1}	k_h kg s^{-1} / MPa m^{-1}10^{-5}
Upward	0.024 a	117.3 a	135.6 a
Downward	0.029 a	40.9 b	38.8 b

instantaneously prior to shoot water potential determination, was multiplied by the respective leaf area (Fig. 2) to obtain total leaf transpiration (Fig. 3 b). Average water flux (F) through the shoot, obtained by summing leaf transpirational fluxes, was about three times higher in upward than in downward shoots (Tab. 3). Consequently, using water flux equation ($F = k_h\, d\Psi/dx$), the *in vivo* shoot hydraulic conductivity was about three times higher in upward shoots (Tab. 3).

Stomatal conductance (Fig. 4) as well as transpiration rate (Fig. 3 a) were significantly lower in leaves of downward shoots at all nodes along the shoot.

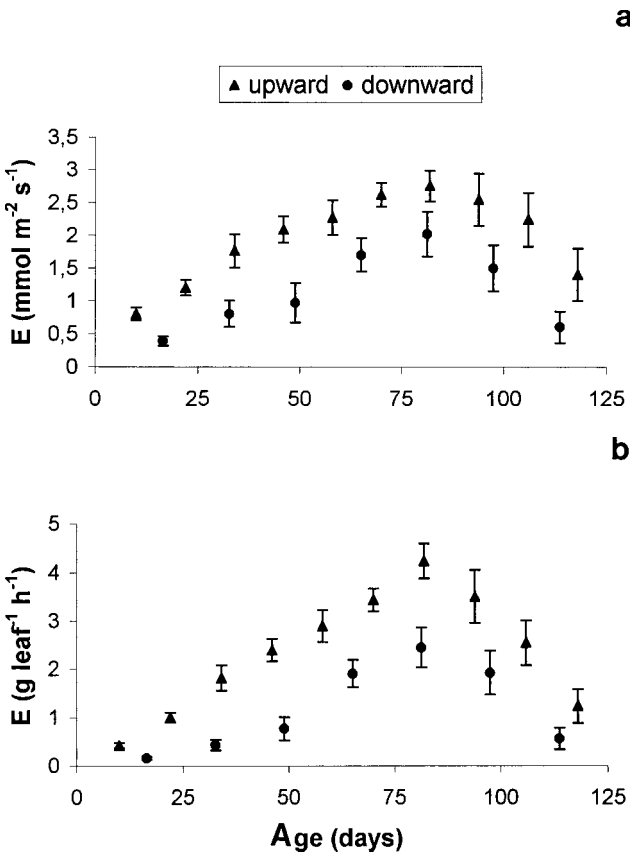

Fig. 3: Average transpiration rate (E) between 10.00 and 14.00 h (solar time) of individual leaves of field-grown shoots (cv. Nebbiolo) trained to different orientations, expressed as water vapour flux per unit leaf area (a) and water vapur flux related to the total leaf area (b). Means ± standard error (n=7).

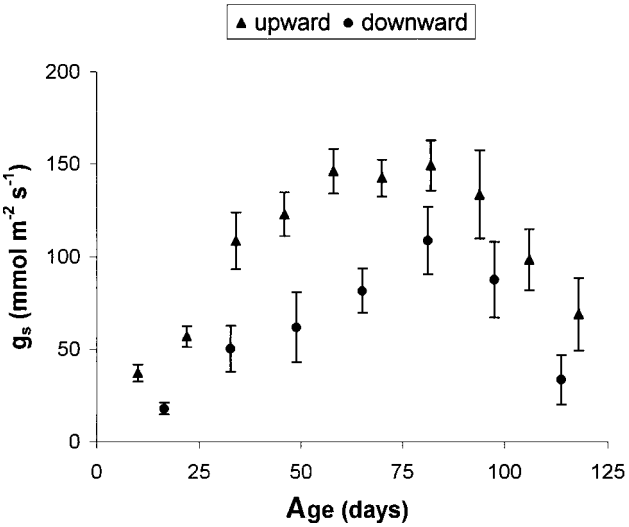

Fig. 4: Average stomatal conductance between 10.00 and 14.00 h (solar time) of individual leaves of field-grown shoots (cv. Nebbiolo) trained to different orientations. Means ± standard error (n=7).

Shoot hydraulic conductivity of cut sections was also significantly lower in downward shoots at all positions along the shoot. k_h decreased from the shoot base towards the shoot apex both, in upward and downward shoots (Tab. 4). Relative differences between the two orientations were higher in basal portions, where k_h in upward shoots was 5.2 times higher than in downward shoots, than in apical

Table 4

Hydraulic conductivity (k_h), specific conductivity (k_s) and leaf specific conductivity (k_l) of upward or downward trained shoots of field-grown grapevines. Measurements were either taken on growing plants (*in vivo*) or on 0.5 m long shoot portions cut from basal, medium, and apical portions of the shoot (for details see Tab. 1)

	Shoot portion	k_h ($kg \cdot s^{-1} / MPa \cdot m^{-1}\ 10^{-5}$) Upward	k_h Downward	k_s ($kg \cdot s^{-1} / MPa \cdot m^{-1}$) Upward	k_s Downward	k_l ($kg \cdot s^{-1} / MPa \cdot m^{-1}\ 10^{-5}$) Upward	k_l Downward
In vivo	whole shoot	135.6 a	38.8 b	178.6 a	142.2 b	315.2 a	153.5 b
After cutting	basal	238.2 a	45.7 b	301.1 a	200.6 b	298.3 a	102.8 b
	medium	165.8 a	27.5 b	293.3 a	177.9 b	315.7 a	124.9 b
	apical	25.3 a	8.4 b	109.2 a	114.8 a	284.3 a	116.1 b
	average	143.1 a	27.2 b	234.5 a	164.2 b	299.4 a	114.6 b

portions, where k_h in upward shoots was only 3.0 times higher than in downward shoots. As expected, k_s showed less differences along the shoot, and was less affected by the downward orientation, suggesting an adaptation of the xylem tissue to the downward position. On the contrary, leaf specific conductivity (k_l) remained more or less constant from the base to the apex of the shoots, but was always significantly lower in downward than in upward shoots (Tab. 4).

Average conductivity values of cut shoots were in close agreement with calculated conductivity values based on the water flux equation applied *in vivo* to whole shoots, although maximum conductivity was higher for cut shoots than *in vivo*. (Tab. 4).

Discussion

The results of this experiment confirm previous observations that downward shoot orientation reduces shoot growth, xylem hydraulic conductivity and stomatal conductance (MAY 1966, KLIEWER *et al.* 1989, SCHUBERT *et al.* 1995, 1999). Canopy architecture of field-grown grapevines in this experiment was different from that of pot-cultivated vines in other reports (free orientation *vs*. shoot bending and fixing to a wire, multi-shoot plants *vs*. single-shoot plants); however this did not change the physiological effects of the downward orientation.

These results have some interesting implications for grapegrowing. Downward shoot positioning is a well-known technique to lower vegetative growth and to increase sugar accumulation in berries (TASSIE and FREEMAN 1992). However, when shoots grow downwards not only leaf area is reduced, but also the carbon fixing capacity per unit leaf area is limited by a decrease in stomatal conductance. In addition, water transport in shoots is limited, and thus may affect the transport of mineral nutrients to the leaves (WILLIAMS 1987). As a consequence shoots should be positioned downward if light and other environmental factors are not limiting photosynthesis (SMART 1974), water transport capacity (SCHULTZ and MATTHEWS 1993), and mineral nutrient uptake (ROBINSON 1992).

Which mechanism regulates growth in upward and downward shoots? In a previous paper we demonstrated for potted grapevines that reduced shoot growth is associated with a decrease of shoot hydraulic conductivity, due to reduced xylem development (SCHUBERT *et al.* 1999). We also put forward the hypothesis that downward orientation hinders the development of xylem vessels by a specific, yet unknown mechanism; in turn, reduced average vessel diameter causes a reduction of the hydraulic conductivity. Under field conditions, extrapolating leaf transpiration data to evaluate water flow in shoots, we assessed that water flux in downward shoots was about three times lower than in upward shoots. However, the shoot water potential gradient was not different between the two orientations. Therefore, also in field-grown vines, conductivity effects are the major causes of reduced flow in downward oriented shoots.

Conductivity determined *in vivo* under field conditions showed the same variation between orientations than conductivity measured on pressurized cut shoots. This was surprising, since we measured hydraulic conductivity on cut shoot portions after removal of eventual embolism, and one would expect conductivity to increase under these conditions. SCHULTZ and MATTHEWS (1993) found a discrepancy of about one order of magnitude between the two measurements for potted grapevines. However, they utilized in pressure-flow experiments single internodes without nodal sections and, as a consequence, their k_h values were overestimated in comparison to ours, since nodes reduce flow along the shoot (SALLEO *et al.* 1982).

In our experiment, a decrease in hydraulic conductivity of the downward shoots was associated with a reduction in stomatal conductance (g_s) of leaves. For downward shoots one may suppose that g_s controls water flow at lower k_h and, as a consequence, that these leaves would transpire less than leaves of upward shoots. Under water stress conditions similar observations have been made and the leaf water status was negatively affected by the stress (MEINZER and GRANZ 1990, LOVISOLO and SCHUBERT 1998). In the present experiment, on the contrary, no water stress was induced by downward positioning (as shown by the lack of changes in shoot water potential), thus one cannot easily assume the existence of a hydraulic signal acting on sto-

mata. It can be hypothesized that a non-hydraulic signal affects stomatal conductance in this case (JACKSON 1997). With other plants such observations have led to the hypothesis that cytokinins in the xylem sap can induce stomatal opening (BLACKMAN and DAVIES 1983, FUSSEDER *et al.* 1992, BANO *et al.* 1993), although direct evidence for the grapevine is still lacking and the mode of action of cytokinins on stomatal regulation is uncertain (INCOLL and JEWER 1987, DAVIES *et al.* 1994).

At any rate, in this experiment leaves of downward shoots were adjusted to keep the water potential gradient similar to that of upward shoots. As a consequence, in downward shoots transpiration was reduced proportionally to the reduction of the hydraulic conductivity and also the development of the individual leaves showed a decreasing trend from the base towards the apex. This resulted in a more or less constant k_l along the shoot in upward and in downward orientated shoots. This means that leaves along the shoot have been supplied by the xylem tissue proportionally to their transpirational surface (TYREE and EWERS 1991), although leaves of downward shoots received less water than those of upward shoots. Without a decrease of stomatal conductance, the shoot water potential gradient would have increased in downward shoots, which is associated with the risk of vessel embolism (SALLEO *et al.* 1985; SCHULTZ and MATTHEWS 1988).

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