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Grapevine shoot growth and stomatal conductance are reduced when part of the root system is dried

by

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Summary: Split-root plants, where the root system was divided between two containers, were used to study the effect of partial drying of the root system on shoot growth and stomatal conductance of grape cultivars Chardonnay and Shiraz (syn. Syrah). When part of the root system was allowed to dry while the other part was well-watered, shoot growth was significantly reduced. Changes in both shoot growth and stomatal conductance in response to half-drying took place in the absence of any change in shoot water status suggesting the involvement of a non-hydraulic signal in mediating this response. Recovery of both shoot growth rate and stomatal conductance appeared to start before rewatering of the dried half of the root system, and coincided with the time when there was no further decrease of soil water content in the dried container. This appears to be first report of a significant decrease in shoot growth in response to partial drying of the root system of grapevines.

Key words: Shoot vigour, split-root, grape, half-drying.

Introduction

The control of vegetative growth, so that it is in balance with reproductive growth, is one of the major management problems in vineyards. Excessive shoot and foliage growth, as well as insufficient growth, have the potential to substantially affect the profitability of grape-growing. The establishment and maintenance of vines which combine optimal productivity with appropriate leaf and shoot growth is challenging not only in practical viticulture, but also at the level of plant physiology.

Drying of part of the root system may significantly reduce shoot growth, even if satisfactory water relations are maintained by supply of water from the hydrated parts of the root system (Davies and Zhang 1991). This has been demonstrated for a range of plant species, particularly through the use of split-root plants where the root system is divided between two or more containers and part of the root system is allowed to dry while the other part is well-watered. In the case of woody plant species, split-root plants have been used to study the effect of partial soil drying on shoot growth. For example, Tan and Buttery (1982) found that stem and leaf dry weight of half-dried peach seedlings was reduced by 11 to 12 % relative to control plants with both containers watered; similarly, leaf area of passionfruit was reduced by 15 % (Turner *et al.* 1996).

As for shoot growth, drying half of the root system reduced stomatal conductance of peach (Tan and Buttery 1982; Poni *et al.* 1992), pear (Poni *et al.* 1992) and sycamore (Khalil and Grace 1993). The magnitude of the response was found to be strongly correlated with the amount of roots in the drying soil (Tan and Buttery 1982). Poni *et al.* (1992) found that total plant transpiration was decreased in response to half-drying and this was associated with changes in stomatal conductance. On the other hand, Turner *et al.* (1996) found that half-drying had no effect on stomatal conductance and suggested that the reduction in plant water-use was a consequence of reduced leaf area.

The first references to the use of split-root plants for the study of grapevine water relations appears to have been those of Düring (1990, 1992) who used plants with roots divided between two containers grown in a controlled environment. He reported a partial reduction of net photosynthesis (Pn) and stomatal conductance (g_S) in response to drying of one half of the root system, without any associated change in shoot water status: 4 d after the start of drying, Pn and g_S had decreased to 70 and 50 % respectively of the control with both containers watered. Using vines (Trebbiano/Teleki 8B) grown outside in containers, Poni *et al.* (1992) maintained one half of the root system without irrigation for two months: treated plants received the same amount of water per plant as control plants with both containers watered. There was no effect on shoot growth rate (SGR). In this experiment, apple, peach and pear were used in addition to grapevine and the results for all 4 species were pooled for some parameters: g_S, Pn and transpiration rate (E) of treated plants decreased to ca. 80 % of control after 9 d of soil drying without any change in leaf water potential (Ψ_L). Plants were harvested at the end of the experiment and the fresh weight of leaves and stems of treated plants (all species averaged) was reduced by 17 % relative to the controls.

The experiments described in this study were conducted to test if, under controlled conditions, grapevine shoot growth and stomatal conductance are reduced when half of the root system is dried. They were part of a program which led to the development of a strategy for control of grapevine shoot vigour now known as partial root-zone drying (Dry *et al.* 1996; Dry 1997).

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Material and Methods

Split-root plants: In the experiments described in this paper, split-root plants, with the roots divided between two containers, were produced using two different methods. In experiment 1, thick cuttings, 40-50 cm in length, of Chardonnay (clone I10V1) canes were selected in winter and the base of the cutting sawn for 15-20 cm towards the tip with a bandsaw and placed in a heat-bed (25 °C) inside a cool-room (2 °C). After root formation, cuttings were planted such that each half of the cutting base was in a different 7-l plastic container. With experiment 2, plants of cv. Shiraz (clone BVRC12) were propagated from dormant cuttings taken in winter from a single grapevine and subsequently grown in plastic bags in a greenhouse. In late spring, single green shoots from two plants were approach-grafted 20 to 25 cm above the soil surface. The graft was wrapped in clear plastic tape and the plants grown in a shade-house for the remainder of the season. In the following winter, the original shoots were cut back to approximately 15 cm above the graft union and a two-node spur retained on each side, both above and below the graft union, *i.e.* 4 two-node spurs per plant. At the same time, the plants were transferred to two 7-l containers and grown in the shade-house during spring and early summer with 4 shoots per plant (two shoots on each side, one above (upper) and one below (lower) the graft union)). The two-year-old split-root vines were then transferred to the open for two months prior to the start of the experiment on February 26 (designated day 1 (D1)).

Experiment 1: The plants were grown in a temperature-controlled greenhouse for 5 months (mean maximum and minimum daily temperatures were 27 and 17 °C respectively). Four weeks prior to the start of the experiment, each plant was cut back to a single lateral shoot which was trained vertically. Vines were blocked (4 replicates) according to shoot height and stomatal conductance and treatments allocated at random. Treatments were: a) both containers irrigated twice daily (WW); b) one container not irrigated from 0900 h on day 2 (D2) until 1500 h on D11 (WD); c) both containers not irrigated from D2 until D6 when one container was irrigated (DD); from D11, all containers of all treatments were irrigated. One container of the DD plants was watered on D6 because the leaves had started to wilt. On D1 (February 16) shoot length averaged 120 cm. A reference node (designated node "-6") was labelled 7 nodes proximal to the shoot tip (the most distal separated node was designated "+1"). Shoot length increase relative to the reference node was measured daily or every second day; shoot growth rate (SGR) was calculated as average increase per day since the previous measurement. The internode length between nodes 0 and +1 was measured daily from D3 and the increase since the previous day calculated (when measurement of this internode started, it was the most distal visible internode). The rate of leaf elongation was determined by measuring the length of the main vein of leaves at nodes -2 and 0 from D2 to D11. Gas exchange of leaves was determined using a portable gas exchange system (LCA-3, Analytical Development Co., Hoddesdon, UK). The distal part of the main lobe was inserted into the cuvette which was positioned normal to the sun; air temperature during measurement ranged from 25 to 33 °C and maximum photon flux density Q ranged from 690 to 1300 $\mu mol \cdot m^{-2} \cdot s^{-1}$. Stomatal conductance was measured at one to three-day intervals in sunny conditions between 1100 and 1200 h on the same 4 leaves per shoot. Leaf water potential (Ψ_L) was measured with a pressure chamber on D3, D6, D7 and D14 (average of two leaves per plant; leaves sampled were proximal to those used for gas exchange). Soil water content (SWC) was measured by time domain reflectometry (TDR, Trase, Soilmoisture Equipment Corp., Santa Barbara, CA, USA) using 15 cm wave guides inserted vertically from the soil surface at 1430 h daily or every second day. Maximum and minimum air temperatures during the experimental period were 19 to 28 °C and 12 to 22 °C respectively and relative humidity ranged between 30 and 55 %.

Experiment 2: On January 18, the two upper shoots were pruned back to one strong lateral shoot at the base of the main shoot which was subsequently trained vertically upwards by attaching to a string (all lateral shoots were removed on this shoot as they appeared). The two lower shoots were cut back to 6 nodes on February 24 by removing the distal portion of the shoot and all laterals removed from the remaining nodes. Plants were blocked on the basis of stomatal conductance and treatments allocated at random (three replicates per treatment). Treatments were: a) both containers irrigated daily (C); b) one container not irrigated from D1 until D23, the other container irrigated daily (T). From D1 to D13 inclusively, there were two, 15 min irrigations per day; from D14 to D22 the frequency was increased to 4, 15 min irrigations per day to accommodate changes in ambient conditions and increased leaf area. The plants were placed on low benches and the sides of the black plastic containers were covered with reflective insulation (Sisalation®) to reduce soil temperature.

The increase in the length of the two upper shoots (reference node = 6 nodes proximal to the shoot tip) was measured daily and the SGR calculated as $cm \cdot d^{-1}$ since the previous measurement. The increase in node number per shoot was determined at intervals from 4 to 6 d. For the T plants, the shoots on the side with the irrigated container were designated as wet and those on the side of the non-irrigated container as dry. Soil water content was measured every three days, on average, by time domain reflectometry. Gas exchange measurements were conducted every 3.5 days, on average, between 1300 and 1600 h using a portable LiCor photosynthesis system (Li-6200, Li-Cor, Lincoln, Nebraska, USA) on the same 4 leaves per upper shoot. The distal part of the main lobe was inserted into a 1.0-l chamber which was positioned normal to the sun. Measurements were conducted during cloudless periods on exposed leaves with a flow rate of 500 to 600 $\mu mol \cdot s^{-1}$. Leaf water potential was measured between 1300 and 1530 h on D18 and D22 on one leaf per shoot using the pressure chamber method.

The soil medium for both experiments was 4:2:1 coarse pine bark, sharp white sand and coarse yellow river sand (v:v:v) plus 1.5 $g \cdot l^{-1}$ $FeSO_4$, 2.0 $g \cdot l^{-1}$ Osmocote Long Life®, 2.0 $g \cdot l^{-1}$ pH amendment (= two parts dolomite, one part gypsum, one part agricultural lime); steam sterilised. Topsoluble Plant Food® (21:5:18 N,P,K plus trace elements) was applied weekly during the growing season at the rate of 2.5 g

per plant and week. Both experiments were conducted on the Waite campus of The University of Adelaide. All statistical analyses were conducted using PRISM™ Version 2 (GraphPad Software Inc., San Diego, CA, USA). A paired t-test was used for comparison of two treatments, and a one-way analysis of variance for three or more treatments with Tukey's post-test for comparing pairs of treatments.

Results

Experiment 1: The reduction in g_S, Pn and SGR (Fig. 1) for DD plants coincided with the decrease in soil water content from D1 to D6 (Fig. 2). From D6 to D11, when DD plants were converted to WD, all three parameters partially recovered to 60-70 % of the control (WW) level, with full recovery taking place after both containers had been irrigated on D11. For WD, the reduction in g_S, Pn and SGR relative to WW plants also coincided with the decrease in water content of the dried container but the rate at which the shoot parameters decreased was slower than for DD. The maximal reduction of SGR (74 % of WW) occurred on D5 at about the time that the soil water content reached its lowest level (8 %); similarly, the maximal reduction of g_S and Pn (ca. 66 % of WW) occurred 2 d later. Recovery of all three parameters appeared to start prior to rewatering of the dry container on D11, followed by complete recovery by D14. Ψ_L was significantly lower on DD plants than either WW and WD by D3 (Tab. 1). After one container was rewatered on D6, Ψ_L had recovered to the WD level by D7, but was still significantly lower than WW. By D14, Ψ_L of DD was still lower than WW, but the difference was not significant. By comparison, Ψ_L of WD was not significantly lower than WW at any time except on the afternoon of D7; the difference on this occasion may be explained by the transient decrease in soil water between irrigations.

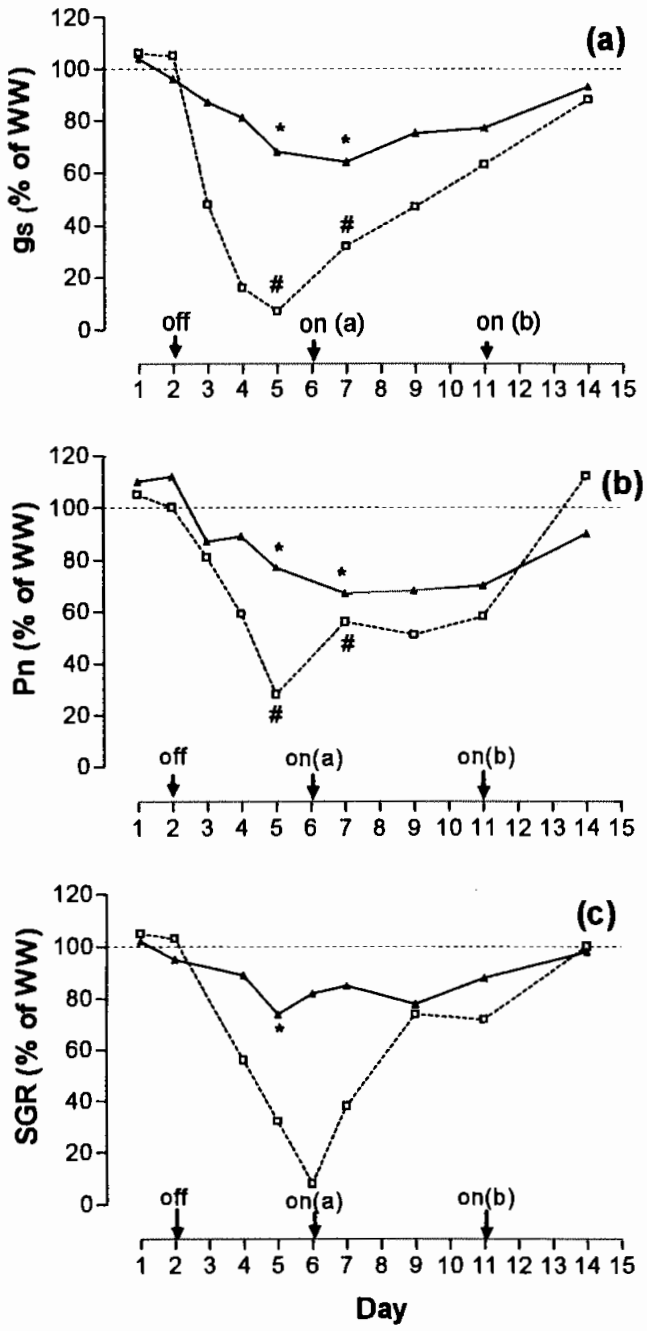

Fig. 1: Effects of wet/dry combinations on gas exchange and shoot growth of Chardonnay, Exp. 1. WD (▲) and DD (□) treatments expressed as % of WW; on(a): DD changed to WD; on(b): all containers irrigated. * indicates those days when WD significantly different ($p<0.05$) from WW and # those days when DD significantly different ($p<0.05$) from WD. (**a**) stomatal conductance (g_S; $mmol \cdot m^{-2} \cdot s^{-1}$): DD significantly different ($p<0.05$) to WW on D3 to 11 inclusively; (**b**) net photosynthesis (Pn; $\mu mol \cdot m^{-2} \cdot s^{-1}$): DD significantly different ($p<0.05$) to WW on D3 to 11 inclusively; (**c**) shoot growth rate (SGR; $cm \cdot d^{-1}$): DD significantly different ($p<0.05$) to WD and WW on D4 to 7 inclusively.

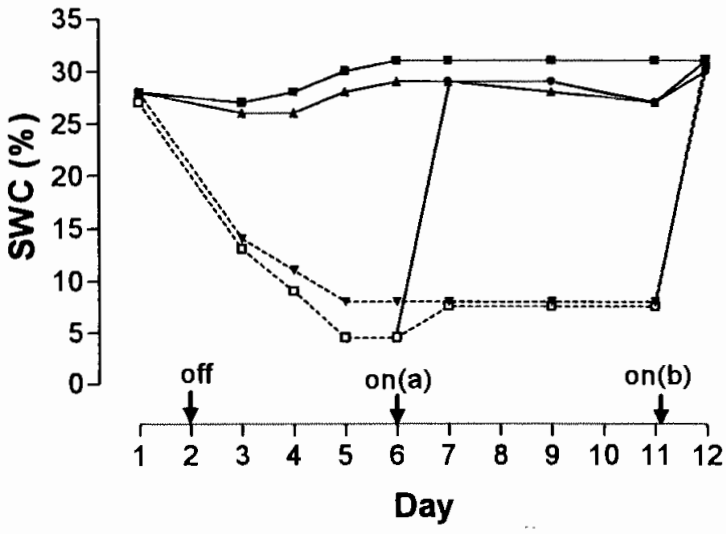

Fig. 2: Volumetric soil water content (SWC, %): average of both containers WW (■); irrigated container of WD (▲); non-irrigated container of WD (▼); average of both containers DD to day 6 and non-irrigated container only thereafter (□); irrigated container of DD from D7 (●); Chardonnay, Exp. 1. On(a): DD changed to WD; on(b): all containers irrigated.

The rate of internode elongation of DD shoots was lowest up to D6, but not after rewatering of one container of DD plants on D6. Similarly, the only differences in the rate of leaf elongation between DD and the other treatments occurred prior to, but not after, D6. There was no difference between WW and WD plants for the rates of internode or leaf elongation. From D1 to D14, SGR and g_S (both expressed as % of WW) were positively correlated: $r = 0.71$ ($p<0.05$) and 0.96 ($p<0.001$) for WD and DD respectively.

Experiment 2: Shoot growth rate (SGR) increased for both control (C) and treated (T) plants from the start of measurement to reach a maximum on D25 (Fig. 3). The SGR of T plants was significantly lower from D17 to D25. The relative reduction in SGR of T plants occurred at the time when there was no further decrease of soil water content in

Table 1

Effects of wet/dry combinations on leaf water potential (MPa); Chardonnay, Exp. 1
(see text for explanation of treatments)

Day	Time (h)	WW	WD	DD	Significant difference ($p<0.05$)	Significant difference ($p<0.01$)
3	1500	-0.56	-0.72	-1.09	WD and DD	WW and DD
6[a]	0530	-0.42	-0.43	-0.68		WW and DD WD and DD
7	1440	-0.49	-0.63	-0.68	WW and DD WW and WD	
14	1130	-0.39	-0.36	-0.45		

[a] DD to WD on day 6 (pm); all containers watered from day 11.

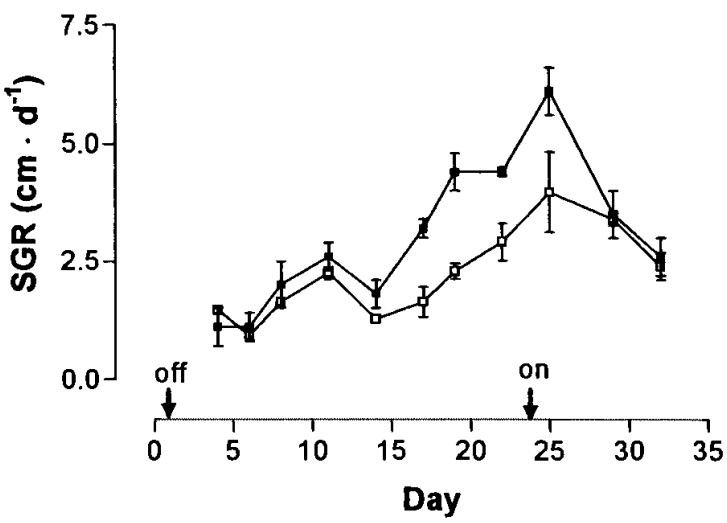

Fig. 3: Effects of partial drying on shoot growth (SGR, mean ± se, $cm \cdot d^{-1}$) of Shiraz, Exp. 2: 'control' vines (C, ■) and 'treated' vines (T, mean of 'wet' and 'dry' shoots, □). T significantly different ($p<0.05$) to C from D17 to D25. One container of T not irrigated from D2 to D23.

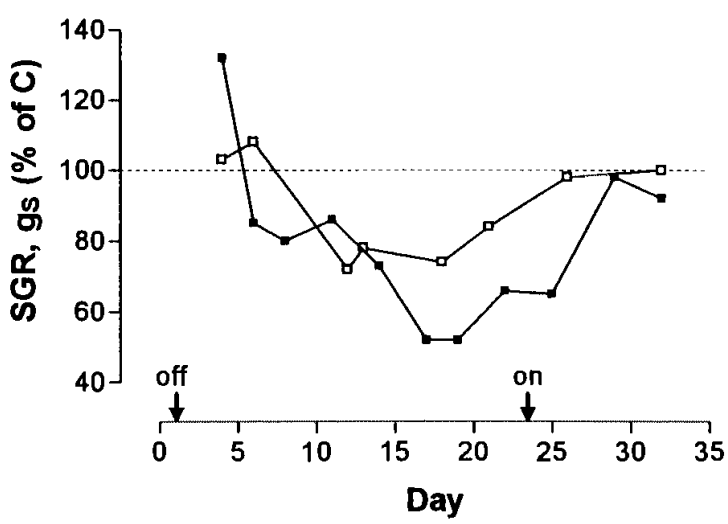

Fig. 4: Effects of partial drying on shoot growth rate (SGR, ■) and stomatal conductance (g_S, □) of Shiraz, Exp. 2: 'treated' (T) as % of 'control' (C). One container of T not irrigated from D2 to D23. SGR and g_S of T significantly different ($p<0.05$) to C for D17 to D25 and D12 to 18 respectively.

the dry container, and SGR stayed at that level until rewatering on D23.

The initial reduction of both SGR and g_S of T plants relative to C (Fig. 4) coincided with the decrease in soil water content of the dry container from D2; SGR decreased to a minimum of 52 % of the C plants on D17 and g_S decreased to a minimum of 72 % of C on D12. Recovery of SGR appeared to start after D19, g_S after D18, and both recovered before the dry container was rewatered on D23; this coincided with the time when there was no further decrease of soil water content in the dry container. SGR and g_S completely recovered by D29. There was no difference between wet and dry shoots of T plants for either SGR or g_S (except on D18 when dry shoots had significantly lower g_S).

The shoot length increment to D25 was reduced by 28 % in response to treatment, in association with a reduction in number of new nodes and mean internode length (Tab. 2). For Ψ_L, there was no significant difference between shoots of C and T plants; similarly there was no significant difference between wet (W) and dry (D) shoots of T plants. Stomatal conductance and SGR were found to be linearly related when mean values of upper shoots were calculated for the period D11 to D22: $r = 0.61$ ($p<0.05$).

Discussion

The DD plants behaved as expected: the reduction in g_S, Pn and SGR by 70 % or more relative to WW was very similar to the results of Tan and Buttery (1982), Düring (1992) and Turner *et al.* (1996). They observed a similar response within 4-7 d, coincidental with a decrease in soil water content and associated with a significantly lower Ψ_L. Similarly, recovery of both gas exchange and SGR was delayed by several days after rewatering whereas Ψ_L recovered almost immediately. SGR partially recovered to the WD level after rewatering one container but this was not the case for either g_S or Pn, which remained lower than the WD level until both containers were watered on D11. This suggests that SGR is more responsive to soil drying than g_S and also it recovers more rapidly. SGR decreased in response to drying of half the root system with both cultivars of *Vitis*

Table 2

Effects of half-drying on shoot growth components (increment from D1 to D25; mean ± standard error) of Shiraz (Exp. 2). Both containers irrigated (C); one container not irrigated from D1 to D23 (T)

	C	T	T (as % of C)	Signif.
Length (cm)	78 ± 7	56 ± 8	-28	<0.05
Node number	9.3 ± 0.6	7.5 ± 0.5	-19	<0.05
Mean internode length[a] (cm)	8.4 ± 0.4	7.5 ± 0.6	-11	ns

[a] Mean internode length = length/node number.

vinifera, and with cv. Ramsey (*Vitis champinii*) in another related experiment (Dry 1997), indicating that the response is not restricted by genotype. SGR of half-dried plants decreased by 30 to 50 % relative to the control after 5-22 d of drying (Figs. 4.1 c, 4.5). This was a similar response to Gowing *et al.* (1990), but the magnitude of the response was greater than that reported by Tan and Buttery (1982) and Turner *et al.* (1996) for the shoot growth components of other species. By comparison, Poni *et al.* (1992) were not able to detect any effect on shoot length after several weeks of half-drying with cv. Trebbiano, but it is unlikely that the different response was the result of a difference in cultivars. In this study, SGR decreased in response to half-drying with both cultivars tested and the lowest rate of shoot growth relative to the control occurred coincidentally with the time when there was no further decrease of soil water content in the dry container.

As for SGR, both g_S and Pn of half-dried plants decreased coincidentally with the reduction in soil water content of the non-irrigated container. The magnitude of the response of g_S and Pn to drying of half the root system in our experiments, *i.e.* 20-35 % decrease, is similar to that reported by Düring (1992) and Poni (1992) for grapevine, greater than that for passionfruit where g_S was not affected at all (Turner *et al.* 1996) or peach (Tan and Buttery 1982) but less than that reported for sycamore (Khalil and Grace 1993). Therefore, unlike the fully-dried treatment, half-drying of the root system only results in partial stomatal closure. This may be beneficial because plant water-use efficiency is increased with partial stomatal closure (Düring 1992).

Recovery of both gas exchange and SGR of half-dried plants relative to controls appeared to start before the rewatering of the dry container with both cultivars. SGR of Chardonnay with the DD treatment increased from 8 % to 72 % of the control (WW) value between D6 and D11 while one container remained dry (Fig. 1 c). For Shiraz, the evidence was less convincing: SGR increased from 52 to 66 % of the control value between D17-19 and D23 (Fig. 4). Furthermore, this relative recovery of the shoot function of half-dried plants appeared to coincide with no further decrease in soil water content of the dry container. For example, in Exp. 1, SGR and g_S recovered from D5 to D7 and minimum SWC was reached on D6 (Figs. 1, 2). Both SGR and g_S recovered completely within a few days of both containers being watered and one could speculate that this may have taken place even if the dry container had not been rewatered. Khalil and Grace (1993) observed a partial recovery of g_S during the day prior to rewatering of the dry container in their half-drying experiment; however, in their case, stomata were almost fully closed prior to the partial recovery.

The reduction in SGR and g_S of half-dried grapevines in these experiments was not associated with any significant change in shoot water relations, except for D7 in Exp. 1. This one instance may have been a consequence of excessive drying of the wet container. The irrigation frequency was increased from D14 in Exp. 2 when it became obvious that the water requirements of the half-dried plants were not being met by the schedule in place to D14. Düring (1992) decreased the leaf area of WD plants relative to WW in order to reduce transpiration, but this was not done in our experiments. The lack of any effect on Ψ_L confirms the observations of Gowing *et al.* (1990) and others that changes in stomatal conductance are more closely linked to changes in soil water status than to the leaf water status.

The rates of leaf and internode elongation were only affected on DD plants prior to D6 in Exp. 1, a typical response to water stress (Williams and Matthews 1990). After D6, when one container was watered, and Ψ_L had recovered, there was no longer any significant effect on expansive growth. Similarly, the decrease in shoot length in response to half-drying in Exp. 2 appeared to be more of an effect on the rate of initiation of nodes than on internode elongation. However, it is difficult to draw any firm conclusions because average internode length is calculated over the whole shoot length increment and thus it is not possible to differentiate between internodes which have elongated at different stages of shoot development. Gowing *et al.* (1990) found that the rate of leaf initiation, *i.e.* the rate of node production, was more sensitive to half-drying than the rate of leaf elongation.

If the wet (W) and dry (D) shoots of half-dried plants are compared, there was no difference in SGR of upper (U) shoots for either cultivar (lower (L) shoots not measured). However, g_S of D shoots tended to be lower than that of W shoots at the time when mean g_S of treated plants was at its lowest level relative to controls. One possible explanation is that the graft union of the approach-grafted Shiraz

vines was not perfect and a putative signal was not fully translocated from the D trunk to the W shoots. On the other hand, there was no significant difference in Ψ_L between W and D shoots of half-dried Shiraz: this may indicate that the graft union did not interfere with the movement of water from the W trunk to the D shoots (which presumably was occurring by D18 because the SWC of the dry container had reached its lowest level by that time).

There was a positive linear relationship between gas exchange and shoot growth rate for half-dried plants, either when expressed as a percentage of control plants over time (Exp. 1) or when actual values per shoot were used (Exp. 2). This suggests that the two physiological processes may be influenced by the same root signal, as proposed by Gowing *et al.* (1990). On the other hand, SGR may simply respond to changes in assimilate supply.

The water requirements of half-dried plants grown in containers appear to be supplied by half the root system so long as the wet half is irrigated frequently; this confirms the observations of others (*e.g.* Turner *et al.* 1996). The experience from Exp. 2 indicates that, if water is not applied frequently, the wet container will dry excessively and there is the risk of an hydraulic effect on shoot growth and gas exchange. It is possible that even the control containers were not being irrigated frequently enough up to D14 because there was an actual decrease in SWC (Fig. 4) and SGR of control Shiraz (Fig. 3) from D11 to D14. Changes in Pn in response to half-drying in Exp. 1 were strongly correlated with changes in g_s; this is similar to the results of Tan and Buttery (1982), Düring (1992), Poni *et al.* (1992) with other woody plant species, and suggests that stomatal conductance is the dominant influence on changes in Pn.

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