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Partial drying of the rootzone of grape. I. Transient changes in shoot growth and gas exchange

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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 gas exchange of Shiraz (syn. Syrah) *(Vitis vinifera*), Kober 5 BB *(Vitis berlandieri* x *Vitis riparia*) and 110 Richter *(Vitis berlandieri* x *Vitis rupestris*). The initial decrease in both shoot growth rate and gas exchange in response to half-drying coincided with the decrease in soil water content of the dried half of the root system. Recovery of shoot function of half-dried grapevines occurred without rewatering of the dried half of the root system, and commenced when there was no further decrease in soil water content. There was no effect of half-drying on leaf water potential at the times of greatest inhibition of shoot growth rate and stomatal conductanc$_e$ relative to control; this suggests the involvement of a non-hydraulic signal originating from the roots in drying soil. Changes in stomatal conductance in response to half-drying were strongly correlated with shoot growth rate.

K e y w o r d s : split-root, *Vitis*, half-drying, recovery, stomatal conductance, photosynthesis, shoot growth, drought stress.

Introduction

Split-root grapevine plants, where the root system was divided between two containers, have been used to study the effect of partial drying of the root system on shoot growth and stomatal conductance of *Vitis vinifera* cvs Chardonnay and Shiraz (syn. Syrah) (Dry and Loveys 1999). When part of the root system was allowed to dry while the other part was well-watered, shoot growth and stomatal conductance were 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. An important observation from these experiments was that recovery of both shoot growth and stomatal conductance started before rewatering of the dried half of the root system of split-root plants at the time when there was no further reduction in soil water content of the dried half. The only previous reference to this phenomenon appears to be that of Khalil and Grace (1993) who observed a partial recovery of stomatal conductance during the day prior to rewatering of the 'dry' container in experiments with sycamore *(Acer pseudoplatanus* L.) seedlings. However, in their experiment, stomata were almost fully closed prior to the partial recovery, unlike the experiments described in Dry and Loveys (1999) where stomatal closure, prior to recovery, was only partial, *i.e.* there was no more than 35 % reduction in g_S relative to the control.

If the shoot function of partially-dried plants is affected by a positive signal produced by roots in contact with drying soil, and if recovery of shoot function coincides with no further decrease in water content of the soil surrounding those roots, then it follows that recovery may take place because there are no more roots being dried and thus no further production of the signal.

The experiments described in this paper were conducted to test the hypothesis that recovery of shoot growth and gas exchange coincides with no further decrease in soil water content of the dried half of the root system. They were part of a program which led to the development of a strategy for control of grapevine shoot vigour and improvement in water-use efficiency now known as 'partial rootzone drying' (Dry *et al.* 1996; Dry 1997; Dry and Loveys 1998)

Material and Methods

The method of production of split-root grapevines was described in Dry and Loveys (1999). Experiments 1 and 3 were conducted in a glasshouse at the Institut für Rebenzüchtung Geilweilerhof, Germany and experiment 2 was conducted in the open on the Waite Campus of the University of Adelaide, Australia.

E x p e r i m e n t 1 : Each 2-year-old vine (Kober 5 BB *(Vitis berlandieri* x *Vitis ripari*a)) was grown in two 5-l-containers in the open for one month and moved into the glasshouse on June 22. The soil medium was 'Einheitserde' (standard soil mixture with a high organic matter content) with the addition of Basacote 6M ® (BASF, Germany) to continuously provide a source of mineral nutrition (14 % N, 10 % P_2O_5, 13 % K_2O, 2 % MgO) and

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micro-elements. The plants were trained to a single vertical shoot (all laterals removed) and had 13 ± 1 leaves at the start of the experiment on July 5 (D0). Plants were blocked on the basis of preliminary stomatal conductance measurements and treatments allocated at random (three replicates per treatment). The treatments were: a) both containers irrigated daily (WW); b) one container irrigated daily, the other not irrigated from day 1 (WD); c) both containers not irrigated from day 1 (DD). From D8, one of the containers of the DD treatment was irrigated. Shoot length was measured daily. Gas exchange measurements were conducted on the same leaf 2-3 times between 1300 and 1500 h; on D4, measurements were carried out 9 times between 0830 and 1630 h. Rates of gas exchange of leaves were determined using a mini-cuvette system (H. Walz, Effeltrich, Germany; Düring 1993). The distal part of the leaf blade was inserted into a cuvette chamber. Measurements were carried out at constant ambient conditions (light saturation at 850 µmol quanta·m^{-2}·s^{-1}; 350 ppm CO_2; leaf temperature 21°C; constant dew point temperature). From D7 (p.m.) to D9 (a.m.), there were no gas exchange measurements due to equipment failure. Soil water content was determined gravimetrically in the top 10 cm every 2-5 d. Leaf water potential (ψ_L) was measured with a pressure chamber on D2, D4, D7, and D18 at approximately 1300 h on one leaf per plant.

Experiment 2: Each 3-year-old vine (cv. Shiraz, clone 12) was grown in two 7-l-containers. One week prior to the start of the experiment on January 16, all vines were thinned back to 4 shoots per plant; those shoots were topped, reduced to 10-12 mature leaves per shoot and all lateral shoots removed except for one terminal lateral, usually at the most distal node. The main shoot and the terminal lateral were trained vertically upwards. Each container was irrigated with two, 2 l·h^{-1} drippers. Treatments were: a) both containers irrigated 4 times daily ('control'); b) one container not irrigated from January 18 (D3) until D18, the other container irrigated 4 times daily ('treated'). Treatments were chosen at random with 5 'treated' and two 'control' vines. All containers were irrigated from D18. Soil water content was measured every second day on average by time domain reflectometry (TDR) (Trase, Soilmoisture Equipment Corp., Santa Barbara, CA, USA) using 15 cm wave guides inserted vertically from the soil surface. The increase in the length of the terminal laterals of two shoots per plant was measured every two days on average and the shoot growth rate (SGR) calculated as cm·day^{-1} since the previous measurement. Stomatal conductance (g_S) was measured on the same 4 leaves per shoot every second day on average between 1030 and 1230 h with a portable porometer (Delta-T AP4, Delta-T Devices, Cambridge, UK). Leaf water potential was measured with a pressure chamber on one leaf per shoot on D10 between 1400 and 1500 h; the ambient temperature at the time was 38-40 °C. The soil medium comprised 4 parts composted pine bark, 2 parts sharp white sand and 1 part coarse yellow river sand plus 1.5 g·l^{-1} $FeSO_4$, 2.0 g·l^{-1} Osmocote Long Life ®, 2.0 g·l^{-1} pH amendment (= 2 parts dolomite, 1 part gypsum, 1 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·$plant^{-1}$·$week^{-1}$. The relationship between soil matric potential and volumetric water content was determined for this soil mix by the filter paper method of Greacen *et al*. 1989; B. R. Loveys, unpubl.

Experiment 3: Four 2-year-old 110 Richter *(Vitis berlandieri* x *Vitis rupestri*s) split-root vines were moved to a glasshouse on May 4 and transplanted to PVC containers (20 x 20 cm section, 47 cm high) with a single glass side. All plants were trained to a single shoot (all laterals removed) with 12 leaves per shoot at the start of the experiment. From May 22 (D6) until June 5 (D20), one container of each plant was not irrigated ('dry'); the other was irrigated twice daily ('wet'). The soil medium was the same as for Expt. 1. Gas exchange measurements were conducted twice each day between 0900 and 1200 h using a Walz infrared gas analyser on the same two leaves per plant from D1. An index of the rate of soil drying was determined by daily measurement of the average depth (relative to the soil surface) of the margin between wet and dry soil in each container on the glass wall.

Results

Experiment 1: Stomatal conductance and SGR of DD plants decreased relative to WW in response to the decrease in soil water content of the dried containers (Fig. 1). By the afternoon of D5, g_S had decreased by 73 % relative to the control, and by D7, SGR had decreased by 45 %. Over the same time period, soil water content decreased from ca. 0.55 g·g^{-1} to a minimum of ca. 0.25 g·g^{-1} on D7. After rewatering of one of the containers on D8 (while the other remained dry), there was a partial and rapid recovery within 3 d for both g_S (a.m. and p.m.) and SGR. During the next 10 d, with one container still dry, g_S and SGR recovered to the level of the WW plants.

For the half-dried WD plants, SGR was not significantly different to the controls over the whole period of measurement. However, g_S of WD decreased relative to WW, coincidentally with the decrease in soil water content of the 'dry' container (Fig. 1), and was significantly lower on D3 by which time the soil water content was ca. 0.25 g·g^{-1} (compared to ca. 0.55 g·g^{-1} in the 'wet' container). Recovery of g_S of WD plants relative to controls after D11 coincided with no further decrease in soil water content and was completed by D14, at which time the soil water content of the 'dry' and 'wet' containers was ca. 0.16 and 0.55 g·g^{-1}, respectively (Fig. 1). Stomatal conductance of DD plants was significantly lower than WW from 1100 h on D4: the DD average (1200 to 1600 h) was 64 % lower than WW. By comparison, g_S of WD plants was only significantly less than WW at 1500 h.

Half-drying had no significant effect on Ψ_L relative to the control. On the other hand, Ψ_L of DD plants was significantly reduced relative to both WW and WD on D7 (just prior to rewatering of one container of DD plants on D8). By D18, when one container of both WD and DD plants was 'dry', there was no significant difference between any treatment combination (data not presented). There was no correlation between Ψ_L and g_S measured concurrently on the same shoot for any treatment (data not presented).

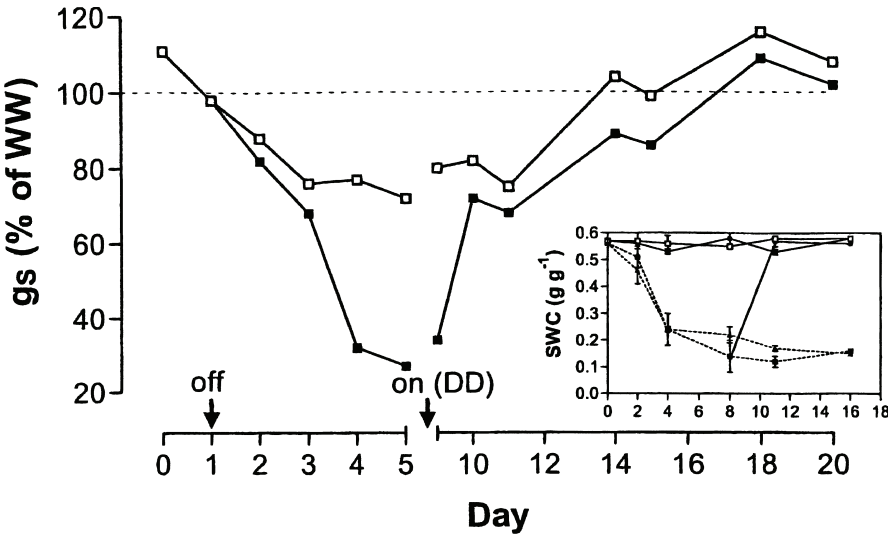

Fig. 1: Effect of wet/dry combinations of 5 BB split-root vines on stomatal conductance (g_S, mmol·m^{-2}·s^{-1}) of WD (□) and DD (■) treatments expressed as % of WW; Expt. 1. Off: one container of WD and both containers of DD not irrigated from D1; on: DD changed to WD. g_S measured in pm (mean of 2-3 measurements between 1300 and 1500 h). DD and WD are significantly different ($p<0.05$) to WW on D3 to D11 inclusively. Insert: Gravimetric soil water content (SWC, g·g^{-1}): average of both containers WW (□); irrigated container of WD (●); non-irrigated container of WD (▲); average of both containers DD to D8 and non-irrigated container only thereafter (■).

The lower 6-8 cm of 'dry' containers of WD plants was still moist with many white roots on D22. By comparison, there were fewer new, white roots at the bottom of the 'wet' containers of WD plants. There were relatively few new roots in the lower 3-4 cm of the containers of WW plants, and many fewer than the 'wet' containers of WD plants. For the DD plant, of which one container had been rewatered 14 d previously, there was much new root growth in the 'wet' container.

Experiment 2: The reduction of SGR and g_S of 'treated' plants relative to 'control' coincided with a decrease in soil water content of the 'dry' container from D3 (Fig. 2). 'Treated' SGR and g_S had decreased by ca. 35 % relative to the control by D9 and D10 respectively and soil water content of the 'dry' container also decreased to the minimum of ca. 7 % at the same time. The lowest value of g_S on 'treated' plants relative to the control, on D10, was not associated with any significant effect of treatment on Ψ_L (-1.17 and -1.14 MPa for 'control' and 'treated' respectively). Both, g_S and SGR of 'treated' plants recovered after D10 and recovery was complete by about D14 and D17 respectively while the soil water content of the 'dry' container remained at ca. 7 % (Fig. 2).

Experiment 3: Stomatal conductance decreased in response to drying of one container: average g_S for the period from D10 to D12, relative to periods immediately before and after, was 68 and 71 % respectively (Fig. 3). The response of Pn (net photosynthesis, assimilation rate) was similar to that of g_S. Water use efficiency (estimated by Pn/g_S) was highest from D10 to D12. Actual values of g_S and Pn were least on D11, after 5 d of half-drying. Both g_S and Pn started to recover from D11 and recovery was complete by D15 (after 9 d of half-drying; Fig. 3). The large decrease of both g_S and Pn from D10 to D11 coincided with

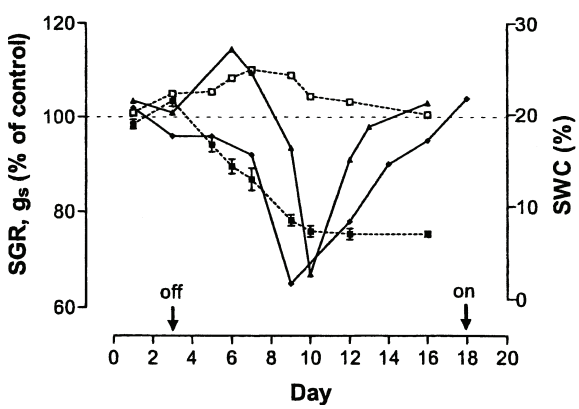

Fig. 2: Effect of half-drying split-root Shiraz on shoot growth rate (SGR, ◆) and stomatal conductance (g_S, ▲); 'treated' (T) as % of 'control' (C), Expt. 2. One container of T not irrigated from D3 ('off') to D18 ('on'). T is significantly different ($p<0.05$) to C on D9 and D12 for SGR, D10 for g_S. Volumetric soil water content (SWC, dotted lines) measured by TDR (mean ± se, %): 'wet' container (□) and 'dry' container (■) of T plants.

the slowing in the rate of soil drying and recovery of g_S and Pn after D11 coincided with the attainment of the maximum depth of the wet/dry margin (Dry *et al.* 2000, this issue; Fig. 1 a).

Discussion

Recovery of shoot function of half-dried grapevines was observed to take place without any change in soil water content of the dried half of the root system. There were some minor differences between shoot growth rate and gas

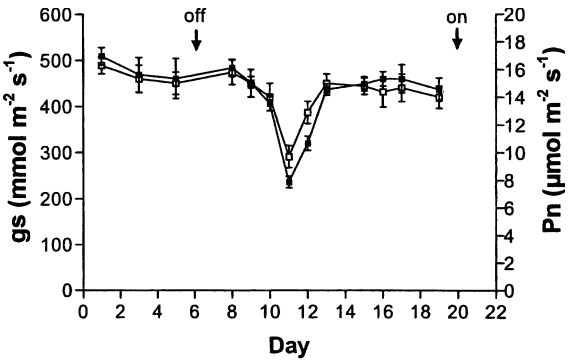

Fig. 3: Effect of half-drying 110 R split-root vines on stomatal conductance (g_S, mean ± se, mmol·m^{-2}·s^{-1}, ■) and assimilation rate (Pn, mean ± se, µmol·m^{-2}·s^{-1}, □); Expt. 3. 'Dry' container not irrigated from D6 ('off') to D20 ('on').

exchange with respect to both the time at which recovery commenced and the rate of recovery.

Poni *et al*. (1992) studied the effect of half-drying on 4 species (apple, pear, peach and grape). In their experiments, gas exchange of half-dried plants appeared to recover relative to the controls in the absence of rewatering of the dry half of the root system; however, the authors made no reference to this phenomenon. They may have overlooked it because the actual values of g_S and net photosynthesis (Pn) for control and half-dried treatments were plotted over time. Using their data (derived by interpolating from their graphs), when g_S of the half-dried treatment as % of the control is plotted over time, it is obvious that recovery, after partial stomatal closure, commenced 10 d after the onset of half-drying and was completed ca. 18 d later. No soil water content data were provided by Poni *et al*. (1992) so it is not possible to conclude if recovery coincided with no further decrease in soil water content of the dried container.

Recovery started between 5 and 10 d after the onset of soil drying in our experiments, which is comparable with the results of both Khalil and Grace (1993) and Poni *et al.* (1992). The rate of recovery, *i.e.* the time from onset to completion, varied from 3 to ca. 7 d; this is less than the 18 d or so calculated from the data of Poni *et al.* (1992) for *Vitis vinifera.* This difference may be a function of the soil type, size of the root system and the number of root tips dried, the rate of soil drying, the growth stage of the plants or differences in genotype. In the experiment of Poni *et al.* (1992), treatment was not imposed until ca. 50 d after budburst when shoot growth rate was starting to slow.

There did not appear to be any relationship between the magnitude of depression of SGR or g_S and the rate of recovery. For example, SGR was inhibited by ca. 35 % relative to the control but recovery occurred in 8 d (Expt. 2); for g_S 20-30 % inhibition was associated with recovery in 2 d (Expt. 3), 4 d (Expt. 2), ca. 10 d (Expt. 1) or 18 d (Poni *et al.* 1992).

Recovery of shoot function started about the time when there was no further decrease in soil water content of the dried half of the root system. Differences in timing of recovery relative to the soil water status of the 'dry' container may be due to differences between experiments with respect to rate of soil drying of the different soil mixes, methods of soil water determination and/or differences between species. For Khalil and Grace (1993), soil water content of the 'dry' container was still decreasing when recovery started, recovery was only partial and it was only observed for one day. Therefore, our paper appears to be the first report of: a) a recovery of shoot function coincidentally with no further decrease in soil water content of the dried half of the root system; and b) complete recovery of shoot function without any change in water status of the soil containing the dried roots. Recovery of g_S started after the soil water content of the 'dry' containers had decreased to 0.16 g.g^{-1} with half-dried plants of sycamore (Khalil and Grace 1993) and this is almost identical to the gravimetric SWC at recovery in Expt. 1.

The initial reduction of shoot growth rate and gas exchange coincided with the decrease in soil water content of the dried half of the root system as reported in Dry and Loveys (1999). SGR and g_S values of half-dried plants became significantly different to the fully-watered controls at a range of volumetric soil water contents. However, because different soil mixes were used in these experiments, the roots in the 'dry' containers in each case may have responded at a similar value of soil water potential. It is likely that roots respond to soil water potential rather than bulk water content. The matric potential at 7 % volumetric SWC for the soil mix used in Expt. 2 was estimated to be approximately -100 kPa: therefore, g_S and SGR of half-dried plants decreased relative to controls when the matric potential of the rootzone of the 'dry' container decreased from field capacity (ca. -10 kPa) to -100 kPa. This was a similar result to Ebel *et al*. (1994) who found that leaf expansion rate of half-dried sorghum plants was not significantly different to controls until the soil in the 'dry' container had decreased to ca. -100 kPa.

The magnitude of the reduction of SGR and g_S , *i.e.* 20-30 %, was similar to that measured in Dry and Loveys (1999) and in some other studies (Tan and Buttery 1982; Poni *et al.* 1992; Khalil and Grace 1993). That the half-drying treatment induces only partial stomatal closure before recovery provides some evidence for a non-hydraulic signal because experiments where the whole of the root system is dried usually produce complete closure over the same time period.

There was no effect of half-drying on Ψ_L at the times of greatest inhibition of SGR and g_S relative to the control, as reported in Dry and Loveys (1999). This provides additional evidence in favour of a non-hydraulic signal originating from the roots in contact with drying soil. On some occasions, Ψ_L of half-dried plants was slightly lower than controls. Although differences were not statistically significant, this may have been the result of an inadequate water supply to the 'wet container, *i.e.* irrigation was not frequent enough to meet the entire needs of the plant. Khalil and Grace (1993) made the same observation and concluded that, because the real differences in Ψ_L were small, they were unlikely to induce any important perturbation in shoot function. Drying of the whole root system of plants in Expt. 1 caused almost complete stomatal closure by D7. The response of these fully-dried plants is an indication that a sig-

nificant reduction in shoot water potential may override a non-hydraulic signal produced by drying roots. Such a direct control of stomatal function by leaf water status may play an important role when the soil dries to such an extent that bulk water relations are perturbed (GOWING *et al.* 1990). A combination of decreased leaf area (as a result of decreased rate of shoot growth and thus leaf initiation, plus reduction in size of expanding leaves) and decreased transpiration rate would allow the plant to extend its growing season given a finite water supply.

After the DD plants in Expt. 1 were converted to half-dried on D8 by watering one of the dry containers, g_S recovered to the WD level within 3 d; thereafter, the DD plants behaved in a similar way to WD plants, *i.e.* they completely recovered over the next 7 d or so while one container remained unwatered. This was similar to the results reported in DRY and LOVEYS (1999).

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