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Partial drying of the rootzone of grape. II. Changes in the pattern of root development

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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 gas exchange and root growth of 110 Richter (*Vitis berlandieri* x *Vitis rupestris*). The initial decrease in 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 gas exchange of half-dried grapevines occurred without any further change in soil water content of the dried half of the root system, and coincided with the point at which there was no further decrease in soil water content. For half-dried plants, there was a relative increase in root development in moist soil layers, both in the 'wet' container as a whole or in the lower part of the 'dry' container. Recovery of gas exchange of half-dried plants occurred at the time when there were no more roots dried in the 'dry' container. We propose that, for half-dried plants, the part of the root system in dry soil can survive because water moves from 'wet' roots to 'dry' roots.

K e y w o r d s : split-root, *Vitis*, half-drying, drought stress, recovery, root growth, gas exchange.

Introduction

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 rate (SGR) and stomatal conductance (g_S) of grape. When part of the root system was allowed to dry while the other part was well-watered, both SGR and g_S were significantly reduced relative to control plants which had both halves of the root system well-watered. The initial decrease for both SGR and g_S in response to half-drying coincided with the decrease in soil water content of the dried half of the root system (Dry and Loveys 1999; Dry *et al.* 2000, this issue). Recovery of shoot function of half-dried grapevines, relative to controls, coincided with the point at which there was no further decrease in soil water content of the dried container (Dry *et al.* 2000, this issue).

The experiment described in this study was conducted to test the hypothesis that recovery of gas exchange of half-dried 110 Richter (*Vitis berlandieri* x *Vitis rupestris*) occurs because there are no more roots being dried. This experiment was part of a program which led to the development of a strategy for control of grapevine shoot vigour and the 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 were conducted in a glasshouse at the Institut für Rebenzüchtung Geilweilerhof, Germany. Four 2-year-old 110 Richter (*Vitis berlandieri* x *Vitis rupestris*) split-root plants were moved to a glasshouse on May 4 and transplanted to PVC containers (20 x 20 cm, 47 cm high) with a single glass side at an angle of 20º such that roots growing vertically downwards intercepted the glass wall. The soil medium was described in Dry *et al.* (2000, this issue). The glass sides were covered to exclude light and covers were only removed for up to 15 $min \cdot d^{-1}$ for measurements. The root ball for each half of the root system was reduced to approximately 12 x 12 x 10 cm and planted next to the glass wall such that the base of the root ball was, on average, 10 cm below the soil surface. This resulted in at least 34 cm of new soil between the base of the root ball and the base of the container. 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'). 'New' roots were defined as those which had grown from the original root ball since re-potting.

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)

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of the margin between wet and dry soil in each container on the glass wall. The growth rate of individual roots in each container was measured daily from D8 to D19: three to four fine, white roots (<2 mm diameter) were selected (from among those which had grown downwards for at least 2 d prior to the start of measurement) and the mean increase in length per day for each container was calculated. The increase in the area of new roots which had grown in contact with the glass wall (mainly below the base of the root ball) was determined every second day on average: a transparent plastic sheet was placed on the glass wall and the roots were drawn on the plastic with a marking pen. The position of the wet/dry margin was also marked. The area of the roots on the plastic sheet was measured with a continuous belt planimeter (Delta-T Devices Ltd., Cambridge, UK) and the average increase ($cm^2 \cdot d^{-1}$) of all roots and percentage of 'new' root area dried was calculated.

On D21, roots from both wet and dry containers of one plant were harvested: the root ball was carefully removed and the soil at different depth classes (0 to 12, 12 to 18, 18 to 26 and >26 cm) excavated from the container with a hand trowel. Roots were extracted by hand, weighed immediately ('fresh weight') and dried for 5 d at 50 ºC, then reweighed ('dry weight'). The correlation between root dry weight and root area on the glass (measured on D18) was calculated. The root areas for the different depth classes (0 to 5, 5 to 10, 10 to 15, 15 to 20, > 20 cm) were measured on the remaining three plants on D22: only the apparently living roots were included, while the relatively few dead and decaying roots were excluded.

Results

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 (Dry *et al.* 2000, this issue; Fig. 3). The response of net photosynthesis Pn was similar to that of g_S. 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) (Dry *et al.* 2000, this issue; Fig. 3). The large decrease of both g_S and Pn from D10 to D11 coincided with the slowing in the rate of soil drying (as indicated by the depth of the wet/dry margin; Fig. 1 a).

Soil water content data from Dry *et al.* (2000, this issue; Fig. 1) was included for comparison in Fig. 1 a (plotted on the same time scale relative to the onset of soil drying) because the same soil medium was used. The percentage of 'new' root area dried almost reached its maximum value at the same time as the minimum value of soil water content was attained, i.e. D11 (Fig. 1 b). Recovery of g_S and Pn after D11 coincided with the attainment of the maximum depth of the wet/dry margin (Fig. 1 a) and the highest percentage of 'new' root area dried (Fig. 1 b). The rate of change in root area per day (RRA; Fig. 1 c) was positively correlated with root dry weight. RRA peaked from D8 to D10 in both 'wet' and 'dry' containers with no

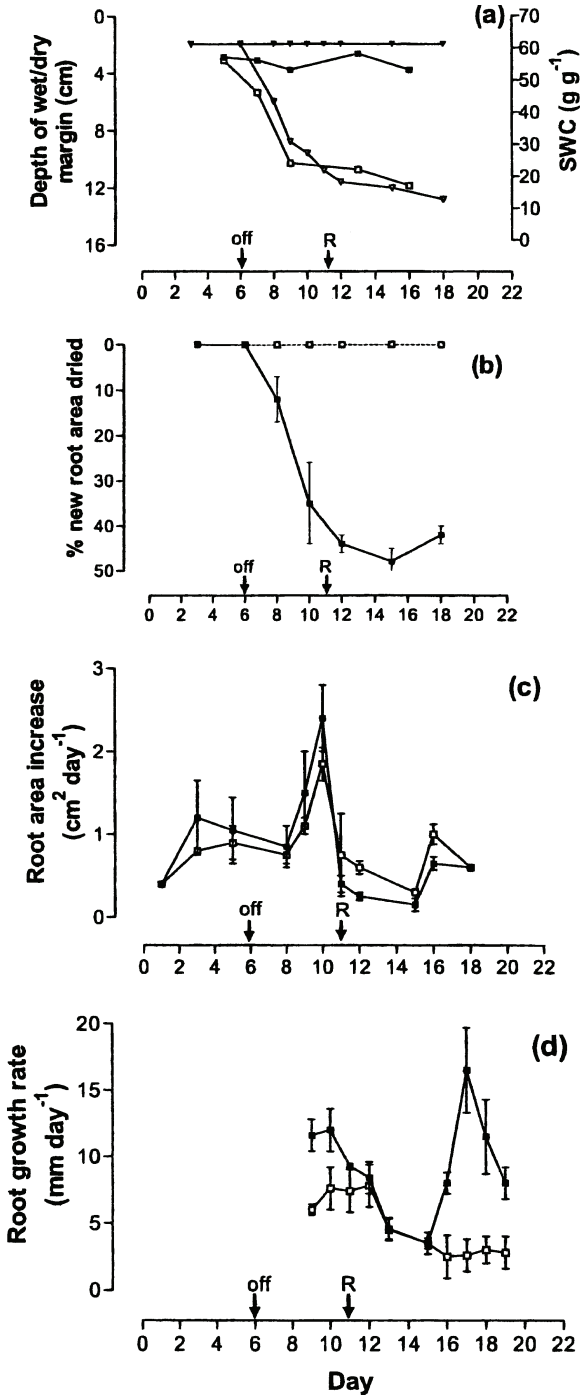

Fig. 1: Effect of half-drying 110 R split-root vines on root development in 'wet'( ) and 'dry' ( ) containers. 'Dry' container not irrigated from D6 ('off') to D20; R indicates day when recovery started (from Fig. 3, Dry *et al.* 2000). (**a**) Depth (mean ± se, cm) of wet/dry margin below soil surface on glass wall of containers. Gravimetric soil water content (SWC, $g.g^{-1}$): data from Fig. 1, Dry *et al.* 2000, adjusted to same time scale relative to cessation of irrigation of 'dry' container; 'wet' ( ) and 'dry' ( ) containers. (**b**) Percentage of 'new' root area dried (mean ± se). (**c**) Rate of increase in root area in contact with glass wall (mean ± se, $cm^2 \cdot d^{-1}$). (**d**) Growth rate (mean ± se, $cm \cdot d^{-1}$) of individual roots on glass wall.

significant effect of container treatment on the changes over time. The rate of growth of roots on the glass in the 'dry' container was significantly greater than that in the 'wet' container from D9 to D10, and again from D16 to D19 (Fig. 1

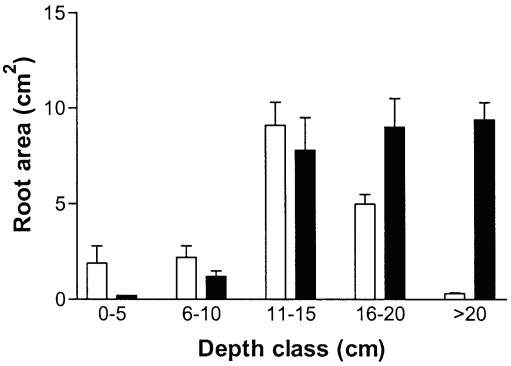

Fig. 2: Effect of half-drying 110 R split-root vines on the area (cm^2) of white and suberised roots on the glass surface (mean ± se of 3 plants) of 'wet'(□) and 'dry' (■) containers. 'Dry' container not irrigated from D6 to D20.

d). There was a significantly larger root area for >15 cm depth in 'dry' than 'wet' containers on D22, particularly deeper than 20 cm (Fig. 2), but no difference in the total amount per container. The average depth of roots on the glass on D22 was 22.6 ±1.5 cm and 34.0 ±2.5 cm for 'wet and 'dry' containers, respectively.

By D12, there were no fine, white roots in the 'dry' container between 0 and 5 cm and very few between 5 and 10 cm depth; many of the roots between 5 and 15 cm depth were suberised ('brown'). By comparison, there were many white roots in the 'wet' container between 5 and 15 cm. On D19 there were relatively thick, white, descending roots in the 'dry' container which had grown to ca. 30 cm depth and a few brown roots above the wet/dry margin; by comparison, the roots in the 'wet' container of the same plant were not growing on the glass wall below ca. 16 cm depth. Excavation of soil from containers after the experiment revealed that there were many roots in the 'wet' container deeper than 20 cm on the side away from the glass wall. Nevertheless, dry weight of roots in the whole container and the area of roots on the glass on D21 were positively correlated: dry weight = 0.124 x area - 0.03; $r^2 = 0.78^{**}$.

Discussion

Recovery of gas exchange of 5 BB vines in this experiment which started on D11 (5 d after the onset of soil drying of the 'dry' container), coincided with no further decrease in soil moisture in the 'dry' container as indicated by the depth of the 'drying margin' on the glass wall (which correlated strongly with actual measurement of soil water content in the same soil mixture in Dry *et al.* (2000, this issue)). As a result, there was no substantial increase in the area of new roots that had dried from D12. If the root development on the glass wall was representative of the situation in the rest of the container (this was likely to be the case for at least the top 15 cm or so of the container, but not necessarily for the lower part), then it is reasonable to accept the hypothesis that recovery occurred because there were no more roots being dried.

It therefore follows that the next hypothesis which needs to be tested is that recovery occurs because there are no more roots being dried and therefore no further export of a signal from those roots. Using split-root plants, several authors have suggested that the amount of roots in drying soil determines the degree of response to half-drying and some have implicated the actual number and/or proportion of root tips in contact with dry soil as the most important factor (Tan and Buttery 1982; Jensen *et al.*1989; Saab and Sharp 1989; Zhang and Davies 1989; Ebel *et al.* 1994). For example, Ebel *et al.* (1994) found that leaf expansion rate decreased by 15 % relative to the control when one container was dried whereas the decrease was ca. 25 % when two were dried. Using a similar system with peach seedlings, Tan and Buttery (1982) found decreases of 4, 12 and 25 % in shoot weight with one, two or three out of 4 containers dried, respectively. As increasing numbers of roots encounter drying soil, the intensity of the signal increases (Zhang and Davies 1989); therefore, it should follow that as decreasing numbers of roots encounter drying soil, the intensity of the signal decreases. With regard to potential decrease in the flux of the signal from roots to shoots, and thus recovery of shoot function, there are several possibilities. Firstly, transpirational flow of water from dry roots to shoots may be maintained (as a result of rehydration of 'dry' roots by 'wet' roots during the night; Saab and Sharp 1989); however, there is a reduction in signal production as drying of new roots slows and thus there is diminished export of the signal. Secondly, signal production may be maintained in dry roots but transpirational flow from dry roots is reduced: as a result, the flux of the signal from roots to shoots is also reduced. Khalil and Grace (1993) favour the second possibility and the evidence in support of all possibilities will be discussed in a later paper**.** Drying roots are known to produce abscisic acid (ABA), *e.g.* Robertson *et al.* (1990), Loveys *et al*. (in press), and the possible role of ABA in the response of grapevines to partial drying will be examined in a later paper.

If recovery of shoot growth can take place without rewatering of the soil occupied by the 'dried' half of the root system, then this suggests that the 'wet' roots may supply water to the 'dry' roots, thus maintaining the water-absorbing capacity in case of rewatering, allowing the plant to resume root growth under favourable soil conditions. Turner *et al.* (1996) found that water uptake by the 'wet' roots of half-dried plants increased relative to those of the 'control' plants. Using sap flow sensors installed in the roots on either side of citrus trees treated with 'partial rootzone drying', Loveys and Dry (unpubl.) found that there was substantial water flow during the night from the roots on the irrigated side of the tree towards the 'dry' roots. This occurred to such an extent that the soil around the 'dry' roots was partially rehydrated during the night.

If partial rootzone drying is to be used for vigour control in the field, the benefits of a single brief period of shoot growth depression during the season are likely to be marginal. This is probably the actual situation in many drip-irrigated vineyards with significant winter rainfall and summer drought: drying of the soil between the rows in spring may produce a signal from that part of the root system in

the mid-rows which results in reduced shoot growth. However, recovery is likely to occur within a relatively short period, because the water requirements of the vines are supplied by the roots underneath the drippers, and shoot growth is restored to its previous rate. This is not to say that this on-off depression is not beneficial because if it happens at the right time, there may be some reduction in leaf area. Furthermore, it may be responsible in part for the characteristic 'switching-off' of shoot growth commonly observed in vineyards in Mediterranean-type climates. However, it is not possible to manipulate this phenomenon under such circumstances.

Therefore, significant and long-term reduction in shoot growth will only be possible if the recovery is minimised. It is unlikely that this will be achieved by a strategy whereby one half of the root system is permanently irrigated while the other half is subjected to a succession of wet and dry cycles because recovery will take place at the end of each drying period and a wetting period of appropriate length would be required to regenerate the root system on that wet/dry side so that it could respond to the next drying cycle. Although this strategy has not been tested in the field, it is unlikely to produce the desired result because it is analogous to the upper and lower parts of the profile of conventionally-irrigated vineyards, *i.e.* the roots of the surface soil go through a series of wet/dry cycles during the season whereas the lower part of the root system may be in permanently moist soil. Therefore, a strategy whereby the drying of half the root system is alternated from one container to the other container, or from one side of the vine to the other, was tested on potted vines and on field vines with split-root systems. Recovery at the end of each drying period may be hypothetically minimised or even prevented by timing the switch so that it occurs at, or just before, the start of recovery. The results of this study led to the development of a strategy for control of grapevine shoot vigour now known as 'partial rootzone drying' (Dry *et al*. 1996; Dry 1997; Dry and Loveys 1998; Loveys *et al*. (in press)).

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References

Dry, P. R.; 1997: Response of grapevines to partial drying of the root system. Doctoral Thesis of the University of Adelaide, Australia.

- -; Loveys B. R; 1998: Factors influencing grapevine vigour and the potential for control with partial rootzone drying. Aust. J. Grape Wine Res. **4**, 140-148.

- -; - -; 1999: Grapevine shoot growth and stomatal conductance are reduced when part of the root system is dried. Vitis **38**, 151-156.

- -; - -; Düring, H.; 2000: Partial drying of the rootzone of grape. I. Transient changes in shoot growth and gas exchange. Vitis **39** (1), 3-7.

- -; - -; - -; Botting, D. G.; 1996: Effects of partial rootzone drying on grapevine vigour, yield composition of fruit and use of water. In: C. S. Stockley, A. N. Sas, R. S. Johnstone, T. H. Lee (Eds.): Proc. 9th Aust. Wine Ind. Techn. Conf., 128-131. Adelaide, Australia. (Winetitles: Adelaide).

Ebel, R. C.; Stodola, A. J. W.; Duan, X.; Auge, R. M.; 1994: Non-hydraulic root-to-shoot signalling in mycorrhizal and non-mycorrhizal sorghum exposed to partial soil drying or root severing. New Phytol. **127**, 495-505.

Jensen, C. R.; Henson, I. E.; Turner, N. C.; 1989: Leaf gas exchange and water relations of lupins and wheat II. Root and shoot water relations of lupin during drought-induced stomatal closure. Aust. J. Plant Physiol. **16**, 415-428.

Khalil, A. A. M.; Grace, J.; 1993: Does xylem sap ABA control the stomatal behaviour of water-stressed sycamore (*Acer pseudo-platanus* L.) seedlings? J. Exp. Bot. **44**, 1127-1134.

Loveys, B. R.; Dry, P. R.; Stoll, M.; McCarthy, M. R.; 2000: Using plant physiology to improve the water use efficiency of horticultural crops. Acta Hortic. (in press).

Robertson, J. M.; Hubick, K. T.; Yeung, E. C.; Reid, D. M.; 1990: Developmental responses to drought and ABA in sunflower roots 1. Root growth, apical anatomy and osmotic adjustment. J. Exp. Bot. **41**, 325-337.

Saab, I. N.; Sharp, R. E.; 1989: Non-hydraulic signals from maize roots in drying soil: Inhibition of leaf elongation but not stomatal conductance. Planta **179**, 466-474.

Tan, C. S.; Buttery, B. R.; 1982: The effect of soil moisture stress to various fractions of the root system on transpiration, photosynthesis, and internal water relations of peach seedlings. J. Am. Soc. Hortic. Sci. **107**, 845-849.

Turner, D. W.; Menzel, C. M.; Simpson, D. R.; 1996: Short term drying of half the root system reduces growth but not water status or photosynthesis in leaves of passionfruit. Sci. Hortic. **65**, 25-36.

Zhang, J.; Davies, W. J.; 1989: Sequential response of whole plant water relations to prolonged soil drying and the involvement of xylem sap ABA in the regulation of stomatal behaviour of sunflower plants. New Phytol. **113**, 167-174.

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