

## Osmoregulation in water stressed roots: Responses of leaf conductance and photosynthesis

by

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**S u m m a r y :** Kober 5 BB vines were subjected to either moderate and slow soil dehydration or to repeated, severe and rapid stress and irrigation cycles. Moderate soil dehydration to 50 % of the soil water capacity led to a small but significant decrease of the osmotic potential at RWC = 100 %, i.e. to osmoregulation in root tips, but not in other parts of the roots. Osmoregulation was associated with the maintenance of a high water status in the root tips and high rates of leaf gas exchange. In a second experiment three severe and rapid drying cycles led to a decrease of the osmotic potential at RWC = 100 % in root tips as well as in unsuberised and suberised roots, the maximum rate being 2.3 bar. In this experiment osmoregulation in roots contributed to a partial increase of the root water status. The observation that, despite a low soil moisture content, leaf conductance and rate of photosynthesis had slightly recovered is discussed.

**K e y w o r d s :** osmoregulation, water stress, root:shoot communication, leaf conductance, photosynthesis.

### Introduction

Adaptation of most higher plants to atmospheric or soil water stress involves the reduction of cell dehydration by either avoidance (e.g. by leaf shedding, leaf blade movement or rolling and stomatal closure) or tolerance of stress, which involves a lowering of the osmotic potential (TURNER and JONES 1980; Jones *et al.* 1981; MORGAN 1984). In grapevines the accumulation of solutes due to water stress (osmoregulation) has been demonstrated in apices and fully expanded leaves (DÜRING 1984). Meanwhile the occurrence of osmoregulation in leaves of grapevines has been confirmed by ZAMBONI and IACONO (1988), Rodrigues *et al.* (1993) and SCHULTZ and MATTHEWS (1993). Solute accumulation enabling the maintenance of turgor despite fluctuations in water status has been rarely studied in roots of grapevines (DÜRING 1984). More information on this phenomenon would be useful because roots are believed to function as "sensors" which "measure" soil dehydration possibly by alterations of their water status (DAVIES and ZHANG 1991). As a consequence, hydraulic and/or chemical signals moving from root to shoot are assumed to induce adaptation processes to the shortage of water supply, e.g. stomatal closure (LOVEYS and DÜRING 1984, TARDIEU and DAVIES 1993).

The aim of the present work was to induce osmoregulation in the roots and to determine if it has any influence on the maintenance of the root water status and, thereby, the communication between roots and shoots at decreasing soil moisture.

### Material and methods

2-year-old Kober 5BB vines (*Vitis berlandieri* x *Vitis riparia*) were grown in containers (32 l) which were filled with a sand/"Einheitserde" (standard soil) mixture (3.5/2 v/v); the substrate contained Basacote 6 M (BASF, Germany) to provide continuously mineral nutrition (14 % N, 10 % P<sub>2</sub>O<sub>5</sub>, 13 % K<sub>2</sub>O, 2 % MgO and microelements). 1 week before the experiment was started the vines were pruned back to 7–9 mature leaves per plant to have a similar leaf area per plant. In experiment A, vines were watered daily: up to August 3 (day 1), irrigation was applied to fully saturate the soil; after that date, the amount was slightly reduced in order to induce a slow decline in soil water content. Plants of experiment B were severely stressed 3 times during the experiment with irrigation only on day 5 and 13. Soil water content was recorded twice each day using a "Trase Systems" equipment (TDR, Time Domain Reflectometry, Soilmoisture Equipment Corp., Santa Barbara, Ca. USA) with 15 cm wave guides. Rates of gas exchange of leaves were determined using a "Miniküvettsystem" (H. Walz, Effeltrich, Germany); technical details have been presented earlier (DÜRING 1993). Measurements were performed at constant ambient conditions twice each day from 12 a.m. to 3 p.m. on 2 fully expanded leaves (light saturation at 850 µmol quanta m<sup>-2</sup> s<sup>-1</sup>, 350 ppm CO<sub>2</sub>, 25 °C leaf temperature and 17 °C dew point). Gas exchange data in the Table are mean values of 4 measurements. On days 13 and 20 the relative water content [(RWC = (fresh weight - dry weight) / (saturated weight - dry weight) x 100)] and the osmotic potential at RWC = 100 % were determined in different parts of the root system: suberised (brown) roots, unsuberised (white) roots and root tips (ca. 3 mm long). Determinations of the osmotic potential were carried out using a vapor pressure Osmometer 5500 (Wescor, Logan, Utha, USA) (for details: DÜRING 1984); data in the Table are mean values of 18 replicates.

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## Results

As is shown in Figure and Table (experiment A) a moderate decrease of soil moisture from 54 % (maximum water capacity) to ca. 27 % within 20 d, (ca. 1.4  $\delta b$ ) led to a decline of the osmotic potential (at RWC = 100 %) of root tips but not of other parts of the root systems. The RWC values of the roots and leaf conductance declined slightly throughout the experiment while rates of photosynthesis remained almost constant or even increased (day 20) indicating higher water use efficiency (photosynthesis/leaf conductance).

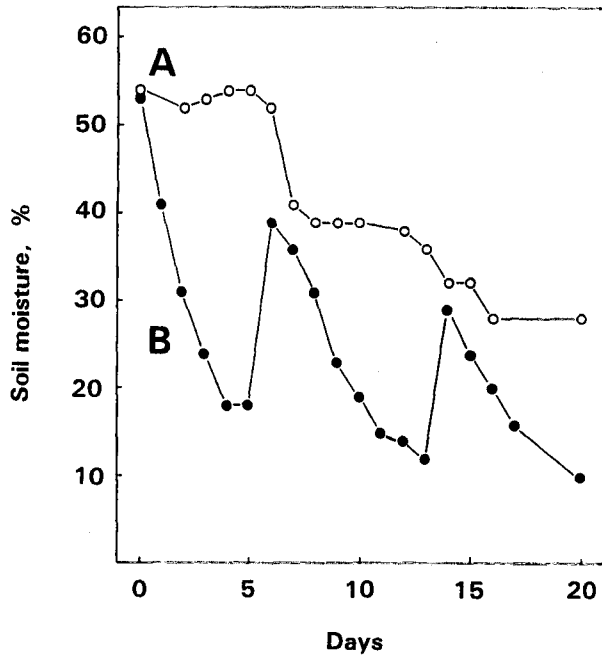


Figure: Soil moisture during the experiments. A: Moderate soil dehydration by limited daily irrigation. B: Repeated severe stress and irrigation cycles.

In experiment B vines were exposed to three drying cycles with two irrigations (Figure and Table, experiment B). Note that in this experiment soil moisture declined more rapidly to minimum values of 18, 11 and 10 %, respectively. 13 d after the start of this experiment, i.e. at the end of the second drying period, the osmotic potential determined at RWC = 100 % of the three types of roots had not significantly changed and RWC had decreased by 62 % (tips), 49 % (unsuberised roots) and 23 % (suberised roots); at the same time leaf conductance and photosynthetic rate had significantly decreased. By contrast, at the end of the third drying period (day 20) the osmotic potential of the three types of roots had decreased by 1.5–2.3 bar, indicating osmoregulation. Compared to day 13 these osmotic changes were associated with an increase of the RWC values of the root tips and higher rates of leaf gas exchange.

The results indicate that (1) slow soil dehydration leading to a moderate soil drought induces osmoregulation in root tips which is associated with a high water status in the roots and the maintenance of gas exchange of leaves, and (2) that it is only after several consecutive episodes of severe stress and irrigation that osmoregulation occurs

Table

Soil moisture, osmotic potential (at RWC = 100 %) of root tips, unsuberised and suberised roots, root RWC, leaf conductance and photosynthesis of Kober 5BB vines (for details see Figure). Values followed by the same index do not differ significantly

	Day		
	0	13	20
<b>Experiment A</b>			
Soil moisture, %	54	37	27
Root osm.pot., -bar			
- root tips	3.0 <sup>a</sup>	3.4 <sup>a</sup>	3.9 <sup>b</sup>
- unsuberised roots	3.0 <sup>a</sup>	3.0 <sup>a</sup>	3.2 <sup>a</sup>
- suberised roots	2.8 <sup>a</sup>	2.9 <sup>a</sup>	2.8 <sup>a</sup>
Root RWC, %			
- root tips	95	93	87
- unsuberised roots	96	92	86
- suberised roots	95	92	92
Leaf conductance, mmol CO <sub>2</sub> m <sup>-2</sup> s <sup>-1</sup>	94 <sup>a</sup>	88 <sup>a</sup>	78 <sup>a</sup>
Photosynthesis, μmol CO <sub>2</sub> m <sup>-2</sup> s <sup>-1</sup>	11.6 <sup>a</sup>	11.5 <sup>a</sup>	13.3 <sup>a</sup>
<b>Experiment B</b>			
Soil moisture, %	54	11	10
Root osm.pot., -bar			
- root tips	3.0 <sup>a</sup>	3.1 <sup>a</sup>	4.5 <sup>b</sup>
- unsuberised roots	3.0 <sup>a</sup>	3.3 <sup>a</sup>	5.3 <sup>c</sup>
- suberised roots	3.0 <sup>a</sup>	3.2 <sup>a</sup>	5.1 <sup>c</sup>
Root RWC, %			
- root tips	95	33	68
- unsuberised roots	93	44	-
- suberised roots	94	71	73
Leaf conductance, mmol CO <sub>2</sub> m <sup>-2</sup> s <sup>-1</sup>	94 <sup>a</sup>	11 <sup>b</sup>	4 <sup>c</sup>
Photosynthesis, μmol CO <sub>2</sub> m <sup>-2</sup> s <sup>-1</sup>	11.6 <sup>a</sup>	2.0 <sup>b</sup>	4.7 <sup>c</sup>

in root tips and other parts of the root system enabling a limited recovery of root water status and leaf gas exchange at constant low soil moisture.

## Discussion

Osmoregulation in roots and the maintenance of a positive root water status under conditions of soil water deficit were shown to have a positive influence on gas ex-

change of the leaves. Assuming that under drought conditions chemical signals, like ABA, are synthesised in the roots and are transported in xylem to the leaves (LOVEYS and DÜRING 1984) it can be speculated that, as a result of osmoregulation, the roots may reduce their sensitivity as sensors and, as a consequence, this may hinder the production of signals. This view, which is part of a concept proposed by KRAMER (1988), would explain the partial recovery of gas exchange at the end of experiment B. It may be argued that the partial recovery of gas exchange is due to osmoregulation in the leaves in experiment B (DÜRING 1984). However, the maintenance of the bulk leaf tissue turgor due to osmoregulation was shown to be not directly associated with stomatal responses and photosynthesis of vine leaves (RODRIGUES *et al.* 1993); similar inconsistencies between the mesophyll water status and stomatal behaviour of grapevine leaves have been reported by KRIEDEMANN and SMART (1971) and DÜRING (1990).

Solute accumulation in roots has also been observed in *Quercus robur* and *Betula verrucosa* subjected to water stress (OSONUBI and DAVIES 1978). In these experiments water stress treatment resulted in the formation of long thin roots. Obviously another major benefit of turgor maintenance in root cells is the maintenance of cell elongation; e.g. root elongation of wheat seedlings was similar at a range of soil water potentials as a result of full turgor maintenance by osmoregulation in the roots (GREACEN and OH 1972). Although we were not able to measure root elongation in our experiments we observed a few long roots growing to deeper, more humid soil layers. In addition, a dense network of small roots was found in the upper soil layer.

## References

- DAVIES, W. J.; ZHANG, J.; 1991: Root signals and the regulation of growth and development of plants in drying soil. *Ann. Rev. Plant Physiol. Plant Mol. Biol.* **42**, 55–76.
- DÜRING, H.; 1984: Evidence for osmotic adjustment to drought in grapevines (*Vitis vinifera* L.). *Vitis* **23**, 1–10.
- ; 1990: Stomatal adaptation of grapevine leaves to water stress. *Proc. 5th Int. Symp. Grape Breeding*, 12–16 Sept. 1989, St. Martin, FR of Germany. *Vitis*, Special Issue, 366–370.
- ; 1993: Rapid stomatal and photosynthetic responses of *Vitis berlandieri* leaves after petiole excision in water. *Vitis* **32**, 63–68.
- GREACEN, E. L.; OH, J. S.; 1972: Physics of root growth. *Nature* **235**, 24–25.
- JONES, M. M.; TURNER, N. C.; OSMOND, C. B.; 1981: Mechanisms of drought resistance. In: Paleg, L.; Aspinall, D. (Eds.): *Physiology and Biochemistry of Drought Resistance in Plants*, 15–37. Academic Press, Sydney.
- KRAMER, P. J.; 1988: Changing concepts regarding plant water relations. *Plant Cell Environ.* **11**, 565–568.
- KRIEDEMANN, P. E.; SMART, R. E.; 1971: Effects of irradiance, temperature, and leaf water potential on photosynthesis of vine leaves. *Photosynthetica* **5**, 6–15.
- LOVEYS, B. R.; DÜRING, H.; 1984: Diurnal changes in water relations and abscisic acid in field-grown *Vitis vinifera* cultivars. II. Abscisic acid changes under semiarid conditions. *New Phytol.* **97**, 37–47.
- MORGAN, J. M.; 1984: Osmoregulation and water stress in higher plants. *Ann. Rev. Plant Physiol.* **35**, 299–319.
- OSONUBI, O.; DAVIES, W. J.; 1978: Solute accumulation in leaves and roots of woody plants subjected to water stress. *Oecologia* **32**, 323–332.
- RODRIGUES, M. L.; CHAVES, M. M.; WENDLER, R.; DAVID, M. M.; QUICK, W. P.; LEEGOOD, R. C.; STITT, M.; PEREIRA, J. S.; 1993: Osmotic adjustment in water stressed grapevine leaves in relation to carbon assimilation. *Austral. J. Plant Physiol.* **20**, 309–321.
- TARDIEU, F.; DAVIES, W. J.; 1993: Integration of hydraulic and chemical signalling in the control of stomatal conductance and water status of droughted plants. *Plant Cell Environ.* **16**, 341–349.
- SCHULTZ, H. R.; MATTHEWS, M. A.; 1993: Growth, osmotic adjustment, and cell-wall mechanics of expanding grape leaves during water deficits. *Crop Sci.* **33**, 287–294.
- TURNER, N. C.; JONES, M. M.; 1980: Turgor maintenance by osmotic adjustment: A review and evaluation. In: Turner, N. C.; Kramer, P. J. (Eds.): *Adaptation of Plants to Water and High Temperature Stress*, 155–172. Wiley-Interscience, New York.
- ZAMBONI, M.; IACONO, F.; 1988: Étude des variations du potentiel osmotique et de l'élasticité cellulaire dans des vignes soumises à un stress hydrique. *Conn. Vigne Vin* **22**, 241–249.

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