Effects of partial rootzone drying on grapevine physiology and fruit quality

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Declaration

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Manfred Stoll October 2000

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Summary

Growth, productivity and fruit quality of grapevines are closely linked to soil water availability. Withholding of water for any length of time results in slowed growth. If drought continues yield may be lost. Vines can be manipulated to stimulate early defence mechanisms by decreasing soil water availability. By using an irrigation technique, which allows for separate zones with different soil moisture status, it is possible to stimulate response mechanisms of the root system which are normally related to water stress. The difficulty of separating 'wet' and 'dry' zones was initially overcome by using split-root plants with root systems divided between two containers. Such experiments on split-root model plants resulted in the development of an irrigation technique termed *partial rootzone drying* (PRD). Results from irrigation experiments using PRD have shown that changes in stomatal conductance and shoot growth are some of the major components affected (Dry *et al*., 1996). The idea of using irrigation as a tool to manipulate stress responses in this way had its origin in the concept that root-derived abscisic acid (ABA) was important in determining stomatal conductance (Loveys, 1984). Later experiments on split-root plants have demonstrated that many effects of water stress can be explained in terms of transport of chemical signals from roots to shoots without changes in plant water status (Gowing *et al*., 1990). The necessary chemical signals are provided by the dry roots, and the wet roots prevent the development of deleterious water deficits.

The general hypothesis tested during this study was that partial drying of the root system gives rise to a change in the supply of root-derived chemical signals which determine changes in grapevine physiology, thereby affecting fruit quality.

Experiments were conducted on split-root vines (*Vitis vinifera* L. cvs. Cabernet Sauvignon and Chardonnay) grown in pots of different sizes, on field-grown vines which had either their root system divided by a plastic membrane (*Vitis vinifera* L. cv. Cabernet Sauvignon on own roots or grafted on Ramsey rootstocks) or conventional vines with a non-divided root system (*Vitis vinifera* L. cv. Cabernet Sauvignon, Shiraz and Riesling) with a commercial PRD irrigation design. The irrigation treatments were vines receiving water on both sides (control) and PRD-treated vines, which only received water on one side at any time. The frequency of alternation of 'wet' and 'dry' sides was determined according to soil moisture and other influences such as rainfall and temperature. In most of the experiments the irrigation was alternated from one side to the other every 10 to 15 days.

Chemical signals from roots: the role of ABA and cytokinins

Studies on chemical signals have concentrated on ABA and cytokinins (CK). An improved stable isotope dilution protocol, which enables analysis of ABA and CK from the same tissue sample, was developed. Analysis of cytokinins focused on zeatin (Z), zeatin riboside (ZR), zeatin glucoside (ZG) and iso pentenyl adenine (iP).

Roots are relatively inaccessible, particularly in field situations. To enable easier access to roots of field-grown vines, split-root vines were planted in a trench which was refilled with a sandy soil. This created a homogenous soil substrate and did not restrict root growth while still allowing access to roots under field conditions. Analyses of root samples of field-grown vines have shown that cytokinins and ABA may originate in roots and their concentrations can be substantially altered during an irrigation cycle. Alternating soil water conditions showed that [ABA] in roots on the 'dry' side was significantly higher compared with the 'wet' side. Due to a reduction in CK on the 'dry' side of PRD-treated vines, the ratio between ABA and CK was substantially changed during an irrigation cycle.

The ABA levels in root tissue and in petiole xylem sap were negatively related to stomatal conductance. This further suggests that ABA, mostly synthesized on the 'dry'

side of the root system, might be responsible for a decline in stomatal conductance. Furthermore, a higher pH of petiole xylem sap was observed in PRD-treated vines which may also contribute to the regulation of stomatal conductance. Studies on stomatal patchiness showed that non-uniform stomatal aperture occurred in field-grown vines under natural environmental conditions and was more abundant under PRD conditions. The degree of stomatal opening, determined by using a water infiltration technique, correlated with measurement of stomatal conductance.

Exogenous application of a synthetic cytokinin (benzyl adenine) can override the possible ABA-mediated stomatal closure resulting from PRD treatment, providing further evidence for the *in vivo* role of these growth regulators in the control of stomatal conductance. The effect of benzyl adenine was transient, however, requiring repeated applications to sustain the reversal. In addition, CKs may also be important in influencing grapevine growth. Following several weeks of repeated spray applications with benzyl adenine, it was found that the development of lateral shoots in PRD-treated vines was enhanced compared to PRD-treated vines sprayed with water only. This supports the idea that the reduction in lateral shoot development seen in PRD-treated vines is due to a reduced production of CKs (Dry *et al*., 2000a). By measuring shoot growth rate it was found that one common feature of PRD-treated vines, which were not sprayed with CK, was a reduction of lateral shoot growth. It can therefore be speculated that the reduction in lateral growth is related to a reduced delivery of cytokinins from the roots. Zeatin and zeatin riboside concentration in shoot tips and prompt buds/young lateral shoots were reduced by the PRD treatment providing further evidence in support of this hypothesis.

Water movement from 'wet' to 'dry' roots

Roots, being a primary sensor of soil drying, play an important role in long- and short-term responses to PRD. Using stable isotopes of water and heat-pulse sap flow sensors water movement was traced from wet to dry roots in response to PRD. The redistribution of water from roots grown in a soil of high water potential to roots growing in a soil of low water potential may be of significance with regard to the movement of chemical signals and the control of water balance of roots. Measurements of the relative water content (RWC) have shown a slower decline of RWC of the 'dry' roots of PRD vines relative to roots of vines which received no water, despite similar water content in soil surrounding those roots. The redistribution of water may help to sustain the response to PRD for longer periods possibly releasing chemical signals and to support the activity of fine roots in drying soil.

Field vines, irrigated with PRD over several growing seasons, altered their root distribution relative to the control vines. PRD caused a greater concentration of fine roots to grow in deeper soil layers and this may contribute to a better water stress avoidance. The effect on root growth may be augmented by the water movement and by the large difference in ABA to cytokinin ratio, which are also known to alter root growth.

PRD makes more efficient use of available water

In experiments where both control and PRD-treated vines received the same amount of water many differences between the vines were demonstrated. Under conditions where water supply was adequate for both treatments, the stomatal conductance and growth of the PRD-treated vines was restricted as has been observed in many previous experiments. As total water input was reduced, however, the stomatal conductance of PRD-treated vines became greater than control vines, suggesting that the latter were experiencing a degree of water stress, whereas the PRD-treated vines were not. This may have been due to the greater depth of water penetration in the case of the PRD-treated vines, where water was applied to a smaller soil surface area. This distinction between PRD-treated and control vines, at very low water application rates, was also reflected in pruning weights and crop yields which were actually greater in PRD-treated vines. It was concluded that at low water application rates, the PRD-treated vines were more tolerant of water stress and made more efficient use of available water.

Reduction in vigor opens the canopy

The initial aim of the research which led to the development of PRD was to achieve better control of undesirable, excessive shoot and foliage growth which, from a viticultural point of view, has many disadvantages. Grapevine shoot growth rate responds very sensitively to drying soil conditions. The irrigation strategy used in the PRD experiments maintained a reduction of both main shoot and lateral shoot growth. In response to PRD a decrease in shoot growth rate and leaf area was observed. Much of the reduction in canopy biomass was due to a reduced leaf area associated with lateral shoots, thus influencing the canopy structure. This was one major factor improving the light penetration inside the canopy.

Control of vegetative vigour results in a better exposure of the bunch zone to light and, as a consequence, in improved grape quality. It is likely that changes in canopy density, as a result of PRD, is causing changes in fruit quality components. Anthocyanin pigments such as derivatives of delphinidin, cyanidin, petunidin and peonidin were more abundant in berries from PRD vines; by comparison the concentration of the major anthocyanin, malvidin, was reduced. When leaves were deliberately removed from more vigorous control vines, which improved bunch exposure, the differences in fruit composition were much reduced. This further supports the idea that a more open canopy, in response to PRD, improves fruit quality by affecting the canopy structure. Fruit quality consequently determines the quality, style and value of the finished wine. Wines from this study have been produced and data on wine quality from commercial wineries are also available. Sensory evaluations have demonstrated that high wine quality from PRD-treated vineyards can be achieved without any yield-depressing effects.

This study has provided evidence to support the original hypothesis. The major findings were:

a) Chemical signals, altered under PRD and mostly originating from roots, play an important role in the root to shoot communication in grapevines.
b) The movement of water from ‘wet’ to ‘dry’ soil layers may help to sustain chemical signals as a response of grapevines to PRD and to support the activity of fine roots in drying soil.
c) A reduction in vegetative growth, in particular of lateral shoots, was sustained using PRD and affected the canopy structure which in turn, due to a better light penetration into the canopy, improved the fruit quality.
d) The reduction in irrigation water applied did not have a detrimental effect on grape yield and thus the efficiency of water use was improved.
e) Application of relatively low irrigation rates showed that PRD-treated vines were more tolerant of water stress and made more efficient use of available water.

List of Abbreviations

ABA	abscisic acid
BA	benzyl adenine
b. wt.	berry weight (g)
CK	cytokinins
CP	capacitance probe
^{o}C	degrees Celsius
df	degrees of freedom
FrW	fruit weight (kg)
FrW / PW	ratio of fruit weight to pruning weight
gs	stomatal conductance ($mmolm^{-2}s^{-1}$)
iP	iso-pentenyl adenine
LA	leaf area (m^2)
LLA	lateral leaf area (m^2)
MLA	main leaf area (m^2)
n	number of samples
n.d.	not detectable
n.s.	not significant
P	probability for data
PAR	photosynthetically active radiation ($\mu molm^{-2}s^{-1}$)
pH	$-log[H^+]$
Pn	photosynthetic rate ($\mu mol\ CO_2m^{-2}s^{-1}$)
PRD	partial rootzone drying
PW	pruning weight (kg)
RH	relative humidity (%)
SGR	shoot growth rate (mm/day)
s.e.	standard error of the mean
SWC	soil water content (volumetric: % or mm)
TA	titratable acidity (gL^{-1} as tartaric acid)
TDR	time domain reflectometry
TSS	total soluble solids (^{o}Brix)
VPD	vapour pressure deficit (Pa)
VSP	vertical shoot positioning
[x-hormone]	plant hormone concentration
Z	zeatin
[9G] Z	zeatin glucoside
ZR	zeatin riboside
Ψ_L	leaf water potential (MPa)
Ψ_m	soil matric potential (MPa)

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