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Vineyard Assimilation: The manipulation of grapevine leaf gas exchange through irrigation management

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Introduction

Strategies for improved water use efficiency

During the past ten years the Australian winegrape industry has experienced a period of massive expansion fuelled by demand for high quality, reasonably priced wines in world markets. Since 1987 the area planted to grapevines has increased from 60,000ha to the current area of 146,000ha. This expansion has occurred in a climate of decreasing availability of water for irrigation and an increase in its cost. There is therefore considerable pressure on the winegrape industry to increase its efficiency of water use. These pressures have resulted in a move away from less efficient forms of irrigation such as overhead sprinklers and flooding and an increased employment of pressurized systems such as drip and under-vine sprinklers. An increased awareness of the benefits of soil moisture monitoring for irrigation scheduling is also contributing to better efficiency of water use. The Australian wine industry is based predominantly on traditional European varieties of *Vitis vinifera* and while these may offer some genetic diversity in terms of their water use efficiency, this attribute is unlikely to be a major consideration in new vineyard development. The dominant property considered will be oenological characteristics and the need to provide the winemaker with reasonable yields of high quality grapes. Rootstocks too may introduce further genetic diversity in their response to water deficits, but this resource remains largely untapped as rootstock selection is likely to be driven by other considerations such as pest and disease resistance and improved performance under saline conditions. A strategy which is able to improve water use efficiency by exploiting the innate drought response mechanisms of grapevines, across a broad range of own-rooted and grafted genotypes, would therefore be a useful management tool. It is well known that partial stomatal closure can bring about improvements in water use efficiency (Bergmann *et al*., 1982; Davies *et al*., 1978; Düring *et al*., 1997; Turner, 1997), due to the non-linear relationship between stomatal conductance and assimilation, and possibly due also to changed resource allocation which may favour reproductive development under conditions of water deficit. Through relatively simple changes to the irrigation management of grapevines, we have been able to manipulate stomatal conductance and bring about an improvement in water use efficiency.

Achieving partial stomatal closure

Increasing evidence suggests that as some plants experience water deficits, the roots can interact with the drying soil to influence leaf function through the transport of signaling substances (Gowing et al., 1990; Tardieu et al., 1992; Zhang and Davies, 1990a,b; Loveys et al., 2000). These xylem-mobile substances primarily affect stomatal behaviour and act to reduce transpiration and possibly leaf area to reduce canopy water loss. Manipulation of soil water therefore becomes a potential tool for the vineyard manager who wishes to exploit these responses. However, the appropriate degree of water deficit may be difficult to achieve and maintain in commercial practice. The deliberate imposition of water stress has been used to manipulate grapevine vegetative and reproductive development and the oenological characteristics of the fruit. For example, reduced irrigation prior to veraison has been shown to cause a reduction in berry size (Matthews *et al*. 1987). Wine made from fruit of fully irrigated vines was unlike wine from early or late season deficit treatments, and there were distinctions evident between 'early season deficit' and 'late season deficit' wines in appearance, flavour, taste and aroma (Matthews *et al*. 1990). Tasters of these wines indicated that 'late deficit' wines had a greater intensity of blackcurrant aroma compared with 'fully irrigated' wines. The concentration of anthocyanins and phenolics was higher in 'deficit' wines although levels of residual sugar, titratable acid, pH and ethanol were similar to 'fully irrigated' wines. Goodwin and Macrae (1990) reported that reduced irrigation during defined periods of berry growth after veraison reduced berry fresh and dry weight and sugar concentration.

The withholding of irrigation water during specific periods is known as regulated deficit irrigation (RDI) and the results have been summaried by Coombe and McCarthy (2000). Berry growth was most sensitive to water stress during pericarp cell division (pre-veraison) and higher levels of water stress were needed to reduce berry size compared with vegetative growth. A reduction in berry size and hence cropping level often results from the RDI treatment, although smaller berries which result in higher anthocyanin concentration may improve fruit quality. Water stress during the ripening period (post veraison) may reduce solute and flavour compound accumulation in berries. This type of irrigation management is practised when there is a need to reduce vigour and manipulate berry size. Although water application is significantly reduced during the RDI period there may be little effect on the long term water use efficiency since post-RDI irrigation rates are normal and yield may be reduced. Improving water use efficiency through the reduced gas exchange which will occur during the period of RDI is therefore not the primary reason for implementing this irrigation management technique. However, a sustained effect on stomatal conductance can be achieved with another irrigation management technique called partial rootzone drying.

Partial rootzone drying (PRD) and its physiological basis

We have investigated the possibility of stimulating some of these water deficit responses in a more controlled and sustained way with a view to improving water use efficiency. This has resulted in the development of an irrigation technique which we have called partial rootzone drying (PRD) (Dry *et al*., 1996. Loveys *et al*., 2000). Implementation of PRD requires that an irrigation system is established such that the rootzone can be simultaneously exposed to both wetted and drying soil. The main effects of PRD in grapevine are that water use efficiency is increased, vegetative vigour is reduced while crop yield and berry size are not significantly reduced. The reduction in canopy density can result in better light penetration to the bunch zone and a consequent improvement in grape quality (Dry *et al*., 1996).

The idea of using PRD as a tool to manipulate water deficit responses in this way had its origin in the observation that root-derived abscisic acid was important in determining grapevine stomatal conductance (Loveys, 1984) and the later demonstration (Gowing *et al.,*

1990) that split-root plants could be used to show that many of the effects of water stress could be explained in terms of the transport of chemical signals from root to shoot without changes in water relations. It was argued (Loveys, 1991) that it should be possible to manipulate vegetative development if, through management of irrigation, both wet and dry root zones could be maintained. The necessary chemical signals would be derived from the dry roots and water supplied from the wet roots would prevent the development of severe water deficits. Experiments with potted and field-grown grapevines showed that both shoot growth and transpiration could be significantly reduced by PRD (Dry *et al*., 1996; Dry and Loveys, 1999; Loveys *et al*., 1998). One of the important features of PRD is that the wetted side of the vine is alternated on a 10 to 14 day cycle. This was found to be necessary because the effects of partial drying could not be sustained for long periods if one part of the root system remained permanently in dry soil while the remaining part was permanently irrigated (Dry *et al*. 1996). This has been attributed to the transient nature of ABA accumulation in roots in dry soil (Loveys *et al*. 2000). The important role of ABA in driving the PRD response has been emphasized in experiments where the effects of PRD on stomatal conductance and on root ABA can be reproduced by applying synthetic ABA to one side of split-root vines. In an experiment with potted Cabernet Sauvignon vines 3μM($\pm$)ABA solution was applied to one side of the root system and water to the other side. The controls received water to both sides. Water was withheld from one side of the PRD vines. After 6 days stomatal conductance was significantly ($P<0.05$) reduced in both PRD and ABA-treated vines when compared with fully watered control vines. Analysis of ABA in the roots showed that the ABA treatment had raised the endogenous ABA content by almost exactly the same amount as the root drying treatment. Furthermore, ABA, expressed from the petioles, was significantly higher in both the PRD and the ABA-treated vines than in the controls, providing more evidence that the transport of root-supplied ABA to the leaves is an important component of the PRD response.

The long term application of PRD to grapevines results in a reduction in lateral shoot development (Dry *et al*. 1996) and this observation prompted experiments to determine treatment effects on endogenous cytokinins. PRD treatment significantly reduced the concentration of zeatin and zeatin riboside in the roots, shoot tips and lateral buds of Cabernet Sauvignon vines (Stoll *et al*. 2000). Furthermore, exogenous foliar applications of the synthetic cytokinin benzyl adenine to Chardonnay vines fully reversed the effects of PRD on stomatal conductance and lateral shoot development (Stoll *et al*. 2000). These results suggest an important role for plant hormones in changes in grapevine leaf gas exchange which occur as a result of strategic irrigation management practices designed to manipulate water use efficiency.

Commercial application of PRD

We now have a working hypothesis to explain how grapevines respond to irrigation practices specifically designed to manipulate canopy gas exchange through the stimulation of water deficit responses. The creation of wet and dry areas within the root zone, as in PRD, appears to be one way of achieving this. In comparison with other deficit irrigation strategies such as RDI, PRD does require the installation of additional irrigation hardware to enable the ability to create the necessary discontinuity in root wetting patterns. There are many ways of achieving this. For example, by the addition of a second drip line, with emitters spaced alternately to the first; with sub-surface drip lines placed close to either side of the vine row; with sub-surface drip lines placed down the middle of the row; and with half-circle under vine sprinklers. Some growers have modified their flood irrigation practices to irrigate alternate sides of the vine rows at each irrigation. The evaluation of PRD in vineyards has now progressed well beyond the experimental stage and there are significant areas of PRD installed in vineyards in Australia, New Zealand, Spain, Israel, USA, South America and

South Africa. To date most installations have involved the installation of a second drip line either above or below ground. We are aware of developments by several irrigation equipment manufacturers to eliminate the need to install two separate drip lines by fusing two conventional lines into one unit. Further research is underway in Australia to determine the optimum configuration for above and below–ground installations such as spacing of 'on' and 'off' drippers relative to vine spacing. The predominant experience from commercial trials has been that if PRD is properly applied, there should be no significant yield reduction, although irrigation amount may be halved.

Conclusions

The development of PRD has refined our ideas about the factors which control vine leaf gas exchange and has drawn attention to the probable role of root-derived chemical signals in modifying stomatal behaviour. Commercial field trials of PRD, now extending to hundreds of ha, are beginning to yield information about the effectiveness of this type of irrigation management in improving the efficiency of water use. At the same time, these trials are exploring the relationships between yield and fruit quality in a commercial setting, at irrigations levels which are considerably less than potential evapotranspiration.

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