

## Irrigation, nitrogen, and rootstock effects on volume loss of berries from potted Shiraz vines

S. Y. ROGIERS<sup>1,2</sup>, J. M. HATFIELD<sup>1,2</sup> and M. KELLER<sup>2,3</sup>

<sup>1</sup>) Cooperative Research Centre for Viticulture, Glen Osmond, SA, Australia

<sup>2</sup>) National Wine and Grape Industry Centre, Charles Sturt University, Wagga Wagga, NSW, Australia

<sup>3</sup>) Washington State University, Irrigated Agriculture Research and Extension Center, Prosser, Washington, USA

### Summary

**Shiraz (synonym Syrah) berry volume increases in two phases and this may be followed by shrinkage during the later stages of ripening. Irrigation regime, nitrogen application rate and rootstock were tested for their effects on the onset of volume loss and extent of volume loss. Maximum berry volume correlated well with volume of berries at 35 d after flowering, the end of the cell division phase. Post-maximum berry shrinkage was not as severe of vines grown with split-root irrigation as compared with standard irrigation. However, these berries were smaller at harvest due to less pre-veraison expansion. Berries grown on vines with standard irrigation had greater post-maximum volume loss than those berries grown in a deficit irrigation treatment. Despite this, maximum berry volume correlated well with final volume in all treatments. N application rate had an effect on the onset of post-veraison expansion but not on the amplitude of maximum berry volume or final berry volume. Deficit irrigation delayed the onset of volume loss by 11 d. Rootstock also had an effect on the onset of volume loss with berries from vines grafted on the rootstock 101-14 Mgt losing volume 7 d earlier than berries from vines grafted on Ramsey. These results suggest that onset and degree of volume loss in Shiraz is sensitive to external influences.**

**Key words:** ripening, grape berry, berry weight, berry shrinkage, deficit irrigation, nitrogen, rootstock.

**Abbreviations:** DI=deficit irrigation, SRI=split root irrigation, STD=standard irrigation.

### Introduction

*Vitis vinifera* L. cv. Shiraz (synonym Syrah) berries can lose volume during later stages of ripening and if this is severe enough they can show symptoms of shrivelling. The timing of the volume loss and the degree of volume loss have large implications for not only yield but final berry composition. An increase in sugar concentration may be a consequence of this water loss, however, anthocyanins and acidity may diminish during the late part of ripening (SOMERS 1976). Basic information is required as to whether the onset of weight loss in Shiraz can be altered or the degree of weight

loss can be manipulated. This information can later be used for field trials through the manipulation of standard vineyard practises.

Water stress can impact on grape berry development. Deficit irrigation can reduce final berry size in cv. Shiraz (McCARTHY 1997) but it is uncertain if it affects the degree of weight loss during the later phase of ripening. Weight loss likely results in grape berries when water inflow into the berry cannot keep pace with evaporative water loss. It is possible that this could be ameliorated by reducing the extent of post-veraison xylem disruption inside the berry (ROGIERS *et al.* 2000, 2001). While water deficit clearly interferes with both cell division and cell enlargement in grapes (WILLIAMS *et al.* 1994), resulting in smaller maximum berry volumes, continued xylem connection to the post-veraison berry could enhance water uptake by the berry and therefore reduce volume loss. Indeed, mild soil water deficit applied to tomato during the early stages of fruit development resulted in increased xylem connection into the ripening fruits, whereas partial rootzone drying (PRD) imposed during the same period had the opposite effect (DAVIES *et al.* 2000). Therefore, one objective of the present study was to vary water levels during flowering and early berry development to see if it changed the extent of volume loss in ripening Shiraz berries.

In addition to soil water status, nitrogen availability can also have an effect on berry size, as can rootstock, along with an influence on yield and composition (KELLER *et al.* 2001). Ramsey, for instance, is a vigorous rootstock producing high yields (CIRAMI *et al.* 1984; HEDBERG *et al.* 1986) and conferring drought tolerance (McCARTHY *et al.* 1997). 101-14 Mgt is a low-moderate vigour rootstock, while Shiraz on its own roots results in a medium to high vigour canopy (DRY and GREGORY 1991). Both nitrogen and rootstocks may affect berry volume either through their influence on vegetative vigour or through an effect on fruit set and thus berry numbers.

The objective of this work was to gain information on factors that impact on the onset of volume loss and/or the degree of volume loss in Shiraz berries. We examined the impact of deficit irrigation, N application and rootstock on berry volume during development. A pot system was used to test the effects of these treatments because non-destructive, precise and accurate measurements of berry volume changes in the field are extremely difficult. It is also easier to carry out experiments on berry volume in a controlled situa-

tion where effects of rain and soil differences can be minimised. However, before any results from such studies can be integrated into a practical vineyard situation, rigorous testing of specific treatment effects in specific field situations will be required.

### Material and Methods

The vines used in this study formed part of two larger studies examining the effects of nitrogen, irrigation and rootstock on vine physiology. The opportunity was taken to learn more about Shiraz berry shrivel by making additional measurements on berry volume during the season.

**Nitrogen and irrigation:** Potted Shiraz (clone PT23) vines were utilised in this study. These vines were on their own roots, their second season of growth, first season of fruit and grown in a medium of river sand: loam: peat moss at 2:2:1. The vines had two shoots that were trained upright with one bunch per plant and were placed in a bird proof enclosure. The pots were 11 l in size and those used for the SRI treatment had a partition down the middle. The vines were exposed to three N application treatments and three irrigation treatments in a factorial design. After an initial base application of 0.5 g N prior to bloom (14 November), a total of 0 g, 1.5 g or 3.0 g of N was applied as  $\text{NH}_4\text{NO}_3$  at 8 intervals from bloom to veraison. Vines were either daily irrigated (STD), deficit irrigated (DI), or exposed to daily irrigation of half the root zone. In this split-root irrigation (SRI) treatment, irrigation was alternated weekly between the two halves of the split roots from bloom to harvest. The DI treatment was started at bloom (18 November), where at the first sign of leaf wilting water was applied to field capacity. This treatment was terminated at the beginning of veraison (9 January) and followed with STD irrigation until harvest. The SRI treatment was initiated at bloom and terminated at harvest. One berry from one bunch was chosen at random from 5 vines per treatment for height and width measurements twice weekly using hand callipers, to calculate berry volume. Shoot length was measured at harvest, and yield components were determined by weighing the bunches and counting the number of berries per bunch. In this study, 50 % bloom occurred at 18 November, 2000 and 50 % veraison occurred 61 d subsequent to this (18 January, 2001). Volume was last measured at 102 d after flowering (DAF, 28 February) and berries were harvested at 118 DAF (16 March).

**Rootstock and irrigation:** Three year-old potted Shiraz vines (clone PT23) grafted to own roots, Ramsey or 101-14 Mgt, were used for this component of the study. The vines were trained to three upright shoots in a bird proof enclosure, and where possible selected for two bunches per shoot. The 26 l PVC pots were fertilised monthly with a complete liquid fertiliser (MEGAMIX PLUS®, Rutec, Tamworth, Australia), providing approximately 4 g nitrogen during the season plus other nutrients. The vines were exposed to two irrigation treatments: daily irrigation (STD) and deficit irrigation (DI), where from fruit set on, watering to field capacity occurred at the point of leaf wilting. In this study, 50 % bloom occurred at 12 November, 2000 and 50 % veraison occurred 57 d subsequent to this (8 January, 2001).

The first drying cycle of the DI treatment commenced on 12 December, and continued on an average of 7 d cycles for the remainder of the season. However, if leaf wilting occurred prior to the 7 d interval the vines were watered. Leaf photosynthesis and stomatal conductance were measured with a portable LCA-4 system (Analytical Development Company, Hoddesdon, England) as a non-destructive indicator of plant water status. Measurements were taken midway through the drying cycle of the last fully expanded leaf at mid-morning. Across the three rootstocks, photosynthesis averaged at  $9.83 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  in the STD treatment and  $4.12 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  in the DI treatment. Stomatal conductance ( $g_s$ ) averaged at 231 in the STD treatment and  $56 \text{ mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$  in the DI treatment. To assess rootstock and irrigation effect on berry growth, one berry from each of two bunches was chosen at random from 4 vines for successive height and width measurements. Measurements were made at least twice weekly in the early morning from 33 to 95 DAF at which point the bunches were harvested (15 February).

**Statistical analysis:** The Genstat® software package (IACR, Rothamsted, UK) was used for statistical data analysis. Results were tested using factorial analysis of variance (ANOVA) and *F* test. Duncan's multiple range test was used for *post-hoc* comparisons of means where appropriate. In the Figs presented an LSD bar was placed only above those data points for a particular day where there was a significant treatment effect. No LSD bar indicates no significant effect of the treatment on that day. Selected parameters also were subjected to product-moment (linear) correlation analysis.

### Results

**Nitrogen and irrigation:** Berry volume increased in two growth phases, reached a maximum and subsequently declined. Irrigation strategy had an effect on pre-veraison and maximum berry size on own-rooted vines (Fig. 1 A). At the onset of berry volume measurements

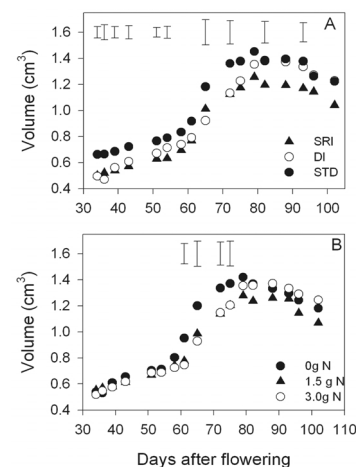


Fig. 1: Changes in berry volume of Shiraz on their own roots during the post fruit set to harvest period. Bars represent least significant differences ( $p < 0.05$ ) between means of irrigation treatment (A) or N fertiliser application rate (B);  $n = 15$ ; absence of bars indicates no significant differences.

(34 DAF), berries from the SRI and the DI treatments were 0.1 cm<sup>3</sup> (17 %) smaller than berries from the STD treatment. Maximum volume occurred 79 to 88 DAF in all three irrigation treatments, and berries from the SRI treatment were again smaller (by 0.17 cm<sup>3</sup> equivalent to 12 %) than the berries from the STD treatment. Maximum volume was positively correlated with volume at 34 DAF (Fig. 2 A). The extent of post-veraison expansion was not, however, affected by irrigation treatment (Tab. 1). Post maximum volume loss was 1.6-fold greater for berries of vines grown in the STD as compared to the SRI or DI treatments (Tab. 1). The counter effects of less expansion between fruit set and 30 DAF and less post maximum volume shrinkage resulted in a non-significant difference in final berry volume, at 102 DAF (Fig. 1 A). Final berry volume was also positively correlated with maximum volume (Fig. 2 B), although on a less than 1:1 relationship, which shows that larger berries lost more volume than smaller berries.

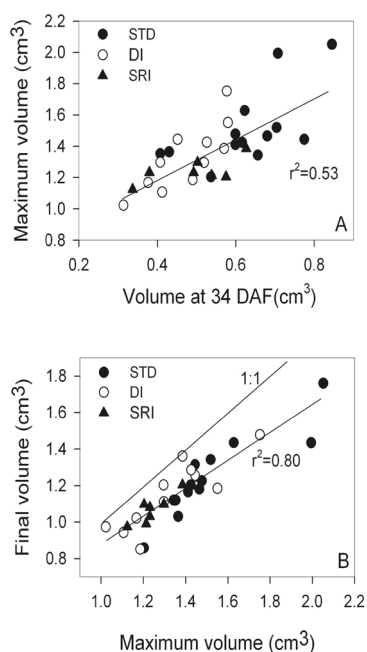


Fig. 2: Linear correlation of maximum volume with volume at 34 DAF ( $p < 0.0001$ ) (A), and final volume with maximum volume ( $p < 0.001$ ) (B) of berries from Shiraz vines on their own roots treated with SRI, DI, or STD irrigation regimes. The 1:1 line was added to show the relationship that would occur if all berries lost volume equally, regardless of their size.

Shoot length at harvest was not affected by irrigation (Tab. 1), however yield (g per vine) was less of vines grown in the SRI treatment as compared to the STD treatment (Tab. 2). This can be explained through berry number because there were 35 % less berries in the SRI treated vines than the STD treated vines. Yield and berry number of DI treated vines were in-between these two extremes. Soluble solids was highest of berries grown in the STD treatment (27.8 °Brix) and lowest in the SRI treatment (25.8 °Brix).

N application rate did not affect pre-veraison volume (Fig. 1 B), amplitude of post-veraison expansion (Tab. 1) or post-maximum berry volume loss (Fig. 1 B and Tab. 1), however, there was an effect on the onset and rate of post-veraison expansion (Fig. 1 B). Berry expansion began earlier

Table 1

Effects of irrigation and N application rate on amplitude of post-veraison expansion, amplitude of post-maximum volume loss and total shoot length at harvest of pot-grown Shiraz grapes. Main effects are shown (ns = not significant); values followed by the same letter do not differ significantly. There were no significant interactions

Treatment	Post-veraison expansion (cm <sup>3</sup> )	Post-maximum volume loss (cm <sup>3</sup> )	Shoot length at harvest (cm)
Irrigation	ns	$P < 0.05$	ns
SRI	0.52	0.18 b	276
DI	0.55	0.18 b	288
STD	0.63	0.28 a	313
N rate	ns	ns	$P < 0.001$
0 g	0.62	0.21	195 b
1.5 g	0.49	0.25	360 a
3.0 g	0.60	0.17	322 a

Table 2

Effect of irrigation on yield and soluble solids of ungrafted Shiraz grapes (ns = not significant); values followed by the same letter do not differ significantly. There was no significant effect of N on these parameters

Treatment	Yield (g/vine)	Number of berries per bunch	Soluble solids °Brix
Irrigation	$P < 0.05$	$P < 0.01$	$P < 0.05$
SRI	41 b	55 c	25.8 b
DI	48 ab	73 b	26.9 ab
STD	58 a	86 a	27.8 a

(at 58 DAF as compared to 65 DAF) and was 1.77-fold faster in the early post-veraison period of the treatment receiving no additional N as compared to the other N treatments. Neither N nor irrigation, however, had a significant effect on the timing of the volume maximum (Fig. 1). Shoot length at harvest (including lateral growth) was affected by N with vines given 0 g of N having 40 to 50 % less shoot growth than vines receiving the other two N treatments (Tab. 1). N did not have an effect on yield, berry number or soluble solids.

**Rootstock and irrigation:** Irrigation also affected berry volume on grafted vines. Vines watered daily had a larger maximum volume as compared to vines under a deficit irrigation regime (1.74 vs 1.56 cm<sup>3</sup>, Fig. 3). This difference in volume was no longer apparent beyond 85 DAF. Those berries which were larger at the onset of measurements (33 DAF) tended to be larger at the volume maximum (Fig. 4 A). There was also a significant irrigation effect on the timing of the volume maximum (Tab. 3). The maximum occurred 11 d later in the DI than the STD treatment. In this study water stress was not applied until after fruit-set and there was no effect of irrigation on yield per vine or number of berries per bunch.

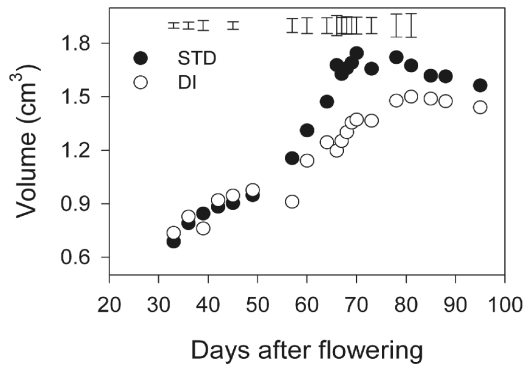


Fig. 3: Changes in berry volume of Shiraz during the post fruit set to harvest period. Bars represent least significant differences ( $p < 0.05$ ) between means of irrigation treatment; data of the three rootstocks were pooled ( $n = 24$ ); absence of bars indicates no significant differences.

There was no significant effect of rootstock on maximum berry volume or final volume, however, there was a significant effect on the timing of the volume maximum (Tab. 3). 101-14 Mgt advanced and Ramsey delayed the volume maximum compared with self-grafted Shiraz.

There was a significant effect of rootstock on the degree of post-veraison expansion (Tab. 3). Berries on Shiraz grafted to Ramsey had the least expansion ( $0.63 \text{ cm}^3$ ), while those on self-grafted Shiraz had the greatest ( $0.76 \text{ cm}^3$ ). There was no effect of rootstock on post-maximum volume loss but, as in ungrafted vines, irrigation treatment did have a significant effect (Tab. 3). Post-maximum volume loss in the STD treatment was double that of the DI treatment ( $0.31$  vs  $0.16 \text{ cm}^3$ ). There was no relationship between post-veraison expansion and the degree of volume loss, or maximum volume and the degree of volume loss. However, as in the ungrafted vines, final volume was closely correlated to maximum volume (Fig. 4 B).

Rootstock impacted on yield per vine and berry number per bunch. Vines grafted onto Ramsey had 25 % more berries compared with either 101-14 Mgt or Shiraz, yet there were no correlations between yield and post-veraison expansion, maximum volume, post-maximum volume loss, or final volume. Shoot length at harvest did not differ between treatments and averaged at 1.94 m. There were no signifi-

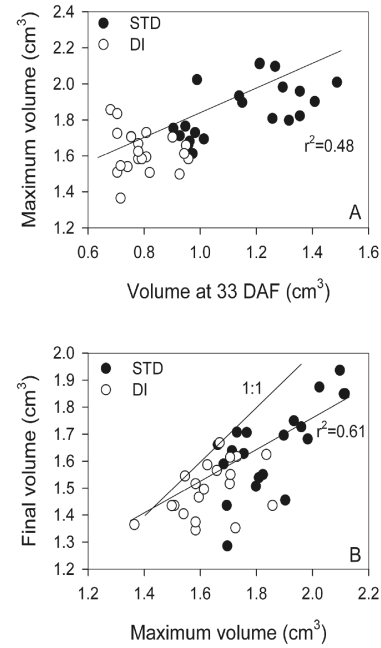


Fig. 4: Linear correlation of maximum volume with volume at 33 DAF ( $p < 0.0001$ ) (A), and final volume with maximum volume ( $p < 0.001$ ) (B) of berries from grafted Shiraz vines grown in STD or DI. The 1:1 line was added to show the relationship that would occur if all berries lost volume equally, regardless of their size.

cant correlations between maximum volume, final volume, or days to volume maximum with shoot growth from flowering to veraison, shoot growth from veraison to harvest or average shoot length at harvest (data not shown). As in the ungrafted vines, °Brix values were higher in the STD treated vines than the DI treated vines ( $23.0$  vs  $19.0$ ). Self-grafted vines had  $22.4$  °Brix at harvest and this was significantly higher than the other two rootstocks.

## Discussion

Deficit and split-root irrigation reduced berry volume throughout development of both own-rooted and grafted Shiraz vines (Figs 1-4). That these differences were apparent very early in development (by 35 DAF) indicates that

Table 3

Effect of irrigation and rootstock on post-veraison expansion, post-maximum volume loss of Shiraz grapes. Main effects are shown (ns = not significant); values followed by the same letter do not differ significantly. There were no significant interactions

Treatment	Days to volume maximum	Post-veraison expansion ( $\text{cm}^3$ )	Post-maximum volume loss ( $\text{cm}^3$ )
Irrigation	$P < 0.01$	ns	$P < 0.05$
DI	85	0.68	0.16
STD	74	0.70	0.31
Rootstock	$P < 0.01$	$P < 0.05$	ns
Ramsey	83 a	0.63 c	0.19
101-14 Mgt	80 b	0.70 b	0.32
Shiraz	76 c	0.76 a	0.19

cell division was inhibited. The increase in volume of grape berries after bloom can be attributed to an increase in cell number (2-fold) and to an increase in cell volume (300-fold) (COOMBE 1976). Cell division in the mesocarp is thought to cease 20-30 DAF (HARRIS *et al.* 1968) and in the skin 35-40 DAF (NAKAGAWA and NANJO 1966). Thus the first volume measurements in this study were taken at approximately the end of the cell division phase. The effect of water stress on cell division after flowering has also been proposed by HARDIE and CONSIDINE (1976). In the present study, there was a significant correlation between volume of berries at 30-35 DAF and the maximum volume (Figs 2 A, 4 A). Therefore the cell division phase of berry growth has a significant impact on the potential maximum size of berries. Berries from the SRI and the DI treatments may have had a smaller maximum volume than berries from the STD treatment because there were fewer pericarp cells to expand initially and there was less expansion of those cells that were present. The effects of irrigation on maximum berry volume seen here are comparable to those of a large irrigation study of field vines where differences in maximum berry weight were attributed to a combination of irrigation treatments and seasonal conditions (McCARTHY 1997, 1999).

Deficit irrigation did not delay the volume maximum of berries on own-rooted Shiraz (Fig. 1), but resulted in an 11-d delay in grafted vines (Fig. 3). The absence of an effect of water deficit on the onset of weight loss in own-rooted vines is consistent with results of the field trial cited above (McCARTHY 1997), where the timing of the volume loss in Shiraz berries was at 90 DAF, regardless of irrigation regime. This potential difference between grafted (even self-grafted) and ungrafted vines deserves further investigation. The final volume of berries from deficit-irrigated vines in this study was not different from the STD treatment and this may be attributed to a greater degree of post-maximum volume loss for berries from the STD treatment (Tabs 1, 2). The pericarp cells of the STD berries may have had more water available for loss. Moreover, berries with a larger surface area could be more prone to evaporative water loss than smaller berries. A study on the rates of cell division and expansion during DI would provide useful insights into the dynamics of berry growth. It is also possible that berries that grow more slowly are able to maintain an increased hydraulic connection to the vine due to reduced xylem disruption. This would allow them to alleviate evaporative water loss in the very latest stages of ripening through continued xylem import.

DI consistently reduced maximum berry volume and the extent of volume loss. This supports the finding by DAVIES *et al.* (2000) that soil drying during flowering and early fruit development enhanced the hydraulic (xylem) connection between tomato fruit and the rest of the plant. In addition, irrigation can also have an indirect effect on berry volume through its effect on berry number. Water stress during flowering and fruit set can result in lower berry numbers through fruit abscission and this may lead to larger berries since competition for photosynthate supply and water is reduced. In this study there were 15-35 % fewer berries on vines grown in the SRI or DI treatments and they were smaller, not larger

than berries of vines grown in STD irrigation. The larger berry size in the STD treatment was thus not due to a smaller berry number per vine.

Shoot growth can also have an impact on berry volume. Extensive shoot growth can divert the water and photosynthate supply away from berry growth and ripening. In this study, there were no negative correlations between maximum berry volume and shoot growth between fruit set and veraison or shoot growth between veraison and harvest. This is likely because overall yield compared with leaf area (*i.e.* the crop load) was very low. The differences in maximum berry size between the irrigation treatments were therefore not due to competition with shoot growth.

Vines grown in the 11 l pots (nitrogen x irrigation study) had berries which were on average smaller than those of the 26 l pots (rootstock x irrigation study). Even though the soil of the vines grown in the 11 l pots was irrigated to field capacity daily, the overall volume of water may not have been sufficient to allow for optimal berry growth. If these vines did indeed experience a water stress, however, it was not severe since there were no signs of leaf wilting in the STD or SRI treatments at any time.

The effect of SRI on minimising berry size is comparable to studies on tomato fruit. A SRI treatment enhanced the extent of hydraulic isolation of the fruit and there was a reduction in the size and the fresh weight of the fruit (DAVIES *et al.* 2000). However, our data are currently insufficient to support or otherwise this conclusion. The authors suggested that reduced fruit size may be the result of growth-retarding, root-borne signals emanating from those roots in contact with the drying soils. The effect on fruit size relative to the vegetative parts of the plant was reduced, however, and this may be because xylem-borne signals may not be able to penetrate the fruit as effectively late in development as the phloem-derived water supply dominates. Recent studies on phloem and xylem continuity into Shiraz berries during and after the volume maximum also indicated that phloem inflow relative to xylem inflow increased (ROGIERS *et al.* 2000). Since the variability in post-veraison expansion only contributed 34 % ( $r = 0.58$ ,  $P < 0.001$ ) to the variability in maximum berry size, root signals prior to veraison could have accounted for most of the difference in berry size.

In this study, N had an effect on rate of post-veraison berry expansion but not on maximum berry volume (Fig. 1, Tab. 1). The accelerated rate of post-veraison expansion with 0 g of N could be the result of less vigorous vegetative growth in this treatment (Tab. 1) leaving more water and photosynthates available for berry growth. A decrease in vegetative growth may also increase relative sink strength of the fruit (DRY *et al.* 1996; DAVIES *et al.* 2000). Low N at bloom usually reduces fruit set, particularly in combination with water stress (KELLER *et al.* 1998). In this study, however, there was no effect of N on number of berries per vine (data not shown), likely because these vines had a very light crop load. Therefore, the N effect on the rate of post-veraison expansion was not a consequence of berry number.

Not only irrigation, but rootstock also had an influence on the timing of the volume maximum, with the earliest maxi-

mum occurring for berries grown on 101-14 Mgt (Tab. 2). The time of 50 % flowering varied over 5 d within this study, with no influence of rootstock or irrigation on its timing. Therefore, time of anthesis did not contribute to the variation in the timing of the volume maximum. A smaller berry number may lead to more photosynthates and water available for the remaining berries, however there was not a consistently lower berry number for 101-14 Mgt compared to the other rootstocks. 101-14 Mgt is considered to be of low vigour compared to Shiraz and Ramsey. In this study, however, not shoot length at veraison nor final shoot length were smaller for vines on this rootstock as compared to Shiraz on own roots or Ramsey. If smaller canopies had been produced by 101-14 Mgt this could have led to less competition for water between berries and shoots and thus advancing the volume maximum. However, the lack of any significant correlations between maximum berry volume, final volume, or days to volume maximum and shoot growth from flowering to veraison, shoot growth from veraison to harvest or average shoot length at harvest indicate that there was little effect of vegetative growth on berry volume.

It should be noted that comparisons of berry volumes were made at a particular berry age, as opposed to a particular soluble solids concentration, because berry volume itself has an effect on the °Brix levels (*i.e.* higher Brix was probably a consequence of volume loss rather than a cause). The present data do indicate that while there was an effect of irrigation on *maximum* berry volume there was no effect on final berry volume. Therefore, larger berries lost more volume than smaller berries.

### Acknowledgements

This research was supported by the Commonwealth Cooperative Research Centre Program and conducted through the CRC for Viticulture with support from Australia's grapegrowers and winemakers through their investment body the Grape and Wine Research and Development Corporation, with matching funds from the Federal Government. We would like to gratefully acknowledge Dr. BRUNO HOLZAPFEL and the PhD students JASON SMITH and JESSICA WADE for allowing access to their experimental vines and for helpful discussions while preparing this manuscript. We are also indebted to DAVID FOSTER and ROBERT LAMONT for technical assistance.

### References

- CIRAMI, R. M.; MCCARTHY, M. G.; GLENN, T.; 1984: Comparison of the effects of rootstock on crop, juice and wine composition in a replanted nematode-infested Barossa Valley vineyard. *Aust. J. Exp. Biol. Med. Sci.* **24**, 283-289.
- COOMBE, B. G.; 1976: The development of fleshy fruits. *Annu. Rev. Plant Physiol.* **27**, 507-528.
- DAVIES, W. J.; BACON, M. A.; THOMPSON, D. S.; SOBEIH, W.; GONZÁLEZ RODRÍGUEZ, L.; 2000: Regulation of leaf and fruit growth in plants growing in drying soil: Exploitation of the plants' chemical signalling system and hydraulic architecture to increase the efficiency of water use in agriculture. *J. Exp. Bot.* **51**, 1617-1626.
- DRY, P. R.; GREGORY G. R.; 1988: Grapevine Varieties in Viticulture, Vol. 1. In: B. G. COOMBE, P. R. DRY (Eds.): Resources in Australia. Aust. Ind. Publ. Pty Ltd; Adelaide, South Australia.
- DRY, P. R.; LOVEYS, B. R.; BOTTING, D. G.; DÜRING H.; 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).
- HARDIE, W. J.; J. A. CONSIDINE; 1976: Response of grapes to water-deficit stress in particular stages of development. *Am. J. Enol. Vitic* **27**, 55-61.
- HARRIS, J. M.; KRIEDEMANN, P. E.; POSSINGHAM, J. V.; 1968: Anatomical aspects of grape berry development. *Vitis* **7**, 106-119.
- HEDBERG, P. R.; MCLEOD, R.; CULLIS, B.; FREEMAN, B. M.; 1986: Effect of rootstock on the production, grape and wine quality of Shiraz vines in the Murrumbidgee Irrigation Area. *Aust. J. Exp. Agric.* **26**, 511-516.
- KELLER M.; ARNINK K. J.; HRAZDINA G.; 1998: Interaction of nitrogen availability during bloom and light intensity during veraison. I. Effects on grapevine growth, fruit development, and ripening. *Am. J. Enol. Vitic.* **49**, 333-340.
- KELLER, M.; KUMMER, M.; VASCONCELOS, M. C.; 2001: Reproductive growth of grapevines in response to nitrogen supply and rootstock. *Aust. J. Grape Wine Res.* **7**, 12-18.
- MCCARTHY, M. G.; 1997: The effect of transient water deficit on berry development of cv. Shiraz (*Vitis vinifera* L.). *Aust. J. Grape Wine Res.* **3**, 102-108.
- MCCARTHY, M.G.; 1999: Weight loss from ripening berries of Shiraz grapevines (*Vitis vinifera* L. cv. Shiraz). *Aust. J. Grape Wine Res.* **5**, 10-16.
- MCCARTHY, M. G.; CIRAMI, R. M.; FURKALIEV, D. G.; 1997: Rootstock response of Shiraz (*Vitis vinifera*) grapevines to dry and drip-irrigated conditions. *Aust. J. Grape Wine Res.* **3**, 95-98.
- NAKAGAWA, S.; AND NANJO, Y.; 1966: Comparative morphology of the grape berry in three cultivars. *J. Japan. Soc. Hort. Sci.* **35**, 117-126.
- ROGIERS, S. Y.; KELLER, M.; HOLZAPFEL, B. P.; VIRGONA, J. M.; 2000: Accumulation of potassium and calcium by ripening berries on field vines of *Vitis vinifera* (L) cv. Shiraz. *Aust. J. Grape Wine Res.* **6**, 240-243.
- ROGIERS S. Y.; SMITH, J. A.; WHITE, R.; KELLER, M.; HOLZAPFEL, B. P.; VIRGONA, J. M.; 2001: Vascular function in berries of *Vitis vinifera* (L) cv. Shiraz. *Aust. J. Grape Wine Res.* **7**, 47-51.
- SOMERS, T. C.; 1976: Pigment development during ripening of the grape. *Vitis* **14**, 169-277.
- WILLIAMS L. E.; DOKOOZLIAN N. K.; WAMPLE R.; 1994: Grape. In: B. SCHAFER, P. C. ANDERSEN (Eds.): Handbook of Environmental Physiology of Fruit Crops. Vol. I. Temperate Crops, 85-133. CRC Press, Boca Raton.
- WILLIAMS L. E.; MATTHEWS M. A.; 1990: Grapevine. In: B. J. STEWART, D. R. NIELSEN (Eds.): Irrigation of Agricultural Crops (Agronomy Monographs no. 30), 1019-1055. ASA-CSSA-SSSA, Madison, Wisconsin, USA.

Received July 15, 2003