The Interactive Effect of Pruning Level and Irrigation Strategy on Water Use Efficiency of *Vitis vinifera* L. cv. Shiraz

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A partial rootzone drying (PRD) irrigation technique (0.5 ML/ha) was compared with a standard irrigation treatment (1 ML/ha) at three different pruning levels of 30, 60 and 120 nodes per grapevine in *Vitis vinifera* L. cv Shiraz. The PRD irrigation technique was applied to a single side of the grapevine rootzone at a time, 45 cm from the trunk, and the sides were switched in 10-day cycles. For the standard irrigation treatment, both sides of the grapevine were irrigated. At the end of an irrigation cycle, the PRD treatment resulted in reduced midday readings of stomatal conductance and stem (ψ_s) and leaf (ψ_t) water potential relative to the control treatment. During the switch between irrigation cycles, when the soil water profile of both the 'wet' and 'dry' sides of the PRD-treated grapevines was refilled, stomatal conductance, ψ_s and ψ_t were restored to the same levels as for the control experiment. As node number per grapevine increased, berry size and winter pruning weight were reduced and yield increased. In the first season of the experiment, the PRD treatment did not have a significant effect on berry size, yield and pruning weight, although shoot length was reduced in response to PRD for all the pruning treatments. In a subsequent season, PRD was found to reduce yield, primarily through a reduction in berry set. Water use efficiency measured as t/ML irrigation water applied was increased significantly as crop load increased, and was enhanced in response to the PRD irrigation technique.

Irrigation is required when grapevines are grown in arid regions, which may lead to increased grapevine vigour in terms of vegetative growth. Both pruning weight and shoot growth rate have been shown to increase under irrigation (Smart & Coombe, 1983; Bravdo & Hepner, 1986). Furthermore, irrigation has been reported to increase average leaf area per shoot (Carbonneau & Casteran, 1979; Van Rooyen et al., 1980). A strategy that has been widely used to reduce shoot vigour in grapevines is the application of water deficit (Smart & Coombe, 1983; Dry & Loveys, 1998). This has been found to have significant effects on internode elongation and the duration of shoot growth, especially when the water deficit occurs early in the season (Williams & Grimes, 1987). However, in most experiments where shoot growth is reduced as a result of a water deficit, a concomitant reduction in yield has been observed (McCarthy & Staniford, 1984; Matthews & Anderson, 1988; Goodwin & Jerie, 1992; Poni et al., 1993). The use of regulated deficit irrigation (RDI) as an irrigation strategy applies a mild constraint to the grapevines through the application of precisely controlled amounts of water at critical stages in the season (Goodwin & Jerie, 1992; McCarthy, 1996, 1997). However, where RDI treatments have brought about a large reduction in vigour, it has often been accompanied by a significant penalty in terms of yield, resulting from reduced berry size (Dry & Loveys, 1998; Kriedemann & Goodwin, 2003).

Partial rootzone drying (PRD) was developed as an irrigation technique that reduces shoot growth in grapevines through partial drying of the root system, but maintains water relations by a supply of water from a hydrated part of the root system (Dry et al., 2000a, 2000b). One-half of the root system is watered at a time, for a specified period, while the soil surrounding the other half gradually becomes dry. The technique maintains the roots in the early stages of drying by transferring irrigation to the opposite half of the root system at intervals. Studies on grapevines and other plant species have shown that, when part of the root system was dried, there is a reduction in stomatal conductance and shoot growth rate without an apparent water deficit, as indicated by decreases in ψ₁ (Blackman & Davies, 1985; Zhang et al., 1987; Saab & Sharp, 1989; Gowing et al., 1990; Dry & Loveys, 1998; Dry et al., 2000a, 2000b; Loveys et al., 2000; Stoll et al., 2000). Abscisic acid (ABA) is a possible candidate for a root-derived signal in the grapevine, as ABA levels in roots and xylem sap closely follow the changes in stomatal conductance observed with PRD (Stoll et al., 2000). Interestingly, early studies with PRD showed no change in berry size or yield as a result of partial drying of the root system in field-grown grapevines over three seasons (Dry, 1997) and in commercial trials (Dry et al., 2000c). This holds significant implications for the application of the technique commercially, in that when correctly applied it may not

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cause a reduction in yield. However, in later experiments using PRD for field-grown grapevines, a significant reduction was found in the yield of PRD-treated grapevines of cvs. Moscatel and Castelao (Dos Santos $\it et~al., 2003$; Du Toit $\it et~al., 2003$). This yield reduction was associated with an observed reduction in pre-dawn ψ_L in PRD-treated grapevines relative to fully-irrigated grapevines, albeit intermediate between lower ψ_L observed in non-irrigated grapevines (Dos Santos $\it et~al., 2003$).

The number of nodes per grapevine left at pruning has significant implications for both crop load and grapevine vegetative growth. Higher node number per grapevine at winter pruning (20 to 160 nodes) increases the number of bunches per grapevine, leading to a higher average yield, while both berry weight and bunch weight are reduced as crop load increases (Miller & Howell, 1998). Grapevine vegetative growth measured as winter pruning weight decreases as node number per grapevine increases, although leaf area per shoot and leaf size shows the reverse effect, with both parameters increasing with higher node number per grapevine (Miller & Howell, 1998). The effect of the interaction of irrigation and pruning level on yield and vegetative growth has not been studied extensively. However, the work of Freeman et al. (1979, 1980) showed that, as node number per grapevine increases (20 to 160 nodes), the effect of water deficit on yield becomes increasingly significant. Clearly, at higher bunch number per grapevine there is potentially an increased sensitivity to water deficit, which could result in decreased yield. This may be due to the decreased ratio of leaf area:crop load, or restricted photosynthetic production per unit crop load under conditions of water constraint.

The PRD irrigation strategy can create more open canopies through a reduction in shoot growth rate and canopy development (Dry, 1997; Stoll, 2000; Du Toit *et al.*, 2003), although there may be a limit to which the balance between vegetative and reproductive growth can be exploited at higher crop loads (Howell, 1999). Therefore, the potential exists that at higher node number per grapevine, PRD may result in insufficient vegetative growth to enable the ripening of a larger crop. The aim of the current study was to explore the effect of PRD on yield components, vegetative growth and grapevine physiology. Within this, the interactive effect of PRD and pruning level at 30, 60 and 120 nodes per grapevine was assessed in order to determine the limitations of PRD in terms of vegetative and reproductive growth.

MATERIALS AND METHODS

Experimental site

The vineyard site was at Nuriootpa, in the Barossa Valley, South Australia (34°48'S, 139°14'E, elevation 274 m). The general

climate of the region is Mediterranean, warm, with a maximum January temperature mean of 29°C and a minimum January temperature mean of 14°C. The long-term climatic averages are shown in Table 1 (Government Bureau of Meteorology, Australia). Annual rainfall in the region is moderate (506 mm), with high summer evaporation and low relative humidity. The soil of the experimental site was classified as a Light Pass fine sandy loam (Northcote *et al.*, 1954). The climatic data for the seasons of the study are shown in Table 2.

Irrigation and pruning strategy

The experiment was on 10-year-old Shiraz grapevines on own roots. The experimental design was a split-plot, with six fully randomised treatments, each consisting of five replicates of two-vine plots. Four buffer vines were assigned between each consecutive treatment. The trellis type was a permanent bilateral cordon without shoot positioning (sprawled canopy). The row and vine spacing was 3.0 m and 2.25 m respectively, and rows were oriented in an east-west direction. The treatments were: three pruning levels determined by node number at winter pruning of 30, 60 and 120 nodes superimposed over either PRD or a 'control' irrigation strategy. The grapevines were spur-pruned and two-node spurs were used for the 30-node treatment, while a combination of two- and four-node spurs was used for the 60- and 120-node treatments. For the PRD and control treatments, two 4L/h drippers were set up 45 cm on either side of the grapevine trunk. For PRD, a specially designed dual dripline (Netafim, Adelaide, Australia) was used that allowed for the sides of the irrigation to be switched without the dripper position being shifted. For PRD, only one side of the grapevine's root system received water at any time, whereas both sides of the root system were watered for standard-irrigated grapevines. The time between PRD cycles was approximately 10 days, and the 'wet' side received an additional irrigation mid-way through a cycle. On average, the length of water application per irrigation was 20 h. The level of irrigation for the control was according to the maximum limit for the Barossa Valley, South Australia, at 1 ML/ha, and was applied in continuous cycles from mid-December (pre-véraison) up to harvest of each growing season and was not adjusted according to rainfall. In the seasons 2000-2001 and 2002-2003, the PRD treatment received half the irrigation water of the control. In 2000-2001, the total water applied was 1.0 ML/Ha and 0.5 ML/Ha for the control and PRD respectively. In 2002-2003, the total water applied was 1.2 ML/ Ha and 0.6 ML/Ha for the control and PRD respectively. In 2001-2002, the same amount of irrigation water was applied to both treatments, namely 1.0 ML/Ha.

TABLE 1
Long-term monthly and annual climatic averages for temperature and rainfall in Nuriootpa, Barossa Valley, South Australia (46-year average).

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Annual average
Mean max temperature (°C)	28.8	28.6	25.7	21.4	17.0	14.2	13.2	14.3	16.8	20.2	23.8	26.3	20.9
Mean min temperature (°C)	13.6	13.9	11.8	9.0	6.7	5.1	4.4	4.8	5.8	8.0	9.9	11.8	8.7
Mean rainfall (mm)	18.8	18.5	22.2	38.2	55.0	56.3	66.2	63.6	60.0	49.4	29.3	24.3	500.5

TABLE 2
Average monthly maximum temperature, minimum temperature and rainfall at Nuriootpa (Barossa Valley, South Australia) for the seasons of the study: 2000 to 2003.

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Annual average
2000													
Mean max temperature (°C)	28.2	31.5	25.8	21.0	15.8	13.5	13.7	14.1	17.9	19.3	26.3	28.0	21.3
Mean min temperature (°C)	14.8	16.9	12.7	10.0	5.8	4.6	4.7	5.0	7.8	7.7	13.7	11.9	9.6
Mean rainfall (mm)	0.8	68.2	19.0	59.4	56.2	59.0	67.2	58.2	113.4	111.8	89.0	66.2	768.4
2001													
Mean max temperature (°C)	33.9	31.5	25.3	21.7	17.6	14.6	13.6	14.6	18.2	17.3	22.0	23.9	21.2
Mean min temperature (°C)	17.4	16.4	11.6	7.6	5.9	6.2	4.2	5.2	8.0	7.9	9.8	10.2	9.2
Mean rainfall (mm)	13.2	15.2	32.8	19.4	53.6	63.8	39.4	77.2	94.9	58.4	32.0	10.6	510.5
2002													
Mean max temperature (°C)	27.6	26.6	25.9	24.1	18.8	14.4	14.6	14.7	17.8	20.9	26.5	28.2	21.7
Mean min temperature (°C)	12.7	12.3	10.4	9.8	7.1	5.6	4.7	3.3	6.0	7.4	10.9	13.5	8.6
Mean rainfall (mm)	32.0	0.2	21.6	3.8	72.2	51.0	50.0	27.6	47.0	20.8	20.6	32.2	379.0
2003													
Mean max temperature (°C)	30.9	28.4	23.9	21.9	17.5	13.9	13.7	13.1	16.4	17.5	26.5	28.8	21.0
Mean min temperature (°C)	14.6	15.1	10.3	8.5	7.8	6.4	4.3	4.3	6.6	6.5	11.8	14.3	9.2
Mean rainfall (mm)	6.2	67.9	3.2	18.4	59.0	72.4	56.2	106.4	67.2	42.8	18.4	34.2	552.3

Gas exchange measurements

The stomatal conductance of the leaves was determined using a portable porometer (Delta-T AP4, Delta-T Devices, Cambridge, UK). On cloudless days, measurements were made during two intervals, 'morning' from 09:30 to 11:00 and 'midday' from 12:00 to 13:30. For all treatment replicates, six sun-exposed leaves of similar maturity, approximately the fifth leaf from the shoot apex, were selected for measurement. For measurement, the terminal part of the main lobe was placed into the cup on the porometer head unit, positioned normal to the sun. The porometer was calibrated prior to each use, and was re-calibrated within the daily period subject to changes in environmental conditions, e.g. relative humidity or temperature.

Leaf and stem water potential

Leaf (ψ_1) and stem (ψ_s) water potentials were measured with a manual pump-up pressure chamber (PMS Instrument Co, Albany, USA). Measurements were taken in the 2002-2003 season only on leaves of similar maturity to those selected for gas exchange measurements. For the measurement of ψ_s , clear plastic bags were placed over two leaves per treatment replicate at 09:00, followed by a second opaque bag. The opaque bags were specially constructed from plastic that was black on the interior and white on the exterior to prevent light penetration to the leaf and to minimise leaf heating. These leaves were left to equilibrate until readings were taken at midday (solar noon). For the measurement of ψ_{I} , an additional two leaves per treatment replicate were selected. Leaves were detached from the shoot by cutting through the base of the petiole. They were transferred to a plastic bag and measured immediately. Water potential pressure readings were recorded when sap was first observed to exude from the cut end of the petiole. All readings were performed within 1.5 h after commencement.

Shoot growth rate

A reference node was tagged seven nodes below the shoot tip of six main shoots per treatment replicate and the distance from that node to the shoot tip was measured at weekly intervals from October to January of 2000-2001 and 2001-2002. Shoot growth rate was calculated on a weekly basis as the average increase in shoot length since the previous measurement (cm/week). When individual shoots ceased growing, they were excluded from the sample set. Data points for the excluded shoots were given a value of zero and included in the average shoot growth rate at later stages of the season, together with the remaining growing shoots. In cases where shoots stopped growing due to damage rather than a physiological cessation of growth, samples were substituted with replacement shoots. The grapevines had sprawling canopies and did not undergo canopy management during the experimental period.

Pruning weight (PW)

Pruning weight was defined as the mass of mature, one-year-old shoots (canes) removed from the grapevine in the dormant period following the growing season. The three pruning treatments were pruned to 30, 60 and 120 nodes. All the shoots removed from a single grapevine were bundled together and weighed in the field with a spring balance. PW was expressed as kg/grapevine.

Yield components

All bunches were removed at a single harvest date when the slowest-ripening treatment reached 23.5 to 24°Brix. The bunches were placed in buckets and weighed using a spring balance in the field to give an average harvest weight in kg/grapevine. Bunch number per grapevine was counted as the fruit were harvested. The value for final fruit weight was adjusted from the values of the berry weight obtained at 23.5 to 24°Brix to enable comparison of

yield figures at similar °Brix. An estimate of fruit weight removed during sampling was also made and used to adjust the final fruit weight value. Mean bunch weight was calculated from this adjusted value (fruit weight/bunch number). Yield components were estimated from six randomly selected bunch samples per replicate removed at harvest to derive berry number per bunch and mean berry weight (g) by ignoring the weight of the bunch rachis. Fruit weight/pruning weight (FW/PW) = fruit weight (kg/grapevine)/pruning weight (kg/grapevine) was calculated from the adjusted yield value per grapevine. Yield was also estimated in terms of t/Ha and water use efficiency (WUE) in terms of t per ML of irrigation applied.

Canopy measurements of solar radiation

The bunch exposure index was determined by measurement of the PAR with a ceptometer (model SF-80, Decagon Devices, Cambridge, UK) inserted horizontally within the bunch zone, parallel to the planting line. Readings were taken at solar noon, perpendicular to the angle of the sun. Ambient solar radiation was measured at half-hourly intervals during the sampling period. PAR measurements within the grapevine canopy were subsequently expressed as a percentage of ambient solar radiation.

Statistical analysis

The data were analysed statistically with the Genstat 6 software package, using a split-plot ANOVA to separate the effects of irrigation and pruning type and observe interactive effects. Where further clarification of the ANOVA results was required, Tukey's HSD post-hoc test was used to separate the individual treatments. For shoot growth analysis, sample sets were separated into pruning level categories, and cumulative differences were compared for the entire data set.

RESULTS

Plant water status and stomatal conductance

For the 2001 and 2003 seasons, where the PRD treatment was irrigated to half the level of the control treatment, both morning and midday measures of stomatal conductance for time points measured at the end of the PRD cycle, where the soil on the 'dry' side of PRD-treated grapevines was at its lowest was significantly reduced by the PRD treatment, irrespective of pruning level (Tables 3 and 4). Mid-cycle in 2000-2001, shortly after the switching period, morning stomatal conductance readings were similar for the PRD and control treatments. However, in 2003, the morning and midday measurements of stomatal conductance taken midcycle, three days after the switching period, were significantly decreased in the PRD-treated grapevines relative to the control treatment. In the 2002-2003 season, corresponding measures of plant water status were determined to further clarify the changes in stomatal conductance observed. Where PRD received half the irrigation water of the control, a significant decrease in ψ_s and ψ_t at the mid-cycle and end-cycle stages of the PRD treatment was recorded (Table 5). At all stages, ψ_s was less negative than ψ_t , as it is representative of whole-vine, root and soil water equilibrium. The effect of the irrigation treatment on ψ_s and ψ_t was independent of node number per grapevine.

In the 2001-2002 season, when both treatments received the same irrigation level, stomatal conductance was measured in a diurnal cycle corresponding to points and the end of a cycle (Fig. 1A) or immediately following the switch (Fig. 1B). Despite there being no difference in the amount of irrigation applied, the PRD treatment consistently reduced stomatal conductance relative to the control treatment, whereas this effect was restored during the switch period.

TABLE 3 Stomatal conductance (mmol/m²/s) in PRD- and standard-irrigated Shiraz vines pruned to different node numbers in the 2000-2001 season, where the PRD treatment was irrigated to 50% of the control. Measurements were taken in the morning between 09:30 and 11:00 (data were analysed by split-plot ANOVA, n = 30, * = P < 0.05; ** = P < 0.001; ns = not significant; T = treatment, P = pruning; T x P = interactive effect).

					Node number	
Sampling date	Stage of cycle	Irrigation treatment	30	60	120	Average
20/01/01	end-cycle	Control	169	151	132	151
		PRD	107	109	80	99
11/03/01	end-cycle	Control	129	128	121	126
		PRD	65	105	64	78
14/03/01	mid-cycle	Control	124	134	148	135
		PRD	150	133	158	147
15/03/01	mid-cycle	Control	98	98	99	98
		PRD	70	82	84	79
		Probability	Т	Р	ТхР	
		20/01/01	**	ns	ns	
		11/03/01	**	ns	ns	
		14/03/01	ns	ns	ns	
		15/03/01	*	ns	ns	

TABLE 4

Stomatal conductance (mmol/m²/s) in PRD- and standard-irrigated Shiraz vines pruned to different node numbers in the 2002-2003 season, where the PRD treatment was irrigated to half the level of the control. Measurements were taken in the 'morning' from 09:30 to 11:00 or at 'midday' from 12:00 to 13:30 (data were analysed by split-plot ANOVA, n = 30, * = P < 0.05; ** = P < 0.01, n = 100 significant; n = 101 not determined; n = 102 reatment, n = 103 interactive effect).

				M	orning			Midday			
			N	ode numl	er	Average	N	ode numb	er	Average	
Sampling date	Stage of cycle	Irrigation treatment	30	60	120		30	60	120		
16/01/03	mid-cycle	Control	257	295	257	269	264	241	263	256	
		PRD	233	261	261	251	198	188	199	196	
22/01/03	end-cycle	Control	241	251	256	249	254	236	242	244	
		PRD	202	177	198	192	167	174	180	173	
31/01/03	end-cycle	Control	nd	nd	nd	nd	189	228	210	209	
		PRD	nd	nd	nd	nd	154	146	133	144	
6/02/03	mid-cycle	Control	231	247	212	230	199	208	205	204	
		PRD	195	191	178	188	137	118	149	135	
		Probability	T	P	ΤxΡ		T	P	T x P		
		16/01/03	ns	ns	ns		**	ns	ns		
		22/01/03	**	ns	ns		**	ns	ns		
		31/01/03	nd	nd	nd		**	ns	ns		
		6/02/03	*	ns	ns		**	ns	ns		

Shoot growth and pruning weight

Shoot growth was compared between the PRD and control treatments in the different pruning levels of the study for the 2000-2001 season, when PRD was irrigated to half the level of the control treatment; and in 2001-2002, when the PRD and control treatments received the same irrigation volume. The incremental rate of increase in shoot length was determined over consecutive weeks, and the response was similar for grapevines pruned to 30 (Fig. 2A) and 60 nodes (results not shown). For these two pruning treatments, shoot growth rate was not affected by the PRD treatment in either of the growing seasons. Rather, PRD caused a significant reduction in cumulative shoot growth over time in the 120-node grapevines, independent of the amount of irrigation water applied (Fig. 2B).

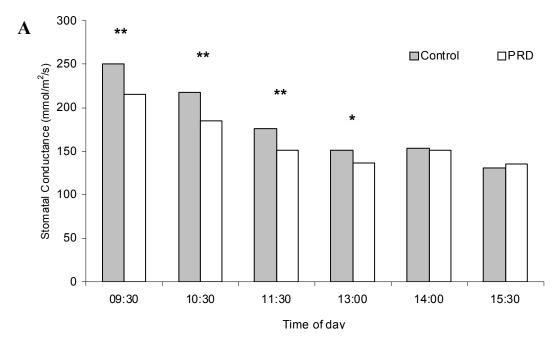
Despite these negligible or small differences observed in shoot growth rate, average shoot length at winter pruning was decreased by PRD in 2000-2001 and 2002-2003 (Tables 6 and 7) for all the pruning level categories. When the effect of pruning level on shoot length alone was observed, increased node number resulted in a decrease in 2002-2003, but not in 2000-2001 (Tables 6 and 7). Shoot weight was not significantly affected by PRD where PRD was run at »50% of the control treatment in 2000-2001 and 2002-2003, but was decreased significantly as node number per grapevine increased. A corresponding decrease in final pruning weight was observed as node number increased, but it was not significantly affected by the PRD treatment. No significant interactive effect (T x P) was observed between PRD and node number for any of these components for either season.

The 2001-2002 season, during which the PRD and control treatments received the same level of irrigation, was characterised by cooler than average minimum and maximum temperatures

during the growing period (September to March). Rainfall during the growing period of 2001-2002 was lower than for the 2000-2001 season (Table 2), but higher than average rainfall fell in January 2002. These unusual climatic conditions may account for the continued shoot growth observed up to the end of January in the 2001-2002 season (Figs. 2C, 2D), while this had ceased by December in 2000-2001 (Figs. 2A, 2B). As a result of the extended period of shoot growth, grapevine vigour in 2001-2002 was increased relative to that seen in the preceding or following seasons. Average pruning weight per vine in 2001-2002 was up to 200% greater than the weights seen in 2000-2001 or 2002-2003 (Table 8). In 2001-2002 there was no significant effect of PRD on average shoot length, although increased node number per grapevine resulted in significantly shorter shoots.

Yield components

The effect of PRD and node number on yield components was compared between the 2000-2001 and 2002-2003 seasons, when the PRD treatment was run at 50% of the control treatment. In both these seasons, shoot number per grapevine, yield and bunch number were significantly increased as node number increased (Tables 6 and 7). However, a more detailed statistical analysis (Tukey's HSD, results not shown) revealed that the split-plot ANOVA result was weighted by a significant difference between the 30-node treatments and 120-node control. The yield of the 120-node PRD treatment therefore did not differ significantly from the other treatments (Bindon et al., 2008). In 2000-2001, yield was not significantly affected by PRD, but in 2002-2003 its application brought about a reduction in yield. Closer examination of the yield components showed that in the latter season, berry number per bunch was significantly reduced in response to PRD in the 30 node per grapevine treatment. This resulted in a PRD-



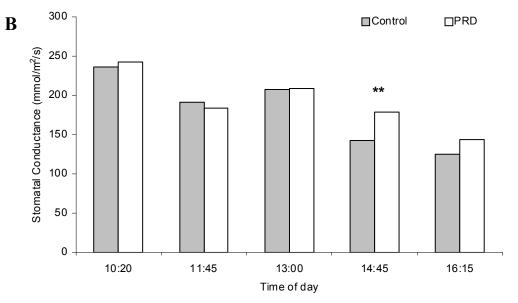


FIGURE 1 Diurnal pattern of stomatal conductance in PRD-irrigated and standard-irrigated Shiraz vines where both treatments received the same irrigation level in the 2001-2002 season. A: End-cycle, B: Switch (ANOVA; n = 30; * = P < 0.05; ** = P < 0.01).

induced reduction in both bunch number and yield at that pruning level category that was greater than that for the other pruning treatments. Furthermore, the reduction in berry number per bunch was greater than the small reduction in berry size due to PRD.

Bunch weight and berry weight decreased significantly as node number per grapevine increased. In 2000-2001, berry number per bunch decreased as node number per grapevine increased, but in 2002-2003 there was no clear effect of node number per grapevine on berry number per bunch. With higher node number per grapevine, the yield/PW ratio increased, such that larger crop loads were supported by reduced vegetative growth, which could explain the reduced carbon partitioned to reproductive growth. WUE in terms of t of fruit produced per ML of irrigation water

applied was improved with PRD in both 2000-2001 and 2002-2003 (Tables 6 and 7), but this improvement was reduced where PRD restricted yield in 2002-2003.

In 2001-2002, when PRD was run at 100% of the control, there was no significant effect on berry weight due to altered pruning level, despite significantly higher bunch numbers per grapevine as node number increased (Table 8). Consequently, yield was significantly increased as node number increased due to increasing bunch number alone, without the restriction in berry weight at higher node numbers observed in other seasons of the study. There was no significant effect of PRD on any yield component observed in 2001-2002 (Table 8). Also, unlike the other seasons of the study, when PRD was run at 50% of the control, the yield

TABLE 5 Midday stem (ψ_s) and leaf (ψ_L) water potential in PRD- and standard-irrigated Shiraz vines pruned to different node numbers in the 2002-2003 season, where the PRD treatment was irrigated to half the level of the control (data were analysed by split-plot ANOVA, n = 30, ** = P < 0.01; T = treatment, P = pruning; T x P = interactive effect).

			Node number							
			ψ _S (-MPa)				ψ_L (-MPa)			
Sampling date	Stage of cycle	Irrigation treatment	30	60	120	Average	30	60	120	Average
22/01/03	end-cycle	Control	0.74	0.75	0.79	0.76	1.04	0.99	0.96	1.00
		PRD	1.08	1.05	1.13	1.09	1.26	1.20	1.32	1.26
31/01/03	end-cycle	Control	0.86	0.90	0.91	0.89	1.02	1.08	1.09	1.06
		PRD	1.29	1.26	1.28	1.28	1.38	1.23	1.47	1.36
6/02/03	mid-cycle	Control	1.08	1.11	1.13	1.11	1.24	1.26	1.27	1.26
		PRD	1.36	1.23	1.34	1.31	1.52	1.41	1.57	1.50
		Probability	T	P	T x P		T	P	T x P	_
		22/01/03	**	ns	ns		**	ns	ns	
		31/01/03	**	ns	ns		**	ns	ns	
		6/02/03	**	ns	ns		**	ns	ns	

TABLE 6 Vine growth and yield components for Shiraz vines pruned to different node numbers in the 2000-2001 season, where the PRD treatment received half the irrigation water of the control treatment (data were analysed by split-plot ANOVA; n = 30; n = 100 significant; n = 100 treatment, n = 100 pruning; n = 100 treatment, n = 100

		30 node	60 node	120 node	P (T)	P (P)	P (TxP)
Berry number/ bunch	Control PRD	92.6 89.6	77.5 82.4	68.7 71.8	ns	< 0.001	ns
Berry Weight (g)	Control PRD	0.83 0.83	0.80 0.77	0.67 0.56	ns	< 0.001	ns
Bunch number	Control PRD	65.9 67.7	124.5 111.8	208.1 188.5	ns	< 0.001	ns
Bunch weight (g)	Control PRD	82.3 79.7	67.5 67.4	50.2 44.6	ns	< 0.001	ns
Yield (kg/vine)	Control PRD	6.26 6.19	8.84 8.17	11.06 8.89	ns	< 0.001	ns
Yield (t/Ha)	Control PRD	7.94 7.86	11.22 10.37	14.04 11.28	ns	< 0.001	ns
WUE (t/ML)	Control PRD	7.94 15.72	11.22 20.74	14.04 22.56	< 0.001	< 0.001	ns
PW (kg)	Control PRD	2.42 2.40	2.41 2.49	2.02 1.6	ns	0.001	ns
Yield/PW ratio	Control PRD	2.59 2.60	3.64 3.29	5.55 5.58	ns	< 0.001	ns
Shoot no. per vine	Control PRD	50.0 52.2	66.4 68.2	82.8 84.2	ns	< 0.001	ns
Weight per shoot (g)	Control PRD	48.4 45.6	36.2 36.4	24.0 19.0	ns	< 0.001	ns
Shoot length	Control PRD	148.5 131.5	143.4 131.0	137.8 112.7	< 0.05	ns	ns
PAR (% ambient)	Control PRD	37 33	41 36	42 59	ns	< 0.05	< 0.05

TABLE 7 Vine growth and yield components for Shiraz vines pruned to different node numbers in the 2002-2003 season, where the PRD treatment received half the irrigation water of the control treatment (data were analysed by split-plot ANOVA; n = 30; n = 100 significant; n = 100 treatment, n = 100 pruning; n = 100 treatment, n = 100

Yield component		30 node	60 node	120 node	P (T)	P (P)	P (TxP)
Berry number/bunch	Control PRD	149.9 113.4	128.6 118.6	103.8 113.2	< 0.05	< 0.05	< 0.05
Berry Weight (g)	Control PRD	0.89 0.78	0.77 0.82	0.71 0.60	ns	< 0.01	ns
Bunch number	Control PRD	71.0 73.6	117.5 113.2	192.0 160.1	ns	< 0.001	ns
Bunch weight (g)	Control PRD	142.9 92.9	105.2 103.7	76.6 72.4	< 0.01	< 0.001	< 0.01
Yield (kg/vine)	Control PRD	10.14 6.8	12.39 11.75	14.48 11.57	< 0.05	0.001	ns
Yield (t/ha)	Control PRD	12.87 8.63	15.72 14.91	18.38 14.68	< 0.05	0.001	ns
WUE (t/ML)	Control PRD	12.87 17.26	15.72 29.82	18.38 29.36	< 0.001	< 0.001	ns
PW (kg)	Control PRD	2.80 2.36	2.10 2.06	1.77 1.31	ns	0.001	ns
Yield/PW ratio	Control PRD	3.83 2.95	5.93 5.88	8.73 8.97	ns	< 0.001	ns
Shoot no. per vine	Control PRD	45.3 45.2	62.3 65.1	93.6 89.3	ns	< 0.001	ns
Weight per shoot (g)	Control PRD	61.6 52.7	33.6 31.6	19.0 14.7	ns	< 0.001	ns
Shoot length	Control PRD	164.4 129.3	142.1 111.5	105.3 91.5	< 0.001	< 0.001	ns
PAR (% ambient)	Control PRD	11 13	12 17	9 47	< 0.001	< 0.01	< 0.001

of 120-node PRD was equivalent to the 120-node control. There was no improvement in WUE due to the PRD irrigation in that season, as both the control and PRD treatments received the same amount of irrigation.

Bunch exposure

An irrigation (PRD and control) by pruning (node number) (T x P) effect on the véraison measure of bunch exposure was found at 0° in both 2000-2001 and 2002-2003 (Tables 6 and 7). The strong PRD effect on bunch exposure detected at véraison in 2002-2003 was primarily due to this interactive (T x P) effect, caused by a very high level of light penetration in the canopies of the 120-node

PRD treatment in both seasons, relative to all the other treatment categories. At harvest, the (T x P) effect was no longer statistically significant due to leaf senescence (results not shown).

DISCUSSION

Stomatal conductance and plant water status

Stomatal conductance was shown to be affected by the PRD treatment for both the seasons when PRD was run at 50% of the control, and the single season when PRD was at 100% of the control. Based on this response it is evident that the partial drying of the root system was sufficient to confer a decrease

TABLE 8 Vine growth and yield components for Shiraz vines pruned to different node numbers in the 2001-2002 season, where the PRD treatment received the same amount of irrigation water as the control treatment (data were analysed by split-plot ANOVA; n = 30; ns = not significant; T = treatment, P = pruning; $T \times P = interactive$ effect).

Yield component		30 node	60 node	120 node	P (T)	P (P)	P (TxP)
Berry number per bunch	Control PRD	125.9 109.8	123.0 99.7	105.2 123.1	ns	ns	ns
Berry Weight (g)	Control PRD	1.09 1.21	1.04 1.12	1.07 1.00	ns	ns	ns
Bunch number	Control PRD	58.1 56.8	80.6 81.8	133.2 124.0	ns	< 0.001	ns
Bunch weight (g)	Control PRD	136.6 131.4	128.1 111.8	105.6 121.1	ns	ns	ns
Yield (kg/vine)	Control PRD	8.07 7.53	10.27 9.34	13.80 15.37	ns	< 0.01	ns
PW (kg)	Control PRD	3.68 3.64	3.98 3.66	4.10 4.06	ns	ns	ns
Yield/PW ratio	Control PRD	2.59 2.10	2.66 2.58	3.57 3.85	ns	< 0.05	ns
Shoot length (cm)	Control PRD	162.1 154.0	152.3 153.5	129.6 112.1	ns	< 0.001	ns

in stomatal conductance, irrespective of the amount of water applied. However, we propose that, under the conditions of the 2002-2003 season, the PRD-treated grapevines experienced water deficit relative to the control treatment. In 2002-2003, PRDtreated vines reached a ψ_{I} lower than -1.2 MPa, and this value was reduced to -1.5 MPa as the season progressed. According to Hsiao (1973), the reduction of ψ_L to between -1.2 and -1.5 MPa can be broadly defined as 'mild' water stress, whereas a reduction to below -1.5 MPa is 'severe' water stress. In terms of this broad definition, PRD-treated vines would have experienced 'mild' water stress relative to the control treatment. In other words, the PRD response was not a non-hydraulically-mediated reduction in stomatal conductance, as reported by Stoll et al. (2000), as this would require a reduction in stomatal conductance in response to soil drying, with no change in ψ_S or ψ_L . The latter response to a PRD treatment was also found in another study on PRD in Cabernet Sauvignon (Bindon et al., 2007). Since early studies with PRD proposed a non-hydraulically-mediated signal, e.g. ABA from roots in soil in the early stages of drying, it would be expected that stomatal conductance could be reduced without conferring a reduction in either ψ_1 or ψ_2 (Blackman & Davies, 1985; Zhang et al., 1987; Saab & Sharp, 1989; Gowing et al., 1990; Dry & Loveys, 1998; Dry et al., 2000a, 2000b; Loveys et al., 2000; Stoll et al., 2000). However, in the study by Dos

Santos *et al.* (2003), despite the yield reduction observed from PRD, it was reported to be more effective in the control of shoot vigour than a conventional deficit irrigation treatment at the same level of water applied. We propose that the maintenance of soil-derived signals, such as ABA from parts of the root system in soil undergoing cyclic drying (PRD), could effectively confer the control of shoot vigour.

Grapevine vigour, yield and berry size

A general observation is that shoot vigour is inversely proportional to shoot number per grapevine, which is determined by node number per grapevine at pruning (Clingeleffer & Sommer, 1995). Shiraz, however, is described as a 'high vigour' variety, which can show extremely high levels of shoot growth when pruning is severe and environmental factors are not limiting (Dry & Loveys, 1998). This was demonstrated in the 2001-2002 season, where water was not limiting due to a cool, wet spring in 2001-2002, and pruning weights were far higher than those of the other seasons in the study. This allowed for a far higher crop load to develop to maturity without a restriction in berry weight or final sugar level obtained.

However, it is evident that for Shiraz grown in the Barossa Valley under average seasonal conditions of higher temperature and water limitation, lower node number per grapevine (30 and

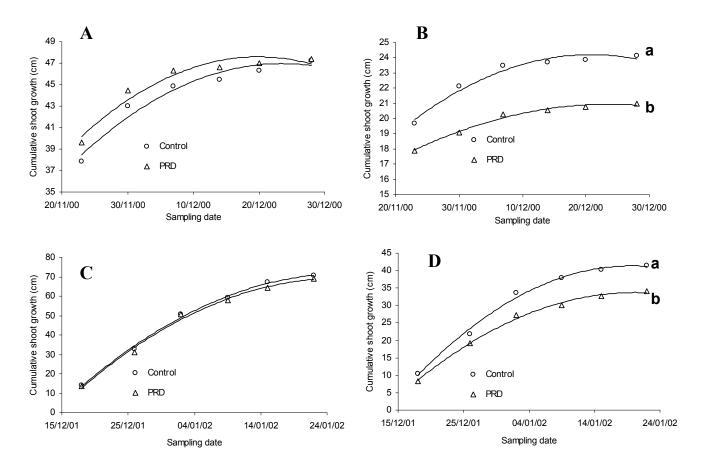


FIGURE 2

Effect of PRD on cumulative shoot growth in Shiraz grown at Nuriootpa where PRD received 50% of the irrigation of the control treatment in 2001-2002. **A:** 30 node, **B:** 120 node or 100% of the irrigation of the control treatment in 2002-2003, **C:** 30 node, **D:** 120 node (ANOVA; n = 30; **a,b** = indicates significant difference where P < 0.05 for **B** and P < 0.01 for **D**).

60 nodes) at pruning will lead to a higher shoot vigour and the application of the PRD irrigation strategy may not necessarily curb canopy growth as measured by winter pruning weight and light penetration in the canopy. With harsher pruning, resulting in a high shoot growth rate in the spring, canopy size may largely be established by the time soil water is depleted in the early summer and irrigation is required. Therefore, in this region, the application of deficit irrigation strategies like PRD later in the growing season may be insufficient to control grapevine vigour. However, in grapevines pruned to a higher node number, i.e. 120 nodes or minimal pruning, a larger crop load may lead to a reduction in shoot growth rate, which could potentially restrict grapevine vigour. This would most likely be caused by a restriction in carbon partitioning to vegetative growth in favour of reproductive growth. Although the reduction in shoot growth rate that occurred in response to the PRD treatment in this study was not sufficient to confer a reduction in final pruning weight, it may be possible to further optimise PRD to reduce vigour and enhance canopy openness (PAR) using the PRD technique, as was the case in the current study. In general, the production of Shiraz in South Australia is on average 7.9 kg/vine or 10.9 kg/ha (Gray et al., 1997). However, this ranges between maximum and minimum values of 0.6 and 35.7 t/ha respectively. The results of the current study therefore fall within the expected range for this cultivar in the region.

Water deficit in the earlier stages of fruit development can lead to a reduction in berry size (Ojéda et al., 2001). Previously, PRD has been shown to cause no change in berry size or yield as a result of partial drying of the root system in field-grown grapevines of a number of grape varieties (Dry, 1997; Stoll, 2000; De la Hera Orts et al., 2002; Antolín et al., 2006) and in many commercial trials (Dry et al., 2000c). However, in some cases there have been reports of PRD causing a small reduction in berry weight and yield, within the range reported in the current study (Dry et al., 2000c; Dos Santos et al., 2003; Du Toit et al., 2003). The data from the current study show that PRD did not affect yield primarily through a reduction in berry weight, as is usually the case under both pre- and post-véraison water deficit (Matthews et al., 1987; Matthews & Anderson, 1989; McCarthy, 1997; Ojéda et al., 2001; Petrie et al., 2004). Rather, the reduction in berry number per bunch in 2002-2003 was greater than the small, non-significant reduction in berry size due to PRD, which would be expected to be the yield component most sensitive to a water deficit within a single season. This response to PRD was most likely the carry-over effect of a deficit experienced by the grapevines in a previous season, although the response to water deficit in subsequent seasons is usually reduced shoot fruitfulness, leading to lower bunch numbers (Buttrose, 1974, Matthews & Anderson, 1989; Petrie et al., 2004). However, in some instances, water deficit has been shown to cause a yield reduction due to

a reduction in berry set, with a resultant cluster-thinning effect (Alexander, 1965; Hardie & Considine, 1976).

Thus, despite a significant reduction in stomatal conductance in response to the PRD treatment in all seasons of the study, indicating stress signalling by the plant, berry weight was not reduced significantly by the water deficit. The implication of this was that WUE was enhanced by PRD, although this difference was smaller in the final season due to reduced berry number per bunch with PRD. The strong reduction in berry weight by increased node number (120 nodes) was expected in terms of the adjustment of carbon partitioning between reproductive and vegetative sinks to maintain 'vine balance'. The concept of 'vine balance' was first proposed by Partridge (1926), and describes the relationship between photosynthetic carbon availability and its distribution among storage organs and sinks in the grapevine. It may be possible for a grapevine of a certain size to bring a large crop to maturity and still produce sufficient storage carbohydrate for shoot growth the following season. However, the potential risk with increasing the crop on a grapevine is that the restriction of carbon resources may prevent the crop ripening to full capacity, as well as reduce its capacity for growth from year to year. In addition to decreasing berry size due to a restriction in carbon supply, increasing bud load per grapevine has been reported to decrease the rate of ripening and final sugar levels attained at harvest (Edson et al., 1993; Miller et al., 1993; Miller & Howell, 1998). In this study, the decrease in berry weight as node number increased in the 2000-2001 and 2002-2003 seasons indicated a restriction in carbon availability in the 120-node grapevines. Although TSS levels reached 24°Brix in the 2000-2001 season, TSS did not accumulate beyond this point but began to decline (Bindon et al., 2008). This indicates that, although a higher crop load could reach maturity (up to 18 t/Ha) in the 120-node control treatment, the restriction in sugar accumulation in this treatment indicates that the threshold in yield:PW was reached. This effect appeared to be exacerbated in the 120-node PRD treatment, where the application of PRD did not limit ripeness relative to the control (Bindon et al., 2008), but yield was comparable with the 60-node treatments.

In an experiment on potted Tempranillo grapevines, Antolín et al. (2006) compared the PRD treatment with grapevines irrigated with either the same amount of irrigation water, or a double amount. Where PRD was compared with a control at the same level of irrigation, increases in berry weight would be expected to equivalent levels of vines irrigated to twice the PRD treatment. This response indicates that the PRD treatment itself has the potential to alter the source-sink relationship, thereby allocating additional carbon to reproductive growth. The mechanism for this has not yet been investigated in grapevines. However, for a field investigation on Shiraz using PRD at 100% the water applied to the control treatment, no change in berry weight was found (Du Toit et al., 2003). Nevertheless, a limitation of the current study was the lack of an additional 'control' where PRD was compared to standard irrigation at the same level of water in one season. However, in 2001-2002, albeit non-significant in the current study, a slight increase in berry weight was observed in response to PRD for the 30- and 60-node grapevines. The higher shoot vigour observed in that season, resulting in no difference in berry weight even between pruning levels, indicates that there was no photosynthetic limitation. Additional work is therefore needed to assess the response of field-grown grapevines to PRD and a control treatment with equivalent irrigation.

CONCLUSIONS

The responses to the PRD irrigation strategy shown in the current study bring to light some important questions surrounding the application of PRD as a deficit irrigation strategy. Firstly, despite rigorous irrigation scheduling, the PRD treatment resulted in the grapevines experiencing water deficit relative to the control treatment, as defined by reduced midday ψ_r and ψ_s . Additionally, it can be concluded that the PRD irrigation strategy would need to be applied earlier in the growing season than in the current study in order to reduce shoot vigour more effectively. The irrigation method may therefore not be suitable for soils with a high waterholding capacity or regions of higher winter rainfall. Increasing the node number in this study conferred the most effective reduction in shoot vigour and pruning weight. The study has also shown that larger crop loads, of up to 15 t/Ha, can be carried by Shiraz grapevines under PRD in the Barossa region, without a significant ripeness penalty. However, it should be noted that this appears to be a threshold for the region, such that higher cropping levels (120 node) will potentially demonstrate both a yield penalty and ripeness penalty when water deficit is applied. Nevertheless, the current study has shown that there is a large potential gain in the WUE of grapevines through the application of PRD, even at higher node numbers. This net gain in WUE remains the most beneficial aspect of the PRD irrigation method. However, this WUE gain with PRD may be reduced in progressive seasons due to a carry-over effect of reduced berry set.

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