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The plasticity of berry shrivelling in 'Shiraz': A vineyard survey

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Summary

Berry water loss during late ripening is a cultivar dependent-trait and is accentuated in wine grape varieties such as 'Shiraz'. 'Shiraz' berry development was monitored in twelve vineyards over two seasons to characterise the extent of weight loss that can occur within a grape growing region. From veraison onwards, berry fresh mass was greatest in vineyards using excessive irrigation and least in vineyards using cautious irrigation strategies. In the first season, berry fresh mass increased, reached a maximum and subsequently declined. Conversely, in the second season, characterised by rain and high humidity, berry fresh mass increased, then stabilised without a consistent decline. In both seasons, berry sugar import rates were highest shortly after veraison but then declined gradually, terminating several weeks after the weight maximum. Notwithstanding that berries with large maximum weights tended to undergo greater rates of weight loss, these berries remained heavier at harvest compared to those berries that were smaller prior to the onset of weight loss. Canopy size, yield and crop load were not key determinants of berry weight loss rates. Berry anthocyanin and sugar accumulation were closely correlated during early ripening but anthocyanin degradation took place during the late weight loss phase.

K e y w o r d s : anthocyanins, grapevine, berry ripening, sugar accumulation, *Vitis vinifera.*

Introduction

'Shiraz' grapes tend to undergo a sustained decline in water content during late ripening (Smart *et al*. 1974, McCarthy 1999 McCarthy and Coombe 1999, Sadras and McCarthy 2007). This loss in fresh mass does not occur every season and its severity appears to vary with region and between vineyards within a region. Berry shrivel in 'Shiraz' begins at 90 to 100 d after flowering and changes in the water economy of the berry have been implicated in the process. Reduced phloem flux into the berry (Rogiers *et al*. 2006b) combined with ongoing berry transpiration (Rogiers *et al*. 2004b, Greer and Rogiers 2009) and potentially water flow from the berry back to the vine (Tyerman *et al*. 2004, Bondada *et al*. 2005, Keller *et al*. 2006, Tilbrook and Tyerman 2009) may all contribute to berry shrivel. Xylem flow into the berry is much reduced from veraison onwards, however, pedicel girdling (Rogiers *et al.* 2001) and xylem mobile element accumulation (Rogiers *et al*. 2000) studies revealed that water flow into the berry through this vascular system during the weight loss phase can continue under some conditions.

The severity of grape berry weight loss following the weight maximum is dependent on cultivar (Tilbrook and Tyerman 2008) as well as abiotic and biotic stresses such as temperature (Bonada *et al*. 2013) and evaporative demand (McCarthy and Coombe 1999, Greer and Rogiers 2009). The diurnal pattern of shrinkage that occurs in many fruits is the result of atmospherically driven transpiration (Lang 1990, Morandi *et al*. 2007, Dichio *et al*. 2003). Current warming trends have shifted grapevine phenology so that berry ripening occurs earlier, coinciding with higher seasonal temperatures and evaporative demand (Webb *et al*. 2007, Petrie and Sadras 2008), and this may worsen berry shrivelling. Sun and wind are likely to exacerbate berry dehydration and elevated temperature can hasten the progression of cell senescence (Bonada *et al*. 2013). Large canopies may therefore reduce the severity of shrivel in warm grape-growing regions through shade and reduced air movement, thereby decreasing bunch temperature.

Shrivelling in 'Shiraz' results in the concentration of existing sugars (McCarthy and Coombe 1999, Rogiers *et al*. 2006) and this may lead to higher alcohol levels in the wine. Early onset of programmed cell death within the mesocarp has been associated with 'Shiraz' shrivel (Tilbrook and Tyerman 2008, Krasnow *et al*. 2008, Fuentes *et al*. 2010) and membrane breakdown may lead to altered flavour profiles of the wine as new secondary metabolites are formed (Baysal and Demirdöven 2007). Grape berry colour is another important quality parameter for red wines. Anthocyanins are responsible for berry colour with the amount and composition dependent on variety, seasonal conditions and management practises. Water availability, light and temperature influence anthocyanin accumulation in several grape varieties (Crippen and Morrison 1986, Dokoozlian and Kliewer 1996, Bergqvist *et al*. 2001); however it is uncertain how the dynamics of anthocyanin concentrations change during this shrivelling phase. The breakdown of membranes during cell senescence may result in the synthesis and degradation of cell compounds important to berry colour and flavour (Coetzee and du Toit 2012).

This study addresses the variability in berry weight loss of 'Shiraz' vines grown in a warm viticultural region. A survey was conducted, over two seasons, across 12 vineyards located in a warm inland region of Australia to characterise the diversity in weight loss rates and to elucidate factors that impact on 'Shiraz' berry size and weight loss during the

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later phase of ripening. Weather, irrigation, yield, vegetative growth, and crop load were investigated. Berry sugar and anthocyanin concentrations as a function of weight loss through late ripening were also characterised.

Materials and Methods

Study sites: Own-rooted 'Shiraz' was sampled across 12 commercial vineyards in the Murrumbidgee Irrigation Area (MIA), NSW over two growing seasons. Specifically, these properties were situated within a 50 km radius in Griffith, Yenda and Leeton and were managed over a range of irrigation regimes. The vineyards were located on relatively light soils (sandy loam, sandy clay loam, sandy clay) and the vines were between 4 and 11 years with the exception of one site (vineyard 9, Tab. 1) which consisted of 38-year old vines. Vines were spaced 1.5 m in rows 3.6 m apart and they were spur-pruned, trained on one or two wires in a single or double cordon. In each vineyard, 10 five-vine replicates were distributed in a Latin square in an area of 10 rows by 50 vines. The area in the vineyard was chosen at a specified distance from the irrigation water outlet (usually 25 vines into the row). Each replicate in every vineyard was sampled weekly by removing 50 berries from each side of a five-vine replicate (100 berries total). The berries were transported on ice to the laboratory, recounted and weighed. Samples were collected from the first week of January (pre-veraison) until commercial harvest. At this time, yield per vine was determined by hand-harvesting and determining bunch number and fresh mass of all fruit within a plot. As a surrogate for canopy size, all dormant shoots from every 5-vine plot were pruned and weighed the winter after sampling. Crop load was determined by dividing pruning weights into yield.

Berry composition: After juicing, TSS was measured on a 50 berry sub-sample using a temperature sensitive handheld refractometer (PR-101 ATAGO, Tokyo, Japan). The other 50 berry subsample was frozen at -20 °C, then thawed at 4 °C prior to anthocyanin extraction. Anthocyanin concentration was determined spectrophotometrically (UV-2101PC Shimadzu, Kyoto, Japan) using the method of Williams *et al*. (1995) following an ethanol extraction of ground (UltraTurrax T25, Janke & Kunkel, IKA Labortechnik, Staufen, Germany) whole berries.

Statistics: GenStat (release 15.0; VSN, Hertfordshire, UK) was used for linear regression analysis between berry and vine parameters. Only data for Season 1 are presented, since there was no general decline in berry fresh mass over the late ripening period of Season 2. Results of the statistical analyses are presented in the tables and figures. Values presented in the text are means ± standard error (SE).

Results

Weather: January of Season 1 consisted of seven days where the daily maximum was in excess of 40 °C and there were no daily maximums that dropped below 30 °C (Fig. 1A). The mean daily January temperature of Season 1

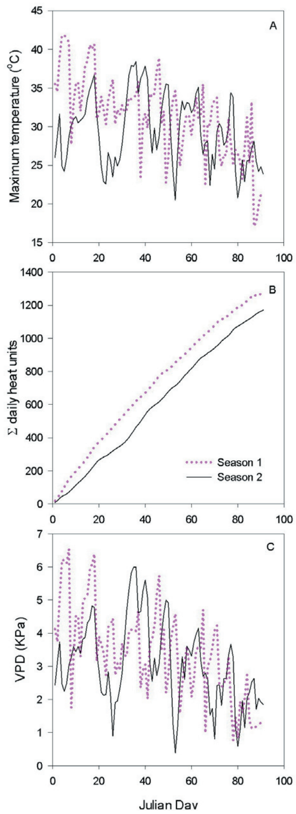

Fig. 1: (**A**) Daily maximum temperature (°C), (**B**) sum of daily heat units and (**C**) VPD during two ripening seasons in a warm grape growing region of NSW, Australia.

Table 1

Berry weight loss and sugar parameters of 12 'Shiraz' vineyards during the late ripening phase of Season 1 (means ± s.e.). Numbers in parentheses refer to the amount of water applied over the season

Site	Irrigation system (ML/ha)	Weight maximum (g)	Rate of weight loss (mg·day^{-1})	TSS at the weight maximum (°Brix)	Berry sugar at the weight maximum (mg sugar·berry^{-1})
1	Furrow (1.0)	1.00 ± 0.05	4.047 ± 1.8	15.4 ± 0.65	155 ± 11.5
2	Drip (1.0)	1.15 ± 0.03	6.666 ± 0.9	17.9 ± 0.29	205 ± 7.3
3	Furrow	1.17 ± 0.03	5.476 ± 0.9	14.4 ± 0.47	168 ± 8.9
4	Furrow	1.22 ± 0.03	7.357 ± 1.0	15.2 ± 0.28	185 ± 5.1
5	Furrow (5.0)	1.31 ± 0.04	0.785 ± 1.0	14.9 ± 0.30	196 ± 8.5
6	Flood (6.0)	1.35 ± 0.05	4.048 ± 0.61	19.1 ± 0.49	256 ± 10.4
7	Furrow (6.0)	1.37 ± 0.03	6.31 ± 1.2	18.1 ± 0.32	249 ± 8.1
8	Flood	1.42 ± 0.03	4.679 ± 1.8	15 ± 0.52	212 ± 7.3
9	Furrow (6.0)	1.45 ± 0.01	11.4 ± 1.6	19.5 ± 0.44	283 ± 7.5
10	Flood (8.5)	1.45 ± 0.06	5.285 ± 0.9	16.9 ± 0.50	242 ± 10.7
11	Drip (2.5)	1.47 ± 0.02	5.71 ± 1.2	14.5 ± 0.61	212 ± 9.2
12	Furrow	1.54 ± 0.03	8.09 ± 0.9	16 ± 0.34	243 ± 8.2

was higher by 5.6 °C than that of the following season and this resulted in 100 more cumulative heat units by the end of the ripening period (Fig. 1B). Along with the temperature differences, VPD as averaged over the ripening period was greater in Season 1 at 3.41 ± 0.15 kPa but only 3.05 ± 0.13 kPa in Season 2 (Fig. 1C).

Berry fresh mass: Berry fresh mass, as meaned across the 12 vineyards, increased and peaked later in the first season as compared with the second season (Fig. 2A).

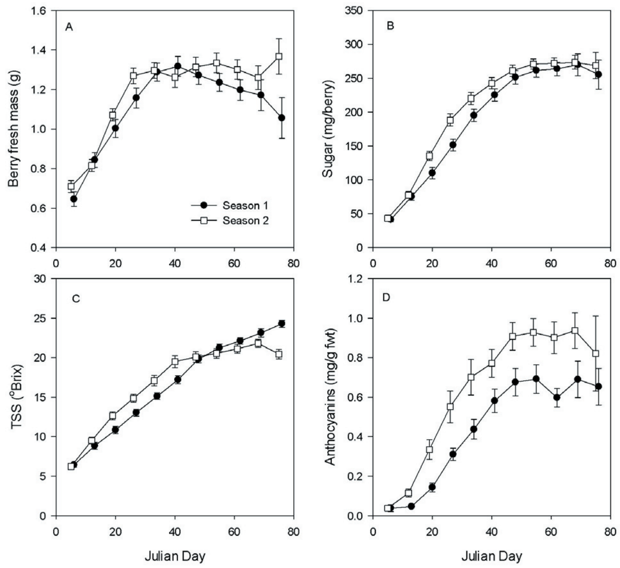

Fig. 2: (**A**) Berry fresh mass, (**B**) sugar per berry, (**C**) TSS, and (**D**) concentration of anthocyanins as a function of Julian day over two seasons. Each data point represents the average of 12 vineyards.

The peak occurred at 1.3 g in both seasons but this transpired at 41 Julian days (days after January 1) in Season 1 and 26 Julian days in Season 2. Berry fresh mass declined continuously during the latter part of Season 1, while in Season 2 it remained fairly constant. This may be related to the four significant rain events (85 mm total) that occurred after the weight plateau had been attained (Fig. 3C), while in Season 1 rainfall accumulated to less than 8 mm during this period (Fig. 3A). In the first season, one particular vineyard was not harvested until 84 Julian days and 31 mm of rain over four days corresponded with a 100 mg increase in berry fresh mass (Fig. 3B).

Maximum berry weight responded to irrigation regime (Fig. 4A). This developmental phase ranged from 1.00 (vineyard 10, cautious flood irrigation) to 1.54 g (vineyard 5, furrow irrigation) in Season 1 and 1.06 g (vineyard 13, cautious drip irrigation) to 1.65 g (vineyard 11, excessive drip irrigation) in Season 2. These differences in berry size were already evident at the first sampling date when berries were pea size. Final berry weight ranged from 1.01 to 1.37 g in Season 1 and 0.99 to 1.50 g in Season 2 and was dependent on when the crop was harvested.

Berry weight loss rates: The *rate* of shrinkage during the later phase of ripening for Season 1 varied widely across the vineyards and ranged from 0.8 to 11.4 mg·day^{-1} with an average at 6 mg·day^{-1} (Tab. 1). Vineyard 5 stood out from the others in that it bore berries with almost negligible weight loss. Rate of weight loss

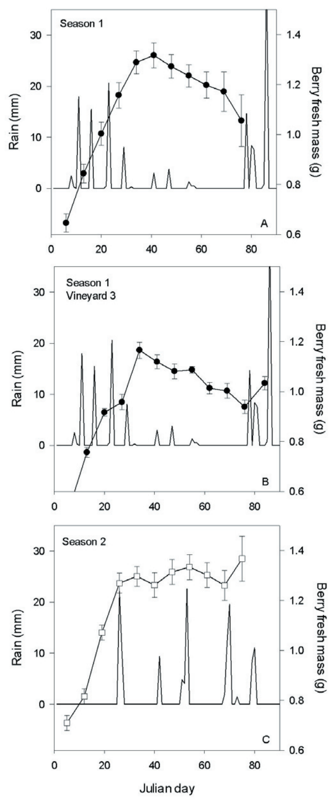

Fig. 3: Berry fresh mass in response to rain events in (**A**) Season 1 as averaged across all vineyards, (**B**) Season 1 of Vineyard 3 which was harvested following a late-season rain event, and (**C**) Season 2 as averaged across all vineyards.

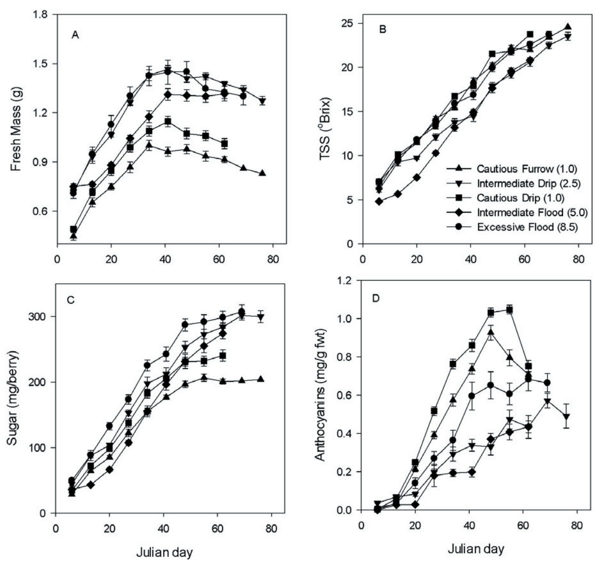

Fig. 4: Berry fresh mass, TSS, sugar per berry and anthocyanin concentrations in response to irrigation regime. Number in parenthesis refers to the ML applied per ha. Each data point represents the average of ten 5-vine replicates.

was not closely associated with the amplitude of the weight maximum (Tab. 3), however, berries which were relatively small at the weight maximum subsequently entered a period with a slow rate of weight loss. Conversely, large berries with a maximum weight at around 1.4 g could undergo either high or low weight loss rates. Final berry weight was tightly correlated with maximum berry weight ($r^2 = 0.90$, $p < 0.001$) (Fig. 5).

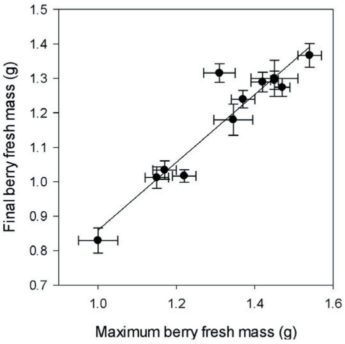

Fig. 5: Final berry fresh mass correlated against maximum berry fresh mass of twelve vineyards in Season 1. Each data point represents the average of ten 5-vine replicates.

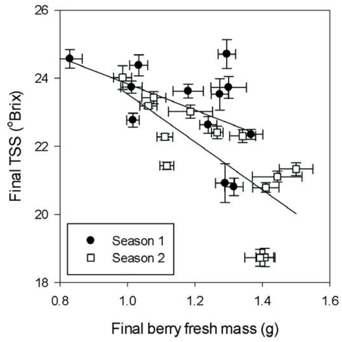

Fig. 6: Harvest time final TSS as a function of final berry fresh mass in Season 1 and Season 2. Each data point represents the average of ten 5-vine replicates within one vineyard.

Berry sugar accumulation: Berry sugar content reached a plateau at 46 to 47 Julian days (Fig. 2B). Total soluble solids concentration however continued to rise linearly in Season 1 (Fig. 2C) due to berry shrinkage during this period. In Season 2, however, TSS reached a plateau mimicking the berry sugar trend since berry fresh mass did not decline. In Season 1, sugar varied between 155 to 283 mg/berry while TSS ranged from 14.4 to 19.5 °Brix at the weight maximum (Tab. 1). Final TSS was not significantly ($P > 0.05$) correlated to final berry fresh mass in this season, but in the second season it was ($R^2 = 0.54$, $P < 0.01$) (Fig. 6).

Berry sugar accumulation rates were at their highest in the early ripening period and reached a greater maximum in the second season as compared with the first (Fig. 7A). A decline in sugar accumulation rates was initiated at 30 to 40 Julian days and reached zero or negative values close to harvest. Sugar accumulation rates prior to the weight maximum ranged from 31 to 47 mg berry·week^{-1}. Rate of weight loss was not closely associated with sugar content at the weight maximum or TSS at the weight maximum (Tab. 3).

As expected, the rate of TSS increase after the weight maximum was tightly correlated with the rate of weight loss ($R = 0.90$, $p < 0.001$) (Fig. 8), ranging from 0.15 to 0.37 °Brix·day^{-1}. One vineyard with a very low rate of weight loss did not follow the overall trends. At this late stage of ripening, this vineyard had vines that bore berries with a relatively high rate of sugar accumulation (26 mg berry·week^{-1}) and TSS increase (0.33 °Brix·day^{-1}) compared with the other vineyards. This vineyard had two trellis wires, had the highest yields (18.1 kg fruit·vine^{-1}), was lagging behind the other vineyards in its veraison date, and only attained 20.8 °Brix prior to harvest.

Yield components and weight loss: Across the twelve vineyards, yield ranged from 9.6 to 18.1 kg·vine^{-1} in Season 1 and 8.1 to 19.5 kg·vine^{-1} (Tab. 2). Season 1 berry maximum weight, rate of weight loss and final weight were not negatively correlated with yield (Tab. 4). Similarly the rate of sugar accumulation prior to the weight maximum was not correlated, however berry TSS declined with increasing yield. Winter vine pruning weight was used as a surrogate for canopy size during the ripening period and ranged from 1.3 to 2.6 kg·vine^{-1} in Season 1 with

Table 2

Pruning weight, yield and crop load of 12 'Shiraz' vineyards during Season 1 and Season 2 (means ± s.e.)

Site	Season 1 Pruning weight (kg·vine^{-1})	Season 1 Yield (kg·vine^{-1})	Season 1 Crop load (kg fruit·kg pruning weight^{-1})	Season 2 Pruning weight (kg·vine^{-1})	Season 2 Yield (kg·vine^{-1})	Season 2 Crop load (kg fruit·kg pruning weight^{-1})
1	1.34 ± 0.15	11.9 ± 1.2	9.06 ± 0.57	2.00 ± 0.19	8.4 ± 1.0	4.0 ± 0.5
2	1.34 ± 0.07	11.1 ± 0.54	8.41 ± 0.29	1.72 ± 0.07	12.6 ± 0.8	7.1 ± 0.4
3	1.46 ± 0.07	14.1 ± 0.8	9.61 ± 0.15	2.20 ± 0.08	16.9 ± 0.8	7.5 ± 0.2
4	1.50 ± 0.15	16.8 ± 1.8	11.24 ± 0.62	1.99 ± 0.21	12.6 ± 1.5	6.2 ± 0.3
5	2.60 ± 0.10	18.1 ± 0.64	7.04 ± 0.33	2.86 ± 0.10	19.5 ± 1.2	4.7 ± 0.4
6	1.60 ± 0.06	9.6 ± 0.47	6.02 ± 0.25	1.47± 0.09	8.1 ± 0.4	5.6 ± 0.5
7	1.36 ± 0.07	12.7 ± 0.44	9.45 ± 0.41	1.92 ± 0.09	14.8 ± 0.8	7.5 ± 0.3
8	2.29 ± 0.15	17.2 ±0.56	7.74 ± 0.40	1.87 ± 0.07	-	-
9	2.00 ± 0.12	9.9 ± 0.80	5.13 ± 0.51	1.83 ± 0.09	13.9 ± 0.6	7.6 ± 0.5
10	1.52 ± 0.07	15.3 ± 1.0	9.96 ± 0.35	1.90 ± 0.11	11.5 ± 0.8	5.9 ± 0.3
11	1.98 ± 0.10	16.7 ± 0.91	8.48 ± 0.28	1.97 ± 0.06	16.8 ± 0.5	8.4 ± 0.2
12	1.46 ± 0.08	16.1 ± 0.41	11.13 ± 0.74	1.71 ± 0.07	11.4 ± 0.4	4.8 ± 0.2

Table 3

Berry weight loss rates in Season 1 as a function of other berry parameters

Rate of berry weight loss (mg·day^{-1}) *vs*	F pr	R^2
Weight maximum (g)	0.34	< 0.01
TSS at the weight maximum (°Brix)	0.14	0.13
Berry sugar at the weight maximum (mg sugar·berry^{-1})	0.10	0.18
Final berry mass (g)	0.74	< 0.01

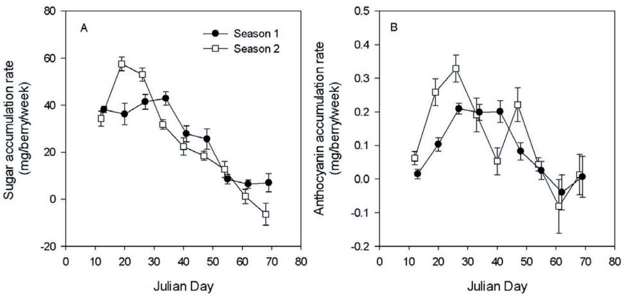

Fig. 7: Changes in (**A**) sugar accumulation rates and (**B**) anthocyanin accumulation rates during Season 1 and 2. Each data point represents the average of 12 vineyards.

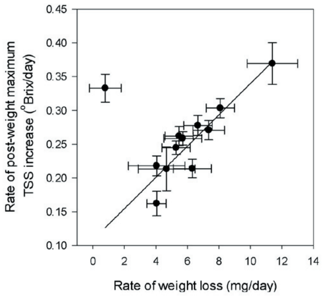

Fig. 8: Rate of post-weight maximum TSS increase as a function of berry weight loss rates. Each data point represents the average of ten 5-vine replicates within one vineyard.

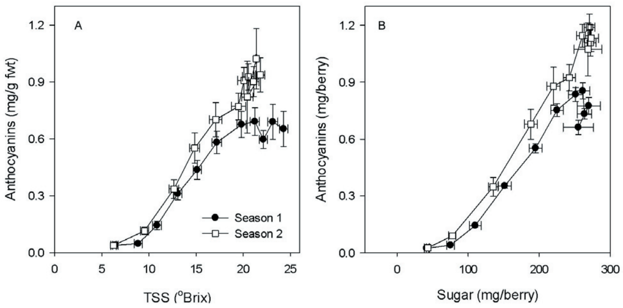

Fig. 9: Seasonal differences in (**A**) berry anthocyanin concentrations as a function of berry sugar concentrations, and (**B**) anthocyanin content per berry as a function of sugar content per berry. Each data point represents the average of 12 vineyards.

slightly larger canopies at 1.47 to 2.86 kg·vine^{-1} in Season 2 (Tab. 2). In Season 1, there were no linear relationships between pruning weights and any of the berry parameters listed above with the exception of final berry mass which increased with pruning weight (Tab. 4). Conversely, crop load ranged from 5.1 to 11.2 kg fruit·kg of pruning weight^{-1} in Season 1 (Tab. 2) and this vine parameter was positively correlated with maximum berry weight but negatively correlated with berry sugar content at the weight maximum (Tab. 4). Relative to the first season, crop load in Season 2 was less in nearly all the vineyards.

A n t h o c y a n i n s : Similar to sugar content, berry anthocyanin concentrations reached a maximum at approximately 46 Julian days in Season 1 and 2 (Fig. 2D). Anthocyanin concentrations were responsive to irrigation regime with the greatest levels in the cautious drip (up to 1.05 mg·g^{-1} fwt) and cautious furrow (up to 0.95 mg·g^{-1} fwt) vineyards while the lowest levels were apparent in the intermediate drip (up to 0.58 mg·g^{-1} fwt) and intermediate flood (up to 0.42 mg·g^{-1} fwt) vineyards (Fig. 4D). Upon examining the relationship between berry sugar concentration and anthocyanin concentration it was evident that, in Season 1, the colour concentration remained stable while the sugar concentration continued to increase as berries continued to shrink (Fig. 9A). In Season 2, however, both sugar and anthocyanin concentrations remained stable. On a per berry basis, sugar levels remained stable but the anthocyanin levels declined by 22 % in the later part of Season 1 (Fig. 9B). In Season 2, anthocyanin degradation did not occur to the same extent at less than 10 %.

Discussion

B e r r y w e i g h t l o s s : Seasonal differences in the severity of berry weight loss were likely a factor of precipitation during this late stage of ripening. Water droplets can be absorbed directly through the pedicel or small cracks in the skin (Lang and Thorpe 1989). Moreover, vine rehydration as a result of rain may increase water flow into the berry through the vascular system, even at this late stage

Table 4

Berry size and sugar in Season 1 as a function of yield, pruning weight and crop load

Yield *vs*	F pr	R^2
Weight maximum (g)	0.38	<0.01
Rate of sugar accumulation to the weight maximum (mg/berry/week)	0.14	0.12
Berry sugar at the weight maximum (mg sugar·berry^{-1})	0.26	0.03
TSS at the weight maximum (°Brix)	*0.002	0.62
Final berry mass (g)	0.27	0.03
Rate of weight loss (mg·day^{-1})	0.25	0.04
Pruning weight *vs*	F pr	R^2
Weight maximum (g)	0.24	<0.01
Rate of sugar accumulation to the weight maximum (mg/berry/week)	0.77	<0.01
Berry sugar at the weight maximum (mg sugar·berry^{-1})	0.78	<0.01
TSS at the weight maximum (°Brix)	0.44	<0.01
Final berry mass (g)	*0.05	0.23
Rate of weight loss (mg·day^{-1})	0.28	0.02
Crop load *vs*	F pr	R^2
Weight maximum (g)	*0.004	0.54
Rate of sugar accumulation to the weight maximum (mg/berry/week)	0.36	<0.01
Berry sugar at the weight maximum (mg sugar·berry^{-1})	*0.003	0.55
TSS at the weight maximum (°Brix)	0.10	0.17
Final berry mass (g)	0.50	<0.01
Rate of weight loss (mg·day^{-1})	0.89	<0.01

of development. Despite impediments in phloem flow into shrivelling berries (McCarthy and Coombe 1999), the capacity for some phloem and xylem transport likely continues (Rogiers *et al.* 2000, 2001, 2006a). Evidence for continuing xylem function was provided through hydrostatic gradient studies of several varieties (Bondada *et al*. 2005) and the presence of intact young tracheary elements of peripheral bundles (Chatelet *et al*. 2008). Possibly almost as critical to the water economy of the berry is evaporative demand. Low humidity can increase berry transpiration rates (Morandi *et al*. 2007), exacerbating berry weight loss. Along with the low rainfall, the high VPD during the ripening period of Season 1 most certainly contributed to greater berry transpiration. Moreover, because 'Shiraz' berries remain hydraulically connected to the vine during this late stage of ripening (Tyerman *et al*. 2004, Bondada *et al.* 2005, Keller *et al*. 2006), increased backflow from the berry to the vine driven by high leaf transpiration may have further aggravated the weight loss.

Aside from climatic factors, irrigation regime also had an influence on maximum and final berry size with larger berries formed in those vineyards where copious water was applied. A water deficit shortly after fruit set can result in reduced cell division rates in the pericarp (Coombe 1960, Harris *et al.* 1968). This combined with curtailed cell expansion likely contributed to the differences in berry size already apparent at veraison in this study. 'Shiraz' berries from a split root irrigation and deficit irrigation study on potted vines also had smaller maximum and final volume than berries exposed to standard irrigation (Rogiers *et al.* 2004a). Likewise, a large irrigation study of field vines found differences in maximum berry weight and this was attributed to a combination of irrigation treatments and seasonal conditions (McCarthy 1997, 1999). A key observation of this study is that berries that were relatively large at their maximum weight were more likely to undergo greater rates of weight loss. The increased rates of weight loss from large berries may simply be a consequence of the presence of more water within the mesocarp cells. High weight loss rates, however, did not necessarily result in smaller berries at harvest. Harvest date itself was likely a large contributor to final berry fresh mass.

In the second season, nearly all the vineyards had larger canopies as compared with the first year and this most likely decreased bunch exposure, berry transpiration and thus berry dehydration. Within a season, however, vine characteristics such as canopy size, yield and crop load did not have an effect on berry weight loss rates. This can be explained by canopy architecture. Because some vineyards employed a double cordon system, large canopies did not necessarily result in greater shading. Double cordons are used to increase yield and improve light penetration to the bunch zone (Louarn *et al*. 2008), therefore increasing, rather than decreasing the evaporative demand at the bunch level.

S u g a r a c c u m u l a t i o n : The rate of sugar import into the berry prior to the onset of weight loss was lower in the first season as compared to the second season and this may have been a consequence of temperatures in excess of 40 °C during this period. High temperature can alter the distribution pattern of carbohydrates (Sepúlveda and Kliewer 1986; Sepúlveda *et al*. 1986) despite reasonable photosynthetic activity (Mullins *et al*. 1992) by diverting assimilates towards the shoot tip, as opposed to the trunk, root and clusters (Sepúlveda *et al*. 1986). Sugar import rates were highest prior to the onset of the weight loss but gradually slowed through the weight loss phase, reaching near zero values several weeks prior to harvest. This corroborates earlier work confirming a decline in the accumulation of potassium, a phloem mobile element, into berries after the weight-maximum (Rogiers *et al.* 2006). Reduced sugar unloading into berries may be the result of down-regulation of sucrose (Davies *et al.* 1999) or hexose transporters (Fillion *et al.* 1999).

As the rate of berry weight loss increased, so did the rate of TSS increase through that weight loss phase, and as expected smaller berries had higher sugar concentrations at harvest. However, because environmental and endogenous factors prior to the weight loss phase have a significant influence on berry sugar accumulation rates into the berry prior to the weight maximum and berry sugar content at the weight maximum, higher weight loss rates did not necessarily result in berries with greater sugar concentrations. Sugar accumulation prior to the weight maximum appears to be more critical to sugar concentration at harvest as opposed to the concentrating effect during shrinkage.

Vineyard 5 stood out with very low ° Brix and weight loss rates but high rates of sugar accumulation prior to harvest. The high rate of TSS increase in this vineyard may be due to continuing sugar import via phloem unloading rather than a concentration effect of existing sugars in the berry. Excessive flood irrigation was used in this vineyard and a liberal amount of N was applied (130.0 kg N·ha^{-1}). This resulted in relatively profuse vegetative growth and pruning weights were 2.6 kg·vine^{-1}. Maximum berry size was not unlike those of other vineyards but the final berry size was relatively large at 1.32 g. It appears that the profuse vegetative growth occurred at the expense of berry sugar accumulation. The vines were also the youngest (at 4 years old) in the survey. For this reason, they probably held a smaller carbohydrate reserve store compared to older vines (Holzapfel *et al*. 2010) and the excessive vegetative growth most likely delayed veraison and resulted in incomplete ripening prior to harvest. High yields and vigour often reduce grape quality (Jackson and Lombard 1993) by delaying maturation (Bravdo *et al*. 1985).

B e r r y c o l o u r : Analogous to the heat-induced inhibition of sugar accumulation during the early ripening phase of Season 1, anthocyanin accumulation was also slowed. Because sugars are the initial precursors of anthocyanins, a strong correlation exists between the concentrations of anthocyanins and sugars in the skin (González-SanJose and Diez 1992, Hrazdina *et al*. 1984, Kataoka *et al*. 1983, Matushima *et al*. 1989, Pirie and Mullins 1977). Anthocyanins increase during ripening (Fernandez-Lopez *et al*. 1992), although a maximum concentration is often reached prior to harvest (Pirie and Mullins 1977, Ribéreau-Gayon 1971, Somers 1976). In Season 1 of this study, anthocyanin concentrations reached a maximum between ten and twenty days after the onset of the fresh mass plateau and subsequently declined during the weight loss phase. The breakdown of membranes as a result of cell senescence may have contributed to this degradation (Coetzee and du Toit 2012). The increase in sugar concentration at the very late stage of ripening is therefore at the expense of a loss in colour and this is undesirable since in some wine regions payment is based on colour as opposed to sugar concentrations.

Conclusion

This vineyard survey has identified a number of key factors that impinge on weight loss rates of 'Shiraz' berries. These include: (1) berry size prior to the weight loss phase, (2) rain during the weight loss phase, (3) VPD, (3) irrigation, and (4) canopy architecture. In order to decrease the severity of weight loss in warm viticultural regions where disease pressure is low, it may be of benefit to adopt canopy styles that improve bunch shading in the afternoon when VPD is most extreme. If berry colour is the predominant factor defining berry quality then the crop should be harvested prior to the very late stage of shrivelling.

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