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The effect of light intensity and temperature on berry growth and sugar accumulation in *Vitis vinifera* 'Shiraz' under vineyard conditions

S. K. Abeysinghe, D. H. Greer and S. Y. Rogiers

National Wine and Grape Industry Centre, Charles Sturt University, Wagga Wagga, Australia

Summary

Temperature and light are key climatic factors which affect grapevine physiology in the growing season. Our aim was to investigate the interactive effects of temperature and light intensity on reproductive growth responses of 'Shiraz' vines in vineyard conditions. Well-watered vines were covered with no shade, light, medium and heavy shade covers in a vineyard over three consecutive seasons. Several heat events, *i.e.*, air temperatures exceeding 40 °C for several days, occurred in two of the seasons. Heavy shade reduced canopy temperatures by 3.2-6 °C in the cooler season and by 4-6 °C in the warmer seasons, relative to air temperature and compared with the open canopy. The onset of berry growth was delayed by the heavy shade but the rate of sugar accumulation was not affected. During the season with the most severe heat events, berry dry matter accumulation was significantly higher in the shaded treatments compared to the unshaded vines. The hypothesis was confirmed that medium and heavy shade conferred high levels of protection on the berry ripening process from high summer temperatures and the concurrent exposure to light intensities.

Key words: berry growth dynamic; heat event; photon flux density; shading; sugar accumulation; temperature.

Introduction

In some parts of Australia, the frequency of high temperature periods has increased markedly during the grape growing season in the recent past (Greer and Weedon 2013). High temperatures, those above about 40 °C, and high light conditions, that is, full summer sunlight, can impair physiological functions such as flowering, berry growth and sugar loading, with resultant costs on yield and quality attributes of grapes (Greer and Weston 2010). However, studies addressing the interactive effects of high light intensities with high temperatures on grapevine performance are relatively uncommon, especially in vineyard conditions.

Temperatures surrounding the vines determine berry growth and development. However, varietal differences showed different responses especially for high temperatures (Soar *et al.* 2009, Sadras and Soar 2009). The optimum temperature for fruit set of grapevines apparently ranged between 20-26 °C d temperatures whereas high temperatures (~ 30 °C) markedly reduced fruit set (Buttrose and Hale 1973, Ebadi *et al.* 1995). The optimum temperature for grape berry growth was reported to be 20-30 °C but the effect of temperature depended on the growth stage of the berries (Kobayashi *et al.* 1965, Ewart and Kliewer 1977). However, a higher sugar content in berries was reported when vines were exposed to 30/10 °C compared with those that were exposed to warmer nights (~ 30 °C), due to favourable conditions for sugar loading into berries (Coombe 1987, Mori *et al.* 2005). The temperatures above ~ 20 °C also reduce the acidity of berries in different varieties and high temperature conditions, therefore, influence the acidity of the wine (Buttrose *et al.* 1971, Kliewer 1971, Kliewer 1973, Lakso and Kliewer 1978). The optimum temperature for the formation of anthocyanins is reported to be between 17-26 °C (Pirie 1978), depending on the variety. However, the reproductive growth is unfavourably affected by elevated air temperature above these threshold temperatures (Klein *et al.* 2007, Sacks and Kucharik 2011).

High temperature effects on grapevine performance and berry development have been extensively examined under field and controlled conditions. For example, Kliewer (1977) investigated high temperature (37/32 °C) effects of 'Emperor' grapes and reported inhibition of anthocyanin synthesis and accumulation of total soluble solids (TSS) compared to control vines. Furthermore, in high temperature conditions (40/20°C), glucose and fructose content decreased in 'Chardonnay' berries relative to control conditions (Sepulveda *et al.* 1986). Elsewhere, the flowering process was completely retarded, along with smaller berries and low sugar accumulation in 'Semillon' exposed to 40/25 °C (Greer and Weston 2010). Moreover, during a heat event in the 2008/2009 growing season, rates of the sugar accumulation in 'Semillon' berries decreased by 50 % and percentages of shrivelled berries increased (Greer and Weedon 2013). These studies confirmed, for many grape cultivars, that exposure to high temperatures was detrimental to several aspects of reproductive growth.

High light effects on grapevine physiology have been explored with diverse methodologies. Petrie and Clingeleffer (2005) demonstrated that high light intensities caused decreased flower numbers of 'Chardonnay', by 13 % per inflorescence, when open and covered mini chambers were used to alter the micro climate surrounding the buds, 14 d

Crrespondence to: Dr. D. H. Greer, National Wine and Grape Industry Centre, Charles Sturt University, Locked Bag 588, Wagga Wagga, NSW 2678, Australia. E-mail: dgreer@csu.edu.au

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prior to bud break. At harvest, 'Shiraz' berries exposed to sunlight were 20 % larger, had lower seed weight, juice pH and lower titratable acidity compared to 'Shiraz' berries in opaque boxes (Ristic *et al.* 2007). In addition, there was a higher TSS in 'Sangiovese' berries exposed to full sun compare to 40 % and 70 % shaded berries (Cartechini and Palliotti 1995). Furthermore, berries of 'Cabernet Sauvignon' vines exposed to full sunlight had a 20-48 % higher sugar content compared to shaded berries (Ribereau-Gayon 1959). Similarly, in 'Semillon' vines, yield was increased by 11-20 % on open vines compared to vines in 70 % shade (Greer and Weedon 2012a). Moreover, solar radiation acts as a source of heat through radiation and by convection and conduction in the vineyard (Crippen and Morrison 1986). In addition, photon flux density is tightly coupled with temperature in a synergic effect (Antcliff and Webster 1955, Iland *et al.* 2011). During heat events, therefore, high temperatures are likely to be exacerbated by the high photon flux densities (PFDs) in the vineyard, which impact negatively on grapevines (Webb *et al.* 2009).

One strategy adopted to reduce the effects of high temperature and high light has been to cover grapevines with shade cloth as a means of protecting bunches from heat damage. Imposing shade cover, however, alters the solar radiation interception by the vines which is important to the light stimulated physiological functions, such as photosynthesis and biosynthesis of phenolic substances in the berries (Iland *et al.* 2011). Some consequences included reduced yield and plant biomass (Greer *et al.* 2010), probably through an effect on photosynthesis (Greer *et al.* 2011, Caravia *et al.* 2016). But shading apparently had no effect on rates of leaf expansion in 'White Riesling' (Schultz 1992), shoot growth (Buttrose 1969b, Greer *et al.* 2010) or composition of anthocyanins (Renata *et al.* 2007). Thus, shade cover does have a number of negative but also neutral effects on the growth and development of grapevines.

Contrasting to those above, studies that have addressed the interactive effects of high light intensities with high temperatures on grapevine performance are relatively rare, especially in vineyard conditions. Exceptions to this knowledge gap include studies by Spayd *et al.* (2002) and more recently by Greer and Weedon (2012b). These studies have shown that effects of high temperatures on berry development, as outlined above, were exacerbated by high light intensities. For example, the effect of increasing temperatures on Semillon berry growth were positive at low PFDs but negative at high PFDs for vines grown in controlled growth conditions (Hulands *et al.* 2014). By contrast, in the same study, increasing temperatures had negative effects on sugar accumulation at low PFDs but less of an effect at high PFDs, though more sugar was accumulated (Hulands *et al.* 2013). These studies suggest the interactive effects of temperature and light intensity are complex and the effects may vary with the individual plant process. Thus, given that the high temperatures across the growing season are frequently accompanied by high light intensities (Gladstones 1992), and these conditions may well increase in frequency in a changing climate, it is essential to understand how berry traits in the vineyard are affected during these extreme climatic conditions from production and wine quality perspectives.

The *Vitis vinifera* cultivar 'Shiraz' is a widely grown and economically important grapevine cultivar within Australia. Although some early studies have investigated the effects of temperature and light intensity on 'Shiraz' growth (Buttrose 1969a, Ebadi *et al.* 1996), there are relatively few studies that have quantified the response of this cultivar to high temperatures in vineyard conditions. However, when 'Shiraz' berries in vineyard conditions were exposed to an open heating system and berry temperatures were elevated by 2-3 °C above ambient conditions, berry weight and TSS did not change, suggesting the vines were able to tolerate the small changes in temperature. (Soar *et al.* 2009, Sadras and Soar 2009). Consistent with these results, berry growth and sugar accumulation of vineyard-grown 'Shiraz' vines treated in a greenhouse system to 3-d heat episodes of 6.5 to 7.3 °C (approx. 40 °C) above ambient were unaffected except when the vines were treated at fruit set (Soar *et al.* 2009). By contrast, when high temperature (> 35 °C) exposure of 'Shiraz' vines was reduced by 2 °C below ambient by overhead shade, soluble solids concentrations and the rate of accumulation were both decreased, although sugar per berry was unaffected (Caravia *et al.* 2016). These results of soluble solids decreasing are at odds with the characteristic attribute of 'Shiraz' grapes late in the growing season to lose berry water (shrinkage), which leads to an apparent increase in soluble solids concentration and a reduction in berry weight, yield and potentially an altered wine style (McCarthy 1999, Rogiers *et al.* 2000, Petrie *et al.* 2004). Despite these characterisations of 'Shiraz' vines and berries thus far undertaken what remains uncertain is how the reproductive process is affected by the concurrent exposures to both extremely high temperatures (> 40 °C) and high light intensities at the height of the growing season.

Accordingly, the hypothesis of the present study was that the dynamics of berry growth, sugar and dry weight accumulation of 'Shiraz' berries exposed concurrently to high temperatures and high light intensities would be detrimentally affected in comparison to exposure to high temperatures alone. To assess this hypothesis, vineyard-grown 'Shiraz' vines were treated to different shade treatments over three growing seasons to determine total soluble solid accumulation and sugar content during naturally occurring high temperature events.

Material and Methods

Experimental site and vines: The 10 year old own rooted *Vitis vinifera* L cv. 'Shiraz' vines grown at the Charles Sturt University vineyard (Latitude 35.05°S and longitude 147.35°E) were used for this study. The vines were trained to a horizontal bilateral cordon and the Vertical Shoot Position (VSP) trellis system. In each season, budbreak occurred in late September and harvest of the vines occurred in mid-February. Vines were drip irrigated at a rate of 3.1 $L \cdot h^{-1}$ for 14 h per week until flowering and 28 h per week thereafter until the harvest.

Light treatments: Four light treatments were applied at pre-budbreak each season by using artificial shade cloth of differing densities and weave (Shade Australia, Sydney, Australia); notably, no light reduction (hereafter referred to as control), 10 % light reduction (hereafter referred to as light shade), 30 % light reduction (medium shade) and 50 % light reduction (heavy shade). For each treatment, shade cloth was placed over six vines distributed across two panels between support posts. In all measurements, only the three middle vines were used to avoid any edge effects. Each treatment was replicated in the same row.

The shade support structure consisted of a wooden horizontal T bar (1.6 m width) and two vertical metal support bars (0.8 m length) which were attached to the middle of the wooden bar at the top end. The frame was fastened to the wooden support post of the vine row at both ends.

Photon flux density: The photon flux density (PFD) was measured with quantum sensors (SQ-110, Apogee, Logan UT, USA) placed 25 cm below the shade cloth of each treatment and 2.25 m above the ground for control canopy. The mean hourly PFD was recorded by data loggers (CR 1000, Campbell Scientific, Townville, Australia) connected to the quantum sensors and the mean daily PFDs were calculated by averaging the mean hourly PFD across each day (from 0600 to 1800 h).

Air temperatures: Screened air temperatures (HMP50, Vaisala, Helsinki, Finland) were monitored above the canopy in a protected white screen and logged as described above with the data loggers.

Canopy temperatures: Canopy temperatures were monitored, using infra-red radiometer temperature sensors (SI-100, Apogee, Logan, UT, USA) at 0.3 m out from the vine on both the eastern and western sides of the canopy. The mean daily canopy temperatures were calculated by averaging the mean hourly canopy temperature across each day.

Bunch temperature: Bunch temperatures were monitored using thermocouples (418-152, T C measurements, Oakleigh, Victoria, Australia) which were connected to the data loggers as described above. The mean daily bunch temperatures were calculated by averaging the mean hourly bunch temperature across each day.

Berry diameter: A total of 15 berries from 5 randomly selected bunches per treatment were measured at weekly intervals in the 2011/12 growing season while 30 berries from 10 randomly chosen bunches were measured in subsequent seasons to reduce variability. Berry diameters of the selected berries were measured by digital microcalipers (Carbon Fibre Composites, ThermoFisher Scientific Australia Pty. Ltd, Victoria, Australia) from when the berries were 3-4 mm in size (E-L stage ~ 27) through to harvest.

Dry weight: The berries that were sampled at weekly intervals as above were also used to determine the dry weights in the 2013/14 growing season only. The berries were weighed and dried in a drying oven for 2 weeks at 60 °C. At harvest, 240 berries from all sample vines per treatment were processed for dry weight determination for each of the three growing seasons using the same process.

Total soluble solid concentration: A total of 60 berries from five randomly chosen bunches of each treatment (15 berries per treatment) were destructively harvested at weekly intervals. Berry sampling was initiated when the berries were 5-6 mm in diameter (E-L stage ~ 30) and continued through to harvest. After the harvest, 300 berries per treatment from all six vines were assessed for TSS and a digital refractometer (PR-101, Atago, Tokyo, Japan) was used for assessment at both instances.

Sugar concentration: Sugar content was determined according to Iland *et al.* (2004) and Greer and Weedon (2014) from berry diameters and the TSS. The percentages of shrivelled berries in the control and three shade treatments were determined visually at harvest in 2012/13 and 2013/14 seasons.

Statistical analysis: The data were analysed using a Generalised Linear Model (GLM) with R, Version 3.0.3 statistical software (The R Foundation for statistical computing, Vienna, Austria). The main and interactive effects of factors were determined using the GLM approach and statistical significance was calculated at the 5 % level. The Boltzmann sigmoid function was fitted to berry growth using Origin V8.1 (OriginLab Corporation, Northampton, MA, USA).

Results

Photon flux densities in the shade treatments: The daily maximum PFD above the vines of the different shade treatments varied between 500 and 2,500 µmol·m^{-2}·s^{-1} (Fig. 1). The average daily maximum PFDs of the treatments from the least to the most shaded treatment, as an example, averaged between 100 and 120 d after budbreak (DAB), from 2147 ± 50, 1997 ± 58, 1518 ± 65 and 955 ± 30 µmol·m^{-2}·s^{-1}, respectively.

The light shade treatment reduced irradiance by 10 % during each of the growing seasons while for medium shade, irradiance was reduced by 33% and the heavy shade reduced irradiance by 55 % compared to the control treatment.

Air temperatures across the growing season: The daily maximum air temperatures were typically 20-25 °C at the start of each growing season (Fig. 2 a-c). However, in the 2011/12 growing season, the daily maximum temperatures increased to be between 30 and 36 °C through early to late in the season and peaked at 38 °C, thus remained below 40 °C. The minimum air temperatures

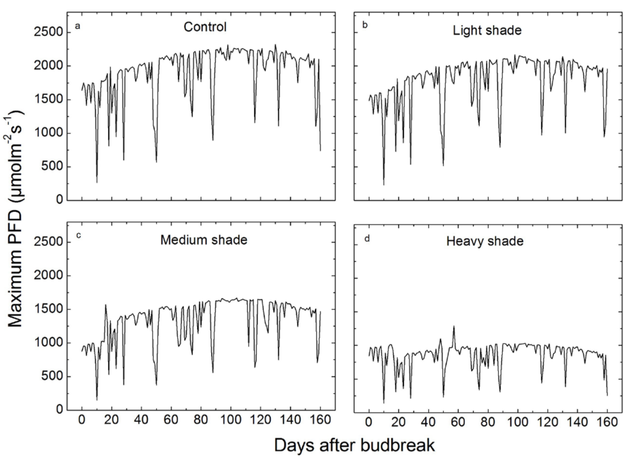

Fig. 1, a-d: The daily maximum PFD during the 2012/13 growing season for each of the four shade treatments, as indicated, for 'Shiraz' vines growing in vineyard conditions.

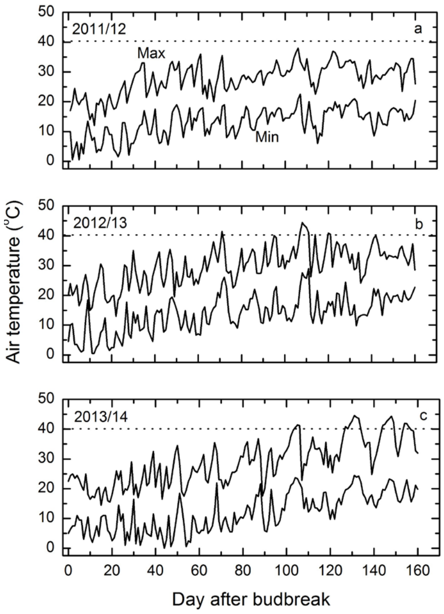

Fig. 2, a-c: The mean daily maximum (max) and minimum (min) air temperatures during the three growing seasons as indicated. The dotted line is drawn to indicate when the maximum air temperatures exceeded 40 °C.

ranged between 10 and 20 °C across the growing season. By contrast, in both the 2012/13 and 2013/14 growing seasons, the maximum air temperatures exceeded 40 °C on several occasions, during the mid-season in 2012/13 (10 times) and in the later berry ripening stage in the 2013/14 growing season (21 times). It was notable also that the maximum air temperatures in both seasons reached 44.5 °C. In both seasons, minimum air temperatures were again typically between 10 and 20 °C but during the heat events, the minima reached up to about 25°C.

Canopy temperatures across the growing season: The daily maximum canopy temperatures for the control, light and medium shade treatments exceeded 40 °C for 3-7 d in the 2011/12 growing season, but the canopy of the heavy shade treatment remained below 40 °C (Fig. 3). By contrast in the 2012/13 season, the canopy temperatures of the heavier shade treatments, approached 40 °C while for the control and light shade treatments, canopy temperatures exceeded 40 °C for 6 d (not shown). In contrast to the two previous growing seasons, the canopy temperatures exceeded 40 °C for 11-29 d, in the 2013/14 growing season in all treatments with the shortest duration under heavy shade and the longest duration in the unshaded canopy (Fig. 4). Furthermore, in the 2011/12 season, the daily maximum canopy temperatures during a set period

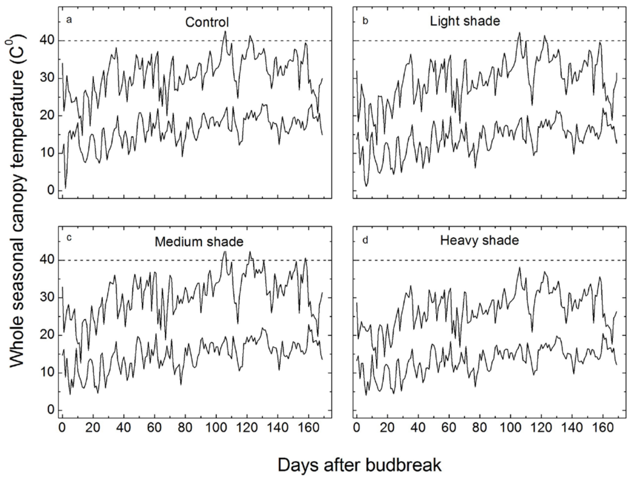

Fig. 4, a-d: The seasonal pattern of the daily maximum and minimum canopy temperatures during the 2013/14 growing season for each of the four shade treatments, as indicated, for 'Shiraz' vines growing in vineyard conditions.

of between 100 and 120 DAB, averaged 30.8 ± 0.8 °C for the heavy shaded canopy and 34.7 ± 0.9 °C for the control (unshaded) canopy while the light and medium shade canopy temperatures varied between these limits. Thus, the heavy shade treatment temperature was comparable with air temperature while the canopy temperatures of all other treatments exceeded air temperature, by as much as 4 °C. Across the 2012/13 growing season, the daily maximum canopy temperatures averaged 36.3 ± 0.8 °C for the same period, in the control and light shade treatments and 32.3 ± 0.8 °C in the medium and heavy shade treatments, therefore, in keeping with maximum air temperatures also exceeding 40 °C. Thus, across the 2013/14 season, the daily maximum canopy temperatures over the set period averaged 34.2 and 35.9 ± 1.0 °C, for the control and light shade treatments and 34.9 and 31.7 ± 0.9 °C in the medium and heavy shade canopy, respectively, thus, only the heavy shade reduced canopy temperature below air temperature.

Bunch temperatures: Bunch temperatures (not shown) followed a similar pattern of canopy temperatures in each of the three growing seasons.

Berry growth: Berry expansion in each season was generally similar for the bunches in each of the four treatments, with few apparent differences (Tab. 1). Across all seasons, there were no treatment effects on the final berry size. However, there were significant differences between the seasons. Notably, final berry size was significantly (P < 0.001) smaller in the 2013/14 season (by 3 mm) compared to the other two seasons. Moreover, there were no treatment or growing season effects on the relative

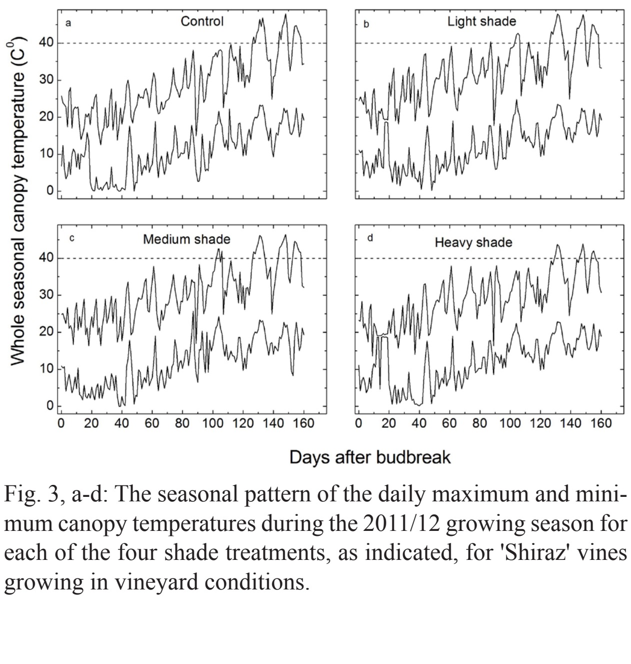

Fig. 3, a-d: The seasonal pattern of the daily maximum and minimum canopy temperatures during the 2011/12 growing season for each of the four shade treatments, as indicated, for 'Shiraz' vines growing in vineyard conditions.

Table 1

Dynamics (Mean ± SE, n = 30) of Shiraz berry diameter growth in each of four shade treatments over three growing seasons; 1, 2011/12, 2, 2012/13, 3, 2013/14, including the maximum diameter, rate of expansion and the timing of when berry growth started and stopped and the duration of the growth period, measured in days after budbreak. In all cases, these data were obtained from the fit of the Boltzmann sigmoid function to the berry expansion data across the period of growth. Also shown are the probabilities (*P*) that the treatment, season and the interactive season x treatment effects were significant for each attribute

Shade Treatment	Season	Maximum diameter (mm)	Relative growth rate ($mm \cdot d^{-1}$)	DAB to 20 % expansion	DAB to 80 % expansion	Duration of expansion (d)
Control	1	13.7 ± 1.6	1.5 ± 0.3	112.1 ± 5	116.4 + 1	4.3 ± 2
Light	1	14.0 ± 1.0	1.2 ± 0.9	114.6 ± 3	118.6 ± 1	4.0 ± 2
Medium	1	13.9 ± 1.0	1.5 ± 0.8	121.1 ± 4	123.7 ± 1	2.6 ± 4
Heavy	1	14.6 ± 1.2	0.8 ± 0.7	122.9 ± 5	125.6 ± 1	2.7 ± 3
Mean		14.0 ± 1.2	1.3 ± 0.7	117.7 ± 4	121.1 ± 1	3.4 ± 3
Control	2	13.8 ± 1.0	0.9 ± 0.4	121.2 ± 2	123.6 ± 1	2.4 ± 1
Light	2	14.1 ± 0.7	1.4 ± 0.8	121.3 ± 1	122.5 ± 1	1.2 ± 1
Medium	2	14.4 ± 0.9	0.6 ± 0.4	118.9 ± 2	123.8 ± 4	4.9 ± 1
Heavy	2	13.8 ± 0.8	0.3 ± 0.1	118.9 ± 2	126.4 ± 2	7.5 ± 1
Mean		14.0 ± 0.9	0.8 ± 0.4	120.1 ± 2	124.1 ± 2	4.0 ± 1
Control	3	10.6 ± 1.6	0.4 ± 0.6	112.0 ± 2	123.5 ± 3	11.4 ± 3
Light	3	11.0 ± 2.5	0.7 ± 0.6	119.3 ± 1	128.1 ± 2	8.8 ± 1
Medium	3	11.1 ± 1.0	0.9 ± 0.2	121.5 ± 4	127.1 ± 3	5.5 ± 5
Heavy	3	11.1 ± 0.8	0.7 ± 0.3	119.7 ± 3	123.6 ± 2	4.0 ± 3
Mean		10.9 ± 1.5	0.7 ± 0.4	118.1 ± 2	125.6 ± 2	7.4 ± 3
Treatment *P*		0.232	0.103	0.002	0.004	0.461
Season *P*		0.001	0.142	0.001	0.351	0.115
Treatment x Season *P*		0.926	0.568	0.005	0.001	0.121

rates of berry expansion, which ranged between 0.7 and 1.3 $mm \cdot day^{-1}$ on average. By contrast, there were highly significant ($P < 0.001$) treatment x season interactions on the timing as to when berry expansion was completed (attaining 80 % of total size), which varied between 123-128 DAB.

Berry dry weight accumulation: The accumulation of berry dry weight in each of the four treatments followed a sigmoidal pattern in the 2013/14 growing season (not shown). Furthermore, across the shade treatments, there were highly significant ($P < 0.05$) treatment effects on when berry dry matter accumulation commenced, progressively later from the control vines at 116 DAB to the heavy shade treatment vines at 125 DAB (Tab. 2). In addition, there were highly significant treatment differences as to when berry dry matter stopped accumulating, and again there was a delay from the control vines at 141 DAB to the heavy shade treatment vines at 144 DAB. Consequently, the duration of berry dry matter accumulation varied significantly, from 19-21 d for the light and heavy shade treatment vines, to 25-28 d for the control and medium shade treatment vines. However, at harvest there were significant ($P < 0.05$) treatment differences, where the berries from the control, light shade and medium shade treatments averaged 364 ± 21 $mg \cdot berry^{-1}$, 468 ± 16 $mg \cdot berry^{-1}$, and 420 ± 9 $mg \cdot berry^{-1}$, respectively, while those berries in the heavy shade treatment averaged 425 ± 21 mg, with the control berries significantly lower and light shade berries significantly higher in dry weight.

Table 2

The dynamics (mean ± se, n = 15) of Shiraz dry weight accumulation of berries in each of four shade treatments during the 2013/14 growing season, including the estimated maximum dry weight, the relative rate of dry weight accumulation and the timing of when dry weight accumulation started and ended and the duration of accumulation, in days after budbreak. In all cases, these data were obtained from the fit of the Boltzmann sigmoid function to the berry accumulation data over the growth period. Also included is the statistical analysis of these data, including the *P* values for the main treatment effects

Shade Treatment	Maximum dry weight ($mg \cdot berry^{-1}$)	Rate of dry weight accumulation ($mg \cdot d^{-1}$)	DAB to 20 % of final dry weight	DAB to 80 % of final dry weight	Duration of accumulation (d)
Control	363.8 ± 32	7 ± 0.1	115.7 ± 1	140.8 ± 4	25.1 ± 1
Light	467.5 ± 16	5 ± 0.2	107.3 ± 4	128.4 ± 5	21.1 ± 4
Medium	420.4 ± 9	8 ± 0.3	117.8 ± 1	145.8 ± 1	28.0 ± 1
Heavy	424.6 ± 21	4 ± 0.2	124.9 ± 1	143.5 ± 1	18.6 ± 5
Mean	419.1 ± 10	6 ± 0.2	116.4 ± 2	139.6 ± 3	23.2 ± 3
Treatment *P*	0.036	0.405	0.001	0.001	0.001

Total Soluble Solids accumulation (TSS): In the 2011/12 growing season, TSS accumulation in the berries of the control and light-medium shade treatments was not significantly different (Fig. 5 a). However, the TSS of berries in the heavy shade treatment was significantly ($P < 0.001$) lower, by 1.4-1.8 °Brix compared with the other treatments. The difference was somewhat transient, because at harvest, there were no treatment differences in TSS. Similarly, across the 2012/13 growing season, the TSS accumulation of berries on vines in the medium and heavy shade treatments was significantly reduced, by up to 4.8 °Brix and 2.4 °Brix, respectively, compared to those berries on vines in the control and lightest shade treatments (not shown). At harvest, berries from the

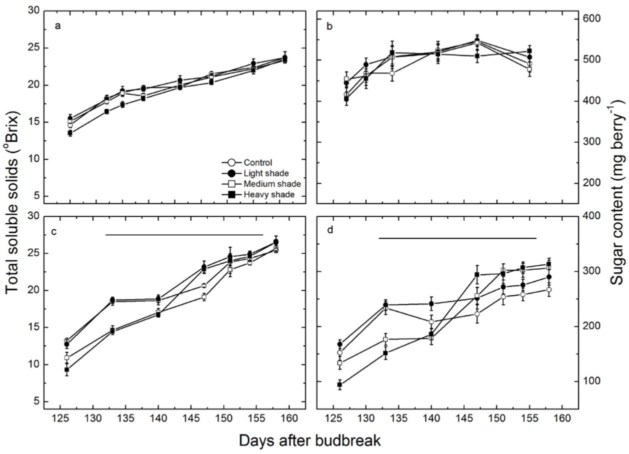

Fig. 5, a-d: Changes in total soluble solids concentration and sugar content (mean ± SE, n = 30) of 'Shiraz' berries as a function of days after budbreak and during the ripening period of the 2011/12 (**a**, **b**) and 2013/14 (**c**, **d**) growing seasons. A sustained heat event occurred in the 2013/14 growing season and the horizontal line indicates this period.

heavy shade treatment remained significantly lower in TSS than those in the other treatments. For the 2013/14 growing season (Fig. 5 c), patterns of accumulation of TSS mirrored the previous season. Thus, a delay in accumulation of soluble solids again occurred in berries from the medium and heavy shade treatments, such that differences in TSS between these and berries from the other two treatments were highly significant ($P < 0.001$). However, in contrast to the previous growing seasons, the treatment effects on TSS accumulation were not sustained from two events: the heat event occurring at about 130 DAB and the recommencement of accumulation of TSS in the medium and heavy shade treatments from about 140 DAB. At harvest, TSS in heavy shade berries was significantly ($P < 0.01$) higher compared with the other treatments.

Accordingly, the effect of heat events on the accumulation of TSS was specifically compared in the period from 125 to 165 DAB in each of the three seasons. There was a significant ($P < 0.05$) interaction between the treatment x season and highly significant ($P < 0.001$) main effects of season, time of sampling and treatment. The treatment x DAB interaction was therefore examined separately for each season. The changes in TSS across the period for the shade treatments in the 2013/14 growing season (Fig. 5) were statistically significant ($P < 0.001$) but not for the 2011/12 growing season. During the heat event of the 2013/14 season (Fig. 5 c), TSS stopped accumulating and was strongly perturbed for bunches in all treatments. However, there was also an apparent strong recovery in TSS when the heat event started to subside for all treatments, but especially so for the heavy shade treatment, and probably indicative of berry shrinkage in the other treatments (Tab. 1).

Berry sugar accumulation: In the 2011/12 season, there were some treatment differences in the berry sugar content (referring to sugar per berry as opposed to TSS which represents sugar concentration). Notably bunches in the heavy shade treatment initially had a significantly ($P < 0.05$) lower sugar content than bunches in the other shade treatments but these differences had largely disappeared by about 130 DAB. The differences in berry sugar content were minimised at the end of the seasons (Fig. 5 b). By contrast in the 2012/13 season, the sugar content of berries on bunches on the heavy shade treatment vines was significantly lower compared with the berries of bunches in all other treatments (not shown). This difference was evident from shortly after ripening commenced and persisted through to harvest. At harvest, there were slight differences in the berry sugar contents in the control to medium treatments. However, a different pattern of sugar accumulation occurred in the 2013/14 growing season (Fig. 4d), where sugar contents of berries in bunches of the two lightest shade treatments were initially significantly higher from ~ 125-140 DAB compared to the berries of bunches in the two heaviest shade treatments. However towards harvest, the sugar content of berries in bunches of the two heaviest shade treatments had increased markedly and were significantly higher compared to the control and light shade treatments from ~ 147-160 DAB. The dynamic analyses of these data revealed a significant ($P < 0.05$) interaction between treatment x season (Tab. 3) on the maximum sugar content in the berries. In all cases, there was a similar relative rate of sugar accumulation. Across all seasons, there were no significant differences in the timing of the ripening process, berries in all treatments and seasons started ripening at 111 to 128 DAB and finished ripening at 124 to 135 DAB.

Also, during the heat event, the rates of sugar accumulation of berries on bunches in the control and light shade treatments decreased significantly from about 13 mg berry^{-1}·day^{-1} to about 4 mg berry^{-1}·day^{-1} at 140 DAB in the middle of the heat event (Abeysinghe *et al.* 2016). There were further small changes in the rates of ripening thereafter, with some recovery apparent. Prior to the heat event, the rate of sugar accumulation of bunches in the medium and heavy shade treatments were significantly lower, at about half the rates of the other treatments. However, there were no marked decreases in the rates during the heat event while a slight increase in the rate of ripening even occurred in bunches in the heavy shade treatment. However, from about 140 DAB, these bunches maintained a significantly higher sugar content than bunches of the control and light shade treatments. This was clear evidence that the 30-50 % shade was providing protection to the ripening process from the heat event.

Shrivelled berries: There was a significant ($P < 0.05$) seasonal effect on the percentage of berry shrivel at harvest (Tab. 4). However, there were no treatment effects on the percentage of shrivelled berries.

Discussion

Each of the three growing seasons varied in the extent of heat exposure that the 'Shiraz' vines were subjected to. No heat events (*i.e.* air temperatures > 40 °C) occurred in the 2011/12 growing season while in the 2012/13 growing season, four heat events occurred, mostly of one day duration except for one event (starting at 104 DAB) which had temperatures over 40 °C for 5 consecutive days, thus 10 d in total were above 40 °C. This trend continued into the 2013/14

Table 3

The dynamics (Mean ± SE, n = 15) of Shiraz sugar accumulation across the growing seasons of berries in each of the four shade treatments during three seasons; 1, 2011/12, 2, 2012/13, 3, 2013/14. In all cases, these data were obtained from the fit of the Boltzmann sigmoid function to these data across the period of berry ripening and measured in days after budbreak. Also shown are the probabilities, *P*, that the treatment, season and the interactive season x treatment effects were significant for each attribute

Shade Treatment	Season	Maximum sugar content (mg·berry^{-1})	Relative sugar accumulation rate (mg·d^{-1})	DAB to 20 % of final sugar content	DAB to 80 % of final sugar content	Duration of accumulation (d)
Control	1	522.2 ± 10	23.0 ± 0.1	111.4 ± 4	127.4 + 5	16.0 ± 5
Light	1	507.2 ± 10	29.0 ± 0.1	114.5 ± 3	124.7 ± 5	10.2 ± 4
Medium	1	491.5 ± 10	33.0 ± 0.1	118.4 ± 2	125.7 ± 5	7.3 ± 5
Heavy	1	477.9 ± 10	26.3 ± 0.1	116.9 ± 3	127.8 ± 2	10.9 ± 1
Mean		499.7 ± 10	27.8 ± 0.1	115.3 ± 3	126.4 ± 4	11.1 ± 3
Control	2	386.0 ± 20	25.0 ± 0.1	123.7 ± 5	128.7 ± 4	5.0 ± 6
Light	2	379.5 ± 11	28.9 ± 0.1	119.0 ± 3	128.3 ± 3	9.3 ± 7
Medium	2	381.1 ± 17	30.0 ± 0.1	121.5 ± 2	132.8 ± 2	11.3 ± 4
Heavy	2	342.7 ± 13	20.1 ± 0.1	122.1 ± 4	131.1 ± 5	9.0 ± 8
Mean		372.3 ± 15	26.0 ± 0.1	121.6 ± 4	130.2 ± 3	8.7 ± 6
Control	3	266.9 ± 12	22.1 ± 0.1	121.0 ± 3	129.5 ± 5	8.5 ± 5
Light	3	290.1 ± 13	29.7 ± 0.1	120.6 ± 4	133.2 ± 6	12.6 ± 4
Medium	3	306.5 ± 13	21.1 ± 0.1	129.9 ± 1	141.4 ± 6	11.5 ± 5
Heavy	3	313.5 ± 10	26.1 ± 0.1	128.4 ± 4	139.6 ± 4	11.2 ± 1
Mean		294.3 ± 13	24.7 ± 0.1	125.0 ± 3	135.9 ± 5	10.9 ± 4
Treatment *P*		0.023	0.452	0.652	0.623	0.961
Season *P*		0.001	0.994	1.000	1.000	1.000
Treatment x Season *P*		0.048	0.996	1.000	1.000	1.000

Table 4

Percentage of berry shrivel at harvest (Mean ± SE, n = 12) of 'Shiraz' under the four shade treatments in the seasons 2012/13 (2) and 2013/14 (3). Also included is the statistical analysis of these data including the *P* values for the main and interactive effects of treatment x season

Shade Treatment	Season	Shrivel berry (%)
Control	2	9.4 ± 0.2
Light	2	8.0 ± 0.1
Medium	2	4.5 ± 0.3
Heavy	2	0.5 ± 0.1
Mean		5.6 ± 0.2
Control	3	37.8 ± 0.2
Light	3	30.0 ± 0.4
Medium	3	24.2 ± 0.3
Heavy	3	2.9 ± 0.2
Mean		23.7 ± 0.3
Treatment *P*		0.514
Season *P*		0.042
Treatment x Season *P*		0.245

growing season, where four heat events also occurred but each was from 3-8 d duration and 21 d in total when air temperatures exceeded 40 °C. An analysis of heat events in the Riverina, NSW indicated a 5 d heat event was relatively rare but the 2008/09 growing season was characterised by a 14-d heat event (Greer and Weedon 2013), thus the present heat event in 2013/14 was extreme in comparison to past events. In this case, this was also the highest temperatures that 'Shiraz' vines were exposed to in contrast to all previous studies on this cultivar. Further support comes from the fact that the average canopy temperatures of the control vines exceeded average air temperatures by 1-4 °C and approached mean temperatures of 45 °C. The shade covering the vines during the 2011/12 growing season maintained canopy temperatures close to the control canopy at around 40 °C. However, the heavy shade reduced canopy temperatures by about 4 °C, to a mean temperature of 35.6 °C. Similar effects occurred in the more extreme heat events of the 2013/14 growing season, with the heavy shade covering reducing the canopy temperatures by 2-4 °C and maintained average canopy temperatures to no higher than 41 °C. Whereas for the vines in the control, light and medium shade treatments, average canopy temperatures ranged between 43 and 45 °C. By contrast, during the 2012/13 growing season, the 5-d heat event where air temperature averaged 42.6 °C, the open canopy averaged 39.1 °C and the medium and heavy shaded vine canopies averaged 36.9 and 37.6 °C, thus 1.5 to 2.2 °C cooler than the control. Thus, the heavy shade consistently kept the canopy cooler by 2-4 °C even during the most extreme heat event. Whereas the light shade conferred no protection and the medium shade was only effective if the heat event was short and not too hot. Elsewhere for 'Shiraz' vines, 62 % shade cover reduced maximum temperatures by 2 °C (Caravia *et al.* 2016), therefore, in keeping with present study. In addition, canopy temperatures of Sangiovese vines were decreased by 2 °C with 70 % light attenuation (Cartechini and Palliotti 1995). Similarly, for 'Semillon' vines, a comparable light attenuation gave decreases in canopy temperature of 3-5 °C below air temperatures (Greer *et al.* 2010). For grapefruit, similar levels of shade cover caused a 5 °C decrease in canopy temperatures as was also shown for coffee plants (Geromel *et al.* 2008). Thus, the shade covering in the present study, especially the higher density shade, was particularly effective in reducing canopy temperatures in keeping with these many other studies. The shade cover reduced light interception of the 'Shiraz' vines from full interception in the control canopy to a 55 % reduction in the heavy shade treatment. These differences were generally in accord with previous studies (Greer and Weedon 2012b, Caravia *et al.* 2016). There were no significant season (temperature) x light interception interactions on the maximum berry diameters of these 'Shiraz' grapevines nor on the relative berry growth rates but there were significant ($P < 0.005$) interactions in the timing of the start and finish of the 'Shiraz' berry expansion process. Across all seasons, as light interception decreased, berry expansion was progressively delayed up to 6 days and also longer to expand, by 4-5 d. Expansion also started earlier and finished soonest in the cooler 2011/12 season and started and finished later in the warmest 2013/14 season. It was notable that light interception had no effect on the berry size but the seasonal temperatures had a significant effect, with berry size reduced significantly in the 2013/14 season, consistent with deleterious effects of the extreme heat event. This conforms with Hulands *et al.* (2013), where 'Semillon' berries were highly responsive to light interception, where increases in PFD generally caused an increase in berry size while at moderate temperatures (25 °C) but caused a decrease in size at higher temperatures (35 °C). In contrast, 'Shiraz' berry growth was unaffected when vines were exposed to slightly elevated canopy temperatures (0.9-1.1 °C) and slightly increased berry temperatures (2.3-3.2 °C) compared with control vines (Sadras and Soar 2009) and probably at markedly lower temperatures compared with the present study.

The season x light interception interactions on berry dry weights and berry growth rates were not determinable in the present study as the dry weights were only determined in the 2013/14 season. However, there was a significant trend for the berry dry weights and rates of dry matter accumulation to decrease as light attenuation increased, such that berry weights were 10 % lower in the heavy shade treatment compared to the light shade treatment. While this may infer a temperature effect, given the heavy shade treatment was also the coolest treatment, no further evaluation was possible. However, there were significant light interception effects on the dynamics of berry dry matter accumulation. Notably, the start of the dry matter accumulation process was earliest for vines in the light shade treatment and a progressive delay occurred with each treatment decrease in light interception. Thus, an 18-d-delay occurred for the berries of vines in the heavy shade treatment in comparison with those on light shade vines. The termination of dry matter accumulation was also significantly affected by the treatment. For the berries on vines in the two most shaded treatments, this occurred between 144 and 146 DAB, whereas, for berries on vines in the light shade treatment, termination of berry dry matter accumulation was about 14 d earlier. For the control vines, the dynamics of berry dry matter accumulation conformed more closely to the more heavily shaded treatments. Thus, there was clear evidence that the dynamics of dry matter accumulation in 'Shiraz' berries were affected by light interception, with phenology progressively delayed as light interception decreased. Unfortunately, again there were no data on seasonal effects to assess the influence of temperature on the dynamics of dry matter accumulation in the present study. However, the timing of dry weight accumulation in hydrocooled and control 'Semillon' bunches was highly dependent on temperature and most favourable at 30 °C (Greer and Weedon 2016).

There was a significant season x light interception interaction on the brix accumulation and this was caused by the decrease in soluble solids concentration (TSS) from 21.0 to 13.7 °Brix (averaged over 140-154 DAB) from the 2011/12 to the 2013/14 growing seasons. This was consistent with the high temperatures in the last season having an apparent deleterious effect on accumulation of soluble solids, although the effect was transitory, as soluble solids concentrations were not different at harvest. Within each season, however, there were varying effects of the light interception treatments, with no significant effects in the 2011/12 (averaged 21.0 °Brix) or the 2013/14 (averaged 13.8 °Brix) growing seasons. By contrast, in the 2012/13 growing season, the soluble solids concentration increased significantly as light interception decreased, from 16.7 °Brix in the control treatment to 19.7 °Brix in the heavy shade treatment.

Light interception had few apparent effects on the dynamics of accumulating soluble solids during the berry ripening period. There were few treatment differences in soluble solids accumulation of 'Shiraz' berries of vines in the control and light shade treatments, however, for the berries of vines in the medium and heavy shade treatments, accumulation of TSS was delayed by up to 5 °Brix in all or some of the seasons, particularly during the middle of the ripening process (~ 110-145 DAB). This suggested low PFDs were unfavourable to the dynamics of soluble solids accumulation process and perhaps a consequence of low photosynthesis and reduced sugar supply (Greer and Weston 2010). Likewise, Caravia *et al.* (2016) reported delayed soluble solids accumulation in 'Shiraz' berries with 62 % shade over vines compared with control vines. Furthermore, 'Semillon' berries under 70 % shade also showed delayed accumulation, by 4-5 °Brix, compared to berries in an open canopy (Greer and Weedon 2012b). It was most notable in the 2013/14 season, where the differences in light interception had the most effect on the process of soluble solids accumulation, where the control and light shade treatments slowed down markedly during the high temperature period for over 15 d. This resulted in the soluble solids appearing to stagnate at a constant concentration for around 20 d (~ 130-150 DAB). By contrast, the berries in the medium and heavy shade continued to accumulate soluble solids throughout this high temperature exposure. Clearly, there were detrimental effects of the high temperatures on soluble solids accumulation process in the 'Shiraz' grape berries, as has been well described elsewhere for other cultivars (Mullins *et al.* 1992, Matsui *et al.* 1986, Greer and Weston 2010, Kliewer and Torres 1972, Kliewer *et al.* 1972).

There was a weakly significant ($P < 0.05$) light interception x seasonal interaction on the amounts of sugar accumulated. There were marked seasonal differences in the total amounts of sugar accumulated in the 'Shiraz' berries, averaged over all treatments, ranged from 294 (2013/14) to 500 mg·berry^{-1} (2011/12) and suggestive of a negative effect of high temperatures on the ripening process. Notably, in the 2013/14 season, the control and light shade treatments initially had accumulated more sugar than the other two treatments but during the high temperature event (over 15 d), sugar stopped accumulating (light shade) or even declined (control) but thereafter berries in both treatment resumed accumulating sugar, albeit at reduced rates. By contrast, the berries in the medium and heavy shade continued to accumulate sugar throughout this high temperature event, such that these berries accumulated over 300 mg sugar·berry^{-1} in contrast to berries in the control and light shade which accumulated 20-40 mg·berry^{-1} less sugar. These results clearly suggested the medium and heavy shade treatments provided protection from this heat event but also that light shade did confer some protection, given the higher sugar content in these berries compared to the control berries. These data, therefore, support the hypothesis that high light intensities exacerbated the detrimental effects of high temperatures on the 'Shiraz' berry ripening process. The seasonal differences in the total amounts of sugar accumulated in the 'Shiraz' berries, as indicated, was consistent with the effect of temperature, given the differences in temperature regimes across the three seasons. For example, the high sugar content accumulated in berries of all treatments in the 2011/12 occurred because the season was characterised by relatively fewer high canopy temperature incidences compared to the other seasons during the ripening period. The 2012/13 season was marked by about 7 d of high temperatures during this period, and the sugar contents for this season averaged over all treatments declined by 1.3-fold whereas the sustained high temperatures of the 2013/14 growing season caused a 1.7-fold decrease over all treatments compared to the 2011/12 season. Thus, it was evident that the temperature regime of the growing season had a marked effect on the total amounts of sugar accumulated by the berries and that the high temperatures were clearly detrimental to the sugar accumulation process. This conclusion was supported by Kliewer *et al.* (1972) for Thompson seedless and Greer and Weston (2010) for 'Semillon' berries, and both concluded that high temperatures impeded photosynthesis for several days and consequently reduced assimilate supply to the berries. Similarly, the sugar accumulation process was arrested for 5 d and the accumulation rate was reduced at harvest when high temperatures were applied at different stages of the ripening period in Semillon berries (Greer and Weston 2010) and the present results conform to these conclusions.

Conclusions

Altering light interception by differing shade cloth over "Shiraz" vines was clearly able to reduce the deleterious effects of high temperatures on the berry ripening process. Greater protection was conferred as the light interception was decreased. During the most severe heat event, reduced light interception conferred some protection but shade cloth density above 30 % conferred adequate protection, since only a small (2 %) depreciation in accumulated sugar occurred compared to the heavy 50 % shade density. These results conform to the hypothesis that concurrent radiation exposure of grapevines coupled with prevailing high temperature exacerbate the deleterious effects of high temperatures and measures to reduce the light exposure would be beneficial to maintain berry quality in regions with high summer temperatures.

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