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The Interactive Effects of Temperature and Light Intensity on *Vitis vinifera* cv. 'Semillon' Grapevines. II. Berry Ripening and Susceptibility to Sunburn at Harvest

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Summary

High light intensities and high temperatures occurring during the development of grape berries are known to have persistent effects on their growth and ripening processes and also induce sunburn and, therefore, reduce berry quality. *Vitis vinifera* cv. 'Semillon' grapevines were grown in controlled environments, exposed at three stages of berry development to short-term temperature and light treatments and, at the time of harvest, assessed for impacts on berry ripening and susceptibility to sunburn. Despite treatments being imposed during development, there were highly significant interactions between temperature and light intensity and the growth stage on berry size and sugar content when measured at harvest. Berries treated to the conditions at the early stage of development (pea size) were largely unaffected and there was no carryover at harvest. By contrast, when treated at the mid (veraison) and late stages, the treatment effects were very persistent especially the highest temperature and light intensity, which caused continued marked reductions in berry size and sugar content compared to when the treatments were applied. Although rates of ripening for berries treated early in development in all conditions actually increased at harvest whereas mostly the ripening rates declined for those berries treated at 30 and 38 °C and at the mid and late stages. There were similar interactive effects of temperature and light intensity on the susceptibility of the berries to sunburn, with nearly 100 % of berries affected when exposed to the highest temperature and the highest light intensity of 660 μmol m^{-2} s^{-1}. Again, stage of development had a marked influence with no sunburn occurring with vines treated early and most susceptible when treated late in development. These results suggest growers need to protect bunches in the late stages of development from exposure to high light intensities by maintaining an adequate canopy cover over bunches, especially when temperatures approach heat conditions.

Key words. berry size – controlled environment – photon flux density – rate of ripening – temperature – sunburn

Introduction

In a recent study, Hulands et al. (2013) demonstrated that berry growth and sugar accumulation of 'Semillon' grapevines were strongly affected by high temperatures and high light intensities. Most notably, these conditions caused berries to decrease in size and also reduced accumulation of sugar into the berries especially at 30 and 38 °C where these processes were increasingly affected. This is well in keeping with effects of high light intensities and temperatures on other varieties such as 'Cabernet Sauvignon' and 'Grenache' where berry mass declined at high compared to low irradiance, when concurrently exposed to high temperatures above about 38 °C (Bergqvist et al. 2001). Similarly, both a delay and a change in the rate of ripening occurred when 'Emperor' vines where grown in 8 % of full sunlight compared with those at full sun (Kliewer 1977b). Kliewer (1977a) also noted the reduction in berry size of 'Cabernet Sauvignon' and 'Tokay' berries as well as a concomitant reduction in sugar content with increasing temperature from 25 to 40 °C.

In addition to the effects of high light and temperature on 'Semillon' berries, there was a marked change in susceptibility to these conditions at different stages of berry development. For example, temperature and photon flux density had no marked effects on berry growth or sugar accumulation early in berry development whereas late in development these same conditions caused a significant decline in berry growth and a marked reduction in sugar content (Hulands et al. 2013). By contrast, Kliewer (1977a) noted with 'Cabernet Sauvignon' vines in particular that when exposed to high temperatures (37.5 and

40 °C) during the bloom – fruit set period had persistent effects on berry size and this was attributed to effects of temperature on cell enlargement. Furthermore, Hale and Buttrose (1974) also observed an effect of high temperatures on 'Cabernet Sauvignon' berry size when exposed to high temperatures in the early and mid stages of development but not when exposed during the late rapid growth phase. Thus, there does appear to be some cultivar variance in response high temperatures at the different stages of development. However, it remains to determine how persistent the effects the high light intensities and temperatures at the different stages of Semillon berry development had on the full growth of the berries at harvest.

One other consequence of fruit being exposed to high irradiance and/or high temperatures is a high incidence of sunburn, that is, brown lesions occurring on the fruit surface (Wünsche et al. 2001). Many different fruit, such as apples (Felicetti and Schrader 2009a), tomatoes (Cantore et al. 2009) and grapes (Greer et al. 2006; Chorti et al. 2010) are affected by such exposures. Damaged grape berries can often shrivel and increase markedly in soluble solids concentration (Kliewer and Lider 1968). These skin blemishes are often indicative of poor fruit quality (Schrader et al. 2009) and, therefore, of low economic returns to growers. Although the effects of high temperature and high irradiance on incidence of sunburn have been well investigated (Zhang et al. 2008; Chen et al. 2008; Felicetti and Schrader 2009b; Schrader et al. 2009), the majority of these studies have used field conditions where high temperatures were coupled to the high irradiance. Therefore, it is difficult to resolve the exact cause of the damage. By contrast, there are few papers where high light and temperature have been uncoupled to examine the specific interaction on sunburn severity.

Thus the objective of the present study was to assess the impacts on 'Semillon' berry growth and development, including susceptibility to sunburn, at harvest after exposures to a range of temperature and light intensities imposed during selected stages of berry development (sensu Hulands et al. 2013).

Materials and Methods

Plant material and growth conditions

Fifteen dormant potted *Vitis vinifera* cv. 'Semillon' grapevines (6 years old) were placed in a controlled environment chamber (TH6000, Thermoline Scientific, Smithfield, NSW, Australia) as described by Hulands et al. 2013). The photon flux density (PFD) was 700 μmol m^{-2} s^{-1} at plant height over a 12 h photoperiod and day/night temperatures were 25/15 ± 0.2 °C and vapour pressures were 1.0/0.6 ± 0.1 kPa. The vines were supplied with an automatic watering system and well supplied with nutrients.

Light and temperature treatments

At an early stage of development (berry size, approx 7 mm diameter), mid stage (berry ripening starting) and late stage (mid ripening, with soluble solids at approx. 16 °Brix), five vines each were transferred for 7 days to two additional controlled environment chambers with day/night temperature set at 30/20 ± 0.2 °C and 38/28 ± 0.2 °C. Five vines remained in the control growth conditions. Six bunches were selected within each stage and temperature regime from each vine and exposed at the bunch surface to a photon flux density of approximately 300 or 600 μmol m^{-2} s^{-1}. In each case, three replicates were used and three additional bunches were also selected and exposed to the prevailing chamber PFD. Further treatment details can be found in Hulands et al. (2013).

Berry diameter and soluble solids concentration

Once the bunches had reached a soluble solids concentration of 22 °Brix (135 days after budbreak), the vines were removed from the growth conditions. In each case, the bunches were removed and berry diameter measured on three berries per bunch with a microcaliper and then soluble solids concentration of each berry was measured, using a digital refractometer (PR-101, Atago, Tokyo, Japan). The total number of berries per bunch was also counted. The bunches were then assessed by counting the number of berries of each bunch that had symptoms of sunburn, and other damage, by scoring visually, symptoms of size and colour of brown lesions on the skin surface. In the case of severe sunburn, the whole berry was affected.

Statistics

All data were analysed using SAS ver. 9.13 statistical software (SAS Institute, Cary, NC, USA) with a general linear model (GLM) in all cases and least squares means and standard errors calculated. In all cases, the analyses used a fully randomised design and statistical significances determined at the 5 % level. Interactions between growth stage, temperature and light treatments and between growth stage, temperature and DAB treatments were investigated statistically using the GLM approach. All soluble solids concentrations were converted to amounts of sugar per berry using the procedure of Greer and Weston (2010b).

Results

Residual treatment effects on berry diameter

The harvest occurred 135 days after budbreak, which was 67, 24 and 13 days after the treatments at the early, mid and late stages of development, respectively. There were marked treatment differences apparent in berry diameter

(Fig. 1) with the interaction between temperature, PFD and growth stage highly significant (P = 0.003; r^2 = 0.54).

After exposure of bunches to 25 °C and the different PFDs within each growth stage, there were no statistical differences in berry diameter, which ranged between 12 and 13 mm across all stages. A similar result occurred for bunches treated at 30 °C and the different PFDs across all growth stages except that at the mid stage, where berries treated to a low PFD were significantly larger than those treated to the mid and high PFDs. Perhaps of note, however, was that berry diameters of bunches treated at the late stage were typically 11.5 ± 0.5 mm while at the early and mid stages, berry diameters were 12.8 ± 0.3 and 13.0 ± 0.3 mm, respectively, suggesting that the treatments had a greater effect during the late compared with the earlier stages of development.

In contrast, bunches treated at 38 °C were markedly affected by exposure to the different PFDs, with berry diameters significantly lower in the high PFD compared to the low PFD, across all stages of development (Fig. 1). Furthermore, berry diameters of these high PFD treated bunches were significantly lower than those exposed to the low PFD (8.5 ± 0.2 mm *cf.* 12.4 ± 0.4 mm) after treatment at 38 °C compared with those bunches treated at 30 °C (12.0 ± 0.6 *cf.* 13.0 ± 0.2 mm). Thus, there were no doubts that the high light and high temperature exposures, especially at the late stage of development, had persistent effects on berry growth, and caused marked berry shrinkage.

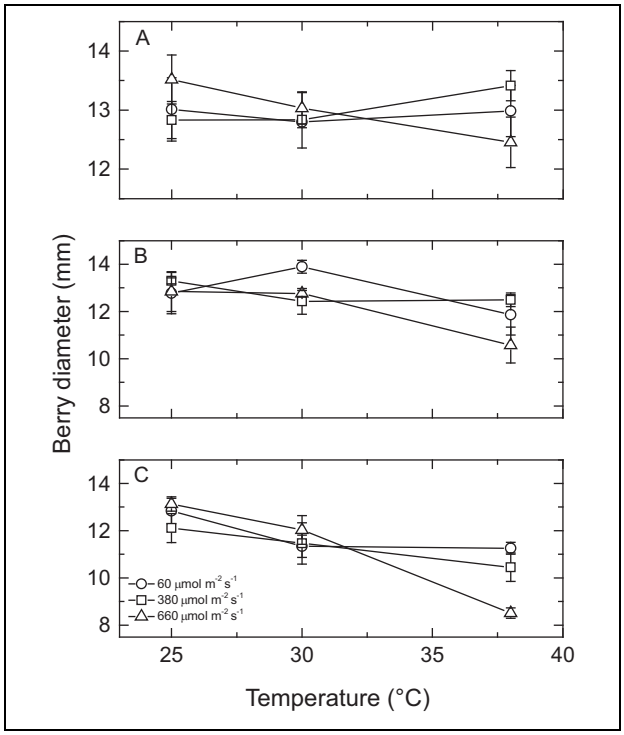


Fig. 1. Berry diameter at harvest (mm). The effect at harvest on berry diameter (Mean ± SE, N = 9) of 'Semillon' bunches treated to each of three PFDs (as indicated) as a function of temperature. The exposures occurred at each of three stages of bunch development; A, at pea size (68 DAB), B, at veraison (111 DAB) and C, at mid ripening (116 DAB).

Residual treatment effects sugar content

There was a high significant interaction (P = 0.0014, r^2 = 0.56) between temperature, PFD and the growth stage when the berry sugar content at harvest was considered and again indicative of residual treatment effects.

In most cases, the sugar contents had increased at harvest from when the bunches had been treated and were typically in the range of 0.27 to 0.35 g berry^{-1} (Table 1). However, in bunches from treatment at the early stage of development, there were few differences in sugar content that were significant between those treated to the different PFDs and temperatures. An exception was those treated at the highest PFD had a significantly (P < 0.05) lower sugar content when treated at 38 °C compared to those treated at 25 and 30 °C. A similar result occurred for bunches treated at the mid stage of development, but the sugar content also declined significantly between 30 and 38 °C for bunches treated at the lowest PFD and between 25 and 38 °C at the mid PFD. For those late stage treated bunches, a consistent effect occurred with those bunches treated to the highest PFD in that a significant decrease in sugar content again occurred when treated at 38 compared with 30 °C. Furthermore, those bunches treated at the highest PFD and temperature had the absolute lowest sugar content of all other bunches, reinforcing the marked impact of these treatment conditions on the ripening process. There were also significant decreases in sugar content between the 38 °C and 25 °C treated bunches at the mid and lowest PFD, confirming the marked impact of the high temperature on ripening. In addition, there were significant linear relationships between sugar content and temperature for the low PFD (P = 0.0448, r^2 = 0.64) and for the highest PFD (P = 0.0051, r^2 = 0.827) at the late stage of development. There was also a trend toward a linear temperature response at the highest PFD and at the early and mid stages of development in as much that the sugar content in berries was significantly lower at 38 compared with 25 °C.

Rates of ripening between the end of each treatment and harvest (Table 2) averaged 5.0 ± 0.6 mg berry^{-1} day^{-1} for the early stage and 5.7 ± 0.6 mg berry^{-1} day^{-1} for the mid stage treated vines and for the most part there was little effect of temperature or PFD on the rates. However, at the mid stage, the rate of ripening for bunches treated at 660 µmol m^{-2} s^{-1} was about 70 % lower at 38 than at 25 or 30 °C and similarly for those treated at 60 µmol m^{-2} s^{-1} but there was no temperature effect for those treated at 330 µmol m^{-2} s^{-1}. However, when averaged over the PFDs there was a temperature effect with a distinct optimum rate at 30 °C. By contrast, the rates of ripening

Table 1. Sugar content at harvest (g berry^{-1}). The effect at harvest on sugar content (mean ± SE, n = 9) of berries on 'Semillon' bunches treated previously to each of three photon flux density (PFD) treatments at each of three temperature treatments and at each of three different stages of bunch development. Also shown are the values averaged over the three PFDs and averaged over the three temperatures on each occasion (mean ± SE, n = 27).

Growth stage	Temperature (°C)	PFD (µmol m^{-2} s^{-1})			
		60	330	660	*Mean*
Early	25	0.321 ± 0.042	0.310 ± 0.027	0.371 ± 0.043	*0.334 ± 0.021*
	30	0.293 ± 0.007	0.356 ± 0.033	0.348 ± 0.030	*0.332 ± 0.016*
	38	0.305 ± 0.014	0.358 ± 0.023	0.259 ± 0.025	*0.308 ± 0.017*
	Mean	*0.306 ± 0.014*	*0.341 ± 0.016*	*0.326 ± 0.023*	
Mid	25	0.327 ± 0.046	0.373 ± 0.010	0.352 ± 0.073	*0.350 ± 0.026*
	30	0.438 ± 0.028	0.311 ± 0.036	0.340 ± 0.024	*0.363 ± 0.024*
	38	0.253 ± 0.050	0.300 ± 0.034	0.260 ± 0.038	*0.271 ± 0.022*
	Mean	*0.339 ± 0.034*	*0.328 ± 0.018*	*0.317 ± 0.029*	
Late	25	0.362 ± 0.048	0.316 ± 0.034	0.390 ± 0.032	*0.356 ± 0.022*
	30	0.237 ± 0.031	0.245 ± 0.047	0.337 ± 0.035	*0.273 ± 0.025*
	38	0.209 ± 0.016	0.279 ± 0.047	0.177 ± 0.016	*0.222 ± 0.021*
	Mean	*0.269 ± 0.029*	*0.280 ± 0.024*	*0.301 ± 0.035*	

Table 2. Rates of ripening (mg berry^{-1} day^{-1}) of 'Semillon' berries on bunches exposed to each of three photon flux densities (PFD) and three temperatures at each of three different stages of bunch development. The rates were determined between the post treatment sugar content and that at harvest (mean slope ± SE, N = 9). Thus, for the early treatment, the duration (60 days) was much longer than for the late treatments (12 days) and may have encompassed a non-linear change in sugar content.

Growth stage	Temperature (°C)	PFD (µmol m^{-2} s^{-1})		
		60	330	660
Early	25	5.3 ± 0.1	4.9 ± 0.4	5.8 ± 0.6
	30	4.7 ± 0.1	5.6 ± 0.5	5.6 ± 0.5
	38	4.5 ± 0.2	5.7 ± 0.3	4.6 ± 0.4
Mid	25	6.8 ± 0.5	6.4 ± 0.2	5.8 ± 0.2
	30	7.4 ± 0.1	7.8 ± 0.8	6.3 ± 0.1
	38	2.1 ± 0.1	6.8 ± 0.9	1.8 ± 0.5
Late	25	8.4 ± 0.4	−7.8 ± 0.3	13.8 ± 0.5
	30	−1.4 ± 0.5	16.4 ± 0.7	−7.1 ± 0.1
	38	−7.5 ± 0.5	6.3 ± 0.5	−21.9 ± 0.9

at the late treatment stage were highly variable. Negative rates occurred when the sugar content declined between treatment and harvest, with the result that the average rate at this stage was −0.1 ± 6.6 mg berry^{-1} day^{-1} over all treatments. However, there were also marked effects of temperature on the rates of ripening. At the lowest and highest PFDs, there was a marked decrease in the rate of ripening, become increasingly negative from 30 to 38 °C. This was most notable at the highest PFD when berries apparently lost sugar at a rate of nearly 22 mg berry^{-1} day^{-1}. There was an opposite trend at 330 µmol m^{-2} s^{-1}, because of a negative rate of ripening at 25 °C and positive rates at 30 and 38 °C.

Treatment effects on susceptibility to sunburn

There was a highly significant ($P < 0.0001$, $r^2 = 0.88$) interaction between temperature, PFD and growth stage on the proportion of each bunch exhibiting berries with sunburn symptoms at harvest (Fig. 2). For those treated at the early stage of development, there were no symptoms of sunburn (not shown) after any of the treatment exposures.

By contrast, the proportions of bunches exhibiting sunburn at the mid stage of development were highly dependent on temperature, with virtually no bunches affected at 25 °C and less than 8 % of the bunch at 30 °C. At 38 °C, the PFD had a marked effect, with those bunches treated at the low and medium PFD having about 10 % of the bunch with sunburn but at the high PFD, this increased to 50 ± 11 %. This trend was more pronounced at the late stage of development where, after treatment to the high PFD at 30 °C, was a marked increase in percentage of bunches with sunburn (26 ± 3 %).

The PFD during the exposure at 38 °C had a dramatically greater effect than at 30 °C, with nearly 20 % of the bunch with sunburn occurring after exposure to the lowest

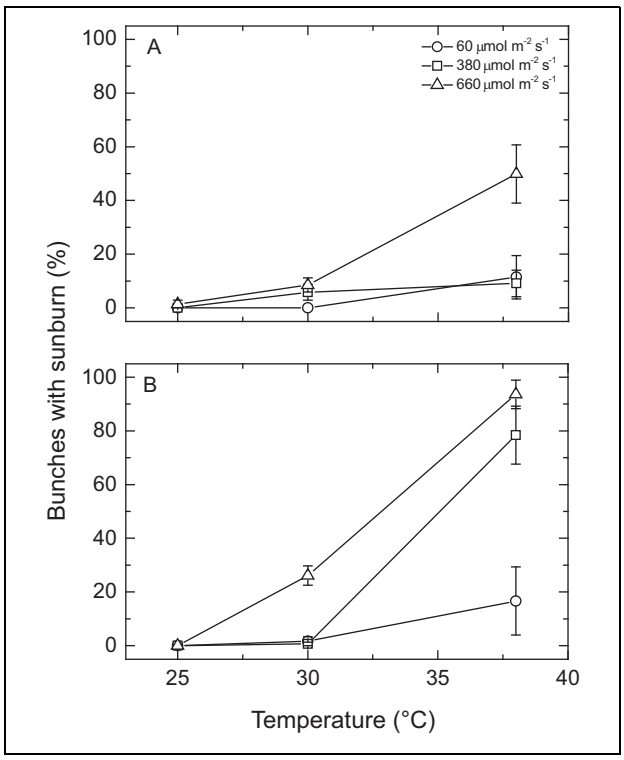


Fig. 2. Sunburn of 'Semillon' berries (%). The effect at harvest on the percentage of the bunch with sunburned berries (Mean ± SE, N = 9) for 'Semillon' bunches treated to each of three PFDs (as indicated) as a function of temperature. The exposures occurred at each of two stages of bunch development; A, at veraison (111 DAB) and B, at mid ripening (116 DAB). There was no evidence of sunburn in any berry on the bunches treated at the early stage of development.

PFD. Bunches treated to both the medium and high PFDs had much greater proportions affected; 78 ± 10 % and 94 ± 5 %, respectively, and these differences were just significant ($P < 0.05$). Thus, although there was an indication of sunburn occurring after treatment in the mid stage of development, it was at the late stage when the bunches became most susceptible to the temperature and PFD exposures.

Discussion

Residual treatment effects

While the treatments had immediate effects on berry diameter growth (*cf.* Hulands et al. 2013), it was clear that these effects also persisted right through to harvest. For the berries treated early in development, all increased in diameter from 9–10 mm to 12–13 mm. The light and temperatures treatments had only small effects, except there was a trend for the berries treated at the highest light intensity to decline in size with increasing temperature, although these berries were small at the time of treatment anyway. A similar trend was also apparent in berries treated at the mid and late stages, in that the high light, high temperature treated berries were the smallest and high light, low temperature treated berries were the largest. For both stages, it was apparent that berries in the high light, high temperature treatment decreased in size between the time of treatment and harvest. In addition, at the late stage, the reduction also occurred with berries treated at 30 °C and high light as well. This shows the short-term exposures to high light and high temperatures had very persistent effects on berry growth as also shown by Hale and Buttrose (1974) and Kliewer (1977a). Somewhat longer treatments at 20 and 30 °C at different growth stages of bunches of 'Aki Queen' vines appeared to cause no persistent effects on berry fresh weight (Yamane et al. 2006). However, when 'Cabernet Sauvignon' and 'Tokay' vines were treated during the bloom-set period (longer, but overlapping with the early stage of the present study) there were highly persistent reductions in berry volume and fresh weight, especially when treated at temperatures above about 32 °C (Kliewer 1977a). The effects, however, were much greater than occurred in the present study and this may have resulted from differences in treatment duration but there may have also been varietal differences in response to the treatments.

After the various treatments, accumulation of sugar in the 'Semillon' berries continued to occur from the time of treatment through to harvest for all bunches treated at both the early and mid stages of development. For these stages, there were no persistent treatment effects at the low and mid PFDs or between the various temperatures. By contrast, the berries treated at the highest PFD, on both occasions, had a 30 % reduction in sugar content between the high and low temperatures. Given that the early and mid stage treatments were applied 67 and 24 days prior to harvest, respectively, these results were consistent with a highly residual treatment effect. This conclusion is strongly confirmed with the treatments applied at the late stage (19 days before harvest), where sugar content declined by over 50 % between the high and low temperatures at the highest PFD. It was noteworthy that the sugar content of the high light, high temperature treated berries also declined by 40 % during the 14 days between treatment and harvest. This was indicative of the serious impact of this treatment on the ripening process and on the high susceptibility of the late stage of development to these high light and high temperature conditions.

Across all treatment stages and when averaged over all PFDs, the rate of ripening of the 'Semillon' berries was a temperature-dependent function, with an apparent optimum at 30 °C. This conforms with Kliewer (1977a) in that temperatures above 37 °C inhibited sugar accumulation. However, the actual rates of ripening varied with

berry development, consistent with a sigmoid pattern of sugar accumulation, and were maximal about the time of veraison at about 16 mg berry^{-1} day^{-1}. This temperature response was likely to account for the negative effects of the high temperature on sugar accumulation outlined earlier. It is more difficult to establish how high PFDs exacerbate the effects of temperature on the ripening process in the controlled growth conditions as used in the present study. It is unlikely that the source and transport of sucrose was affected as the light was focussed directly onto the bunch. More research is clearly needed to establish how the interaction between PFD and temperature influenced the rate of ripening.

Susceptibility to sunburn

By contrast to the effect of light on ripening, the effect on skin properties is better understood and can result in chlorophyll and other pigment losses (Schrader et al. 2009) as well as enhancement of phenolic compounds (Wünsche et al. 2001; Greer et al. 2006; Chorti et al. 2010). In the present study, there was no sensitivity of the berry skin to the temperature and PFD treatments when applied at the early stage of development and no occurrence of sunburn at the time of harvest was evident. By the time of veraison, however, the situation had changed and a very definite interaction between PFD and temperature had occurred. No bunches had any sunburn when treated at 25 °C and only a few berries were affected when treated at 30 °C. By contrast, at 38 °C and at PFDs below about 400 μmol m^{-2} s^{-1}, only small numbers of berries (ca 10 %) were susceptible to sunburn whereas at a PFD of 660 μmol m^{-2} s^{-1}, the susceptibility increased to well over 40 % of berries on each bunch. The same response occurred in the late stage of development but the effects were magnified at 30 and especially 38 °C, where the percentage of berries per bunch that were sunburned increased to close to 100 % at the highest PFD. Thus, we can conclude that susceptibility of the 'Semillon' berries to sunburn was highest at the late stage of development and that the higher the temperature and the higher the PFD, the greater was the extent of sunburn. Similar results occurred with 'Merlot' berries exposed to high PFDs and high temperatures (Spayd et al. 2002), in 'Chardonnay' berries (Greer et al. 2006), 'Semillon' berries (Greer and Weston 2010a) and in 'Kerner' and 'Portugieser' berries (Düring and Davtyan 2002).

Previous results have suggested that sunburn was primarily caused by high temperatures (Wünsche et al. 2001). However, Smart and Sinclair (1976) and more recently Bergqvist et al. (2001) have shown berry temperatures increase linearly with increasing light intensities. Thus, it is relatively difficult to separate the effect of temperature from that of light intensity in many of these studies in vineyard conditions. By contrast, in the present study, the temperature was effectively uncoupled from the PFD, enabling assessment of berry responses to temperature independently from that of light. There was no doubt that sunburn susceptibility increased both with an increase in temperature but also with an increase in light intensity. However, the interaction between temperature and light intensity was statistically strong ($P < 0.0001$), indicating that the effect of temperature on sunburn was exacerbated by light intensity and vice versa.

Conclusions

The high light and high temperatures imposed well before the berries were fully ripe had very persistent effects on the growth, ripening and susceptibility of the berries to sunburn. Mostly, the latest treatments imposed at the mid ripening stage had the most effect at harvest, reducing berry size and reversing the accumulation of sugar. However, the highest light intensity accompanied by the highest temperature had a persistent effect at harvest after treatments were imposed at all stages of development. These effects had major impacts on berry quality at harvest, with a marked reduction in ripening but the propensity of the berries to sunburn increased also in accord with increasing light and temperature, adding to the poor quality of the berries.

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References

Bergqvist, J., N. Dokoozlian and N. Ebisuda 2001: Sunlight exposure and temperature effects on berry growth and composition of 'Cabernet Sauvignon' and 'Grenache' in the Central San Joaquin Valley of California. Am. J. Enol. Vit. **52**, 1–7.

Buttrose, M.S., C.R. Hale and W.M. Kliewer 1971: Effect of temperature on the composition of 'Cabernet Sauvignon' berries. Am. J. Enol. Vit. **22**, 71–75.

Cantore, V., B. Pace and R. Albrizio 2009: Kaolin-based particle film technology affects tomato physiology, yield and quality. Env. Exp. Bot. **66**, 279–288.

Chen, L.-S., P. Li and L. Cheng 2008: Effects of high temperature coupled with high light on the balance between photooxidation and photoprotection in the sun-exposed peel of apple. Planta **228**, 745–756.

Chorti, E., S. Guidoni, A. Ferrandino and V. Novello 2010: Effect of different cluster sunlight exposure levels on ripening and anthocyanin accumulation in 'Nebbiolo' grapes. Am. J. Enol. Vit. **61**, 23–30.

Düring, H. and A. Davtyan 2002: Developmental changes of primary processes of photosynthesis in sun- and shade-adapted berries of two grapevine cultivars. Vitis **41**, 63–67.

Felicetti, D.A. and L.E. Schrader 2009a: Changes in pigment concentrations associated with sunburn browning of five apple cultivars. I. Chlorophylls and carotenoids. Plant Sci. **176**, 78–83.

Felicetti, D.A. and L.E. Schrader 2009b: Changes in pigment concentrations associated with sunburn browning of five apple cultivars. II. Phenolics. Pla. Sci. **176**, 84–89.

Greer, D.H., S.Y. Rogiers and C.C. Steel 2006: Susceptibility of 'Chardonnay' grapes to sunburn. Vitis **45**, 147–148.

Greer, D.H. and C. Weston 2010a: Effects of fruiting on vegetative growth and development dynamics of grapevines (*Vitis vinifera* cv. 'Semillon') can be traced back to events at or before budbreak. Func. Plant Biol. **37**, 756–766.

Greer, D.H. and C. Weston 2010b: Heat stress affects flowering, berry growth, sugar accumulation and photosynthesis of *Vitis vinifera* cv. 'Semillon' grapevines grown in a controlled environment. Func. Plant Biol. **37**, 206–214.

Hale, C.R. and M.S. Buttrose 1974: Effect of temperature on ontogeny of berries of *Vitis vinifera* L. cv. 'Cabernet Sauvignon'. J. Am. Soc. Hort. Sci. **99**, 390–394.

Hulands, S., D.H. Greer and J.D.I. Harper 2013: The Interactive effects of temperature and light intensity on *Vitis vinifera* cv. 'Semillon' grapevines. I. Berry growth and development. Eur. J. Hort. Sci. **78**, 249–257.

Kliewer, W.M. and L.A. Lider 1968: Influence of cluster exposure to the sun on the composition of 'Thompson Seedless' fruit. Am. J. Enol. Vit. **19**, 175–184.

Kliewer, W.M. 1977a: Effect of high temperatures during the bloom-set period on fruit-set, ovule fertility, and berry growth of several grape cultivars. Am. J. Enol. Vit. **28**, 215–222.

Kliewer, W.M. 1977b: Influence of temperature, solar radiation and nitrogen on coloration and composition of 'Emperor' grapes. Am. J. Enol. Vit. **28**, 96–103.

Schrader, L.E., J. Zhang, J. Sun, J. Xu, D.C. Elfving and C. Kahn 2009: Postharvest changes in internal fruit quality in apples with sunburn browning. J. Am. Soc. Hort. Sci. **134**, 148–155.

Smart, R.E. and T.R. Sinclair 1976: Solar heating of grape berries and other spherical fruits. Agric. Met. **17**, 241–259.

Wünsche, J.N., D.H. Greer, J.W. Palmer, A. Lang and T. McGhie 2001: Sunburn – the cost of a high light environment. Acta Hort. **557**, 349–356.

Yamane, T., S.T. Jeong, N. Goto-Yamamoto, Y. Koshita and S. Kobayashi 2006: Effects of temperature on anthocyanin biosynthesis in grape berry skins. Am. J. Enol. Vit. **57**, 54–59.

Zhang, J., S. Chen, Y. Li, B. Di, J. Zhang and Y. Liu 2008: Effect of high temperature and excessive light on glutathione content in apple peel. Front. Agric. China **2**, 97–102.

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