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To cite this article: Dennis H. Greer & Mark M. Weedon (2019) Can a small differential in canopy temperature influence performance of Semillon in a vineyard?, New Zealand Journal of Crop and Horticultural Science, 47:1, 63-82, DOI: 10.1080/01140671.2018.1523197

To link to this article: https://doi.org/10.1080/01140671.2018.1523197

Published online: 19 Sep 2018.
Can a small differential in canopy temperature influence performance of Semillon in a vineyard?

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ABSTRACT
Vegetative and reproductive growth responses of vineyard-grown Vitis vinifera cv. Semillon vines to canopy temperatures were followed. Canopies were controlled at means of 29.8°C, 31.5°C and 32.7°C. Stem and leaf growth were affected; length and canopy leaf area was maximal in the warmest treatment and smallest in the coolest treatment. Accumulation of biomass of leaves, stems and bunches was highest in the coolest treatment and lowest in warm conditions. Berry expansion was affected by treatment temperatures but most reduced in the warm treatment, whereas accumulation of sugar in the berries was highest in the coolest treatment. There were treatment differences in yield, with a marked reduction in the warm treatment. Clearly, there were detrimental growth responses to the higher temperatures. The temperature differential between treatments of 3°C was comparable with what might occur with climate change and the study shows such a difference can be detrimental to vine growth and development.

ARTICLE HISTORY
Received 12 July 2018
Accepted 7 September 2018

KEYWORDS
Berry growth; biomass accumulation; climate change; leaf area expansion; stem lengths; sugar accumulation; vine architecture

Introduction
Temperature is the main moderating influence of plant growth through the effects on the rates of growth and development. For example, rates of budbreak of deciduous species such as grapevines are a linear function of mean temperature, at least up to 20°C with a base temperature of about 5°C (Moncur et al. 1989), although a base temperature of about 9°C has also been suggested (Oliveira 1998). Similarly, the rates of budbreak of cv. Cabernet Sauvignon were a linear function of mean temperature (estimated from Keller et al. 2010; Keller and Tarara 2010) and increasingly faster between 10°C and 20°C. For other species, including Picea glauca (Rongzhou and Pengxin 2010), a similar relationship holds but for this species and Pseudotsuga menziesii, the relationship between rates of budbreak and temperature was non-linear (Campbell and Sugano 1979). A similar non-linear relationship was evident for rose (van den Berg 1987), with rates increasing over 6-fold between 10°C and 25°C. It was notable that across these diverse species, rates of budbreak at about 17°C to 20°C were about 0.06 buds day$^{-1}$ except for the rose, which was higher at 0.13 buds day$^{-1}$.

Once budbreak has occurred, leaf appearance is initiated and again this process is also highly temperature-dependent. A linear relationship between temperature and rates of leaf
appearance, at least between about 8°C and 25°C has been demonstrated for the grapevine cultivar Mataro (Moncur et al. 1989) and for the cv. Grenache (LeBon et al. 2004) up to a mean air temperature of 23°C. A similar relationship between leaf appearance and temperatures up to 25°C has also been demonstrated for sunflower (Villalobos and Ritchie 1992). By contrast, leaf appearance of Actinidia deliciosa vines was curvilinearly dependent on temperatures between about 12°C and 28°C (Greer et al. 2004). Other processes such as leaf elongation and expansion (Tardieu et al. 2000; Seleznova and Halligan 2006; Parent and Tardieu 2012), shoot growth (Buttrrose 1969; Junttila 1986; Keller and Tarara 2010) and biomass accumulation (Buttrrose 1969) are also highly temperature-dependent.

For many of the growth and development processes, exposure to high temperatures can be at best limiting to at worst deleterious (Mittler 2006). For example, total biomass of two potato cultivars were markedly reduced when exposed to a heat treatment of 31°C for 4 weeks. Similarly, a 5-day exposure to 40°C caused a large decrease in biomass of wheat kernels (Stone and Nicolas 1995). Growth of several grapevines cultivars for 13 weeks at 35°C also caused a marked reduction in whole vine biomass compared to growth at 25°C (Buttrrose 1969). Furthermore, average shoot growth rates of cv. Chenin Blanc vines were severely decreased after a 12-day exposure to 40°C (Sepúlveda et al. 1986). Consistent with this, whole season accumulation of biomass by Semillon shoots exposed to a hot climate was also reduced in comparison with vines that were protected (Greer and Weedon 2014a).

Reproductive growth is also highly susceptible to high temperatures. The flowering process is particularly susceptible, with all flowers on cv. Semillon grapevines abscising after being exposed to a 4-day heat treatment at 40°C and berry expansion was also affected (Greer and Weston 2010b). This was also noted with Cabernet Sauvignon berries exposed at 40°C (Kliwer 1977). Consistent with this, berries of Chenin Blanc and Chardonnay vines exposed to 12 days at 40°C (Sepúlveda et al. 1986) shrivelled badly, consequently the soluble solids increased to over 30° Brix (see also Radler 1965). Thus, many aspects of vegetative and reproductive growth are affected by temperature, particularly those towards the upper range of tolerance. Many of these studies into high temperatures were undertaken in controlled environments (Sepúlveda et al. 1986; Greer and Weston 2010b) given the difficulty of achieving desired temperatures in field conditions.

Greer and colleagues (Greer et al. 2010; Greer and Weedon 2014a, 2016) have had a major focus on determining the effects of high temperatures on the highly economically important grapevine cultivar Semillon. Covering vines with shade cloth was effective at reducing canopy temperatures by 4°C to 6°C and was beneficial in preventing a heat-induced impact on berry ripening (Greer and Weedon 2013) but this strategy was costly in terms of biomass accumulation and the net carbon balance (Greer et al. 2011). Another strategy was to use a hydrocooling system and this was used to maintain canopy temperatures at 30°C to 40°C (Greer and Weedon 2016) and shown to be beneficial for vine growth. Several other studies have documented the effectiveness of intermittently spraying water onto grapevines vines (Gilbert et al. 1970; Kliwer and Schultz 1973; Aljibury et al. 1975) when they were exposed to high temperatures and reductions in berry and canopy temperatures in the order of 8°C to 10°C were achieved. Similar results have occurred with other crops (Brewer et al. 1979; Iglesias et al. 2002; Gindaba and Wand 2005; Pelletier et al. 2016). Much of this work has confirmed high temperatures
were detrimental to the growth and developmental processes of different plant species. However, how the vine architecture, leaf area and stem extension dynamics and biomass distribution are affected has not been determined.

The objective of the present study, therefore, was to evaluate Vitis vinifera cv. Semillon vine vegetative and reproductive growth and development at different canopy temperatures in field-grown vines to quantify the dynamic growth and biomass allocation responses to high temperatures. In addition, the objective was to ascertain if a small difference in canopy temperature, in line with climate change expectations, would reveal differences in response. Canopy temperature control was achieved by using the hydrocooling system of Greer and Weedon (2014a; Greer and Weedon 2016).

Materials and methods

Field site

This study was undertaken on a commercial vineyard in the Riverina region of NSW, Australia over the 2011/2012 growing season as described by Greer and Weedon (2014a). Vines were grown in rows orientated in a north–south direction at 1.8 m spacing between vines and 3.5 m between the rows and trained on a vertically shoot positioned (VSP) trellis and spur pruned. Vines were drip irrigated with drippers at 0.6 m spacing and delivered 2.4 L h\(^{-1}\) for 12 h per week (12.5 L day\(^{-1}\)) until veraison when the irrigation was increased to 24 h per week (24.7 L day\(^{-1}\)) and the nutrition was supplied through the dripper system. Mid-day water potentials (\(\psi\)) of well exposed leaves measured on each vine in each treatment in mid-summer (118 Days after budbreak, DAB) indicated there were no significant differences between the treatments, \(\psi = -1.5\) to \(-1.6 \pm 0.07\) MPa when the hydrocooling treatments were active. Budbreak occurred in early September, flowering in early November and fruit set in mid-November and harvest occurred in early February (9/2).

Canopy temperature control

The canopy temperatures were controlled by the hydrocooling system based on that described by Greer and Weedon (2016) and was installed and started in the vineyard 60 days after budbreak (DAB). This system enabled water to be sprayed on to the vines when set temperatures were exceeded and the vines were sprayed for 60 s and 5 min were left for drying and evaporative cooling to occur. On each occasion, the vines were sprayed with 66 mL per nozzle and up to 800 mL per hour. These small amounts contributed nothing to the irrigation, as all the fine droplets were quickly evaporated. Three temperature treatments were set up, each comprising two panels each of three vines and replicated twice and the temperatures of each treatment were controlled at selected temperatures. The hydrocooling system was typically on between 1000 and 1700 h and sprayed at a maximum of 10 times per hour and the hydrocooling was on demand for 35, 22 and 5 days for the three treatments. Canopy temperatures were measured on each side (East and West) of the centre vine of one panel in each treatment and replicate, using an infrared temperature sensor with a 22\(^\circ\) view (IRRP, Apogee, Logan UT, USA). This was located 1.2 m height off the ground and 0.3 m out in the inter row space and pointed towards
the canopy. The sensors were connected to a datalogger (CR1000, Campbell Scientific Australia, Townsville, Qld) and hourly averages recorded. Air temperature and relative humidity (HMP50, Vaisala, Helsinki, Finland) placed within a protected white screen as well as irradiance measured with a quantum sensor (LI190s, LiCor, Lincoln, NEB, USA) were placed 500 mm above the canopy and measured with the datalogger at similar intervals.

**Vine measurements**

**Budbreak and phenology**
From early September until Mid-October, for each of six vines in each treatment and replicate, phenology was followed on one representative shoot using the modified E-L system of Coombe (1995) and budbreak was determined at E-L stage 4 where the green tips were first visible.

**Shoot growth**
Two shoots on each of three vines in each treatment and replicate and on either side of the vines where tagged shortly after budbreak (total of 12 shoots per treatment) and shoot lengths measured from late October (40 DAB) and continued through to late December (106 DAB) and measured at about 5-day intervals. Starting from about 10 days after budbreak (DAB) in late September, the length and width dimensions of all leaves present and at least 10 mm in width were measured on each of two of the tagged shoots of each vines for all treatments and replicates. These measurements were continued at 9–12-day intervals until about 90 DAB in mid-December. In that time, up to 30 leaves had appeared in some cases but 25 leaves were more typical. The leaf dimension were converted to leaf area by the product of the length and width following Sepúlveda and Kliewer (1983).

**Berry diameter and soluble solids**
From about 105 DAB, berry diameters of three berries from the upper, middle and basal segments of a bunch from one shoot of six vines of each treatment and replicate (total of 36 berries) were measured with a microcaliper at intervals of 3–5 days. These berries were destructively harvested and total soluble solids measured with a digital refractometer (PR-101, Atago, Japan). Berry sugar content was calculated using the berry diameters to estimate berry volume and converting the total soluble solids measurements to sugar concentration according to Greer and Weedon (2014a).

**Yield**
At harvest, all bunches were removed from each vine in the treatments and replicates and counted and the total bunch fresh weight per vine measured. These bunches were then transported to the laboratory and those on the tagged shoots separated into the components (berries, rachis) and number of berries per bunch counted and then the berry fresh weight determined.
**Biomass determination**

At the time of the fruit harvest, all of the tagged shoots were also destructively harvested and taken back to the laboratory. Main stem and lateral leaves were removed from each shoot, counted and areas of individual main stem leaves and total lateral leaf area determined with a leaf area meter (LI-3000, LiCor, USA). These leaves, stem and selected whole bunches were then dried for 2–3 weeks at 60°C and then weighed to determine the biomass. Individual berries and the bunch rachis were also dried in the same conditions and weighed.

**Data analysis**

All data were analysed using generalised linear models (GLM) with SAS V9.3 (SAS Institute, Cary, NC, USA) and least squares means and standard errors determined. All data were analysed assuming a fully randomised design and statistical significance was assessed at the 5% level. The Boltzmann sigmoid function was fitted using Origin V8.1 (OriginLab Corporation, Northampton, MA, USA) to leaf expansion, shoot extension and sugar accumulation over parts of the growing season.

**Results**

**Canopy temperatures and vapour pressures**

The mean daily air temperatures across the growing season (Figure 1A), were typically between 25°C and 35°C in early spring but generally increased over time, such that in mid-summer, the temperatures were ranging between 30°C and 40°C. The treatment canopy temperatures (not shown) averaged 29.8°C (21.6°C (min) – 33.5°C (max), 31.5°C (22.7°C to 35.7°C) and 32.7°C (22.9°C to 38.3°C)), hereafter referred to as low, medium and high canopy temperatures, while the air temperature averaged 35.0°C (23.6°C to 42.9°C). The mean daily vapour pressures (Figure 1B) ranged between 3 and 5 kPa across the season, indicative of the dry climate.

Across the season, the daily maximum photon flux density (not shown) averaged 1200–1400 µmol (photons) m⁻² s⁻¹ in spring and increased to 1400–1600 µmol (photons) m⁻² s⁻¹ in mid-summer.

**Phenology**

Budbreak occurred on the 8th September (Figure 2) and then the first inflorescences were separated on 20th of September and the leaf growth up to node 10 had commenced by the 12th of October. There were no treatments applied at this time so all data were pooled.

**Shoot growth**

Shoot extension across the season had already commenced by the time measurements had started (Figure 3) and it was evident that there were major differences in shoot lengths. Thus, the shoots were separated into those that had fewer than 19 nodes (cf. Greer et al. 2010) defined as medium length shoots, (Figure 3A) and those had more nodes.
defined as long shoots, (Figure 3B). For the low temperature treatment vines, 42% of shoots were medium length, and for the medium and high treatment treatments, 33% and 52% were medium length shoots, respectively. The average length for the medium shoots over all treatments was 611 ± 9 mm. There was a significant ($P < 0.0014$) treatment * DAB interaction and for the vines of the low temperature treatment, the stems were the shortest (598 mm) compared with those vines in the medium temperature treatment which were the longest (622 mm) but the dynamics of growth were not significantly different and the timing of maximum extension averaged 49.6 ± 3 DAB, the window of maximum growth averaged 8.9 ± 0.9 days and the extension rate averaged 0.056 ± 0.003 mm day$^{-1}$.

For the long shoots (Figure 3B), which averaged between 48% and 67% of the measured shoots, there was also a highly significant ($P < 0.0001$) treatment * DAB interaction. The average length over all treatments was 902 ± 13 mm and, again, the differences between the vines in the medium temperature treatment, which again had the longest shoots (945 mm), were significantly longer compared to those vines in the low temperature treatment (847 mm) and high temperature treatment (882 mm). Dynamics of growth were also

\textbf{Figure 1.} The seasonal changes in daily mean air temperature A and mean daily vapour pressures B in the Vitis vinifera cv. Semillon vineyard.
significantly different (Table 1), with the timing of when the maximum extension of the shoots occurred was delayed from 50 to 64 DAB as the temperature treatment increased. By contrast, the window of rapid growth was shortened from about 8 days in the low temperature treatment to about 5 days in the high temperature treatment and the relative extension rate also increased in the same pattern. This suggested the dynamics of long shoot extension were enhanced by higher temperatures.

**Leaf area expansion**

For the leaves appearing in the first preformed (see Seleznyova and Greer 2001) cohort (1–6 nodes), there were no temperature treatment effects (appeared before treatments applied) and the leaves all expanded similarly, as shown for leaves at node 5 (Figure 4A) for example, at rates between 1.49 and 1.55 ± 0.19 cm² day⁻¹ and reached a maximum area of 0.0152 ± 0.0004 m². For the leaves in the second cohort (7–19 nodes), also from preformed primordia (Greer and Weston 2010a), there were also no temperature treatment effects as shown for leaf 12 (Figure 3B), which expanded at an average rate of 1.35 ± 0.22 cm² day⁻¹ and had a maximum leaf area of 0.0127 ± 0.0004 m². However, for leaf 16 (Figure 3C) also probably from a preformed primordium, there were effects of the temperature treatments, with expansion rates of 1.85 ± 0.08 and 2.1 ± 0.22 cm² day⁻¹, and maximum leaf areas of 0.0093 ± 0.0003 m² and 0.0107 ± 0.0003 m², for the high and medium temperature treatments, respectively with the rates and sizes in between for the low temperature treatment. However, those leaves appearing at nodes with *de novo* (Greer and Weston 2010a) formed primordia (> node 20), were affected by the temperature treatments, as shown for leaf 22 (Figure 3D) as an example. The leaves in the high temperature treatment expanded at the slowest rates at 0.74 ± 0.11 cm² day⁻¹ while those in the low temperature treatment expanded at a significantly (*P* < 0.05) higher rate of 1.03 ± 0.07 cm² day⁻¹ but those in the medium temperature

**Figure 2.** Changes in phenology across the early part of the growing season of Semillon grapevines grown in an irrigated vineyard and based on the Coombe (1995) E-L scoring system. Also shown are selected stages in the phenological calendar.
treatment expanded at the significantly highest rate of $1.21 \pm 0.08 \text{ cm}^2 \text{ day}^{-1}$. Notably, the leaves at node 22, and to some extent also those at node 16, had not completed expansion thus the final leaf areas and hence dynamics of growth were not determined.

The leaf size distribution along the shoot at harvest (Figure 5) confirmed that the temperature treatments had little effect on the final areas of almost all the preformed leaves. However, consistent with Figure 4D, those leaves along the shoot from about node 18

**Table 1.** Attributes (mean ± SE, $N = 16$) of fitting the Boltzmann sigmoid function to the long shoot extension of *Vitis vinifera* cv. Semillon vines treated to three different canopy temperature treatments (see text).

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Length (mm)</th>
<th>Timing (DAB)</th>
<th>Window (Days)</th>
<th>RER (mm d$^{-1}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Low</td>
<td>850 ± 3.3</td>
<td>50.0 ± 2.1</td>
<td>7.9 ± 0.5</td>
<td>0.063 ± 0.005</td>
</tr>
<tr>
<td>Medium</td>
<td>943 ± 3.7</td>
<td>53.2 ± 1.1</td>
<td>7.7 ± 0.4</td>
<td>0.065 ± 0.004</td>
</tr>
<tr>
<td>High</td>
<td>883 ± 2.2</td>
<td>63.8 ± 0.5</td>
<td>5.2 ± 0.3</td>
<td>0.096 ± 0.006</td>
</tr>
<tr>
<td>$P$</td>
<td>0.01</td>
<td>0.01</td>
<td>0.05</td>
<td>0.01</td>
</tr>
</tbody>
</table>

Notes: Length represents the estimated maximum shoot length, Timing represents the time of maximum shoot extension, the Window represents the duration of the maximum rate and RER represents the relative extension rate. Also shown is the probability $P$, of the treatments being significant.
in the high temperature treatment had significantly smaller areas from the other treatments and those leaves on vines in the low temperature treatment were intermediate in size in comparison to those of the medium temperature treatment vines (see inset Figure 5). Even though leaves at nodes along the shoot beyond position 20 were not fully expanded, the results suggested the highest temperatures were unfavourable and reduced the rates of expansion whereas the low temperature treatment was perhaps too cool and also reduced rates of expansion compared to the medium temperature treatment.

**Biomass allocation at harvest**

Across all mean temperatures (Figure 6A), there were highly significant ($P < 0.0001$) differences in the total (main stem + laterals) leaf biomass at harvest, with a significant decrease for the vines in the low temperature treatment to the vines in the high temperature treatment. Across all treatments, leaf biomass, ranged from 22 to 30 g, and on average, was $32 \pm 2\%$ of the total biomass. By contrast, stem biomass (Figure 6B) across all treatments (9–14 g) averaged $13.7 \pm 0.9\%$ of the total biomass but was also significantly lower than the leaf biomass, by about two-fold. There were also highly significant ($P < 0.0001$, $r^2 = 0.22$) treatment differences in stem biomass, again with a trend of decreasing stem biomass for the vines in the low to the high temperature treatments.
Figure 5. Final leaf area (mean ± SE, N = 16) distribution of the leaves along the shoot measured at harvest for Semillon vines in the temperature treatments, as indicated. The arrow indicates the last leaf along the shoot to be fully expanded. The inset graph shows the same data for node positions 18–25 but at an expanded scale to express the treatment differences.

Figure 6. Changes in biomass allocation (mean ± SE, N = 12) to the leaves A, stems B, and bunches C and the total shoot biomass D for Semillon vines in the temperature treatments, as indicated. In all cases, there were highly significant (P = 0.025 < 0.001) differences in the biomass between the various treatments.
Bunch biomass (Figure 5C) was more than two-fold higher than the leaf biomass and there were significant ($P = 0.025$, $r^2 = 0.22$) treatment differences between the low and medium temperature treatments (average $61.1 \pm 2.9$ g) compared with the high temperature treatment (average $49.8 \pm 1.9$ g) but not significantly different between two warmer temperature treatments. Across all treatments, bunch dry matter averaged $54 \pm 3\%$ of the total biomass.

There were significant ($P = 0.0036$, $r^2 = 0.31$) treatment differences in the total biomass (Figure 5D) of the shoot. In keeping with the lower accumulation of biomass as stems, leaves and bunches, the vines in the high temperature treatment also had the lowest total biomass. The vines in the low temperature treatment had the highest total biomass and significantly so compared to the other treatments.

**Berry growth**

The diameters of the berries across the later part of the growing season (Figure 7A) were initially similar between the vines of the different treatments. However, there was a markedly slow expansion of the berries of the vines in the high temperature treatment. By

![Figure 7](image_url)

**Figure 7.** Changes (mean ± SE, $N = 36$) in berry expansion **A** and total soluble solids accumulation **B** across the growing season for bunches of Semillon vines in temperature treatments, as indicated. Linear regressions determined between 105 and 125 DAB for the soluble solids accumulation rates were all highly significant ($P < 0.0001$, $r^2 = 0.973–0.981$) and the slopes were, $0.358 \pm 0.020$, $0.328 \pm 0.021$ and $0.298 \pm 0.020°$ Brix day$^{-1}$ for the low, medium and high temperature treatments, respectively.
contrast, for the other treatments, berry growth was greater, with the largest berries in the medium temperature treatment measurement period and significant differences in berry diameter between the treatments. In all treatments, it appeared that the berry expansion process had largely been completed by 125 DAB and thereafter there was some berry shrinkage in all treatments.

In contrast to berry expansion, accumulation of total soluble solids (Figure 7B) occurred in a similar pattern for the berries in all treatments. In addition, there was a significant ($P < 0.032, r^2 = 0.41$) interaction between treatment and day, with a consistently higher TSS in the low and high temperature treatments and significantly lower TSS for those vines in the medium temperature treatment. It was uncertain why berries in the highest and lowest temperature treatments had a similar pattern of soluble solids accumulation.

The sugar content (Figure 8) increased over the later part of the growing season in concert with accumulation of soluble solids concentration and with a highly significant ($P < 0.0001, r^2 = 0.23$) treatment * day interaction occurred. There was a strong and consistent effect of temperature treatment; berries in the low temperature treatment had the fastest accumulation and highest sugar content at 498 ± 7 mg and content declined progressively as the temperature treatment increased to where the content had decreased to 445 ± 7 mg. Sugar accumulation for all treatments were all highly significant ($P < 0.0001, r^2 = 0.969–0.984$) sigmoid functions and the attributes indicated the dynamics were mostly significantly different (Table 2). The shortest window of maximum accumulation and the highest rates occurred in berries of the low temperature treatment vines and the longest window of sugar accumulation and slowest rates occurred in the vines of the high temperature treatment and these differences were highly significant. However, for the vines in the medium temperature treatment sugar accumulation was intermediate in timing and with the relative rate of sugar accumulation but the overall pattern was close to those vines in the high temperature treatment. This indicated sugar accumulation was a temperature-dependent process and optimal nominally in the low temperature treatment.

Figure 8. Accumulation of sugar (mean ± SE, $N = 36$) in berries on bunches of Semillon vines in the temperature treatments, as indicated. In each case, the line is a fit to the Boltzmann sigmoid function.
There were no significant treatment effects on the numbers of bunches per vine (Table 3) and there were 58 to 62 ± 5 bunches vine$^{-1}$ on average. However, there were treatment effects on the yield per vine, which ranged from 9.7 to 12.0 ± 0.8 kg vine$^{-1}$, with the highest yield in the low temperature treatment but this was not significantly different from that for the medium temperature treatment but the yield was significant lower for the high temperature treatment vines. There were no treatment effects on the bunch fresh weights, which ranged from 192 to 233 ± 20 g. There were, however, significant treatment effects on the berry fresh and dry weights. Notably, the berry fresh weights were highest in the low temperature vines and significantly so compared to the medium and high temperature vines. By contrast, berry dry weights were significantly higher in the medium temperature vines compared with those of the other treatments. These data indicated yield and berry weights were temperature-dependent processes.

**Discussion**

The treatments applied to the Semillon grapevines in the vineyard provided a range of temperatures that averaged from 29.8°C to 32.7°C and peaked at 33.5°C to 38.3°C across the season. Although these differences in temperature were relatively small, there were statistically significant differences in the growth and development processes of the Semillon vine responses. It was clear, therefore, that differences of up to 3°C in mean canopy temperature sustained over the growing season were large enough to alter the growth and dynamics of the vines. This has implications for potential changes in climate, where possible temperature increases of about 3°C are plausible to occur over the next few decades if the greenhouse gases are not reduced. As shown here, some aspects of the vine growth were detrimentally affected by the high temperature regime, thus, there is reason to ensure the global temperatures do not increase by this magnitude.
Vine architecture was affected by the temperature treatments in that percentages of medium and long shoots shifted from more (67%) long shoots to more medium shoots (52%) as the temperature treatment increased. By contrast, with this cultivar grown in the vineyard with exposed and shaded conditions, the shoot architecture shifted to more medium shoots in the shaded, hence cooler, conditions (Greer et al. 2010). Nevertheless, these data indicate the shoot architecture of the Semillon vines was sensitive to temperature, pointing to the possible detrimental effects of the high temperatures on the apical meristem, given the increased proportion of medium shoots in the present study. Elsewhere and on a different vine species, Actinidia deliciosa, Foster et al. (2007), suggested necrosis of the apical meristem tissues caused abortion of the meristem, creating the medium shoots and low temperatures (12°C) enhanced this effect (Seleznyova and Halligan 2006). However, no studies of the apical meristem have been undertaken on grapevines to assess this, although, development of the inflorescence primordia were shown (Watt et al. 2008) to be enhanced in a similar climate to the present study compared to a cooler climate. Thus, it remains uncertain if the high temperatures were detrimental to the apical meristem.

In keeping with the vine architecture, shoot lengths of the two cohorts were affected by the temperature treatments, although the effects were most apparent on the long shoots. In both shoot types, the vines treated to the medium temperature (31.5°C) were the longest and those in the low temperature (29.8°C) were the shortest. However, the relative extension rates increased as the treatment temperature increased, by 1.5-fold. Thus shoot length was optimal at about 31°C but growth rates were optimal at 33°C. These results contrast with Aljibury et al. (1975), who demonstrated that a 10°C decrease in leaf temperatures caused a 35% increase in Semillon shoot length. However, given that the shoots were only 10 cm long, it was likely that these were short shoots (cf. Greer et al. 2010) and not comparable with the shoots of the present study. Similarly, hydrocooled shoots of Chardonnay and Chenin Blanc vines were also longer by 18% and 54% (Aljibury et al. 1975) but again, at less than 25 cm, were consistent with being short shoots. By contrast, the rates of shoot extension of Pinot Noir vines were optimal at 35°C and for Carignane shoots, optimal at 25°C (Kliwer 1977), although shoot lengths were not given, these data certainly suggest cultivar differences in shoot growth responses to temperature, especially high temperatures. Furthermore, there were possibly differences in temperature sensitivity of the different shoot length classes but this remains to be determined. For long shoots of Actinidia deliciosa vines, both shoot length and extension rates were markedly increased by temperatures at 28°C compared to 17°C (Greer and Jeffares 1998), consistent with the present study.

The medium shoots of the Semillon vines averaged about 600 mm (19 nodes) in length and the long shoots averaged about 900 mm (> 25 nodes) in length. These shoot sizes conformed to that for Semillon vines measured earlier (Greer et al. 2010), although the shoots were shorter in the present compared to the earlier study in the same vineyard. The two cohorts of shoots also conforms to that of Greer and Weston (2010a), who demonstrated that Semillon vines have between 12 and 18 preformed leaf primordia in dormant buds and that leaves at higher nodes originated from de novo formed primordia produced by the shoot apical meristem (see also Gerrath et al. 2001; Seleznyova and Greer 2001). In addition, rates of shoot development altered at about node 19, with subsequently slower rates of leaf appearance and delayed leaf and internode expansion in the distal nodes of
long shoots (Greer and Weston 2010a). As rates of leaf expansion are also temperature dependent (Seleznyova and Halligan 2006), it was perhaps likely that the growth of those metamers of the long shoots past node 19 were more sensitive to the growth conditions and thus the long shoots expressed greater effects of the temperature than did the medium shoots.

Leaf area expansion was not affected by the temperature conditions, at least for those leaves up to about node 18. This was principally because these leaves had originated as preformed primordia in the previous season (Seleznyova and Greer 2001; Greer and Weston 2010a) and appearance and expansion of these leaves largely occurred prior to the temperature control occurring. However, for leaves originating de novo from primordia produced by activity of the shoot apical meristem (Seleznyova and Greer 2001), that is, those appearing after about 60 DAB (Greer and Weedon 2016), there were marked treatment effects, with leaf expansion slowest in the high temperature vines and fastest in those vines grown in the intermediate temperature. Although most leaves in this cohort did not complete expansion and final leaf sizes remained unknown, it seemed likely that the temperature treatments affected both cell division and rates of cell expansion and a medium temperature (31.5°C) was optimal, as warmer temperatures were unfavourable for these processes. The mean leaf area of the Semillon vines strongly supported this conclusion, in fact, across all temperatures there was a significant \( (P = 0.026, r^2 = 0.92) \) linear relationship between the mean maximum temperature and the mean shoot leaf area (not shown), suggesting perhaps 30°C to 31°C was about optimal for leaf size. Consistent with this conclusion, Greer and Weedon (2016) demonstrated that leaf size and leaf expansion rates were optimal at an average seasonal temperature of 31.3°C and above this, the size and rates declined. Certainly, the lower sizes of the leaves in the low (29.8°C) treatment vines from node positions 18–25 (see inset Figure 5) also conforms to this conclusion.

Amounts of biomass and allocation at harvest were also affected by the temperature treatments and the biomass allocated to the leaves, stem and bunches were highest in the vines of the low temperature treatment in all cases. By contrast, the lowest amounts of biomass accumulated at harvest occurred in the vines in the high temperature treatment. This result conforms to the conclusion that biomass accumulation is favoured by the cooler seasonal temperatures, suggesting about 30°C was the threshold temperature. A similar conclusion, at least for bunch biomass allocation was demonstrated by Greer and Weedon (2016) and for leaf and bunch biomass by Greer and Weedon (2014a) for the same cultivar. From the present study, there was a trend for the biomass allocated to each shoot component to be driven by temperature, with amounts declining with increasing temperature (29.8°C to 32.7°C) at a rate of 1.8 to 2.1 g °C\(^{-1}\) (not shown). This provides strong quantitative support for the conclusion above. Thus, across several studies, the canopy temperature has had marked effects on various aspects of vegetative growth, including stem length (this study; Aljibury et al. 1975) stem and leaf biomass accumulation (this study; Greer and Weedon 2016), and shoot growth dynamics (this study; Greer and Weedon 2014a) and has revealed that not all processes have the same threshold temperature.

Not only the vegetative growth but also the reproductive growth was influenced by the temperature treatments. There was a marked effect of the mean temperatures on berry size, with the Semillon berries of the high temperature vines consistently smallest and berries in the medium temperature treatment consistently largest. Greer and Weedon
(2014b) have demonstrated quantitatively that Semillon berry expansion was optimal at 25°C, did not expand at 30°C and declined in size at 35°C. While the temperatures of this latter study were more precise than for the present study, nevertheless, there was some conformity in that both studies support a threshold temperature of 29°C to 30°C. Results of Greer and Weedon (2014a) confirm this where berry expansion was much slower in control compared to hydrocooled berries.

During the rapid phase of soluble solids accumulation, it was clear that the accumulation was fastest (0.358 ± 0.020 Brix day\(^{-1}\)) for the vines in the low temperature treatment and slowest for those in the medium temperature treatment (0.270 ± 0.012 Brix day\(^{-1}\)), however, TSS accumulation was also high in the high temperature treatment. The high soluble solids concentration may well have occurred because the berries of the high temperature treatment were smallest and, therefore, smallest in volume, enhancing the apparent concentration. Similarly, the berries of the medium treatment were the largest and hence the low TSS evident in these berries may have been a consequence of a dilution effect from the larger volume. Therefore, although there appears to be an effect of temperature on soluble solids accumulation, the effect may have been an artefact of differences in berry expansion. However, at harvest, the total soluble solids concentrations were 19° to 21° Brix. This conclusion conforms to results of Hulands et al. (2013), where a short (7 days) exposure of Semillon vines at mid ripening to 38°C and high light conditions increased the soluble solids concentration to over 30° Brix, consistent with a 18% reduction in berry size. A comparable exposure to 30°C, more in keeping with the present study, raised the soluble solids concentration from 15° to 23° Brix whereas berry diameter increased only slightly (Hulands et al. 2013). Certainly the effect of temperature through hydrocooling treatments elsewhere has shown soluble solids accumulation was affected, for example, hydrocooled cv. Semillon, cv. Chenin Blanc and cv. Chardonnay vines had lower concentrations than control vines (Aljibury et al. 1975). Similar results were also shown for apple fruit, including cv. Topred Delicious (Iglesias et al. 2002) and cv. Cripps Pink and cv. Royal Gala (Gindaba and Wand 2005). However, accumulation of soluble solids in cv. White Riesling, cv. Cardinal and cv. Carignane vines was largely unaffected by a pulsed hydrocooling treatments set at 30°C, although the cv. White Riesling vines did have a higher soluble solids concentration when the vines were sprinkled compared to control vines (Kliwer and Schultz 1973). This result was surprising in that berries in the sun experienced about 37°C while the sprinkled berries averaged about 28°C, suggesting perhaps a different temperature sensitivity for berry ripening of these cultivars compared to that for cv. Semillon.

In contrast to soluble solids accumulation, there were clear and distinct effects of temperature on the rapid phase of sugar accumulation. From early on, the sugar content of the Semillon berries of the low temperature treated vines was always the highest whereas the berries on vines in the high temperature treatment almost always had the lowest sugar content but certainly so from mid ripening. The differences in sugar content between the treatments ranged from 64 to 88 mg berry\(^{-1}\) and these differences were highly significant. However, the amounts of sugar accumulated in the berries of the various treatments were well in keeping with that for Semillon in earlier studies (Greer and Weedon 2014a; Greer and Weedon 2016). In the present study, the rates of sugar accumulation were maximal at 29.8°C and minimal at 32.7°C. This suggests an optimum of 29°C to 30°C for this process. This temperature-dependency of the rates of ripening contrasts to the
comparable but more detailed temperature response for Semillon berries in Greer and Weedon (2014b), where the optimum erred towards 35°C. In part, the difference may result from the imperfect understanding of what aspect of field temperatures controlled the various growth processes, including the contribution that the daily minimum temperatures might make. Nevertheless, the rates of ripening in the present study ranged between 7 and 11 mg berry⁻¹ day⁻¹ and, therefore, well in keeping with rates measured in the earlier studies (Hulands et al. 2014; Greer and Weedon 2014a, 2014b).

There were only small treatment effects on the yield per vine, with the high temperature treated vines significantly reduced in yield compared with those vines in the other treatments. This certainly suggests a threshold temperature for the yield but there were no other effects of the temperature control on the yield as also shown by Gilbert et al. (1970). This contrasts with the study of Greer and Weedon (2014a), where a 32% increase in yield of Semillon vines occurred in hydrocooled compared with control vines. However, the yields of the present study were in keeping with those in other studies of Semillon in the same vineyard (Greer and Weedon 2012, 2014a). Given that the bunch numbers per vine and the bunch fresh weights were not affected by the treatments of the present study, it was not surprising that the Semillon yields were not more strongly affected by the treatments. Despite this, berry fresh and dry weights were affected by the treatment, with berry fresh weights for vines in the lower temperature treatments higher than for the high temperature treatment. By contrast, for the berry dry weights, the vines in the 31.5°C treatment had a significantly higher weight than the other treatments. This would suggest the berry dry weight growth was optimal at about 31°C to 32°C while the berry fresh weight accumulation was optimal at 29°C to 30°C. At least for the berry dry weights, this conclusion is not consistent with that for Semillon berry biomass accumulation being strongly optimal for vines (Greer and Weedon 2014b), but grown in highly controlled temperature conditions. Berry fresh weights for cv. Cardinal, cv. Carignane, and cv. White Riesling all increased by 0.3 to 0.8 g and for the same cultivars, berry dry weights increased by 0.05 to 0.1 g with hydrocooling compared to control vines (Kliewer and Schultz 1973) and comparable with the present results. In addition, Semillon berry fresh weights increased with hydrocooling by 0.4 to 0.5 g in the study by Aljibury et al. (1975).

Conclusions

The temperature treatments were highly effective in controlling the canopy vegetative and reproductive growth of the Semillon vines and although the mean temperature differences were small, the growth differences were marked and highly significant. For example, stem length and shoot leaf areas were largest in vines at the warmest temperature with a high temperature threshold but biomass accumulation for the leaves and stems were optimal at the lowest temperature regime and hence with an apparently lower threshold temperature. Similarly, berry expansion and sugar accumulation were also highest at the lowest temperature regime as was the berry fresh weight, again suggesting a low threshold for these processes but the dry weight was higher at warmer temperatures. By contrast, the yield and its components of bunches per vine and bunch fresh weights were mostly not affected by the temperature regimes. These data suggest that no single temperature response can describe the various aspects of seasonal growth or the growth of the different organs of the vine. Furthermore, there were differences in the apparent
thresholds for the different growth responses and these ranged across all treatment temperatures but appeared to have no relationship to the seasonal climate. This study confirmed temperature control in field conditions was able to quantify some effects on vine performance and shown that a 3°C differential had marked effects and provided clear evidence of the detrimental effects of potential climate – change induced increases in temperature.

**Acknowledgments**

We thank Bob and Sylvie Allen for technical support in the vineyard and to the owners of the vineyard for their contribution to the study allowing the use of the vines.

**Disclosure statement**

No potential conflict of interest was reported by the authors.

**Funding**

This study was a contribution to the Winegrowing Futures program, a Grape and Wine Research and Development Corporation (now Wine Australia) funded initiative to the National Wine and Grape Industry Centre, Charles Sturt University.

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