Warm spring temperatures induce persistent season-long changes in shoot development in grapevines

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INTRODUCTION

Shoot growth and canopy development of plants are strongly influenced by environmental conditions and therefore vary considerably spatially and temporally. Temperature is one of the primary microclimatic factors driving rates of growth and leaf area development (Alleweldt and Hofäcker, 1975; Seleznova and Greer, 2001; Lebon et al., 2004). It is typically assumed that temperature effects are instantaneous, meaning that temperature drives current rates of cell division, photosynthesis and respiration, and thus growth (Jaquinet and Simon, 1971; Seleznova and Greer, 2001; Körner, 2003; Hendrickson et al., 2004; Lebon et al., 2004). The rates and patterns of primary and axillary shoot growth are an integral part of phenotypic plasticity in shoot architecture (Atkin et al., 2006; Beveridge, 2006) and, together with the number of shoots, ultimately determine canopy architecture (Lebon et al., 2004; Louarn et al., 2007). Canopy architecture in turn influences light interception and canopy microclimate (Smart, 1973; Schultz, 1995), which determines the potential amount of carbon that a plant can fix within a growing season (Poni et al., 2003; Weyand and Schultz, 2006). Knowledge of these relationships is important not only to understand better the dynamics of wild plant communities, but it also has implications for horticultural crop production because total carbon fixation and canopy microclimate strongly impact yield formation, fruit ripening and quality, and disease development.

Grapevines (Vitis sp.) have emerged as an important model system for research into the impact of environmental variables on shoot and canopy architecture of woody perennials (Lebon et al., 2004, 2006; Louarn et al., 2007; Pallas et al., 2008), because cultivated vines are vegetatively propagated (permitting the use of clonal material to control genetic variation) and are easily manipulated in the field. Many cultural practices for grapes focus on managing the canopy to obtain an optimal balance between vegetative and reproductive growth (Smart, 1985; Keller, 2010). Viticulturists worldwide spend much of their time modifying canopy configurations that arise from the influence of climate variation on shoot growth.
Moreover, the assumption of a linear relationship between temperature (above a threshold of 10 °C) and growth forms one of the bases of categorization of grape-producing regions according to average seasonal accumulation of thermal time (Amerine and Winkler, 1944; Lebon et al., 2004). The linear approach has not been revised for high temperature thresholds despite evidence that photosynthesis and shoot growth may be lower in vines grown under 35 °C than under 20 °C (Ferrini et al., 1995). Low temperatures (<15 °C) are understood to induce low rates of photosynthesis and shoot growth, and even small temperature differences (1–3 °C) cumulatively can result in large differences in growth of field-grown grapes (Hendrickson et al., 2004). Consequently, lower temperatures during the growing season have been held partly responsible for the observation that grapevines growing in cool regions tend to have shorter shoots with fewer leaves than those plants growing in warm regions (Pratt and Coome, 1978; Hendrickson et al., 2004). Weather around budbreak has received comparatively little attention, although the importance of temperature in the timing of budbreak has long been known (e.g. Currle et al., 1983; Huglin and Schneider, 1998). The association between temperature near budbreak and the size of early-wood xylem vessels in chestnut (Castanea sativa) stems (Fonti et al., 2007) suggests that woody perennials may respond to early-season temperature through persistent physiological and growth responses.

The objective of this study was to evaluate the effects on shoot development of bud rather than air temperatures near budbreak, and to do so independently of other microclimatic variables. Using a forced-convection, free-air cooling and heating system (Tarara et al., 2000), buds and emerging shoots on field-grown grapes were subjected to a range of temperatures. This approach avoided the uncertainty associated with many deterministic field studies that arise when air temperature is the variable measured; air temperature and that of plant tissues are often decoupled, because tissue temperature is determined by its surface energy balance (Grace, 2006). This made it possible to quantify the influence of early-season temperature on plant phenology, shoot growth and architecture, and leaf area development.

**MATERIALS AND METHODS**

*Plant material and temperature treatments*

The experiment was conducted during 2002 and 2003 in a vineyard planted in 1983 to own-rooted grapevines (Vitis vinifera 'Cabernet Sauvignon') at the Irrigated Agriculture Research and Extension Center near Prosser, WA, USA (46°30' N, 119°75'W, elevation 270 m a.s.l., annual precipitation approx. 200 mm). The site has a 3% south-west slope, and the soil is a uniformly deep (>4 m) Warden fine sandy loam with a field capacity of approx. 25% (v/v) and a permanent wilting point of approx. 8% (Evans et al., 1993). Vines were planted with 1.8 m between plants in north–south oriented rows spaced 3.1 m apart, trained to bilateral cordon, and winter-pruned to 35–40 buds per vine. No other canopy manipulations were carried out during the growing season. According to standard commercial practice in the region, the vineyard was drip-irrigated using regulated deficit irrigation (RDI) to limit shoot growth after fruit set as described elsewhere (Keller et al., 2005). Water deficits imposed by RDI also reflect the natural conditions of a Mediterranean climate (wet winter/dry summer pattern), where vineyards are subjected to water deficit by mid-summer. Most of the world’s vineyards are in Mediterranean climates, where the frequency of temperature and rainfall extremes is increasing in association with global climate change.

The temperature of buds and emerging shoots was controlled with a forced-convection, free-air cooling and heating system as described by Tarara et al. (2000), but modified by replacing the single chilling unit with a pair of units that operated alternately. Tissue temperature was controlled continuously and without the use of chambers to minimize modification of other microclimatic variables like solar radiation and humidity. Heated or chilled air was delivered directly to individual buds and emerging shoots through 8.3-cm-diameter tubes whose outlets were set within 5 cm of the experimental tissue with an exit velocity of approx. 1.9 m s⁻¹, which is below the 3.0 m s⁻¹ at which partial stomatal closure is thought to begin in grapevine leaves (Freeman et al., 1982). Temperatures were controlled from the beginning of sap flow (i.e. prior to budswell) until individual flowers on the developing inflorescences were visible to the naked eye, at which stage the shoots had four to eight unfolded leaves. The duration of temperature control varied as a consequence of phenology-based termination of treatments.

Four temperature regimes were applied: ‘ambient’, ‘cool’, ‘warm’ and ‘hot’. To account for the effects of forced-air delivery, a convective control (‘blower’) was included in which ambient air was blown across plant organs at the same rate as the heated or chilled air. ‘Ambient’ buds served as controls whose average temperature was used to calculate the offsets required to maintain the target temperatures for the other treatments, which ensured that typical daily oscillations in temperature were maintained in all treatments (Fig. 1). Heated air was delivered to ‘hot’ buds continuously to maximize the temperature difference between ‘ambient’ and ‘hot’, but a 40 °C upper temperature threshold was
applied to avoid tissue injury. Heated air was delivered to ‘warm’ buds to raise their temperature by one-half the actual difference in temperature between ‘ambient’ and ‘hot’. Chilled air was delivered to ‘cool’ buds to maintain their temperature as close to 10 °C as possible, the purported base temperature for grapevine growth. No chilled air was delivered if bud temperature was below 10 °C. Each temperature-control treatment was applied to five pairs of buds generated from adjacent two- to three-bud spurs to maximize the number of buds that could be treated with each air-delivery tube. Treatment replicates were applied to different vines, with each vine receiving a random combination of treatments. Untreated buds and shoots on each plant remained under ambient conditions throughout the experiment. This design avoided potential confounding effects due to differences in canopy microclimate or whole-plant differences in sink-to-source ratio that might have occurred if all buds or shoots on an individual vine had been subjected to the same temperature control regime. The experimental design did not exclude the possibility that differences in shoot development might have been induced by correlated temperature, temperature, meaning that shoots emerging earlier might have suppressed the growth of shoots emerging later on the same plant. Therefore, on adjacent, similarly pruned but non-treated plants, shoot growth was assessed and compared with ‘ambient’ shoots on treated plants. Budbreak and shoot development also were examined on six additional non-treated plants, each pruned to a combination of two-bud spurs and canes with bud numbers varying from 6 to 20 to induce varying dates of budbreak within each vine.

Bud temperature was estimated from the temperature of cane periderm immediately subtending the treated bud. Because preliminary tests had shown that inserting thermocouples into live buds was often lethal, subtending periderm temperature was the nearest practical proxy for actual bud temperature. The periderm temperature also provided an uninterrupted estimator for the temperature of emerging shoots during the period of temperature control after budbreak. Hereafter for conciseness, the temperature of these buds and shoots as estimated by cane periderm temperature will be referred to as bud temperature. Two type-T thermocouples (copper-constantan, 0.13-mm diameter, 2-mm junctions) were affixed to opposite aspects of the cane. To minimize radiation-induced measurement errors, thermocouple junctions were covered with 1 cm² strips of periderm that had been peeled from a nearby cane. Air temperature was measured with shielded, aspirated thermocouples at the height of the cordon (1.2 m) and at a reference height 2 m above the cordon. A solid-state thermocouple multiplexer (AM25T; Campbell Scientific, Logan, UT, USA) was used to switch among thermocouple signals. Global irradiance was measured with a pyranometer (model 8–48; Eppley Laboratories, Newport, RI, USA). Sensor signals were scanned every 5 s and averaged every 12 min by a datalogger (CR10-X; Campbell Scientific). The 5-s signals entered feedback loops to control forced-air delivery. Soil water content (v/v) under the vines was monitored weekly by the neutron scattering method (503 DR Hydroprobe; CPN International, Pachero, CA, USA) with six PVC access tubes installed to a depth of 1.2 m both under drip emitters and equidistant between emitters.

Measurement of vegetative growth

Phenological stages were assessed using the modified Eichorn–Lorenz system (Coome, 1995). Leaf chlorophyll content was estimated in newly unfolded leaves at nodes two and three using a chlorophyll meter (SPAD-502; Minolta, Osaka, Japan). Shoot growth and cluster development were measured weekly until after fruit set, again at the beginning of ripening (change of fruit colour from green to blue, termed veraison), and at commercial maturity, when grapes were harvested. Shoot length, number of unfolded leaves, and leaf length along the midrib of each unfolded leaf (>15 mm) were measured on all treated shoots. Leaf area was calculated by regressing leaf length against leaf area as determined destructively on leaves of plants adjacent to the treated plants (r = 0.99, P < 0.001, n = 181), using an area meter (model 3100; Li-Cor Biosciences, Lincoln, NE, USA). The numbers of axillary (lateral) shoots and their leaves (lateral leaves) on each treated shoot were counted. Lateral leaf area was estimated by regressing leaf number against area as determined destructively on leaves of plants adjacent to the treated plants (r = 0.94, P < 0.001, n = 80).

Shoot elongation rate (SER), relative shoot elongation rate, leaf appearance rate (LAR; separately for the main shoot only and including all lateral leaves), and leaf-area expansion rate (LER; separately for the main shoot only and including all lateral leaves) were estimated for the following periods: budbreak to first visible flower; first visible flower to anthesis (50 % of flowers open); anthesis to veraison; and veraison to harvest. All indices were calculated separately for each experimental shoot as the time-averaged value over the sampling interval as in classical growth analysis (Hoffman and Poorter, 2002). The duration of leaf expansion for the leaf opposite the basal cluster (fourth node) was estimated as the period from the first time its midrib length was measured (>15 mm) to its final length. Shoot periderm formation was determined at harvest as the number of brown internodes per shoot. After dormant pruning to two-bud spurs, the fresh mass of each cane was recorded. A cane section between the third and fourth nodes was dried to constant mass at 65 °C, ground to pass through a 0.08-mm screen, and then used for determination of non-structural carbohydrates. Soluble sugars were extracted in 80 % (v/v) aqueous ethanol, and starch remaining in the pellet was extracted in 0.1 M KOH and hydrolysed with α-amylase. Glucose, fructose and sucrose were then analysed by sequential enzymatic degradation (Hendrix, 1993), using a microplate spectrophotometer (SpectraMax Plus384; Molecular Devices Corp., Sunnyvale, CA, USA).

Statistical analysis

Data were analysed by ANOVA using a repeated-measures design for variables that were measured more than once, and Duncan’s new multiple range test was used for post-hoc comparisons of treatment means, using Statistica (version 7.1; StatSoft, Tulsa, OK, USA). Where data were normally distributed, correlations between plant response variables were assessed using the Pearson product moment correlation coefficient (r). The association between mean bud temperatures near budbreak and plant response variables was assessed using the
Spearman rank correlation coefficient (\(R\)). For multiple linear regression analysis of selected temperature and plant variables, data were transformed as needed to adjust for distributions deviating from normality and for heterogeneous variances. The relationship between maximum bud temperature and thermal time expressed as cumulative growing degree days (base 10 °C), and plant response variables at a given phenological stage was evaluated by forward stepwise regression with an entry criterion of \(F = 1\).

RESULTS

The temperature-control device performed as designed, continuously maintaining bud temperatures near their target values (Fig. 1). For example, ‘warm’ buds were on average within 0.7 °C (±0.8 °C s.e.) of their target temperature in 2002, and within 0.9 °C (±1.3 °C) of their target temperature in 2003. Before budbreak, ‘hot’ buds were on average 5.8 °C (±1.4 °C; 2002) or 6.6 °C (±1.0 °C; 2003) warmer than ‘ambient’ buds. Because of the 10 °C low-temperature threshold, the average temperature of ‘cool’ buds was closer to that of ‘ambient’ buds than were the temperatures of ‘hot’ buds. Before budbreak, the difference in temperature between ‘cool’ and ‘ambient’ buds was on average 0.7 °C (±0.9 °C; 2002) or 1.4 °C (±0.9 °C; 2003). The buds considered convective controls (‘blower’) were on average within 0.2 °C of the temperature of ‘ambient’ buds in both years. The mean temperature of ‘ambient’ buds before budbreak was 11.2 °C (±0.1 °C) in 2002 and 11.4 °C (±0.1 °C) in 2003. The average maximum temperature of these buds during the same period was 25.5 °C (±0.6 °C) in 2002 and 29.1 °C (±0.3 °C) in 2003. The absolute minimum temperature to which ‘ambient’ buds were exposed was –2.1 °C (±0.3 °C) in 2002 and –3.8 °C (±0.1 °C) in 2003.

Across all temperature regimes, soil water content increased from approx. 15% to 19% (v/v) during the budbreak period in 2002 but decreased from approx. 18% to 17% during the same period in 2003 (Figs 2 and 3). In both years, soil water content in the top 90 cm declined from a maximum of 17–19% around the time of budbreak to a minimum of approx. 12% (Fig. 2) at the time of fruit set (Fig. 3). Consequently, growth of ‘ambient’ shoots ceased around day

\[\text{FIG. 2. Soil moisture in the top 90 cm under grapevines over two growing seasons. Symbols are means from three neutron-probe access tubes placed either beneath or between drip emitters. Error bars are ± s.e. Budbreak occurred between DOY (day of year) 100 and 125 in 2002, and between DOY 93 and 128 in 2003.}\]

\[\text{FIG. 3. Phenological development of grapevine shoots in response to variation in temperature near budbreak. Symbols are treatment means (n = 5 shoot pairs), error bars are ± s.e. Key growth stages (E-L codes; Coombe, 1995) include budbreak (4); 6 leaves separated (13), corresponding approximately to the end of temperature treatments; beginning of bloom (19); full bloom or 50 % anthesis (23); fruit set (27); berries pea-size (31); beginning of ripening or veraison (35); and harvest (38).}\]
of year (DOY) 170–180 in both years (Fig. 4A, B) as intended by implementation of RDI in this vineyard. Soil water content was lower and fluctuated less between the drip emitters than under emitters, but in no case did the water content approach the permanent wilting point (8% v/v). As indicated by small and consistent variances (Fig. 2), all plants had similar available water in the root zone at any given time during the experiment. There was ample soil moisture during the period of

**Fig. 4.** Grapevine shoot growth and leaf-area development in response to variation in temperature near budbreak. Temperature was controlled by blowing heated or chilled air on individual buds and emerging shoots from pre-budswell to the time individual flowers on the developing inflorescences were visible. Symbols are treatment means (n = 5 shoot pairs), error bars are ± s.e.
rapid spring shoot growth, and all experimental plants were subjected to comparable, controlled severities of soil water deficit during the period of fruit development. In both years, soil water content was >15% at the time of treatment termination and before any decrease in shoot growth rates was observed; shoot growth responded consistently to budbreak temperature across years (Fig. 4) irrespective of any shifts in phenological development (Fig. 3).

Phenological development and shoot growth in the ‘ambient’ and ‘blower’ treatments were very similar (Figs 3 and 4) with the exception of shoot length in 2002, where ‘blower’ shoots grew slightly longer than ‘ambient’ shoots (Fig. 4A). This divergence became significant ($P < 0.05$) at full bloom (50% anthesis), which occurred around DOY 170 or more than one month after the ‘blower’ treatment had been terminated (DOY 134). None of the other measured variables differed significantly between these two treatments at any time during the two years. Therefore, shoot responses were indeed due to differences in temperature and were not confounded by convective heat transfer or changes in humidity immediately around the treated buds. Phenology and growth of ‘ambient’ shoots on treated vines and shoots on nearby, untreated grapevines were indistinguishable (data not shown). On other vines that had been left untreated but winter-pruned to leave dormant shoots of six to 20 buds each (canes) in addition to dormant shoots pruned to two buds (spurs), budbreak at the proximal end of a cane was suppressed by the emergence of shoots at the distal end of the same cane. Budbreak on the adjacent spurs occurred simultaneously with budbreak at the distal end of the canes. After the distal portion of the canes had been removed, the two remaining (proximal) buds also burst. Thus, two populations of shoots were created whose mean date of budbreak differed by 16 d. Shoots from the ‘early’ budbreak population grew faster than those from the ‘late’ budbreak population. Between budbreak and anthesis, the rate of shoot elongation in the ‘early’

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**Table 1.** Correlations between mean bud temperature from sap flow to budbreak and grapevine phenological and growth responses across two growing seasons (2002 and 2003)

<table>
<thead>
<tr>
<th>Date of phenological stage</th>
<th>Spearman $R$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Budbreak</td>
<td>$-0.84$</td>
</tr>
<tr>
<td>Flowers separated</td>
<td>$-0.65$</td>
</tr>
<tr>
<td>Anthesis</td>
<td>$-0.67$</td>
</tr>
<tr>
<td>Veraison (beginning of ripening)</td>
<td>$-0.83$</td>
</tr>
<tr>
<td>Time elapsed from budbreak</td>
<td></td>
</tr>
<tr>
<td>Flowers separated</td>
<td>$-0.34$</td>
</tr>
<tr>
<td>Anthesis</td>
<td>$0.41$</td>
</tr>
<tr>
<td>Veraison</td>
<td>$0.39$</td>
</tr>
<tr>
<td>Harvest</td>
<td>$0.60$</td>
</tr>
<tr>
<td>Growth measured at veraison</td>
<td></td>
</tr>
<tr>
<td>Shoot length</td>
<td>$0.77$</td>
</tr>
<tr>
<td>Number of nodes per shoot</td>
<td>$0.79$</td>
</tr>
<tr>
<td>Shoot elongation rate (SER)</td>
<td>$0.78$</td>
</tr>
<tr>
<td>Leaf appearance rate (LAR)</td>
<td>$0.80$</td>
</tr>
<tr>
<td>Leaf area on main shoot</td>
<td>$0.74$</td>
</tr>
<tr>
<td>Lateral leaf area per shoot</td>
<td>$0.84$</td>
</tr>
<tr>
<td>Total leaf area per shoot</td>
<td>$0.84$</td>
</tr>
<tr>
<td>Lateral shoot appearance rate</td>
<td>$0.83$</td>
</tr>
<tr>
<td>Lateral LAR</td>
<td>$0.85$</td>
</tr>
<tr>
<td>Total leaf area expansion rate (LER)</td>
<td>$0.84$</td>
</tr>
<tr>
<td>Lateral LER</td>
<td>$0.84$</td>
</tr>
<tr>
<td>Lateral leaf area as percent of total</td>
<td>$0.86$</td>
</tr>
</tbody>
</table>

All rates are time-averaged for the period between budbreak and veraison. All values are significant at $P < 0.05$. 

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**Fig. 5.** Date (DOY = day of year) of (A) grapevine budbreak, (B) date of veraison, and (C) the time elapsed between budbreak and veraison, as a function of mean bud temperature between sap flow and budbreak. Symbols are treatment means ($n = 5$ shoot pairs), error bars are ± s.e.; asterisks denote Spearman $R$ significant at $P < 0.05$. 

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shoots was twice that in the ‘late’ shoots ($P < 0.001$), and the rate of leaf appearance was 60% higher in the ‘early’ shoots ($P < 0.001$). These results demonstrate correlative inhibition among buds within but not between dormant canes, but they also show that growth of a shoot may be influenced by that of other shoots on the same vine.

Heating buds advanced the date of budbreak and subsequent phenological stages (Table 1 and Figs 3 and 5A, B) but increased the variation among shoots. By contrast, cooling buds delayed budbreak by as much as 10 d. Thus, between ‘cool’ and ‘hot’ buds, budbreak differed by about 3 weeks in both years. The date of veraison also was advanced with an increase in budbreak temperature (Fig. 5B). Thermal time accumulated between sap flow and budbreak was not correlated with date of budbreak ($R = -0.04$, n.s.) or subsequent phenological stages. However, the inclusion of thermal time with temperature (average maximum temperature between sap flow and budbreak) in a linear model did account for more of the variability in the date of budbreak (multiple $R = -0.87$, $P < 0.0001$, s.e. = 3.53) than did temperature alone. This association also held for the dates of anthesis (multiple $R = -0.78$, $P < 0.0001$, s.e. = 3.60) and veraison (multiple $R = -0.72$, $P < 0.0001$, s.e. = 3.62). The differences in phenological development among treatments declined over time (Fig. 3), thus the period between budbreak and subsequent phenological stages tended to increase with budbreak temperature (Fig. 5C).

Although temperature was controlled only during the buds-well and early post-budbreak period, variation in the rate of shoot development continued during the growing season, leading to increasing differences over time in shoot length (Fig. 4A, B), number of unfolded leaves or nodes (Fig. 4C, D), number of lateral leaves (Fig. 4E, F) and leaf area per shoot (Fig. 4G, H). Nonetheless, chlorophyll content was similar across all treatments for leaves that unfolded while under temperature control (data not shown). Later in the season there was no compensatory (i.e. increased) growth of shoots from the buds that had been cooled, whereas buds that had been exposed to the warmest temperatures during budbreak gave rise to shoots that continued to produce new leaves until harvest (Fig. 4C–F). Growth of these shoots continued despite the application of RDI to limit shoot growth after fruit set. Cumulative differences in vegetative growth were due to the combined effects of SER (Fig. 6A), LAR (Fig. 6B), growth of axillary or lateral shoots (Fig. 6C), and LER (Table 2). Most of the growth variables measured at veraison were positively correlated with mean bud temperature from sap flow to budbreak (Table 1 and Fig. 7).

Among shoots arising from ‘cool’ buds, if a main shoot produced any laterals, these did not begin to emerge from axillary buds until the main shoot had formed ≥12 nodes, which generally occurred after anthesis (Table 3). By contrast, among shoots from buds that were subjected to the highest temperatures, lateral shoots emerged when the main shoot had formed as few as six to eight nodes, which occurred well before anthesis. Mean budbreak temperatures >14 °C induced lateral shoots to emerge just before the time at which individual flowers became visible. The number of laterals per shoot was closely correlated with shoot length across the growing season ($r = 0.93$, $P < 0.001$) and at its end ($r = 0.89$, $P < 0.001$). By the time the fruit had reached commercial maturity, the total leaf area of shoots from ‘hot’ buds was 9 times (2002) or 19 times (2003) greater than that of shoots from ‘cool’ buds (Table 3). The proportion of total leaf area due to lateral

![Fig. 6. (A) Average grapevine shoot elongation rate; (B) leaf appearance rate on the main shoot, and (C) leaf appearance rate on all lateral shoots from budbreak to veraison, as a function of mean bud temperature between sap flow and budbreak. Symbols are treatment means ($n = 5$ shoot pairs), error bars are ± s.e.; asterisks denote Spearman $R$ significant at $P < 0.05$.](http://aob.oxfordjournals.org)
leaves increased as bud temperature increased (Fig. 7C). Higher bud temperatures also increased the average internode length and the extent of periderm formation (Table 3); the periderm formation (Table 3); the periderm formation of the number of nodes per shoot (number of internodes with brown periderm was a linear function of the number of nodes per shoot) (\( r = 0.95, P < 0.001 \)). There also was a trend toward lower concentrations of non-structural carbohydrates in the dormant canes from ‘cool’ canes, as were the growth rates of the shoots emerging from these two bud populations. This is consistent with other studies (Howell and Wolpert, 1978; Clingeleffer, 1989) that demonstrated delayed development of basal buds to be a within-cane rather than a within-plant phenomenon in grapevines. Thus it is unlikely that the shoots emerging from heated buds suppressed budbreak of ambient and cooled buds on other spurs on the same plant. Nevertheless, it is possible that the stunted growth of shoots emerging from cooled buds may have been a consequence of the early emerging shoots’ demand for storage reserves. It remains to be demonstrated whether such stunted growth is due to a direct temperature effect or due to persistent effects of relative strengths of carbon sinks early in the growing season.

After budbreak, shoot development in grapevines depends on four processes: internode elongation, appearance of new leaves, leaf expansion and emergence of lateral shoots, which in turn is a function of timing and rate of axillary-bud outgrowth. Higher budbreak temperatures accelerated all four processes, although LER appeared to be less responsive to temperature than were SER and LAR. In most plant species, meristem temperature is the major driver of LAR and LER (Granier and Tardieu, 1998), probably via its effect on sink activity (Körner, 2003). Lebon et al. (2004) reported a linear increase in LAR of grapevines as the air temperature increased from 13 to 24 °C. The present results indicate a sustained curvilinear response in LAR for main shoots and a linear response for lateral shoots over a range in mean tissue temperature near budbreak of about 10–19 °C. Lower rates of leaf initiation at the apical meristem are indicated by the lower number of leaves on shoots that had been subjected to below-ambient temperatures. Considering that up to ten leaf primordia are pre-formed in dormant ‘Cabernet Sauvignon’ buds (Morrison, 1991), it appears that shoots subjected to the lowest budbreak temperatures initiated hardly any new leaves after the treatments were terminated. Less leaf initiation implies lower rates of cell division at the meristem, whereas smaller individual leaves could imply lower rates of cell division, cell expansion, or both. In the present study, both SER and LAR varied as a function of budbreak temperature long after the temperature of shoot apices was no longer controlled. This is somewhat surprising because low temperatures restrict leaves increased as bud temperature increased (Fig. 7C). Higher bud temperatures also increased the average internode length and the extent of periderm formation (Table 3); the periderm formation (Table 3); the periderm formation of the number of nodes per shoot (number of internodes with brown periderm was a linear function of the number of nodes per shoot) (\( r = 0.95, P < 0.001 \)). There also was a trend toward lower concentrations of non-structural carbohydrates in the dormant canes from ‘cool’ canes, as were the growth rates of the shoots emerging from these two bud populations. This is consistent with other studies (Howell and Wolpert, 1978; Clingeleffer, 1989) that demonstrated delayed development of basal buds to be a within-cane rather than a within-plant phenomenon in grapevines. Thus it is unlikely that the shoots emerging from heated buds suppressed budbreak of ambient and cooled buds on other spurs on the same plant. Nevertheless, it is possible that the stunted growth of shoots emerging from cooled buds may have been a consequence of the early emerging shoots’ demand for storage reserves. It remains to be demonstrated whether such stunted growth is due to a direct temperature effect or due to persistent effects of relative strengths of carbon sinks early in the growing season.

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cell division more than they do photosynthesis (Wardlaw, 1990; Körner, 2003). Thus, once the shoot apex had grown past the cool air delivery tube, one might have expected more rapid growth from excess leaf carbohydrates and from reserves stored in the permanent vine structures.

It appears from the present data that the rate of shoot growth is established early in the growing season and is relatively unaffected by the growth rate of neighbouring shoots, except in extreme cases as mentioned above. Others found a strong association between air temperature and early-season rates of shoot growth in field-grown grapevines (Hendrickson et al., 2004). Those authors concluded that differences in growth rates were caused by differences in the supply of assimilates from current photosynthesis rather than by direct effects of temperature on rates of cell division or cell expansion. Budbreak and initial growth are dependent on stored carbon and other reserves (Hale and Weaver, 1962; Wardlaw, 1990), and these may be remobilized more rapidly by high sink activity from a shoot apex that is growing under higher temperatures. Communication of high sink activity implies a temperature-dependent release of a hormonal signal such as auxin (Gray et al., 1998; Aloni, 2001) from the shoot apex to the subtending permanent structure of the vine. Temperature may also have affected the rate of phloem transport for remobilized nutrient reserves during the imposition of the temperature control regimes. Similarly, the rates of photosynthesis and assimilate export of the oldest leaves would have been influenced by the temperature control regimes until these treatments were terminated. The oldest leaves begin to supply assimilates to the shoot apex once about five leaves have unfolded on a grapevine shoot (Hale and Weaver, 1962). Because growth more or less adheres to the principles of compound interest (as new leaves become photosynthetically competent, they permit growth of yet more leaves), growth is proportional to present biomass (Turgeon, 2010). In the present study, both SER and LAR generally were positively correlated with present leaf number and leaf area per shoot.

A positive association between temperature near budbreak and the size of early-wood xylem vessels in chestnut stems (Fonti et al., 2007) indicates another plausible explanation for the persistent effect of budbreak temperature on shoot growth: larger vessels have lower hydraulic resistance. In the present study, higher early-season temperatures may have enhanced the supply of remobilized nutrient reserves to the cambium, causing improved xylem function and thus persistently higher rates of cell division in the shoot apical meristem long after the treatments were terminated. Other recent results suggest an association between shoot vigour and both vessel number and size in grapevines (S. R. B. R. Bondada and M. Keller, unpubl. res.).

Potentially wider xylem vessels in ‘hot’ and ‘warm’ shoots also could have supported axillary shoot growth via lower hydraulic resistance in the transpiration stream. It was found that higher early season bud and shoot meristem temperatures not only accelerated growth in the main shoot but also promoted lateral (axillary) shoot growth throughout the season. The early induction of budbreak in axillary buds on ‘hot’ shoots (at six to eight nodes) is remarkable, as Louarn et al. (2007) and Pallas et al. (2008) reported that such growth required a critical shoot length of ten nodes in V. vinifera. Because the main shoot apex grew past the air delivery tube before temperature-control regimes were terminated and before the first axillary buds began to grow out, high meristem temperature per se cannot be expected to account for the decrease in apical dominance any more than for the

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Fig. 7. (A) Number of nodes per shoot, (B) total leaf area per shoot, and (C) percent of total leaf area comprised by lateral leaves measured at veraison, as a function of mean bud temperature between sap flow and budbreak. Symbols are treatment means (n = 5 shoot pairs), error bars are ± s.e.; asterisks denote Spearman R significant at P < 0.05.
imposed soil water deficits. This was unexpected (cf. Schultz and Matthews, 1988; Lebon et al., 2006), because the goal of applying RDI was to stop shoot growth after fruit set. These shoots developed more leaf area earlier than did ‘ambient’ and much earlier than did ‘cool’ shoots. In addition, if the more vigorous shoots did develop wider xylem vessels, they may have been more vulnerable to cavitation (Lovisolo and Schubert, 1998). Thus, given similar soil moisture at any particular time, it was expected that the shoots arising from heated buds would experience more water deficit and earlier cessation of growth than those arising from cooled buds. However, the opposite was observed, strengthening the earlier cessation of growth than those arising from cooled buds. However, the opposite was observed, strengthening the 

The present results demonstrate a persistent effect of early-season variation in microclimate on grapevines that is strong enough to partly override the influence of seasonal soil water deficit. High temperatures before and during budbreak were found to advance phenological development, accelerate shoot growth and stimulate axillary-bud outgrowth throughout the growing season, while low temperatures induced an opposite effect. These results diverge from the general assumption underlying plant growth models that growth rates are controlled only by current temperatures and do not reflect prior temperatures. A substantial portion of the variability in shoot architecture described by others (Lebon et al., 2004, 2006; Louarn et al., 2007) may be introduced very early in the growing season. Relative differences between and within canopies that are established during the budbreak period may be maintained or amplified over time. Given the recent findings for chestnut (Fonti et al., 2007), it would be interesting to test whether the present results are generally applicable to woody species. Such knowledge could be used to improve input variables in ecophysiological models that describe seasonal changes in shoot and canopy development and to fine-tune cultural practices in horticultural crop production.

**ACKNOWLEDGEMENTS**

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### Table 3. Effect of budbreak temperature regime on vegetative growth of grapevines in two years

<table>
<thead>
<tr>
<th></th>
<th>2002</th>
<th></th>
<th>2003</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Cool</td>
<td>Ambient</td>
<td>Blower</td>
<td>Warm</td>
</tr>
<tr>
<td>Shoot leaf area at anthesis (m²) **</td>
<td>0.10bc</td>
<td>0.16bc</td>
<td>0.18b</td>
<td>0.26b</td>
</tr>
<tr>
<td>Shoot leaf area at veraison (m²)**</td>
<td>0.12bc</td>
<td>0.25bc</td>
<td>0.27bc</td>
<td>0.46b</td>
</tr>
<tr>
<td>Shoot leaf area at harvest (m²)**</td>
<td>0.12bc</td>
<td>0.25bc</td>
<td>0.27bc</td>
<td>0.46b</td>
</tr>
<tr>
<td>Duration of leaf expansion at node 4 (d)</td>
<td>26b</td>
<td>24b</td>
<td>25b</td>
<td>27ab</td>
</tr>
<tr>
<td>Leaf-area expansion rate at node 4 (cm² d⁻¹)</td>
<td>4.3b</td>
<td>3.8a</td>
<td>4.6a</td>
<td>4.4a</td>
</tr>
<tr>
<td>Final leaf size at node 4 (cm²)</td>
<td>109bc</td>
<td>86a</td>
<td>111b</td>
<td>114a</td>
</tr>
<tr>
<td>Mean leaf size at harvest (cm²)</td>
<td>77bc</td>
<td>89a</td>
<td>92a</td>
<td>96a</td>
</tr>
<tr>
<td>Proportion of lateral leaf area (%) †</td>
<td>11d</td>
<td>28bc</td>
<td>28b</td>
<td>49b</td>
</tr>
<tr>
<td>Nodes per shoot at treatment end ‡</td>
<td>6b</td>
<td>5a</td>
<td>4c</td>
<td>6b</td>
</tr>
<tr>
<td>Nodes per shoot at first lateral §</td>
<td>&gt;12a</td>
<td>11b</td>
<td>11ab</td>
<td>9a</td>
</tr>
<tr>
<td>Nodes per shoot at anthesis*</td>
<td>12a</td>
<td>15b</td>
<td>15b</td>
<td>17a</td>
</tr>
<tr>
<td>Nodes per shoot at harvest</td>
<td>15d</td>
<td>19a</td>
<td>23bc</td>
<td>25b</td>
</tr>
<tr>
<td>Mean internode length (cm)</td>
<td>3.8a</td>
<td>4.1a</td>
<td>4.6a</td>
<td>5.0b</td>
</tr>
<tr>
<td>Periderm formation*</td>
<td>8a</td>
<td>11a</td>
<td>15a</td>
<td>18a</td>
</tr>
<tr>
<td>Cane mass (g cane⁻¹)</td>
<td>8.8a</td>
<td>15.5a</td>
<td>27.4b</td>
<td>45.2b</td>
</tr>
<tr>
<td>Cane ‘density’ (g m⁻²)</td>
<td>16.4b</td>
<td>22.4a</td>
<td>30.3b</td>
<td>38.9a</td>
</tr>
<tr>
<td>Cane NSC (% dry mass)**</td>
<td>9.0b</td>
<td>10.0b</td>
<td>9.6b</td>
<td>10.1a</td>
</tr>
</tbody>
</table>

Data are means (n = 5 shoot pairs), and numbers followed by the same letter within rows and within years are not significantly different at P < 0.05.

* Includes both main and lateral leaves.
† Mean for the period fruit set to commercial fruit maturity.
‡ Number of nodes per shoot at the time bud temperature treatments were ended.
§ Number of nodes per shoot at time of first axillary-bud outgrowth.
* Number of nodes per shoot at the time 50% of the flowers had opened.
** NSC, non-structural carbohydrates.
the temperature-control system, Lynn Mills and Babette Grünwald for assistance with field and laboratory measurements, and Carolyn Scagel for statistical advice.

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LITERATURE CITED