Effects of temperature and light (before and after budburst) on inflorescence morphology and flower number of Chardonnay grapevines (*Vitis vinifera* L.)

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Abstract

Plastic mini-chambers were used as tiny 'glass houses' to increase bud temperature in the vineyard. Open containers, with holes cut in them for ventilation, were used as controls, and inflorescences produced in those chambers were compared with inflorescences from modified chambers where either shade cloth or reflective foil were used to alter internal levels of photosynthetically-active radiation (PAR) as well as temperature. Buds were treated for either14 days prior to budburst or for 13 days subsequent to budburst. Temperature and PAR were monitored immediately adjacent to the buds. Applied prior to budburst, the closed mini-chambers increased bud temperatures and reduced flower numbers per inflorescence. Both 'clear' and 'reflective foil' treatments resulted in similar flower numbers. However, the shading treatment increased flower numbers by approximately 13%. Prior to budburst, there was a significant but weak correlation between average temperature and flower number per inflorescence for both the basal and apical inflorescence. Average PAR was not significantly correlated with flower number on either inflorescence, and did not improve the correlation when included with temperature in a multiple linear regression. Subsequent to budburst, flower numbers per inflorescence were decreased by the closed container but were unaffected by either the shading or foil treatment. The correlation between temperature and flower number on the *apical* inflorescence was maintained but the correlation between temperature and flower number on the *basal* inflorescence was no longer apparent. These results suggest that temperatures encountered in a vineyard during budburst can influence the number of flowers per inflorescence to the extent of a 15 to 25% variation in flower number. PAR, apart from influencing bud temperature, does not appear to influence flower number. The effect of temperature on flower differentiation diminishes as budburst advances.

Key words: *grapevine,* Vitis vinifera *L, Chardonnay, inflorescence, flowers, flower numbers, flower differentiation, temperature, sunlight, vineyard yield*

Introduction

Flower numbers at anthesis represent an upper limit for potential yield from a vineyard, and have thus attracted extensive research. Studies by previous authors in controlled environment cabinets (cited below) have suggested that high temperatures at budburst may reduce flower differentiation which is occurring at that time. However, those studies did not establish whether variation in temperature over a range normally encountered in a vineyard could also impact on flower numbers. Experiments reported here were designed to address this issue.

The number of flowers present at anthesis imposes an upper limit on potential yield from a vine because no more flowers can be converted into berries than are present at that time. Total flower number per vineyard is thus a critical (state) variable, and can be represented by the product of the number of grapevines in a vineyard × inflorescences per vine × number of flowers per inflorescence. Within that 'equation', berries per bunch is the second most important factor contributing to yield after bunches per vine (Martin et al. 2000) and can be responsible for approximately 30% of seasonal variation in yield. In identifying such sources of variation in vineyard yield, considerable research effort has been invested in determining the timing of inflorescence initiation and the factors that control it. In contrast, far less research has been carried out on factors that influence flower number per inflorescence, and in determining when the individual flowers are initiated (May 2000). In some earlier work, May (1964) tracked the development of inflorescences before budburst on single node Sultana cuttings at 22/18ºC (day/night) temperature, and established that the inflorescence primordia initially showed branching of the first order, and occasionally, second order. By day 8,

branches of the third order had begun to develop, and by day 12, fourth order branches were developing. Day 12 coincided with the mean day of budburst for the single node cuttings. Consistent with that time course of development, most researchers now suggest that flower formation commences around the time of budburst, coinciding with branching of inflorescence primordia, but subject to environmental influences during that period (see May 2000, and literature cited).

For example, Both Pouget (1981) and Ezzili (1993) have demonstrated that high temperatures during budburst reduce flower numbers per inflorescence. They were, however, working with either potted plants or cuttings, and using temperature extremes (both high and low) that would have been outside the range commonly encountered in a vineyard during budburst. Approaching this same issue from a different perspective, Kubota (1984) altered root temperature and found an 18% increase in flower number per inflorescence when root temperatures were increased from budburst until just after anthesis.

Shifting to vineyard-level observations, Dunn and Martin (2000) attempted to alter the date of budburst by delaying pruning, and thereby change the environment in which budburst occurred. Their average budburst date was delayed by four days but the pruning date did not have a significant effect on flower number per inflorescence. A significant, albeit weak correlation was nevertheless shown between flower number per inflorescence and the date of pruning. However, both mean air temperature, and mean soil temperature were increasing at that time. It was therefore impossible to separate the (possibly) confounding effects of time, and thus shoot phenology, from either soil or air temperature.

In an attempt to circumvent such interacting variables, this present vineyard experiment was designed with plastic mini-chambers as small 'glass houses' to alter bud temperature. Specific treatments included the use of either shade cloth or reflective foil to alter the light environment surrounding buds during budburst. Ambient conditions surrounding buds was thus altered either immediately before budburst, or subsequent to budburst, to determine whether there was a critical period when temperature would alter flower number and inflorescence morphology. Our treatments produced a range of light and temperature environments that were more in keeping with vineyard conditions compared with growth-cabinet experiments cited above.

Materials and methods

Study site

The experiment was established on the outside row of an existing vineyard planted to *Vitis vinifera* L. cv. Chardonnay, and established as part of a clonal trial in 1991 at the CSIRO Plant Industry site at Merbein in Victoria (142°2′E, 34°13′S). E–W rows ran 13° West of North. The vines were planted at a 1.8 m spacing in row, and with 2.8 m between rows. The clones (76B, 95, 96, 277 or 'Bernard clones') were grown on their own roots and watered with undervine sprinklers. In the previous season, the vines were spur pruned on a bilateral cordon located 1.1 m above the ground.

Experimental design

Six bamboo canes (0.5 m long) per vine were placed level with the cordon running due west and supported at the eastern end by the cordon wire and at the western end by a wooden framework. Each cane was attached parallel to the bamboo using a twist tie. A plastic mini-chamber (see below) was attached over the eighth bud on the cane to keep the cane in place and parallel to the bamboo (i.e. running from east to west). The eighth bud was selected from canes with a similar diameter (approximately 10 mm) so that they all had the potential to provide a similar number and size of inflorescences. The ninth bud was excised and the cane cut between it and the tenth bud. This ensured 100% budburst over all treatments.

The plastic mini-chambers (Figure 1) were made from polypropylene (Sarstedt, Technology Park, SA, Australia) and were 77 mm tall and 68 mm in diameter with a nominal capacity of 0.25 L. Two slots were cut on opposite sides of the container rim so that the whole assembly could be slid into place over the cane and the bamboo, and then held in place by securing the lid. The mini-chambers were either left sealed (enclosed) or had five holes cut in them (open). For open chambers, one 58 mm diameter hole was cut in the bottom of the container (which in this case faced up), and four, 45 mm diameter holes were cut into the sides, except for the open foil treatment (see below). Three covering treatments were used. The first was a clear treatment where no cover was placed over the open or closed container. The second was a shaded treatment where a 75% (transmission) shade cloth was placed on top and around the entire circumference of the open or closed container. The third was a reflective-foil treatment to enhance PAR. Aluminium foil was placed around half the side of the container; if this was on an open container then holes were not cut in these two sides. The foil mini-chambers were positioned so that the foil was on the southern side of the cane causing sun reflection back onto the bud throughout the day. The six separate treatments were:

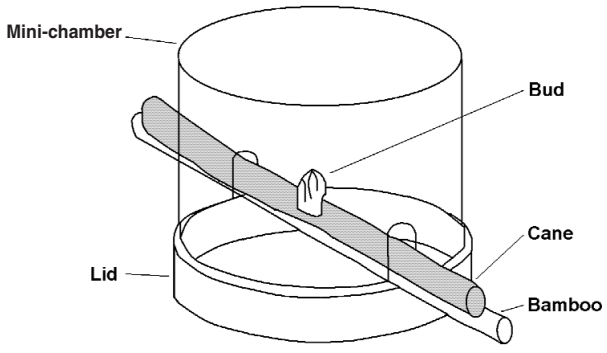

Figure 1. A diagram of a mini-chamber as set up for the enclosed clear treatment.

1. Open, Clear.
2. Open, Foil.
3. Open, Shaded.
4. Enclosed, Clear.
5. Enclosed, Foil.
6. Enclosed, Shaded.

All six treatments were imposed on each vine so that a statistical analysis could be blocked by vine. Treatments were analysed as a two-way factorial, where either open or closed mini-chambers were one factor and the three coverings (clear, shade, and foil) were the other factor. There were two inflorescences per shoot in every case except one (which was omitted from the analysis) and these were analysed as a split plot (upper and lower inflorescence) within the factorial design.

Treatments were imposed on two occasions; the first for a duration of 14 days before budburst (23 August – 5 September 2002), and again on a different set of vines for 13 days duration subsequent to budburst (6–19 September 2002). There were 10 replicate vines used in the first experiment and nine replicate vines used in the second experiment. The stage of shoot growth was rated using the Eichhorn and Lorenz scale (Coombe 1995) on the day that the treatments were removed from the buds.

Environmental analysis

Thermocouples were attached with 'blue tac' (Bostic Findley, Thomastown, Victoria, Australia) to the sides of the cane adjacent to the buds. Light sensors (silicon photodiode, BPW34, Temic Telefunken microelectronic GmbH, Heilbronn, Germany) were placed within the mini-chambers, supported by a wire so they remained in position on the southern side and level with the bud. The light sensors were calibrated against a quantum sensor (Model QSO, Apogee Instruments, Logan, UT, USA) under clear sky conditions (PAR data are thus cited as µmol quanta/m^2.s). Four thermocouples and twelve light sensors were connected to each custom built base unit that contained a reference temperature sensor for the thermocouples and variable resistors for internal calibration of the light sensors. The base units were connected to a Starlog Pro data logger (Model 7001A, 512K, Unidata, Willetton, WA, Australia) via a custom built multiplexer. Unfortunately due to a programming error on the data logger, information was not collected from one of the base units. This meant that temperature measurements the of the open-shaded and enclosed-shaded treatments were monitored by only one thermocouple prior to budburst. Subsequent to budburst the temperature of buds in enclosed foil chambers, and enclosed-shaded chambers, were again monitored by only one thermocouple. All other treatments were monitored by at least two thermocouples. PAR measurements were collected from 36 locations (instead of 48) and these were spread evenly over all the treatments. A reading was collected from one base unit every fifteen minutes so that sensors attached to each unit were logged once per hour. Multiple linear regression was used to separate the effects of PAR and temperature on flower formation. Since a separate light or temperature measurement was unavailable for every bud, the average maximum daily temperature, the average daily temperature, and PAR were used as the predictive variables; individual and mean flower numbers per inflorescence were taken as response variables.

Flower counts

Inflorescences were collected at the beginning of anthesis (18 November 2002). Each inflorescence was placed separately in a paper bag and dried at 60ºC for six days before being weighed. The number of second order branches was counted and the flowers were separated from the rachis. The flowers were sieved through a 1.25 mm sieve to remove the rachis and spread evenly over an A4 piece of overhead projector transparency film on a scanner (Hewlett Packard, ScanJet IIcx, Palo Alto, California, USA). The image which was 355.6 mm (1050 pixels) tall and 216.0 mm (638 pixels) wide was scanned as a 'black and white photo', and stored as a TIFF (Tagged Image Format) file using Desk Scan II (Hewlett Packard, Palo Alto, California, USA). The image was sharpened using the 'sharpen more' filter and then density sliced automatically, to divide it into black and white pixels. Every group of more than 5 black pixels was counted as an individual flower. Image processing was conducted using UTHSCSA Image Tool, version 3 (University of Texas Heath Sciences Centre in Antonio, Texas, USA). The accuracy of flower counts using this image analysis software was confirmed by manually counting the original flowers corresponding to 36 images previously used for automated counting. A very close relationship between manual and automated counts was confirmed (manual count = 0.98 × scanner count – 3.94; r^2 0.98).

Modelling budburst

VineLOGIC (Education package, Version 1, December 2002, Co-operative Research Centre Viticulture, Urrbrae, South Australia) was used to forecast Chardonnay budburst at Mildura (Victoria, Australia) for the years 1950–1998. The weather data from this program were also used to calculate the average temperature over the 14 days prior to, and the 14 days subsequent to the forecast date of budburst.

Results

Bud environment

The effect of mini-chamber treatments on bud temperature was very similar when imposed before and after budburst. The closed treatments were warmer than the open treatments and the shaded treatments were cooler than either the clear, or the foil treatments. The treatments resulted in an average daily temperature range of approximately 3ºC with an average daily maximum temperature range of between 12ºC and 14ºC. Light levels were also affected to a similar extent by the treatments both prior to, and subsequent to budburst. Buds subjected to the foil treatments experienced significantly more sun light than the clear treatments, which in turn received more light than the shaded treatments (Tables 1 and 2). Treatment

Table 1. The influence of sunlight (PAR) and temperature **immediately before budburst** on the development of the apical and basal inflorescence.

	Open container						Closed container									
	No cover		Reflective foil		Shade cloth		No cover		Reflective foil		Shade cloth		Bunch[a]	Container[b]	Cover[c]	Container* cover[d]
Bunch position	**Low**	**Upper**	**Low**	**Upper**	**Low**	**Upper**	**Low**	**Upper**	**Low**	**Upper**	**Low**	**Upper**				
Average temperature (°C)	15.1[y]		15.9[x]		14.7[z]		17.0[z]		17.8[y]		16.0[x]		–	–	–	–
Average maximum temperature (°C)	27.7[y]		31.3[x]		25.8[z]		34.7[z]		39.9[y]		31.9[y]		–	–	–	–
Average PAR[w] (µmol/m²s)	212		454		146		237		442		157		–	–	–	–
Inflorescence dry weight (mg)	504 bc	371 ef	611 a	429 de	643 a	393 de	519 b	320 f	444 cd	310 f	601 a	378 def	*** 27.3	* 66.3	ns	ns
Inflorescence length (mm)	86.4 ab	76.8 cde	89.4 a	82.5 bc	88.9 a	77.2 cde	74.4 ef	66.6 g	76.4 de	69.4 fg	80.9 cd	74.1 ef	*** 2.58	*** 5.65	ns	ns
Secondary arm number	12.7	11.3	14.5	11.5	15.7	11.4	13.5	9.9	13.8	10.2	14.6	11.4	*** 0.418	ns	ns	ns
Flower number	336 b	238 cd	321 b	242 cd	393 d	266 d	277 c	192 f	283 c	201 ef	331 b	228 cde	*** 14.1	** 31.2	* 38.3	ns
Flowers per secondary arm	27.0 a	21.9 cde	22.8 cd	21.3 cde	26.6 a	24.8 ab	23.0 bcd	22.0 cde	22.0 cde	19.5 e	23.7 bc	20.9 de	** 1.73	* 2.69	ns	ns
Stage of shoot development	2.60		2.60		2.90		2.63		2.93		2.6		–	ns	ns	ns

Values (except temperature and light) are means of ten replicates. Statistical significance of main effects (bunch position[a], open or enclosed container[b], and container cover[c]) and the interaction (container * cover[d]) are given by (*) $P < 0.05$, (**) $P < 0.01$, (***) $P < 0.001$, and (ns) not significant. Values were separated using Fisher's LSD, and the results are presented below the measure of significance. Dissimilar letters below the mean values across a row of data imply a statistically significant difference between those means based on the LSD from the open or closed container treatment: [z] mean of one thermocouple, [y] mean of two thermocouples, [x] mean of three thermocouples and [w] Photosynthetically Active Radiation, mean of six light sensors.

differences in the average amount of sunlight experienced by buds were more muted on overcast days (data not shown).

Temperature and sunlight effects prior to Budburst

Changing the environment surrounding the bud for two weeks prior to budburst had a significant effect on flower number (Table 1). The higher temperature treatment (closed container) reduced flower numbers by approximately 17% compared to the cooler treatment (open container). Both clear and foil treatments resulted in similar flower numbers, however the shading treatment increased flower numbers by approximately 13%. There were no significant interactions between light and temperature in driving bud responses.

Of interest in terms of developmental morphology, the lower inflorescence carried significantly more flowers than the upper inflorescence (Table 1). While flower number was affected by the different treatments, the number of second order branches was only significantly influenced by the position of the inflorescence on the shoot. Inflorescence length and weight at anthesis was significantly higher for the lower inflorescence, where the container was open, but was unaffected by the shading treatment. Bunch position was the only factor to have a significant effect on inflorescence weight. Bud development was not accelerated by treatments imposed prior to budburst.

There was a significant but weak correlation between average treatment temperature before budburst and flower number per inflorescence for both the upper and lower inflorescences (Figure 2). The r^2 for the correlation between average daily maximum temperature and flower number per inflorescence was similar to the r^2 values for the regression using average temperatures. The slopes however were not as steep when the regression was calculated using maximum temperatures (–7.3 flowers per °C for the lower inflorescence and –5.5 flowers per °C for the upper inflorescence). The relationship between temperature and flower number was improved when average flower number per inflorescence for each treatment was used as the response variable ($r^2 = 0.80$ and 0.81 for both the lower and upper inflorescence respectively). Mean PAR did not show a significant correlation with flower number for either upper or lower inflorescence, and the r^2 was decreased when PAR was included with temperature in a multi-linear regression.

Temperature and sunlight effects subsequent to budburst

Enclosing developing buds in a clear container for 13 days after budburst also decreased flower number per inflo-

Table 2. The influence of sunlight (PAR) and temperature **immediately after budburst** on the development of the apical and basal inflorescence.

	Open container						Closed container									
	No cover		Reflective foil		Shade cloth		No cover		Reflective foil		Shade cloth		Bunch[a]	Container[b]	Cover[c]	Container* cover[d]
Bunch position	**Low**	**Upper**	**Low**	**Upper**	**Low**	**Upper**	**Low**	**Upper**	**Low**	**Upper**	**Low**	**Upper**				
Average temperature (°C)	15.3[x]		16.1[y]		15.1[y]		17.2[x]		17.7[z]		16.8[z]		–	–	–	–
Average maximum temperature (°C)	27.5[x]		28.9[y]		25.5[y]		33.5[x]		37.5[z]		33.2[z]		–	–	–	–
Average PAR[w] (µmol/m²s)	324		412		162		311		367		161		–	–	–	–
Inflorescence dry weight (mg)	609	403	622	374	514	289	508	295	488	331	525	436	*** 49.1	ns	ns	ns
Inflorescence length (mm)	85.6	77.7	78.6	74.4	73.8	63.7	79.3	64.0	78.4	67.7	84.1	76.4	*** 3.06	ns	ns	ns
Secondary arm number	13.3	11.7	14.3	11.8	11.0	8.5	14.2	10.3	12.7	10.4	14.4	9.89	*** 0.564	ns	ns	ns
Flower number	404 b	271 e	465 a	309 d	406 b	257 ef	345 cd	221 f	357 ef	234 f	355 c	256 ef	*** 28.0	** 36.8	ns	ns
Flowers per secondary arm	31.1 bc	24.5 cdef	40.8 a	27.7 bcd	37.7 a	31.4 b	25.2 cdef	21.6 f	27.9 bcd	22.3 ef	25.8 cde	27.3 cd	*** 2.28	*** 3.98	ns	ns
Stage of bud burst	6.3 abc		6.8 ab		5.4 c		7.0 ab		6.8 ab		9.5 a		–	** 1.15	ns	** 1.99

Values (except temperature and light) are means of nine replicates. Statistical significance of main effects (bunch position[a], open or enclosed container[b], and container cover[c]) and the interaction (container * cover[d]) are given by (*) $P < 0.05$, (**) $P < 0.01$, (***) $P < 0.001$, and (ns) not significant. Values were separated using Fisher's LSD, and the results are presented below the measure of significance. Dissimilar letters below the mean values across a row of data imply a statistically significant difference between those means based on the LSD from the open or closed container treatment: [z]mean of one thermocouple, [y]mean of two thermocouples, [x]mean of three thermocouples and [w]Photosynthetically Active Radiation, mean of six light sensors.

rescence significantly (Table 2). However, the covering treatment did not have a significant effect on flower number during this period. Arm number, inflorescence dry weight and length were only significantly affected by inflorescence position for treatments applied subsequent to budburst (Table 2). Phenology of the buds was accelerated by the closed-shade treatment subsequent to budburst (Table 2). The number of flowers on the apical inflorescence was correlated with average daily temperature for the period subsequent to budburst ($r^2 = 0.14$, $P = 0.005$), but the number of flowers on the basal inflorescence was not correlated with PAR or temperature. Again, adding PAR to the regression model did not improve r^2 (data not shown).

Modelling budburst

The modelled date of Chardonnay budburst ranged from the 19 August (1962) through to the 14 September (1958). The average temperature for the 14 days prior to budburst was 11.4°C, with the lowest (9.5°C) and highest (13.7°C) average temperatures occurred in 1969 and 1982 respectively. Similar trends were seen in the 14 days post budburst where the average temperature was 13.1°C and ranged between 17.5°C (1981) and 10.6°C (1996).

Discussion

Elevating bud temperature, either before or after budburst, reduced the number of flowers produced per inflorescence. Conversely, shading the bud before budburst (and lowering its temperature) increased the number of flowers present (Tables 1 and 2). These results are similar in character to those presented by previous authors (Dunn and Martin 2000, Ezzili 1993, Pouget 1981). By influencing the environment surrounding an individual bud, and not the whole vine, and by imposing treatments both prior to budburst, and those same treatments again subsequent to budburst, several additional conclusions can be drawn from these present results, and are discussed below.

Both Pouget (1981) and Ezzili (1993) subjected buds to sustained and contrasting temperatures, viz. 12 versus 28–30°C, maintaining these temperatures continually throughout a growth cabinet trial. Significant bud responses were reported, but such sustained temperature differences are highly unlikely under 'natural' vineyard conditions. In the present work, and by using a 'passive' system, our buds followed a diurnal temperature variation that was similar to what would commonly occur in the field. Average daily temperature differences between the treatments (Tables 1 and 2) were small compared to the range used by Pouget (1981) or Ezzili (1993). In our

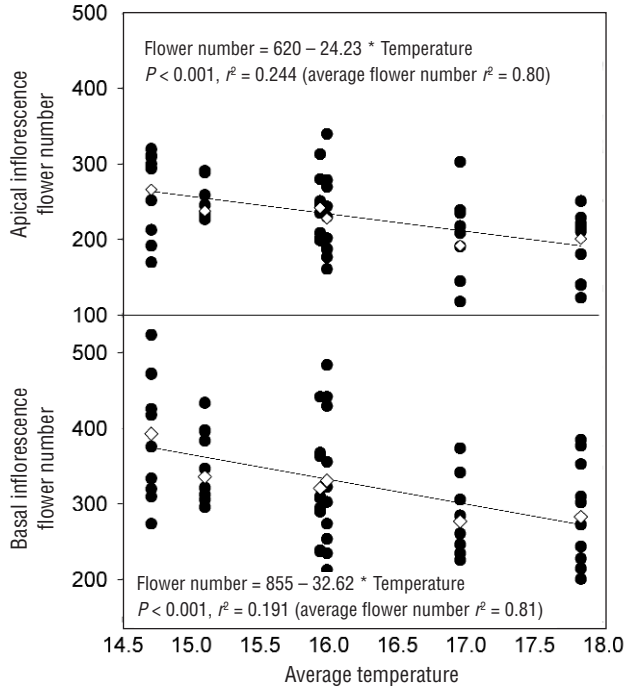

Figure 2. Relationships between average daily temperature and the number of flowers per apical inflorescence (upper graph) and basal inflorescence (lower graph) during the 14 days before budburst.
● Individual flowers
◇ Average flower number.

experiment, the average daily maximum temperature was 12–14ºC higher for the enclosed buds compared to control buds. This was due to radiative heating of vine tissues, and by conductive-convective heating of the air enclosed within the sealed containers. On clear and still days, radiative heating alone may raise (apple) bud temperature by up to 10ºC above ambient for short periods (Landsberg et al. 1974). The VineLOGIC model also suggests that the average ambient temperatures surrounding budburst can vary greatly between seasons (4.2ºC pre budburst, compared with 6.9ºC post budburst). Therefore, the scale of heating in our experiment is of a similar order to that in an open vineyard. Clearly then, temperature variations that are known to occur during budburst in a typical inland Australian vineyard have the potential to impact on flower development.

With respect to the timing of developmental sensitivity to temperature, imposing treatments both before budburst, as well as after budburst, suggested that flower number per inflorescence could be affected by temperature throughout the budburst period. The significant effect of container covering on flower number before budburst, but not after budburst, suggests that flower development (in terms of the number of flower primordia) are more sensitive to the environment before budburst occurs (Tables 1 and 2). Unfortunately, restrictions on the length of the row that could be covered by the array of sunlight and temperature sensors, meant that before-budburst treatments, and after-budburst treatments, could not be imposed as a single experimental block. Further research is required into the critical times and temperatures that influence on-going differentiation of flower primordia within a developing inflorescence. It is possible that as with initiation of inflorescence primordia (Buttrose 1974), only a few hours per day of high or low temperatures are required to influence inflorescence (and flower) development.

While temperature at budburst influences flower formation, the manner by which such differences eventuate is not known (May 2000). Increases in flowers per secondary arm and the lack of a treatment effect on arm number suggest that the increases in flower numbers is likely due to additional branching below the second order (Tables 1 and 2). In this regard, May (1964) observed both first degree, and some second degree branching in inflorescence primordia prior to the beginning of budburst; and branching as far as the fourth degree at budburst. These findings are consistent with our present results where treatments were imposed over the period when the third and fourth order arms would have been differentiating.

Dunn and Martin (2000), following the hypothesis of May (1988), suggested that changes in root temperature alter cytokinin concentration, which subsequently impact on inflorescence development. Root temperature affects the type of cytokinins in xylem exudate (Skene and Kerridge 1967) and such cytokinins have been shown to promote cell division and branching (Miller et al. 1956), as well as cause flower formation on tendrils when applied exogenously (Srinivasan and Mullins 1979). Our treatments, however, influenced flower numbers without altering root temperature, which was the same for all buds (within a block) being part, as they were, of the same vine. While elevated root temperature can increase the number of flowers per inflorescence (as reported by Kubota and Shimamura 1984) and possibly via a change in cytokinin physiology, our results imply that root temperature alone is not *the* controlling factor for flower number in this present experiment. An alternative hypothesis was presented by Pouget (1981) who suggested that warm conditions at budburst accelerated the 'rate' of budburst, providing less time for flower formation. Conversely, low temperatures slowed vegetative growth and allowed inflorescence differentiation to occur over a longer period of time. Indeed, Boss et al. (2003) suggested that the number of flowers per inflorescence may be determined by the duration of expression of genes that inhibit terminal flower formation during the early stages of inflorescence development. Candidate genes include *TERMINAL FLOWER* (*TFL1*), which represses floral meristem production in *Arabidopsis* (Bradley et al. 1997), and may delay flowering in grapevine (Boss el at. 2003). Higher temperatures also make the flower inhibition phenotype of *tfl1* mutants stronger in *Arabidopsis* (Alvarez et al. 1992).

Returning to the interpretation of vineyard observations, Dunn and Martin (2000) showed a weak but significant relationship between *temperature on the date of budburst* and *flower number per inflorescence at anthesis*. By manipulating light and temperature during budburst, we

produced six different average temperatures schemes over a range of approximately 3ºC (Tables 1 and 2). Linear regression gave a similarly weak but significant correlation for both the basal and apical inflorescences for the before budburst treatment (Figure 2). The reduction in flower number of 32.6 (basal) and 24.2 (apical) flowers per ºC for the basal inflorescence and apical inflorescences, respectively, is similar to the figures reported by both Dunn and Martin (2000) and Pouget (1981). The range in average temperatures (4.2ºC) prior to modelled budburst for Chardonnay grapevines at Mildura, suggests that average flower number per inflorescence could vary over a range of at least 100 (±50 flowers per inflorescence) due to either cool or warm weather during this period.

Using linear regression, we have established that the average maximum daily temperature was also related to flower number. While the r^2 value was similar to the figure calculated for average daily temperature, the slope of the line was not as steep due to the greater range in maximum temperatures between the treatments (4°C for average temperatures compared to 12°C for maximum temperatures). The relationship between temperature and flower number per inflorescence was far stronger when flower number per inflorescence was averaged for each treatment. This, however, unjustifiably removed a large amount of variation from the data and could allow a misleading inference that a large proportion of the variation in flowers per inflorescence could be attributed to the average temperature during flowering (Dunn and Martin 2000). Multiple linear regression using light and temperature as predicting variables was used in an attempt to improve the relationship between the environment and flower number. The correlation co-efficient, however became worse when PAR was added to temperature as a predictor for flower number. Moreover, PAR (without temperature) did not have a significant effect on the flower number per inflorescence (data not shown). This does not mean that sunlight per se has no effect on flower number, but rather that the effect of sunlight was actually caused by solar heating of the developing bud (i.e. increasing tissue temperature). The lack of a correlation between temperature and flower number for the 'after-budburst' treatment suggests that the critical period when temperature can affect flower number may have occurred before the treatments were imposed.

At anthesis, inflorescence weight and length were both decreased by enclosure prior to budburst, but not by enclosure that was imposed after budburst. This contrast confirms a greater sensitivity of the developing inflorescences to temperature during the period before budburst. Temperature at budburst may also influence flower and subsequent berry weight. Flower size immediately before anthesis was reduced by management systems that also reduce berry size (Petrie and Clingeleffer unpublished). Therefore, environmental conditions at budburst could impact on final harvest by influencing both flower number and flower size. Variation in flower number would translate into subsequent variation in berry number, while variation in flower size, would translate into final berry size.

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