Effect of pruning time and hydrogen cyanamide on budburst and subsequent phenology of *Vitis vinifera* L. variety Cabernet Sauvignon in central Victoria

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Abstract

This paper presents a detailed description of effects from two pruning times and an application of hydrogen cyanamide on budburst and subsequent phenology in a population of spur-pruned, 13-year-old *Vitis vinifera* L. Cabernet Sauvignon vines grown in central Victoria in 1998/99. Later pruning (17 August), compared with earlier pruning (7 July), delayed the onset of budburst by an average of 4.3 days and 60% budburst by an average of 5.3 days. This difference persisted at anthesis (5.0 days), veraison (4.1 days) and at harvest (0.91°Brix). Application of hydrogen cyanamide on 26 August did not advance the timing of budburst but increased the number of shoots that burst. This was due predominantly to more 'extra' shoots bursting on old wood and at the base of spurs. In the earlier stages of budburst, 'primary' buds on clear nodes of 1 year-old wood (spurs) burst in preference to buds at the base of spurs or on old wood. However, by the end of the 5-week budburst period, the number of 'extra' shoots per vine was similar to the number of primary shoots on clear nodes. Primary shoots with more bunches tended to burst earlier. Conceivably, the number of inflorescences (potential reproductive sites) and the number of flowers (potential number of seeds) on a shoot that arises from a dormant latent bud indicate a 'reproductive potential' that exerts some control over dormancy release. The frequency of budburst was sensitive to fluctuations in air temperature, but limited by the number of buds available to burst. Temperature-based models designed to predict phenological events might be improved by including parameters that take pruning time and reproductive potential into account.

Abbreviations and definitions

Capfall abscission of floral calyptra; **ESP** exchangeable sodium percentage

Keywords: *grapevine, pruning, hydrogen cyanamide, budburst, phenology*

Introduction

Grapevine yields vary considerably from place to place and year to year due to a complexity of factors. In seeking to understand, forecast and control this variation, viticulturists have resolved yield into its components (e.g. May 1972, Tassie and Freeman 1992). One formula that may be used is: (fresh) weight/vine = (nodes/vine × shoots/node × bunches/shoot × berries/bunch × weight/berry) + ('extra' shoots/vine × bunches/'extra' shoot × berries/bunch × weight/berry), where nodes are 'clear' nodes on one-year-old wood and 'extra' shoots are those that arise from other positions on the vine.

Pruning during winter, when grapevines are dormant, is an important cultural operation grapegrowers use to regulate yield (Tassie and Freeman 1992). Pruning is a relatively simple and straightforward method that can be used (i) to directly limit the number of nodes per vine and (ii) to select the type of buds that are available to burst. However, between the time of winter pruning and harvest there are a number of phenological events that may affect the particular components that eventually determine yield. The first major phenological event to occur after winter pruning is budburst.

For individual buds, budburst is generally defined as the first appearance of leaf tip, and during this time there is rapid and unprecedented growth and development of both vegetative and floral meristems. Prior to bursting, buds are in a state of ecodormancy, i.e. prevention of growth due to environmental conditions such as temperature (Lang 1987). Processes that culminate in release of buds from ecodormancy are still not defined (Lavee and May 1997).

In whole vines that support many buds, budburst involves a further level of complexity. Typically, buds burst over a period spanning several weeks and not all of the buds on a vine burst. Although temperature is clearly a dominant factor in the control of the timing of budburst (Pouget 1963, Baldwin 1966, Williams et al. 1985, Pouget 1988, Moncur et al. 1989 and Swanepoel et al. 1990), other factors can also affect the timing of budburst, albeit

to a lesser extent. For instance, soil temperature (Kliewer 1975), pruning (Goodwin, pers. comm.), the time of winter pruning (Ravaz 1912), irrigation practices (Williams et al. 1991) and the application of various chemicals (see Lavee and May 1997) can all affect the timing of budburst. Similarly, the proportion of buds that burst is under the control of a complex of environmental, plant and cultural factors. Components of grapevine yields can be extremely sensitive to both the timing and the proportion of budburst, and both can vary greatly for any given variety within a geographical region. Despite the importance of the process of budburst, there a very few detailed studies (except on Sultana) of the time-course of budburst at an individual vine level.

Delaying winter pruning can delay budburst (Ravaz 1912), whereas timely application of hydrogen cyanamide (H_2CN_2) can advance budburst (Shulman et al. 1983), particularly in warmer climates (George et al. 1988, Cirami and Furkaliev 1991). Responses of grapevines to the timing of winter pruning and application of hydrogen cyanamide can be exploited to manipulate time of budburst and, in turn, to manipulate timing of subsequent phenological events, with potentially important consequences for yield components.

In the experiment reported here, pruning and hydrogen cyanamide treatments were imposed to extend the total duration of budburst and expose sub-populations of bursting shoots to a wider range of environmental conditions than they would have otherwise experienced. This was done primarily to investigate the effects of climatic conditions (particularly temperature) during budburst on aspects of reproductive behaviour and the determination of yield components (Dunn and Martin 2000, in press). This present paper provides a detailed description of the effect of two pruning times and an application of hydrogen cyanamide on budburst and subsequent phenology in a population of spur-pruned, 13-year-old *Vitis vinifera* L. Cabernet Sauvignon vines grown in central Victoria.

Materials and methods

Experimental site

The experiment was established in a row of *Vitis vinifera* L. var. Cabernet Sauvignon (G9V3) vines, grafted onto Schwarzmann rootstocks, which were planted in 1986 in the Melbourne University vineyard at Dookie, Victoria, Australia (36°23' S, 145°25' E). The row contained 72 vines spaced 2.5 m apart and was located in a rectangular, 0.9 ha block where row spacing was 3.3 m and row orientation was east–west. The pruning system consisted of spurs on a bilateral cordon on a single fruiting wire at a height of 1.2 m with a foliage wire at 1.8 m. The vineyard was drip irrigated. Long-term average annual rainfall at the site is 555 mm, mean temperature in January is 22.4°C and heat sum is 1868 growing degree days (base temperature 10°C). Originally, Downes (1949) classified the soil type as a Dookie clay loam. Subsequently, it has been classified (S. Hamilton, pers. comm.) under Northcote (1979), as Gn 4.42, (a non-calcareous rough ped neutral gradational soil) and under Isbell (1996, pp. 91–101), as a brown mesotrophic sodic tenosol (ESP 5.8% at 60 cm and 9.9% at 74 cm).

Experimental design

Four treatments were imposed on 60 vines within a single row of 72 vines, viz. 'Earlier' pruning (E), 'Earlier' pruning + hydrogen cyanamide (E+HCN), 'Later' pruning (L) and 'Later' pruning + hydrogen cyanamide (L+HCN). Vines were pruned to 2-bud spurs spaced at approximately 20 cm along the cordons. 'Earlier-pruned' plots were pruned on 7 July 1998 and 'Later-pruned' plots were pruned on 17 August 1998. The '+ hydrogen cyanamide' (+HCN) plots were sprayed with a solution containing hydrogen cyanamide (Dormex® at 25 mL/L and a non-ionic wetter at 1 mL/L) on 26 August 1998 in accordance with the manufacturer's instructions. A total of 9 L of solution was sprayed on the cordon zone of 30 vines. Neighbouring vines were shielded from spray drift using cardboard screens.

The experimental design was a randomised block, consisting of 5 blocks, 4 plots per block, and 3 contiguous vines per plot. An identification number was assigned to each spur in sequence along the cordon. Nodes on each spur were numbered in ascending acropetal order. Node 0 was the base of the spur while node 1 was the first node separated from the base. There were 3 guard vines at either end of the row. Groups of 3 vines that contained a younger 'replant' were excluded.

Measurements

During the course of budburst every node and inter-spur area in the experiment was assessed 3 times per week (usually on Monday, Wednesday and Friday morning) from 16 September to 21 October. A bud was considered to have burst when the serrated edge of a leaf was visible. This corresponds with modified Eichorn and Lorenz (E-L) stage 04 (Coombe 1995). Shoots were categorised as either 'primary' (i.e. shoots from the first buds that burst on clear nodes) or 'extra' (i.e. shoots arising from old wood, bases of spurs and secondary and tertiary buds on clear nodes). The time of budburst in each plot was defined using two measures. The first was the day on which the first bud in the plot burst. The second was the first day when it was observed that 60% or more of the clear nodes in the plot had burst, in accordance with Coombe (1988). To test for treatment effects on time of budburst, the time units used were days after 16 September. For statistical analysis, bursting shoots were assigned a budburst date midway between the day on which they were first observed and the previous observation day.

The course of anthesis was monitored in flower clusters on 4 shoots per vine. These were selected randomly from primary shoots arising from Nodes 1 or 2 only. Each cluster on these shoots was assessed visually on Mondays, Wednesdays and Fridays from 23 November until 11 December. A visual scoring system was used to define the degree of capfall on each cluster. The scores were: 0 = no capfall, 1 = 1 capfall to 10% capfall, 2 = 10–50% cap-

fall, 3 = 50–90% capfall, 4 = 90% capfall to 1 cap remaining, and 5 = 100% capfall. Mean capfall scores for each plot were calculated for each assessment date. The day of anthesis in each plot was defined as the first assessment date on which it was observed that the mean capfall score was ≥3 (corresponding to 70% capfall). To test for treatment effects on time of anthesis, the time units used were days after 16 November.

The course of veraison was monitored in the same clusters that were assessed at anthesis on 8 dates between 1 February and 25 February. A visual scoring system was used to define the degree of bunch colouration. The scores were: 0 = no berries coloured, 1 = 1 berry coloured to 10% coloured, 2 = 10–50% berries coloured, 3 = 50–90% berries coloured, 4 = 90% berries coloured to 1 berry not yet coloured, and 5 = 100% berries coloured. Mean bunch colouration scores for each plot were calculated for each assessment date. The time of veraison in each plot was defined as the first assessment date on which it was observed that the mean bunch colouration score was ≥3 (corresponding to 70% coloured). To test for treatment effects on time of veraison, the time units used were days after 26 January.

Soluble solid concentration of free-run juice was selected as an indicator of fruit maturity. On the day of harvest (29 March) the same bunches that were monitored at anthesis and veraison were removed and cool-stored in sealed freezer bags overnight. After physical measurements had been made on each bunch, berries were counted and their juice was sampled for further chemical analyses, including the measurement of soluble solid concentration (°Brix) using a refractometer.

The number of bunches per shoot was counted on 5 shoots per vine prior to anthesis and on another 5 shoots per vine after fruit set. These sets of shoots had either 1, 2 or 3 bunches. The number of bunches per shoot was also counted on the 4 shoots per vine that were used to assess the times of anthesis and veraison and to assess maturity at harvest. These shoots had either 0, 1, 2 or 3 bunches. Two sets of data were assembled from these measurements to test for the effects of clusters per shoot on budburst time. Data set 1 consisted of 225 0-, 1- and 2-bunch shoots. Data set 2 consisted of 772 1- and 2-bunch shoots, of which the 1- and 2-bunch shoots in data set 1 were a subset. The time units of budburst for each shoot were days after 16 September. Mean budburst time per plot of 1-bunch and 2-bunch shoots was calculated for statistical analysis.

Air temperature was measured at 15 minute intervals using an automated weather station located approximately 200 m from the experimental site. Air temperature was recorded also at 0900 h and 1500 h daily at the University of Melbourne Dookie College approximately 2 km from the experimental site.

Statistical analysis

Analysis of Variance (ANOVA) was used to test the effects of treatments and clusters per shoot. Residual Maximum Likelihood (REML) analysis was used to test the effect of clusters per shoot on shoot data set 1 because it was unbalanced. Treatment means were compared using Fisher's unrestricted least significant difference ($LSD_{5\%}$, i.e. p = 0.05). Relationships between budburst frequency and temperature were assessed by regression analysis. Statistical analyses were performed using Genstat 5 Release 4.1 (Lawes Agricultural Trust 1997).

Results

Relative to Earlier pruning, Later pruning delayed the mean date of the onset of budburst (bursting of the first bud in each plot) and the mean date of 60% budburst on clear nodes by 4.3 days and 5.3 days respectively (Table 1). This delay persisted at anthesis (5.0 days) and veraison (4.1 days). There was also evidence that a similar delay persisted until harvest. The mean soluble solid concentration of the fruit of Later-pruned vines was 0.91 °Brix lower than for the Earlier-pruned vines on the day of harvest. If it is assumed that juice soluble solid concentration was increasing at a rate of 0.13°Brix/day (derived from curves presented by Coombe 1992 and McCarthy 1999), then a difference of 0.91°Brix would represent a delay of about 7 days.

Hydrogen cyanamide did not significantly affect the times of the onset of budburst, 60% budburst, anthesis or veraison or fruit maturity at harvest, but interacted significantly with Later pruning to delay fruit maturity (Table 1).

Table 1. Effects of two pruning times and application of hydrogen cyanamide (HCN) on the timing of budburst, anthesis and veraison, and the maturity of grapes at harvest, as indicated by juice sugar concentration. The time of budburst was defined as the day when the first bud burst ($Budburst_1$) and the day when 60% of buds had burst ($Budburst_{60}$). Anthesis was defined as 70% capfall. Veraison was defined as 70% berries coloured. Reference dates for budburst, anthesis and veraison were 16 September, 16 November and 26 January, respectively. Harvest was on 29 March.

Treatment	$Budburst_1$	$Budburst_{60}$	Anthesis	Veraison	Maturity
	(Days after reference date)				(°Brix)
Pruning time					
Earlier	1.9	9.0	8.8	9.1	24.96
Later	6.2	14.3	13.8	13.2	24.05
$LSD_{5\%}$	0.4	1.4	1.5	1.7	0.57
Hydrogen cyanamide					
+ HCN	4.0	11.9	11.2	11.8	24.27
– HCN	4.1	11.4	11.4	10.5	24.74
$LSD_{5\%}$	0.4	1.4	1.5	1.7	0.57
Pruning time × hydrogen cyanamide					
Earlier	2.0	8.2	8.6	8.4	25.27
Earlier + HCN	1.8	9.8	9.0	9.8	24.65
Later	6.2	14.6	14.2	12.6	24.21
Later + HCN	6.2	14.0	13.4	13.8	23.89
$LSD_{5\%}$	n.s.	n.s.	n.s.	n.s.	0.81

n.s. indicates no significant interaction

Table 2. Effects of two pruning times and bud position on the mean time of budburst.

Bud position	Pruning time		Bud position mean
	Earlier	Later	
	(Days after 16 September)		
Node 3	9.3	13.8	11.5
Node 2	8.9	13.7	11.3
Node 1	10.3	15.6	13.0
Spur base	13.9	17.7	15.8
Old wood	25.3	27.3	26.3
Pruning time mean	13.5	17.6	15.6
Factor	Pruning time	Bud position	Time × position
$LSD_{5\%}$	0.7	0.9	1.4

On both Earlier and Later pruned vines, buds on nodes 3 and 2 burst at the same time, but buds on node 2, node 1, the spur base and the old wood burst in succession (Table 2). Buds on Earlier pruned vines burst earlier than on Later pruned vines at all bud positions, and differences were greater at higher positions.

The delaying effect of Later pruning on onset of budburst and 60% budburst was apparent in curves representing the time course of budburst for each treatment (Figure 1A). All four curves converged on an upper limit of approximately 90% budburst on clear nodes. Hydrogen cyanamide caused more buds to burst on the vine as a whole (Figure 1B), but this effect did not begin until approximately 8 days after the onset of budburst in the Earlier-pruned treatments and approximately 4 days in the Later-pruned treatments. Similar patterns were observed in the course of anthesis (Figure 2A) and veraison (Figure 2B).

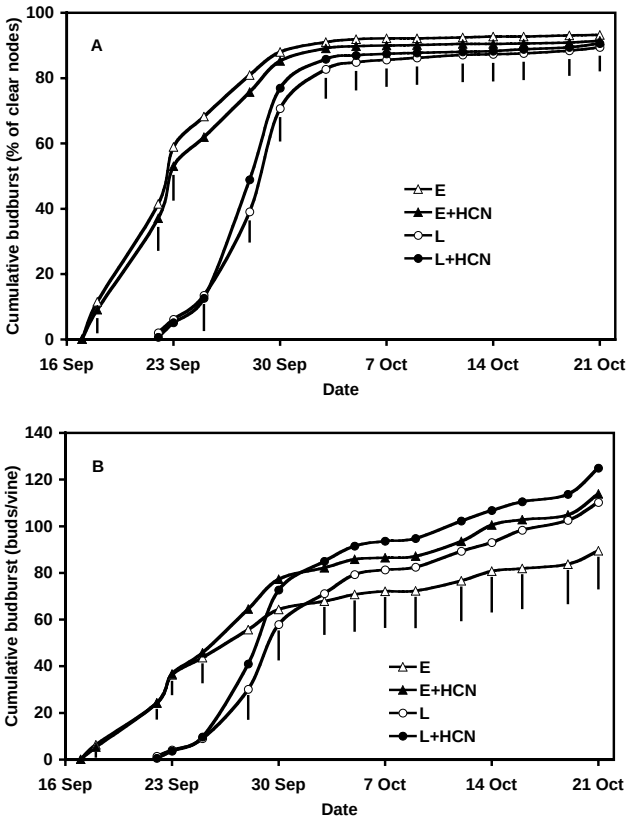

Figure 1. Effects of pruning time and hydrogen cyanamide on the time course of budburst: **A** – cumulative % budburst of clear nodes; **B** – cumulative buds burst per vine.
Treatments were Earlier pruning (E), Earlier pruning + hydrogen cyanamide (E+HCN), Later pruning (L) and Later pruning + hydrogen cyanamide (L+HCN). Points indicate treatment means and vertical bars represent $LSD_{5\%}$ for each date.

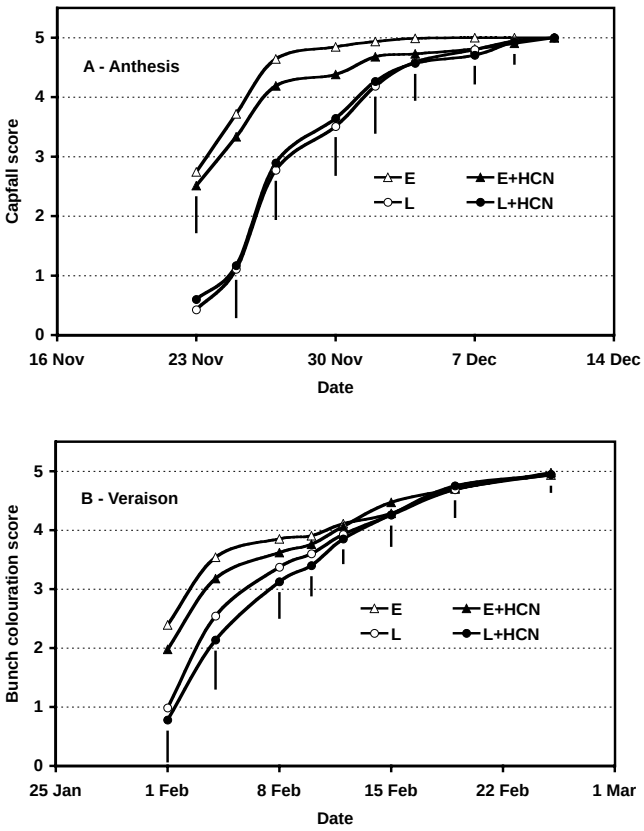

Figure 2. Effects of pruning time and hydrogen cyanamide on the time course of: **A** – anthesis (measured by a visual score of capfall); **B** – veraison (measured by a visual score of bunch colouration). Treatments were Earlier pruning (E), Earlier pruning + hydrogen cyanamide (E+HCN), Later pruning (L) and Later pruning + hydrogen cyanamide (L+HCN). Points indicate treatment means and vertical bars represent $LSD_{5\%}$ for each date.

At the end of the observation period (5 weeks after the first bud in the experiment burst) there were significantly more shoots on the Later-pruned vines than on the Earlier-pruned vines (Table 3). The source of the difference was shoots from clear nodes, rather than shoots from old wood or the spur bases. This was due to a retention of 23% more nodes on the Later-pruned vines, rather than a difference in shoots per node. Possible confounding of the effect of the time of pruning with the effect of retained nodes per vine was tested by including nodes per vine as a covariate in analyses of the times of the onset of budburst, 60% budburst, anthesis and veraison and maturity at harvest. The effect of nodes per vine was not significant in any of these analyses ($p = 0.73$, 0.49, 0.26, 0.42 and 0.003°Brix cf. $LSD_{5\%}$= 0.06°Brix respectively) and the magnitude of differences between the times of phenological events in Earlier and Later pruned vines could not be accounted for by the difference in nodes per vine.

Table 3. Effects of two pruning times and application of hydrogen cyanamide on budburst components. Interactions of pruning time and hydrogen cyanamide were not significant (P > 0.05).

Treatment	Nodes per vine	Shoots per vine				Shoots per node
		Old wood	Spur base	Clear nodes	Whole vine	
Pruning time						
Earlier	54.1	23.8	21.5	56.3	101.7	1.045
Later	66.3	26.5	23.5	67.6	117.6	1.019
$LSD_{5\%}$	5.9	4.7	3.4	6.6	9.2	0.056
Hydrogen cyanamide (HCN)						
+ HCN	61.8	27.8	26.2	65.4	119.4	1.064
– HCN	58.6	22.6	18.8	58.5	99.9	1.000
$LSD_{5\%}$	5.9	4.7	3.4	6.6	9.2	0.056

Hydrogen cyanamide caused 20% more shoots to burst from all parts of the vine (Table 3). Biggest effects were on the spur base and the old wood, from which 39% and 23% more buds burst, respectively. Hydrogen cyanamide also increased budburst from clear nodes by 12%, due to a 6% increase in the number of shoots per clear node.

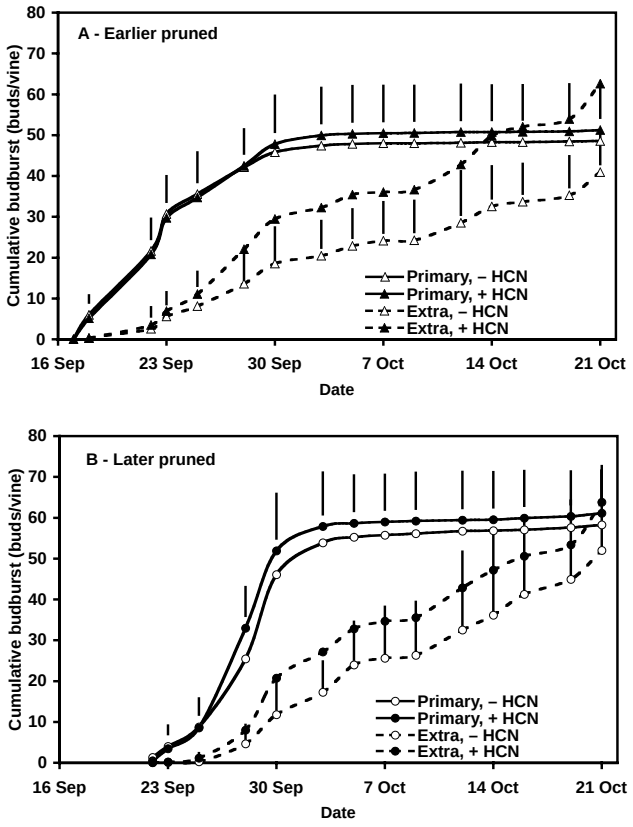

Figure 3. Effect of hydrogen cyanamide (HCN) on the time course of budburst for Primary shoots and Extra shoots on **A** – Earlier-pruned vines and **B** – Later-pruned vines. 'Primary' shoots were defined as those that arose from the first buds that burst on clear nodes. 'Extra' shoots were defined as those that arose from old wood, bases of spurs and secondary and tertiary buds on clear nodes. Points indicate treatment means and vertical bars represent $LSD_{5\%}$ for each date.

There were different patterns in the course of budburst of 'primary' shoots (i.e. shoots from the first buds that burst on clear nodes) and 'extra' shoots (i.e. shoots arising from old wood, bases of spurs and secondary and tertiary buds on clear nodes) (Figure 3). At first, primary shoots dominated budburst in all treatments. Extra shoots began to burst a few days later at a relatively low frequency. Despite the difference in the onset of budburst, the number of primary shoots that burst reached a plateau on both Earlier and Later pruned vines at a similar time (shortly after 30 September). Extra shoots continued to burst at a fairly steady frequency for a further 3 weeks. There were similar numbers of primary and extra shoots on each vine by the end of the monitoring period. In both Earlier- and Later-pruned vines, the major effect of hydrogen cyanamide was to cause an increase in the frequency of bursting of extra shoots. For Earlier-pruned vines (Figure 3A), this difference continued to increase over the whole period, while for later pruned vines (Figure 3B) the difference in the bursting frequency of extra shoots, once established, remained fairly constant.

Analysis of the effect of the number of bunches per shoot on the time that the shoot burst using the smaller data set 1 showed that shoots without bunches burst on average about 3 days later than shoots with bunches (Table 4). Analysis of the larger data set 2 showed that 2-bunch shoots burst on average about 1 day before 1-bunch shoots (Table 4). This effect was also apparent in the budburst frequencies for each pruning treatment (Figure 4). In the random sample of shoots from which this data was derived, there were more 2-bunch shoots than 1-bunch shoots, and more 1-bunch shoots than 0-bunch shoots (Table 4), probably indicating trends in the whole primary shoot population.

Table 4. Effect of bunches per shoot on the time of budburst determined for 2 sets of shoot data. The 1- and 2-bunch shoots in Data set 1 were a subset of Data set 2. Time units are days after 16 September.

Bunches per shoot	Mean budburst time	Shoots	% of sample
Data set 1			
2	10.1	133	59
1	10.6	68	30
0	13.4	24	11
$LSD_{5\%}$	2.3		
Data set 2			
2	11.0	474	61
1	10.0	298	39
$LSD_{5\%}$	0.5		

The Earlier pruning time coincided approximately with the coldest time of the year at the vineyard (Figure 5). The Later pruning time was about half way between the Earlier pruning time and budburst, during which time mean air temperatures fluctuated around a rising trend. Mean air temperatures fluctuated between 8°C and 16°C in the 3 weeks or so leading up to budburst, but were

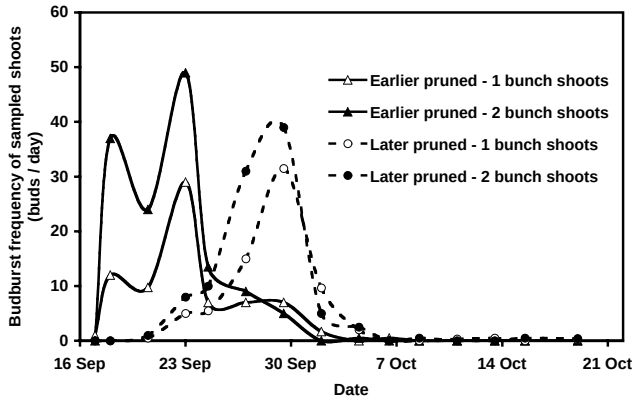

Figure 4. Time course of budburst frequency for 1-bunch and 2-bunch shoots in Earlier- and Later-pruned treatments. The measure of budburst frequency at each date was derived from 136 1-bunch shoots and 247 2-bunch shoots on Earlier-pruned vines and 162 1-bunch shoots and 227 2-bunch shoots on Later-pruned vines.

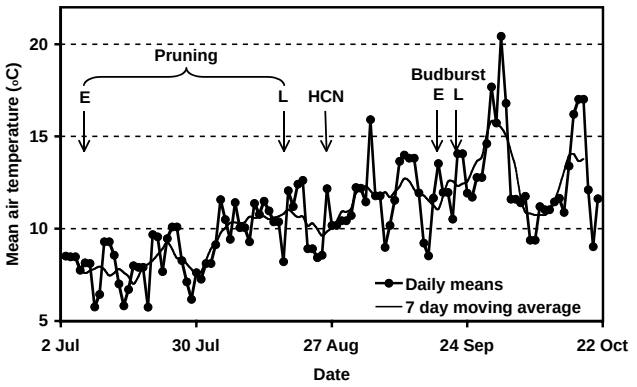

Figure 5. Timing of imposition of Earlier (E) and Later (L) pruning, application of hydrogen cyanamide (HCN) and occurrence of budburst in relation to mean air temperatures.

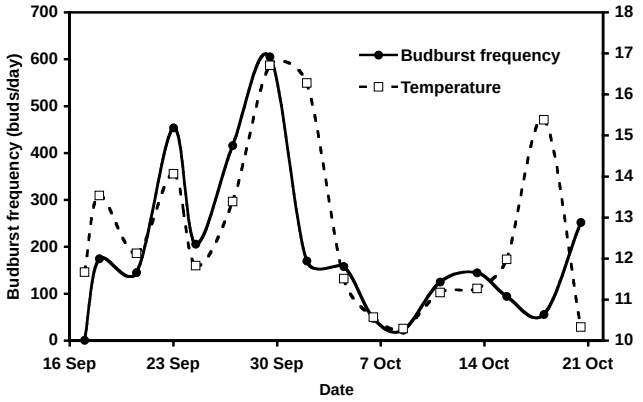

Figure 6. Mean air temperatures during the course of budburst and budburst frequencies for the entire population of buds on 60 vines.

generally above 10°C. Temperatures peaked at approximately 20°C about 2 weeks after the onset of budburst in the Earlier pruned vines and then fell to <10°C before rising and falling again towards the end of the observation period.

During the 5 weeks after the onset of budburst in the Earlier pruned vines the budburst frequency of the entire population of shoots in the experiment generally followed fluctuations in air temperature (Figure 6). However, there were three periods when budburst frequency departed from mean daily air temperature. The first period was at the very beginning (*ca* 17 September), when only the first few buds were bursting on the clear nodes of the Earlier pruned vines (Figure 7A). The second period was after the budburst frequency of primary shoots in the Later-pruned vines had peaked (*ca* 30 September) (Figure 7B). By this time over 80% of the primary buds had burst (Figure 1A). The third period was in the last week of the observation period (October 14 – 21), when the budburst frequency of extra shoots fell as temperatures rose and then rose as temperatures fell (Figure 7). Nearly all the shoots that burst during the last two weeks of the observation period were extras. The budburst frequency of these also fluctuated with temperature until the last week of the observation period, but the peak was not as high as for primary shoots. There was a strong positive correlation ($R^2 = 0.87$) between budburst frequency and mean air temperature on the day of budburst when these points were removed from a regression (Figure 8). The regression indicated a zero budburst frequency at a mean air temperature close to 10°C.

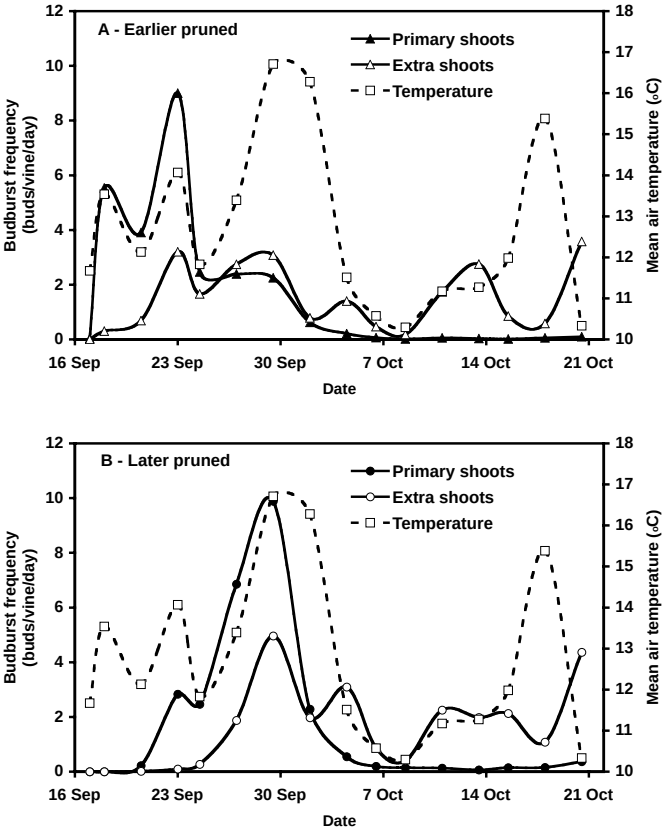

Figure 7. Mean air temperatures on the day of budburst and budburst frequencies of primary and extra shoots on **A** - Earlier-pruned vines and **B** - Later-pruned vines. 'Primary' shoots were defined as those that arose from the first buds that burst on clear nodes. 'Extra' shoots were defined as those that arose from old wood, bases of spurs and secondary and tertiary buds on clear nodes.

The budburst behaviour of primary shoots appeared to be divided into two distinct phases, which were distinguished by the degree to which budburst frequency expressed as a proportion of remaining buds followed air temperature fluctuations (Figure 9). In the first phase,

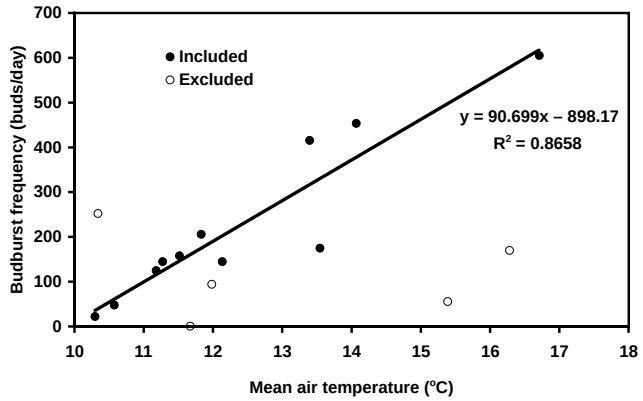

Figure 8. Relationship between budburst frequencies for the entire population of buds on 60 vines and mean air temperatures during the course of budburst. The points excluded from the regression (○) related to times (1) when the very first buds were bursting, (2) when there was a severe limitation in the supply of available buds in the class bursting at the time and (3) when only buds on old wood were bursting.

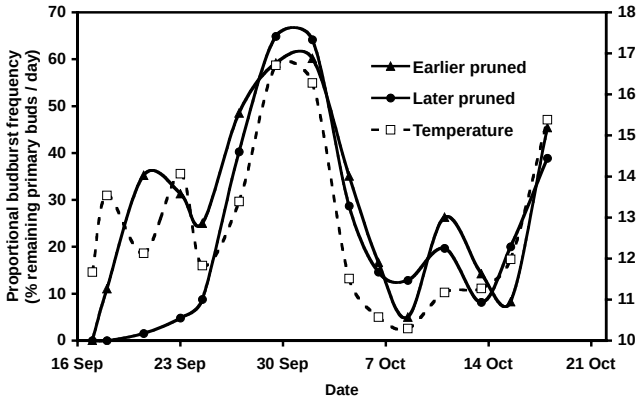

Figure 9. Mean air temperatures and mean budburst frequencies of primary shoots expressed as a proportion of unburst buds remaining on Earlier- and Later-pruned vines. 'Primary' shoots were defined as those that arose from the first buds that burst on clear nodes. 'Extra' shoots were defined as those that arose from old wood, bases of spurs and secondary and tertiary buds on clear nodes.

which lasted for about a week after the onset of budburst in each pruning time treatment, less than 60% of the available primary buds had burst (Figure 1A) and absolute budburst frequencies followed fluctuations in temperatures closely. In the second phase, the absolute budburst frequency of primary shoots declined steadily and appeared to be insensitive to fluctuations in temperature (Figures 7A and 7B), but budburst frequency expressed as a proportion of unburst buds remaining followed temperature fluctuations closely (Figure 9). The proportional budburst frequency of primary buds after 60% of the available primary buds had burst was strongly correlated with mean air temperature on the day of budburst (Figure 10).

Discussion

Applying hydrogen cyanamide to Cabernet Sauvignon vines in this region did not advance the onset of budburst or the time of 60% budburst. Its effect was to increase budburst for buds that otherwise would not have burst. These were predominantly basal buds and latent buds on old wood and, to a much lesser extent, buds from spur nodes 1 and 2. In another experiment (Whiting and Coombe 1984), applying cyanamide about 30 days before budburst did not advance budburst of Sultana or Cabernet Sauvignon grapevines. Lavee and May (1997) suggested that, in this instance, the late application of cyanamide at high concentration may have damaged buds and, thus, delayed their opening. There was no evidence of damaged buds in our experiment. In both experiments the manufacturer's instructions regarding both concentration and timing of application were followed. Hydrogen cyanamide seems to have its greatest effect in warmer regions where budburst is patchy due to insufficient chilling. Perhaps manufacturer recommendations are based on results from trials in sub-tropical and tropical environments and, thus, are not appropriate for central Victoria (Whiting, pers. comm.).

As expected, a difference in the timing of winter pruning led to a difference in time of budburst. The difference of 5 days in budburst time as a result of a 6-week difference in pruning time is consistent with the results of studies for other wine grape varieties in other regions (Ravaz 1912, Antcliff et al. 1957). It is also consistent with results for the table grape variety Muscat Hamburg, grown in south-eastern Queensland (George et al. 1988). However, the difference we observed was much smaller than the 7 week difference in 50% budburst (12 June versus 1 August) that Cirami and Furkaliev (1991) induced in glasshouse-grown Cardinal grapes in South Australia with a pruning time difference of 6 weeks (4 May versus 15 June).

The persistence of the difference between the budburst times of Earlier- and Later-pruned vines at flowering, veraison and maturity confirms long-held knowledge (Ravaz 1912). Some Victorian viticulturists prune earlier to advance the time of harvest and thus reduce the risk of losing crop due to rain-induced damage in autumn (Bailey pers. comm.). The value of varying pruning time in practice would need to be assessed in relation to specific circumstances. Managers of large varietal blocks could prune them in stages in order to reduce overall frost risk in frost-prone areas or to extend the duration of

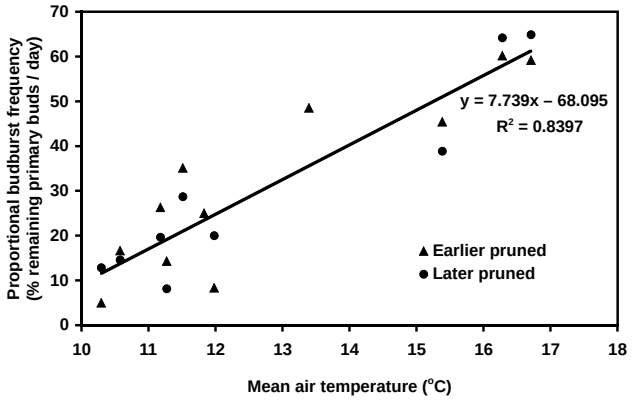

Figure 10. Relationship between mean budburst frequencies of primary shoots expressed as a proportion of unburst buds remaining on Earlier- and Later-pruned vines and mean air temperatures on the day of budburst after 60% of the clear buds had burst.

ripening to obtain more flexibility during harvesting. Alternatively, a difference of 7 days in maturity could make it difficult to optimize the time of machine harvesting of a block and in such an instance it would be sensible to avoid large differences in the time of pruning of different parts of the block.

We observed that different types of bud, as defined by their position on a vine (Table 2) and as indicated by the different types of shoot that they produced (Table 4), burst at different times. There was a hierarchy of bursting, with more distal nodes bursting earlier on spurs, and spur bases bursting earlier than old wood (Table 2). This pattern is consistent with the familiar phenomenon of apical dominance, which is a concept that is generally applied to relationships between buds on a given actively growing shoot. However, apical dominance could persist in some form even during dormancy. Perhaps earlier-pruned vines burst earlier because removal of the distal buds eliminated a source of inhibition of proximal buds at an earlier stage, thus increasing their sensitivity to environmental conditions. Alternatively, the effect of pruning time may be one of pruning itself. Wounding has been shown to increase respiration from dormant buds (Shulman et al. 1983) and it may be possible to construct explanations based on relationships between respiration and dormancy release. However, the role of respiration in dormancy alleviation is not well understood (Lang 1989), with results from various studies being equivocal.

On the spur-pruned Cabernet Sauvignon vines that we studied, single-inflorescence shoots burst from primary buds on clear nodes 1 day later, on average, than double-inflorescence shoots. Buds containing shoots with no inflorescence primordia burst even later again. The difference between budburst of 'fruitful' primary shoots (those with at least one inflorescence) and 'unfruitful' primary shoots (those with no inflorescence) averaged 3 days. Dunn and Martin (2000, in press) demonstrated that for Cabernet Sauvignon, double-cluster shoots had significantly and substantially more flowers (per bunch and per shoot) than single-cluster shoots. If one introduces the concept that flower number (potential seed number) and inflorescence number (potential reproductive sites) indicate a shoot's 'reproductive potential', then one could speculate that shoots with higher reproductive potential burst in preference to those with lower reproductive potential. It is difficult to explain this in evolutionary terms because the genotypes familiar to viticulturists are highly selected, grown unnaturally and not in their native habitat. However, it is possible that vines that supported earlier bursting of the shoots most likely to result in seed dispersal could have gained a selective advantage. There would also be an advantage for a tree-climbing plant such as the grapevine in giving preference to shoots bursting at higher locations.

Antcliff and Webster (1955) have also suggested that grapevine buds do not burst at random, but that those with more inflorescences burst earlier than those with fewer inflorescences. They based this on an analysis of budburst in cane-pruned sultana over a 3-year period. However, the highly significant and negative correlation between budburst and % fruitful shoots (having at least one inflorescence) that they reported may have been due to a combination of two factors. First, the pattern of budburst along canes (i.e. distal buds bursting in advance of proximal buds) coupled with the well established (Antcliff and Webster 1955) trend for sultana buds to have fewer inflorescence primordia toward the base of canes would contribute to this effect. Secondly, secondary and tertiary shoots, which burst later than primary shoots, generally have fewer inflorescences than primary shoots.

Once budburst commenced, the frequency of buds bursting per day was sensitive to fluctuations in air temperature, but limited by the number of buds available to burst (Figures 6 to 10). These patterns may be interpreted as follows. A wave of dormancy release commences in the most apical and fertile buds and then proceeds towards the more proximal and less fertile buds. Once released from dormancy, each bud will grow in response to temperature. Rigorous definition of the rules that govern this behaviour at an intra-vine bud population level could be valuable in the construction of models designed to predict phenological events and the productivity of grapevines in different environments.

The effects of pruning time and reproductive potential on time of budburst are factors that are not considered in models that are currently used to predict budburst (e.g. Pouget 1988, Swanepoel et al. 1990). These temperature-based models assume that, for a given cultivar, vines will be able to burst when a critical number of chilling units have been accumulated, and that budburst will occur when a minimum number of heat units have been accumulated and a minimum mean daily temperature has been attained. In our experiment (and others cited above) the buds on Earlier- and Later-pruned vines of the same cultivar burst at significantly different times despite being exposed to an identical set of environmental conditions. This suggests that the capability of currently-available models designed to predict the time of budburst could be improved by the inclusion of a function or the adjustment of a parameter to take account of the effects of pruning time and reproductive potential.

In summary, delaying pruning by six weeks delayed budburst, anthesis, veraison and maturity by approximately five days. Thus, pruning time may be a source of variation in the timing of key phenological events in the vineyard and may be an important factor to consider in planning vineyard operations. Hydrogen cyanamide did not advance the times of budburst, anthesis, veraison or maturity, but caused more shoots to burst, particularly 'extra' shoots at the base of spurs and on old wood. 'Primary' shoots on clear nodes burst before extra shoots. The frequency of budburst was sensitive to fluctuations in air temperature, but limited by the number of buds available to burst. A primary shoot tended to burst earlier if it had more bunches. Thus, it may be possible to improve temperature-based models designed to predict the timing of phenological events in grapevines by including parameters that take account of pruning time and the reproductive potential of classes of buds.

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