Commonwealth Research Station, C.S.I.R.O., Merbein, Victoria, Australia

Dormancy and Bud Burst in Sultana Vines

by

A. J. ANTCLIFF and P. MAY

Introduction

The phenomenon of dormancy in the buds of woody plants has been reviewed by SAMISH (1954). In many cases buds which have gone into dormancy will not burst during the winter even if brought into temperatures favourable for growth. For some deciduous fruit trees it has been shown that this is due to a chilling requirement which must be satisfied before the buds will burst normally. Insufficient chilling leads to serious disorders which make commercial crop production impracticable. Hence for many varieties, particularly of peaches and apricots, the amount of chilling needed has been determined and the regions in which they can be grown with a reasonable expectation of success have been defined.

Early evidence of chilling requirement in grape vines was indirect. CHANDLER et al. (1937) noted that buds were observed to start earlier and more uniformly on vines shaded during winter. MAGOON and DIX (1943), working with young potted vines, found that the longer they were left in the open during winter the more readily they would burst when moved to a warm greenhouse. However even vines which had spent only 200 hours below 7.2° C would burst and grow quite normally. BRANAS, BERNON, and LEVADOUX (1946) compared weather records with the date of bud burst in the field and concluded that as the amount of chilling increased the amount of warmth subsequently needed to bring vine buds to bursting became less. The dormancy of grape vines was not studied more directly until recently, probably because disorders due to insufficient chilling had not been observed.

Sultana vines in the Murray Valley, Australia, sometimes show disorders suggestive of those observed on some fruit trees after insufficient winter chilling. These are the failure of an unusually large number of buds to burst and a temporary stunting of shoots for several weeks after bud burst. As nothing was known of the course of dormancy in this area, studies have been made and the results are given in this paper.

Since this work was started several papers dealing with dormancy in grape vines have appeared. KONDO (1955) described the course of dormancy in a number of varieties in the Soviet republics of Uzbekistan and South Kazahstan. He defined three phases of dormancy — conditional, organic, and enforced which, however, merged into one another and had to be separated by an arbitrary division. Organic dormancy was the phase in which cuttings would not burst in 20 days at favourable temperatures. The period of deep dormancy, in which cuttings would not burst in 70 to 75 days at favourable temperatures, occurred in early autumn and the intensity of organic dormancy had become much less by the beginning of winter. Conditional dormancy was the state of the buds during the summer of their formation, when, although they would not normally shoot on the vine, they would readily shoot on detached cuttings. Enforced dormancy was the phase after organic dormancy, when the buds would still not burst in the field, but only because of the lack of warm weather. The duration of organic dormancy could be shortened considerably by keeping the buds at a constant temperature of 5° C.

NIGOND (1957) studied the effect of controlled temperatures on dormant buds at Montpellier and also described an effect of cold treatment on vine dormancy. He concluded that temperatures of 1° C to 8° C were more effective than 0° C in shortening organic dormancy. However, Alleweldr (1960) found that keeping buds at 5° C or -5° C for periods of up to 15 days did not decrease the time required for bursting or increase the proportion of buds which burst when they were returned to favourable temperatures.

The results of HUGLIN (1958), who made a comprehensive study of vine buds, agree with the concept of three phases of dormancy, and show that the first phase, in summer, is due to correlative inhibition. The buds will burst readily if the growing tip is removed, and even more readily if the laterals and leaves are removed also. POUGET and RIVES (1958) used rindite, a mixture in which ethylene chlorhydrin is the major constituent, to force growth and compared the burst of treated and untreated cuttings to develop several criteria for determining the end of organic dormancy. WEAVER (1959), RIVES and POUGET (1959), and ALLEWELDT (1959b, 1960) have all found that the dormancy of vine buds can be prolonged with gibberellin.

Our observations and results will be described and discussed in relation to those of these authors.

Results

Changes in the Intensity of Dormancy during Autumn and Winter

The variation in the intensity of dormancy has been studied by taking cuttings at intervals during autumn and winter and growing them at 20°C in water. In 1956 cuttings of several buds were used, comprising nodes 1 to 3, 4 to 6, 7 to 10, and 11 to 14. There was a very poor burst of the lower buds of the cuttings, so in 1957 and 1958 single bud cuttings were used. These were taken from nodes 7 to 10 from canes where the internodes concerned were about 1 cm thick and 8 to 12 cm long. Only canes on which the buds appeared to be healthy and undamaged were sampled. A bud was taken as burst on the day when the edge of the first leaf could first be distinguished between the bud scales. The stages chosen by the other authors quoted should not have differed from this by more than a day or two. The mean time to bursting for a group of cuttings was obtained by averaging the logarithms of the times for the individual cuttings. A logarithmic transformation was found to be appropriate for analysing the results statistically, and calculating the mean in this way avoided giving undue weight to later bursting buds. This mean was usually quite close to the time at which 50 per cent. of the cuttings had

burst, used as the mean by some authors. All cuttings were taken from the Research Station vineyard at Merbein except in 1958 when two other vineyards in the Sunraysia area were also sampled.

The results of the observation are shown in Figure 1.



Fig. 1: Days to bursting at 20° C of buds sampled at various times during autumn and winter

The dotted line in 1957 allows for buds which did not burst. Three vineyards were sampled during part of 1953

After the end of May all single bud cuttings produced shoots and only one point is shown for each time of sampling. For samples taken earlier than this, in which not all buds burst, two points are shown — one counting only those buds which burst, and the other with an allowance made for the buds which did not burst. This was done by ascribing to these buds an arbitrary date of burst after that of the last bud which did burst. While not exact it should give a more accurate estimate of the intensity of dormancy. The figures for 1956 are for nodes 6, 9, and 10 only, counting only buds which burst. These nodes were the nearest with a high percentage burst to those used in the later years.

The general picture is quite clear and agrees with that found by KONDO (1955) and NIGOND (1957). There is a steady decrease in the intensity of dormancy during autumn and winter. In each case early autumn represents the time of most intense dormancy, the intensity becoming much less before the coldest winter period begins. However there are differences in detail. Sultana buds sampled in early autumn took about three months at 20° C to burst. This agrees fairly well with the period of almost three months at 18° C which NIGOND (1957) found for Aramon buds sampled at this stage at Montpellier

but is much less than the six months at 20° C which Kondo (1955) found for the European varieties which he studied. The results shown in Figure 1 do not cover the transition from conditional to organic dormancy but observations under uncontrolled conditions indicated that this occurred, with some variation between individual buds, during late summer, as found by Kondo (1955) and ALLEWELDT (1960).

Temperature Effects on Dormancy

Most experiments were carried out at 20° C. However when buds were grown at other temperatures the relation between temperature and time to bursting agreed very closely with that found by NIGOND (1957). Cuttings taken on July 25, 1957, burst in 25.3 days at 20° C and 33.6 days at 15° C. Cuttings taken on June 3, 1958, burst in 32.9 days at 20° C and 23.7 days at 25° C. Thus the increases in speed of growth were 6.6 and 7.8 per cent. per degree respectively, compared with NIGOND's figure of 6 to 7 per cent. per degree.

In view of the magnitude of this effect it is clear that temperature would need to be very carefully controlled for a critical determination of the intensity of dormancy. A change of only 1° C would lead to an appreciable error. Thermograph records showed that the temperature in the air-conditioned laboratory used to obtain the data of Figure 1 varied over long periods by more than 1° C from the intended 20° C, and the matter was further complicated by the position of sunlit areas in the room. Quite apart from possible sampling error, therefore, Figure 1 cannot be taken to indicate any more than a general decrease in the intensity of dormancy during the period studied. The data would not be suitable for relating short term changes in bursting behaviour, such as occurred at the beginning of June, 1958, with weather records.

Only one attempt at testing the effect of low temperatures was made. Buds sampled on March 28, 1958, were held in a refrigerator at 4° C for 0, 3, 5, or 7 days and then transferred to 20° C. There was no evidence of a reduction in time to bursting after chilling. Only about half of the 20 buds burst in each case and the mean times from placing at 20° C to bursting were 73.0, 78.3, 76.7, and 72.6 days for 0, 3, 5, and 7 days of chilling respectively. The autumn in the areas where sultanas are grown in Australia (shown in locality map, ANTCLIFF and WEBSTER 1955a) is not particularly cold. In 1958 the equivalent of three days below 8° C had not occurred until the beginning of June, by which time buds sampled from the field would burst in about 40 days at 20° C. Similarly the equivalent of seven days had not occurred until later in June when buds from the field would burst in just over 30 days. This suggests that sultanas have, in fact, no chilling requirement and that some other factor during autumn and winter is responsible for reducing the intensity of dormancy, the correlation with cold being purely fortuitous.

ALLEWELDT (1959a, 1960) has come to a similar conclusion for other vine varieties. The data of NIGOND (1957) also support this idea. While suggesting that temperatures of 1° C to 8° C are about twice as effective as 0° C in breaking dormancy they also suggest that temperatures of 18° C or 25° C are still more effective. Thus in one case 400 hours at 18° C were equivalent to 820 hours between 1° C and 8° C or 2140 hours at 0° C; and in another

370 hours at 25° C were equivalent to 823 hours between 1° C and 8° C or 1592 hours at 0° C. In all his experiments the hours of chilling applied were far greater than the resultant reduction in time at warm temperatures needed for bursting, again suggesting that the warm temperatures are actually more effective in breaking dormancy. This contrasts strongly with the position in peaches (OVERCASH and CAMPBELL 1955) where warm periods decrease the effectiveness of the chilling already undergone.

Effect of Ethylene Chlorhydrin on Dormancy

Treatment with ethylene chlorhydrin has often been used to break dormancy in plants, and it was thought that a comparison of bursting times for treated and untreated cuttings taken at intervals during the winter would show when organic dormancy was ended in the field.

In 1956 and 1957 ethylene chlorhydrin was used under conditions which were not strictly controlled and gave somewhat variable results. In 1958 the effect of various concentrations and durations of treatment was tested using single bud cuttings as previously described. The cuttings were treated in an airtight tin of about 20 litres containing the chlorhydrin soaked on cotton wool and kept at 20° C. The results are shown in Table 1. At the earlier time of sampling, treatment for 24 hours gave a significantly greater reduction in

Table 1

Time to bursting at 20° C of single bud cuttings treated for various times with various amounts of ethylene chlorhydrin (in a 201 container)

Date of Sampling	0	- 8 hr 1/3 ml 1 ml	3 ml	1/3 ml	24 hr 1 ml	3 ml	1/3 ml	72 hr 1 ml	3 ml
27. 5. 58	34.6	20.0 22.1	21.1	18.3	18.6	17.4	20.3	29.5	31.0
18. 8. 58	20.1	19.2 17.9	18.8	18.9	19.7	20.4	23.8	28.7	30.7

the time needed for bursting than did treatment for 8 hours. At the later time of sampling the difference for the two higher concentrations was in the other direction and although small, was just significant, suggesting a marginal toxic effect of the longer treatment.

Treatment for 72 hours appears to have been toxic at both times of sampling but at the first the effect of the lowest concentration was only slight.

In comparing the time of bursting of treated and untreated cuttings a treatment of 3 ml per 20 l for 24 hours was adopted as standard for winter 1958. In 1956 a treatment of about 0.5 ml per 20 l for 65 hours had been used, which should have given fairly similar results, but in 1957 a much higher concentration was used, which was always toxic and at later samplings was lethal. Results for 1956 and 1958 are shown in Figure 2. Treated cuttings usually burst in about 20 days, which was also the case for the variety Merlau studied by POUGET and RIVES (1958). These results support KONDO (1955) in

his choice of the stage at which buds will burst in 20 days at favourable temperatures as the transition from organic to enforced dormancy. If this criterion is accepted the transition in the sultanas generally occurred



Fig.2: Days to bursting at $20^{\circ}\,\text{C}$ of buds treated with ethylene chlorhydrin and of untreated buds





treated with ethylene chlorhydrin; \bigcirc — \bigcirc canes in the field

somewhere near the beginning of August. This is about a month before the usual time of bud burst in the field.

In 1956, when cuttings of three or four buds were used, ethylene chlorhydrin affected the proportion of buds which burst. Figure 3 shows for each bud position the percentage of buds on the cuttings which burst during the experiment, and, for comparison, the percentage of buds which burst in spring on vines near those sampled for the cuttings, and which had been pruned to canes of 14 buds. On the untreated cuttings burst of the lower buds was very strongly suppressed. Burst of the corresponding bud position on canes still on the vine was much higher. Treatment of the cuttings with ethylene chlorhydrin stimulated more buds to burst (except on the most basal cuttings, where the short internodes meant that the lower buds were frequently immersed in the water in which the cuttings was reduced by treatment but was still evident. Thus, for cuttings with four buds, per cent. bud burst of the two upper buds was increased from 75 to 90 and that of the two lower buds from 16 to 55.

The Origin of the Inhibition During Dormancy

In 1957 and 1958 a preliminary investigation was made of the origin of the inhibition which delays bud burst during autumn and winter. Single bud cuttings were treated by removing the brown outer bud scales, by soaking in water, by removing the scales and soaking in water, and by removing the scales and soaking in water to which bud scales were added. The last two



Fig. 4: Days to bursting of buds treated in various ways
untreated; ----- outer bud scales removed;
.... soaked in water; --- scales removed and soaked in water;
.... scales removed and soaked in water with scales;
_____ treated with ethylene chlorhydrin

treatments were included in 1958 only, when observations were made at two temperatures and a chlorhydrin treatment was also included for comparison. For the water soaking treatment the cuttings were placed in about three litres of water, 18 cuttings for 65 hours in 1957 and 20 cuttings for 48 hours in 1958; for soaking in water plus scales the scales from about 500 buds were added to about 150 ml of water in which 20 cuttings were placed for 48 hours. The results are shown in Figure 4. Three times of sampling are shown for 1957. Samples were taken in the two previous months and gave similar results to the May and June samples. They are not included in the figure because not all of the buds burst; they could not be included in the statistical analysis nor could their means be as satisfactorily calculated. Because logarithms were used in the statistical analysis a constant difference necessary for significance cannot be given. For P = 0.05 it was about 2 days for means near 20 days and about 4 days for means near 40 days. It can be seen that either removing the scales or soaking in water will reduce the time needed for bursting, the former usually having the greater effect. A combination of these treatments is a little more effective than just removing the scales; on the other hand if scales are present in the water the combined treatment is nearly as effective as ethylene chlorhydrin in stimulating bursting. This effect is discussed later.

Establishment of the Pattern of Bud Burst in Canes before Bud Burst

Earlier studies of bud burst on sultana canes in the field (ANTCLIFF and WEBSTER 1955b; ANTCLIFF, WEBSTER, and MAY 1957) showed a definite pattern of bud burst. The terminal buds burst earliest and the basal buds latest, with a more pronounced variation between bud position at the ends of the cane than in the centre. The following experiment was carried out to investigate whether this pattern is established before bud burst. On July 22, 1957, 24 vines were pruned to 11 canes of 14 buds each. One cane at random was sampled from each vine on July 22, August 9, August 21, August 29, and September 3. These canes were cut into single bud cuttings from node 3 to node 14 and their time to bursting at 20° C determined. The time of burst on a further cane on each vine was observed in the field. Results are shown in Figure 5. All points for the five samples are days to bursting after sampling and are based on complete bud burst. Bud burst was not complete on the canes left on the vines but followed the usual trend, similar to that shown in Figure 3. The points for these canes are the means for the buds which burst and are days after an arbitrary base date, September 7. There were no significant differences between bud positions in time to bursting for the canes taken at the time of pruning. For canes from the next sampling, 18 days later, significant differences were found, and these followed a pattern similar to that found in the field. This pattern was then found virtually unchanged for canes from all the later samplings. The slight differences from the pattern for the canes which burst in the field can probably be accounted for by the difference in the conditions under which bud burst occurred. The more pronounced differences between bud positions at the distal end of the canes in the field are probably due to the generally lower temperatures during their burst, while the fact that differences at the proximal end were not similarly more pronounced is probably due to the failure of a proportion of the buds to burst. The corresponding buds on the cuttings, which were not prevented from bursting, were probably those which burst latest and increased the average time to bursting. Thus the pattern of bud burst must be established at least a month before the buds actually burst.



Fig. 5: Days to bursting at 20° C of each bud position for (top to bottom) canes sampled on 22.7, 9.8, 21.8, 29.8, and 3.9 and for canes in the field

A further feature of the pattern, which can be seen in Figure 5, is a tendency for the bud positions towards the distal end of the cane to be associated in pairs in their time to bursting. A similar effect for per cent, bud burst can be seen in Figure 3. These effects had been noted previously (ANTCLIFF, WEBSTER, and MAY 1957), and an experiment was started in winter 1957 to study them further. Vines were pruned to 14-bud canes, some of which were left intact while in other treatments progressively more and more of the buds at the odd nodes were scraped off, until in the most severe treatment bud one was the only odd bud remaining. Not all treatments necessarily occurred on one vine but there were 22 replications of each treatment. The time of bursting of all buds was observed in spring. The number of buds burst and the mean time of bursting of the buds which burst are shown for each bud position in Table 2. Complete bud burst at the most distal untreated odd node occurred in most treatments and notably when this was node 1 or 3. Also the mean time of bursting at the most distal untreated odd node tended to be a little earlier than it would have been if buds had been present on the more distal odd nodes.

Table 2

Number of buds burst and mean time to bursting at each bud position on 22 canes for treatments with varying numbers of odd buds removed

Odd Buds Romound		Number of Buds Burst									Mean Time to Bursting				
Odd Buds Reini	oveu	None	13	13&11	13 to 9	13 to 7	13 to 5	13 to 3	None	13	13 & 11	13 to 9	13 to 7	13 to 5	13 to 3
													2		
Bud Position	1	1	3	3	2	1	4	22	21.0	26.8	24.5	22.8	31.5	21.0	22.6
	2	8	9	5	6	5	5	4	24.9	24.9	20.3	23.3	27.3	25.9	23.6
	3	8	7	9	14	7	22		25.4	20.5	26.4	22.8	21.0	18.0	
	4	14	14	13	17	13	13	11	23.3	20.8	24.2	24.5	22.3	22.1	21.0
	5	17	16	16	14	21			20.6	19.5	20.1	21.3	16.2		
	6	20	19	16	19	15	17	20	20.5	18.6	22.8	21.2	19.6	18.3	19.3
	7	20	20	20	22				17.9	17.3	18.2	15.6			
	8	17	19	17	20	15	20	18	17.7	19.3	18.7	20.8	16.1	18.9	19.6
	9	18	21	22			N		17.5	15.7	14.6				
	10	19	21	20	20	18	21	20	16.2	16.8	15.2	15.4	15.9	15.3	14.5
	11	21	22						15.5	14.5					
	12	18	22	19	22	22	22	20	15.2	15.0	14.0	14.6	16.2	14.8	15.2
	13	21							13.5						
	14	22	21	22	20	22	22	22	13.4	12.5	11.3	12.1	11.9	12.1	11.8

The Effect of Auxin and Gibberellin on Bud Burst

To test the effect of auxin on bud burst six canes were sampled on August 20, 1957. Single bud cuttings from node 3 to 14 were completely immersed for 24 hours in a solution containing 5 p.p.m. of indole acetic acid and their time to burst at 20° C observed. Only 73 per cent. of these buds burst and their mean time to burst was 20.0 days. For comparison, buds from the third sample in the experiment on pattern of burst, which were taken on August 21, showed a complete bud burst with a mean time to bursting of 13.6 days. Thus the auxin both reduced the proportion of buds bursting and increased the time needed for bursting.

In another experiment, started on July 21, 1959, similar cuttings were treated with ethylene chlorhydrin, indole acetic acid at 10 p.p.m., gibberellic acid at 50 p.p.m., or left untreated. Cuttings from 10 canes were used for each treatment. The treatments with indole acetic acid and gibberellic acid were made by standing the cuttings with their base in the appropriate solution instead of in water for the first three days at 20° C. The values for per cent. bud burst and mean time to bursting are given in Table 3. In this case, where the auxin was available to the bud only from below, it was completely without

Treatment	Per cent. bud burst	Time to bursting
Control	99.2	27.3
Chlorhydrin	98.3	23.7
IAA	99.2	26.9
GA	61.7	85.1

Table 3

Per cent. bud burst and mean time to bursting at 20° C for single bud cuttings given various treatments

effect. Gibberellic acid, however, under the same conditions, had a most marked effect on both per cent. bud burst and mean time to bursting. This prolongation of dormancy agrees with that found by the authors quoted in the Introduction.

General Discussion

The results obtained with controlled temperatures suggest that the sultana does not require chilling to overcome dormancy. Moreover gibberellin, which according to BRIAN (1959) replaces chilling and breaks dormancy in species known to have a chilling requirement, prolongs dormancy in the sultana as in other grape varieties. It is thus most unlikely that the unsatisfactory bursting

sometimes observed on sultanas in the Murray Valley is due to a lack of winter chilling.

Sultanas in this district pass through the three phases of dormancy described by other authors for other grape varieties, but this applies only to the over-wintering buds and not to the vine as a whole. Deep organic dormancy is undergone while the vines are still actively in leaf, and on many vineyards the intensity of organic dormancy is very much reduced by the time the leaves fall. For much of the time that the vines as a whole appear dormant the buds are only in enforced dormancy.

There is a definite distinction between conditional and organic dormancy of the buds, but not between organic and enforced dormancy. Organic dormancy when at its deepest is clearly different from enforced dormancy but it disappears gradually and merges into enforced dormancy. The choice of a point dividing them has to be arbitrary. In any case if warmth is an important factor in overcoming organic dormancy then the distinction between organic and enforced dormancy will have no practical significance. When enough warmth has been received to end organic dormancy, further warmth will lead to a starting of growth. The natural variation in temperature from year to year should lead to nothing more serious than a variation in time of bud burst.

These conclusions do not necessarily conflict with those of FENNELL (1948), who found that *vinifera* grapes could not be grown satisfactorily in Costa Rica and concluded that lack of chilling was involved. The trouble was due at least in part to photoperiodic effects — ALLEWELDT (1959c) has since shown that short day treatment leads to cessation of vegetative growth — and premature development seems to have been more serious than delayed development. The normal growth cycle became impossible and two or more prunings a year were necessary to keep the vines even partially in harmony with the seasons. Thus chilling may have been required, but to prevent premature development rather than to end dormancy. The first buds to burst under abnormally warm conditions will grow strongly, and may be quite capable of inhibiting the burst of further buds as was indicated by the suppression of burst of the lower buds when cuttings of several buds were grown at 20° C.

That there is no need for the vine as a whole to undergo a dormant period is clear from the practice described by BERNSTEIN and FAHN (1960) of producing two crops per year in parts of Israel. The buds producing the winter crop certainly do not undergo any organic dormancy although the buds producing the next summer crop may pass through organic dormancy during the growth of the winter crop.

The course of dormancy and bud burst in sultanas may be governed by variations in auxin and inhibitor concentration such as found by SPIEGEL (1955) in buds and internodes of hybrid grapes. He found an inhibitor whose concentration rose during winter and fell before bud burst and an auxin whose concentration rose sharply just before bud burst, and identified the auxin as indole acetic acid. The inhibitor, which was shown to be leached out on steeping in water, may be the agent in sultana bud scales whose removal permits earlier burst of cuttings in winter, but some further explanation would be needed for the results with buds soaked in water with scales. Possibly soaking activates the destruction of the inhibitor by some other component of the scales. It is very probable that auxin is responsible for the pattern of bud burst. The tests showed that auxin had an inhibitory effect on bud burst, but that it would move only basipetally in the cane. There may be no difference between bud positions in the time at which the buds begin to move. However, if in the process they produce an auxin this will accumulate towards the base of the cane. The concentration will be lower at the terminal buds since there are no buds beyond them to replace the auxin which moves away from them. The even more pronounced effect on cuttings of several buds may indicate that in canes on the vine the auxin is able to move right out of the cane but does not move out of the base of the cuttings.

Summary

Dormancy and bud burst have been studied for sultana vines in the Murray Valley, Australia.

The vines are in deep dormancy at the beginning of autumn and the intensity of dormancy decreases gradually during autumn and winter.

Bud burst of cuttings taken during the dormant period occurs the more rapidly the higher the temperature at which they are held. There is evidence to suggest that sultanas have no chilling requirement and no clear distinction between organic and enforced dormancy.

Treatment with 3 ml of ethylene chlorhydrin in a 201 container for 24 hours is effective in breaking dormancy. The most effective treatment veries slightly with the intensity of dormancy.

Removing the outer bud scales or soaking buds in water decreases the intensity of dormancy.

The pattern of bud burst found on canes in the field is established on pruned canes at least one month before the shoots appear.

Both auxin and gibberellin will delay bud burst and reduce the proportion of buds which burst but auxin will not affect a bud above the point of application whereas gibberellin will do so.

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