REDUCING INFLORESCENCE FORMATION BY SHADING INDIVIDUAL SULTANA BUDS

By P. May*

Summary

For four seasons, individual buds developing on sultana vines in the field were shaded with a number of materials during the period of floral initiation. Heavy shading up to complete darkening consistently reduced the number and size of inflorescence primordia. This reduced fruitfulness could not be related to changes in the spectral quality of the light, which might have upset the phytochrome system, nor to changes in temperature of the buds.

Buds lacking fruit initials, whether shaded or not shaded, had smaller leaf primordia than fruitful buds. It is concluded that shading may reduce bud fertility at least partly by affecting leaf development inside the bud.

I. Introduction

Experimental shading of sultana vines in spring, when inflorescence primordia for the next season are initiated, caused a significant reduction in the number of inflorescences formed (May and Antcliff 1963). This, together with supporting evidence obtained by relating fruitfulness to hours of bright sunshine during the time of inflorescence initiation (Baldwin 1964), suggests strongly that variation in the number of inflorescences formed is, at least partly, due to differences in solar radiation.

The effect of light on floral induction, and to a lesser extent also on floral initiation, has been studied widely and considerable progress has been made in its understanding, particularly where photoperiodic reactions are involved. All investigators have found that the photoperiodic stimulus is perceived by the leaf and translocated from there to the apices where flowers are initiated.

For perennial fruit crops, particularly apples, it has been suggested that the carbohydrate–nitrogen ratio may be of importance for flower initiation and that widening of this ratio in favour of carbohydrate increases flowering. Today this hypothesis is largely abandoned in its simple form. However, it is still held that a certain level of carbohydrate, produced by the leaves under the influence of sunlight, is essential for satisfactory flower production (Kobel 1961).

Thus it is always assumed that light acts on flower induction through the agency of the leaf. This paper reports experiments where shading of individual sultana buds, without shading of leaves, reduced inflorescence formation in the shaded buds.

II. Materials and Methods

All four experiments here described were carried out on mature sultana vines (*Vitis vinifera*) growing in the vineyard of the Horticultural ¦Research ¦Section

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located at Merbein, Vic. No attempt was made to modify the general growth habit
of the vines or to change normal field conditions.

From 1957 to 1960 certain axillary buds were shaded during spring and early
summer for varying periods with various materials in a manner described below.
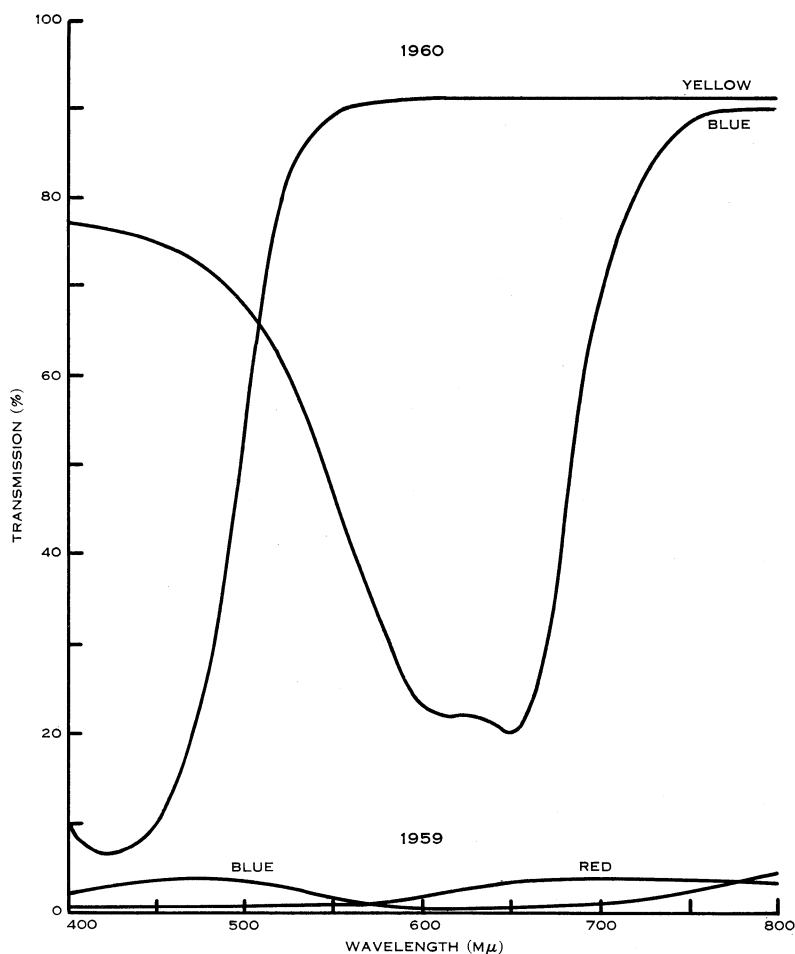As shading of whole vines during October did not affect bud fertility (May and

Fig. 1.—Percentage transmission at wavelengths between 400 and 800 mμ
of red and blue plastic film (1959) and yellow and blue Cellophane (1960) used
for shading sultana buds.

Antcliff 1963), bud shading was commenced during the last week of this month.
Buds arising on nodes 6–10 of strong shoots were treated. This is the most fruitful
region of the shoot where buds at different levels of insertion are comparable in
fruitfulness (Antcliff and Webster 1955a).

After shading was terminated the buds were left on the vines until fully dor-
mant. They were then dissected under low magnification (20–50×), the percentage

of buds with inflorescence primordia ("fruitful buds") was determined, and measurements of the inflorescence primordia, where present, were taken. In 1957–58 the approximate area of the biggest longitudinal section was calculated from the measurements of greatest length and width, while in the following years the primordia were weighed on a microbalance. In 1959–60 and 1960–61 the first five leaf primordia, which make up the bulk of the leafy material of the dormant bud, were also weighed.

The following experiments were carried out:

1957–58: A piece of stiff aluminium foil was placed between stem and leaf petiole and folded over the bud. This excluded all direct sunlight from the bud but admitted a small but uncontrolled amount of reflected light. Shading lasted from October 24 to November 27. The experiment comprised eight treatments, namely all possible combinations of shading and non-shading of buds 7, 8, and 9 on the same shoot, each shoot being regarded as a unit. Each treatment was repeated six times. Thus a total of 144 buds was included, half of which were shaded and half not shaded.

1958–59: Here the treated buds were completely darkened by wrapping several layers of aluminium foil around them and the adjoining parts of stem and leaf petiole. There were 16 treatments, 15 of which differed in commencement and duration of shading, the sixteenth being the untreated control. The shading treatments were applied in a triangular factorial arrangement, i.e. shading commenced on October 23, November 11, November 25, December 9, or December 23, and lasted for 2, 4, 6, 8, or 10 weeks, but ended not later than January 5.

Buds at nodes 7, 8, 9, and 10 on 100 shoots were used. The original design of the experiment, five sets of a 4×4 balanced lattice [bud position $= k$, vine $= r$, cane $= b$ (Cochran and Cox 1950, p. 304)] could not be used for the final evaluation because of many missing values. As a preliminary test showed that variation between canes did not contribute greatly to the total variance, complete randomization of the treatments over all buds was assumed. The statistical analysis for percentage of fruitful buds (after angular transformation) and for inflorescence primordium weight (after square root transformation) was carried out by testing the fit of the data to a model in which each period of shading was assumed to have been effective, the effects of successive periods being cumulative in a simple additive form. Constants for the model were determined by the method of least squares and the analysis repeated using working values from the first-cycle estimates (Fisher and Yates 1957, Table X_2) as a basis for the second cycle.

1959–60: The intensity and quality of the sunlight reaching the buds was varied by a single layer of clear, red, blue, or black plastic film. The light transmission of these materials, as measured in a spectrophotometer against air, is shown in Figure 1. Shades were placed

during the periods October 20–November 17, November 10–December 8, or October 20–December 8.

Buds 6, 7, 8, and 9 on 104 shoots, arising from node 7 of canes pruned to eight buds, were used and the 13 treatments allocated to them at random.

1960–61: Celluloid tubes of 1 in. diameter and about $2\frac{1}{2}$ in. length were placed around the node and the basal part of the subtending leaf's petiole. The inside of the tube was covered by one layer of clear, yellow, or blue Cellophane, or of a metallized polyester film which provided complete darkness. The light transmission of the coloured films of Cellophane are also shown in Figure 1. The celluloid tubing excluded about 15% of the light throughout the visible part of the spectrum. Top and bottom of the tubes were plugged with cotton-wool.

This mode of shading made treating of more than one bud per shoot impossible. Therefore, on each of 165 vines five similar shoots were selected and bud 7 on each had one of the treatments allocated at random. Shading lasted from November 5 to December 14.

TABLE 1

PERCENTAGE OF FRUITFUL BUDS AND WEIGHT (OR SIZE) OF INFLORESCENCE PRIMORDIA FORMED IN
SULTANA BUDS UNDER HEAVY SHADE

Seasons 1957 to 1960

Season	Fruitful Buds (%)			Inflorescence Primordium Size		
	Not Shaded	Transparent Cover	Heavy Shade	Not Shaded	Transparent Cover	Heavy Shade
1957	100	Not applied	70	$0 \cdot 402$ mm^2	Not applied	$0 \cdot 326$ mm^2
1958	96	Not applied	67*	108 μg	Not applied	46 μg*
1959	60	64	25	53 μg	53 μg	65 μg
1960	92	83	65	115 μg	68 μg	65 μg

* Average of all periods during which shading was effective.

III. RESULTS

(a) Effect of Heavy Shading

In each of the four seasons buds were shaded very heavily or completely darkened. The overall results of these treatments on percentage of fruitful buds and average size of inflorescence primordia are shown in Table 1. Some aspects of the results will be discussed in more detail later, but the overall trend is quite clear. Heavy shading or complete darkening of individual buds considerably reduced the likelihood of their becoming fruitful. Covering with transparent material on the other hand had no effect in 1959 and only slight effect in 1960, the latter probably

being due to the fairly heavy shade cast by the cotton-wool plugs inserted in the ends of the celluloid tubes.

Shading also tended to reduce development of the inflorescence primordia, measured either by an estimate of size (1957) or by their fresh weight. In each year the mean for the heavily shaded buds was the lowest. However, the results were less definite, possibly because measurements of inflorescence primordia normally show great variability.

TABLE 2

FRUITFULNESS OF SULTANA BUDS SHADED DURING VARIOUS PERIODS BETWEEN OCTOBER 28, 1958, AND JANUARY 6, 1959, TOGETHER WITH CONSTANTS FITTED BY METHOD OF LEAST SQUARES FOR EACH PERIOD OF 2 WEEKS

Levels of significance refer to differences between each shading treatment and the not-shaded control

| Duration of Shading (weeks) | Date of Commencement of Shading | | | | | Not Shaded |
	28.x.58	11.xi.58	25.xi.58	9.xii.58	23.xii.58	
	Fruitful Buds (%)					
0						96
2	75**	100	92	95	95	
4	71***	83*	90	89		
6	45***	74***	87			
8	52***	73***				
10	65***					
	Constants†					
2	−17·00	−4·66	−8·30	−2·26	−0·99	78·71
	±3·68	±3·68	±3·68	±3·68	±3·68	±2·96

* $P < 0.05$.   ** $P < 0.01$.   *** $P < 0.001$.

† Angular transformation of percentage of fruitful buds.

(b) Critical Period of Shading

May and Antcliff (1963) found that shading of whole vines affected bud fertility during a period of about 6 weeks. They assumed that the critical period, although short for each individual bud, is prolonged for whole vines because of differences in time of development between buds of different shoots and at different levels of insertion. Heavy shading of individual buds during various periods was tested in 1958 and, less extensively, in 1959.

The results for 1958 are summarized in Tables 2 and 3. Most critical for the initiation of inflorescence primordia was the fortnight between October 28 and November 11, when shading brought about a significant reduction in the proportion of fruitful buds. Shading before this period was not tried because bud fertility had not been altered when whole vines were shaded during October (May and Antcliff 1963). Up to December 9 fruitfulness was further reduced by prolonging the treatment. No effect resulted from treatments commenced on or after November 25.

The statistical model described earlier fitted the observed values without any significant deviations. The constants for each period of 2 weeks' shading (Table 2) and for the not-shaded control further illustrate these trends.

As shown in Table 3, average fresh weight of inflorescence primordia also tended to be smaller under the treatments which reduced fruitfulness. The effects are of a similar order but somewhat more irregular. The statistical model again fitted the observed values without any significant deviations, the constants being also shown in Table 3.

The detrimental effect on the growth of inflorescence primordia seems to have extended longer into summer than the effect on inflorescence initiation. This is not surprising as initiation of primordia in buds comparable to those treated here ceases about the second week of December, while preformed primordia continue to grow until the beginning of February (May 1964).

TABLE 3

MEAN WEIGHT OF INFLORESCENCE PRIMORDIA FORMED IN SULTANA BUDS UNDER HEAVY SHADE DURING VARIOUS PERIODS BETWEEN OCTOBER 28, 1958, AND JANUARY 6, 1959, TOGETHER WITH CONSTANTS FITTED BY METHOD OF LEAST SQUARES FOR EACH PERIOD OF 2 WEEKS

Levels of significance refer to differences between each shading treatment and the not-shaded control

Duration of Shading (weeks)	Date of Commencement of Shading					Not Shaded
	28.x.58	11.xi.58	25.xi.58	9.xii.58	23.xii.58	
	Mean Weight of Inflorescence Primordium (μg)					
0						108
2	65**	76*	78	94	87	
4	54***	64**	78	58**		
6	46***	49***	65**			
8	69*	66**				
10	43***					
	Constants†					
2	−0·94 ±0·47	−0·79 ±0·47	−0·49 ±0·47	−0·11 ±0·47	−0·62 ±0·47	9·44 ±0·38

* $P < 0·05$.   ** $P < 0·01$.   *** $P < 0·001$.

† Square root transformation of inflorescence primordium weight.

In 1959 three periods of shading were tested, extending over the whole period of initiation or over its first or second half, but overlapping by 1 week. No significant differences between periods were found for either percentage of fruitful buds or weight of inflorescence primordia, although all three periods differed significantly from not-covered control in both respects. The week commencing November 10, common to the three periods of shading, thus appears to have been the most effective time for reducing fruitfulness.

While the shoots selected for treatment in 1958 arose near the crown of the vine, those treated in 1959 originated from bud position 7 of eight-bud canes. Shoots from terminal buds burst and develop more uniformly than those near the crown (Antcliff and Webster 1955b). This may account for the shorter critical period found in 1959.

(c) Interaction between Shaded and Unshaded Buds on the Same Shoot

A bud is less likely to become fruitful when shaded, but this detrimental effect does not affect other, not-shaded buds on the same shoot. This is illustrated in Figure 2 where the results of the 1957 experiment are shown.

While only 70% of the 61 viable shaded buds became fruitful all 69 not-shaded buds produced inflorescence primordia irrespective of their association with shaded or not-shaded buds on the shoot. There was, however, a weak, statistically non-significant trend for the proportion of fruitful buds to become smaller as the number of shaded buds per shoot increased.
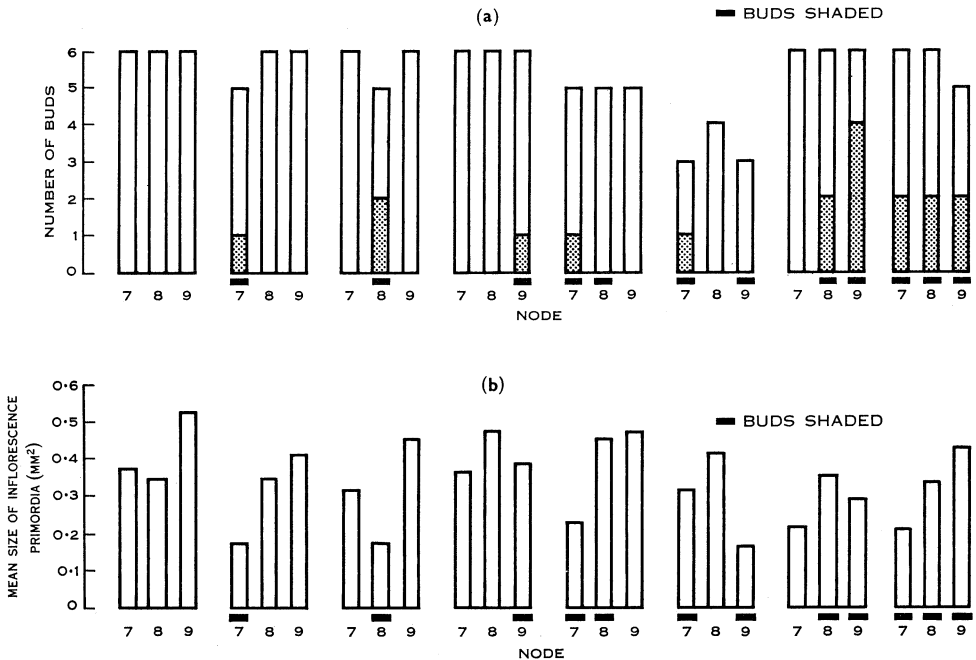
Fig. 2.—(a) Number of fruitful (open rectangles) and unfruitful (stippled rectangles) buds arising on nodes 7, 8, and 9, when one, two, or three buds per shoot were shaded. (b) Mean size of inflorescence primordia of the fruitful buds.

(d) Effect of Light Quality

Measuring the effect of light quality under field conditions is difficult. Nevertheless attempts were made in 1959 and 1960 to test whether the reduction in bud fertility due to shading could be attributed to changes in the ratio of red and far-red radiation. This ratio has been shown to be involved in many photomorphogenic reactions, including flower initiation (Borthwick and Hendricks 1961).

In each of the two seasons two covering treatments were applied which provided similar amounts of photosynthetically active light. But, while one cover excluded a large portion of the blue light, leaving the ratio of red and far-red more or less unchanged, the other excluded mainly the red part of the spectrum, thereby upsetting

the red–far-red relationship. The transmission curves for these materials are shown in Figure 1.

   Table 4 summarizes the results of these treatments. Complete darkening significantly reduced fruitfulness in both seasons. In 1959 buds under the coloured shades, which excluded a large proportion of the visible radiation, were also less fruitful than those under transparent covers. The more transparent coloured shades in 1960, however, did not cause significant infertility, although trends similar to the previous season were again apparent.

TABLE 4

PERCENTAGE OF FRUITFUL BUDS AND WEIGHT OF INFLORESCENCE PRIMORDIA FORMED IN SULTANA
BUDS UNDER SHADES OF DIFFERENT COLOURS IN SEASONS 1959 AND 1960

Levels of significance (on angular transformation of percentage of fruitful buds) between treatments, identified by index figures (1)–(4), are shown. Differences between treatments in inflorescence weight are not significant

Treatment	Fruitful Buds (%)		Inflorescence Weight (μg)	
	1959 Season	1960 Season	1959 Season	1960 Season
Black[1]	24·5***[4], *[3]	65·1**[4], *[2]	39	64
Red†[2]	37·5**[4]	78·7	35	77
Blue[3]	45·2*[4]	75·7	36	62
Clear[4]	64·1	82·8	53	68

   * $P < 0.05$.   ** $P < 0.01$.   *** $P < 0.001$.
   † Yellow in 1960.

   Weight of inflorescence primordia was not affected significantly by any treatment, although in 1959 the mean values tended to be smaller under all covers.

   There was no indication that effects of shading are related to quality of light. It appears that heavy reduction of overall light intensity, irrespective of the spectral composition of the residual light, is responsible for reducing fruitfulness.

(e) Effect of Shading on the Development of Leaf Primordia

   When studying the development of grape buds it had been found that fruitful sultana buds have more and larger leaf primordia than barren buds at the time of inflorescence initiation and from then on until buds burst next spring (May 1964). From this, and from the close positive relationship between the size of leaf primordia and inflorescence primordia in fruitful buds, it was concluded that the initiation and development of inflorescences is at least partly dependent on growth of the vegetative components of the bud.

   When measuring the weight of leaf primordia in 1959 and 1960 similar differences between fruitful and barren buds were found for buds of all treatments, and the

TABLE 5

MEAN FRESH WEIGHT OF THE FIVE MOST BASAL LEAF PRIMORDIA OF FRUITFUL AND BARREN SULTANA BUDS WHICH HAD DEVELOPED UNDER VARIOUS SHADING TREATMENTS, TOGETHER WITH THE NUMBER OF BUDS (n) ON WHICH EACH MEAN IS BASED. ALSO SHOWN ARE CORRELATION COEFFICIENTS (r) BETWEEN WEIGHT OF LEAF AND INFLORESCENCE PRIMORDIA IN THE FRUITFUL BUDS

Seasons 1959 and 1960

| Shading Treatment | 1959 Season | | | | | 1960 Season | | | | |
| | Fruitful Buds | | | Barren Buds | | Fruitful Buds | | | Barren Buds | |
	r	n	Mean Fresh Weight (μg)	n	Mean Fresh Weight (μg)	r	n	Mean Fresh Weight (μg)	n	Mean Fresh Weight (μg)
Black	0·75***	17	543	48	405	0·23 (n.s.)	51	604	23	412
Red†	0·49**	23	555	36	417	0·21 (n.s.)	71	642	16	421
Blue	0·67***	28	567	34	351	0·41***	68	627	17	448
Clear	0·60***	43	592	23	385	0·55***	67	614	15	528
Not shaded	0·45 (n.s.)	15	657	10	365	0·48***	91	621	7	467

** $P < 0.01$.   *** $P < 0.001$.   n.s., not significant.
† Yellow in 1960.

weights of leaf primordia and inflorescence primordia in fruitful buds were positively and in most cases significantly correlated in both years (Table 5).

IV. Discussion

Apart from altering the light regime of the bud, shading affected its general environment, notably its temperature. The magnitude of these effects was tested by exposing thermometers, whose bulbs had been covered by the materials and methods used to shade buds, concurrently to full sunlight. Mean temperatures from several readings are shown in Table 6. The temperature under very heavy shades deviated little from ambient in three seasons but was considerably increased in the fourth, while fruitfulness under these shades was lower in all four seasons. On the other hand clear covers considerably increased temperature in both seasons without affecting bud fertility. Thus the observed effects seem unrelated to changes in temperature brought about by shading.

TABLE 6

TEMPERATURE MEASURED BY MERCURY-IN-GLASS THERMOMETERS SUSPENDED CONCURRENTLY IN FULL SUNLIGHT BUT WITH BULBS SHADED BY THE DIFFERENT MATERIALS AND METHODS USED FOR THE SHADING OF SULTANA BUDS IN EACH OF THE SEASONS 1957 TO 1960

Shading Treatment	Temperature (°C)			
	1957	1958	1959	1960
Black	18	19	22	19
Red†	—	—	21	24
Blue	—	—	25	26
Clear	—	—	24	24
Not shaded	18	18	18	18

† Yellow in 1960.

It appears therefore that changing the light regime was directly responsible for the shading effects. The experiments in 1959 and 1960 did not provide evidence that, in the sultana, floral initiation is connected with the phytochrome system which controls photoperiodic determination of flowering in many plants. This agrees with results by Alleweldt (1964) on *V. rupestris* (cv. St. George) indicating that the number of inflorescences per bud does not depend on length of day. In *V. vinifera* the inflorescence is inserted extra-axillary and leaf-opposed. The level of insertion varies slightly from bud to bud, but is characteristic for the variety. In the sultana the first inflorescence is mostly found at the seventh node. It has been proposed that the decision whether an inflorescence is to be formed is at least partly determined by the development of the leaf primordia on nodes preceding the "floral node" (May 1964). This view receives support from the present results. If shading acted on the initiation of inflorescence primordia directly without affecting leaf primordia larger leaves should have been present in buds which remained barren because of shading. No such effect

was apparent (Table 5), the relationship in leaf weight between fruitful and barren buds being similar for shaded and non-shaded buds.

Shading also caused partial etiolation of the leaves inside the bud. This may be supporting evidence that they are involved in determining inflorescence initiation.

For soybeans, darkening of young leaves reduced their import of assimilates, prevented them from reaching full size and led to their abscission (Thrower 1964). It may well be that a reduced import into the bud, when shaded, contributes to reduced fruitfulness. Up to flowering, unfavourable conditions such as deficiency of water, assimilates, or possibly hormones may all upset the development of the inflorescence, often leading to total abscission. This indicates that, up to this stage, the inflorescence is the weakest "sink" of the shoot system. If import into the bud is reduced by shading, at the time when the inflorescence should be initiated, insufficient assimilates may reach the region of the apex where initiation was to take place.

V. ACKNOWLEDGMENTS

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