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## **Influence of temperature and photoperiod on flower induction and inflorescence development in sweet orange (*Citrus sinensis* L. Osbeck)**

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### SUMMARY

At low temperature (15° C. day/5° C. night) flowering of sweet orange cuttings was not photoperiodically controlled, occurring at 16-, 12-, and 8-hour photoperiods.

When plants were transferred, after varying periods of low temperature (15°/8° C.) to warm conditions (30°/25° C.), growth of the buds commenced within a few days of transfer. Flowering response to length of the cold treatment appeared to be quantitative.

High temperatures (above 30° C.) appeared to impair development of the flower buds.

Temperature had a large influence on the type of inflorescences† formed; more leaves were formed on the inflorescences of plants growing at 24°/19° C. and 27°/19° C. than at 18°/13° C. and 15°/10° C. No significant differences occurred between 11- and 13-hour photoperiod treatments.

These results are discussed in relation to climatic conditions in the field.

RECENTLY Lenz (1969) has shown that flowering in sweet orange can be controlled by photoperiod at a moderate temperature (24° C. day/19° C. night). However, field evidence (Abbott, 1935) is in favour of floral initiation occurring during the winter months when temperatures are low (15° C. day maximum/5° C. night minimum). Thus it was considered necessary to test the influence of photoperiod at these low temperatures to find if short day-length is the primary agent of flower induction, or if low temperatures alone induce flowering.

Similarly, little is known about the development of orange inflorescences, and whether it is influenced by external factors. Haas (1949) found that late-opening flowers set more fruit than ones which flowered earlier, so it was thought possible that changes in temperature and small changes in photoperiod might influence development. The inflorescences of sweet orange can be classified into five main types (Sauer, 1951), as shown in Fig. 1. Both Sauer and Lenz (1966) found considerable differences between the various types of inflorescences in their ability to set fruit. Nothing is known about factors which might influence the proportion of one type of inflorescence to another.

The effects were studied of temperature, over a range likely to occur between induction

† The term "inflorescence" in this paper has been applied to all types of flower-bearing growth arising from axillary buds, as used by Reece (1945).

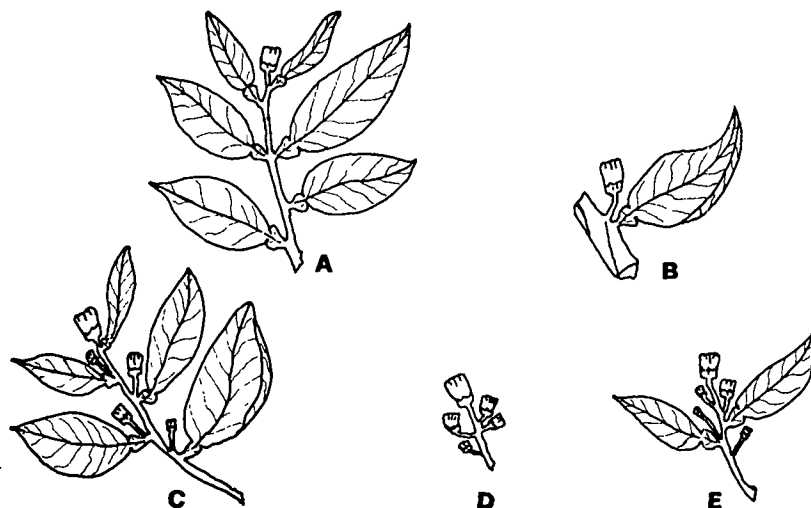


FIG. 1

Inflorescence types of shoots: A, with several leaves and one flower; B, with no leaves and one flower; C, with several leaves (more than half the number of flowers), and many flowers; D, leafless with several flowers; E, with a few leaves (less than half the number of flowers).

and flowering, and of two photoperiods that represented the day-length during late winter and spring.

#### *Materials and methods*

One-year-old orange cuttings of the variety "Washington Navel" were used. They were propagated as described by Gates *et al.* (1961) and grown in sand culture (Lenz, 1967). Plants were grown under glasshouse conditions with a minimum night temperature of 18° C., and were selected for uniformity before transferring to the experimental treatments. The treatments were carried out in the CSIRO phytotron at Canberra in naturally lit cabinets where the plants received 8 hours of natural daylight, and afterwards the photoperiod was extended as required with incandescent light. Upon termination of the natural daylight the temperature was dropped by 5° C.

#### *Influence of day-length on flower initiation*

The plants for this experiment bore developing fruit until the start of the experiment so that no flowers were likely to be initiated on them. (A similar group of plants retained in the glasshouse did not flower until after the fruit ripened.) There were six plants per treatment. The treatments, begun on 5th June 1967, were:

- (i) 8 hours of natural daylight
- (ii) 8 hours of natural daylight+4 hours of incandescent light
- (iii) 8 hours of natural light+8 hours of incandescent light.

All treatments were carried out at 15° C. during the 8-hour day, and 5° C. during the night. After 8 weeks, signs of inflorescence formation were apparent, and the night temperature was increased to 10° C. After 17 weeks from commencement of the experiment flowering was recorded.

*Effects of varying periods of inductive conditions on shoot and flower development*

Plants were kept at 15° C. day/8° C. night temperature (hereafter referred to as 15°/8° C.) with 10 hours of day temperature, photoperiodic and photosynthetic light. This approximates to winter conditions in the Murrumbidgee Irrigation Area (Table VI). In this area orange trees produce three growth flushes per year, the greatest amount of new shoots, including flowering ones, occurring upon the return of warmer conditions in the spring. At fortnightly intervals 10 plants were transferred to 30°/25° C., with 8 hours of day temperature, and 16 hours of photoperiodic and photosynthetic light. It is known that flowering of citrus cuttings does not occur under these conditions (Lenz, 1969). Control plants remained at 30°/25° C. The number of new shoots and inflorescences was recorded after 2 weeks of warm conditions.

*Influence of temperature and day-length on inflorescence development*

Fruit was removed from the plants 4 weeks before commencement of the treatments, so that flowering could be induced. However, the number of flowers initiated was related to subsequent treatment. There were five plants per treatment, and the treatments commenced 28th June 1967. Temperature treatments were:

- (i) 27°/22° C.
- (ii) 24°/19° C.
- (iii) 18°/13° C.
- (iv) 15°/10° C.

For each temperature treatment there were two photoperiod treatments:

- (i) 11 hours
- (ii) 13 hours.

The time to flower opening was recorded by noting the date of flower opening of each flower on the first five inflorescences of each plant. The numbers and types of inflorescences were recorded. The ratio of the number of flowers to number of inflorescence-leaves (hereafter referred to as flower/infl.-leaf ratio) was used as an index of the types of inflorescences produced.

## RESULTS

*Influence of day-length on flower initiation*

Flowering occurred at all day-lengths, indicating that photoperiod is not likely to be the controlling factor (Table I).

There were significantly fewer inflorescences formed on the plants with 16 hours day-length, but this effect was due to fewer shoots being produced. Even at low temperatures

TABLE I  
*Influence of day-length on flowering at 15°/5° C.*

| Day-length          |    |    | Number of new shoots per plant | Number of inflorescences | Flowers per inflorescence | Ratio of flowers/leaves per inflorescence |
|---------------------|----|----|--------------------------------|--------------------------|---------------------------|-------------------------------------------|
| 8 hours             | .. | .. | 116                            | 109                      | 4.28                      | 2.58                                      |
| 12 hours            | .. | .. | 103                            | 102                      | 4.31                      | 3.81                                      |
| 16 hours            | .. | .. | 79                             | 76                       | 4.24                      | 3.71                                      |
| L.S.D. ( $P=0.05$ ) | .. | .. | —                              | 21                       | NS                        | NS                                        |

day-length may have some influence over bud dormancy. There were no differences in the number of flowers per inflorescence or the types of inflorescences produced as indicated by the flower/inf.-leaf ratio.

*Effects of varying periods of inductive conditions*

The low temperature ( $15^{\circ}/8^{\circ}$  C.) treatment caused more buds to become uninhibited after transfer to warm conditions. Flowering was irregular, and there was evidence that the high day temperature of  $30^{\circ}$  C. impaired the formation of flowers. Small aborted flower buds were observed in several instances; a similar effect was noted in plants which had received 4 weeks of inductive treatment, and then were transferred to a glasshouse where temperatures were above  $30^{\circ}$  C. during the day. It seems that about 4 weeks of inductive cool conditions will induce flowering (Fig. 2), but the inhibiting effects of subsequent high temperature precludes any conclusion on this aspect.

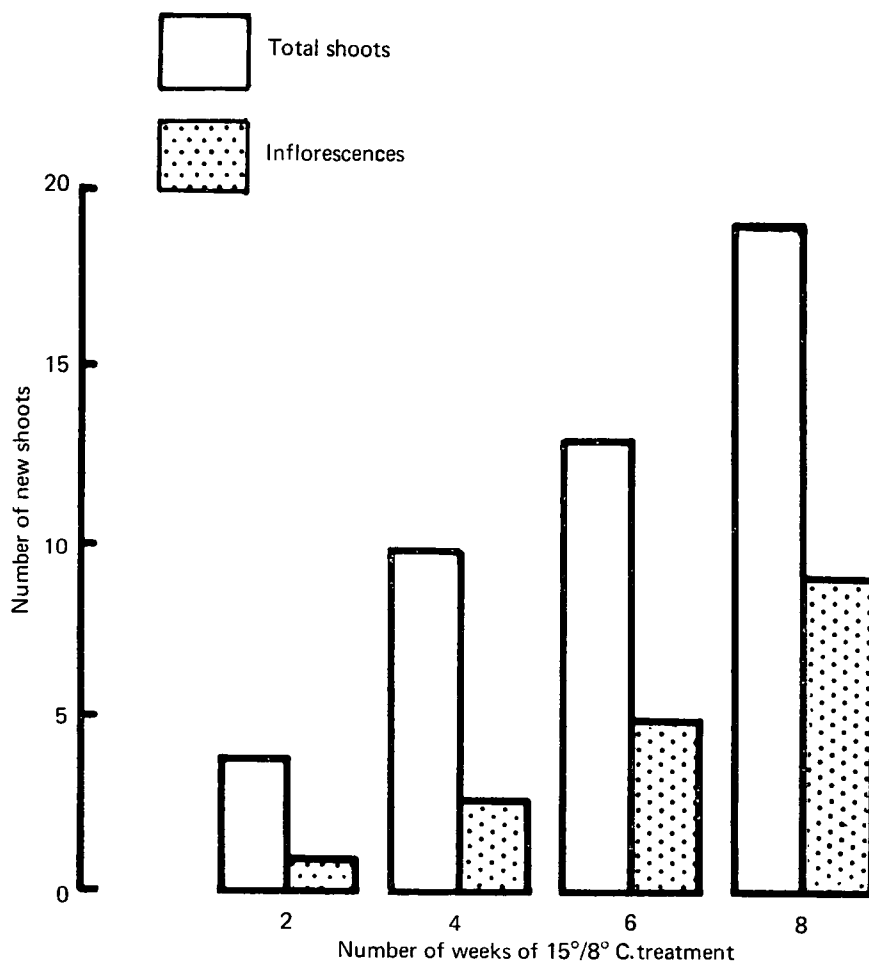


FIG. 2

Influence of varying periods of low temperature on bud inhibition and flower initiation.

*Influence of temperature and day-length on inflorescence development*

Day-length had no consistent effect on the time to flowering (Table II). A statistical analysis of the 18°/13° C., and 15°/10° C. data showed that day-length effects were not significant at the 5% level of probability. Temperature had a large effect on the time to flowering.

TABLE II  
*Mean time to flower in days from commencement of the experiment*

| Temperature treatment | 11-hour day-length | 13-hour day-length |
|-----------------------|--------------------|--------------------|
| 27°/22° C.            | 11.0               | 14.0               |
| 24°/19° C.            | 27.0               | 27.0               |
| †18°/13° C.           | 72.6               | 52.5               |
| †15°/10° C.           | 114.8              | 127.1              |

† Temperature treatments significant at  $P=0.001$ , day-length not significant.

The lower the temperature the more flowers were formed, though the day-length had no influence on the numbers of inflorescences (Table III). The number of flowers per inflorescence stayed constant over the temperature range 15° to 27° C., and was not influenced by photoperiodic treatment (see also Table I).

TABLE III  
*Effects of temperature and day-length on number of inflorescences formed, and on the number of flowers per inflorescence*

| Temperature treatments | 11-hour day-length        |                            | 13-hour day-length        |                            |
|------------------------|---------------------------|----------------------------|---------------------------|----------------------------|
|                        | Number of inflorescences† | Flowers per inflorescence‡ | Number of inflorescences† | Flowers per inflorescence‡ |
| 27°/22° C.             | 9.0                       | 4.1                        | 6.2                       | 4.1                        |
| 24°/19° C.             | 14.0                      | 5.0                        | 22.0                      | 4.3                        |
| 18°/13° C.             | 50.6                      | 4.6                        | 37.6                      | 4.4                        |
| 15°/10° C.             | 102.6                     | 4.5                        | 96.2                      | 3.9                        |

† Temperature treatments significant at  $P=0.001$ , day-length treatments not significant.

‡ Treatments not significant.

Table IV contains the percentages of inflorescences in each of Sauer's five types. Day-length had no significant effect, but temperature had a highly significant effect on the types of inflorescences formed. At 18°/13° C. and below, the many-flowered leafless type of inflorescence (type D) predominated, but at 27°/22° C. the many-flowered leafy type of inflorescence (type C) was the commonest. At 24°/19° C. the proportions of the two types of multi-flowered inflorescences were approximately equal. This effect of temperature is most easily seen if the flower/infl.-leaf ratio is used as an index of the type of inflorescence formed (Table V).

TABLE IV  
Occurrences of the different types of inflorescences expressed as percentages of the total number of inflorescences in each treatment

| Temperature treatments | Inflorescence type†<br>Pp.(hr.)‡ | A   |     |      | B    |      |      | C    |      |      | D    |      |      | E    |      |      |
|------------------------|----------------------------------|-----|-----|------|------|------|------|------|------|------|------|------|------|------|------|------|
|                        |                                  | 11  | 13  | Mean | 11   | 13   | Mean | 11   | 13   | Mean | 11   | 13   | Mean | 11   | 13   | Mean |
| 27°/22° C.             |                                  | 4.9 | 6.5 | 5.7  | 22.0 | 7.5  | 14.8 | 61.0 | 67.8 | 64.4 | 5.9  | 16.0 | 11.0 | 6.2  | 2.2  | 4.2  |
| 24°/19° C.             |                                  | 3.3 | 3.0 | 3.1  | 2.9  | 6.1  | 4.5  | 58.7 | 23.3 | 41.0 | 28.0 | 38.7 | 33.4 | 7.0  | 29.0 | 18.0 |
| 18°/13° C.             |                                  | 0.3 | 0.0 | 0.1  | 6.7  | 6.9  | 6.8  | 21.1 | 15.3 | 18.2 | 52.0 | 66.5 | 59.2 | 20.0 | 11.3 | 15.6 |
| 15°/10° C.             |                                  | 1.0 | 5.0 | 3.0  | 4.6  | 12.6 | 8.6  | 18.0 | 23.0 | 20.5 | 54.6 | 46.5 | 50.6 | 21.8 | 15.1 | 18.4 |
| L.S.D. ( $P=0.05$ )    |                                  | —   | —   | NS   | —    | —    | NS   | —    | —    | 14.5 | —    | —    | 15.5 | —    | —    | 7.3  |

† See Fig. 1.

‡ Pp.(hr.)=photoperiod in hours.

(Photoperiod treatment had no significant effect.)

TABLE V  
*Effect of temperature on the flower/inflorescence leaf ratio*

| Temperature treatments | Ratio of flowers to inflorescence leaves |
|------------------------|------------------------------------------|
| 27°/22° C.             | 1.35a †                                  |
| 24°/19° C.             | 2.28a                                    |
| 18°/13° C.             | 19.60b                                   |
| 15°/10° C.             | 5.27b                                    |

† Statistical analyses carried out on logarithmically transformed data. Treatment means bearing different postscripts differ at  $P=0.05$  (Duncan test, 1955).

#### DISCUSSION

Flower differentiation in sweet orange takes place during January in the Northern Hemisphere (Abbott, 1935; Ayalon and Monselise, 1960). The latter authors used a technique based on ringing a branch and removing all leaves distal to the ring (on the assumption that no inducing stimuli could then reach the buds distal to the ring) and claimed that induction stimuli were only slightly operative during November and December, but had the maximum effect early in January. If this is so, then in Australia one might expect flower initiation to take place in July, so that the plant is probably receptive to inductive conditions during May and June. Table VI shows that both short days and low temperatures occur at this time, but from this work the low temperatures might be expected to have the greatest influence on floral initiation. With the Satsuma orange this does not appear to be so, since Iwasaki and Owada (1960) claimed that higher winter temperature resulted in increased flowering in the spring, temperatures during December and January being decisive. However, this would not be borne out by the data for Washington Navel oranges (Table III) where the amount of flowering was greater at the lower temperatures.

Long photoperiods may prevent flowering during the summer (Lenz, 1969), but the presence of growing fruit will also inhibit flowering.

More flowers may be initiated at low temperatures as a result of the slow rate of development of the buds, so that they remain under inductive conditions for a longer period. Also, the cooler temperatures cause many inhibited buds to develop into shoots which also become floral.

Unfortunately it was not possible to determine accurately the minimum number of weeks of inductive conditions necessary for flower induction, but it appears to be short, probably at least 3 weeks, and to be a quantitative rather than a qualitative effect. Under field conditions the length of time that suitable conditions inductive to flowering occur would not be limiting. The suppression of flower-bud development by high temperatures has been noted more definitely in *Pharbitis* by King (1968), and Hield *et al.* (1966) reported that high temperatures (29°–38° C.) prevented flowering of grapefruit seedlings.

The high flower/infl.-leaf ratio with the 18°/13° C., and 15°/10° C. conditions is due to failure of the leaves on the floral shoots to develop. Minute leaves can be seen when the inflorescence is only a few millimetres long, but they fail to expand, and in some cases

wither or fall off. The mechanism of this phenomenon has not yet been explained, although two hypotheses have been considered:

(a) low temperature may reduce the translocation (or supply) of nutrients and/or hormones so that these substances are limiting, in which case the flowers must be better able to compete against the leaves for these substances. Citrus cuttings grown for long periods at low temperatures become yellow, suggesting nitrogen deficiency even when well supplied.

(b) the flowers may be able to develop at a slightly lower temperature than the leaves.

Further work is needed to elucidate this process.

Because of the observed impairment of flower development by high temperature, the possibility that the low flower/inf.-leaf ratio at 24°/19° C. and 27°/22° C. is due to flower degeneration must be examined. In the experiment described here this seems unlikely because the number of flowers per inflorescence was unaffected by temperature, and a reduction in the number of flowers per inflorescence would be expected if any flower degeneration had occurred.

Fruit-set was recorded in the plants in this experiment, but temperatures after flowering may have had an influence on set, so that the different treatments cannot readily be compared. The percentage of flowers that set fruit was slightly higher for the higher-temperature treatments, though the low-temperature treated plants had more fruit on them because of the greater number of inflorescences. Under field conditions there are large differences in the ability of the various types of inflorescences to set fruit (Sauer, 1951; Lenz, 1966). Since it has been demonstrated that temperature during inflorescence development markedly affects the relative proportions of the different types of inflorescences (Table IV), this effect of temperature might be of some importance in determining fruit-set. Flowering in Washington Navels, in the Murrumbidgee Irrigation Area, takes place during late October and November, so it might be supposed that temperature during September and October would have an effect on inflorescence development. It can be seen from Table VI that these temperatures are relatively low, and would be conducive to the formation of leafless inflorescences. Field data obtained in the spring of 1967 (Table VII) show an appreciable proportion of leafless inflorescences, as was also reported by Sauer (1951). Thus field

TABLE VI  
*Mean monthly temperatures and day-lengths for Griffith*  
*(36-year means, after Fleming and van Aken, 1968)*

| Month           | Mean max.<br>°C. | Mean min.<br>°C. | Mean<br>°C. | Day-length†<br>hours |
|-----------------|------------------|------------------|-------------|----------------------|
| May .. ..       | 18.3             | 5.6              | 11.9        | 11.3                 |
| June .. ..      | 14.8             | 3.8              | 9.3         | 10.8                 |
| July .. ..      | 14.1             | 2.9              | 8.5         | 11.0                 |
| August .. ..    | 16.1             | 3.8              | 9.9         | 11.7                 |
| September .. .. | 19.7             | 5.5              | 12.6        | 12.8                 |
| October .. ..   | 23.1             | 8.7              | 15.9        | 13.9                 |
| November .. ..  | 27.0             | 11.8             | 19.4        | 15.0                 |

† Plus 1 hour to allow for twilight.

temperatures during inflorescence development may have some influence on fruit-set of sweet orange. Work is now in progress to see if such a relationship can be found by analysing data from a long-term experiment.

Similar results to those reported here have been found in subsequent experiments which will be reported at a later date.

TABLE VII  
*Percentage frequencies of inflorescence types occurring on Washington Navel trees in the field*

| Inflorescence type |              |              |              |             |
|--------------------|--------------|--------------|--------------|-------------|
| A                  | B            | C            | D            | E           |
| 22.7<br>±3.7       | 23.9<br>±2.9 | 14.2<br>±2.3 | 32.2<br>±4.5 | 7.0<br>±0.7 |

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