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# The effect of high daytime temperatures on inhibition of flowering in 'Koroneiki' olives (*Olea europaea* L.) under chilling and non-chilling nighttime temperatures

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## Abstract

Regulation of flowering in 'Koroneiki' olives by various regimes of daytime and nighttime temperatures was investigated. The trees flowered profusely under chilling (2.5°C; 569 inflorescences tree$^{-1}$) and non-chilling nighttime temperatures (8.3°C; 729 inflorescences tree$^{-1}$) when daytime temperatures were kept optimal (18.3°C). Chilling nighttime temperatures (2.5°C) did not produce any greater number of inflorescence than non-chilling temperatures of 8.3°C. High daytime temperatures (26.6°C) strongly inhibited flowering at both chilling and non-chilling nighttime temperatures (*i.e.*, 0.5 and 0.0 inflorescences tree$^{-1}$ under chilling and non-chilling temperatures, respectively). Mildly high daytime temperatures (23.9°C) also inhibited flowering but there were significantly more inflorescences per tree at 23.9°C (220 and 127 inflorescences tree$^{-1}$ under chilling and non-chilling nighttime temperatures, respectively) than at 26.6°C. There was no significant difference in the number of inflorescences tree$^{-1}$ between chilling and non-chilling nighttime temperatures at both inhibitory daytime temperatures; *i.e.* 23.9°C and 26.6°C. The trees that were kept vegetative by high daytime temperatures (26.6°C), but given flower inducing nighttime temperature for three months, when returned to optimal flower inducing conditions did not flower before the normal induction period (70-80 days), indicating that inhibitory daytime temperatures canceled any effects of nighttime flower inducing temperatures. Surprisingly, trees kept vegetative in growth chamber at a high daytime temperature (26.6°C) produced fewer inflorescences compared to trees kept vegetative in the greenhouse where temperatures were less controlled but generally, with a few exceptions, remained between 15-20ºC in the night and 25-30ºC during day.

**Key words**: flowering, inflorescence, *Olea europaea* L., olive, temperature effects.



## Introduction

Temperature induced regulation of flowering in olives is extensively studied by Hartmann and associates (Hackett and Hartmann, 1964, 1967; Hartmann, 1953; Hartmann and Opitz, 1980; Hartmann and Porlingis, 1957; Hartmann and Whisler, 1975). Denney and McEachern (1983), reviewed Hartmann and associates work and defined ≤7.2°C as the "daily minimum temperature" for olive flowering while minimum temperatures ranged between 1.7-4.4°C and maximum between 15.6-18.3°C were considered optimal temperatures. Similarly, Lavee (1985) reviewed olive literature and suggested that maximal flower induction in olives required temperature changes "from low (2-4°C) to high (15-19°C)". It takes 70-80 days of exposure to optimal temperature conditions to obtain optimum inflorescence in olive trees (Hartmann and Whisler, 1975).

While possibilities of flower initiation in olive without significant chilling were proposed by Pinney and Polito (1990), we experimentally demonstrated that flowering in 'Arbequina' cultivar can be achieved without any significant chilling hours (Malik and Bradford, 2005b); none of the researchers listed above included 'Arbequina' (an important oil producing cultivar) in their studies. From this finding, it was hypothesized that inhibition of flowering in areas like Weslaco, Texas, is perhaps due to the inhibitory effects of high daytime temperatures rather than lack of sufficient chilling hours. This hypothesis was supported by the results where flowering in 'Arbequina' in the field at Weslaco was achieved through shading and evaporative cooling to protect from inhibitory effects of high daytime temperatures (Malik and Bradford, 2005c). Further confirmation of this concept was provided by growth room experiments where flowering was strongly inhibited by a few degrees higher daytime temperature while the nighttime temperatures were maintained just above chilling temperatures (Malik and Bradford, 2006).

In these studies we further investigate the interactions of day and nighttime temperatures in regulating flowering in olives. First, another early maturing (*i.e.* the trees start flowering within two years) cultivar 'Koroneiki' was tested for flowering under non-chilling conditions and the effectiveness of these temperatures to induce flowering was compared with the extent of flowering in trees that were given optimal chilling temperatures. Similarly, the effect of high daytime temperatures was also studied at non-chilling (low temperature of 8.3°C) and at chilling temperatures (2.5°C). In addition, plants in which flowering had been inhibited during winter induction period due to high daytime temperatures (even though they were given flower-inducing temperatures in the night) were placed back in a growth room with optimal flower inducing conditions to see if flowering in these trees would occur in a shorter period of time. Results of these studies are reported here.

## Materials and methods

Three-year-old olive trees of cultivars 'Koroneiki' (also labeled I-38 which is a clonal selection of 'Koroneiki'; commonly used in Texas) were purchased from Texas Olive Ranch in Carrizo Springs, Texas (N 28.5 latitude; W 99.9 longitude and 184 m elevation). The trees were repotted in 16 L pots filled with peat, perlite, and sand mixture and supplied with nutrients as described previously (Malik and Bradford, 2006). The trees were grown at the USDA-ARS facility (in open field under 30% shade) in Weslaco, Texas for 8 months before testing in growth chamber experiments. During this 8 months period (March 15-November 15, 2006), temperatures in field varied considerably. The average monthly, maximum/minimum temperatures (°C), from March to November were; 27/15, 29/18, 31/24, 32/25, 31/26, 31/25, 30/26, 30/17, and 27/15. Four walk-in type growth chambers that were locally constructed based on our previously published design were used for testing different day and night temperature regimes, as described below for each experiment, on flowering in 'Koroneiki' olives (Malik and Bradford, 2005a). Temperatures in each growth chamber and the greenhouse were monitored at 30 min intervals and the data transferred to Excel spread sheet for processing as described previously (Malik and Bradford, 2006). Time of appearance of floral buds in stage 1, as described earlier (Malik and Bradford, 2007), was noted in each treatment, and total number of inflorescence and number of flowers per inflorescence were measured at the conclusion of the experiment. In addition, height of the trees (m) and the diameter of the trunk (mm), 8 cm above the soil, were measured. The following experimental conditions were used for each of the experiments.

**Experiment 1**: Fifteen replicate trees were tested under each of the following treatments in the four walk-in growth chambers.

Treatment 1. Nighttime temperature 2.5 ± 0.5°C, daytime temperature 18.3 ± 0.5°C.

Treatment 2. Nighttime temperature 2.5 ± 0.5°C, daytime temperature 26.6 ± 0.5°C.

Treatment 3. Nighttime temperature 8.3 ± 0.5°C, daytime temperature 18.3 ± 0.5°C.

Treatment 4. Nighttime temperature 8.3 ± 0.5°C, daytime temperature 26.6 ± 0.5°C.

Nighttime and daytime temperature regimes in growth chambers were maintained for 8 hrs each period. At the end of each period the temperature was gradually increased or decreased as reported previously (Malik and Bradford, 2006). Details of daily temperature changes in each treatment are given in Table 1. The growth chambers utilize natural light (Malik and Bradford, 2005a) and therefore light intensities changed with time in the day and on cloudiness; on a bright day, light intensity measured in the growth chambers was 1303 µmole $m^{-2}$ $s^{-1}$. The above temperature regimes were strictly maintained during the three month winter induction period (November 15 to February 14). By that time, flowering buds became visible under non-chilling conditions such as Treatment 3, but for chilling treatments nighttime temperatures were gradually increased (2.5°C→5.5°C→8.3°C→11.1°C) to release flower buds from dormancy. Denney and McEachern (1983) defined chilling temperatures (after thoroughly reviewing previous research) for olives as "daily minimum temperature ≤ 7.2°C". They also defined optimal temperatures when maximum temperatures are within 15.6-18.3°C and minimum temperatures are within 1.7-4.4°C. We have followed this terminology here, and therefore, for the purpose of differentiating we have referred to 8.3°C as non-chilling temperature here. Temperatures in the greenhouse were less controlled and fluctuated considerably as daytime temperatures varied between 25-30°C and night temperatures between 15-20°C except a few days when the daytime temperatures dropped below 25°C and for only a few hours nighttime temperatures dropped below 15°C in November and then again in January.

**Experiment 1A**: Trees from Treatments 2 and 4 of the above Experiment 1 where flowering was strongly inhibited due to high daytime temperatures, as described above, were placed in optimal flowering conditions in a chamber maintained at Treatment 3 temperature (see Table 1 for details on temperature regimes). Temperature conditions of Treatment 3 have consistently given extensive flowering in the past and in this study (Malik and Bradford, 2005b, 2005c, 2006). In addition to 15 replicate trees for each of Treatments 2 and 4 of Experiment 1, four trees kept in the greenhouse were also placed in the same chamber under optimal flowering conditions of original Treatment 3. Thus, Treatment 1 of Experiment 1A was previously Treatment 2 of Experiment 1. Treatment 2 of Experiment 1A was previously Treament-4 of Experiment 1. Treatment 3 of Experiment 1A was previously trees kept in the greenhouse. After placing all the trees of treatments 1-3 in one growth chamber, the temperature in the growth chamber was maintained at nighttime temperature of 8.3 ± 0.5°C, and daytime temperature of 18.3 ± 0.5°C for ninety days. Under these conditions, inflorescences begin to appear in 70 days.

Table 1. Daily temperature regimes for each treatment in each experiment

| Time | | | Experiment 1 , Treatments | | | | Experiment 1A, Treatments | | | Experiment 2 , Treatments | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| From | Until | Hours | 1 | 2 | 3 | 4 | 1[b] | 2[c] | 3[d] | 1 | 2 | 3 |
| 0:00 | 5:00 | **5:00** | **2.5**[a] | **2.5** | **8.3** | **8.3** | **8.3** | **8.3** | **8.3** | **2.5** | **8.3** | **8.3** |
| 5:00 | 8:00 | 3:00 | 7.2 | 10.0 | 12.8 | 12.8 | 12.8 | 12.8 | 12.8 | 10.0 | 12.8 | 12.8 |
| 8:00 | 10:00 | 2:00 | 12.8 | 23.3 | 15.6 | 23.3 | 15.6 | 15.6 | 15.6 | 18.3 | 20.0 | 15.6 |
| 10:00 | 18:00 | **8:00** | **18.3** | **26.6** | **18.3** | **26.6** | **18.3** | **18.3** | **18.3** | **23.9** | **23.9** | **18.3** |
| 18:00 | 19:00 | 1:00 | 15.6 | 23.3 | 15.6 | 23.3 | 15.6 | 15.6 | 15.6 | 18.3 | 20.0 | 15.6 |
| 19:00 | 20:00 | 1:00 | 12.8 | 18.3 | 12.8 | 18.3 | 12.8 | 12.8 | 12.8 | 12.8 | 18.3 | 12.8 |
| 20:00 | 21:00 | 1:00 | 7.2 | 10.0 | 10.0 | 10.0 | 10.0 | 10.0 | 10.0 | 7.2 | 10.0 | 10.0 |
| 21:00 | 24:00 | **3:00** | **2.5** | **2.5** | **8.3** | **8.3** | **8.3** | **8.3** | **8.3** | **2.5** | **8.3** | **8.3** |

[a]Temperature in °C ± 0.5.

[b]After the conclusion of Experiment 1, its Treatment 2 was placed under this inductive temperature regime.

[c]After the conclusion of Experiment 1, its Treatment 4 was placed under this inductive temperature regime.

[d]Trees from Greenhouse under none inductive conditions throughout (since the start of Experiment 1) were placed under inductive conditions.

The temperature of the growth chamber was raised after 90 days and total number of inflorescence were counted after 2 weeks.

**Experiment 2**: A second experiment was conducted to study differences, if any, between chilling and non-chilling nighttime temperatures on the inhibitory effects of high day time temperatures but approximately 3 degrees less than the temperatures used in Experiment 1 (*i.e.* 23.9°C instead of 26.6°C). Four replicate trees from the greenhouse were placed in each of the following temperature regimes (Table 1).

Treatment 1. Nighttime temperature 2.5 ± 0.5°C, daytime temperature 23.9 ± 0.5°C.

Treatment 2. Nighttime temperature 8.3 ± 0.5°C, daytime temperature 23.9 ± 0.5°C.

Treatment 3. Nighttime temperature 8.3 ± 0.5°C, daytime temperature 18.3 ± 0.5°C.

These temperature regimes were also maintained for three months.

**Statistical analysis**: Results of different replicate of each treatment in the experiment were subjected to one way analysis of variance using SAS software package (version 9.1). The L.S.D. test of significance between means was determined at $P < 0.05$.

## Results and discussion

It is noteworthy that nighttime chilling temperatures of 2.5°C under optimal daytime temperatures (18.3°C) did not produce any greater number of inflorescence compared to 8.3°C nighttime temperatures (Table 2) even though earlier researcher reported a temperature of 2.5°C as optimal chilling temperature for inducing maximal flowering in olives (Badr and Hartmann, 1971; Lavee, 1985). On the contrary, there appeared nearly 28% increase in inflorescences per tree under non-chilling nighttime temperatures (8.3°C) over the trees that were kept under optimal chilling conditions (2.5°C) (Table 2). There was also no difference in number of flowers per inflorescence in trees kept under optimal nighttime chilling conditions versus the ones that were placed in a non-chilling environment (Table 2). While these results are consistent with our previous findings that non-chilling nighttime temperatures (8.3°C) are quite effective for inducing flowering in another cultivar ('Arbequina') of olive (Malik and Bradford, 2005b, 2005c), the present finding go one step further by demonstrating that equally effective flowering, compared to trees kept under optimal chilling conditions (2.5°C), can be achieved in 'Koroneiki' olives when they were never exposed to temperatures below 7.2°C; *i.e.* chilling temperatures. Rallo and Martins (1991) have shown the release of dormant floral buds to produce inflorescence at elevated temperatures (10/21 °C night/day), but the optimal inflorescence only occurred in their explants that were taken from trees that had already experienced hundreds of chilling hours, thus their results are very different from our results described here. It would, however, be pertinent to mention here that 'Arbequina' or Koroneiki' cultivars (important oil producing cultivars) that we used in our experiments were not included in the tests of researchers mentioned above.

High daytime temperatures (26.6°C) strongly inhibited flowering at both chilling (2.5°C) and non-chilling (8.3°C) nighttime temperatures; the non-chilling nighttime temperatures under optimal daytime temperatures do produce extensive flowering (Table 2). Inhibition of flowering by high daytime temperatures (26.6°C) and optimal nighttime temperatures (8.3°C; *i.e.*, non-chilling temperature) is consistent with our previous finding with 'Arbequina' cultivar (Malik and Bradford, 2006). These studies, however, demonstrate for the first time that such inhibitory daytime temperatures (26.6°C) were equally effective in inhibiting flowering even when plants were given optimal nighttime chilling temperatures (2.5°C) (Table 2).

Since daytime temperatures of 26.6°C drastically inhibited flowering in the 'Koroneiki' cultivar (*i.e.*, 0.5±0.4 inflorescence per tree under chilling conditions and 0±0 per tree under non-chilling conditions) we decided to test the effect of nighttime chilling versus non-chilling at relatively lower daytime temperatures (23.9°C) to see if quantitative difference between the two nighttime conditions could be measured. At a daytime temperature of 23.9°C the trees kept at both chilling and non-chilling nighttime temperatures, produced significantly more inflorescences (220.0 ± 17.7 versus 0.5 ± 0.4, and 126.8 ± 30.6 versus 0 ± 0 under chilling and non-chilling nighttime temperatures, respectively) than the trees kept at 26.6°C (Table 2 and 3). Still, even at 23.9°C daytime temperature, flowering was strongly inhibited; *i.e.* 15-25 % of the optimal daytime temperatures, and there was no significant difference between chilling and non-chilling nighttime temperatures (Table 3). Further experiments involving minimal daytime inhibitory temperatures may shed more light between interactions of chilling and non-chilling nighttime temperatures in the presence of mild daytime inhibitory temperatures.

The possibility exists that the flower inhibitory effect of high daytime temperatures may simply suppress the flowering induced by optimal nighttime temperatures thus the flowering would quickly occur if optimal daytime temperatures are given to the trees that were previously kept under high daytime temperatures but inductive nighttime temperatures. Alternatively, the flower inhibitory effect of high daytime temperatures could cancel the flower inducing effects of optimal nighttime temperatures, in

Table 2. The effect of high daytime temperatures under chilling and non-chilling nighttime conditions on flowering in 'Koroneiki' olives

| Treatment | Temperature (°C) minimum/maximum | Inflorescences per tree | Flowers per inflorescence | Diameter (mm) | Height (m) |
|---|---|---|---|---|---|
| Tr. 1 | 2.5/18.3 | 568.7±45.5[a] | 21.6±0.9[d] | 13.2±1.1[f] | 1.4± 0.1[g] |
| Tr. 2 | 2.5/26.6 | 0.5±0.4[c] | 3.8±2.7[e] | 12.3±0.4[f] | 1.5± 0.1[g] |
| Tr. 3 | 8.3/18.3 | 728.7±43.8[b] | 23.9±0.7[d] | 12.5±0.7[f] | 1.4±0.1[g] |
| Tr. 4 | 8.3/26.6 | 0.0±0.0[c] | 0.0±0.0[e] | 13.6±0.7[f] | 1.4± 0.1[g] |

Details of temperature regimes in each treatment are given in the Table 1 under Experiment 1. Mean number of inflorescence per tree, and mean number of flowers per inflorescence, in treatments 2 and 3 are significantly lower ($P < 0.05$) than treatments 1 and 4 respectively. Numbers with similar superscript letters in each column are not significantly different but numbers with different letters are significantly different at $P < 0.05$.

Table 3. The effect of mildly high daytime temperatures under chilling and non-chilling nighttime conditions on flowering in 'Koroneiki' olives

| Treatment | Inflorescences per tree | Flowers per inflorescence | Diameter (mm) | Height(m) |
|---|---|---|---|---|
| Tr. 1 (2.5/23.9) | 220 ± 17.7[a] | 14.9 ± 0.7[d] | 13.3 ± 0.4[f] | 1.4 ± 0.0[g] |
| Tr. 2 (8.3/23.9) | 126.8 ± 30.6[a] | 13.8 ± 0.8[d] | 13.3 ± 0.5[f] | 1.3 ± 0.1[g] |
| Tr. 3 (8.3/18.3) | 873.8 ± 50.5[b] | 20.9 ± 1.3[e] | 13.7 ± 0.3[f] | 1.3 ± 0.1[g] |

Details of temperature regimes in each treatment are given in the Table 1 under Experiment 2. Mean number of inflorescence per tree in treatment 1 and 2 are significantly lower ($P < 0.05$) than treatment 3. Numbers with similar superscript letters in each column are not significantly different but numbers with different letters are significantly different at $P < 0.05$.

Table 4. Flowering in trees whose flowering was initially inhibited in Experiment 1 after placing them under optimal flowering conditions.

| Treatment (Temperature °C, from minimum/ maximum to minimum/maximum ) | Inflorescences per tree | Flowers per inflorescence | Diameter (mm) | Height (m) |
|---|---|---|---|---|
| Tr. 1 (2.5/26.6 to 8.3/18.3)[1] | 504.6 ± 65.2[a] | 19.52 ± 1.5[c] | 12.1 ± 0.3[d] | 1.5 ± 0.1[e] |
| Tr. 2 (8.3/26.6 to 8.3/18.3)[2] | 625.7 ± 41.7[ab] | 21.4 ± 0.8[c] | 12.9 ± 0.5[d] | 1.4 ± 0.1[e] |
| Tr. 3 (Greenhouse to 8.3/18.3)[3] | 873.8 ± 50.5[b] | 20.9 ± 1.3[c] | 13.7 ± 0.3[d] | 1.3 ± 0.1[e] |

[1]After the conclusion of Experiment 1, its Treatment 2 was placed under this inductive temperature regime

[2]After the conclusion of Experiment 1, its Treatment 4 was placed under this inductive temperature regime

[3]Trees from Greenhouse under none inductive conditions throughout (since the start of Experiment 1) were placed under inductive conditions

Details of temperature regimes in each treatment are given in the Table 1 under Experiment 1 and 1A. Numbers with similar superscript letters in each column are not significantly different but number with different letters are significantly different ($P < 0.05$).

which case, putting them back under optimal conditions would take a normal time to flower. To test these possibilities, trees of Treatments 2 and 4 of Experiment 1 were placed back in a growth chamber maintained at optimal daytime temperature (same as in Treatment 3 of Experiment 1). In addition, four replicate trees (there were 15 replicate trees for Treatment 2, and 4, of Experiment 1) kept in the greenhouse were placed in the same growth chamber at optimal flowering conditions (Treatment 3 of Experiment 1). Interestingly, there was no hastening of flowering in trees that were given optimal flower inducing nighttime conditions (at both chilling and non-chilling), but inhibitory daytime temperatures, compared to the trees that were transferred from the greenhouse kept under non-inducing daytime and nighttime temperatures (15-20°C). For example, it took about 75 days for the trees (50% of trees) in Treatment 3 of Experiment 1 to produce inflorescence [inflorescences begin to appear under these conditions without changes in temperatures, and therefore, it was straightforward to note the time of appearance of inflorescence. Trees kept under chilling conditions (*e.g.*, 2.5°C) must be brought to non-chilling condition to produce inflorescence], whereas it took 70 days to produce inflorescences in trees of Experiment 1A. These results indicate that inhibitory daytime temperatures cancel any flower inducing effect of optimal nighttime temperatures. Lavee (1985) described reversal of inhibitory effect of high temperatures that may interrupt winter inductive period in field grown trees, during early induction period, but this reversal does not occur after February. Thus, based on our findings under controlled condition and those of Lavee's observations on field grown plants further studies are needed, to determine the length and intensity of high temperature interruption, at various times during induction period, that are reversible and when they become irreversible.

It is puzzling to note that the trees that were first exposed to chilling nighttime temperatures and inhibitory daytime temperatures (Treatment 1 of Experiment 1A) produced significantly fewer inflorescences compared to the tree that were kept in greenhouse (Table 4). Considering that temperatures in growth chambers were stringently controlled (Malik and Bradford, 2006), while temperatures were not that tightly controlled in the greenhouse, we compared the number of hours in different temperature groups between the two conditions. We found that while trees in the greenhouse and growth chamber were subjected to a similar number of hours of flower inhibitory temperatures (>25°C), the trees in the greenhouse received 4-5 times more hours of temperatures (18-22°C optimal; or 18-23°C) that promote flowering (Fig. 1). The flower promoting temperatures in the greenhouse are different from the nighttime chilling and non-chilling temperatures in growth chambers discussed above [tree under greenhouse conditions never flower in greenhouse and take 70 -75 days of inductive period to flower]. However, it is difficult to assert at this time that the difference in temperature categories between the two conditions (greenhouse versus growth chamber) was responsible for fewer inflorescences in trees initially kept under flower inhibitory conditions in the growth chambers versus in greenhouse. It is, however, `interesting information that deserves further studies; and we intend to conduct detailed studies on interactions between various lengths of flower inhibitory temperatures on various lengths of flower promoting temperatures on the extent of flowering in olives.

In conclusion, "Koroneiki' olives flower profusely at both chilling (2.5°C) and non-chilling temperatures (8.3°C), when daytime

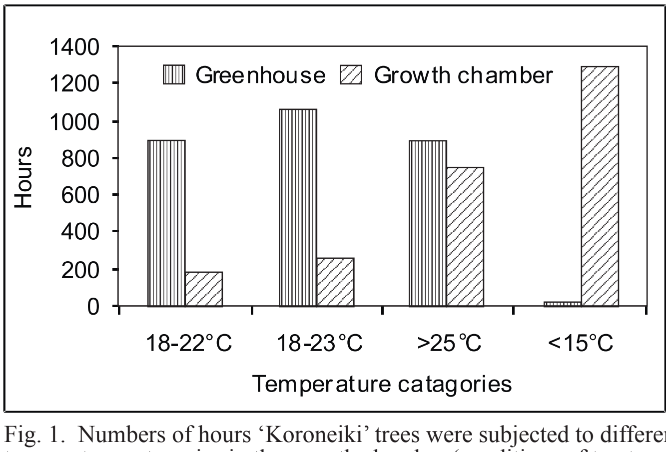


Fig. 1. Numbers of hours 'Koroneiki' trees were subjected to different temperature categories in the growth chamber (conditions of treatment 4 of experiment 1) and greenhouse parallel to the three month induction period in growth chambers.

temperatures are maintained at 18.3°C, and that equal flowering intensity in this cultivar can be achieved under non-chilling conditions. These results are similar to previously reported results with cultivar, 'Arbequina', except that they provide further evidence that chilling temperatures (2.5°C) do not produce higher number of inflorescence than non-chilling temperatures (8.3°C). High daytime temperatures (26.6 and 23.9°C) strongly inhibited flowering at both chilling and non-chilling nighttime temperatures. Inhibitory effects of high daytime temperatures canceled any flower promoting effects of optimal nighttime temperatures because trees kept at a 26.6°C daytime temperature, and optimal nighttime temperatures, when returned to optimal flowering inducing conditions did not flower earlier, but required the 70 days period before inflorescence emergence.

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