**Effects of pre-blossom temperatures on flower development and fruit set in apricot**

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**Abstract**

The influence of pre-blossom temperatures on flower development and fruit set is ascertained in apricot (Prunus armeniaca L.), a species without previous records on the effect of pre-blossom temperature on fruit set, but that is particularly prone to erratic fruit set. A polyethylene cage was used during pre-blossom development of flower buds to increase maximum temperatures by 6-7ºC and mean temperatures by 3ºC in orchard conditions. This increase in temperature accelerated flower bud development, caused a hastening in flowering time and, following hand-pollination, reduced fruit set. At anthesis, flowers that had developed in warmer conditions weighed less and showed less development of the pistil than control flowers. Pistil growth of flowers under warm conditions did not differ from that of control flowers when both populations were compared on a real time scale, in spite of the fact that warmed buds were at an advanced external phenological stage. Thus, hastening of external floral development by warm pre-blossom temperatures was not accompanied by advance in pistil development. This lack of synchrony resulted in premature flowering of flowers with underdeveloped pistils that had a reduced capability to set fruit. The results are discussed in terms of flower quality and its implications in fruit set and subsequent crop load.

Keywords: Apricot, Prunus armeniaca, flower development, fruit set, pistil, anthesis, temperature.

## 1. Introduction

Irregularity of yield is one of the main problems in fruit production (Tromp, 1986). Year-to-year variations in crop production have been traditionally related to weather conditions in spring. Thus, wind and low temperatures affect bee activity and therefore pollination (Dennis, 1979), and frosts can reduce the number of buds, flowers and fruits (Rodrigo, 2000). Likewise, rain or high relative humidity can cause pollination failures and promote floral disease during bloom (Gradziel and Weinbaum, 1999), and temperature in the days following anthesis affects pollen tube growth and the effective pollination period (Williams, 1970). An effort to integrate all these variables influencing crop production in a model system based on multiple regression analysis (Beattie and Folley, 1977) showed that while meteorological variables at flowering time had an effect on the subsequent apple fruit production, surprisingly pre-blossom temperatures had also a clear effect on yield. These results were later further confirmed showing a negative correlation between crop load and warm pre-blossom temperatures in apple (Beattie and Folley, 1978; Jackson and Hamer, 1980; Jackson et al., 1983). Conversely, cold pre-blossom temperatures have been correlated to high yield in pear (Browning and Miller, 1992).

While these mathematical models based on natural orchard conditions establish a clear correlation between pre-blossom temperatures and yield, the mechanisms leading to this relationship remain obscure. Several attempts have been made to evaluate the effects of pre-blossom temperatures on fruit set. This has been achieved mainly through the use of potted trees, but results are not always clear. Experiments on potted apple trees subjected under controlled pre-blossom temperatures have shown that fruit set is enhanced at low temperatures and reduced

at high temperatures (Abbott 1971; Jackson et al., 1983; Miller et al., 1986). Likewise, in pear and apple, low temperatures appeared to promote fruit set on potted trees exposed to different temperature regimes from February to harvest (Tromp and Borsboom, 1994). However, other experiments in apple have shown no significant differences in fruit set (Abbott, 1962; Miller et al., 1987) or even that low pre-blossom temperature reduces final fruit set (Tromp, 1986). In Prunus species, information is also scarce and contradictory. While high pre-blossom temperatures reduced fruit set on sweet cherry potted trees (Beppu et al., 1997), increased temperature of bagged branches did not affect the percentage of fruit set in almond (Egea and Burgos, 1995).

These apparently contradictory results may be related to the different treatment conditions in the different experiments. Thus, depending on the experiments, temperature has been increased during the day (Beppu et al., 1997), overnight (Jackson et al., 1983; Miller et al., 1986, 1987) or continuously, either under constant temperature (Abbott, 1971) or with a day/night regime (Tromp, 1986; Tromp and Borsboom, 1994). Likewise, the duration of the treatments have been different. Temperature has been applied during three months before bloom (Jackson et al., 1983; Miller et al., 1986, 1987), from dormancy to petal fall (Abbott, 1971), from one month before anthesis to petal fall (Beppu et al., 1997), or from dormancy to harvest (Tromp, 1986; Tromp and Borsboom, 1994).

Furthermore, the use of young potted trees further complicates the situation since it cannot entirely reflect the behaviour of adult trees in orchard conditions (Sedgley and Griffin, 1989). As an alternative, temperature conditions can be modified in whole trees by means of plastic-covered trees in the orchard. This

approach has been used to evaluate the effects of temperature and irrigation on fruit growth (Atkinson et al., 1998), but has not been used widely for pre-blossom temperature modification in orchard conditions.

We have used a mobile greenhouse adapted to an adult tree in the orchard, similar to those used to protect valuable hybridizations from freeze injury and insect contamination to test whether elevated pre-blossom temperatures reduce fruit set. This approach increases both mean and maximum temperature, the two parameters shown to affect subsequent fruit set in previous analyses (Beattie and Folley, 1978; Jackson and Hamer, 1980). This work has been done in apricot (Prunus armeniaca L.), a species without previous records on the effect of pre-blossom temperature on fruit set, but which is particularly prone to erratic fruit set (Mehlenbacher et al., 1990). The aim of this work is to evaluate the effect of pre-blossom warm temperatures on flower bud development, flower morphology and subsequent fruit set.

## 2. **Material and methods**

### 2.1. Plant material and temperature monitoring

The experiments were performed in two consecutive years, 1999 and 2000, on different trees from an eight-year-old orchard of the apricot cultivar 'Moniqui', which is particularly prone to erratic fruit set (Rodrigo and Herrero, 1996). When most flower buds presented separation of bud scales and an initial protrusion of sepals, a tree was enclosed within a metallic structure covered by a 0.178 mm thick polyethylene film in order to increase the daytime temperature. Another tree at the same phenological stage was left uncaged as control. Since ventilation was needed to prevent excess heat accumulation and moisture condensation, the cage was partially opened daily during daylight. Temperature measurements inside and outside the cage were logged at 5 min intervals using shaded data loggers (Testostor 175-3, Testo, Germany) placed at 60 cm high from soil level and orientated to the north. At full bloom, when 50% of the flower buds were opened, the cage was dismantled and flowering and subsequent fruit set proceeded under natural orchard conditions.

### 2.2. Flower development

To follow flower bud development, several branches completing over 1500 flower buds per tree were monitored. To characterize the progression of bud phenophases, counts of flower buds at each phenological stage were made every two days until full bloom. Assessments were made using a previously adjusted scale, in which stage values are linearly related to apricot flower bud development: 1.6 (separation of bud scales); 3.0 (protrusion of sepals); 4.2 (broadening of exposed

sepals); 4.9 (expansion and rounding of sepals); 5.5 (initial protrusion of petals); 5.9 (expansion and rounding of petals); 6.1 (anthesis); 7.4 (abscission of petals) (Austin et al., 1998). Linear regressions were performed in both treatments to fit functions of chronological time through the adjusted phenophase data. Slopes were compared and tested to determine if they were significantly different.

In both years, 30 flowers were collected every two days from the outset of the experiment up to anthesis (240 flower buds in all) and preserved in FAA [formalin - acetic acid - ethanol 70%, (1:1:18, v/v/v)] for further analysis. Subsequently, from anthesis onwards, a total of 275 pistils, 47 of them at anthesis and 12 per day thereafter over 19 days, were collected in each treatment and preserved in FAA.

To follow pistil growth from anthesis onwards fresh pistils were individually weighed prior to fixation. Since differences were apparent between treatments, pistil size was also measured in the pistils previously preserved in FAA from the outset of the experiment, when bud scales started to separate. For this purpose, pistils were separated from other bud or flower structures and observed under a Wild Heerbrugg M8 binocular microscope. The images were collected using a Cohu 8310 RGB Colour Camera attached to the binocular microscope and processed using a Quantiment 570 Image Analysis System (Leica Cambridge, England). Pistil size values were obtained by measuring the surface of the image corresponding to the ovary and the length of the style.

On the day of anthesis, individual weights of several flower structures were also obtained separately, these were petals, sepals and stamens, anthers, pistil and peduncles. This was done on 47 flowers per treatment and year. Since no significant differences were found between both years, data from both years were pooled

together. Data were subjected to analysis of variance.

2.3. Pollination and fruit set

Since differences in flower development were apparent quite early in the experiment and the two treatments flowered at different times, to avoid the influence of different pollination conditions in the orchard at full bloom, controlled pollinations were carried out by hand in both treatments. For this purpose, pollen from 'Canino', a cultivar compatible with 'Moniqui' (Rodrigo and Herrero, 1996), was obtained from flowers at the balloon stage by removing the anthers and placing them on paper at room temperature. Pollen was sieved 24 h later through a 0.26-mm mesh and frozen at -20ºC until required. Seven branches were tagged to complete over 1000 flower buds per tree. Receptive flowers were hand pollinated every other day until all flowers were opened. Since the cages were dismantled at full bloom, the first flowers opened were hand-pollinated already in the cage.

To ascertain the final fruit set, in tagged branches weekly counts of flowers and developing fruits were made at anthesis and harvest. Fruit set was expressed as the percentage of fruits per total flowers (Williams, 1970). Finally, fruits of both treatments were weighed at harvest to determine the crop of the tagged branches.

## 3. Results

The polyethylene cage induced a mean increase in the maximum temperature of 7.6ºC in 1999 and 6ºC in 2000. Minimum temperature was slightly altered and reduced 1.5ºC under the cage in 1999 and 0.4ºC in 2000. This resulted in an increase in the mean temperature of 3ºC in 1999 and 2.7ºC in 2000 (Table 1). This increase in temperature was achieved while the pattern of diurnal variation was maintained through the treatment period, increasing from 8:00 to 15:00 hours and decreasing gradually to 19:00 hours (Figure 1). This pattern was consistent over the two years.

The influence of pre-blossom temperature on flower bud development was significantly different in both treatments. Regression slopes, and therefore rates of growth, differed significantly between warm treatment and the control ($P<0.01$) (Figure 2). Thus, warm temperature regime accelerated blooming time in both years. In spite to the fact that flowering time differed between the warm treatment and the control, no big differences in temperature were recorded in the 10 d following anthesis in each treatment. Thus, both treatments had similar mean temperature (9.6ºC in 1999 and 9.7ºC in 2000) during this time.

A comparison of pistil growth at four phenological stages showed that although pistils in both treatments followed the same pattern of growth in the first days of the experiment (from separation of bud scales to expansion and rounding of sepals), differences in ovary size (Figure 3a) and style length (Figure 3b) were found in the subsequent flower bud stages in which both parameters were smaller under warm treatment. Moreover, at anthesis, a proportion of the flowers, in the warm treatment, showed small pistils. While on the control treatment most of the flowers (92%) had a morphologically well developed pistil, in the warm treatment 33% of the flowers

presented pistils not completely developed and 13% of the flowers showed short styles and unswelled ovaries (Figure 4). Thus, number of normal pistils in the warm treatment (54%) were significantly lower than in the control ($\chi^2$ = 136, 2 df, $P$<0.001). However, a daily observation and weighing of these pistils revealed that this proportion of underdeveloped pistils were not arrested in development but, on the contrary, were gradually completing their development, since the proportion of underdeveloped pistils gradually disappeared during the 5 days following anthesis, while no flower drop could be recorded during this time. These differences in pistil development were reflected in clear differences in flower weight at anthesis. While control flowers averaged 169 ± 3 mg, flowers from the warm treatment averaged approximately one third less (114 ± 3 mg).

To evaluate whether these differences were entirely due to differences in pistil weight or other structures were involved, several flower parts (peduncle and receptacle, petals, sepals and filaments, anthers and pistil) from individual flowers were separately weighed. All the structures were significantly heavier in control than in warmed flowers (Table 2). The differences in pistil weight were maintained during the days following anthesis in which control pistils experimented a larger growth than warmed pistils (Figure 5). However, when pistil development from the outset of the experiment was plotted in real dates instead of related to anthesis, the pattern of growth was coincident in both treatments and there were not significant differences in ovary size (Figure 6a). Style length at anthesis was shorter in the warm treatment 10.9 ± 0.6 mm than in the control 16.8 ± 0.5 mm. These differences were maintained when style development was plotted in real dates, resulting in that warm treatment flowers attained a final shorted style (Figure 6b).

Control of number of flowers and developing fruits resulted in a higher fruit set in the control than in the warm treatment (Table 3). This was reflected in a lower crop load in the warm treatment than in the control. The warmed treatment produced heavier fruits than control, probably due to the reduced fruit set that induced a lower competition among fruits.

## 4. Discussion

An increase in temperature during the time of flower bud growth induced earlier flowering and had a clear negative effect on the subsequent fruit set in apricot. Warm conditions accelerated anthesis, but not pistil development, resulting flowers with a reduced pistil weight and shorter style length. This lack of synchrony between the development of the pistil and other floral organs had also a reflection in producing a high proportion of flowers with an altered pistil morphology.

Apricot is particularly prone to erratic fruit production (Mehlenbacher et al., 1990), but the causes for this behaviour are not completely understood. While in other species pre-blossom temperatures do play a part affecting subsequent fruit set (Beattie and Folley, 1977, 1978; Jackson and Hamer, 1980; Jackson et al., 1983), the effect of pre-blossom temperature on apricot fruit set has not been previously explored. Our results suggest that pre-blossom temperatures do influence subsequent fruit set in apricot. This agrees with experimental reports on young potted trees in several other fruit species (Abbott, 1971; Jackson et al., 1983; Miller et al., 1986; Tromp and Borsboom, 1994; Beppu et al., 1997). Conflicting results (Tromp, 1986; Miller et al., 1987; Egea and Burgos, 1995) may be related to variable conditions on the different experiments. Our results show that flower bud development is sensitive to temperature in the period from separation of bud scales to anthesis. Warm temperatures during this time have a deleterious effect on flower quality and fruit set.

The reduction in fruit set appears to be associated with a proportion of abnormal flowers with short styles and unswelled ovaries. Flower abnormalities resulting in female sterility have been reported in a wide number of species (Meyer,

1966; Sedgley, 1990). While abnormally small pistils have been previously described as a variable trait in different apricot cultivars (Suranyi, 1976; Viti and Monteleone, 1991; Guerriero and Bartolini, 1995; Layne et al., 1996), the cause for this failure was so far unknown. Results from both years consistently show that these pistil abnormalities are possibly related to pre-blossom high temperatures.

While a clear correlation between warm pre-blossom conditions and reduced fruit set was previously shown in apple (Beattie and Folley, 1978; Jackson and Hamer, 1980), it has been argued that this might be an indirect effect. Thus, high pre-blossom temperatures whether naturally or experimentally induced lead to early flowering (Sedgley and Griffin, 1989) and hence to an increase in spring frost risk. Likewise, other factors could be affected such as day length and bee activity that could be related to low fruit set rather than just to temperatures (Jackson and Hamer, 1980). Our results show a direct relationship between pre-blossom temperatures and fruit set, since both treatments had the same climatic factors and mean temperature in the days following anthesis. Likewise, the pollination variable was obviated by hand pollinating both treatments.

The fact that good quality flowers are heavier than poor quality flowers appears to be a reported constant in different experiments; no matter if differences in flower quality are produced through warm pre-blossom temperatures (Abbott, 1971; Miller et al., 1986; Beppu et al., 1997), nitrogen summer applications (Williams, 1965), wood age (Robbie and Atkinson, 1994) or orientation of branches where flower buds are located (Robbie et al., 1993). Results reported here show that the lighter flowers from the warm treatment could be related to an underdevelopment of the pistil at the time of flower opening due to a premature flower opening. Further

work is required to elucidate whether internal development of the pistil is associated to pistil growth or the external development of the flower. Likewise, the growth of pollen tubes through the style could be affected by the morphological differences between the styles of both treatments. However, results reported here provide a basis for further study and contributed to explain the effect of pre-blossom temperatures on subsequent fruit set through the induction of a premature flowering not followed at the same rate by pistil development.

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Table 1

Mean, maximum and minimum temperatures (ºC) under control conditions and in the warm treatment through the 7 days previous to anthesis of apricot cv Moniqui in 1999 and 2000.

| | Control | | Warm treatment | |
|---|---|---|---|---|
| | 1999 | 2000 | 1999 | 2000 |
| Mean temperature | 12.4 | 13.2 | 15.4 | 15.9 |
| Mean maximum temperature | 18.3 | 19.4 | 25.9 | 25.4 |
| Mean minimum temperature | 6.5 | 6.6 | 5.0 | 6.2 |

Table 2

Weight of several floral structures at anthesis in individual flowers of apricot cv Moniqui subjected to different pre-blossom temperature regimes (Mean ± SE)

| | Control (mg) | Warm treatment (mg) | F-ratio |
|---|---|---|---|
| Pistil | 6.7 ± 0.2 | 3.9 ± 0.2 | 81.4*** |
| Petals, sepals and filaments | 130 ± 2 | 82 ± 2 | 340*** |
| Anthers | 17.8 ± 0.3 | 16.4 ± 0.3 | 14.8*** |
| Peduncle and receptacle | 15.9 ± 0.4 | 13.3 ± 0.4 | 21.3*** |

*** Contrasts significant at $P \leq 0.001$ (all with treatment d.f. = 1 and error d. f. = 187)

Table 3

Fruit set, fruit weight and crop load under control conditions and in the warm treatment of apricot cv Moniqui in 1999 and 2000.

| | Control | | Warm treatment | |
|---|---|---|---|---|
| | 1999 | 2000 | 1999 | 2000 |
| Fruit set (%) | 36 | 49 | 21 | 32 |
| Fruit weight (g) | 76 | 53 | 88 | 59 |
| Crop load (kg) | 24.7 | 41.7 | 15.8 | 25.1 |

**Figure captions**

Fig. 1. Diurnal variation in temperature for both control and warm treatment in 1999 and 2000. Data are means ± SE of the average values from the data recorded through the treatment period.

Fig. 2. Flower bud phenophases from the outset of the experiment in control and warm treatment in apricot cv Moniqui. Mean ± SE of the average values. Equations and determination coefficient ($R^2$) determined by linear regression.

Fig. 3. Area ($mm^2$) of the section of the ovary (a) and length (mm) of the style (b) in flowers of apricot cv Moniqui in both control and warm treatment at different flower bud development stages. Mean ± SE of the average values. Equations and determination coefficient ($R^2$) determined by linear regression.

Fig. 4. Percentage of flowers at anthesis with different pistil morphology in apricot cv Moniqui in control and warm treatment.

Fig. 5. Fresh weight of pistils in both control and warm treatment during the 19 days following anthesis in flowers of apricot cv Moniqui. Mean ± SE of the average values.

Fig. 6. Area ($mm^2$) of the section of the ovary (a) and length (mm) of the style (b) from the outset of the experiment in relation to anthesis of the control (day 0) in both control and warm treatment in flowers of apricot cv Moniqui. Mean ± SE of the

average values.

Fig. 1

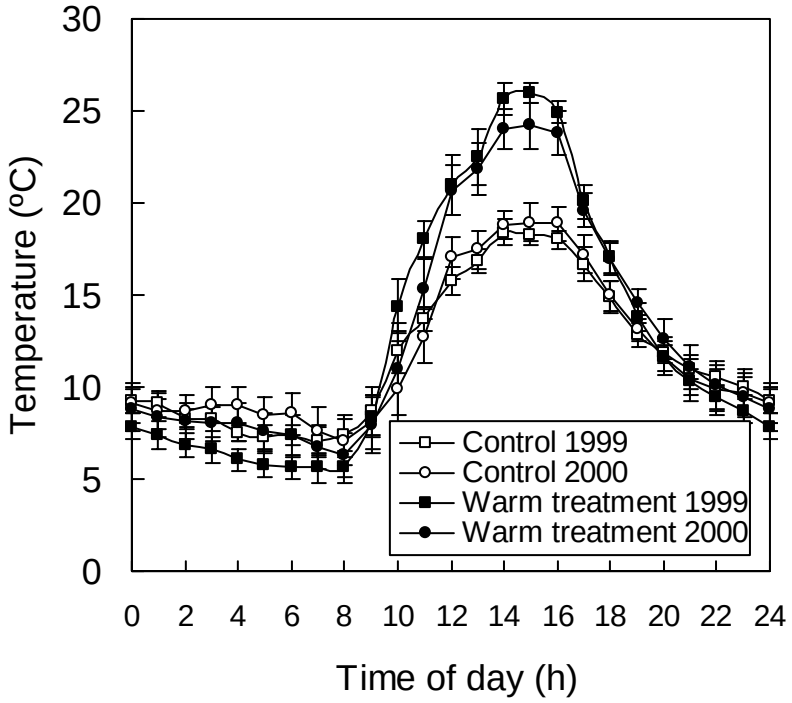

Temperature (°C)
Time of day (h)
Control 1999
Control 2000
Warm treatment 1999
Warm treatment 2000

Fig. 2

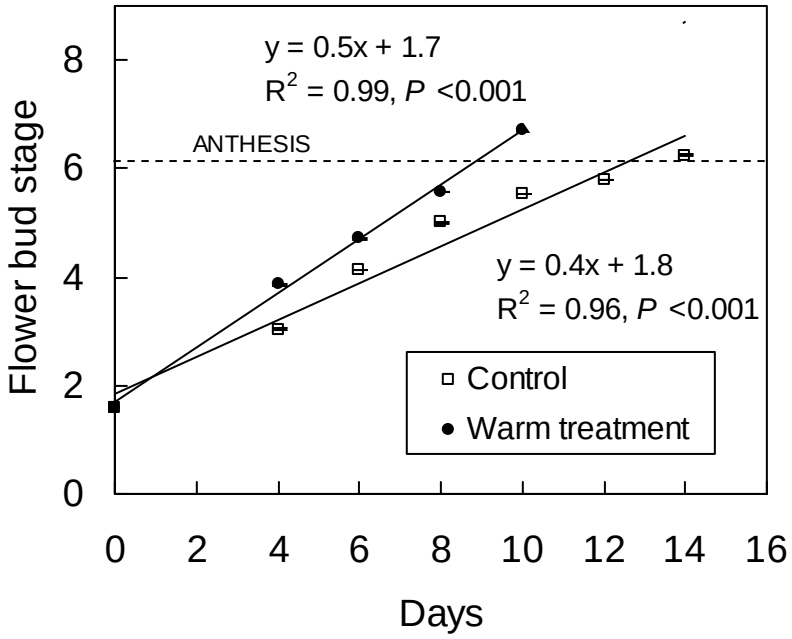

y = 0.5x + 1.7
R2 = 0.99, P <0.001
ANTHESIS
y = 0.4x + 1.8
R2 = 0.96, P <0.001
Control
Warm treatment
Flower bud stage
Days

Fig. 3

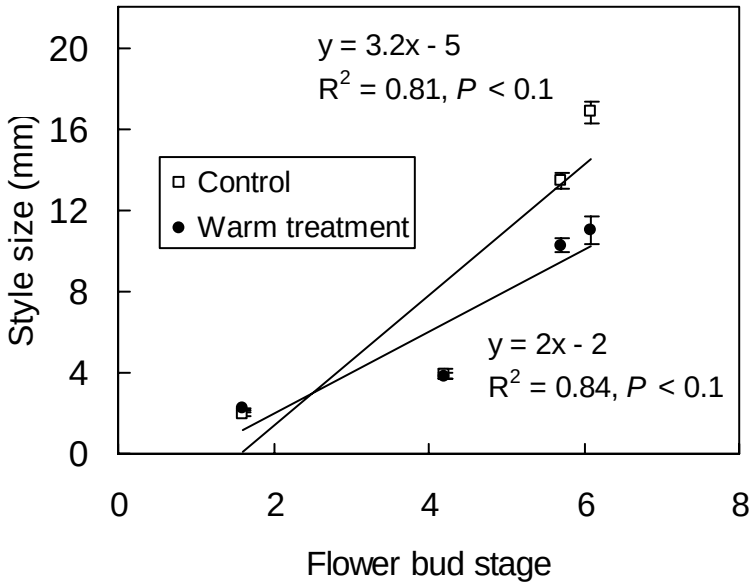

y = 3.2x - 5
R2 = 0.81, P < 0.1
Control
Warm treatment
y = 2x - 2
R2 = 0.84, P < 0.1
Style size (mm)
Flower bud stage
0
4
8
12
16
20
0
2
4
6
8

Fig. 4

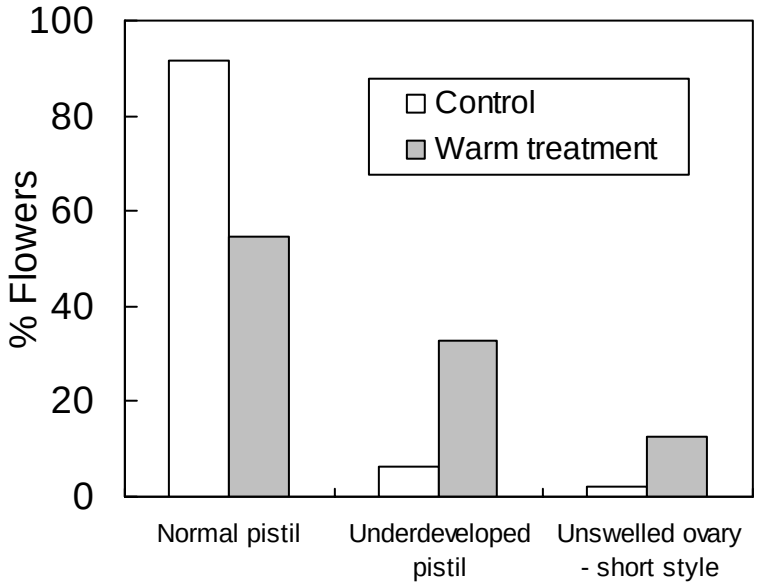

Control
Warm treatment
% Flowers
0
20
40
60
80
100
Normal pistil
Underdeveloped pistil
Unswelled ovary - short style

Fig. 5

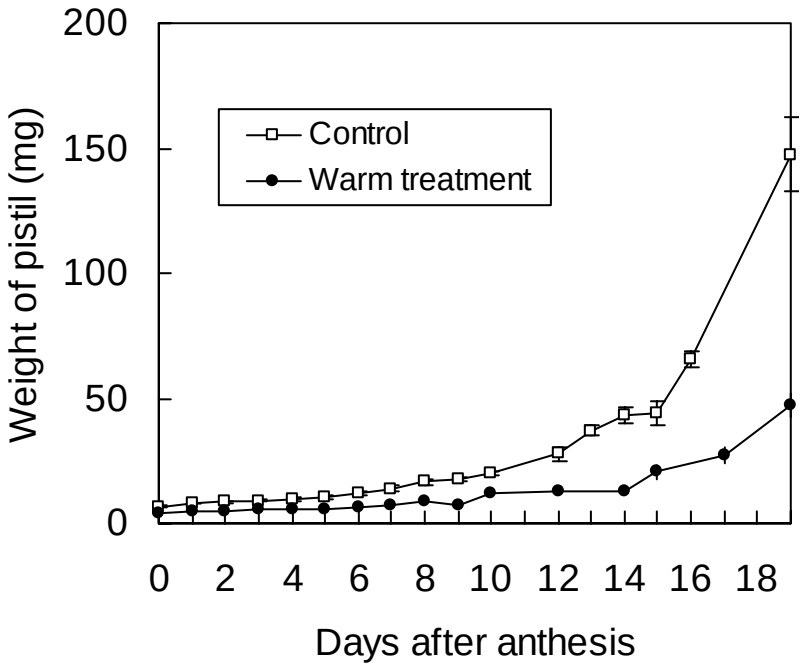
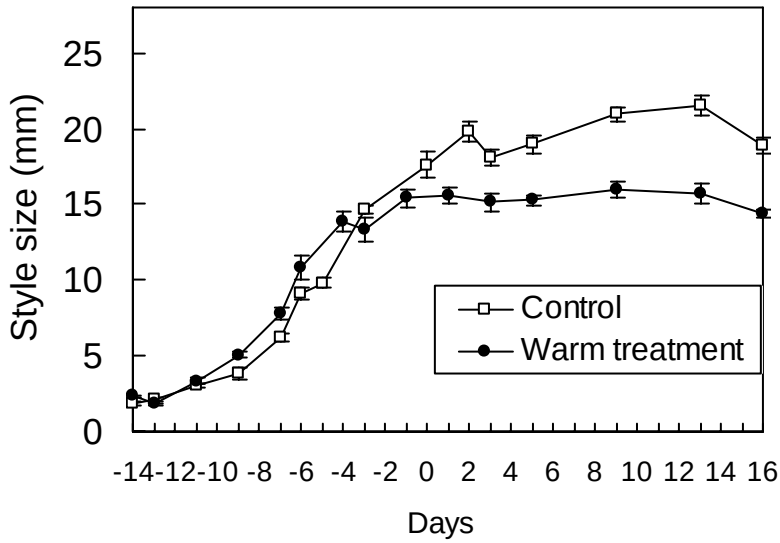

Weight of pistil (mg)
200
150
100
50
0
Control
Warm treatment
0 2 4 6 8 10 12 14 16 18
Days after anthesis

Fig. 6


Style size (mm)
25
20
15
10
5
0
Control
Warm treatment
-14 -12 -10 -8 -6 -4 -2 0 2 4 6 8 10 12 14 16
Days