Flower Production in Olive as Influenced by Various Chilling Temperature Regimes[1, 2]

Hudson T. Hartmann and John E. Whisler
Department of Pomology, University of California, Davis

Abstract. Controlled low temperature chilling caused flower initiation in container-grown olive (*Olea europaea* L.) trees at any time of the year. Optimum inflorescence production under controlled conditions occurred after exposure for 70 to 80 days to a diurnal sine wave temperature pattern, with a 2°C minimum and a 15°C maximum. These same temperatures, but changing abruptly from one to another failed to cause inflorescence formation. A constant intermediate temperature of 12.5°C was also effective in causing flower formation, but a continuous constant low temperature (7°C), or continuously high temperatures above 15°C failed to cause infloresence formation. The cv. Ascolano produced inflorescences under a wider range of temperature patterns than did 'Manzanillo'.

Irregular bearing behavior of olives in California's Central Valley could not be attributed to varying winter chilling patterns. There was no correlation over a 7-year period between amount of winter chilling and subsequent crop size. Sufficient chilling occurs even in warmest winters there for ample flower initiation.

Most commercial production of olives is confined to 2 bands around the world, between about 30° and 45° latitudes, except in areas where temperatures fall below about −10°C, the lethal minimum temperature for olives. In more tropical areas the trees grow well vegetatively but fruit production is low or nonexistent, except in a few localities such as southern Peru where the climate is modified by cold ocean currents.

The olive is a broad-leaved evergreen tree which produces inflorescences in late spring containing about 15 flowers each. Differentiation of a floral axis occurs during late winter in lateral buds produced on previous season's shoots. Flower parts are microscopically evident in the bud in early spring (7, 11). Two flower types, perfect and staminate, are produced in various proportions. The latter results from abortion or failure of the pistil to develop (3).

In 1953, Hartmann (8) noted that inflorescence production was in direct proportion to the amount of winter chilling received, but that growth of vegetative buds was not dependent on chilling. Hartmann and Porlingis (10) reported that certain olive cultivars required considerably less chilling than others for flower initiation. Hackett and Hartmann (4, 5) found that the flowering response to chilling is localized in those portions of the tree exposed to low temperatures, and that the presence of leaves during chilling is a requirement for flower initiation. They also found that photoperiod is not a factor influencing floral initiation. They showed that inflorescence development could be induced by exposure of the trees for about 17 weeks to 12.5°C constant temperature.

In a study comparing chilling olive trees at a constant temperature with chilling at diurnally fluctuating temperatures, Badr and Hartmann (1) found that holding trees at 12.5°C for 10 weeks resulted in inflorescence production, but maintaining similar trees for 10 weeks at a daily temperature regime of 12 hr at 15°C followed by 12 hr at 2°C (or 18°C and 7°C) failed completely to induce flowering.

Milella and Deidda (12) noted that in years with a mean January temperature in excess of about 6.5°C olive trees had a high bud drop and high pistil abortion; they also found that certain olive cultivars had a high chilling requirement but others had a low requirement. In a similar study, but using container-grown trees and greenhouse-controlled temperatures, Porlingis (14) in northern Greece, found considerable variability among olive cultivars in their chilling requirement for maximum flowering. Some produced high numbers of inflorescences when exposed to minimum chilling temperatures of 10° to 14°C, while others produced few flowers at these temperatures, requiring lower winter temperatures for maximum flowering.

The pattern of biologically active endogenous substances in olive buds was found by Hartmann, Fadl, and Hackett (9) to be quite different in a group of container-grown trees exposed to winter chilling temperatures (1756 hr below 7°C), in comparison with similar trees maintained in a greenhouse (minimum 15°C) throughout the winter. Studies by Badr, Hartmann and Martin (2) of biochemical changes associated with chilling and the onset of flowering in olive buds indicated that winter chilling could possibly induce flowering in the olive by altering a balance between endogenous gibberellins and certain inhibitors, including abscisic acid.

The purpose of the present study was to determine with some preciseness the optimum chilling temperature regime for flower initiation in the olive.

Materials and Methods

A series of experiments was conducted with container-grown olive trees in controlled environments. One of the chambers used in these tests is shown in Fig. 1. Light was provided by 3 banks of fluorescent lamps supplemented by incandescent lamps. An intensity of ca 8000 lux was maintained. A 12-hr photoperiod was used in all experiments. Temperature was controlled to the desired patterns by the use of Partlow[3] recording temperature programmers (Model RFCS). Circulatory fans maintained constant air movement and provided some interchange with outside air.

All experimental trees were propagated as rooted cuttings and grown to fruiting size in a prepared soil mix, supplemented with Osmocote fertilizer, in 15-gal containers. Trees were maintained under nonchilling temperatures prior to differential chilling treatment. Subsequent to such treatments, all trees were placed in a common greenhouse environment for flower development to occur.

The percentage of lateral buds forming inflorescences was determined on 20 selected potential fruit-bearing shoots on each tree. All inflorescences developing on each tree were recorded in some experiments. The percentage of perfect flowers on sample branches was determined in some experiments.

In the first experiment (Table 1) a group of 12 similar 5-year-old 'Manzanillo' olive trees in containers was brought into a heated (>15°C) greenhouse on October 15, 1969 while a group of 3 similar trees was subjected to normal winter chilling outdoors at Davis, California (Treatment E). On February 11, 1970, the 12 greenhouse trees were divided into 4 groups of 3 trees each and placed under 4 temperature treatments, shown in Table 1, for 12 weeks.

On August 2, 1971, a second experiment was initiated using 28 'Manzanillo' and 28 'Ascolano' trees of uniform size. These were

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Figure 1. Chamber in which container-grown olive trees were maintained under controlled light and temperature.

Table 1. Flower production in Manzanillo olive after 12 weeks under various temperature regimes. February 11 to May 4, 1970. Davis, California.

Treatment	Percent of buds forming inflorescences[z]
A. Constant 12.5°C	22a
B. Diurnal sine wave temperature fluctuation from 2° to 23.5°C	23a
C. Diurnal temperatures of 11 hr at 2°C and 11 hr at 23.5°C[y]	0
D. Greenhouse. Minimum temperature 15°C, maximum 21° to 32°C	0
E. Outdoor winter chilling	57b

[z] Values followed by different letters are significantly different at the 5% level as determined by Duncan's multiple range test.
[y] Two hrs daily in transitional temperatures.

divided into 7 groups of 4 trees of each cultivar for temperature treatments. The trees had bloomed in May, 1971, and the young fruits were removed about July 1. Temperature treatments were given as listed in Table 2. After about 10 weeks, all trees were moved to the greenhouse, and on December 14 the percentage of buds forming inflorescences was determined.

In a third experiment, 16 similar, container-grown, 5-year-old 'Manzanillo' olive trees which had been in a heated greenhouse all of the preceding winter, were divided into 4 groups of 4 trees each on May 2, 1972 and given the temperature treatments listed in Table 3. On July 29, the trees were moved to a lathhouse, and on August 16 the percentage of buds forming infloresences was determined.

An experiment using container-grown trees of olive cvs. Manzanillo, Sevillano, Ascolano, and Mission, was started on August 2, 1972.

Table 2. Flower production in olive trees exposed to differential temperature treatments for 10 weeks. August 2 to October 11, 1971. Davis, California.

Treatment	Percent of buds forming inflorescences[z]	
	Manzanillo	Ascolano
A. Constant 12.5°C	2.6a	15.6a
B. Diurnal temperatures of 11 hr 2°C and 11 hr 15°C[y]	1.0a	15.4a
C. Diurnal sine wave temperature fluctuation from 2° to 15°C	26.4b	26.8ab
D. Diurnal sine wave temperature fluctuation from 7° to 18°C	4.6a	31.8b
E. Diurnal sine wave temperature fluctuation from 4.5° to 10°C	0.0	0.0
F. Constant 7°C	0.0	0.0
G. Greenhouse. Minimum temperature 15°C	0.0	0.0

[z] Means within columns followed by different letters are significantly different at the 5% level as determined by Duncan's multiple range test.
[y] Two hrs daily in transitional temperatures.

Table 3. Flower production in 'Manzanillo' olive trees exposed to various temperature treatments for 12 weeks. Number of inflorescences per tree. May 2 to July 29, 1972. Davis, California.

Replicate number	Number of inflorescences per tree Temperature treatments			
	A 8°C (constant)	B 2°–15°C (diurnal sine (wave pattern)	C 2°–15°C (2°C 11 hr; 15°C 11 hr)[z]	D 7°–21°C (diurnal sine wave pattern)
1	6	132	0	8
2	0	67	0	1
3	17	413	0	0
4	0	101	0	0
Means	5.8	178.3	0	2.3

[z] Two hrs daily in transitional temperatures.

Table 4. Inflorescence production and flower type in 4 olive cultivars after exposure for 13 weeks to 2 temperature regimes. August 2 to November 2, 1972. Davis, California

Treatment	Manzanillo	Sevillano	Ascolano	Mission
Percent of buds forming inflorescences[z]				
A. Diurnal sine wave temperature fluctuation from 2° to 15°C	11.2b	12.6b	25.6c	22.3c
B. Constant temperature 12.5°C	0.6a	4.0ab	23.9c	42.0d
Percent perfect flowers[z]				
A. Diurnal sine wave temperature fluctuation from 2° to 15°C	57.5cd	66.2d	40.1bc	56.0cd
B. Constant temperature 12.5°C	54.6d	33.8b	44.3bc	11.6a

[z] Figures in columns and rows followed by different letters are significantly different at the 5% level as determined by Duncan's multiple range test.

The developing fruits were removed from each tree. The trees of each cultivar were divided into 2 groups of 3 each and given the treatments listed in Table 4. All trees were removed from the chambers on November 2, after 13 weeks, and placed in a heated greenhouse. Counts were made on November 27 of inflorescence production and percentage of perfect flowers.

We determined the response of olive trees to a daily fluctuating chilling period but of lesser magnitude than the 2° to 15°C differential previously used since, in some countries where olive production has been attempted, the winter chilling pattern is of such a type. On July 9, 1973, 4 'Manzanillo' and 4 'Ascolano' trees growing in 15-gal containers were selected and the young developing fruits were removed. Two trees of each cultivar were subjected to a sine wave temperature fluctuation varying from 15°C to 2°C. The remaining 2 trees of each cultivar were subjected to a sine wave temperature pattern varying from 12.5° to 7°C. After 12 weeks exposure the trees were moved to the greenhouse, and inflorescences counted (Table 5).

In nature, continuous favorable chilling rarely occurs. Therefore an experiment was designed to determine if an unfavorable temperature pattern (7° to 12.5°C) interspersed at intervals among favorable patterns (2° to 15°C) would affect flower initiation as compared to continuous exposure to a favorable pattern. A group of 8 uniform 'Manzanillo' trees growing in 15-gal containers was placed in a heated greenhouse on October 1, 1973, so the trees would have no exposure to chilling temperatures. On November 26, they were divided into 2 groups of 4 trees each and given the chilling regimes indicated in Table 6.

Results

Flowering could be induced in olive trees at any time of year they were subjected to favorable chilling temperatures although, in nature, the trees bloom in spring following the usual winter chilling period.

Trees held in a heated greenhouse during winter with no exposure to chilling failed to flower (Table 1, treatment D). In addition, trees exposed to diurnal alternate chilling (2°C) and high temperatures (23.5°C), with abrupt change from 1 temperature to another, also failed to flower (treatment C). In contrast, trees exposed to these same maximum and minimum daily temperatures but provided on a gradually changing sine wave pattern did flower (treatment B). Likewise, trees held at constant 12.5°C flowered, as observed previously by Hackett and Hartmann (6) (treatment A). However, maximum flowering was obtained with trees receiving outdoor winter chilling (treatment E).

Highest inflorescence production in 'Manzanillo' olive was obtained with a diurnal sine wave temperature pattern having a 15°C maximum and a 2°C minimum (Table 2). Fewer inflorescences were produced on trees exposed to a similar fluctuating temperature pattern of 7° to 18°C, to 12.5°C constant, or to a 2° to 15°C temperature pattern changing abruptly from 1 extreme to the other.

Figure 2. Shoots from Manzanillo olive trees (*above*) and Ascolano olive trees (*below*). Those on the left were from trees held for 12 weeks at a sine wave temperature pattern having a 7°C minimum and a 12.5°C maximum. Those on the right were from trees maintained for the same length of time and with the same temperature pattern but with a 2°C minimum and a 15°C maximum.

Table 5. Flower production in 'Manzanillo' and 'Ascolano' olive following treatment for 12 weeks under 2 temperature regimes. July 9 to September 30, 1973. Davis, California.

Treatment	Av no. of inflorescences per tree		Percent of buds forming inflorescences	
	Manzanillo	Ascolano	Manzanillo	Ascolano
Diurnal sine wave temperature fluctuation from 2° to 15°C	233	116	34	23
Diurnal since wave temperature fluctuation from 7° to 12.5°C	0	0	0	0

Table 6. Effect of 2 chilling temperature regimes on flower development in Manzanillo olives. Davis, California.

Treatment	No. of inflorescences per tree[x]	Percent of buds forming inflorescences[x]	Percent perfect flowers[x]
A[z]	962a	49a	17a
B[y]	822a	39b	28a

[z] Biweekly temperature regime of diurnal sine wave fluctuations of 2° to 15°C interspersed by a biweekly temperature regime of sine wave fluctuation of 7° to 12.5°C until 10 weeks at 2° to 15°C were provided. Treatments started November 26, 1973; concluded March 11, 1974.

[y] Continuous diurnal sine wave temperature fluctuations of 2° to 15°C for 12 weeks. Treatments started November 26, 1973; concluded February 7, 1974.

[x] Figures in columns followed by different letters are significantly different at the 5% level as determined by Duncan's multiple range test.

Table 7. Relationship between the amount of winter chilling in California olive districts and size of the olive crop the subsequent season.

Winter season	Days of "effective chilling"[z]					State olive yield (tons)
	Tulare	Tehama-Glenn	Butte	Mean of Tulare, Tehama-Glenn, and Butte[y]	San Diego	
1966–67	72	80	61	71	34	14,000 (1967 crop)
1967–68	53	62	65	58	19	86,000 (1968 crop)
1968–69	54	49	44	50	23	70,000 (1969 crop)
1969–70	95	82	84	89	13	52,000 (1970 crop)
1970–71	83	78	70	79	17	55,000 (1971 crop)
1971–72	64	73	57	65	31	24,000 (1972 crop)
1972–73	75	56	50	64	21	73,000 (1973 crop)
Means	71	69	62	68	23	

[z] Number of days between October 1 and April 1 in which the maximum temperature was between 12.5° and 23.5°C and the minimum temperature was between −4° and 7°C.

[y] The Tulare County value was weighted by 2x since its olive production is about equal to that of the other 2 districts combined.

Trees held at a constant 7°C, or with a minimum temperature of 15°C, failed to bloom. The percentage of buds forming inflorescences under 12.5°C constant temperature was surprisingly low in view of the high inflorescence production previously reported with such a treatment by Hackett and Hartmann (6). 'Ascolano' trees responded with flower production over a wider range of temperature treatments than did 'Manzanillo'. A sine wave fluctuating pattern from 7° to 18°C, gave maximum flowering (Table 2, D). These results indicate that 'Ascolano' may be more responsive in flowering to a variety of naturally-occurring winter chilling patterns than 'Manzanillo'.

Inflorescence production was highest when trees were held under a diurnal sine wave chilling temperature pattern of 2° to 15°C, as compared to a similar temperature pattern but at a higher level (7° to 21°C), or to a constant 8°C, or a 2° to 15°C pattern which changed abruptly from one temperature to the other (Table 3).

A comparison of plants grown at 2 temperature regimes, both known to induce flower formation in olives, showed important cultivar effects on flowering (Table 4). With 'Manzanillo', 'Sevillano', and 'Ascolano', flutuating temperatures gave higher inflorescence production than did constant 12.5°C temperature, but with 'Mission' the reverse was true (Table 4). For 'Sevillano' and 'Ascolano', the differences were not significant. 'Sevillano' and 'Mission' produced significantly greater numbers of perfect flowers under the fluctuating temperature regime as compared to a constant 12.5°C, whereas 'Manzanillo' and 'Ascolano' did not.

Subjecting either 'Manzanillo' or 'Ascolano' trees to a diurnal sine wave fluctuating temperature pattern of 7° to 12.5°C resulted in no inflorescence production (Table 5). However, similar trees subjected to the same temperature pattern but at a 2° to 15°C range, produced relatively high numbers of inflorescences (Fig. 2).

Interspersing periods of ineffective chilling patterns among periods of effective patterns showed no cancelling effect (Table 6). In fact, a significantly higher percentage of buds produced inflorescences when this was done, as compared to trees receiving continual effective chilling. No significant differences resulted from these 2 treatments in the percentage of perfect flowers produced.

Discussion

In discussions of vernalization (low temperature promotion of flowering), the types of plants responding are invariably listed as certain winter annuals and some biennials (15). The olive tree is a woody perennial which also responds to vernalization treatments. Many olive cultivars have an absolute requirement for chilling in order for flower formation to take place. There is a quantitative relationship in that the longer the exposure to natural winter chilling, the greater the number of inflorescences that develop. There is an additional requirement for the presence of leaves during the chilling period, indicating that some factor in the leaves contributes to the morphological changes in lateral buds from vegetative to floral growing points. The flower-forming stimulus resulting from the combination of leaves plus bud-chilling apparently is nontranslocatable. On greenhouse-grown trees, only those shoots exposed to outdoor winter chilling (by being placed through the greenhouse wall) develop infloresences.

Attempts are often made commercially to grow olive cultivars with a high chilling requirement in certain areas of the world where the trees grow well but sufficient chilling does not occur to initiate enough flowers to produce profitable crops. For example, along the coastal regions of central California, the summers are cool and the winters mild, producing a constant chilling pattern to which 'Mission' olive trees respond by continuously initiating low numbers of flowers. Mature fruits, half-grown fruits, and well-developed inflorescences can be found together at any one time through much of the year. In such mild winter regions, certain cultivars described by Porlingis (14) as being capable of flowering with little chilling should be tried. Such cultivars are grown commercially in parts of Greece where very mild winters occur (e.g., Chania, Crete, averaging 86 hours below 7°C (13) as compared to 1400 in California's Central Valley).

According to Wellensiek's hypothesis (16), vernalization takes place when dividing cells are present along with a concomitant cold treatment. Effects of temperature on flower initiation in olives supports this hypothesis. In earlier tests by the authors, where trees were maintained for 2½ months at a constant low temperature of 2°C (but with the soil-root mass held at 10°C to avoid tree wilting), there was a complete absence of inflorescence production when the trees were subsequently placed in a warm greenhouse. At such a chilling temperature there would be little or no actively dividing cells. On the other hand, (Tables 1 and 2) flowering also does not occur in olive trees maintained in a warm greenhouse during the winter where no chilling is possible. Flowering does take place, however, under conditions where warm temperatures each day permit the activities of dividing and metabolizing cells plus a daily cold period to provide the necessary vernalization stimulus.

Although olive trees exposed to a sine wave temperature pattern having a 15°C maximum and a 2°C minimum produced high numbers of inflorescences, exposure of trees to these same maximum and minimum temperatures, but with an abrupt change from one to another, failed to induce inflorescence production (Table 3). Perhaps the recovery of cells to a metabolically active state (at the 15°C level) after an 11 or 12-hr exposure to 2°C is too slow to permit flower induction processes to commence before the tissues are again exposed to low temperature. With a pattern of gradually changing temperatures, however, the tissues are subjected most of the time to intermediate temperatures where cell activity is more likely to occur, undergoing the minimum temperatures necessary for production of a flower-producing stimulus for a relatively short time. A 12.5°C constant temperature (at which olive flower initiation will occur) apparently is a compensation level where cell activity takes place, and, at the same time, the temperature is low enough to provide a vernalization stimulus.

California olives are produced principally in the interior Sacramento and San Joaquin Valleys. Yields vary widely from year to year. Alternate bearing is one reason for the variation, with a very heavy crop usually being followed by a light crop. In addition, the question arises whether a light crop might develop following a winter having a particularly unfavorable chilling pattern, whereas a heavy crop may appear following a winter providing ample amounts of an effective chilling pattern.

The present study indicates that about 70 to 80 days with temperature maxima at 15°C and minima of 2°C provide sufficient chilling to result in good inflorescence production. In the 7-yr period, 1966–67 through 1972–73, counts were made of the number of days each winter such a chilling pattern occurred, using temperature data from thermographs located in the 3 principal California olive-producing areas; i.e., Tulare County, Tehama-Glenn Counties, and Butte County. The winter climate in these 3 regions is quite similar, all having a mean January temperature of about 7°C. Since, in nature, maximum and minimum temperatures vary from day to day, the acceptable maximum was arbitrarily broadened to a range of 12.5° to 23.5°C, and the minimum to 2° to 7°C. Each year the number of days of "effective chilling" in each district were used to obtain a state-wide average. Since the Tulare County district produces about as many olives as the 2 other districts combined, the Tulare temperature values were weighted to give them twice the value of those from the other 2 districts. These state-wide number of days of "effective chilling" was then related to the amount of the state's olive crop for each of these 7 years (Table 7). The correlation coefficient for these data was −0.36, indicating little relationship between the amount of "effective chilling" established in this manner, and the following olive crop. In fact, certain heavy production years (e.g. 1968-86,000 tons) were preceded by winters having low amounts of "effective chilling".

It may be concluded from this that in California's Sacramento and San Joaquin Valleys for the olive cultivars grown there, sufficient "effective chilling" is provided for flower initiation even in the warmest winters, colder winters providing a surplus amount of chilling. In contrast, in southern California, where the state's olive plantings were first made, commercial production no longer exists, due primarily to the low yields obtained with the cultivars growing there. In the years 1966–67 through 1972–73, there was a mean of only 23 days of "effective chilling" in San Diego County, compared to 71 in Tulare County, 69 in the Tehema-Glenn district, and 62 in Butte County (Table 7). The low number of days of "effective chilling" in San Diego was caused by the temperatures in most winter nights failing to reach the minimum values required.

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Developmental Studies of Pyriform Fruits of Grapefruit[1, 2]

Arthur C. Gibson[3, 4]
University of Arizona, Agricultural Experiment Station, Tucson

Abstract. A study of the structure and development of gynoecia from normal and pyriform samples of 'Red Blush' grapefruit (*Citrus paradisii* Macfad.) revealed that stages in organogenesis and histogenesis were essentially similar. Activity of a subovarian intercalary meristem prior to anthesis was responsible for enlargement of the ovary base and increase in thickness of the ovary wall during the last half of pistil ontogeny. Other meristematic areas accounted for development of locules, central core, ovary top, style, and stigma, but these regions were not involved in the elongation process. The evidence suggests that floral apices which form pyriform fruits tend to produce wider gynoecia, which are more robust than normal ones throughout the subsequent months of development. Size of pistils may be an important factor in relation to variation in fruit shape in grapefruit, and, therefore, prevention of pyriform fruit development is probably intimately related to the control of the growth rate of apices in a given year.

Fruit size and shape are particularly variable in species that produce fleshy fruits. Whereas heritable factors account for and also limit the range of expression of morphological characteristics within a cultivar, variation in fruit shape on a single plant is caused by relative differences in cell volume and number, size of intercellular spaces, and distribution of cell divisions in developing ovaries. Many climatic and growth factors affect the development of fruits by controlling cell division and enlargement (7, 8). The combined effects of various factors on fruit ontogeny are complex and difficult to monitor, although cellular changes can be studied directly with comparative ease.

Growers of *Citrus* in desert regions have noted a high incidence in some years of pyriform or "sheepnosed" fruits in cultivars as compared with coastal grown specimens (1, 6). This commonly occurs in grapefruit, but all cultivars of *Citrus* may possess these symptoms to lesser degrees. Fruits are elongate at the pedicel end and tend to have thick, rough peels. Abnormalities in fruit shape and peel thickness usually appear together, but in grapefruit each characteristic is influenced independently by a set of climatic factors even though one factor may affect several different characteristics (1). The problem of why fruit shape changes is intriguing because normal and pyriform fruits may be produced on the same tree in alternate years. Similarly, a particular scion-stock combination grown in different localities shows different degrees of elongation of fruits in any given year with trees growing in sandy soils having the highest incidence of elongation. Trees with heavy fruit set tend to have well-rounded fruits in comparison to those with light fruit set.

Accounts of the anatomical stages in flower and fruit development are available for 'Eureka' lemon (2) and other cultivars of *Citrus* (9). Those studies serve as useful guides for comparisons with grapefruit, which has not been studied. However, no description adequately discusses when and how ovary shape develops and where meristematic activity occurs at each stage of development. The primary objective of this study was to describe the meristematic zones of the pistil and to compare the histogenesis of gynoecia of developing normal and pyriform fruits.

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