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Title: EFFECTS OF FLORAL POSITION, STAMEN QUALITY, HAND POLLINATION, AND TEMPERATURE DURING REPRODUCTIVE DEVELOPMENT ON MEADOWFOAM SEED SET AND SEED YIELD

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Abstract Approved:

Dr. Gary D. Jolliff

Inconsistent seed yields of meadowfoam (Limnanthes alba Benth.) interfere with profitable production of this new oilseed crop. Significant correlation of field grown meadowfoam seed yields with years having temperatures above 24$^{0}$C in mid-May at Corvallis, OR., led to the hypothesis that ambient temperature during reproductive development affects meadowfoam seed yields. The objective of this experiment was to determine the effect of three day/night temperature regimes (16/10, 24/10, 32/10$^{0}$C),

imposed for seven days during bud, early flowering or peak bloom stages on seed yield, seed number per flower, and seed weight of meadowfoam when grown under a controlled environment. In separate experiments, studies were performed to verify the effectiveness of a hand pollination technique in field-grown meadowfoam; and influences of flower location and stamen quality on seed set in hand-pollinated growth chamber-grown meadowfoam were examined. No significant differences in seed set were found among flowers at different locations on the plants, nor in flowers having normal or abnormal anthers. Supplementally hand-pollinated flowers of field-grown meadowfoam set more seed than bee-pollinated flowers on the same plants. Temperature and floral stage treatments did not result in significant seed number or seed size (1000-seed weight) differences, but high temperature ($32^{0}$C) imposed at the bud stage did increase seed yield (total weight of all seeds produced per plant). High temperature did not increase seed yield when imposed at early flowering or peak bloom. Temperature during reproductive development does appear to play an important role in determining meadowfoam seed yield, and further research is necessary to determine the extent of seed yield response to temperature in the field.

# EFFECTS OF FLORAL POSITION, STAMEN QUALITY, HAND POLLINATION, AND TEMPERATURE DURING REPRODUCTIVE DEVELOPMENT ON MEADOWFOAM SEED SET AND SEED YIELD

by

Elena L. Alba

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Professor of Crop Science in Charge of Major

Redacted for privacy

Head of Department of Crop Science

Redacted for privacy

Dean of Graduate School

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## INTRODUCTION

Meadowfoam is a winter annual native to the Pacific Coast areas of southern Oregon, California, and Vancouver Island, British Columbia. Meadowfoam seed contains 25 to 33% oil primarily composed of $C_{20}$ and $C_{22}$ fatty acids, with unsaturation at the fifth and/or the thirteenth carbon atoms. This unusual structure allows meadowfoam seed oil to remain clear and fluid at temperatures as high as $180^{0}C$, making it potentially useful as an industrial lubricant additive. Other uses have been suggested, and the first commercial sale of the oil was to a Japanese firm in 1985 for use in cosmetics.

Meadowfoam is a crop of special interest in the Willamette Valley of Oregon because it is adapted to the mild, wet winters and the poor internal drainage typical of approximately 80,000 hectares of soils in the region. In recent decades annual ryegrass for seed has been the only adapted cash crop which growers could produce on these soils. Air pollution caused by the burning of ryegrass seed crop residue, and severe fluctuations in the price of annual ryegrass seed have resulted in a serious need for alternative crops. High seed yields could make meadowfoam a profitable alternative for farmers, but seed yields from experimental

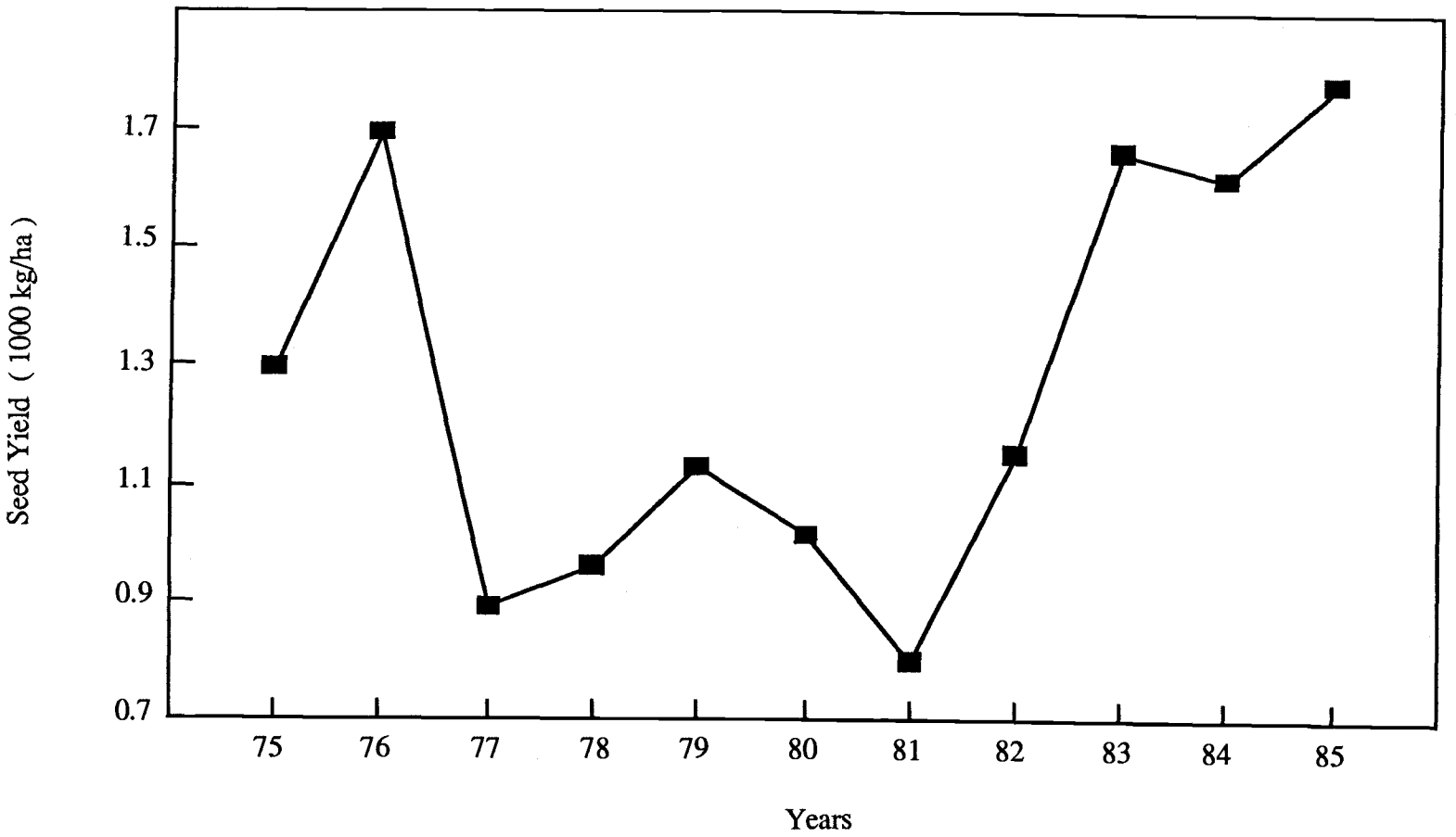


Figure 1. Meadowfoam seed yields at Hyslop Corp Science Field Laboratory, Corvallis, Oregon, from 1975 to 1985.

production trials at Oregon State University have been inconsistent, varying from 788 to 1760 kg/ha (Fig. 1). The factors contributing to yearly fluctuations in seed yield in the Willamette Valley of Oregon have not been identified. A significant positive correlation was found between seed yield and the number of days having average maximum temperature above $24^{0}$C from May 10th to May 17th (Appendix Table 13). The objective of this research was to test the hypothesis that temperature variation during reproductive development can affect seed yield. Additional experiments were performed to validate sampling techniques, examine differences in flower quality, and verify the effectiveness of a hand pollination procedure.

# CHAPTER I

## REVIEW OF LITERATURE

Temperatures during reproductive development are known to affect plant processes contributing to final seed yield by influencing seed number, seed size, or both. The number of seeds produced by a plant is dependent upon: the number of reproductive structures that differentiate and successfully develop, successful pollination and fertilization, and finally sufficient dry matter accumulation to mature the seed. Environmental stress present during any one of these phases could prevent a plant from reaching its full genetic potential for seed yield. Gamete differentiation and development, pollination, and fertilization are especially sensitive to temperature extremes (Leopold and Kriedemann, 1975; Stanley and Liskens, 1974). Elevated temperatures during premeiotic or meiotic stages can disturb cell division and result in reduced gamete viability (Carlson and Williams, 1985). Low temperatures induce male sterility in some cereals and in strawberry (Kinet et al., 1985), whereas favorable temperatures promote pollen germination and pollen tube growth (Savithri et al., 1980). Whole flower abortion often results from the exposure of emerging flower buds to either high or low temperature extremes (Brevedan et al., 1978).

The rates at which many reproductive processes occur are highly temperature sensitive, and their response may influence seed

yields. Thompson and Liu (1973) showed that warm temperatures during and after pollination increased the rate of pollen tube growth, fertilization, and embryo development in Italian prune, resulting in increased fruit set. In onion, warm temperatures during flower opening hastened stigma receptivity and increased seeds produced per ovary (Chang and Struckmeyer, 1976). During avocado flowering, temperatures below $17^0$C disturbed the normal reproductive cycle and prevented embryo development, resulting in lowered fruit set, while temperatures above $33^0$C caused abnormal pollen growth and early ovule degeneration (Sedgley, 1977).

Seed size is largely determined by genetic code (Egli, 1981), however, variations in the rate and duration of seed growth within a species or cultivar have been shown to result in part from differences in thermal environment. The metabolic processes associated with seed growth tend to accelerate as temperatures increase within a specific temperature range (Egli and Wardlaw, 1980), above and below which growth is slowed or stopped. Seed growth rate is also affected by the availability and distribution of photosynthate within the plant. Wardlaw (1968) has stated in general that seed "sink strength" (sink capacity plus sink activity) is dependent upon the number and size of seed cells, their metabolic rate, and their distance from the source of photosynthate. Growth substances which may regulate photosynthate distribution also affect seed sink strength. Sink strength affects the rate of grain fill, and may therefore influence final seed mass (Cochrane and Duffus, 1983).

Jones et al. (1984) found that unfavorable temperatures (15 or 35$^0$C) during the lag phase (rapid endosperm cell division) in maize resulted in reduced kernel mass due to the production of fewer and smaller endosperm cells, and fewer starch granules in the endosperm cells. Final seed weight has been found to be highly correlated with endosperm or cotyledon cell number in several plant species (Egli et al., 1980; Gray and Ward, 1985; Cochrane and Duffus, 1983). In wheat, unfavorable lag phase temperatures (above 30$^0$C) reduce endosperm sink strength by limiting cell size, with little effect on cell number (Hoshikawa, 1962; Wardlaw, 1970). Information is unavailable regarding temperature effects on either cell size or cell number in meadowfoam seed.

Egli (1981) has reported that duration of seed growth is negatively correlated with temperature in many plant species, though it may be less variable than seed growth rate; and that duration of seed growth is strongly related to final yield. Jones et al. (1985) found the duration of the effective grain fill period in maize to be primarily mediated by temperature during this stage rather than by its previous thermal history. Pearson and Shaw (1981) also noted that duration of caryopsis growth in dallis grass (Paspalum dilatatum) increased by temperature reduction, and that florets produced at 21/16$^0$C day/night temperatures were heavier than those produced at 31/25$^0$C. Ong (1983) found that the duration of the main grain filling period in pearl millet (Pennisetum typhoides, S.and H.) was decreased by 0.7 days for each 1$^0$C rise in temperature from 19 to 25$^0$C, and that each 1$^0$C temperature increase resulted in a decrease of 0.38 mg in average grain weight.

The limited amount of published information on meadowfoam response to environmental variables reveals that soil fertility, water availability and stand density may interact to produce a complex effect on seed yield (Calhoun and Crane, 1978; McGahuey, 1986; Johnson et al., 1980; Pearson, 1983; Brown, 1976). Few temperature related studies of meadowfoam reproduction are reported in the literature. Huynh (1971) found that L. douglasii pollen germinated easily in vitro at $25^0$C. Mason (1952) reported that the percent of fertile pollen was greatest in the first flowers to open on a meadowfoam (L. spp.) plant. He speculated that light and temperature might have an effect on pollen viability. In a meadowfoam hand-pollination study under greenhouse conditions, Devine and Johnson (1978) reported up to 70% seed set in L. alba at $30^0$C.

Temperature has been shown to affect meadowfoam phenology. Early-season warm temperatures shortened the period of vegetative growth and reduced seed yields of L. alba in a California cultural trial (Higgins et al., 1971). In another California trial, a few hot days in late spring caused termination of flowering in normally indeterminate flowering L. alba plants (Jain et al., 1977), hence limiting subsequent seed production. Temperature parameters were not defined in these studies. A preliminary study by Franz (unpublished data) showed that during L. alba flowering, daytime maximum temperatures higher than $16^0$C shortened the lag period after anthesis when pollination could result in successful fertilization.

Preliminary work has been carried out on meadowfoam to investigate the effects of environmental conditions other than temperature on the number of seeds produced. A water-stress study by Pearson (1983) demonstrated an increase in seeds per flower where L. alba was irrigated during an unusually dry May (the bud and flowering period for meadowfoam in the Willamette Valley of Oregon). Pearson (1983) and McGahuey (1986) both showed that nitrogen fertilization in L. alba decreased the number of seeds set per flower while increasing the number of flowers produced per plant. These researchers speculated that competition for available photosynthate and/or bee pollinators, along with increased disease infection in the dense floral canopies of fertilized plants could account for the reduction in seeds per flower. Pierce and Jain (1977) also noted a negative correlation of seeds per flower to flowers per plant in L. spp., though they did not comment on cause and effect relationships. Brown et al. (1979), Brown (1976) and Gentry and Miller (1965) have noted the high degree of variability in numbers of seeds produced per flower in native stands or progeny of native stands of meadowfoam. Arroyo (1975) suggests that fluctuations in pollinator availability and seasonal variations in soil moisture are probably strong contributing factors to final seed set in these stands. These researchers do not mention any likelihood of a relationship between temperature stress during flowering and seed set. Typically, however, temperature fluctuations are concomitant with other weather conditions which may directly affect pollinator activity or soil conditions. Cool wet weather occurring during bee foraging periods inhibits the

insects' activities and possibly hinders efficient pollination (Burgett, 1976). This could result in a reduced number of seeds produced, even though the temperature may not be low enough to damage gamete viability or seriously hamper the biochemical processes involved in reproduction. Conversely, bright clear days accompanied by a noticeable rise in temperature due to the accumulation of unobstructed radiant energy may be highly conducive to pollinator activity, but if the frequency of warm dry days is high, evapotranspiration may deplete available soil moisture and limit seed filling (Pearson, 1983).

Studies of environmental effects on L. alba seed yield components have shown that oil content of the seed is highly correlated with seed weight (Johnson et al., 1980). Nitrogen fertilizer trials and seeding rate studies have failed to show a consistent seed weight response to treatments (Johnson et al., 1980; Pearson, 1983), while harvest dates, irrigation and genetic variation, do affect meadowfoam seed weight and oil content (Johnson et al., 1978; Johnson et al., 1980; Pierce and Jain, 1977; Pearson, 1983). Yield records from Oregon State University field trials from 1977 to 1985 have shown a significant correlation ($r^2=0.96$) between total seed yield and number of seeds produced per hectare, whereas seed size (grams per 1000 seed) has not been correlated with total yield (unpublished data).

The evidence presented above suggests that temperature could have a significant effect on meadowfoam seed yield. Whether that effect may be direct through plant physiological processes, or indirect through interaction with other contributing factors

requires further examination. Quantitative studies on the effects of specific temperature treatments on meadowfoam seed yield and its components will help to clarify the contribution of climate to variable annual meadowfoam yields.

# CHAPTER II

## EFFECTS OF FLORAL POSITION, STAMEN QUALITY, HAND POLLINATION AND TEMPERATURE DURING REPRODUCTIVE DEVELOPMENT ON MEADOWFOAM SEED SET AND SEED YIELD

## INTRODUCTION

Meadowfoam is a new oilseed crop in Oregon. It is adapted to poorly drained soils (Calhoun and Crane, 1978) and has oil with unique chemical properties (Higgins et al., 1971). Seed yields from experimental production trials at Oregon State University have varied from 788 to 1760 kg/ha within the last ten years. The cause of these fluctuations has not been identified. A significant positive correlation was found between seed yield from 1975 to 1985, and the occurrence of average maximum temperatures above $24^{0}C$ during flowering (unpublished data). The objective of this study was to evaluate the effects of three temperature regimes during three stages of floral development on meadowfoam seed yields.

Unfavorable temperatures have been shown to disturb meiotic cell division in soybean (Carlson and Williams, 1985), slow pollen tube growth and embryo development in Italian prune (Thompson and Liu, 1973), and cause early ovule degeneration in avocado (Sedgley, 1977). All of these temperature effects resulted in decreased

fecundity. Seed size is also known to be affected by temperature through various mechanisms. Unfavorable temperatures during the lag phase of seed growth resulted in reduced size and number of endosperm cells in maize (Jones et al., 1984), and reduced endosperm cell size in wheat (Wardlaw, 1970). This reduced the sink strength and rate of seed growth of these crops. Egli (1981) has reported that the duration of seed growth is negatively correlated with temperature in many plant species, and is strongly related to final seed yield.

Few temperature related studies of meadowfoam reproduction are reported in the literature. Higgins et al. (1971), and Jain et al. (1977) have shown that meadowfoam phenology is affected by high temperatures. Burgett (1976) has described the inhibiting effect of low temperatures on insect pollinator activity. Arroyo (1975) suggested that fluctuations in pollinator availability and seasonal variations in soil moisture are strong contributing factors to final seed set in meadowfoam. Pearson (1983) and McGahuey (1986) both noted a negative correlation between seed set and floral density. These findings point to interaction of environmental variables. Quantitative studies on the effects of specific temperature treatments which prevent confounding interaction among other environmental factors are needed to help clarify the contribution of climate to inconsistent meadowfoam seed yields.

Testing of temperature effects on meadowfoam seed yield requires the use of sampling techniques which have not previously been reported for this crop. Floral position within a plant canopy influences seed production through competition for nutrient supply

or pollinator availability in some plants (Pyke, 1981; Wyatt, 1980). Experiment I was conducted to determine an appropriate sample flower selection method based on the degree to which floral position affects seed set in hand-pollinated meadowfoam. Experiment II was conducted to determine whether flowers with abnormal stamens (filaments very short, anthers darkened and apparently lacking pollen) are able to bear a full complement of five seeds, and are therefore useful as sample flowers. Meadowfoam plants grown in growth chambers with relatively low light intensity have produced a high frequency of such abnormal flowers in previous experiments.

Insect pollinators were not available in controlled environment growth chambers used in these experiments, so Experiment III was performed to verify the effectiveness of hand pollination. Experiment IV combined the findings of Experiments I, II and III in establishing sampling procedures and a hand-pollination technique, in order to test the effects of temperature at different floral stages on meadowfoam seed yield.

# MATERIALS AND METHODS

Four experiments were conducted using meadowfoam seed (Limnanthes alba Benth., cv. Mermaid) from a single lot produced at Corvallis, Oregon in 1983. Seeds for growth chamber and greenhouse experiments were germinated without light for seven days in perlite-filled trays at $10^0$C in a germination refrigerator. the seedlings were grown vegetatively for 38 days in a growth chamber at $16^0$C under an 8/16 hour light/dark cycle using fluorescent and incandescent light producing photosynthetically active radiation (PAR) of approximately 275 $uEm^{-2}s^{-1}$. Twenty-one days after planting, the seedlings were transplanted into 10 x 10 cm fiber pots containing a peat, sand, clay loam soil mixture adjusted to a pH range of 5 to 6 by the addition of $CaCO_3$ and $Ca(OH)_2$. Soil fertility was maintained by weekly additions of 50 mls of a modified Hoagland's solution (Ore. State Univ. Dept. of Crop Science, New-Crops Project annual report, 1983) until the plants were 75 days old. Protandry in L. alba necessitates hand pollination to achieve measurable seed set in the absence of insect pollinators. Hand pollination in these experiments was performed once daily for as many days as each flower remained open, by touching a freshly dehiscing anther to each lobe of receptive stigmas. L. alba stigmas are first receptive to pollen when the style has elongated to nearly the height of the stamens, and before the stigmatic lobes have spread (Devine and Johnson, 1978). The duration of this receptive period is variable and is dependent on the ambient temperature and possibly other variables.

The field experiment was seeded in peat pellets on September 6, 1984, and transplanted to 30 centimeter rows with 30 centimeters between plants within rows on November 11. At the time of transplanting, 300 kg/ha of 16-20-0 fertilizer was incorporated into the soil. On November 1, 4 kg/ha Propachlor was applied to the soil surface to control weeds.

Experiment I

In a completely randomized design, six meadowfoam plants at late bud stage were selected for hand pollination treatments and were placed in a greenhouse in pairs to receive the following treatments:

Group 1: All flowers on four primary stems (arising directly from the plant crown) of each plant were hand pollinated daily until petal closure.

Group 2: All flowers on four secondary stems (arising from nodes on primary stems) of each plant were hand pollinated daily until petal closure.

Group 3: Two to four flowers from each of eight separate stems (primary and/or secondary) of each plant were hand pollinated daily until petal closure. This process continued for as long as groups 1 and 2 had unopened flowers on their treatment branches.

The number of mature seeds produced per hand-pollinated flower were recorded, and data analyzed by analysis of variance. No seeds were produced on flowers which were not hand pollinated.

Experiment II

The experiment was a completely randomized design in which a single plant bearing both normal flowers and flowers with abnormal stamens was maintained in a growth chamber at $16^0$C and a 16/8 hour light/dark cycle (approximately 275 $uEm^{-2}s^{-1}$) throughout flowering. Pollen from normal flowers of a second plant grown under the same conditions was used to hand pollinate fifteen normal and fifteen abnormal flowers. The number of mature seeds produced per flower was recorded and data analyzed by analysis of variance.

Experiment III

In the spring of 1985, in a completely randomized design, ten field-grown meadowfoam plants were randomly selected at Hyslop Crop Science Field Laboratory, and thirty of the first sixty flowers to open on each plant were tagged at anthesis and hand pollinated. The pollination technique used was identical to that used in the growth chambers and greenhouse, except that insect pollinators were also permitted to visit the tagged flowers. The remaining thirty flowers were also tagged, but were not hand pollinated. The number of mature seeds produced per flower was recorded and analyzed by analysis of variance and paired T-test.

Experiment IV

This experiment was conducted in a split plot design with two replications. Independant treatment variables were temperature (mid-day maximums of 16, 24 and 32$^{0}$C) as main plots, and floral stage (bud, early flowering and peak bloom) as sub-plots. Each replicated treatment had ten observations (mean seed yield and yield components from thirty hand-pollinated flowers per plant, on ten plants).

Three weekly plantings of meadowfoam seed were made to provide replicate plants at bud (abbreviated B; floral branches elongated but no petals open), early flowering (abbreviated EF; not less that 5% nor more than 20% of visible flower buds open) and peak bloom (abbreviated P; not less than 50% of visible flower buds open) stages on the date of temperature treatment. At 45 days after seeding, all plants within a planting date (floral stage) group were transferred to a Conviron 'PGV-36' growth chamber (16/8 hour light/dark cycle and 18/13$^{0}$C day/night temperature cycle) to induce flowering. The first 30 flowers to open on 30 plants of each floral stage group were tagged and hand pollinated daily until petal closure. Flowers which opened subsequent to the first 30 were not hand pollinated and did not produce measureable seed set. Six plants of each floral stage group were used as pollen sources for that group. Hand pollinations were performed with care to assure that flowers in all treatments received uniformly large quantities of freshly dehisced pollen, to prevent inadequate pollen supply from limiting seed set. Irrigation and fertilizer application also were maintained uniformly so that water and mineral deficiencies would not limit yield.

Ninety days after the first seeding date, 12 plants (10 for hand pollination and 2 for pollen source) from each planting date group were randomly selected and placed in one of three growth chambers where elevated temperatures were imposed. In all temperature regimes a minimum nighttime temperature of $10^0$C was maintained from 2200 h to 0200 h. A daytime maximum temperature of 16, 24 or $32^0$C was maintained from 1130 h to 1330 h in one of the three growth chambers, respectively, with temperatures ramped between these high and low temperature periods (Fig. 2). The factorial combination of three temperatures and three floral stages provided nine treatments. Following seven days of temperature elevation, all plants were returned to the PGV-36 chamber, and the temperature regime of that chamber was reset to $18/13^0$C. Each planting date group was moved to a greenhouse bench 112 days after seeding to complete the seed maturation process. Pre- and post-treatment light intensity in the PGV-36 chamber averaged 750 $uEm^{-2}s^{-1}$, but light intensity during the seven days of elevated temperatures was approximately $330uEm^{-2}s^{-1}$ (maximum light intensity for two of the chambers).

Seeds were harvested at maturity and allowed to dry at room temperature for eight weeks before weight measurements were taken. The weight of all seeds produced per plant was measured with a Metler analytical balance. Total seed number and number of seeds produced per flower were recorded for each plant, and mean seed size (mg) was then calculated.

Treatment effects were measured as differences in average number of seeds produced per flower, seed size, and seed yield

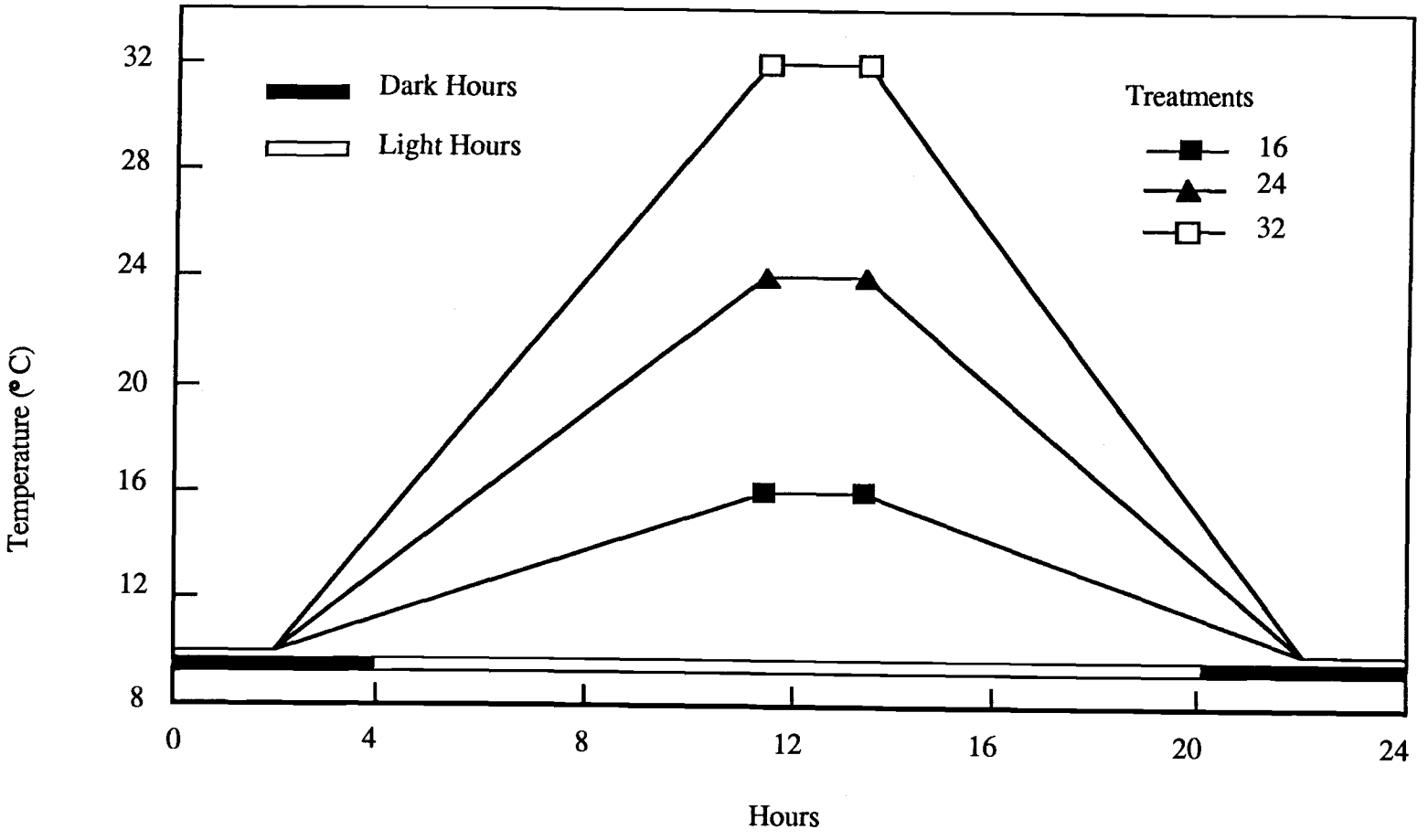


Figure 2. Patterns of light/dark cycle and temperature treatment regimes for study of temperature effects on meadowfoam seed yields.

(total weight of all seeds produced per plant). Data were analyzed by analysis of variance, and LSDs were calculated for comparison of treatment means.

# RESULTS

## Experiment I

The mean number of meadowfoam seeds produced per flower was similar at the three floral positions tested (Table 1), though a non-significant trend toward increased seed set was seen in flowers located on separate stems versus those on the same stem. Flowers born close together on secondary stems tended to have lower seed set than those close together on the larger primary stems. Since meadowfoam plants in these growth chamber experiments typically produced seven to ten primary stems, and the lower three to four flowers on these stems opened before most other flowers on the plant, we determined that a simple method of uniform sample flower selection was to sample the first 30 flowers to open on each plant.

## Experiment II

Seed set in hand-pollinated flowers with abnormal stamens was similar to that of flowers with normal stamens (Table 1). Apparently, the gynoecium of meadowfoam was not adversely affected by the conditions which caused staminal abnormality in this experiment. Because meadowfoam flowers with abnormal stamens did not have significantly reduced mean seed set and because some of these flowers were able to produce five seeds (the maximum number possible), we determined that it was not necessary to selectively avoid them in meadowfoam yield studies.

Table 1. Treatment means and statistical comparisons for number of seeds produced per meadowfoam flower in three experiments using hand-pollination.

| Experiment | Number of Samples | Treatments | Mean Seeds/flower | Comparison Statistic |
|---|---|---|---|---|
| I | 2 plants | Group 1* | 2.98 | |
| | 2 plants | Group 2 | 2.49 | $LSD_{.05}$ 1.40 |
| | 2 plants | Group 3 | 3.22 | |
| II | 15 flowers | normal stamens | 3.33 | |
| | 15 flowers | abnormal stamens | 3.00 | $LSD_{.05}$ 0.71 |
| III | 10 plants | 30 supplementally hand-pollinated flowers/plant | 3.53 | Paired $T_{.05}$ Value |
| | 10 plants | 30 bee-pollinated flowers/plant | 3.13 | 2.92 |

* Group 1 - all flowers of 4 primary stems per plant
Group 2 - all flowers of 4 secondary stems per plant
Group 3 - individual flowers of separate stems

Experiment III

Supplementally hand-pollinated field-grown flowers had higher seed set than did flowers pollinated soley by insects (Table 1). This indicates that the hand pollination technique used was effective in bringing about fertilization under field conditions as well as in the growth chambers. We have judged its use in growth chamber experiments as justified.

Experiment IV

Seed Number

All nine temperature/floral stage treatments resulted in average seed set greater than three seeds per flower, and 28 individual plants produced an average of more than four seeds per flower. However, the data indicate that within the temperature parameters tested, no treatment differed significantly from the others in its effect on meadowfoam fecundity (Table 2). Plant to plant variation in seed set was high in all treatments, which made differences between treatment means difficult to discern.

When temperature was increased from 16 to $24^{0}$C at the bud (B) stage, seed set was virtually unchanged (Fig. 3). However, when the temperature was increased to $32^{0}$C at B stage, slightly higher seed set resulted. Plants exposed to increased temperature at the early flowering (EF) stage responded differently than those exposed at the bud stage (Fig. 3). EF plants exposed to $24^{0}$C had slightly more seeds per flower than those held at $16^{0}$C, but EF plants

Table 2. Treatment means and statistical comparisons for seeds per flower, seed size and yield (total weight of all seed produced per plant) meadowfoam under three temperatures and three stages of floral development.

| Treatments | Seeds per Flower | Seed Size | Seed yield |
|---|---|---|---|
| Temperature | | mg | g |
| $16^0$C | 3.36 | 9.50 | 0.960 |
| $24^0$C | 3.28 | 9.89 | 0.952 |
| $32^0$C | 3.19 | 10.55 | 0.965 |
| Stages | | | |
| Bud | 3.37 | 9.78 | 1.046 |
| Early Flower | 3.17 | 9.75 | 0.905 |
| Peak Bloom | 3.23 | 10.41 | 0.929 |
| Temperature | N.S. | N.S. | N.S. |
| Stages | N.S. | N.S. | ** |
| Temp x Stage | N.S. | N.S. | * |
| temps within stages | | | N.S. |
| stages within temps | | | * |

**, * Significant at the 0.01 and 0.05 probability levels, respectively.

N.S. = Non Significant

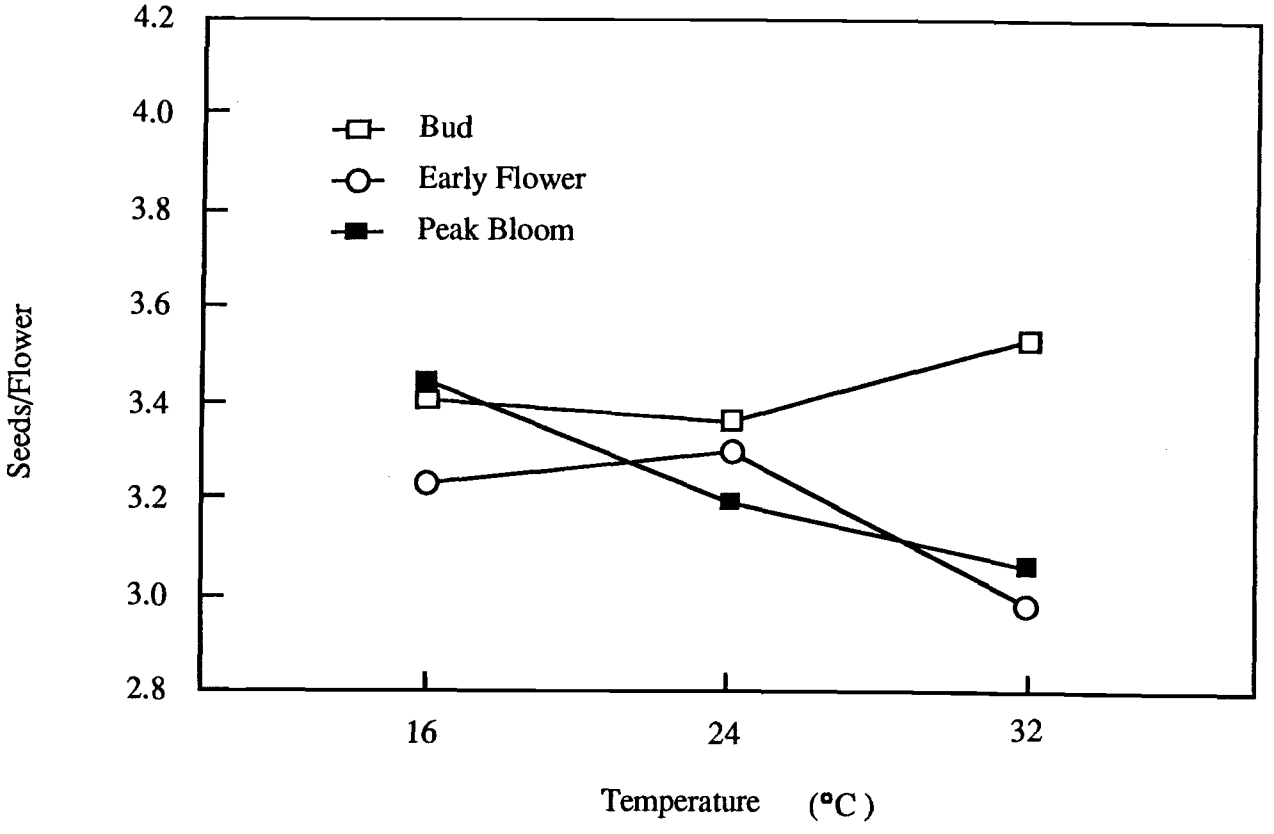


Figure 3. Effects of three temperature treatments at three stages of reproductive development on number of seeds per flower in meadowfoam plants.

exposed to 32$^0$C had 8 and 10% fewer seeds per flower than those held at 16 and 24$^0$C, respectively. Plants in peak bloom (PB) seemed to respond less favorably to elevated temperatures than did the younger plants. Seed set in PB plants was highest when temperature was held at 16$^0$C. Exposing PB plants to 24$^0$C caused a 7% reduction in seed set compared to those at 16$^0$C. Increasing the temperature to 32$^0$C at peak bloom caused seed set to be 11% lower than that produced at 16$^0$C.

The mean number of seeds produced per flower at each of the three temperatures did not differ significantly (Table 2). Seed set at 16 and 24$^0$C was quite similar among all floral stages, although the rank among stages for seed set differed between the two temperatures (Fig. 3). Seed set varied more noticeably among floral stages at the 32$^0$C temperature. When exposed to 32$^0$C, plants at B stage produced 13 and 15% more seeds per flower than EF or PB plants, respectively.

## Seed Size

A trend toward greater seed size at higher temperatures was observed when temperatures were increased during B or PB stages (Fig. 4). Seed size also increased when temperature was increased from 24 to 32$^0$C during the EF stage, but this increase was not seen when temperature was increased from 16 to 24$^0$C at that stage. Despite these trends, seed size was not significantly different among treatments (Table 2). When temperature was increased from 16 to 32$^0$C during the B stage, seed size was increased by 13%. Increasing the temperature only 8$^0$ from 16 to 24$^0$C accounted for

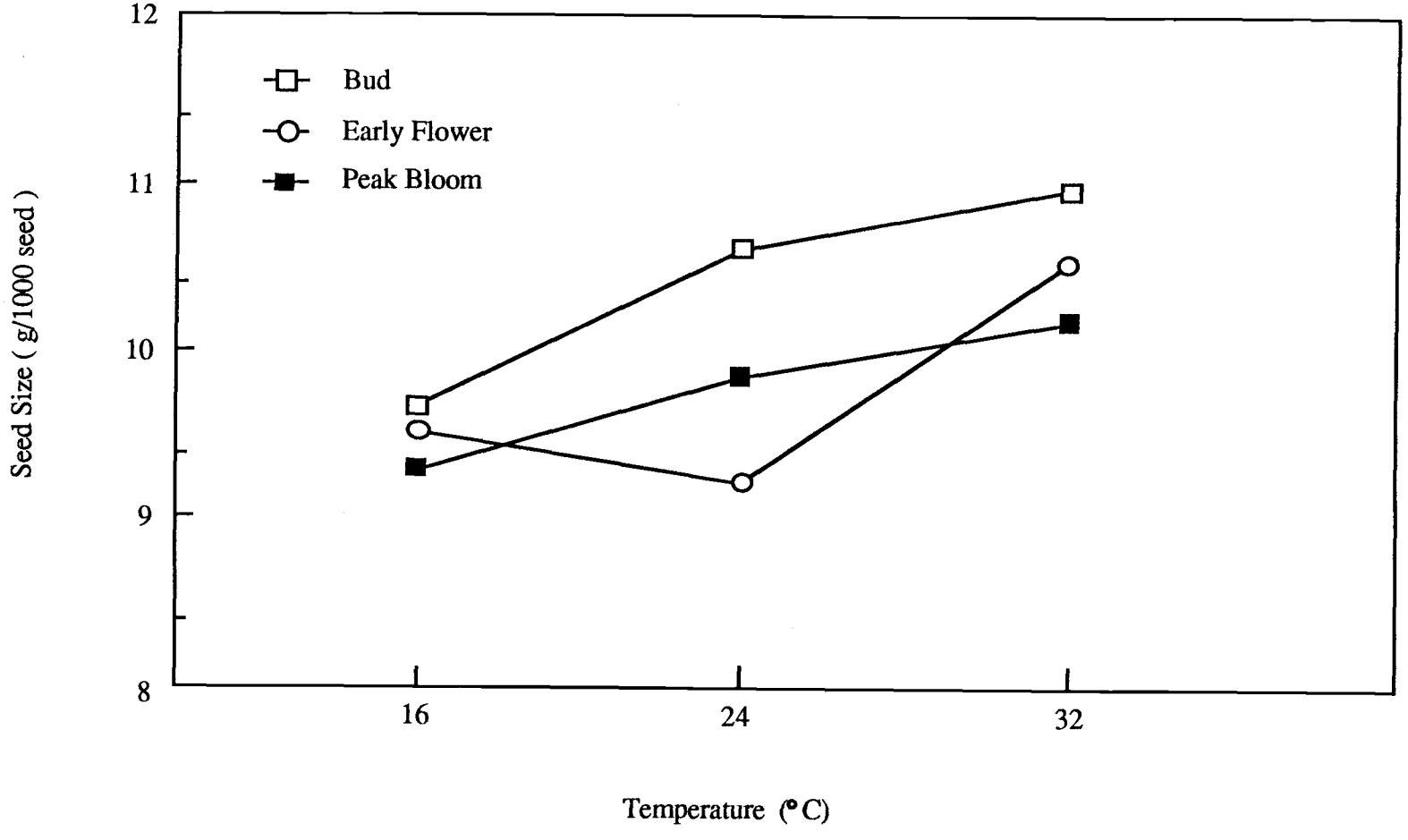


Figure 4. Effects of three temperature treatments at three stages of floral developement on meadowfoam seed size.

73% of the total increase in seed size at this stage. Seed size was increased by 9% when temperature was increased from 16 to 32$^0$C during the PB stage. Approximately two-thirds of the total seed size increase was obtained by increasing the temperature from 16 to 24$^0$C. A 10% increase in seed size was also noted in early flowering stage plants exposed to a temperature increase from 16 to 32$^0$C. However, unlike the B and PB plants, increasing the temperature from 16 to 24$^0$C during EF caused a decrease in seed size.

Seed size was quite uniform among floral stages at 16$^0$C, but showed more variability when 24 or 32$^0$C were imposed. B stage plants under the higher temperature treatments tended to produce heavier seed than the more mature plants . EF plants tended to produce heavier seed than PB plants at 16 and 32$^0$C, but not at 24$^0$C.

## Seed Yield

Highly significant differences for seed yield did result from the combined responses of seed set and seed size to temperature treatments at different stages of development (Table 2). The main effects of temperature on seed yield were not independently statistically significant, but showed significant interaction with the stage of floral development when applied (Table 2). Figure 5 illustrates the effects of treatments on seed yield (total weight of all seed produced per plant). Increasing the temperature from 16 to 24 or 32$^0$C during EF did not affect the seed yield. Increasing the temperature from 16 to 32$^0$C caused a 13% decrease in

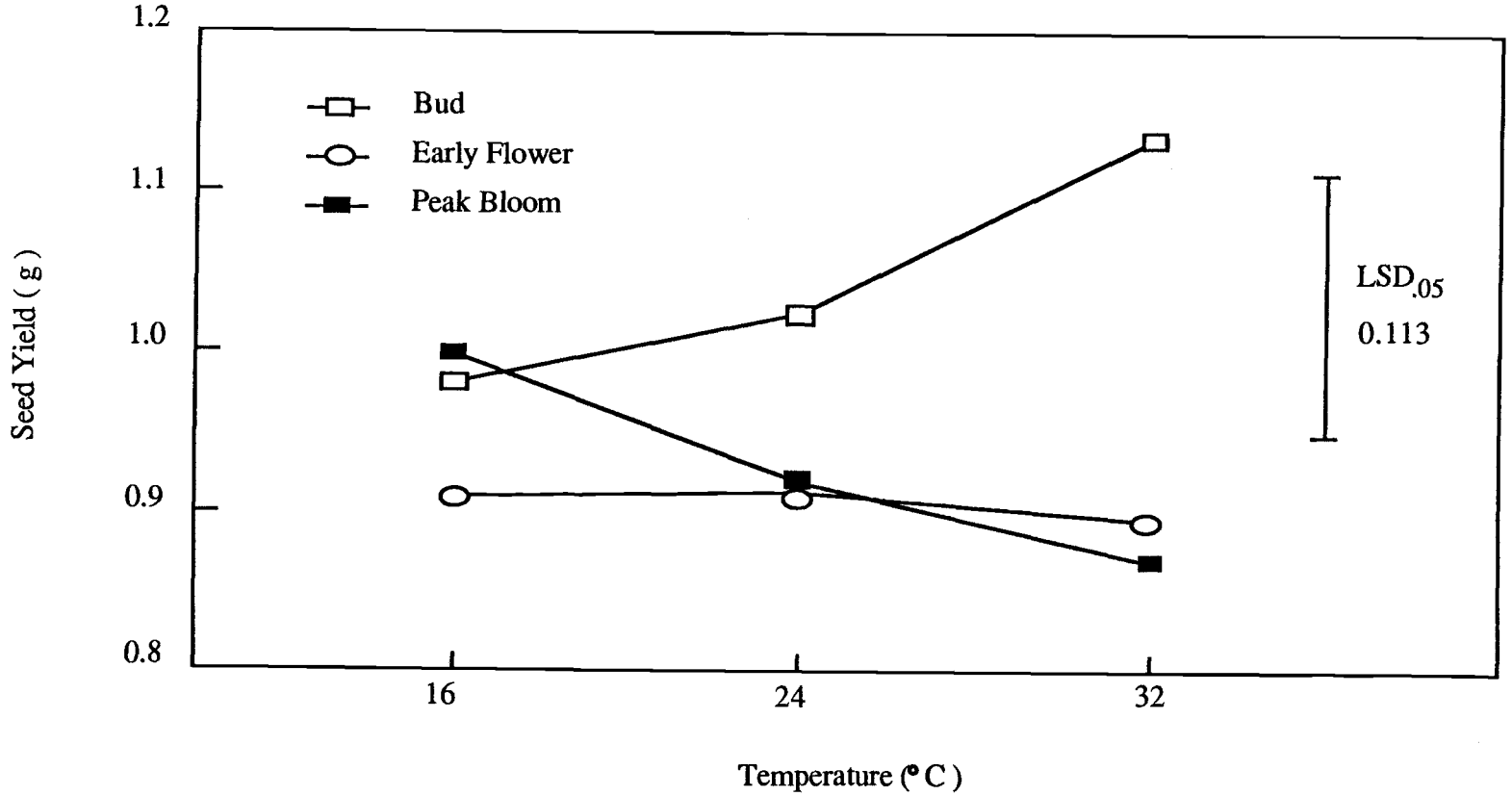


Figure 5. Effects of three temperature treatments at three stages of floral development on yield ( total seed weight per plant ) in meadowfoam. The vertical bar indicates the LSD(0.05) for comparing stages of development within each temperature treatment.

yield when applied at the PB stage, and a 16% increase in yield when applied at the bud stage. Only 28% of the increased seed yield of B stage plants was caused by increasing the temperature from 16 to 24$^{0}$C; increasing the temperature from 24 to 32$^{0}$C was responsible for 72% of the total yield increase. About 60% of the total yield decrease for PB plants occured when temperatures were increased from 16 to 24$^{0}$C, and 40% when temperatures were increased from 24 to 32$^{0}$C. Figures 3 and 4, in combination, illustrate the apparent compensation which occured between seed size and seed number in response to treatments in EF and PB plants at 24 and 32$^{0}$C.

B plants exposed to 32$^{0}$C produced greater seed yield than any of the other eight treatments. EF and PB plants at 32$^{0}$C produced approximately 23% less seed yield than that of the B plants. At 24$^{0}$C, B plants produced 10% greater yield than either EF or PB plants, but this difference was not statistically significant. Seed yields were approximately equal for all floral stages at 16$^{0}$C since the number of seeds produced per flower and the mean seed size were approximately equal among all floral stages at this temperature.

Stage of floral development at the time of temperature increase had a significant effect on seed yield (Table 2). When averaged over the temperature treatments, B stage plants produced 13.5 and 11% greater mean yield than EF and PB stage plants, respectively (Table 2). There was no significant difference, however, between mean yields of EF and PB stage plants. Similarly,

no significant yield differences were seen at different temperatures within each floral stage.

# DISCUSSION

In our study, seed set was similar for all hand-pollinated flowers, regardless of their position on the flowering stems, although the effects of inter-floral competition on seed set have been well documented for other plant species (Stephenson, 1981). The meadowfoam plants in this experiment each produced an average of 65 flowers, and only 30 of the flowers on each plant were hand pollinated . Unpollinated flowers did not produce seed. Pollination of only about half the flowers on each plant may have put such a minimal demand on the plants' photosynthetic capacity that statistically significant evidence of competition among the various floral locations was not discernable. Inter-floral competition could, however, be an important consideration in determining sampling techniques for future studies where insect pollinators may be used. If more than half of the flowers on each plant were fertilized by insects, then positional differences in seed set caused by inter-floral competition may be more apparent due to the increased demand for plant photosynthate.

The results of Experiment II suggested that the gynoecium of meadowfoam flowers apparently does not respond to low light in the same negative way or with the same intensity as does the androecium. Further study will be necessary to quantify the effects of reduced light intensity on pollen production. Although seed set does not appear to be hindered by low light so long as adequate pollen is provided, yield studies using insect pollinators under

limited light conditions should take into consideration the possibility of a lack of available pollen limiting seed set.

Hand pollination of field-grown meadowfoam was successful in causing an increase in seeds produced per flower compared to pollination solely by bees. This indicates that suboptimal bee pollination may be limiting seed production in the field, and that hand pollination can provide a useful tool in studying environmental effects on meadowfoam seed set in conditions where insect pollinators are necessarily excluded. Caution must be excercized in applying seed set results achieved in an artificial environment to predicted performance of meadowfoam plants grown under field conditions. The fact that supplementally hand-pollinated flowers produced an average of only 70% of their maximum genetic potential suggests that there remain unidentified limiting factors in addition to suboptimal pollen vectoring which warrant further study.

Although the yield components of seeds per flower and seed size did not independantly show significant responses to temperature/floral stage treatments, their combined contribution resulted in highly significant treatment differences for seed yield. All floral stages tested at $16^0$C performed similarly, as was expected, since this temperature was nearly the same as the pre- and post-treatment temperature. When averaged across the three floral stages, elevating the temperature to $24^0$C for one week was not enough to cause a significant difference in mean seed yield than from that of $16^0$C. At $32^0$C significant differences in seed yield were noted between the floral stages. This high temperature

increased seed yields when imposed at the bud stage, but did not increase yields when imposed during early flowering or peak bloom. In fact, yield of peak-bloom-stage plants tended to be decreased by the $32^{0}C$ temperature.

The results of this experiment indicate that optimum temperatures for seed yield may vary with the stage of floral development. Optimum temperatures for seed set also appear to differ from those for seed size in some cases. The highest temperature ($32^{0}C$) tested in this study favored increased seed size in all floral stages, but tended to decrease seed set when imposed at early-flowering and peak-bloom-stages. The intermediate temperature ($24^{0}C$) favored an increase in seed size and comparative decrease in seed number when applied at bud or peak-bloom-stages, but had the opposite effect when applied at early flowering. While seed size and seed number appear to respond in a compensating manner, it is unknown as to which may be the cause and which the responding effect. In general, seed yield increased when plants were exposed to higher temperatures at bud-stage, but not during subsequent stages of floral development.

It should be noted that, in this experiment, hand pollination was normally begun on the day following each flower opening, when the stigma appeared receptive. Flowers on the plants at peak-bloom-stage which were exposed to increased temperature may have had reduced seed yield because the majority of their seed was in an early stage of development during the temperature treatment. In particular, the number of seeds produced per flower on the peak-bloom-stage plants tended to decrease with increasing temperature.

Conceivably, increased temperature may have promoted abortion of developing seeds. Studies have not been performed to identify the duration of seed development stages in meadowfoam. In most crops the lag phase (rapid cell division) occurs shortly after fertilization, and is sensitive to adverse temperature (Jones et al., 1984; Wardlaw, 1970). The seeds born on bud stage plants in this experiment were largely formed after the conclusion of the temperature treatment, and therefore could not have been exposed to an unfavorably high temperature during the lag phase. Conversely, exposure to the high temperature prior to pollination may have increased the growth rate of reproductive structures in these bud-plants and thereby increased their sink strength relative to other plant organs. Various plant processes have different sensitivities to environmental factors (Hofstra, 1984), and it is possible that the sink strength of meadowfoam flowers was increased in this trial at the high temperature, without damage to the reproductive structures. This may also have occurred in field grown meadowfoam during years when early warm weather coincided with bud-stage floral development. Further study is needed to determine temperature limits for meadowfoam reproduction, and to identify the characteristics which are most temperature sensitive (eg. seed set, seed cell number or size, oil content, etc.).

# CHAPTER III

## SUMMARY AND CONCLUSIONS

Data from field production of meadowfoam in the Willamette Valley of Oregon indicated that temperature variation during mid-May could account for a significant portion of the variation in annual seed yields. After establishing effective sampling and hand-pollinating techniques, this experiment tested the yield response of meadowfoam to three temperature/floral stage treatment regimes. Confounding influence of variations in pollen vectoring, soil conditions, and other environmental factors which can not be adequately controlled in the field were eliminated by the use of growth chambers and hand-pollination.

Seed set was similar among hand-pollinated flowers of different locations on meadowfoam flowering stems. Caution is warranted, however, when selecting sample flowers on plants which have been insect-pollinated because competition among floral locations may be significant due to the greater percentage of flowers per plant receiving pollen.

Seed set was also similar for flowers with normal and abnormal stamens. So long as an adequate supply of pollen is made available, the gynoecium of flowers with abnormal stamens appear to be able to perform normally.

Supplemental hand-pollination of field grown meadowfoam resulted in greater seed set than did insect-pollination alone.

This indicated that the hand-pollination technique used was effective in causing fertilization, and justified its use in controlled atmosphere conditions where insect-pollinators were not available.

Seed yield was greatest for plants exposed to $32^{0}C$ at the bud stage, while exposure to this high temperature at later stages of development tended to reduce seed yield. Yields of plants exposed to lower temperatures did not significantly differ, regardless of their stage of development at the time of exposure. Yield components of seeds per flower and seed size showed no differences among treatments, but did tend to compensate for one another when temperature was elevated at early flowering and peak bloom stages of floral development.

Temperature during floral development appears to be an important factor in determining meadowfoam seed yield. This information will be valuable in interpreting findings of future field experiments and in understanding year-to-year variations in yield of commercial plantings. Future study of meadowfoam seed yield should include sufficient sample size to alleviate the problem of plant to plant variation masking treatment differences. Knowledge of meadowfoam response to temperature may also be useful in selection criteria for crop improvement and in grower recommendations for production site locations. Cultivars developed to bloom relatively later in the season when temperatures are likely to exceed $16^{0}C$ might potentially have better seed set and more dependably high yields than the currently available commercial varieties. However, yield gains accomplished with later blooming

cultivars could be lost if soil moisture is exhausted before the completion of seed fill, or if harvest is hampered by early rainfall.

# BIBLIOGRAPHY

Arroyo,M.T.K. 1975. Electrophoretic studies of genetic variation in natural populations of allogamous Limnanthes alba and autogamous Limnanthes floccosa (Limnanthaceae). Heredity 35:153-164.

Brevedan,R.E., D.E. Egli, and J.E. Leggett. 1978. Influence of N nutrition on flower and pod abortion and yield of soybean. Agron. J. 70:81-84.

Brown,Charles R., 1976. Fecundity response to stress in three taxa of the genus Limnanthes. p. 82-85. In: Vernal pools: their ecology and conservation. Ed. S.K. Jain, Institute of Ecology, Univ. of California,Davis, No. 9.

Brown,C.R., H. Hauptli, and S.K. Jain. 1979. Variation in Limnanthes alba: A biosystematic survey of germ plasm resources. Econ. Bot. 33:267-274.

Burgett,D.M. 1976. Meadowfoam pollination trials. In: New Crops Research Project Annual Report, Research Period, September 1,1975 to December 31,1976. Crop Science Department, Oregon State University, Corvallis, Ore.

Calhoun,W., and J.M. Crane. 1978. Seed yields of meadowfoam as influenced by N, seeding rates, and soil-water table levels. Agron J. 70:924-926.

Carlson,D.R. and C.B. Williams. 1985. Effect of temperature on the expression of male sterility in partially male-sterile soybean. Crop Sci. 25:646-648.

Chang,W.N. and B.E.Struckmeyer. 1976. Influence of temperature, time of day, and flower age in pollen germination, stigma receptivity, pollen tube growth, and fruit set of Allium cepa L. J. Amer. Soc. Hort. Sci. 101:81-83.

Cochrane,M.P. and C.M. Duffus. 1983. Endosperm cell number in cultivars of barley differing in grain weight. Ann. Appl. Biol. 102:177-181.

Devine,M.B. and J.W. Johnson. 1978. Mode of pollination and reproduction of meadowfoam. Crop Sci. 18:126-128.

Egli,D.B. 1981. Species differences in seed growth characteristsics. Field Crops Research 4:1-12.

Egli,D.B. and I.F.Wardlaw. 1980. Temperature response of seed growth characteristics of soybeans. Agron. J. 72:560-564.

Franz,R.E. 1984. Oregon State University, Corvallis, Ore. Unpublished data.

Gentry,H.S. and R.W. Miller. 1965. The search for new industrial crops IV. Prospectus of Limnanthes. Econ. Bot. 19:25-32.

Gray,D. and J.A. Ward. 1985. Relationships between seed weight and endosperm characteristics in carrot. Ann. Appl. Biol. 106:379-384.

Higgins, J.J., W. Calhoun, B.V.Willingham, D.H. Dinkel, W.L. Raisler, and G.A. White. 1971. Agronomic evaluation of prospective new crop species, II, The American Linmnanthes. Econ. Bot. 25:44-54.

Hofstra,G. 1984. Response of source-sink relationship in soybean to temperature. Can. J. Bot. 62:166-169.

Hoshikawa,K. 1962. Studies on the ripening of wheat grain. 4. Influence of temperature upon the development of the endosperm. Proceedings of the Crop Science Society of Japan 30:228-231.

Huynh,K.L. 1971. The morphological development of the pollen of Linmanthes douglasii (Limnanthaceae). Grana 11:58-61.

Jain,S.K.,R.O. Pierce, and Holly Hauptli. 1977. Meadowfoam: potential new oil crop. In: California Agri. Exp. Stn. Univ. of California, Davis, Cal. 31:18-20.

Johnson,J.W., M.B. Devine, and G.A. White. 1978. Influence of date of harvest on yield and agronomic characteristics of meadowfoam. Agron. J. 70:1103-1104.

Johnson,J.W., M.B. Devine, R. Kleiman, and G.A. White. 1980. Nitrogen fertilization of meadowfoam. Agron. J. 72:917-919.

Johnson,J.W., M.B. Devine, G.A. White, and R. Kleiman. 1980. Yield and agronomic characteristics of meadowfoam with planting dates and rates. Agron. J. 72:617-619.

Jones,R.J., S. Ouattar, and R.K. Crookston. 1984. Thermal environment during endosperm cell division and grain filling in maize: effects on kernel growth and development in vitro. Crop Sci. 24:133-137.

Kinet,J.M., Sachs, R.M. and G. Bernier. 1985. Control by temperature and water stress. p.89-107 In: The physiology of flowering Vol.III. CRC Press, Boca Raton, Fl.

Leopold,A.C. and P.E. Kriedemann. 1975. In: Plant growth and development. McGraw Hill Book Co., Inc. New York.

Mason,C.T.,Jr. 1952. A systematic study of the genus Limnanthes R. Br. p. 455-507. Univ. of California Press, Berkeley and Los Angeles.

McGahuey, M.L. 1986. Nitrogen fertilizer rate and application timing effects on growth and seed-oil yields of meadowfoam. MS thesis, Oregon State University, Corvallis, OR.

Ong, C.K. 1983. Response to temperature in a stand of pearl millet (Pennisetum typhoides S. and H.). J. Exp. Bot. 34:337-348.

Pearson,C.H. 1983. Physiological and yield responses of meadowfoam to water stress and nitrogen fertilization. Ph.D. Thesis. Oregon State University, Corvallis, OR.

Pearson,C.R. and G. Shaw. 1981. Effects of temperature on seed production and seed quality and growth of Paspalum dilitatum. J. App. Ecol. 18:897-905.

Pierce,R.O. and S.K. Jain. 1977. Variation in some plant and seed oil characteristics of meadowfoam. Crop Sci. 17:521-526.

Pyke,G.H. 1981. Effects of inflorescence height and number of flowers per inflorescence on fruit set in Telopea speciosissima. Aust. J. Bot. 29:419-424.

Savithri,K.S., P.S. Ganapathy, and S.K. Sivha. 1980. Sensitivity to low temperature in pollen germination and fruit set in Cicer areitinum L. J. Exper. Bot. 31 (121):475-481.

Sedgley,M. 1977. The Effect of temperature on floral behavior, pollen tube growth and fruit set in the avocado. J. Hort. Sci. 52:135-141.

Stanley,R.G. and H.F. Liskens. 1974. In:Pollen biology biochemistry management. Springer-Verlag Co., Berlin.

Stephenson,A.G. 1981. Flower and fruit abortion: proximate causes and ultimate functions. Annu. Rev. Ecol. Syst. 12: 253-279.

Thompson,M.M. and L.J. Liu. 1973. Temperature, fruit set, and embryo sac development in 'Italian' prune. J. Amer. Soc. Hort. Sci. 98:193-197.

Wardlaw,I.F. 1968. The control and pattern of movement of carbohydrates in plants. Bot. Rev. 34: 79-105.

Wardlaw,I.F. 1970. The early stages of grain development in wheat: response to light and temperature in a single variety. Aust. J. Biol. Sci. 23:765-774.

Wyatt,R. 1980. The reproductive biology of Asclepias tuberosa: I. Flower number, arrangement and fruit set. New Phytol. 85:119-131.

# Appendix

Appendix Table 1. Number of meadowfoam seeds produced per hand-pollinated flower as affected by flower position.

| Flower position | Number of flowers pollinated | Seeds per Flower |
|---|---|---|
| Group 1. All flowers of 4 primary stems per plant: | | |
| Plant 1 | 26 | 3.08 |
| Plant 2 | 24 | 2.83 |
| Mean | 25 | 2.96 |
| Group 2. All flowers of 4 secondary stems per plant: | | |
| Plant 1 | 18 | 2.67 |
| Plant 2 | 20 | 2.30 |
| Mean | 19 | 2.49 |
| Group 3. Individual flowers of separate branches: | | |
| Plant 1 | 28 | 3.71 |
| Plant 2 | 26 | 2.73 |
| Mean | 27 | 3.22 |

Appendix Table 2. Analysis of variance for number of meadowfoam seeds produced per flower as affected by flower position.

| Source | Sum of squares | Degrees of freedom | Mean squares | F-value |
|---|---|---|---|---|
| Total | 1.13 | 5 | | |
| Treatments | 0.55 | 2 | 0.28 | 1.42 |
| Error | 0.58 | 3 | 0.19 | |

LSD = 1.40

*Flower positions: Group 1. All flowers on four primary stems.
Group 2. All flowers on four secondary stems.
Group 3. Individual flowers on separate stems.

Appendix Table 3. Number of meadowfoam seeds produced per hand-pollinated flower on 15 normal flowers and 15 flowers with abnormal* stamens.

| Flower number | Flowers abnormal | Flowers normal |
|---|---|---|
| 1 | 3 | 4 |
| 2 | 5 | 3 |
| 3 | 4 | 4 |
| 4 | 1 | 4 |
| 5 | 4 | 3 |
| 6 | 5 | 5 |
| 7 | 2 | 2 |
| 8 | 3 | 3 |
| 9 | 2 | 3 |
| 10 | 2 | 3 |
| 11 | 1 | 2 |
| 12 | 4 | 4 |
| 13 | 4 | 5 |
| 14 | 2 | 3 |
| 15 | 3 | 2 |
| Total | 46 | 50 |
| Average | 3.0 | 3.33 |

*Filaments very short, anthers darkened and apparently lacking pollen.

Appendix Table 4. Analysis of variance for number of meadowfoam seeds produced per flower on 15 normal flowers and 15 flowers with abnormal* stamens.

| Source | Sum of squares | Degrees of freedom | Mean square | F-value |
|---|---|---|---|---|
| Total | 25.80 | 29 | | |
| Treatments | 0.50 | 1 | 0.50 | 0.55 |
| Error | 25.30 | 28 | 0.90 | |

LSD = 0.71

*Filaments very short, anthers darkened and apparently lacking pollen.

Appendix Table 5. Mean number of meadowfoam seeds produced per flower on 10 field-grown meadowfoam plants with 30 flowers bee-pollinated and 30 flowers supplementally hand-pollinated.

| Plant number | Supplementally hand-pollinated flowers | Bee-pollinated flowers |
|---|---|---|
| 1 | 2.83 | 3.10 |
| 2 | 4.07 | 3.40 |
| 3 | 3.50 | 3.40 |
| 4 | 2.97 | 2.80 |
| 5 | 3.73 | 3.13 |
| 6 | 3.80 | 3.74 |
| 7 | 3.77 | 2.73 |
| 8 | 4.03 | 3.00 |
| 9 | 2.04 | 1.87 |
| 10 | 4.57 | 4.13 |
| Mean seeds per flower | 3.53 | 3.13 |
| Variance | 0.54 | 0.38 |

Calculated T-value at 0.05 level = 2.92
Tabulated T-value at 0.05 level = 2.69

Appendix Table 6. Mean number of meadowfoam seeds produced per flower on 30 flowers of each of 10 plants in 2 replications of 3 temperatures and 3 floral stages.

| | Temperature applied | | | | | |
|---|---|---|---|---|---|---|
| | 16°C | | 24°C | | 32°C | |
| Floral Stage | R I* | R II* | R I | R II | R I | R II |
| Peak bloom | 3.93 | 4.27 | 3.10 | 4.33 | 2.93 | 3.71 |
| | 3.77 | 3.13 | 2.83 | 2.73 | 3.33 | 2.13 |
| | 2.53 | 3.40 | 2.77 | 2.89 | 3.23 | 3.66 |
| | 4.07 | 4.07 | 3.15 | 3.60 | 3.30 | 3.10 |
| | 4.03 | 3.66 | 1.90 | 3.63 | 2.20 | 3.27 |
| | 2.03 | 4.03 | 4.13 | 3.57 | 1.93 | 3.13 |
| | 3.47 | 2.93 | 4.00 | 3.23 | 3.23 | 2.34 |
| | 3.67 | 3.33 | 2.60 | 4.00 | 4.07 | 3.70 |
| | 3.70 | 3.00 | 2.70 | 3.37 | 3.20 | 2.07 |
| | 2.65 | 3.20 | 2.60 | 2.70 | 3.67 | 3.00 |
| Early flower | 3.38 | 3.50 | 3.63 | 3.83 | 3.75 | 2.87 |
| | 4.07 | 4.20 | 2.83 | 3.37 | 3.63 | 3.93 |
| | 3.66 | 2.87 | 3.50 | 3.28 | 2.73 | 2.87 |
| | 2.79 | 3.90 | 2.93 | 3.87 | 2.71 | 3.23 |
| | 3.70 | 3.67 | 4.13 | 4.10 | 3.60 | 2.73 |
| | 2.79 | 2.57 | 3.53 | 3.37 | 3.10 | 3.53 |
| | 3.42 | 2.50 | 2.17 | 3.48 | 3.14 | 1.07 |
| | 3.97 | 3.77 | 3.10 | 3.13 | 3.83 | 1.57 |
| | 2.54 | 3.00 | 2.60 | 4.24 | 3.10 | 3.07 |
| | 1.60 | 2.80 | 1.70 | 3.20 | 3.13 | 2.03 |
| Bud | 3.70 | 2.80 | 1.43 | 3.80 | 3.25 | 3.69 |
| | 3.73 | 3.43 | 3.37 | 3.60 | 3.38 | 4.33 |
| | 4.30 | 3.53 | 4.23 | 3.90 | 4.28 | 3.10 |
| | 3.80 | 3.07 | 3.57 | 3.80 | 3.70 | 4.23 |
| | 4.07 | 3.67 | 3.70 | 4.00 | 4.00 | 4.43 |
| | 1.97 | 3.63 | 3.90 | 2.90 | 4.17 | 3.83 |
| | 2.20 | 4.07 | 2.37 | 3.07 | 3.43 | 3.07 |
| | 1.63 | 3.83 | 3.57 | 4.03 | 2.64 | 3.31 |
| | 3.30 | 3.97 | 2.80 | 3.70 | 1.83 | 3.79 |
| | 3.60 | 4.20 | 1.90 | 3.47 | 2.77 | 3.40 |

*R I and R II refer to replications I and II, respectively.

Appendix Table 7. Mean number of meadowfoam seeds produced per flower, under 3 temperatures and 3 floral stages.

| | | Temperature | | | |
|---|---|---|---|---|---|
| Floral Stage | | $16^0$C | $24^0$C | $32^0$C | Stage means |
| Peak bloom | mean | 3.44 | 3.19 | 3.06 | 3.23 |
| | sd[1] | 0.596 | 0.628 | 0.617 | |
| Early flowering | mean | 3.23 | 3.30 | 2.98 | 3.17 |
| | sd | 0.670 | 0.642 | 0.734 | |
| Bud | mean | 3.41 | 3.36 | 3.53 | 3.37 |
| | sd | 0.739 | 0.741 | 0.656 | |
| | Temp means | 3.36 | 3.28 | 3.19 | 3.29 |

[1] standard deviation
means calculated from two replications of 30 hand-pollinated flowers on each of 10 plants per treatment

Appendix Table 8. Meadowfoam seed weight (milligrams) produced per plant by 30 flowers on each of 10 plants in 2 replications of 3 temperatures and 3 floral stages.

| | Temperature applied | | | | | |
|---|---|---|---|---|---|---|
| | 16°C | | 24°C | | 32°C | |
| Floral Stage | R I* | R II* | R I | R II | R I | R II |
| Peak bloom | 10.29 | 7.13 | 9.81 | 8.99 | 8.92 | 7.19 |
| | 7.46 | 11.72 | 10.70 | 12.41 | 8.52 | 12.12 |
| | 11.32 | 10.74 | 7.52 | 9.71 | 10.15 | 10.32 |
| | 8.72 | 10.10 | 10.92 | 9.74 | 9.52 | 10.71 |
| | 10.29 | 9.45 | 9.40 | 8.57 | 13.92 | 8.76 |
| | 12.59 | 8.76 | 8.03 | 8.35 | 10.38 | 9.47 |
| | 9.89 | 12.90 | 9.43 | 10.34 | 9.38 | 9.83 |
| | 9.95 | 10.94 | 10.35 | 9.29 | 8.43 | 15.45 |
| | 6.95 | 11.30 | 13.05 | 9.94 | 11.09 | 11.18 |
| | 8.30 | 6.94 | 11.14 | 9.25 | 8.42 | 9.62 |
| Early flower | 10.38 | 10.73 | 8.11 | 10.86 | 9.28 | 10.08 |
| | 11.35 | 11.98 | 8.41 | 9.59 | 9.91 | 11.58 |
| | 8.37 | 10.85 | 8.51 | 9.57 | 9.42 | 11.28 |
| | 9.26 | 9.70 | 9.25 | 9.05 | 9.39 | 10.00 |
| | 6.99 | 8.48 | 7.90 | 9.71 | 8.38 | 12.77 |
| | 8.65 | 8.69 | 8.76 | 9.80 | 10.06 | 8.44 |
| | 7.76 | 11.20 | 10.00 | 8.13 | 8.92 | 17.78 |
| | 7.18 | 9.16 | 9.16 | 8.86 | 9.15 | 12.00 |
| | 9.28 | 7.54 | 9.01 | 9.50 | 11.06 | 9.66 |
| | 13.50 | 9.29 | 10.04 | 9.87 | 8.29 | 12.97 |
| Bud | 9.72 | 10.31 | 14.52 | 12.39 | 11.22 | 12.16 |
| | 11.34 | 12.13 | 9.59 | 9.58 | 12.20 | 11.52 |
| | 6.99 | 7.21 | 9.96 | 9.35 | 8.84 | 10.93 |
| | 10.88 | 10.05 | 10.41 | 10.25 | 10.30 | 10.13 |
| | 9.48 | 9.54 | 9.15 | 9.92 | 11.47 | 8.74 |
| | 7.21 | 10.13 | 10.32 | 11.49 | 14.12 | 10.39 |
| | 11.02 | 8.77 | 10.18 | 8.53 | 10.90 | 10.12 |
| | 12.16 | 7.76 | 13.23 | 9.13 | 14.12 | 12.58 |
| | 10.71 | 7.58 | 10.93 | 8.22 | 12.84 | 11.60 |
| | 11.86 | 8.57 | 15.98 | 9.06 | 10.11 | 8.57 |

*R I and R II refer to replications I and II.

Appendix Table 9. Mean weight (milligrams) per meadowfoam seed produced per plant under 3 temperatures and 3 floral stages.

| Floral Stage | | Temperature | | | Stage means |
|---|---|---|---|---|---|
| | | $16^0C$ | $24^0C$ | $320_C$ | |
| | | mg | | | |
| Peak bloom | mean | 9.30 | 9.85 | 10.18 | 10.41 |
| | sd[1] | 0.003 | 0.002 | 0.002 | |
| Early flowering | mean | 9.52 | 9.21 | 10.53 | 9.75 |
| | sd | 0.002 | 0.001 | 0.002 | |
| Bud | mean | 9.68 | 0.61 | 10.96 | 9.78 |
| | sd | 0.002 | 0.002 | 0.002 | |
| | temp means | 9.50 | 9.89 | 10.55 | 9.98 |

[1] standard deviation
means calculated from two replications of 30 hand-pollinated flowers on each of ten plants per treatment

Appendix Table 10. Meadowfoam seed yield (total seed weight produced per plant in grams) produced by 30 flowers on each of 10 plants in 2 replications of 3 temperatures and 3 floral stages.

| | Temperature applied | | | | | |
|---|---|---|---|---|---|---|
| | 16°C | | 24°C | | 32°C | |
| Floral Stage | R I* | R II* | R I | R II | R I | R II |
| Peak bloom | 1.173 | 0.912 | 0.893 | 1.052 | 0.785 | 0.748 |
| | 0.843 | 0.912 | 0.899 | 1.018 | 0.852 | 0.776 |
| | 0.862 | 1.095 | 0.624 | 0.796 | 0.985 | 1.094 |
| | 1.064 | 1.232 | 1.037 | 1.052 | 0.942 | 0.996 |
| | 1.245 | 1.002 | 0.536 | 0.934 | 0.919 | 0.946 |
| | 0.768 | 1.095 | 0.996 | 0.894 | 0.602 | 0.653 |
| | 1.029 | 1.135 | 1.131 | 1.003 | 0.910 | 0.668 |
| | 1.094 | 1.094 | 0.807 | 1.040 | 1.028 | 0.958 |
| | 0.771 | 1.017 | 1.057 | 1.004 | 1.065 | 0.693 |
| | 0.664 | 0.770 | 0.869 | 0.749 | 0.926 | 0.837 |
| Early flower | 1.048 | 1.127 | 0.884 | 1.249 | 0.871 | 0.867 |
| | 1.339 | 1.509 | 0.715 | 0.969 | 1.012 | 0.367 |
| | 0.887 | 0.933 | 0.894 | 0.909 | 0.813 | 0.970 |
| | 0.750 | 1.135 | 0.814 | 1.050 | 1.017 | 0.970 |
| | 0.902 | 0.669 | 0.980 | 1.194 | 0.714 | 1.047 |
| | 0.675 | 0.933 | 0.929 | 0.990 | 0.779 | 0.895 |
| | 0.792 | 0.840 | 0.650 | 0.984 | 0.916 | 0.569 |
| | 0.854 | 1.035 | 0.852 | 0.833 | 1.026 | 0.564 |
| | 0.659 | 0.679 | 0.703 | 1.168 | 0.851 | 0.889 |
| | 0.648 | 0.780 | 0.512 | 0.948 | 0.929 | 0.791 |
| Bud | 1.079 | 0.876 | 0.610 | 1.412 | 1.100 | 1.301 |
| | 1.157 | 1.249 | 0.969 | 1.035 | 1.196 | 1.498 |
| | 1.145 | 0.764 | 1.265 | 1.094 | 1.096 | 1.017 |
| | 0.902 | 0.925 | 1.114 | 1.168 | 1.143 | 1.287 |
| | 1.240 | 1.050 | 1.016 | 1.191 | 1.330 | 1.163 |
| | 1.204 | 1.104 | 1.207 | 1.000 | 1.304 | 1.195 |
| | 1.157 | 1.070 | 0.723 | 0.785 | 1.123 | 0.931 |
| | 0.476 | 0.893 | 1.111 | 1.105 | 1.087 | 1.208 |
| | 0.783 | 0.902 | 0.911 | 0.913 | 0.706 | 1.276 |
| | 0.540 | 1.080 | 0.918 | 0.942 | 0.839 | 0.874 |

*R I and R II refer to replications I and II, respectively.

Appendix Table 11. Meadowfoam seed yield (total seed weight per plant in grams) under 3 temperatures and 3 floral stages.

| Floral Stage | | Temperature $16^0C$ | $24^0C$ | $32^0C$ | Stage Means |
|---|---|---|---|---|---|
| | | | g | | |
| Peak bloom | mean | 0.998 | 0.920 | 0.869 | 0.929 |
| | sd[1] | 0.168 | 0.154 | 0.143 | |
| Early flowering | mean | 0.910 | 0.911 | 0.893 | 0.905 |
| | sd | 0.234 | 0.182 | 0.176 | |
| Bud | mean | 0.980 | 1.024 | 1.134 | 1.046 |
| | sd | 0.217 | 0.190 | 0.190 | |
| | temp means | 0.963 | 0.952 | 0.965 | 0.960 |

[1] standard deviation
means calculated from two replications of 30 hand-pollinated flowers on each of ten plants per treatment

Appendix Table 12. Analysis of variance on the effects of 3 temperatures imposed during 3 floral stages on seed yield of meadowfoam.

| Source | df[1] | Seeds per flower | Seed wt. | Yield[+] |
|---|---|---|---|---|
| | | | mg | g |
| Replication | 1 | 2.04 | $0.77 \times 10^{-8}$ | 0.220 |
| Temp | 2 | 0.48 | $0.17 \times 10^{-4}$ | 0.003 |
| Error A | 2 | 1.43 | $0.70 \times 10^{-5}$ | 0.057 |
| Floral stage | 2 | 1.09 | $0.85 \times 10^{-5}$ | 0.343** |
| Temp x stage | 4 | 0.56 | $0.26 \times 10^{-5}$ | 0.105* |
| Error B | 168 | 0.43 | $0.33 \times 10^{-5}$ | 0.033 |

*,** Significant at the 0.05 Or 0.01 probability levels, respectively.

[1]df = degrees of freedom.

[+]Total weight of all seed produced per plant

LSD for yield = 0.11 grams.

Appendix Table 13. Coefficients of determination derived from linear regressions of climatic data against yield of meadowfoam seed from 1975 to 1983.

| Period | Climatic feature | $r^2$ value |
|---|---|---|
| May (entire month) | total precipitation | (-)0.36 |
| | # of days of measureable rain | (-)0.13 |
| | average minimum temperature | (+)0.04 |
| | # of days of minimum temp below 6.5°C | (-)0.00 |
| | # of days of minimum temp below 0°C | (-)0.00 |
| | average maximum temp | (+)0.51 |
| | # of days of maximum temp below 16°C | (-)0.50 |
| | # of days of maximum temp below 20°C | (-)0.34 |
| June (entire month) | total precipitation | (-)0.14 |
| | average minimum temp | (+)0.08 |
| | average maximum temp | (+)0.09 |
| May 1-9 | highest temp | (+)0.00 |
| | # of days of maximum temp above 20°C | (+)0.00 |
| May 10-17 | highest temp | (+)0.39 |
| | lowest temp | (+)0.00 |
| | # of days of maximum temp above 18°C | (+)0.12 |
| | # of days of maximum temp above 20°C | (+)0.28 |
| | # of days of maximum temp above 24°C | (+)0.55* |
| | # of days of maximum temp above 28°C | (+)0.32 |
| May 18-25 | highest temp | (+)0.02 |
| | lowest temp | (+)0.00 |
| | # of days of maximum temp above 18°C | (+)0.17 |
| | # of days of maximum temp above 20°C | (+)0.02 |
| | # of days of maximum temp above 24°C | (+)0.06 |
| | # of days of maximum temp above 28°C | (+)0.16 |
| May 15-31 | total precipitation | (-)0.35 |
| | precipitation during bee foraging | (-)0.20 |
| | average minimum temp | (+)0.06 |
| | average maximum temp | (+)0.25 |

(+),(-) indicate positive and negative correlation with meadowfoam seed yield, respectively
* siginficant at the .05 probability level

Appendix Table 14. Schedule of meadowfoam seeding, transplanting and growth chamber use for 3 temperature and 3 floral stage treatments.

| | Replication I | | | Replication II | | |
|---|---|---|---|---|---|---|
| | PB* | EF** | B*** | PB | EF | B |
| seed (45/date) | 12/19 | 12/26 | 01/02 | 02/28 | 03/06 | 03/13 |
| move to vegetative chamber (Hyslop) | 12/26 | 01/02 | 01/09 | 03/06 | 03/13 | 03/20 |
| transplant to fiber pots | 01/09 | 01/16 | 01/23 | 03/20 | 03/27 | 04/03 |
| move to floral induction chamber (PGV-36) | 01/30 | 02/06 | 02/13 | 04/10 | 04/17 | 04/24 |
| begin temp. regimes with 10 plants per treatment in chambers C-1,C-2 and PGV-36 | 03/21 | 03/21 | 03/21 | 06/01 | 06/01 | 06/01 |
| end temp treatments return all plants to PGV-36 | 03/28 | 03/28 | 03/28 | 06/08 | 06/08 | 06/08 |
| move to greenhouse | 04/03 | 04/10 | 04/17 | 06/17 | 06/24 | 07/01 |
| collect seed/flower data | 05/03 | 05/10 | 05/17 | 07/15 | 07/22 | 07/29 |
| collect seed weight data | 07/03 | 07/10 | 07/17 | 09/09 | 09/16 | 09/23 |

*PB - peak bloom
**EF - early flowering
***B - bud

Hoagland's Nutrient Solution, modified from Plants in Action: A Laboratory Manual of Plant Physiology by Leonard Machlos and John G. Torrey. W. H. Freeman and Co. 1956.

| Stock solution | Amount per 2 liters final solution |
|---|---|
| 1) 1 M $Ca(NO_3)_2$ | 10 ml |
| 2) 1 M $KNO_3$ | 10 ml |
| 3) 1 M $MgSO_4$ | 4 ml |
| 4) 1 M $KH_2PO_4$ | 2 ml |

5) Fe EDTA*: (5 mg Fe/ml stock)

6) Micronutrients:

1 liter stock contains:

2.86 g $H_3BO_3$

1.81 g $MnCl_2 \cdot 2H_2O$

0.11 g $ZnCl_2$

0.05 g $KCuCl_2 \cdot 2H_2O$

0.025 NaMoO $\cdot 2H_2O$