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Pollination and Seed Set in Meadowfoam

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Meadowfoam (*Limnanthes alba* Hartw. ex Benth. ssp. *alba*, Limnanthaceae) is an oilseed crop that requires insect (primarily honey bee) pollination to set seed. Effective honey bee colony management will increase meadowfoam yields, which will improve the economic competitiveness of this valuable resource for Oregon.

The purposes of this publication are to:

- Review the flowering characteristics and seed-set requirements of meadowfoam
- Offer suggestions for effectively managing honey bee colonies for improved meadowfoam pollination and subsequent yield

The first recorded farm-scale planting of meadowfoam (cultivar ‘Foamore’) in Oregon took place in 1975 to 1976. The Oregon Agricultural Experiment Station released a second cultivar, ‘Mermaid’, exclusively to the Oregon Meadowfoam Growers Association in 1984. Since then, a number of cultivars have been released, including ‘Floral’ (1993), ‘Knowles’ (1998), ‘Wheeler’ (2000), ‘Ross’ (2003), ‘Starlight’ (2004), ‘GA-2’ (2013), and ‘Crane’ (2014).

All of the released cultivars are open-pollinated and require bee pollination to set seed. Commercial seed yields average about 1,000 pounds per acre in the Willamette Valley of Oregon, with a record yield of more than 1,700 pounds per acre. In research plots, yields of 2,000 pounds per acre are not uncommon, but vary greatly from year to year.

With occasional exceptions, each meadowfoam flower has the potential to produce a maximum of five seeds. Greenhouse pollination studies using hand pollination have repeatedly produced greater than four seeds per flower, but honey bee-pollinated field populations typically average a little over three seeds per flower.

The seed-set disparity observed between greenhouse and field pollination, as well as yearly yield fluctuations in field research plots, have aroused speculation that inadequate pollination may be limiting seed set. Effective bee management is essential to maximize pollination and seed set.

Flowering characteristics

Meadowfoam is a short, fleshy-stemmed plant that produces 1 to 12 flowers per stem and 1 to 10 stems per plant under solid stand field production. Some of the stems may be branched. During peak bloom, it is common for 4 to 6 million new flowers per acre to open each day.

Before flowering, clusters of buds appear at the top of each stem. The flowers on each stem develop in a sequential order from bottom to top. Each flower is attached to the stem by a peduncle (Figure 1). Stems and peduncles elongate before the flowers open.

Each flower has 10 stamens, and each stamen contains a pollen-producing anther, the male reproductive structure (Figure 1). Five small nectaries are located at the base of the stamens, directly above the sepals. The 10 stamens surround the female reproductive structure (pistil). The pistil is made up of five stigmas (female receptors of pollen), a common style, and five ovaries, each of which contains one ovule (Figure 1). The five ovaries are located at the base of the style. Each ovary has the potential to produce one seed, technically known as a nutlet. Before initial flower opening, five petals and five sepals cover the stamen and pistil.

Once flower opening commences, flower sepals and petals open during the day, exposing the stamens and pistil to potential bee pollinators, and close at night. Bee visitation is required to start the nightly petal- and sepal-closing mechanism. Flowers on caged plants in the field that lack pollinator exposure do not close at night.

Flowers continue to open and close until successful pollination and fertilization occur, and then the petals and sepals permanently close around the reproductive

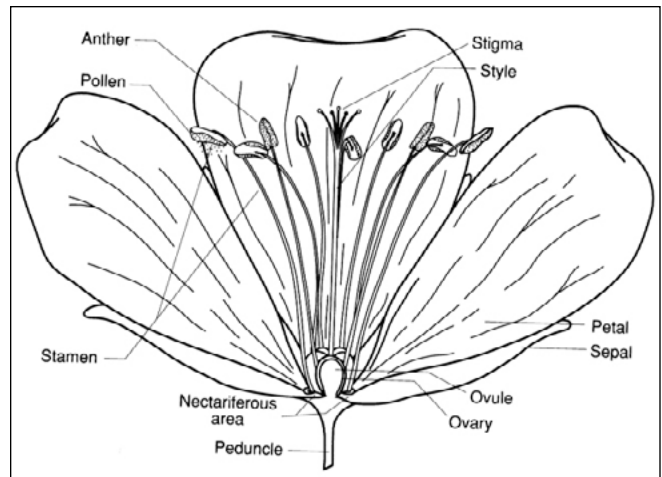


Figure 1. Longitudinal section of a 'Mermaid' meadowfoam flower with one stamen and two petals removed (x7).

structures. In some cultivars there is a tendency for petals to turn slightly pink in color after fertilization has occurred.

Meadowfoam pollen is heavy and sticky enough to inhibit wind pollination, and thus requires insects (primarily honey bees) for pollen transport. Within each flower, pollen is shed before the stigmas are receptive (Figures 2a and 2b). This asynchronous development of male pollen before the female stigma becomes receptive is called protandry, and it can be a period of several hours to 4 days, depending on temperature. The female style elongates as it matures and generally rises above the stamens before the stigmas expand and become receptive (Figure 2c).

Pollen produced within any given flower is capable of setting seed within the same flower. However, in the field, pollen for fertilization usually comes from another

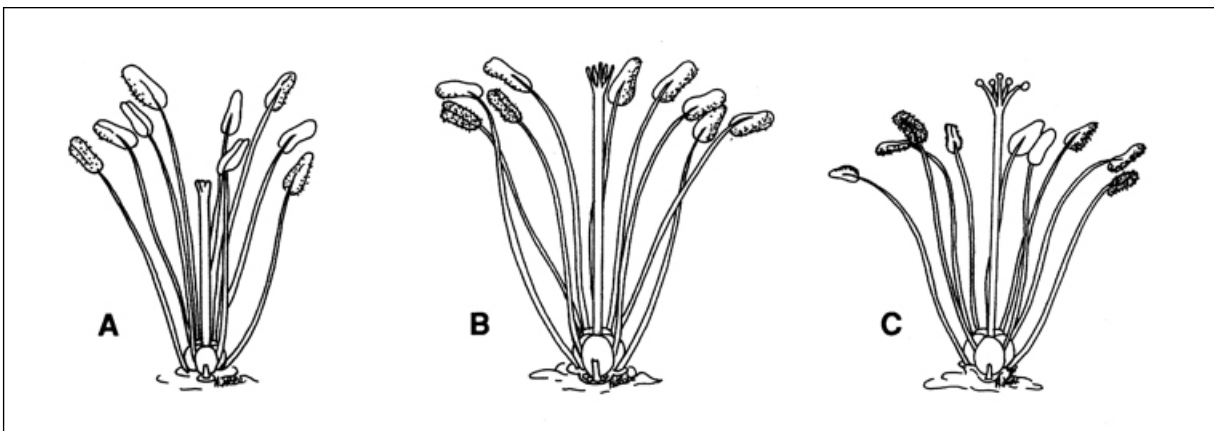


Figure 2. Sequential reproductive development of a 'Mermaid' meadowfoam flower: A) Flower opening with initial pollen availability (dehiscence) and unreceptive stigmas; B) Maximum pollen shed with unreceptive stigmas; C) Maximum stigmal receptivity with reduced pollen availability.

flower, either on the same or a different plant. Factors that promote cross-pollination include:

- Pollen is shed and may lose viability before the stigmas are receptive (protandry).
- Bees and other insects forage for the pollen before the stigmas are receptive.
- Remaining pollen adheres to stamens located below the receptive stigmas.

Plant breeders have made some efforts to develop cultivars of meadowfoam that are self-pollinating (autogamous), through wide crosses with *L. floccosa* ssp. *grandiflora* and *L. alba* ssp. *versicolor*. No cultivars have yet been released, and it is not clear whether the benefits of autogamous cultivars will compensate for potential reductions in yield potential due to inbreeding depression in *L. alba*.

Pollination

The pollination period for meadowfoam ranges from 2 to 4 weeks during May and early June, depending on the weather (Figure 3). Individual flowers open for 1 to 4 days, depending on the temperature. Pollination occurs when insects inadvertently transfer pollen from the anthers of one or more flowers onto the stigma or stigmas of a receptive flower.

One study revealed that 1, 6, and 11 honey bee visits to receptive flowers produced an average of 1.6, 2.3, and 3.3 seeds per flower, respectively. Six million flowers per acre multiplied by six visits per flower equals an average demand of 36 million pollination visits per acre during



Figure 4. Honey bee collecting pollen from a meadowfoam flower

an average day at peak bloom. Thus, the demand for honey bees is important and warrants close attention.

Pollen germination on a stigma is followed by pollen tube growth down the style into the ovule, where the union of sperm and egg cell results in the embryo formation and potential seed production.

When pollen is abundant, either honey bee pollen foragers or honey bee nectar foragers can successfully accomplish pollination. The daily foraging periods of the pollen- and nectar-collecting honey bees overlap in the afternoon. Pollen-collecting honey bees (Figure 4) are most prevalent from about 11 a.m. to 2 p.m., when the majority of available pollen is collected. Nectar-collecting honey bees forage primarily between 2 p.m. and 7 p.m.

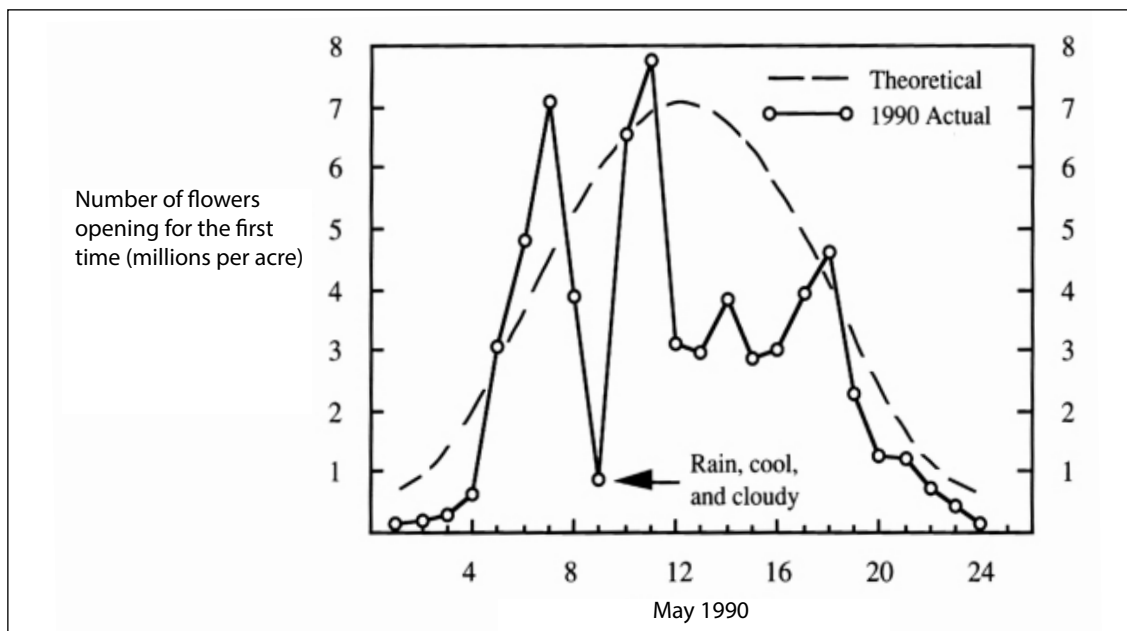


Figure 3. 'Mermaid' flower opening patterns



Figure 5: Blue orchard bee nesting blocks erected in a meadowfoam field



Figure 6: Blue orchard bee foraging on a meadowfoam flower

Osmia lignaria propinqua Cresson (Figures 5, 6, and 7), a blue orchard bee, has also been shown to be a good alternative pollinator for meadowfoam (see Jahns and Jolliff in “References,” page 7). Other insect pollinators such as halictid bees and hover flies can also contribute to meadowfoam pollination.

Factors affecting pollination and seed set

Plant

Genetic variability. Meadowfoam cultivars are genetically variable, resulting in a range of individual plant yield responses within a solid stand.

Flower position and timing. Flowering starts at the bottom of each stem and proceeds to the top. The peduncle elongates 1 to 10 inches, pushing the flower bud to the surface of the crop canopy. The flower then opens and is exposed for pollinator visitation. Younger flowers rise above older flowers as the flowering stems and the individual peduncles elongate.

Consequently, throughout the bloom period, the older flowers become covered in the canopy of younger flowers. These older flowers are less accessible to honey bees than the flowers at the top of the canopy. The rate of flower elongation depends on temperature, making it as unpredictable as the weather.

Thus, it is important to have enough honey bees available at the appropriate time to achieve the desired pollination before large numbers of older flowers are “buried” in the canopy. The first two-thirds of the flowers to open on a stem produce more seeds per



Figure 7: Blue orchard bee nesting block

flower than the last one-third of the flowers on top of the stem.

Embryo abortion. Embryo abortion has been observed in individual meadowfoam plants. The risk of reduced seed development, by as much as one seed per flower over an entire plant, increases with temperatures above 80°F.

Stigmatal receptivity. The stigmas of individual meadowfoam flowers become receptive to deposited pollen at specific times. Pollen deposition before or after prime stigmatal receptivity (Figures 2a and 2b, page 3) is less likely to maximize seeds per flower than at greatest stigmatal receptivity (Figure 2c, page 3).

The greater the number of pollinator visitations per flower during the stigmatal receptivity period, the greater the likelihood that pollen will be deposited at or near peak stigmatal receptivity, which maximizes seed set.

Pollen deposition. The deposition of about 25 viable pollen grains to any or all of the five stigmas per flower is required to maximize seed set in meadowfoam flowers grown in the greenhouse.

A 2-year field study showed that one honey bee visitation per flower deposited between 15 and 22 pollen grains per stigma, but six honey bee visitations deposited between 43 and 47 grains per stigma.

Though the rate of pollen deposition to maximize seed set in the field has not been determined, multiple honey bee visits per flower increase the likelihood of adequate pollen deposition for maximum seed set.

Honey bee

Nutritional requirements. Honey bees require both nectar and pollen to maintain and expand their colonies. The low nectar availability found in meadowfoam flowers inhibits honey production, which limits colony growth and maintenance. Pollen coming from meadowfoam flowers, however, does not appear limiting for bee colony growth.

Canopy penetration. Meadowfoam plants in a solid stand grow together, entwining the stems and flowers of adjacent plants. Production practices such as seeding rate, row spacing, and nitrogen fertilization influence the distribution of flower opening over time and flower location in the canopy.

The majority of foraging bees do not actively seek out flowers in the depths of the canopy because the entwined plants restrict their movement. Increasing the number of foraging honey bees might increase pollination and seed set of these secondary flowers.



Figure 8. Top view of a standard Langstroth hive with 10 frames and bees. There are approximately 24,000 bees in this hive.

Weather

Temperature. Temperature strongly affects honey bee activity, and the day and hour when the plants need to be pollinated. Temperatures below 55°F will hinder flower opening as well as honey bee flight.

In western Oregon, rainfall, low temperature, and low solar radiation typically occur simultaneously. All of these factors contribute to a reduction in the rate of flower opening (Figure 3, page 3). On a single warm day, following a period of unfavorable weather that has inhibited flowering, as many as 8 to 10 million flowers per acre may open. This could result in an enormous pollination requirement when these flowers become receptive to pollen.

As temperature rises, there is a tremendous demand for pollen deposition onto the receptive stigma(s) of individual flowers. The prime stigmatal receptivity period may be as long as 24 hours when temperatures are below 70°F and as short as 1 hour when temperatures are above 90°F.

Wind. At wind speeds greater than 15 to 20 miles per hour, honey bee flight and meadowfoam pollination are restricted to areas adjacent to hives.

Managing honey bees

Colony strength and grade

In 1960 and 1978, Oregon and Washington departments of agriculture mandated colony-strength regulations for hives employed in commercial pollination of agricultural crops. The regulations were designed to assure growers that the colonies that they rent meet minimum biological standards. Currently, these regulations are not being enforced, but the standards set forth can still serve as minimum colony-strength requirements and help identify the quality of the colony being rented for pollination. Consider these regulations as recommendations and use them to define colonies in pollination contracts.

Based on the above-mentioned Oregon regulations, a Grade A field colony must have approximately 24,000 adult bees (10 standard Langstroth combs completely covered with bees, as shown in Figure 8 and Figure 9, page 6). Grade A field colonies also should have about 1,000 square inches of comb occupied by brood. One standard Langstroth comb, if fully occupied, has 270 square inches of brood. For more information on colony strength and grade, refer to



Figure 9: A standard deep Langstroth comb with adult bees. This comb side would be rated 100 percent covered with adult bees. There are approximately 1,200 worker bees in this photograph.

Evaluating Honey Bee Colonies for Pollination: A Guide for Growers and Beekeepers (see "Resources," page 7).

Colony Food Reserves

Honey bee colonies rented for pollination should have optimal food resources. Honey is the energy source for bee flight. Without adequate honey reserves stored in the hive, starvation may cause pollination deficiencies and eventual colony loss. A colony unable to forage for 2 or 3 days during poor weather can easily consume about 10 pounds of honey. Each colony should have a minimum of at least 40 pounds of honey reserves for colony maintenance and efficient pollination during meadowfoam pollination.

Pollination recommendations

Colony numbers

Three honey bee hives per acre are recommended to ensure adequate pollination. During long bloom periods with prevalent cool, wet conditions, more than three hives per acre may be required to fulfill peak pollination demands.

Spacing colonies

Proper hive placement (Figure 10) has been shown to increase yields in some crops. During unfavorable foraging periods, bees tend to work areas close to the hive. Hence, appropriate distribution of hives around the fields will result in efficient pollination during unfavorable weather. On meadowfoam fields greater than 10 acres, a minimum colony spacing of 32 hives every 10 acres should provide efficient pollination based on the average of 3 hives per acre for many seed and berry crops (see Delaplane and Mayer in "References," page 7).

Timing

Move hives into meadowfoam fields when 5 to 10 percent of the flowers are in bloom. The introduction of hives at 10 percent bloom will help to discourage colonies from initially foraging on competing plants. However, if the introduction of hives is delayed past 10 percent bloom, severe yield reductions may result.

In 1987, caged field studies revealed that 2 days after 10 percent bloom was established, peak bloom occurred. A 1-week delay in honey bee colony introduction would have left 83 percent of the available flowers opened from 1 to 7 days without pollination. Because of the way female stigmas age, 50 percent of the previously unpollinated flowers may not have been able to set seed, a situation that dramatically reduces seed yield.

Honey bee hives can be removed from the field when less than 5 percent of the bloom remains.



Figure 10. Honey bee colonies placed in a meadowfoam field

Competing bloom

If possible, avoid planting meadowfoam within 2 miles of commercial acreages of competing bee-attractive crops, such as crimson clover or a late-blooming rapeseed variety. Superior nectar resources of these crops may attract honey bees away from meadowfoam and significantly reduce pollination.

Weeds commonly in bloom during meadowfoam flowering include the mustards and wild radish. A small percentage of bees may visit these blooming weeds, but this should not concern meadowfoam growers as these weeds provide nutritional diversity for bees that in turn enhances colony health.

Resources

OSU Extension publications

Oregon State University Extension Service publications available online at <https://catalog.extension.oregonstate.edu/>

Evaluating Honey Bee Colonies for Pollination: A Guide for Growers and Beekeepers (PNW 623) <https://catalog.extension.oregonstate.edu/pnw623>

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Delaplane, K.S., and Mayer, D.F. 2000 "Crop pollination by bees." CABI Publishing, New York, NY

Jahns, T.R., and Jolliff, G.D. 1990 "Survival rate and reproductive success of *Osmia lignaria propinqua* Cresson (Hymenoptera: Megachilidae) in caged meadowfoam, *Limnanthes alba* Benth. (Limnanthaceae)." *Journal of the Kansas Entomological Society* 64: 95-106.

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