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Breeding Advances and Germplasm Resources in Meadowfoam: A Novel Very Long Chain Oilseed

Steven J. Knapp and Jimmie M. Crane*

Meadowfoam (*Limnanthes alba* Benth., Limnanthaceae) produces a very-long chain seed oil with novel physical and chemical characteristics (Earle et al. 1959; Smith et al. 1960; Bagby et al. 1961; Miller et al. 1964; Isbell 1997). These characteristics have propelled the development of meadowfoam as a specialty oilseed crop and the development of industrial markets for meadowfoam oil and oil derivatives.

Meadowfoam has been produced on a limited scale for more than 20 years in Oregon (Fig. 1). Markets for the oil began emerging in 1992. Production has steadily increased with progress in marketing the oil and the development and marketing of a variety of specialty chemicals from meadowfoam fatty acids and triglycerides (Isbell 1997). Oregon growers have ensured a supply of oil for the meadowfoam industry.

Meadowfoam has an important role as a rotation crop in the Willamette Valley of Oregon and is primarily grown by grass seed producers. The rotational fit of meadowfoam is excellent, particularly for growers with weed or other pest problems in grass seed production fields. Weed control and other crop rotation benefits have stimulated production in Oregon. Although miniscule on a global scale, meadowfoam has had a significant economic impact in Oregon (seed production), California (seed and oil processing), and Illinois (marketing and product development). The number of hectares of meadowfoam produced outside Oregon is not publicly recorded. Meadowfoam has been produced on a pilot scale in New Zealand and Virginia (US) and field tests have been carried out in the United Kingdom, the Netherlands, France, and elsewhere.

The development of the meadowfoam industry has been impeded by low and erratic seed yields. Although meadowfoam production has steadily increased since 1993 (Fig. 1), meadowfoam seed yields have not increased and are not much greater today than they were 10 to 15 years ago in Oregon. Significant seed yield increases are needed to solidify and sustain the growth of the meadowfoam industry.

The goal of our research has been to increase the productivity of meadowfoam by developing superior cultivars, discovering and developing novel phenotypes, and advancing our understanding of the genetics of economically important traits. Our breeding work has concentrated on increasing seed yield, seed oil concentration, lodging resistance, and *Scaptomyza* resistance, developing self-pollinated lines and cultivars, and developing novel oils. We review recent progress in meadowfoam breeding, describe meadowfoam germplasm resources, and review breeding and genetics research needs for meadowfoam.

EARLY GERMPLASM SCREENING AND SPECIES SELECTION

The development of meadowfoam as a crop began with the discovery of the novel fatty acid profile of the seed oil (Earle et al. 1959; Smith et al. 1960). The oil has four key characteristics that have stimulated the development of the meadowfoam industry. The oil has (1) very high concentrations of very-long-chain (C_{20} and C_{22}) fatty acids (~980 g/kg), (2) very low concentrations of saturated fatty acids (~10 g/kg), (3) very high concentrations of $\Delta 5$ double bonds (~840 g/kg), and (4) excellent oxidative stability (Earle et al. 1959; Smith et al. 1960;

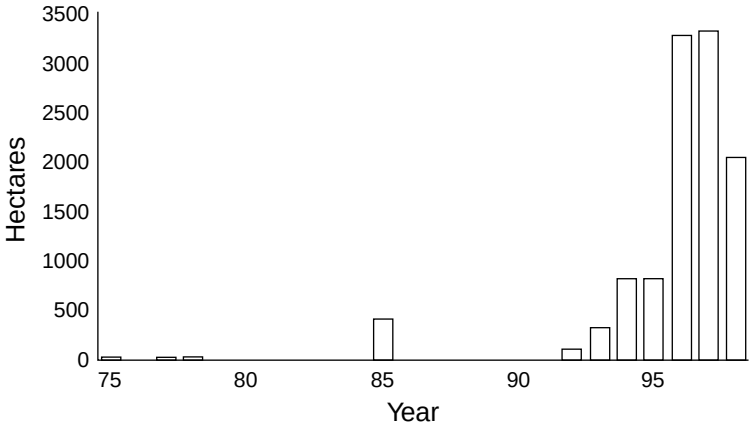

Fig. 1. Hectares of meadowfoam produced in Oregon between 1974–75 and 1998–99.

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Bagby et al. 1961; Miller et al. 1964; Isbell 1997).

The early germplasm screening and species selection work produced several key findings that have since dictated the course of meadowfoam research and development. *First*, the novel fatty acids of meadowfoam are found throughout the genus in similar proportions and concentrations (Bagby et al. 1961; Earle et al. 1959; Miller et al. 1964; Smith et al. 1960). This discovery showed that novel oils were produced by all of the known species and that species could be selected for commercial development on the basis of agronomic performance alone. *Second*, *L. alba* and *L. douglasii* were shown to produce greater biomass and seed yields than other meadowfoam species (Gentry and Miller 1965; Higgins et al. 1971; Pierce and Jain 1977; Jain et al. 1977; Brown and Jain 1979; Brown et al. 1979; Jain and Abeulgasim 1981; Krebs and Jain 1985; Jain 1989). This discovery narrowed the focus of crop development research to these two species. *Third*, the lack of non-shattering phenotypes in *L. douglasii* and presence of non-shattering phenotypes in *L. alba* (Jain 1989; Dole and Jain 1992) narrowed the focus of cultivar development research in Oregon to *L. alba* and led to the development of Foamore (PI 543894), the first non-shattering cultivar (Calhoun and Crane 1974).

GERMPLASM RESOURCES

Limnanthes (meadowfoam) is a genus of 17 species and subspecies belonging to two Sections (Inflexae and Reflexae) of the Limnanthaceae (Mason 1952) (Table 1). The USDA maintains germplasm for several of these species. Our laboratory maintains an *L. alba* germplasm collection and concentrates on the development of *L. alba* germplasm and cultivars. *L. alba* is a predominantly allogamous, self-compatible, diploid (x = 5) in Section Inflexae (Mason 1952; Jain 1978).

Two inter-fertile *L. alba* subspecies have been described (*L. alba* ssp. *alba* and *L. alba* ssp. *versicolor*). Partially fertile inter-specific hybrids can be made between *L. alba* and secondary gene pool species of Section Inflexae (e.g., *L. gracilis* and *L. floccosa*) (Table 1). Hybrids between *L. alba* and tertiary gene pool species of Section Reflexae species (e.g., *L. douglasii*) are sterile. The genetic diversity of several related species can be accessed through inter-specific crosses. We assigned species and subspecies to primary, secondary, and tertiary gene (germplasm) pools on the basis of the fertility of inter-subspecific and inter-specific hybrids with *L. alba* (Table 1).

The *primary gene pool* of *L. alba* is comprised of *L. alba* ssp. *alba* and *L. alba* ssp. *versicolor*. Crosses between these subspecies are fertile and seem to undergo normal meioses (Mason 1952; Knapp and Crane 1998, unpubl. data). Partially fertile progenies have been produced from crosses between *L. alba* and all of the species we assigned to the secondary gene pool (Table 1). Fertile progenies have not been produced from crosses between *L. alba* and the species we assigned to the tertiary gene pool. One backcross to *L. alba* greatly increases the fertility of progeny from crosses between primary and secondary gene pool species. Secondary gene

Table 1. Meadowfoam germplasm resources held by the United State Department of Agriculture (USDA) National Plant Germplasm System (NPGS) and the Oregon State University (OSU) Center for Oilseed Research (CORE).

Limnanthes species	No. accessions	Source
Primary gene pool		
L. alba	18	USDA NPGS
L. alba	~ 30	OSU
L. alba ssp. *alba*	4	USDA NPGS
L. alba ssp. *versicolor*	1	USDA NPGS
L. alba ssp. *versicolor*	5	OSU
Secondary gene pool		
L. gracilis	2	USDA NPGS
L. gracilis ssp. *parishii*	1	USDA NPGS
L. gracilis ssp. *gracilis*	1	USDA NPGS
L. floccosa	5	USDA NPGS
L. floccosa ssp. *bellingeriana*	2	USDA NPGS
L. floccosa ssp. *pumila*	2	USDA NPGS
L. floccosa ssp. *grandiflora*	1	USDA NPGS
L. floccosa ssp. *floccosa*	1	OSU
L. floccosa ssp. *californica*	1	OSU
L. montana	1	USDA NPGS
Tertiary gene pool		
L. bakeri	2	USDA NPGS
L. douglasii	3	USDA NPGS
L. douglasii ssp. *douglasii*	1	USDA NPGS
L. douglasii ssp. *nivea*	5	USDA NPGS
L. douglasii ssp. *rosea*	2	USDA NPGS
L. macounii	1	USDA NPGS
L. striata	2	USDA NPGS

pool species, however, are vastly inferior to *L. alba* for agronomically important traits and have limited utility for enhancing meadowfoam seed and oil yield in the short run.

The USDA National Plant Germplasm System (NPGS) holds seed of 23 *L. alba* and 15 secondary gene pool accessions (Table 1). The working collection is maintained by USDA-ARS Plant Introduction Station (Pullman, WA). Passport data on the working collection can be accessed through the Germplasm Resource Information Network or GRIN (http//:www.ars-grin.gov). The OSU Center for Oilseed Research (CORE) presently holds 30 or more *L. alba* accessions, in addition to families and lines from numerous segregating populations and mapping populations (Table 2). The CORE accessions are comprised of unreleased germplasm populations (selected and unselected), recollected wild populations, newly discovered and collected wild populations, unreleased inbred lines, novel genetic stocks, unreleased experimental cultivars, and released cultivars.

The *L. alba* germplasm collection held by the USDA is primarily comprised of wild populations, most of which were collected between 1962 and 1972. These accessions have not been regenerated since being deposited and have slowly and steadily degraded. Although meadowfoam seed can be kept alive in low humidity cold storage for ~15 years, much of the seed in the collection is more than 25 years old. These accessions will eventually be completely lost unless the collection is regenerated or the accessions are recollected and routinely regenerated.

Table 2. Meadowfoam germplasm accessions held by the Oregon State University (OSU) Center for Oilseed Research (CORE).

Accession	Description
Knowles (OMF69)	Released insect-pollinated cultivar
OMF78	Experimental insect-pollinated cultivar
OMF86	Experimental insect-pollinated cultivar
OMF103	Experimental insect-pollinated cultivar
OMF156	Experimental insect-pollinated cultivar
OMF78-C_1	Experimental insect-pollinated cultivar
OMF58	Unselected insect-pollinated germplasm population (diverse pedigree)
OMF59	Unselected insect-pollinated germplasm population (diverse pedigree)
OMF157	Unselected insect-pollinated germplasm population (OMF62 × OMF154)
OMF62	High oil insect-pollinated germplasm population
OMF87	High oil insect-pollinated germplasm population
OMF154	Large seeded insect-pollinated germplasm population
OMF-Redding (OMF66)	Wild *L. alba* ssp. *versicolor* population
OMF158	Wild *L. alba* ssp. *versicolor* population (recollected PI 283705)
OMF159	Wild *L. alba* ssp. *versicolor* population (recollected PI 374791)
OMF160	Wild *L. alba* ssp. *versicolor* population (recollected PI 374801)
OMF161	Wild *L. alba* ssp. *versicolor* Population (recollected PI 374802)
OMF63 S_5	Self-pollinated inbred line
OMF64 S_5	Self-pollinated inbred line
OMF66 S_5	Self-pollinated inbred line
OMF104-Bulk S_1	Bulk of self-pollinated S_1 *L. alba* ssp. *versicolor* progeny
OMF104-Bulk S_2	Bulk of self-pollinated S_2 *L. alba* ssp. *versicolor* progeny
OMF104-Bulk S_3	Bulk of Self-Pollinated S_3 *L. alba* ssp. *versicolor* progeny
Mermaid S_5	Insect-pollinated inbred line
Globus	Fused sepal mutant
LAG64-1 F_4	Self-pollinated *L. alba* × *L. gracilis* ssp. *parishii* inbred line
LAG64-2 F_4	Self-pollinated *L. alba* × *L. gracilis* ssp. *parishii* inbred line
LAG64-3 F_4	Self-pollinated *L. alba* × *L. gracilis* ssp. *parishii* inbred line

There are three cultivars in the USDA and CORE collections: two *L. alba* cultivars (Foamore and Mermaid) and one *L. alba* ssp. *alba* × *L. floccosa* ssp. *grandiflora* cultivar (Floral). 'Foamore' (PI 543894) (Calhoun and Crane 1975) and 'Mermaid' (PI 601232) (Calhoun and Crane 1984; Jolliff 1986) have been released to the USDA working collection. 'Floral' (PI 562386) (Jolliff 1994) has been deposited in the USDA NPGS National Seed Storage Laboratory (Fort Collins, Colorado), but has not been released to the USDA working collection.

Many wild *L. alba* populations could be extinct. Seed of the wild *L. alba* populations collected by Dr. S.K. Jain (University of California, Davis) and his students over the years (Pierce and Jain 1977) has been lost and many of the original collection sites for *L. alba* have been disturbed by human development. *L. alba* cannot be safely preserved in situ. As noted by Knapp and Crane (1997), the site of the OMF-Redding population was destroyed by human development soon after seed was collected. Several *L. alba* populations have undoubtedly had similar fates over the last 20 years in California.

Six wild *L. alba* populations from the University of California, Davis meadowfoam collection have been used in our breeding work. We received seed samples of four wild *L. alba* ssp. *alba* populations (UC-302, UC-305, UC-308, UC-312) from Dr. Jain in 1987. These were bulked and intermated under cages at Corvallis, Oregon in 1988–89. We used the bulk population (UC-Bulk) to develop OMF58. We received seed of two additional *L. alba* accessions (UC-Sonoma and UC-Calaveras) from Dr. Jain in 1988. These accessions were intermated en masse with 21 *L. alba* accessions in an isolated field at Corvallis, OR in 1992 to develop OMF59 (Table 2). Pierce and Jain (1977) described the origin of some of the UC accessions. The geographical origins of several accessions are not known. Most of the collected diversity of *L. alba* was pooled in OMF58 and OMF59.

A census of wild populations has not been taken for many years, the number and distribution of present day wild populations is not known, and germplasm has not been systematically collected from the wild for many years. Historical records (Mason 1952; Pierce and Jain 1977; www.ars-grin.gov) show that germplasm has apparently not been collected from parts of the natural range of *L. alba*, particularly along the easterly margins of the range along the Sierra Nevada foothills.

Several *L. alba* ssp. *versicolor* populations were collected by Jimmie Crane and Daryl Ehrensing in May of 1993 from sites nears Redding, California. They collected seed from sites (populations) of four previously collected populations (PI 283705, PI 374791, PI 374801, and PI 374802) and from a new *L. alba* var. *versicolor* population (OMF-Redding or OMF66) near the other four sites. Seed of the recollected populations (OMF158, OMF159, OMF160, and OMF161) is held in the CORE meadowfoam collection (Table 2). OMF-Redding was found to be a source of self-pollinated phenotypes (Knapp and Crane 1997). Seed of OMF-Redding, OMF158, OMF159, OMF160, and OMF161 has not yet been regenerated or deposited in the NPGS working collection (Table 2).

Self-pollinated inbred lines have been developed from OMF66 and from two other wild *L. alba* ssp. *versicolor* populations (PI374791 and PI374801) (Knapp and Crane 1997). These inbred lines (OMF63-S_5, OMF64-S_5, and OMF66-S_5) are being increased for release as enhanced germplasm. Seed of OMF63-S_5, OMF64-S_5, and OMF66-S_5 will be sent to the working collection in July of 1999. We are presently developing a diverse self-pollinated population (OMF104-Bulk) from a bulk of wild *L. alba* ssp. *versicolor* populations. Two cycles of inbreeding and mass selection for self-pollination have been completed in this population. The third cycle will be completed in 1998–99. OMF104-Bulk S_3 seed will be released in July of 1999.

INSECT-POLLINATED GERMPLASM AND CULTIVAR DEVELOPMENT

The development of enhanced insect-pollinated germplasm is the core of our breeding program. Aside from partially self-pollinated wild populations and strongly self-pollinated lines (Knapp and Crane 1997), most *L. alba* germplasm is allogamous and insect-pollinated and most of the genetic diversity of this species resides in insect-pollinated populations. We have primarily used recurrent mass, half-sib family, and S_1 family selection in these populations with a strong focus on increasing seed yield and lodging resistance.

Meadowfoam germplasm screening began in 1966 and cultivar development began in 1971 at Oregon State University. 'Foamore', the first cultivar developed for this crop, was released in 1974 (Calhoun and

Crane 1975). 'Foamore' was eclipsed by 'Mermaid' (Calhoun and Crane 1984; Jolliff 1985) and 'Mermaid' was eclipsed by 'Floral' (Jolliff 1994). 'Foamore' and 'Mermaid' were developed by mass selection for seed yield in wild *L. alba* ssp. *alba* populations, while 'Floral' was developed by mass selection for seed yield in an interspecific population (*L. alba* ssp. *alba* × *L. floccosa* ssp. *grandiflora*). All three cultivars are insect-pollinated. 'Floral' is difficult to distinguish from *L. alba* and has few if any obvious *L. floccosa* ssp. *grandiflora* traits. The latter is a diminutive species with very low biomass. 'Floral' (Jolliff 1994) was the primary cultivar grown in commercial fields in Oregon between 1993 and 1998. Over 3000 ha of 'Floral' were grown in Oregon in 1997–98. 'Foamore' and 'Mermaid' have not been grown in Oregon for several years.

Several new experimental insect-pollinated cultivars have been developed from the breeding program we initiated in 1991. 'Knowles', OMF78, and OMF86 were the first of these. 'Knowles' (tested as OSU-EXP-OMF69), a newly released insect-pollinated cultivar (Crane and Knapp 1999; Knapp and Crane 1999), was developed by one cycle of recurrent half-sib family selection for increased seed yield, seed oil concentration, and lodging resistance in OMF58. OMF78 was developed by one cycle of recurrent half-sib family selection for increased seed yield and seed oil concentration in OMF59. OMF86 was developed by two cycles of recurrent half-sib family selection for increased seed yield, seed oil concentration, and lodging resistance in OMF58. OMF78 and OMF86 have not yet been officially released.

'Knowles', OMF78, OMF8, 'Mermaid', and 'Floral' were grown in replicated yield trials at Hyslop Farm (Corvallis, OR) in 1996–97 and 1997–98. The mean seed yield of 'Floral' was 783 kg/ha versus 688 kg/ha for 'Mermaid'. The mean seed yield for 'Knowles' and OMF78 were 1,014 kg/ha and 1,016 kg/ha, respectively. The seed yields of 'Knowles' and OMF78 were significantly greater than the seed yields of 'Mermaid' and 'Floral' ($LSD_{0.05}$ = 83 kg/ha), but still may not be great enough to dramatically affect the price of meadowfoam oil. Over 1000 ha of 'Knowles' were planted in Oregon in October of 1998. 'Knowles' and OMF78 are presently being tested at four sites in the western US (Davis, California; Medford and Corvallis, Oregon; and Mt. Vernon, Washington).

OMF86 has the strongest upright growth habit and the greatest lodging resistance of any cultivar we have developed or tested thus far. The seed yield of OMF86 was not significantly different from Knowles in 1996–97 (1,222 versus 1,200 kg/ha), but was significantly less than Knowles in 1997–98 (713 versus 829 kg/ha) ($LSD_{0.05}$ = 83 kg/ha). Because of this, OMF86 may not be released as a new cultivar.

The first wave of new cultivars will undoubtedly have short commercial lives and be rapidly superceded by other new cultivars (OMF156 and others). The cultivar replacement process is especially dynamic in meadowfoam because of the short breeding history of this crop. Even though self-pollinated cultivars have tremendous appeal and commercial promise, insect-pollinated germplasm and cultivars are the cornerstone of our breeding program and the development of insect-pollinated cultivars is presently more advanced than the development of self-pollinated cultivars.

SELF-POLLINATED CULTIVAR DEVELOPMENT

The self-pollinated germplasm described earlier lacks many of the traits necessary for commercial production (Knapp and Crane 1997; Crane and Knapp 1999), e.g., OMF63-S_5, OMF64-S_5, and OMF66-S_5 grow flat and produce less seed than elite insect-pollinated *L. alba* cultivars. Several new self-pollinated inbred lines have been developed from crosses between insect-pollinated *L. alba* ssp. *alba* cultivars (e.g., 'Knowles') and self-pollinated *L. alba* ssp. *versicolor* lines (e.g., OMF64). Some of these lines may be released as enhanced germplasm or cultivars. With further development, self-pollinated cultivars might significantly impact the meadowfoam industry by reducing production costs (honeybee hive rentals) and increasing the stability of seed yields across years.

Meadowfoam seed yields tend to be volatile across years. Poor honeybee pollination, rightly or wrongly, is routinely blamed for low seed yields. Oregon growers experienced some of this volatility the last two years. The mean seed yield of all cultivars in our yield trial was significantly greater ($LSD_{0.05}$ = 45 kg/ha) in 1996–97 than 1997–98 (1,094 kg/ha versus 654 kg/ha). Similar seed yields were produced in commercial fields in those years. The yield decline in 1997–98 was partly blamed on poor pollination. Although pollination undoubtedly plays a role in seed yield volatility across years, there are no experimental data that directly

incriminate pollination as the primary cause of low seed yields. Yield tests of insect- and self-pollinated cultivars across years should shed light on this. If poor pollination is the primary problem, then self-pollinated cultivars should experience less seed yield volatility across years than insect-pollinated cultivars.

BREEDING BASICS

As note earlier, *L. alba* is self-compatible and predominantly allogamous (Jain 1978; Brown and Jain 1979). Although naturally self-pollinated progeny are found in certain wild *L. alba* ssp. *versicolor* populations (Knapp and Crane 1997), most populations lack self-pollinated progeny and strongly self-pollinated progeny have not been found in wild (unselected) populations. The frequency of self-pollinated progeny among F_2 progeny from crosses between self- and insect-pollinated lines is very low (unpublished data) because the self-pollinated phenotype (seeds per flower) is a function of two threshold traits (protandry and heterostyly). The genetics of self-pollination are poorly understood in meadowfoam. Molecular breeding experiments are underway in our laboratory to dissect the genetics of self-pollination. We suspect that the genetics are complex and that two or more quantitative trait loci (QTL) underlie phenotypic differences for self-pollination, heterostyly, and protandry.

The versatility of the mating system of meadowfoam means that diverse breeding methods and schemes can be employed. We have used several breeding methods to develop the germplasm described in this review: recurrent mass and family selection and backcross breeding in insect-pollinated populations and backcross, pedigree, single seed descent, and bulk breeding in crosses between self- and cross-pollinated lines. We used recurrent half-sib family selection for early breeding experiments so that families could be grown in large plots (2 × 7 m) for direct combining. Half-sib seed can be easily produced on field grown plants spaced 1 m or more apart in isolated nurseries. Such plants typically yield 15 to 45 g of seed (~1,500 to 4,500 seeds per family). This is sufficient to plant one or two replications per family in 2 × 7 m plots. Individual plants do not produce enough seed to test families in more than one year or location in 2 × 7 m plots, so one cycle of selection is typically completed with families tested in one year and one location. We test families in non-isolated fields and produce selected populations by bulking remnant seed of selected families.

We have begun using S_1 rather than half-sib family recurrent selection in insect-pollinated populations. This switch was made for a few reasons. First, half-sib family seed must be produced on spaced plants in field isolations, whereas S_1 family seed can be produced in the greenhouse. Selected S_1 families are intermated under cages in the field, thus circumventing the need for a field isolation. Second, S_1 family selection should produce greater gains from selection than half-sib family selection. The S_1 family selection cycle is longer than the half-sib family selection cycle (three versus two years), but the theoretical gains are greater for the former. Third, the process of developing S_1 families is a natural starting point for discovering and selecting novel phenotypes and developing inbred lines. We produce S_1 family seed in screened greenhouses by manually pollinating individual flowers within a plant with cotton swabs. Numerous flowers on a single plant can be pollinated in one to two minutes. The process of selfing a plant typically spans eight to 12 days with repeat pollinations every two to three days. We typically produce 100 to 200 S_1 seeds per plant. This is enough seed to plant two rows 2 m long. We bulk harvest S_1 plots with a forage harvester and thresh the seed with a stationary thresher.

Developing inbred lines is straightforward in meadowfoam. We have developed and are developing several inbreds for breeding and genetics experiments by manually selfing greenhouse grown plants. Many meadowfoam populations are depressed by inbreeding and lines are frequently lost in inbreeding experiments (Jain 1976, unpubl. data). We have observed inbreeding depression in several *L. alba* ssp. *alba* populations. Some *L. alba* ssp. *versicolor* populations, however, seem to have no genetic load (Knapp and Crane 1997), e.g., inbreeding coupled with selection for increased self-pollination led to increased fecundity in OMF64. The effects of inbreeding and heterosis needs to be systematically and intensively studied in the self- and cross-pollinated gene pools of meadowfoam. Meadowfoam is an excellent candidate for hybrid seed production; however, a system for producing hybrid seed has not been discovered or developed for this crop. With such a system, single-cross hybrids could be produced between self-pollinated inbred lines, thereby short-circuiting inbreeding depression and producing simultaneous gains from self-pollination and heterosis. The development of a hybrid seed production system would have a revolutionary impact on meadowfoam.

Crosses are easily produced in meadowfoam. We emasculate flowers one day before buds break and typically pollinate emasculated flowers one to two days later. Anthers are excised using forceps. The seed to seed generation time for greenhouse grown plants ranges from 120 to 150 days. We typically complete three generations per year in the greenhouse. One of the keys to speeding up the greenhouse cycle is rapidly germinating freshly harvested seed. Meadowfoam seed typically must be after-ripened for one month before a new generation can be started; however, we discovered that freshly harvested seed, when heat treated, can be immediately germinated. Physiologically mature seeds are held at 50°C for 48 h to break dormancy. This trick reduces the seed to seed generation times by three months over the course of one year.

We have had situations where we needed to field test segregating backcross progeny (e.g., BC_1S_1 progeny) for pre-anthesis traits and backcross to the recurrent parent. Because producing crosses in the field is difficult and impractical, we grow the recurrent parent in the greenhouse so that the field and greenhouse generations will nick. Stems of flowering plants are collected from field grown plants. The cut stems are placed in water in the greenhouse and pollen is harvested from flowers as they open and the anthers dehisce. We have produced crosses from flowering stems held this way for one to five days in the greenhouse. The females, of course, must planted ahead so that they nick with field grown male plants. We have not developed or tested a protocol for storing meadowfoam pollen.

KEY AGRONOMIC PROBLEMS AND PRODUCTION BARRIERS

The most serious pest of meadowfoam in Oregon is *Scaptomyza*, a fruit fly that bores into developing buds and crowns, thereby destroying seed or whole plants. The taxonomy of this pest is unclear. Glenn Fischer and Daryl Ehrensing at OSU are studying the life cycle, control, and integrated management of *Scaptomyza* and have developed promising control measures. Floral, Knowles, and several other cultivars are susceptible to *Scaptomyza*. We attribute some of the seed yield decline for all cultivars and the very low seed yield of 'Floral' in our 1997–98 yield trial to *Scaptomyza* damage. *Scaptomyza* damage was severe in our 1997–98 yield trial (Hyslop Farm, Corvallis, Oregon) and tends to be more severe on our experiment farm than elsewhere. This situation undoubtedly exists because meadowfoam, although rotated, is continuously grown within the confines of the experiment farm.

As stated earlier, resistance or tolerance to *Scaptomyza* has been found in OMF78. We developed an experimental insect-pollinated cultivar (OMF156) from *Scaptomyza* tolerant half-sib families and are increasing this cultivar for further tests. The genetic basis for resistance is not known. The biology, control, and genetics of resistance to *Scaptomyza* must be further elucidated to help avert losses to this pest.

As noted earlier, poor pollination of insect-pollinated cultivars is frequently cited as one of the key factors underlying low seed yields in meadowfoam. The perception is that seeds yields are diminished when the weather for pollination is unsatisfactory or when honeybees are not optimally managed. This has been the driving force behind the development of self-pollinated cultivars. The first self-pollinated cultivars are being increased for testing in 1998–99. The cost of producing meadowfoam should be significantly lower for self- versus insect-pollinated cultivars (honeybee rentals typically comprise 30% to 35% of the cost of production). If seed yields are comparable for self- and insect-pollinated cultivars, then the release and commercial production of self-pollinated cultivars should decrease production costs and meadowfoam oil prices.

The commercial development of meadowfoam has been limited by the growing conditions under which this crop thrives. The Willamette Valley of Oregon (45°N and 123°W) seems to be ideal for producing meadowfoam. Several traits and factors listed below underlie the narrow ecological niche of this crop.

1. Meadowfoam (specifically *L. alba*) grows naturally in riparian habitats (vernal pools) in northern California (Mason 1952). The crop tolerates and thrives in saturated soils. Many Willamette Valley soils are saturated from late November to early April or later. Soil drying is typically coupled with increased ambient air and soil temperatures in the Willamette Valley. These factors accelerate flower and fruit develop and senescence. The long wet growing season and dry harvest season in the Willamette Valley are ideal for meadowfoam.
2. Meadowfoam thrives in cool weather (growing temperatures between 4° and 16°C), but is typically killed by ambient air temperatures below 5°C for prolonged periods (more than four days). We speculate that meadowfoam lacks frost tolerant and winter hardy types, but concede that the germplasm

collections have not been systematically screened for either trait. The development of winter hardy cultivars would dramatically expand the range of production for this crop.

3. Meadowfoam can be sown as a spring annual to circumvent winter damage, but the growing season is dramatically compressed and seed yields are typically very low. There is certainly no harm in experimenting with spring or summer planting, but be prepared for failure.
4. Seed dormancy restricts planting to soil temperatures below 15°C (Toy and Willingham 1966, 1967). Secondary dormancy is induced when fully imbibed seeds are planted in soils warmer than 16°C (Toy and Willingham 1967). Selection for non-dormancy has not been done in meadowfoam, the genetic basis for seed dormancy is not known, and germplasm has not been screened for non-dormant phenotypes. We speculate that nothing can be gained by planting earlier (via the development of cultivars lacking secondary dormancy) without developing heat tolerant cultivars. Oregon farmers typically have no difficulty planting meadowfoam in early October after soils temperatures have cooled to 15°C or lower.

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