4 Pollinating Bees Crucial to Farming Wildflower Seed for U.S. Habitat Restoration

James H. Cane

Background

Native plant communities and ecosystems of the western United States are increasingly besieged by invasive weeds and grasses of Eurasian origins. Federal land managers oversee 40 million ha in the Great Basin region of the western United States. Its valleys are cold desert steppe vegetated by grassy shrublands; these are interrupted by forested mountains. The Great Basin and Columbia Plateau ecoregions (figure 4.1) together include about one-half of North America's remaining 43 million ha of sagebrush (*Artemesia* spp.) plant communities (Wisdom et al., 2005). The health and extent of these communities are fast diminishing, with dire consequences for many plant and animal inhabitants. The most charismatic of these is the sage grouse, but 206 other species warrant conservation concern (Wisdom et al., 2005). Cheatgrass (smooth brome, *Bromus tectorum*), a flammable annual grass from the Mediterranean, has invaded 11 million ha of the Great Basin northward into the Columbia Plateau, an area equivalent to that of Cuba, Hungary, or Virginia. Cheatgrass is quite literally fueling a dramatic increase in the frequency and extent of wildfire across the region, degrading native plant communities and presumably their dependent native bee faunas. In Nevada alone, 1,000 wildfires burned 200,000 ha of rangeland from 2000 to 2002, half of it sagebrush communities (Wisdom et al., 2005). Besides direct fire suppression efforts, land managers have also sought to break this intensified fire cycle by rehabilitating native plant communities, primarily through direct seeding following wildfire (Monsen & Shaw, 2001). This reseeding strategy to restore native plant communities on western public rangelands, if successful, may be comparable to fire suppression in cost but will have more enduring habitat value.

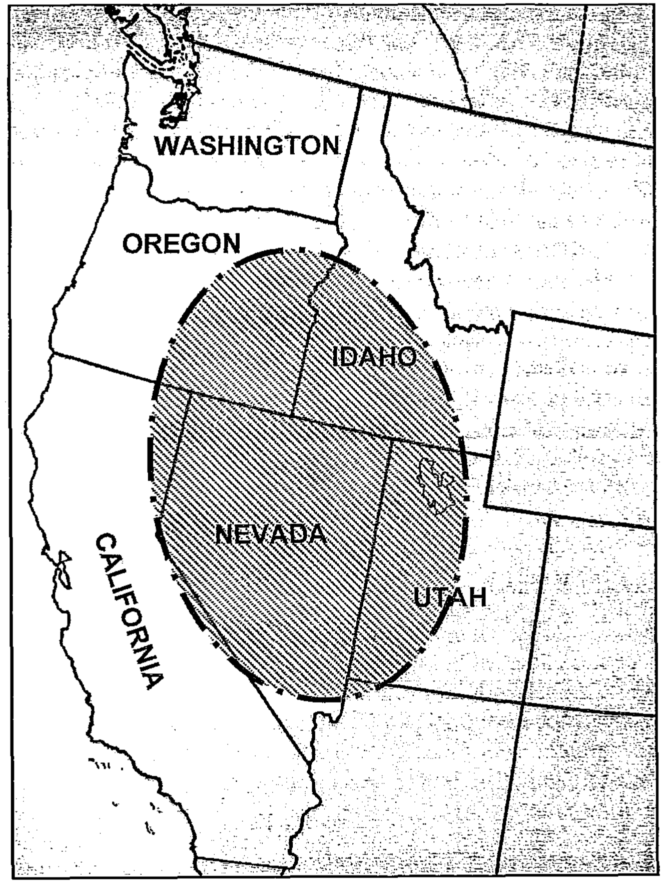

Figure 4.1 A map of the western U.S. Intermountain Region showing the hydrological Great Basin (shaded circle), which botanists often recognize as a single floristic region.

Recent Great Basin reseeding efforts to rehabilitate rangelands have been ambitious. However, native wildflowers are barely represented in these seed mixes, in terms of either volume or diversity, a circumstance that a new research program seeks to redress. The program scale has no precedent. From 1999–2004, massive wildfires burned across the western United States. In response, federal agencies distributed more than 6,500 metric tons of seed. Since the 1970s, the reseeding mixes have consisted of about one-third each of exotic grasses, native grasses, and native shrubs (Monsen & Shaw, 2001). Native flower seed constituted a mere 0.5% of the mix, most of that being a native yarrow, *Achillea millefolium* L. Dramatically more wildflower seed, about 150 tons each year, is sought by western land managers to rehabilitate the hundreds of thousands of hectares that annually burn in the Great Basin and adjacent biomes (Scott Lambert, National Seed Coordinator, Bureau of Land Management, 2007 personal communication). The sage grouse is hoped to be a major beneficiary; this endemic bird is otherwise fast becoming endangered. Native shrub seed for such restoration continues to be harvested directly from nature. Though cost effective for shrubs, wild harvest is impractical and unreliable for native wildflowers, as it yields paltry quantities of expensive seed. For example, wild-harvested seed of *Hedysarum boreale* was recently being marketed for US$110 per kilogram and that of *Sphaeralcea ambigua* for US$180 per kilogram. Budgetary constraints and harvest inefficiencies will forever limit the volumes of most wild-harvested wildflower seed that can be bought to satisfy these reseeding programs.

A cadre of innovative commercial growers are farming fields of the native grasses and, more recently, experimentally farming several of the native wildflower species desired for restoration seed. With the advent of the Great Basin Native Plant Selection and Increase Project in 2001, farming practices are being developed for 16 eudicot flowering species (table 4.1) native to the Intermountain Region, especially the Great Basin, but including the Columbia Plateau to the north and the Colorado Plateau to the

Table 4.1 Wildflower species desired for rangeland rehabilitation in the U.S. Intermountain West.

Family	Species
Apiaceae	*Lomatium dissectum* (Nutt.) Math. & Const.
	L. triternatum (Pursh) Coult. & Rose
Asteraceae	*Balsamorhiza sagittata* (Pursh) Nutt.
	Crepis acuminata Nutt.
Cleomaceae	*Cleome lutea* Hook
	C. serrulata Pursh
Fabaceae	*Astragalus filipes* Torr.
	Dalea ornatum (Dougl.) Barneby
	D. searlsiae (Gray) Barneby
	Hedysarum boreale Nutt.
	Lupinus argenteus Pursh
	L. sericeus Pursh
Malvaceae	*Sphaeralcea grossularifolia* (H. & A.) Rydb.
	S. munroana (Dougl.) Spach.
Plantaginaceae	*Penstemon speciosus* Dougl.
Polygonaceae	*Eriogonum umbellatum* Torr.

southeast. They were chosen in part for being regionally widespread, common within native plant communities, broadly adapted at mid- and lower elevations, tolerant of fire, and palatable to wildlife and for having practical promise for farming (e.g., mechanical harvest). By harnessing the efficiencies and reliability of modern agriculture, the hope is to dramatically boost seed production while slashing seed costs.

Applied Pollination Paradigms

For the successful farming of wildflower seed, each flowering crop's pollination needs must be understood and satisfied by practical means. Three of the four approaches to agricultural pollination are relevant and context-specific: (1) renting hives of managed honey bees, (2) managing nesting of nonsocial bees in provided substrates, and (3) practicing on-farm pollinator stewardship to favor unmanaged nesting populations of local wild bee communities. The fourth alternative, which is purchasing disposable hives of bumble bees, will likely prove impractical for reasons discussed herein. A novel mix of these pollination strategies is being developed for farmed wildflowers.

Applied pollination ecology is practiced in two traditional arenas, agriculture and wildflower conservation. Their unusual marriage in this program brings novel challenges and opportunities. In agriculture, extensive monocultures of food, forage, and fiber crops are farmed far beyond their geographic points of origin. Most pollinated crops are either herbaceous annuals or woody perennials, such as orchard fruits. Each crop's pollination needs and benefits are generally well understood (Free, 1993; Klein et al., 2007). Most crops are derived from decades, if not centuries, of artificial selection and sometimes controlled hybridization. Prolonged plant breeding often modified their reproductive biologies, inadvertently or intentionally eliminating physiological or mechanical barriers to selfing while favoring passive autopollination. The wild progenitors of a few crop species are extinct (e.g., onions, *Allium cepa*) and, with them, knowledge of their former natural pollinator faunas.

Farming Great Basin wildflowers for restoration seed contrasts sharply with farming our traditional crops, with profound consequences for pollination needs and pollinator management. Only two of the species are annuals; the rest are perennial, but herbaceous. They are being grown in or near their native geographic ranges. We are ignorant of their pollination needs and benefits, often for entire genera, sometimes even for tribes (Cane, 2005, 2006a) or families (e.g., Cleomaceae). The Association of Seed Certification Agencies (AOSCA) has promulgated new standards and protocols for native seed collection and certification called the "source identified class." It dictates ≤5 generations in cultivation before returning to geographically explicit wild seed sources. Artificial and inadvertent selection are being minimized and genetic diversity maintained in order to retain regional adaptations relevant for wildflower establishment once seeded back into wildlands. These objectives, strategies, and problems have no precedent in agriculture, although the tools and farming practices are mostly borrowed and adapted from traditional agriculture.

The second realm of applied pollination ecology addresses the breeding and pollination biology of wildflowers in a context of species conservation. Most of the funding focuses on specific threatened or endangered plant species growing in situ. Failed sexual reproduction has been a tenable explanatory hypothesis for rarity of endangered wildflowers, but more recent accumulating evidence implicates other factors, primarily habitat loss, for the endangerment of most continental flowering species that are pollinated by insects (Tepedino, 2000). Unlike crop plants, these rare wildflowers enjoy adequate natural pollination service, partly because their floral densities fall far short of those experienced in cropped monocultures, and so the densities of unmanaged wild pollinators typically suffice. Many ecologically important plant genera lack such endangered species (or they have not been studied). Consequently, studies of endangered wildflowers leave us surprisingly ignorant of the breeding biologies and pollinators of the numerous native wildflowers that dominate plant communities targeted for ecological restoration (Cane, 2006a), including those of the Great Basin. Thus neither agricultural nor conservation contexts for applied pollination research provide a satisfactory blueprint to address pollination needs of farmed native wildflowers whose harvested seed will later be used to rehabilitate and restore native plant communities.

Pollination Needs

None of these Great Basin wildflowers that are under study in this project is wind pollinated, and none proliferates vegetatively. Only one species, *Crepis acuminata*, can set considerable seed without pollinators; most of its populations include numerous polyploid individuals that can reproduce asexually through apomixis (Babcock & Stebbins, 1938). Even for the more self-fertile species, comparatively little seed results from autopollination (unaided pollen transfer; figure 4.2). The two *Cleome* species constitute a partial exception, as mechanical jostling of densely grown flowering stands nearly doubled fruit set in cages (37% vs. 19% (Cane, 2008)). Nevertheless, all nine species studied at my laboratory have produced dramatically more seed with pollinator visitation (see figure 4.2). Northern sweetvetch (*Hedysarum boreale*) sets no fruit or seed at all if pollinators are excluded from its flowers (Swoboda, 2007). The species also vary in their degrees of self-fertility, a trait useful for colonization. Outcrossing has yielded more modest gains in seed or fruit production (figure 4.3). These gains are nonetheless substantial. For example, outcrossing by *Astragalus filipes* doubles seed yields and could thereby halve seed prices from the same field. For a few cases, such as *H. boreale*, flowers pollinated freely by bees set more seed than even our manual outcrossing treatments, suggesting further nuances for maximal seed set (Swoboda, 2007). Overall, if literally tons of wildflower seed will be produced cheaply and profitably, then fruit and seed set must be maximized through judicious use of reliably abundant and effective pollinators.

Pollinator guilds of each of these wildflower species consist exclusively of insects. For 12 species, I have systematically sampled 1–6 floral visitor guilds in 1–3 states, along with any bees in our experimental common garden in Logan, Utah. Native bees, sometimes joined by honey bees, dominate most of the guilds, with up to 29 bee species represented in pooled guild samples of no more than 200 individuals. The small floral visitor

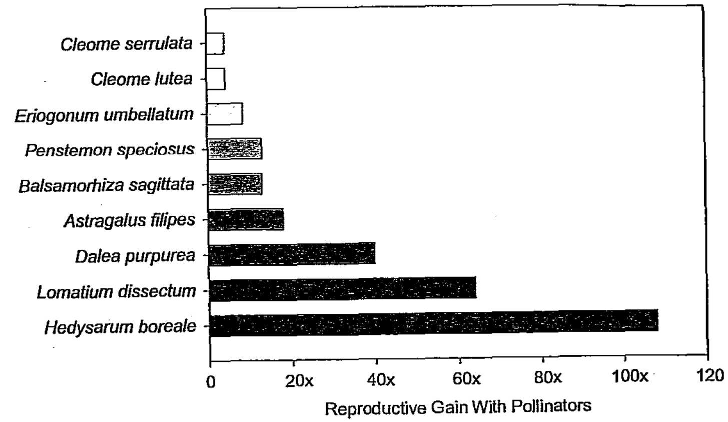

Figure 4.2 Western wildflowers grown for rangeland restoration and their requirements for pollinators. Using seed yield per inflorescence, reproductive gain was calculated as the average yield of seeds from flowers open to pollinator visits, divided by the yield from flowers bagged in mesh netting that excluded pollinators but allowed wind pollination and autopollination. Treatments were either paired within plants or randomly assigned among plants. Pollinator numbers were not supplemented. Note that the abscissa is a multiplier, not a percentage.

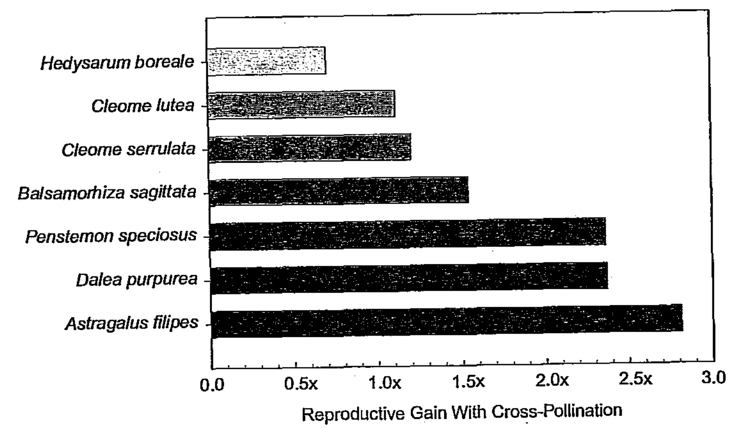

Figure 4.3 Self-fertility of western wildflowers grown for rangeland restoration in the Western United States. Flowers netted or caged to exclude insect visits were manually pollinated with pollen from either the same or a different plant. Plants (8–25 per species) were grouped for each replicate treatment.

guild at *Penstemon speciosus* constitutes one exception. Its two specialist *Osmia* bees are joined by another prominent visitor and likely pollinator, the pollen wasp, *Pseudomasaris vespoides* (Masaridae), which frequents flowers of this genus (Tepedino, 1979). The two *Cleome* species are again exceptional, too, their prodigious and accessible nectar attracting diverse nectarivorous insects, primarily butterflies, bees, and wasps. Their wild populations have yet to be systematically sampled. Curiously, although these *Cleome* flowers are visited and readily pollinated diurnally, I have found that their anthers dehisce and stigmas become receptive nocturnally (Cane, 2008). In desert basins (but not at the common garden) their flowers might also be visited by moths. The other wildflowers are all diurnally pollinated. Overall, it has become clear that each of these wildflower species needs pollinators. Bees are the predominant and diverse group of visitors populating nearly all of their floral guilds. Bees seem likely, therefore, to be generally essential for these wildflowers' seed production.

Pollinator Options

Honey Bees

The European honey bee (*Apis mellifera*) continues to be the versatile workhorse of agricultural pollinators. In many developed countries, hives of honey bees are typically rented from professional migratory beekeepers who transport palletized hives to pollinate sequentially flowering crops. Honey bees are, therefore, the obvious default choice to pollinate farm fields of wildflowers, too. Even at a rental cost of US$100 per hive, a strong colony's 10,000 foragers are cheap, each rented forager costing the grower 1 cent. As an added advantage, once a beekeeper is contracted and arrives with rental hives, a grower has no further pollination inputs or concerns.

But honey bees do have drawbacks, some of which are specific to the practicalities of wildflower seed production:

1. Some of today's native seed growers are distant from regions in which migratory beekeepers pollinate crops. Delivering small numbers of rental hives to a small, out-of-the-way wildflower grower will often be inconvenient at best.
2. Mite-borne diseases have decimated feral honey bees and thinned the ranks of hobbyist beekeepers, while doubling costs for commercial hives. Hence, feral or locally owned colonies may not exist.
3. For certain seasons and regions, pollination demand exceeds hive availability, most notably in the early spring when tree fruits and almonds bloom in the western United States.
4. Field size for a given wildflower seed crop is likely to remain small by some agricultural standards. If a given cultivated wildflower species has but mediocre attraction for foraging honey bees, their broad floral preferences and flight vagility will allow them easy access to alternative floral hosts in neighboring fields, fallow areas, or surrounding wild lands.
5. Lastly, honey bees may be ineffective pollinators for a given wildflower species. For these reasons, honey bees will be impractical pollinators for some native wildflower seed crops.

For a few traditional crops, nontraditional bees are superior pollinators and can be effectively managed in the large numbers that are needed. Sometimes these alternative pollinators are useful only in particular cultural or economic contexts for a given crop, such as the use of *Osmia cornifrons* (Megachilidae) to pollinate apples only in Japan, or the use of several *Bombus* species whose commercial colonies are shipped great distances to pollinate tomatoes in North America, Europe, and the Mediterranean, but only in greenhouses (see chapters 3 and 9, this volume). Whatever the pollinator, economics and practical considerations for managing the bees and the crop constrain our options for reliably supplying large numbers of dedicated pollinators to a given crop monoculture.

Bumble Bees

My bee surveys revealed bumble bees to be often ubiquitous and sometimes common members of these wildflowers' pollinator guilds. They avidly visit and effectively pollinate two of the four species of legumes, *Astragalus filipes* and *Hedysarum boreale*. In our common garden and in trial cultivation plots, unmanaged bumble bees also have proven to be excellent pollinators of *Penstemon speciosus*, although they were not seen at this *Penstemon* in the wild. Stewardship of unmanaged bumble bee populations in and around native seed farms (see chapter 2, this volume) might therefore pay dividends in seed yields to growers. However, commercial bumble bee colonies are costly for open-field pollination, with individual foragers costing about one hundredfold more than rented honey bees. Purchased bumble bee colonies are short-lived, shifting production from workers to drones and queens after a few months. Hence, they are disposable. For now, they are economically practical only when foragers pollinate highly valuable crops in confinement, such as greenhouses (see chapter 3, this volume). Off-season or early season fruit production in greenhouses gives growers profitable marketing advantages that justify the costs of disposable bumble bee colonies. However, there is no incentive in being the first grower of the year with fresh wildflower seed, and so no justification exists for greenhouse cultivation and its attendant bumble bee colony purchases. For native seed crops flowering in open fields during the growing season, pollinators less expensive than commercial bumble bees should be able to satisfy pollination needs.

Currently Managed Nonsocial Bees

Some managed but nonsocial bees are likely to find use in pollinating wildflower seed crops. In North America, farm management protocols exist for three species. The alfalfa leafcutting bee (*Megachile rotundata*) and the blue orchard bee (*Osmia lignaria*) nest above ground in cavities, whereas the alkali bee (*Nomia melanderi*) nests underground. As with any bee, nesting needs, flight seasonality, floral host preferences, and pollination efficacy together will define their promise as pollinators of a native wildflower species for seed production. The question then remains: Can we sustainably manage these bees in large enough numbers to adequately stock wildflower production fields?

Management methods and markets are mature for the alfalfa leafcutting bee (see chapter 7, this volume); this bee has revolutionized alfalfa seed production over the past 40 years (Stephen, 2003). It does require summer's warmth for development and flight, precluding its use for pollinating springtime wildflowers. It is particularly adept at pollinating small-flowered legumes such as alfalfa. The prairie clovers (*Dalea*) are also small-flowered, summer-blooming, herbaceous perennial legumes, two of which are desired for Great Basin reseeding (see table 4.1). A third (prairie) species, *Dalea purpurea*, was commercially available for immediate transplant into our outdoor trial garden, and so I used it as a surrogate for the Great Basin species that were being grown from seed. As expected, the alfalfa leafcutting bee was found to freely forage at its uncaged flowers, choosing to provision its nest cells solely with *D. purpurea* pollen. Stigmatic contact appeared inevitable because the bees scrabbled for pollen on the dense inflorescences. I obtained substantial seed sets per plant (>20,000 seeds, and up to 80% seed set; Cane, 2006a).

Honey bees, bumble bees, and several wild solitary bee species were also seen visiting these *Dalea* flowers concurrently with the alfalfa leafcutting bee, so the leafcutting bee's specific contribution to pollination awaits assessment. In cages, at least, alfalfa leafcutting bees are useful in cross-pollinating small-flowered specialty seed crops (e.g., carrots; Tepedino, 1997) or hybrid foundation seed or in regenerating small lots of seed for seed repositories, showing more versatility than might be expected from their floral foraging preferences. This leafcutting bee could likewise be flown in field cages to bulk up small lots of seeds harvested from wild stands of forbs. This could yield the several kilos of clean foundation seed to be later sown by growers (*Lomatium* is an apt candidate, also being of the carrot family). The field pollination needs of several of the summer-blooming, small-flowered wildflowers such as *Dalea* spp. could be satisfied by alfalfa leafcutting bees as well, managed in the same way as for fields of seed alfalfa (see chapter 7).

Ground-Nesting Bees of Agriculture

The pollinator guilds of all of the target wildflower species I have surveyed thus far include multiple species of ground-nesting bees, sometimes to the exclusion of any other kind (e.g., for *Lomatium dissectum*). Numerous other ground-nesting bees effectively pollinate various crop species as well (Cane, 1997), but only the alkali bee, *Nomia melanderi*, is intensively managed (Johansen et al., 1978). Like the alfalfa leafcutting bee, it flies soon after midsummer and is used to pollinate seed alfalfa (Cane, 2002; see also chapter 7, this volume). It may prove useful to pollinate species of *Dalea* and *Cleome*; *C. lutea* is suspected to be a key natural floral host of the alkali bee (Richard Rust, personal communication, 2006).

Unlike the alfalfa leafcutting bee, the alkali bee presents daunting nest establishment challenges typical of other ground-nesting bees. It requires silty subirrigated soils with salty surfaces. Managed aggregations can be densely populous (more than 5 million females) and can endure for 50 years or more (Cane, 2008). However, where naturally silty, subirrigated soils are absent, these earthen nesting sites can be difficult and expensive to construct. Nest sites are then populated by coring, transporting, and inserting hundreds or even thousands of large 30 kg soil blocks bearing overwintering prepupae. The blocks are punched from the parent aggregation using custom hydraulic tools. Native seed crops might be profitably produced adjacent to managed alkali bee aggregations, a novel strategy of bringing the crop to the bee rather than vice versa. However, unless wildflower seed growers have the long-term commitment of many alfalfa seed growers to maintain nesting populations of the alkali bee, active management of this and other ground-nesting bee species is impractical or impossible for agricultural pollination, including wildflower seed production.

In only a few cases have wild but unmanaged ground-nesting bees proven to be both effective and adequately abundant across the entire range of cultivation for any one crop. In the southeastern United States, the southeastern blueberry bee (*Habropoda laboriosa*; Apidae) and bumble bees are together responsible for pollinating farmed rabbiteye blueberries (*Vaccinium ashei*) on all but the largest farms (Cane & Payne, 1993). At some North American gardens and commercial fields of squashes and pumpkins (*Cucurbita* spp.), the squash bees (esp. *Peponapis pruinosa*; Apidae) satisfy pollination needs (Hurd et al., 1971; Tepedino, 1981; Roulston et al., 1996; Shuler et al. 2005). A collaborative survey of pollinators amid cultivated squashes and pumpkins is demonstrating the predominant pollination service of *Peponapis* bees throughout most of the Western Hemisphere (Cane et al., unpublished data). Nesting populations of *P. pruinosa* can apparently increase enough to pollinate cultivated squashes and pumpkins at field sizes up to at least 75 ha. (R. Hammon, personal communication, 2006). Both *H. laboriosa* and *P. pruinosa* are ground-nesting floral specialists that effectively pollinate their respective crops (Tepedino, 1981; Sampson & Cane, 2000). Importantly, both crops are typically grown at a location for years at a time, accommodating the slow growth of pollinator populations detailed subsequently.

Untried Bees to Manage

Potentially manageable, effective pollinators exist among North America's 4,000 non-social bee species. Most promising are the 139 species of North American *Osmia*, for half of which species we already know basic nesting habits and many of which are cavity nesters (Cane et al., 2007). Some have proven themselves amenable to artificial nesting substrates to pollinate various perennial crops (e.g., apples, raspberries, almonds; see, e.g., Bosch, 1995; Torchio, 2003; Cane, 2005, 2006b). Unlike species of *Megachile* or *Hoplitis*, which overwinter as prepupae, all *Osmia* overwinter as adults. As a group, *Osmia* are therefore more phenologically versatile, some species emerging with the first warm days of spring (e.g., *O. lignaria*; see chapter 6, this volume). Others, such as *O. bruneri* (Frohlich, 1983) or *O. sanrafaelae* (Parker, 1985), require days of warm incubation that delay their emergence until midsummer. To match on-farm bloom phenology, emergence date for a given *Osmia* species can be manipulated somewhat to shift it earlier or later by several weeks. Alternatively, populations can be sourced from places with cooler or warmer climates to better match a seed crop's local blooming schedule. If a wildflower is farmed for seed where its natural bloom time is advanced or retarded, novel matches of bee and wildflower are possible. One or more species of *Osmia* are usually present and sometimes prevalent in the guilds of floral visitors that I have thus far sampled at the wildflowers targeted by this project (e.g., dominating every one of 21 *Astragalus filipes* populations sampled in four states). Some of these cavity-nesting *Osmia* occur in more than one floral guild. For instance, I have sampled *O. bruneri* at three of the four legumes (*Hedysarum boreale*, *Astragalus filipes* and *Lupinus sericeus*). Such floral versatility foreshadows managing one *Osmia* bee species for several different flowering crops.

Unmanageable Bees to Try

Unmanaged wild bees pollinate these wildflowers in nature, so why not rely on this strategy for farmed wildflower seed crops as well? In wildflower fields of several native seed growers, I have found ground-nesting native bees foraging and nesting, albeit in sparse numbers. In home and market gardens, ratios of bloom to nearby nesting opportunities can yield satisfactory densities of such wild pollinators. However, at larger commercial field sizes, wild pollinator numbers typically become greatly diluted (e.g., Scott-Dupree & Winston, 1987), hence the need to supplement with managed pollinators. To be profitable, most family and corporate farms of the developed world must depend on either mechanization and economies of scale or niche marketing. Farmed flowering monocultures present a "sea of bloom" to bees, with plentiful pollen and nectar rewards. Insufficient undisrupted nesting opportunities may limit growth and ultimate size of nonsocial bee populations, judging from the inadequate pollination service provided by unmanaged bees in larger fields and orchards.

Nesting opportunities for wild bees are often restricted to the field perimeter, which likely explains their sparsity in the larger fields and orchards of commercial agriculture. When nesting is restricted to field margins, simple edge:area relationships dictate that nesting densities must double for every fourfold increase in field size to maintain constant floral visitation intensity in the field. The predicament is obvious for those nonsocial cavity-nesting bee species that nest in abandoned beetle burrows in dead wood or in pithy dead twigs or stems. These nesting opportunities are scarce or nonexistent within larger fields and orchards in many farming regions. Bumble bees may fare no better, because most species nest either above ground in tree hollows or underground in abandoned nests of rodents or other small mammals.

Even for ground-nesting nonsocial bee species, fields and orchards rarely offer sufficient nesting habitats to match the prodigious pollination needs of traditional crops. These constraints likely foreshadow similar problems for wildflower seed growers who expect to depend on unmanaged pollinators. Most ground-nesting species seek patches of exposed, sunlit bare soil, sometimes as vertical embankments. Farming practices and crops themselves often limit these opportunities, owing to impenetrable shady canopies

(e.g., seed alfalfa, cranberries), impermeable plastic mulches (e.g., commercial strawberries); or dense interalley turf (e.g., tree fruit orchards, blueberries). Even for crops such as sunflower with suitably exposed soil (Wuellner, 1999), controlling weeds during bloom by interrow cultivation buries these bees' nest entrances. Deeper nesting species escape tillage damage once their nesting season is done. Not so for bees nesting shallowly in the soil, whose nests are destroyed by cultivation. Their stewardship may require year-round no-till practices. These shallow nesters include all of the species of *Megachile* (Eickwort et al., 1981) and *Osmia* (Cane et al., 2007) that nest shallowly underground, which are the very species I have sampled from pollinator guilds of *Astragalus*, *Crepis*, *Hedysarum*, *Lupinus*, and *Penstemon* (see table 4.1, figure 4.2). This group of ground-nesting bees also includes effective pollinators of traditional crops (Hobbs, 1956; Cane et al., 1996). Whether or not they can ultimately satisfy the pollination needs of native seed growers remains to be seen.

Growers will need patience with the realized reproductive outputs of unmanaged solitary bees; they multiply slowly for an insect. A female of a nonsocial species starts life with 30 or so eggs. Half or more of these will yield males. Females of most species will typically provision only one or two nest cells daily during good weather. Larval diseases and nest parasites and predators can subtract substantially from a mother bee's reproductive output. Hence, in the first years that a crop blooms, starting numbers of unmanaged bees will fall far short of densities needed to satisfy the sudden pulse in pollination need. Numbers of unmanaged pollinators will likely remain inadequate for some years while their populations gradually grow. Overstocking of managed species, such as honey bees, may further retard this growth through floral resource competition. Wild bees may initially be more populous if availed another adjacent, usable flowering crop in the preceding years. The circumstances on most wildflower seed farms tend to match those found to favor pollination of traditional crops by unmanaged wild bees: fields adjacent to wildlands, small field size, little insecticide use, and either alternate floral resources nearby (for floral generalists) or a perennially grown crop that blooms year after year (for its floral specialists). Even under these conditions, adequately abundant managed pollinators will be needed initially to pollinate the crop, serving as a bridge between the first years of a new wildflower crop and the year when the numbers of wild bees finally grow to satisfy pollination needs. If and when patient stewardship results in sufficiently populous ground-nesting pollinators to service bloom, they might be the least expensive and simplest means of pollinating a given wildflower crop.

Flow of Research

Research for this program must progress simultaneously on multiple fronts to keep apace of grower needs (Bosch & Kemp, 2002). I am following a logical sequence of steps:

1. Plots of source-identified wildflowers are needed in our common garden for later caged pollination trials. Using wild populations in situ is logistically impractical if they are separated by hundreds of kilometers. Manual pollination treatments and later seed harvest can

require daily attention, with intervening protection from herbivores, seed predators, and a curious public (Cane, 2005). Because most of these wildflowers are unavailable from nurseries, my collaborators collect seed from the wild, which are then germinated and grown in the greenhouse. Once transplanted outside, I await first flowering, typically 1–3 years later for these perennials.

2. To characterize the small subset of potential pollinators from each bee community, I systematically net sample guilds of each wildflower's floral visitors throughout their geographic ranges. The locations of floral host populations and estimated bloom dates are gleaned from specimens housed in the region's herbariums.

3. To obtain starting populations of the subset of potentially manageable cavity-nesting species, both drilled nesting blocks with multiple-sized holes and drilled stick nests are manufactured and deployed. Most are placed in the wild, preferably in the presence of target wildflower hosts, but we have enjoyed some success placing them around grower's wildflower fields, too. With luck, some of the cavity-nesting species thus obtained match those surveyed at a wildflower's visitor guild. Each nest's progeny are identified by sacrificing only one individual, preferably a male. This leaves the rest to fly, forage, and nest the following year in confinement with one of the common garden stands of wildflowers.

4. Their prowess as pollinators is assessed against our own manual pollination treatments from the preceding year.

5. Stocking densities of the bees are estimated that give both abundant seed yields and sustainable population growth of the bees when limited to a particular floral species for forage.

Two case studies show that success proceeds apace of progress with each of these components while overcoming idiosyncrasies of bees, bloom, and weather. For *Balsamorhiza sagittata*, which is estimated to take more than 5 years from seed to bloom, I experimented with the species' breeding biology using nearby wild populations (Cane, 2005). It was found to require insect pollinators (see figure 4.2) and to benefit from outcrossing (see figure 4.3). Two widespread cavity-nesting bees, *O. californica* and *O. montana*, were commonly sampled visiting its flowers. Both were earlier reported to forage at *Balsamorhiza* and *Wyethia* (Torchio, 1989). When collecting pollen, they were seen to vigorously pat pollen-bearing surfaces of the stigmatic lobes using their ventral abdominal scopae, thereby inevitably pollinating as well. Populations readily increased using my practical nesting system (Cane, 2006b). An estimated stocking density of several hundred females per hectare satisfies pollination needs (Cane, 2005). These two *Osmia* species answer for all of the objectives of the program and are ready to manage as pollinators for seed production of any *Balsamorhiza* species.

I have pursued a different approach and a different path to pollinator management with my studies of *Dalea* (Cane, 2006a). To accelerate my research schedule, I obtained transplants of a Great Plains species, *D. purpurea*, for our common garden in Logan. It served as a surrogate species while I awaited seed and maturation of the two Great Basin species, neither of which has been previously cultivated nor is found within 250 km of Logan. Pollination trials in our common garden revealed a necessity for pollinators (see figure 4.2) and great benefits from outcrossing (figure 4.3). Its rich Midwestern pollinator guild suggests many choices for pollinators, a guess borne out in our common garden, where honey bees, bumble bees, alfalfa leafcutting bees, and various wild species eagerly sought its flowers. Fertile seeds formed at 60–80% of available flowers. A small, managed nesting population of alfalfa leafcutting bees preferentially provisioned numerous nest cells with the bright orange pollen of *D. purpurea* flowers. Because inflorescences of the two Great Basin *Dalea* spp. closely resemble those of *D. purpurea*, I am optimistic that either honey bees or managed alfalfa leafcutting bees will handily pollinate farmed Great Basin *Dalea*. Initially small populations of wild bees seen visiting newly planted *Dalea* could multiply in subsequent years in response to simple stewardship practices, ultimately satisfying the pollination needs of farmed *Dalea*.

Summary

Federal, state, and private land managers in the western United States annually seek tons of affordable seed from dominant native wildflowers for use in their wildland rehabilitation and restoration programs. The prohibitive price of wild-collected wildflower seed stymies that effort. Seed costs and practicality necessitate the farming of wildflowers for their seed. Heterogeneous cultivation needs, seed harvest methods and site-specific restoration seed mixes all dictate that farmers grow these species in monocultures rather than meadow mixes. However, individual native seed growers can be expected to be farming more wildflower species as their skill and success meet demands.

I am finding that bees are needed to pollinate nearly all of the target wildflower species desired for restoration and rehabilitation in Great Basin plant communities. Actively managed bees will initially be necessary, at least as a "bridge" for growers in early production years. If and when wild bees proliferate to become abundant on farms, then some farms and seed crops will eventually enjoy substantial pollination services from passively managed local native bee communities. Context, practicality, and cost will determine the mix of bees used. Options under study for actively managed pollinators include honey bees, currently managed nonsocial species (*M. rotundata*, *O. lignaria*), and additional cavity-nesting species of *Osmia*, *Megachile* and *Hoplitis* that show pollination prowess and nest management potential. Native bees will need to be sustainably managed on seed farms, as it is impractical and costly to replenish managed populations by annually trap-nesting wild bee populations. Unmanaged farm populations of bumble bees and ground-nesting bees should benefit from some simple pollinator stewardship practices, including a hiatus in cultivation during bee nesting, wise insecticide use, and planting supplemental forage crops nearby.

Pollinator lessons learned with the Great Basin Plant Selection and Increase Project should translate to other regions and biomes in which native wildflower seed is increasingly sought for restoration around the United States, including the Upper Colorado Plateau, the Mojave Desert, and the Great Plains. Successful seeding and restoration of native wildflowers will have far-reaching positive ecological impacts on damaged Great

Basin plant communities and their dependent native bee communities. These gains will dwarf the comparatively small economic impact of a peculiar native seed industry and the novel mix of bees that it will use to produce its wildflower seed.

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5 Honey Bees, Bumble Bees, and Biocontrol

New Alliances Between Old Friends

Peter G. Kevan, Jean-Pierre Kapongo, Mohammad Al-mazra'awi, and Les Shipp

Introduction

Bees are well known for their ability to carry microscopic particles. After all, they are important pollinators, and most pollen is microscopic (Wodehouse, 1959). Bees also are known to carry fungal spores and bacterial cells, some of which are pathogens of the bees themselves, or of plants (Morse & Nowogrodzki, 1990; Shaw, 1999). The capacity of bees to vector spores, bacteria, and viruses can be turned to our advantage by using them to transport biological control agents, a technique known as pollinator biocontrol vector technology (Kevan et al., 2001, 2003, 2004, 2005). This chapter describes the range of biocontrol agents useful for this technique and the targets against which they can be used. These biocontrol agents all have good potential for control of weeds, plant pathogens, or insect pests. The safety of the vector is considered next, along with the fact that it must be harmonized with efficacy against the target problem. Following from and closely linked to those two parts of the pollinator biocontrol vector technology is the matter of concentration of the biocontrol agent in an effective formulation and the efficiency of its acquisition and delivery by the vector. Dispenser designs are discussed as they influence the efficiency of pickup of the formulated biocontrol agent by the pollinators and so constitute another component of the technology. Finally, we briefly consider environmental safety and issues of nontarget effects.

The elements involved in this new technology are:

1. A crop in need of protection
2. A pest (weed, disease, or herbivore) that adversely affects crop production
3. Pollinating insects that visit the flowers of that crop

Bee Pollination in Agricultural Ecosystems

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