

SELF-INCOMPATIBILITY OF U.S. GREAT BASIN *SPHAERALCEA* (MALVACEAE) AND REGIONAL PREVALENCE, POLLINATION EFFICACY, AND FLORAL INFIDELITY OF THEIR OLIGOLECTIC *DIADASIA* BEES

James H. Cane^{1,*}, Byron G. Love²

¹WildBeecology Consulting, Logan UT 84322 and emeritus research entomologist, PIRU

²USDA-ARS Pollinating Insect Research Unit (PIRU), Utah State University, Logan, Utah USA

Abstract—Three globemallows – *Sphaeralcea coccinea*, *S. grossularifolia* and *S. munroana* (Malvaceae) – are widespread, summer-flowering perennial forbs found throughout the sagebrush-steppe and neighbouring biomes of the western USA. Their seed is desirable for rehabilitating degraded rangelands. This study had four objectives: 1) determine each species' breeding biology, 2) quantitatively characterize their regional pollinator guilds, and evaluate 3) pollination efficacy and 4) floral constancy of a bee that is an abundant *Sphaeralcea* specialist.

All three globemallows are self-incompatible. On average, 43-76% of manually outcrossed flowers formed capsules (schizocarps) averaging 7-9 seeds each (potential of 11 seeds). In contrast, autogamy and geitonogamy yielded few capsules, half of them seedless. Autogamy yielded few mature seeds despite proximity of anthers and stigmas.

Floral visitors to *S. grossularifolia* and *S. munroana* were systematically surveyed across the American sagebrush-steppe. Bees foraging at wild and cultivated populations were non-social ground-nesters. Three globemallow pollen specialists (oligoleges, particularly *Diadasia diminuta*) were frequent and often abundant, as were several common generalist halictid bees among the 38 species collected. Single floral visits by pollen-foraging females of *D. diminuta* deposited sufficient pollen to effect full seed set (means of 42 and 34 grains per stigma at *S. coccinea* and *S. grossularifolia*, respectively).

Newly planted *Sphaeralcea* plots were colonized within several years by *D. diminuta*. Females foraging a mixed experimental garden frequently switched between globemallow species during foraging bouts, evidence that these floral specialists will facilitate hybridization rather than behavioral isolation of *Sphaeralcea*. The abundant pollinators at these *Sphaeralcea* species should deliver sufficient outcrossing at most locales, including both wildlands and farmed fields.

Keywords—Anthophila, Apiformes, globemallow, oligolecty, specialization, pollinator

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*Corresponding author:

jim.cane2@gmail.com

INTRODUCTION

The globemallows (*Sphaeralcea*: Malvaceae) constitute a monophyletic, amphitropical genus of 40+ herbaceous, perennial wildflower species found mostly in arid basins and foothills of western North and South America, where they can be common and abundant. They comprise the second largest genus in their tribe, the Malveae, and the largest North American genus in the Malvaceae (Tate et al. 2005). Taxonomy within the

group can be confounded by polyploidy (Laduke 1986; Holmgren et al. 2005) and a proven capacity to hybridize (Dreher 2014).

Although *Sphaeralcea* are common and familiar, their pollination and breeding biology is rarely documented. In North America, a warm desert species (*S. laxa* Woot. & Standl.) is self-incompatible (Hubbard et al. 1993), as are four Argentinian species of *Sphaeralcea* (Gutiérrez et al. 2024). Other species can be hybridized too, based on limited crosses (Dreher 2014). Several close

relatives of *Sphaeralcea* (Tate et al. 2005) present either a mixed breeding system (García-Franco & Arroyo 1995) or one reflecting incompatible ploidy levels (Tate & Simpson 2004). More broadly, some species of Malvaceae are self-compatible, but others are obligate outcrossers (reviewed in Raju & Rani 2016). These few studies suggest that other species of *Sphaeralcea* may be self-incompatible too.

Oligolectic bees from several genera are known to specialize on *Sphaeralcea* pollen (Danforth 1991; Linsley & MacSwain 1957; Sipes & Tepedino 2005). Among these are 12 closely-related species of *Diadasia* bees (Apidae), with 11 more congeners specialized for other malvaceous genera (Sipes & Tepedino 2005; Tepedino et al. 2016). Very few digitized specimens of these species have been collected in the sage-brush steppe, the region of this study (<http://www.discoverlife.org>). Surprisingly, no *Sphaeralcea* species has been methodically surveyed for its guild of bees or their relative abundances at flowers.

Fourteen species of *Sphaeralcea* are described from the U.S. Intermountain West, with four common species ranging northward into the Great Basin cold desert shrub-steppe and the neighbouring Snake River Plain. Native plant communities in this region have been widely degraded or even displaced by historic overgrazing plus invasion by exotic annual grasses that carry more frequent fires and outcompete native wildflower seedlings for spring moisture. As a consequence, sage-steppe specialists, notably the sage grouse, are in such steep decline as to be candidates for listing as endangered species (Wisdom et al., 2005). In response, the U.S. Bureau of Land Management coordinated and funded an extensive, concerted, multi-year research effort to overcome all possible barriers to farming, storing and sowing native seed of common native shrubs, grasses and wildflowers of basin sage-brush steppe and adjoining plant communities (<https://research.fs.usda.gov/treesearch/42005>). These included the *Sphaeralcea* species evaluated here.

Understanding the reproductive needs of target wildflowers and nesting/foraging traits of their pollinators can be critical in two contexts, seed farming, and later, rehabilitating wildland plant communities. Farmed native seed in the U.S. is grown in monoculture fields (to ensure seed

purity). Some farms are distant from the wildlands where many of their pollinators reside (e.g., Shock et al. 2012), whereas others adjoin wildlands. In general, farmers remedy pollination needs by renting hives of honey bees (*Apis mellifera* L.), which can pollinate many but not all crops. Knowing the difference before growing a given wildflower seed crop is critical for the farmer, as it is an expensive multiyear land and labor commitment.

Seed destined for wildland restoration is generally custom mixed at the seed storage warehouse. Cheaper seed (Eurasian and native grasses, some shrubs) comprises the bulk of the mix, with more expensive seed (most native forbs) relegated to much smaller fractions. As a consequence, even successful plantings result in widely spaced wildflowers (Ott et al. 2016), with consequences for pollination and so self-perpetuation of the wildflower species. Compared with self-fertile species, host plant sparsity is far more problematic for self-incompatible species, as their ovule fertilization will require pollen from distant conspecific individuals. Sparse, widely spaced host plants will greatly slow foraging by their oligolectic pollinators too, thereby constraining their lifetime reproduction. Where several *Sphaeralcea* species grow in neighbouring fields or wildland patches, floral constancy by colonizing oligoleges (or ubiquitous honeybees) could limit *Sphaeralcea* hybridization, or conversely, these bees could forage indiscriminately among *Sphaeralcea* species.

The objectives of this study were four-fold. 1) Characterize the breeding biology for each of three widespread globemallows of the U.S. sagebrush-steppe: *Sphaeralcea coccinea* (Pursh) Rydberg, *S. grossularifolia* (H. & A.) Rydberg and *S. munroana* (Douglas) Spach. Capsule and seed set was measured for manually pollinated plants grown in our greenhouse. 2) Survey and compare the taxonomic composition and relative abundances of floral visitors at patchy populations of *Sphaeralcea* that we encountered across the Great Basin and adjacent Snake River Plain. 3) Document colonization of new *Sphaeralcea* plantings by its specialist bees. 4) Evaluate the pollination efficacy of one of its common specialist bees, *Diadasia diminuta* (Cresson), in terms of single-visit pollen deposition at two available *Sphaeralcea* species in

our common garden. The results are then interpreted for both native seed growers and land managers rehabilitating sagebrush-steppe plant communities, including the likely role of its specialist bees in either speciation or hybridization of their *Sphaeralcea* hosts.

MATERIALS AND METHODS

BREEDING BIOLOGY OF *SPHAERALCEA*

Ten potted plants each of *S. coccinea*, *S. grossularifolia* and *S. munroana* were grown in our greenhouse from young plants provided by Therese Meyer, Great Basin Research Center and Seed Warehouse, Ephraim, Utah. To determine when floral stigmas first became receptive, ten newly opened flowers were tagged. For each of the next three days, we immersed several of their clipped styles in hydrogen peroxide. Unlike stigmas from day-old flowers, stigmas that were 2-3-days-old generated bubbles, revealing

peroxidase activity of a receptive stigma (Zeisler 1938). By the second day, their styles also had elongated to extend beyond the staminal column (Fig. 1c). As bloom progressed, we enclosed three budded racemes on each of 9-17 plants per species in fine nylon mesh bags. Once bagged flowers were two days old, they were tagged and assigned one of three manual pollination treatments: autogamy (unassisted self-pollination), geitonogamy (transfer of self pollen) and xenogamy (outcrossing). Flowers were not emasculated, both because the delicate styles could be damaged while cutting the many surrounding stamens, plus herkogamy minimized chances for autopollination. Flowers in the autogamy treatment remained bagged until after bloom. Geitonogamous pollination involved daubing recipient virgin stigmas with anthers of an untaged flower from the same plant. Donor

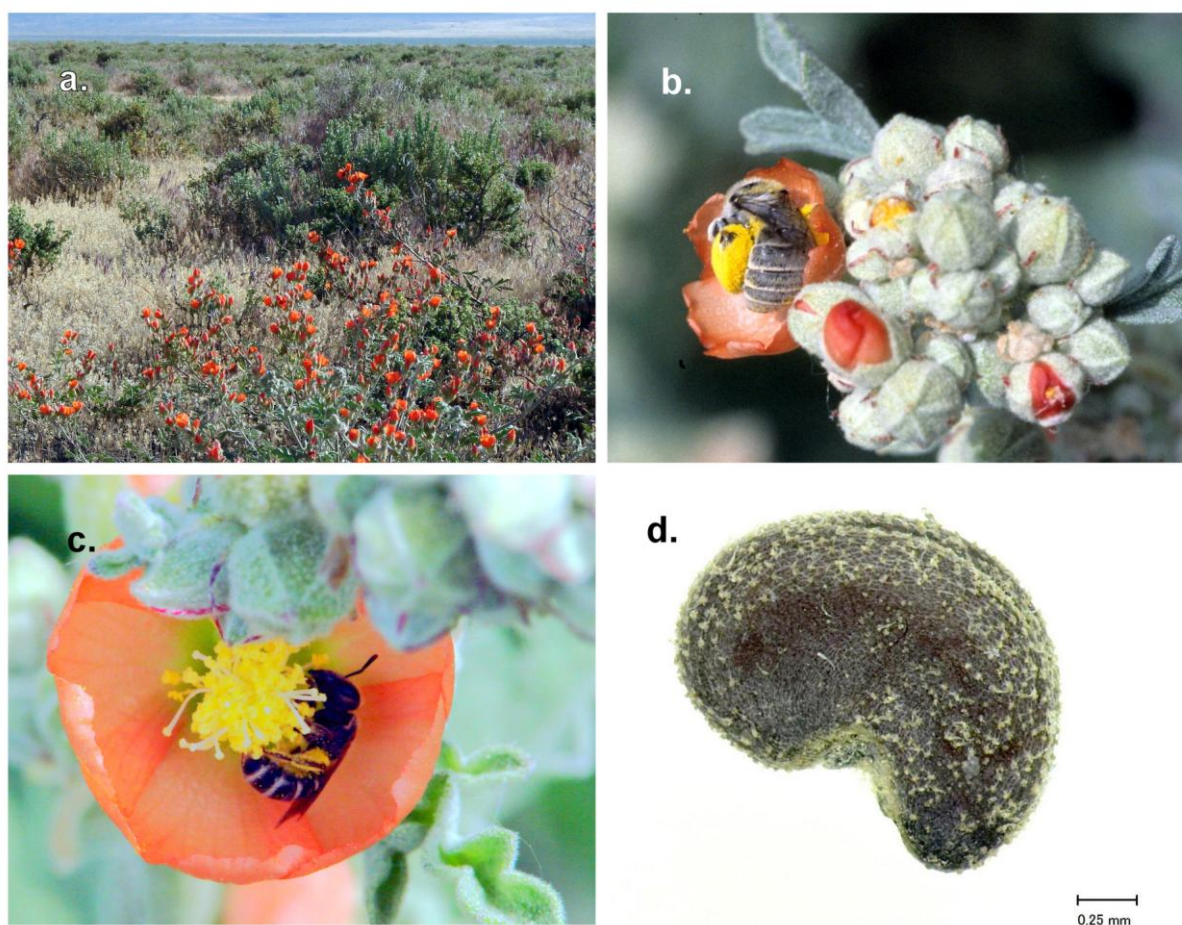


Figure 1 a) *Sphaeralcea* flowering amid sagebrush near Austin, Nevada. b) Female of the oligolege *Diadasia diminuta* foraging in a *Sphaeralcea* flower. c) Female *Halictus ligatus* bee foraging in *Sphaeralcea* flower. Note the multiple white styles of pistil. d) Seed of *Sphaeralcea*

pollen for xenogamy was taken from flowers of other, untagged racemes of conspecifics.

We evaluated our use of a clipped stamen to daub pollen on stigmas of another recipient flower for pollen transfer. While being viewed microscopically, clean stigmas of two trial flowers were lightly brushed ten times using anthers of another flower, taking care to not touch the anthers of the recipient flowers. Every stigma ($N = 24$) thus brushed received pollen, often piled 4-6 grains deep, with 15-30 grains in contact with each stigma's surface. We therefore used this floral daubing method for our manual pollination treatments.

CAPSULE AND SEED PRODUCTION

Once capsules were mature, but before their seed was shed, each raceme's complement of capsules was counted, then clipped and later dissected to count each capsule's content of mature seeds. The three species and three pollination treatments were compared using general mixed models for their percent sets of capsules per

raceme pollinated (arcsin transformed) and yields of seeds per capsule (square-root transform) (Littell et al. 1996). Data was analysed as a split plot design, with *Sphaeralcea* species and pollination treatment as fixed effects and plants as unreplicated blocks. Plotted residuals were judged to be adequately normal. Where differences were found among treatments ($P \leq 0.05$), treatments were compared by Tukey-Kramer *a posteriori* tests. For comparison, we also collected 24 maturing capsules from eight plants from a wild population (east of Snowville, Utah) and counted their content of seeds.

POLLINATOR GUILDS OF SPHAERALCEA

We characterized the guild of bees that visit flowers of the two common *Sphaeralcea* species that we encountered - *S. grossularifolia* and *S. munroana* - found at 20 wild populations in basin and foothill sage-steppe habitats across a 100,000 km² region. We could not confidently distinguish these two *Sphaeralcea* species, reflecting their close morphological, floral (Fig. 2) and genetic

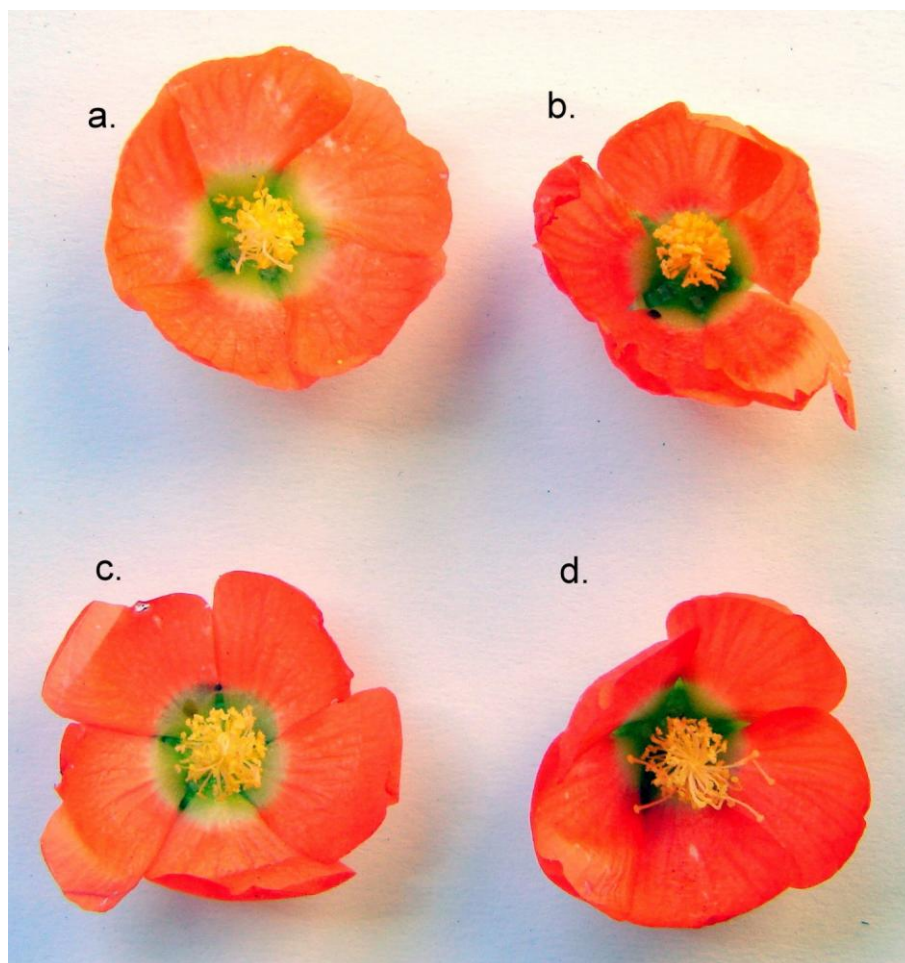


Figure 2. Flowers of the four species of *Sphaeralcea* studied: a) *S. coccinea*; b) *S. grossularifolia*; c) *S. parvifolia*; d) *S. munroana*

similarities (Holmgren et al. 2005). For each site survey, one or both authors netted bees individually at flowering *Sphaeralcea*. Bees were surveyed during fair, warm, relatively calm weather between 0900–1500h in populations with abundant bloom. Plants were sequentially and briefly inspected once for floral visitors during a walking scan census, thereby providing a quantitative “snapshot” of local guild composition and density at the time (detailed in Cane & Love 2016). We counted and sampled all flowering individuals in small populations, or for larger populations, we netted bees from counted flowering individuals encountered along a 2-m-wide walking transect through the patch. By counting all plants that we inspected for visiting bees, we could calculate densities of each bee species per 100 plants across sites. We expected 20 surveys to be sufficient for characterizing the guild and relative abundances. Collected bees were pinned, labelled and identified to species using published keys and comparison with specimens in the USDA-ARS National Pollinating Insect Collection in Logan, Utah, where vouchers of all collected specimens are databased and deposited.

Females of the bees *D. diminuta* and *D. lutzii* Ckll. are sister species considered by some to be a species complex (Sedonia Sipes, pers. comm.). Unworn specimens were generally distinguishable, but older worn females of the two species were not, even with reference to existing determined museum specimens. Both species are oligoleges of *Sphaeralcea* throughout their ranges (Sipes & Tepedino 2005); *D. diminuta* ranges further north into the Great Basin and Snake River Plain than does *D. lutzii*. For practical reasons, therefore, we pooled worn females with the more common *D. diminuta*, realizing that this decision may or may not under-represent *D. lutzii* sampled at some locations.

POLLINATION EFFICACY BY THE BEE *DIADASIA DIMINUTA*

The pollination efficacy of *D. diminuta* females was evaluated using single-visit pollen deposition at ten virgin flowers each of potted *S. coccinea* and *S. grossularifolia*. These large plants were kept in an insect-free greenhouse until the hour of experiment. At that time, we placed an individual potted plant among the patch of four flowering globemallows that we had been planted several years earlier in an outdoor research plot (see more

details below), one that supported a population of *D. diminuta*. As an individual foraging female freely visited the virgin flowers on the potted plant, the visited flowers were marked, removed and returned to the laboratory. We repeated this with the other potted plants. The large pollen grains enabled direct counting of stigmatic pollen loads of on each style using a stereomicroscope (most flowers had eight styles). Only pollen grains directly contacting the stigmatic surfaces were counted. Counts on all eight stigmas of the first six flowers were sufficiently consistent within a flower (mean of std dev = 9.3), so thereafter, pollen loads were counted on a random subset of three stigmas per flower for the remaining flowers.

FLORAL FIDELITY BY FORAGING FEMALE *DIADASIA DIMINUTA*

A 3.3m × 16m garden plot adjacent to Utah State University in North Logan, Utah was planted with ~100 transplants of the four widespread orange-flowered globemallow species of the U.S. sagebrush-steppe: *S. coccinea*, *S. grossularifolia*, *S. munroana* and *S. parviflora* Nelson. We grew all four from seed. Half of the plot was organized in four neighbouring single-species rows. For the other half, additional transplants were available for all but *S. parviflora*; these were added and tagged in an intermixture. After three years, wild *D. diminuta* had colonized the garden site and multiplied. Late in bloom of year 4, when male bees had died off and all females of *D. diminuta* were gathering pollen, we tracked foraging individuals as they flew through the array of transplants. For two days at mid-morning, two teams visually followed females through the array, recording the identities of sequentially visited plants. Female *D. diminuta* are fast, erratic fliers, so we generally could only record short visitation sequences.

We characterized foraging preferences as summed counts of observed flights that were between either conspecific or heterospecific plants. The visit counts were compared by logistic regression against a null hypothesis of equal visitation to the four species. The probabilities of flights between specific species pairs were confounded by planting design, as not all species were available in neighbouring rows. We therefore averaged the three nearest neighbour distances between every pairing of the four *Sphaeralcea* species in the plot. On these distances we regressed the sum of interspecies flights observed by

foraging female *Diadasia*, fitted using an inverse polynomial equation (SigmaPlot 12.5).

RESULTS

BREEDING BIOLOGY OF *SPHAERALCEA*

For all three *Sphaeralcea* species, xenogamous pollination yielded far more capsules (Fig. 3) and seeds (Table 1) than either geitonogamy or autogamy. Pollination treatment groups differed significantly in their production of seeded capsules ($F_{[2,70]} = 54$, $P < 0.001$) and mature seeds per capsule ($F_{[2,91]} = 128$, $P < 0.0001$). Of the 100 treated racemes, 27 yielded no capsules (representing 556 flowers), being 15 from autogamy, 11 from geitonogamy and just one from xenogamy. For those racemes setting at least one capsule, capsule production resulting from autogamy and geitonogamy were similar for all three globemallows ($P = 0.93$) and far inferior to that of outcrossed flowers ($P \leq 0.001$) (Fig. 3). Similarly, seed yields resulting from our manual pollinations of greenhouse plants also differed by pollen source. The autogamy and geitonogamy treatments delivered equivalent seed sets per capsule ($P > 0.8$). They were far inferior to outcrossing ($P < 0.0001$), which enhanced seed production per capsule 2-5-fold (Table 1). Outcrossing of *S. grossularifolia* set 30% fewer seeds per capsule than the other two species ($F_{[2,91]} = 12.5$,

$P < 0.001$) (Table 1), but like the other two species, autogamy and geitonogamy were equivalent ($P = 0.8$) and inferior for seed production per capsule (Table 1). The 24 capsules collected from the population of wild globemallows contained two to three-fold more seeds per capsule (18.8 ± 8.9 seeds) than our manually outcrossed greenhouse flowers (Table 1).

POLLINATOR GUILDS OF *SPHAERALCEA*

Native bees were the predominant visitors to *Sphaeralcea* flowers encountered during our systematic surveys. We collected ≥ 39 species of native bee (Table 2) from 4600 inspected wild *Sphaeralcea* plants (median 109 per site) growing in 20 populations across the Great Basin, Colorado Plateau and Snake River Plain (Fig. 4). Eleven of the bee species were considered incidental, being represented by a single specimen (Table 2). Excluding incidentals, soil-nesting typifies 98-100% of the individuals, depending on the identities of the few *Megachile* collected. Bees were often numerous at globemallow flowers, averaging 14 foragers for every hundred flowering individuals, and sometimes as many as a bee at every plant. The most common floral generalist, *Agapostemon angelicus* Ckll., represented 8% of the sampled bees (Table 2). Four of the more abundant bees taken in this study are taxonomic floral

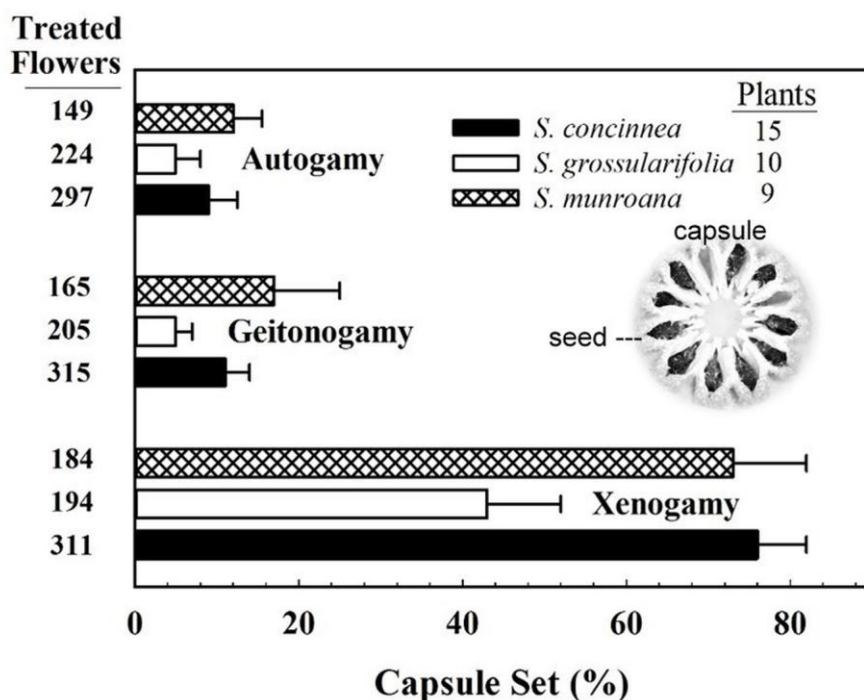


Figure 3. Set of seeded capsules by three species of *Sphaeralcea* in response to manual pollination treatments

Table 1. Three pollination treatments applied to flowers of *S. coccinea*, *S. grossularifolia* and *S. munroana*, comparing both average seed set per capsule and seed yield per 100 flowers pollinated.

Reproductive response	<i>Sphaeralcea</i> species	Pollination treatment [†]			No. of plants	Sum of capsules or flowers
		Autogamy	Geitonogamy	Xenogamy		
Seeds per formed capsule	<i>S. coccinea</i>	2.6 ± 2.3	2.4 ± 1.6	8.6 ± 2.3*	17	319
	<i>S. grossularifolia</i>	2.0 ± 3.1	2.3 ± 3.0	5.7 ± 3.0*	10	105
	<i>S. munroana</i>	1.7 ± 2.7	1.7 ± 1.9	8.0 ± 2.7*	9	177
Seeds produced per 100 flowers pollinated	<i>S. coccinea</i>	23	33	649*	17	923
	<i>S. grossularifolia</i>	14	30	279*	10	623
	<i>S. munroana</i>	32	45	647*	9	498

[†]All statistical comparisons are between treatments within species. Numbers are means ± their standard errors. Bold-faced numbers with asterisks are statistically different from other treatments within their species (row) ($P \leq 0.05$).

specialists (oligoleges) of *Sphaeralcea*, being three *Diadasia* (Sipes & Tepedino 2005) and one *Colletes* (Moldenke & Neff 1974). They collectively represented 52% of all sampled bees (Table 2, Fig. 5). Where present, these oligoleges predominated in the local *Sphaeralcea* guilds (Table 2). One oligolectic bee, *D. diminuta* (Fig. 1b), was the most frequently present (70% of sites) and abundant bee (29% of all visitors) found visiting wild *Sphaeralcea* (Table 2). Some older females were conceivably *D. lutzi*, as their diagnostic hair bands were worn away. Populations of *D. diminuta* also foraged in two small research fields planted to these native *Sphaeralcea* (one near Boise, Idaho, another at the Malheur Agricultural Experiment Station near Ontario, Oregon), plus three different wildflower gardens on the campus of Utah State University, Logan, Utah.

POLLINATION EFFICACY OF *DIADASIA DIMINUTA*

Floral visits by female *D. diminuta* bees regularly left considerable pollen on stigmas of both evaluated *Sphaeralcea* species. Females were seen to harvest and pack pollen from *Sphaeralcea* flowers, but none extended her tongue to explore for nectar. For 65 stigmas of *S. coccinea*, single visits deposited 42 ± 10.4 pollen grains (range 11–67 grains). At *S. grossularifolia*, single visits resulted in 34 ± 8.5 grains being deposited (31 stigmas, range 10–54 grains). Of 3560 grains counted, only 4 were not of *Sphaeralcea*, resembling those of a weedy Malvaceae, *Malva neglecta* Wallr. which bloomed nearby. Ten flowers each of *S. coccinea* and *S. grossularifolia* visited once by foraging female *D. diminuta* bees received an average sum of 336 and

272 pollen grains, respectively, on their eight stigmas.

FLORAL INFIDELITY BY FORAGING FEMALE *DIADASIA DIMINUTA*

We followed 68 foraging female *D. diminuta* as they visited a total of 374 flowers on 213 *Sphaeralcea* plants in our Logan research plot. Floral constancy among them varied with the *Sphaeralcea* species, measured as the subset of females seen arriving from a conspecific plant ($X^2 = 31.6$, $P < 0.0001$). Obviously, the nearest neighbouring plant was a conspecific within the same row. Bees were more likely to move sequentially between conspecific plants of *S. grossularifolia* ($N = 39$) than for any of the other three species ($N = 10, 22$, and 8 moves). The spatial proximity of species pairs explained much of the variation in our counts of interspecific flights by foraging *Diadasia* ($r^2 = 0.83$, $P \leq 0.01$), with bees most likely to switch to species growing in neighbouring rows. Overall, as foraging *D. diminuta* flew between *Sphaeralcea* plants in the plot, they switched rows (and so species) as often as they moved between conspecific plants in the same row (70 versus 69 moves).

DISCUSSION

All three manually pollinated *Sphaeralcea* species proved to be largely xenogamous. They rely on bees for their necessary outcrossing and seed production. Bagged as well as manually self-pollinated flowers seldom set seeded capsules, and when they did, fewer seeds resulted (Table 1), a result in line with reports for five other *Sphaeralcea* species (Hubbard et al. 1993; Gutiérrez et al. 2024). Multiplying seed set per capsule by the likelihood

Table 2. The bee species collected at flowers of three species of *Sphaeralcea*, including the count of sites where they were present, the sum of bees caught and their relative abundance where found.

Genus	Species ^{1,2}	Number of sites where present	Total bees	Bees per 100 flowering plants where present
Diadasia	diminuta	14	157	10.2
Diadasia	lutzi	11	73	22.9
Colletes	sphaeralcea	11	44	12.9
Agapostemon	angelicus	16	45	8.3
Eucera	edwardsii	8	29	3.0
Halictus	tripartitus	10	32	4.9
Lasioglossum	sp.	7	32	4.8
Colletes	phacelliae	2	9	1.6
Megachile	sp.	5	12	1.5
Dialictus	sp.	5	11	3.4
Melissodes	sp.	4	16	6.3
Halictus	farinosus	4	6	1.9
Perdita	xanthochroa	1	9	5.3
Eucera	lutziana	5	8	1.1
Diadasia	nitidifrons	2	8	42.9
Melissodes	dagosa	2	5	1.2
Halictus	ligatus	2	7	5.2
Agapostemon	femoratus	4	4	1.7
Osmia	trevoris	1	4	4.1
Nomada	sp.	3	3	0.8
Dialictus	prasinogaster	1	3	1.6
Andrena	sp.	3	3	0.6
Ceratina	pacifica	1	2	2.1
Halictus	rubicundus	2	2	1.4
Sphecodes	sp.	2	2	0.7
Bombus	huntii	1	2	0.4
Eucera	actuosa	1	2	0.1
sum			536	

¹ Single individuals of 11 additional bee species were also taken: *Agapostemon virescens*, *Andrena lupinorum*, *Anthidium emarginatum*, *A. schwarzii*, *Ceratina nanula*, *Colletes simulans fulgidus*, *Dialictus hudsoniellum*, *Epeolus* sp., *Melecta pacifica*, *Osmia calla* and *O. grinellae*.

² **Boldface** indicates known oligoleges of *Sphaeralcea* and related Malvaceae

of capsule set, xenogamy yielded 20-30x more seed per 100 flowers than the other treatments (Table 1). For the wild population, 24 capsules from eight plants contained an average of 18.8 ± 8.9 seeds at openly pollinated flowers, 2-3x more seed than from our manually outcrossed flowers in the greenhouse (Table 1). For those wild plants, we have no measure of failed pollination or aborted capsules, unlike our manual pollinations.

Oligolectic *Diadasia* bees are core pollinators of *Sphaeralcea* in the Great Basin and adjacent

ecoregions (Fig. 5). They are frequently joined by polylectic halictid bees (e.g. *Agapostemon*, *Halictus*, *Lasioglossum*) (Table 2). Older floral collection records for the bee *C. sphaeralcea* Timb. indicate that it too is a *Sphaeralcea* oligolege (Moldenke & Neff 1974). A quite different bee fauna was found visiting *S. parviflora* at 3 sites on the Colorado Plateau (Gateway Colorado, Negro Bill Canyon and Cisco Utah) (white circles with dashes in Fig. 4). Plants were not counted there. The bees included *D. diminuta* and *A. coloradensis* Crawford,

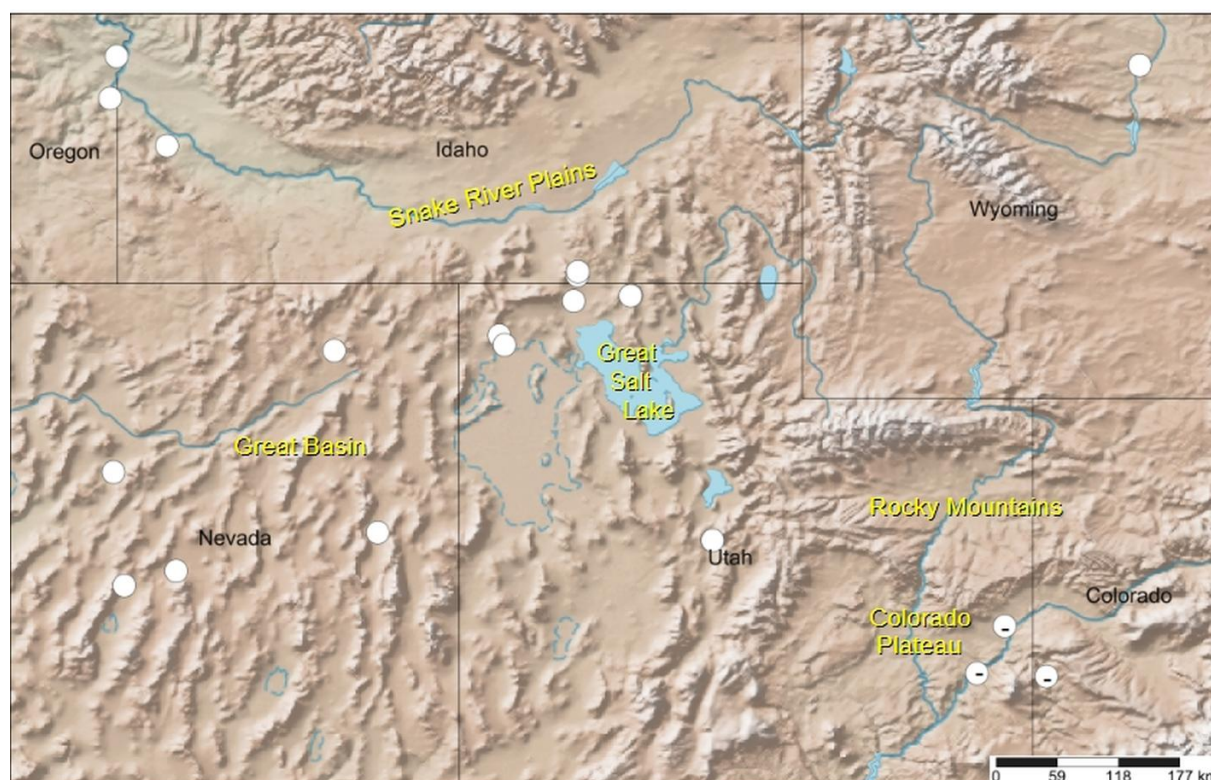


Figure 4. Topographic map marking the western U.S. locations (white circles) where guilds of bees were systematically surveyed at *Sphaeralcea* flowers. Bees at *Sphaeralcea* on the Colorado Plateau (three circles with dashes) were collected haphazardly and so those bees are not included in Table 2 or Figure 5.

as well as a new species of *Hesperapis* plus a number of panurgine bees not seen across the Great Basin, including: *Calliopsis* (*Hypomacrotera*) *subalpinus* (Ckll.), *Panurginus* aff. *beardsleyi*, and *Perdita* (*Octomaculata*) *xanthochroa* Timb. Overall, bee abundance at globemallow flowers surveyed here (1.3 bees per 10 plants) is less than visitation intensity at other common surveyed wildflowers of the sage-brush steppe, such as *Phacelia hastata* Dougl. and *Lomatium dissectum* (Nutt.) Math & Const. (2–3 bees per ten plants) but comparable to native bee densities at *Balsamorhiza sagittata* (Pursh) Nutt. and *Dalea ornata* (Doug.) Eaton & Wright (Cane & Love 2016). The ground-nesting habits of all members of the *Sphaeralcea* bee guild should facilitate their colonization of sites with their pollen host, as opposed to cavity-nesters that require suitable woody nesting substrates in often treeless arid basins.

We were surprised to find resident populations of *D. diminuta* at even small, seemingly isolated patches of globemallows. How did colonists find those host populations? Other genera of Malvaceae are generally absent from the arid

basins and foothills of the Intermountain West. The one exception, alkali mallow (*Malvella leprosa* (Ortega) Krapov), only grows along muddy alkali flats. Sipes & Tepedino (2005) suggested that *D. diminuta* is in fact an eclectic oligoledge, being a bee species that will collect pollen from 2–3 disparate plant families (Cane & Sipes 2006). In the case of *D. diminuta*, they reported that half of 25 sampled females carried pure loads of *Sphaeralcea* pollen, but the other 12 carried mixed loads or pure loads of Asteraceae pollen. In the USDA-ARS National Pollinating Insect Collection, 574 *D. diminuta* from the Intermountain West have floral host labels. Of these, nearly 70% (395 bees) were netted at *Sphaeralcea* flowers. However, another 21% were taken at Asteraceae (20 genera), although 83% of these are male *D. diminuta* (compared to only 41% at *Sphaeralcea*). Many species of Asteraceae bloom in Intermountain basins and foothills when *D. diminuta* is active. Conceivably, these widespread Asteraceae might serve as “stepping stones” by which nesting populations of *D. diminuta* can eventually access widely spaced populations of *Sphaeralcea*, their usual pollen host, although

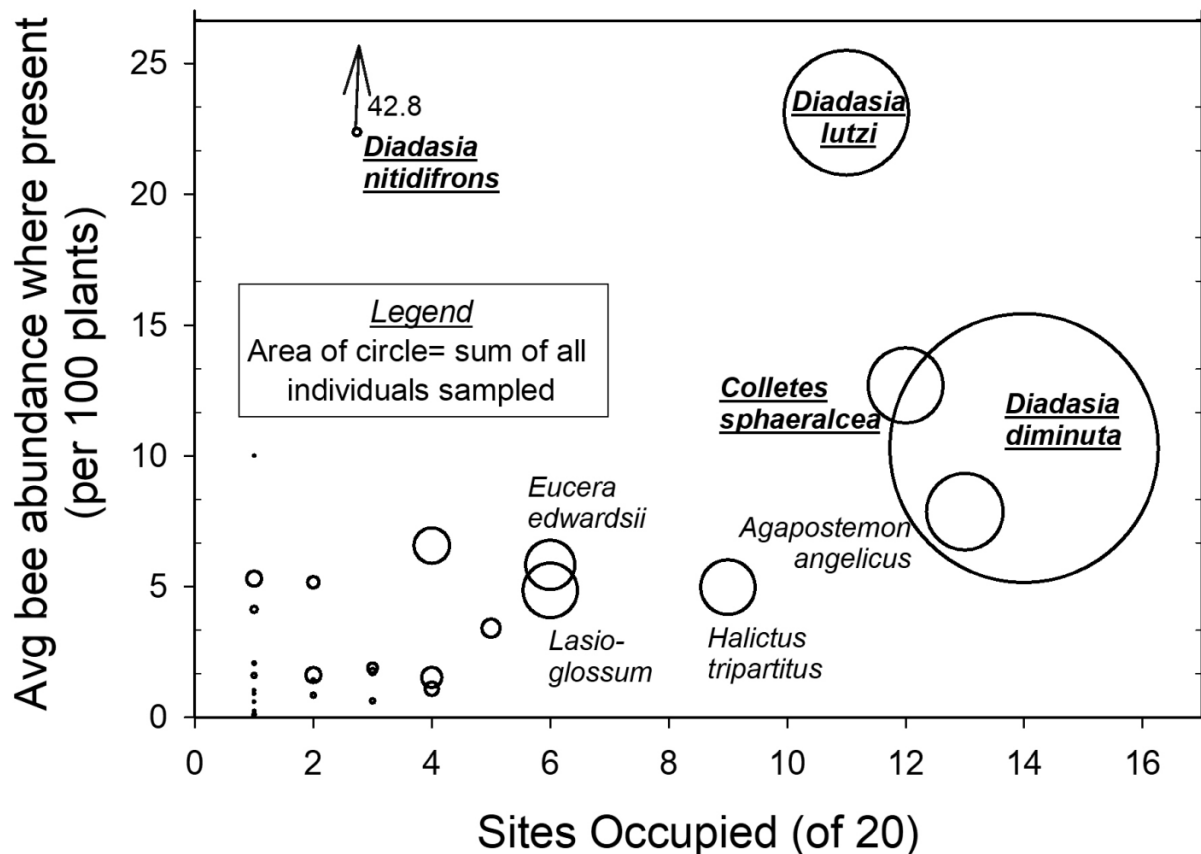


Figure 5. Guild plot of the bee species sampled across sites at *Sphaeralcea*, depicting the count of sites where present, average abundance where present, and the sum of bees systematically collected (circle diameter).

collection data indicate that these alternative floral hosts are primarily visited by nectaring males. Obtaining unambiguous field evidence that addresses this hypothesis may be laborious to obtain, as the instances where female *Diadasia* are found visiting flowers of one or another Asteraceae are likely to be scattered and infrequent.

Female *D. diminuta* bees are effective pollinators of the evaluated *Sphaeralcea* species. Flowers visited once by a forager received pollen far in excess of the average 8-12 ovules and seeds produced per flower, even allowing for some of those grains to be ineffective self pollen. Species of *Diadasia* are also effective pollinators of two *Ferrocactus* species (McIntosh 2005) and another malvaceous genus, *Iliamna* (Tepedino et al. 2016), including one dependent on *D. diminuta* in particular (Mesler and Carothers, in press). In light of these *Sphaeralcea* species being obligate outcrossers, the consistent local abundance and regional ubiquity of oligolectic *D. diminuta* bees

(Table 1, Fig. 5) renders them the most important of the bees at *Sphaeralcea* in the region.

In mixed patches of these orange-flowered *Sphaeralcea*, indiscriminate foraging by female *D. diminuta* should also yield hybrid seed among interfertile species. Similar foraging infidelity was found for oligolectic *Osmia californica* Cress. and *O. montana* Cress. bees gathering pollen in an experimental array of their *Balsamorhiza* floral hosts (Cane 2011). As with *Sphaeralcea*, some species of *Balsamorhiza* also hybridize. Understanding the broader significance of foraging infidelity among oligolectic bees for gene flow between hosts that can hybridize awaits additional studies.

Successful farming and later deployment of *Sphaeralcea* seed for restoration in the Intermountain West will depend on accommodating the salient traits of the plant and its pollinators. The ground-nesting habits of its pollinators preclude grower management, but good stewardship (e.g. no insecticides during

bloom) will be critical and challenging, given needs for seed weevil control (Hammon and Franklin, 2012). The indeterminate flowering of globemallows can be vexing for seed growers. Most seed production potential is lost when the plants are destructively harvested once for seed (Rick Dunne, Wind River Seed, *pers. comm*). However, the ripe capsules will hold their seed well if not battered by wind. Because globemallows can be interfertile (Dreher 2014) and even oligolectic *Diadasia* readily move between the species during a foraging trip, accessions of different *Sphaeralcea* species should not be grown in adjacent fields, at least until their species delineations are better resolved (Sriladda et al. 2021).

The eventual presence and abundance of *D. diminuta* bees foraging at all four cultivated globemallow populations demonstrates the species' colonizing ability. Wild *Sphaeralcea* were not found near these cultivated sites. For instance, at the Malheur Experiment Station site, the nearest uncultivated land where *Sphaeralcea* could grow was 2-3 km distant. At that site, the bees' distinctive turreted nest entrances were found within the rows, suggesting that they will readily nest in seed production fields. Weedy *Malva neglecta* is often present in these agricultural valleys; it might serve as an alternate pollen host for colonizing *Diadasia*, as might various Asteraceae. Following colonization, several successive annual bee generations will be needed to multiply their populations to fully service a commercial seed field. In the interim, polylectic halictid bees, such as *Agapostemon*, can be expected to pollinate newly established wild populations, whereas on farms, growers could conveniently supply hived honey bees for seed production, although pollination efficacies of these polyleges should be evaluated for globemallows.

Blending small fractions of wildflower seeds into wildland seed mixes is unlikely to establish sustainable wildflower populations for three reasons. First, sparse seed in a blend will yield isolated plants. Widely spaced plants are unlikely to be visited by pollinators, both because they may be unaware of single plants, plus the energetic and time costs of searching and flight outweighs the small flower rewards available. Second, the weak self-compatibility of *Sphaeralcea* (Table 1)

exacerbates this problem, for even if a plant does attract a competent pollinator, that bee would need to have flown from a distant conspecific host to be carrying essential outcross pollen (Table 1). As stated by Ghazoul (2005): "...reproductive success in self-incompatible plants is likely to be strongly correlated with local population density". Lastly, from the bee's perspective, widely scattered plants of forbs such as globemallow cannot support a viable nesting population, whose females need to efficiently collect locally abundant pollen to provision their offspring. Instead, cross-pollination of globemallows and other wildflowers would benefit from separately seeded small patches in suitable microsites or "islands" (Hulvey et al 2017). Concentrating the expensive seed in small areas favourable to establishing *Sphaeralcea* holds better promise to grow sizable host patches that will both facilitate needed cross-pollination and enable female bees to profitably forage and multiply, thereby yielding an enduring population.

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AUTHOR CONTRIBUTION

Concept and design, data collection both Cane and Love, data analysis and, writing Cane, edits Cane and Love.

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The authors report no potential conflict of interest.

GENERATIVE AI DISCLOSURE STATEMENT

No AI tools were used were used in research or writing.

DATA AVAILABILITY STATEMENT

The data used to write this article are available as supporting information.

APPENDICES

Additional supporting information may be found in the online version of this article:

Appendix I. Data set and analyses.

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