

BREEDING SYSTEM AND INTERACCESSIONAL HYBRIDIZATION OF *PURSHIA TRIDENTATA* PLANTS GROWN IN A COMMON GARDEN

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ABSTRACT.—*Purshia* spp. (Rosaceae) comprise a widespread western North American species complex that is important as landscape dominants, wildlife habitat, browse for wild and domestic ungulates, and seed reserves for small mammals. This study examined aspects of the phenology, compatibility, pollination biology, and progeny fruit characteristics of multiple accessions of bitterbrush (*Purshia tridentata*), as well as a putative hybrid between bitterbrush and *Purshia stansburiana*. Except for open- and wind-pollination treatments, mass pollination was accomplished at anthesis within white paper sacks, which were used to isolate treatment branches. Bitterbrush appears to be largely self-incompatible and requires some agent, either wind or animal, to effect pollination. While the majority of pollination of bitterbrush flowers is undoubtedly accomplished by insects, some pollination by wind is possible (ambophily) when shrubs are closely spaced, as flowering is fairly synchronous. Flower duration varied among shrubs, but generally lasted from 12 to 24 hours, depending on weather conditions. Flower development stage had little effect on fruit set, indicating prolonged stigma receptivity. Populations of bitterbrush exhibit considerable interfertility, as well as substantial hybridization with congeners. Intrapopulation crosses were only slightly more successful than interpopulation crosses. One of the populations analyzed exhibits characteristics consistent with its putative hybrid nature, having more than one pistil per receptacle, smaller but longer fruits, and a greater reliance on insects for pollination. Both maternal and paternal effects are important in fruit development. Taxonomic relationships within the complex are discussed.

RESUMEN.—Las especies del género *Purshia* abarcan un amplio complejo de especies del área occidental de Norteamérica, las cuales son importantes como dominantes del paisaje, hábitat de la vida silvestre, follaje para ungulados silvestres y domesticados y reservas de semillas para mamíferos pequeños. En este estudio se examinan aspectos de la fenología, compatibilidad, biología de la polinización y características de la progenie de diversos lotes de la maleza amarga (*Purshia tridentata*) y de un híbrido putativo entre esta misma especie y *Purshia stansburiana*. Con la excepción de los tratamientos de polinización abierta y por viento, la polinización masiva se logró en la etapa de antesis dentro de bolsas de papel blanco, las cuales se usaron para aislar las ramas del tratamiento. Al parecer, la maleza amarga es mayormente auto-incompatible y necesita de algún agente, ya sea del viento o algún animal, para efectuar la polinización. Aunque la polinización de las flores de maleza amarga sin duda se lleva a cabo principalmente a través de insectos, es posible que ocurra cierto grado de polinización mediante el viento (ambofilia) cuando los arbustos se encuentran cercanamente espaciados, debido a que florecen de manera bastante sincronizada. La duración de la flor varió entre arbustos, pero por lo general duró de 12 a 24 horas, dependiendo de las condiciones climatológicas. La etapa del desarrollo de la flor tuvo poco efecto en la producción de frutos, indicando así una prolongada receptividad del estigma. Las poblaciones de maleza amarga mostraron tanto una interfertilidad considerable como una hibridación substancial con sus congéneres. Las cruces intrapoblacionales fueron solamente un poco más exitosas que las interpoblacionales. Una de las poblaciones analizadas exhibió varias características consistentes con su naturaleza híbrida putativa debido a que tuvo más de un pistilo por receptáculo, frutos más pequeños pero alargados y una dependencia mayor de los insectos para la polinización. Tanto los efectos maternos como los paternos son importantes para el desarrollo de los frutos. Se discuten las relaciones taxonómicas dentro del complejo de especies.

Bitterbrush and cliffrose (*Purshia* spp., Rosaceae) comprise a widespread western North American species complex, occurring on approximately 10 million ha (38,610 miles²) (McArthur et al. 1983). Species of the complex are important as landscape dominants, wildlife habitat, browse for wild and domestic ungulates, seed reserves for small mammals, and contributors to rare species flora, wildland nitrogen fixation, and aesthetic beauty (McArthur et

al. 1983, Young and Clements 2002). Originally described as separate genera, bitterbrush and cliffrose (*Purshia* and *Cowania*, respectively) have now been combined under the genus *Purshia* (Henrickson 1986, Kartesz 1999, USDA–NRCS 2011) based on the capacity for members of the complex to hybridize (Smith 1964, Stutz and Thomas 1964, Blauer et al. 1975, Koehler and Smith 1981, Reichenbacher 1994).

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Antelope bitterbrush, *Purshia tridentata*, one of the most widespread species in the complex, encompasses significant phenotypic and genetic variation across its geographic and elevational range (Blauer et al. 1975, Shaw and Monsen 1983, Young and Clements 2002). Several ecotypes and growth forms have been described (Alderfer 1976, Winward and Findley 1983). Prized for its value as browse for wild and domestic ungulates, bitterbrush—its ecology and management—has been the subject of considerable research. Specific topics of research are phenology and ecophysiology, including nitrogen fixation, habitat classification, revegetation techniques, animal relationships, management strategies, and response to disturbance (Righetti and Munns 1982, Tiedemann and Johnson 1983, Busse 2000, Young and Clements 2002). Less is known regarding the specifics of its reproductive biology. Preliminary work has been done on breeding system and artificial hybridization (Blauer et al. 1975), as well as reproductive success and flowering phenology of multiple accessions (Shaw and Monsen 1983). However, more complete information on the reproductive biology is needed for genetic understanding and better management of this important species complex.

As part of a larger project examining intra-generic variation in *Purshia*, we documented aspects of the phenology, compatibility, and pollination biology of multiple accessions of *Purshia tridentata*, as well as a putative hybrid between *P. tridentata* and *P. stansburiana*. We also followed reproductive success of intra- and interaccessional crosses and examined fruit characteristics of the resulting progeny. This study compliments earlier work on flowering phenology, seed production, and morphological studies of putative hybrids. Specifically we addressed these issues: (1) whether *Purshia tridentata* flowers are self-compatible, (2) what role wind plays in pollination, (3) if pollination treatment effects differ with maternal population, (4) if intra-accessional crosses are more successful than interaccessional crosses, and (5) maternal and paternal contributions to seed and fruit characteristics.

METHODS

The study took place in a common garden consisting of over 700 plants grown from seeds

collected from 39 populations of *Purshia tridentata*, 6 populations of *Purshia glandulosa*, 16 populations of *Purshia stansburiana*, and 6 putative hybrid populations (see McArthur et al. 1983 for details on populations). The garden was established in 1981 in Springville, Utah, for the purpose of examining variation among *Purshia* populations for multiple traits related to forage quality, growth, and production. Plants were randomly planted out at 10-foot (3.1 m) intervals in a grid array and maintained for some 15 years.

Phenology of *Purshia tridentata*

To determine individual flower phenology, we tagged 10 buds on each of 5 randomly selected shrubs, each shrub representing a different accession of *P. tridentata*. The 5 accessions used were Izee, Oregon; Blackfoot, Idaho; Soda Springs, Idaho; Elko, Nevada; and Kaibab, Arizona. Buds were initially tagged beginning at 16:00 on the afternoon of 2 May 1989. We scored flower development hourly for the next 2 days beginning at 7:00 on 3 May. Flowers were assigned to 1 of 8 developmental stages ranging from closed bud through complete dehiscence of all anthers. We followed flowering phenology of terminal branches on 5 branches of each of 3 shrubs: one from Bishop, California, and 2 from the Canyon Mountains, Utah, though from different collections. Flowers were numbered sequentially from the branch tip down, and the order of flower-opening was recorded.

We also examined stigma receptivity as a function of floral development by hand-pollinating flowers that were at different stages of development. We bagged 3 branches with unopened buds on each of 3 randomly-selected shrubs representing different accessions of the *Purshia* complex. Accessions used were of *P. tridentata* from Oakley, Idaho; *P. glandulosa* from the Chief Range, Nevada; and a hybrid (*P. tridentata* $\times$ *P. stansburiana*) population (see paragraph below) from Thoreau, New Mexico. Branches were bagged using white bakery bags fitted with glycine windows in the bottom to allow determination of floral development stage before addition of pollen to the bag. The development stage of 10 flowers on each branch was recorded at the time of pollination. We accomplished pollination by adding open flowers with dehiscing anthers from adjacent shrubs to the bag through a slit

cut in the end. We then sealed the slits with packing tape and shook the bags to aid in pollen dispersal. We pollinated each of the 3 branches on different days, 2–3 days apart. Flowering was sufficiently synchronous within bags to allow for this type of mass pollination.

Breeding System

We selected 4 populations for intensive study: Bryce Canyon, Garfield Co., Utah (BC); Canyon Mountains, Millard Co., Utah (CM); Fairview, Sanpete Co., Utah (FV); and Thoreau, McKinley Co., New Mexico (TH). Three of the 4 populations (BC, CM, FV) are *P. tridentata*. The population from Thoreau is considered to be of hybrid origin (*P. tridentata* × *P. stansburiana*) based on leaf, flower, and fruit characteristics (Stutz and Thomas 1964). In May 1989, we applied the following treatments to separate branches on individual shrubs of each of the 4 selected populations:

- (1) control—open pollination of unmanipulated flowers,
- (2) bagged only—white bakery bags over unmanipulated flowers as a test for autogamy,
- (3) emasculated—flowers emasculated and then bagged as a test for apomixis,
- (4) selfed—flowers bagged with self pollen added as a test for geitonogamy, and
- (5) wind—flowers bagged using tulle mesh to exclude insect pollinators.

The 5 treatments were applied to 8 plants each of the CM and FV populations, 5 plants of the BC population, and 2 plants of the TH population. We also emasculated flowers on open-pollinated branches of 4 shrubs of the Canyon Mountain population to see if emasculation itself had any effect on fruit production. Bags and emasculation treatments were applied just prior to bud opening. At the onset of flowering, we accomplished mass pollination of the self-pollination treatment by adding whole flowers of the same bush that had dehiscing pollen through a slit made in each paper bag, which we then reclosed with tape (mass pollination using this technique was successful in the past; Blauer et al. 1975). We shook the bags several times in the following days to help disperse pollen within the bag. After flowering was complete, we replaced the paper sacks with tulle net bags on all treatments. We added tulle net bags to open pollination treatments in order to protect developing fruits from insect damage and ensure collection of seeds.

After fruits had ripened and begun to separate from the perianth, we removed treatment branches by clipping. We then sorted and counted receptacles and fruits present within each bag. Seeds were removed from the achenes by hand rubbing and sorted according to appearance—plump or shriveled. The response variables measured were (1) number of fruits initiated per flower, (2) number of mature fruits produced per flower, and (3) number of good seeds produced per flower. Response variables were measured on a per flower basis because occasional plants of *P. tridentata* and all hybrid populations have more than one pistil per flower.

Interaccessional Crosses

In 1990, we expanded the study to examine intra- and interpopulation compatibility of the 4 core antelope bitterbrush accessions in a diallelic crossing design supplemented by additional antelope bitterbrush (*P. tridentata*) and Stansbury cliffrose (*P. stansburiana*) pollen-donor accessions. We applied the following treatments to separate branches of 6 individual shrubs of each of the 4 accessions, for a total of 12 branches per shrub: one self pollen; one open pollination; one Lassen, California, source; one nearby random antelope bitterbrush source; 2 separate bushes of each of 3 of the 4 core study accessions (omitting the hybrid Thoreau population as a pollen donor); and 2 bushes of Stansbury cliffrose. We also included self- and open-pollination treatments to verify breeding system results obtained from the first year. In 1989, some bags tore due to rain and winds, making us question the relatively high seed set obtained in the self-pollination treatment. Branches were first bagged with white bakery bags prior to bud break and the appropriate pollen added through slits in the bag as described above. Once fruit development had begun, we replaced bakery bags with tulle net bags that we later collected and processed as previously described. We then recorded fruit number, fruit length in mm, and seed weight to the nearest 0.1 mg. Seeds were removed from the achenes by hand rubbing and sorted by appearance.

Statistical Analyses

The 1989 breeding system data were analyzed using the MIXED models procedure of SAS version 9.1 (SAS Institute, Inc. 2007). Response variables were ratios of fruit initiated,

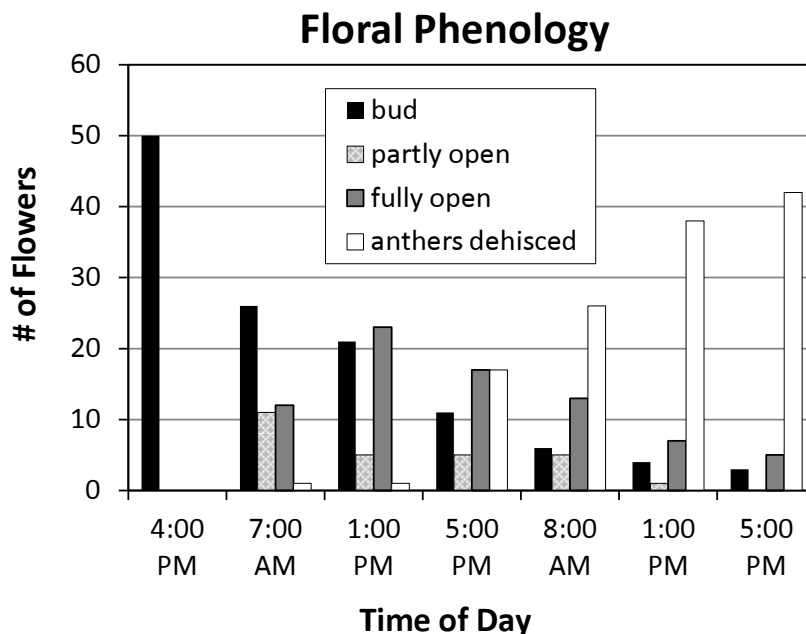


Fig. 1. Phenology of flower opening for 50 bitterbrush (*Purshia tridentata*) flower buds followed over a 24-h period.

fruit matured, and plump (filled) seed to number of flowers treated. Main effects were maternal population and pollination treatment. Where the population by treatment effect was significant, we determined treatment differences within population by examining simple main effects (Winer 1971) of the least-squares means, applying a Tukey–Kramer adjustment of the *P* value. A paired *t* test was used to compare open-pollinated flowers with emasculated open-pollinated flowers using a paired *t* test. We log-transformed data as needed to meet the requirement of normality.

Data from 1990 interaccessional crosses were analyzed using the GLIMMIX procedure, the response variables being the number of mature fruit and seed produced per flower, and main effects being maternal population, pollen population, and their interaction. To assess inter- versus intra-accessional pollination success, we compared seed and fruit production from controlled pollinations using the 3 geographically central core populations—BC, FV, and CM—as both pollen recipients and pollen donors. These represented same- and interaccession crosses. We also included *P. stansburiana* as a pollen source. The Thoreau population was analyzed separately.

Maternal and paternal population influences on fruit length and seed weight were also

analyzed using GLIMMIX. We used all 4 maternal populations and 6 pollen populations, including *P. stansburiana*, in the analysis, but we did not include self- and open-pollination treatments. Additionally, we analyzed individual plant variation of reproductive variables, both within and among the BC, FV, and CM populations, using best linear unbiased predictors (BLUPS) of random effects in GLIMMIX.

RESULTS

Phenology

Flower opening was not specific to any particular time of day; flowers began opening anytime from early morning through late afternoon and early evening (Fig. 1). Flowers took 2–5 hours to open completely, depending on time of day and, presumably, temperature. Flowering, from first opening through anther dehiscence, was generally completed within 24 hours. However, flower duration varied with shrub. For 3 of the 5 shrubs, tagged flowers lasted approximately 10–12 hours. Flowers on the other 2 shrubs lasted closer to 24 hours. The order of flower opening along the branch varied both among branches and among shrubs. No pattern in flower order was observed, with the single exception that the second flower

TABLE 1. Maternal population means across all pollination treatments for reproductive success variables. Means followed by different letters indicate significant differences among populations based on least-squares means with an adjusted significance level of 0.05.

	Bryce Canyon	Canyon Mtns.	Thoreau	Fairview	Attained significance
1989					
Fruit initiated/flower	0.888 a	0.868 a	2.350 b	0.797 a	$P < 0.0001$
Fruit matured/flower ^a	0.369 a	0.411 a	0.737 b	0.363 a	$P = 0.0107$
Filled seed/flower ^a	0.348 a	0.384 a	0.621 b	0.322 a	$P = 0.0109$
1990					
Fruit matured/flower	0.489 a	0.489 a	0.706 b	0.408 a	$P < 0.0001$
Filled seed/flower	0.479 a	0.500 a	0.527 b	0.336 a	$P < 0.0001$

^aSignificant interaction between maternal population and pollination treatment

from the stem tip was consistently one of the earliest (either first or second) to open. Other factors, such as branch aspect and incident light, apparently affect flower opening more than position on the branch.

Bud/flower development stage had little effect on fruit set. Fruit set for opening buds was approximately 75%, whereas that of partially-opened flowers to those whose anthers were fully dehiscent was 87%–88%. Pollen retains viability for a least several days under normal field conditions (Sanderson 1969), allowing time for unopened buds to open completely. The high fruit set attained by fully dehiscent flowers indicates that, in the absence of pollination, stigmas may remain receptive for several days.

Breeding System

In 1989, maternal population had a significant effect on all 3 reproductive variables, with the Thoreau population differing from the other 3 populations. Consistent with its hybrid nature, the Thoreau population frequently had more than one pistil per receptacle, resulting in an average of 1.6 to 2.9 times the number of fruit initiated, fruit matured, and filled seed produced on a per flower basis than that produced by the other 3 populations (Table 1). The population $\times$ pollination treatment interaction term was highly significant for all 3 reproductive success variables, reflecting differences among populations in degree of treatment significance (Table 2). When populations were analyzed separately, the hybrid Thoreau population did not show any significant treatment effect, although the relative pattern was consistent with the other populations. The error term for the Thoreau population was an order of magnitude higher than for the other

populations, reflecting both the low number of shrubs used (2) and variation between the 2 plants.

When the Thoreau population was omitted from the analyses, only the pollination treatment term was significant ($P < 0.0001$ in all cases). The bagged only (geitonogamy) and emasculation (apomixis) treatments did not differ from each other and only differed from the self-pollinated treatment in number of fruit matured. Netted (wind-pollination) and control treatments were not significantly different from each other, except for the number of mature fruit per flower, but always differed from the other 3 treatments. The emasculation process itself did not appear to have any negative effect, as all 3 fruit set and seed production measures were not significantly different for emasculated and non-emasculated flowers of open-pollinated branches (data not shown).

In 1990, differences among maternal populations in the mean number of fruits and seeds per flower were significant when averaged across all pollination treatments, the Thoreau population again having the highest values (Table 1). Pollination treatment was also significant ($P < 0.0001$). The self-fertilization treatment resulted in extremely low fruit production across all populations, averaging 1.2% of flowers pollinated, as compared with 84.7% for open-pollinated branches. The number of good seed produced by self-pollinated flowers was also very low, averaging 1.1% of pollinated flowers, compared with 76.4% for the open-pollination treatment. There were no differences in seed weights produced by open- and self-pollinations. Artificial outcross (xenogamy) pollinations produced somewhat less mature fruit and good seed per flower as compared with open pollination (55.1% and 54.0%,

TABLE 2. Pollination treatment response means by maternal population using 1989 data. Means followed by different letters indicate significant differences among populations based on least-squares means with an adjusted significance level of 0.05. The 3- and 4-population means indicate treatment differences using all 4 populations in the analysis or with the Thoreau population omitted.

	Emasculated	Bagged only	Selfed	Net bags	Control
Fruit initiated / flower					
Bryce Canyon	0.784 a	0.779 a	0.804 ab	0.987 ab	1.061 b
Canyon Mtns	0.695 a	0.821 a	0.657 a	1.065 b	1.104 b
Thoreau	2.486 a	1.983 a	1.957 a	1.988 a	3.321 a
Fairview	0.774 abc	0.601 a	0.721 ab	0.856 abc	1.033 c
4-population means	1.184 a	1.046 a	1.041 a	1.224 a	1.630 b
3-population means	0.751 a	0.734 a	0.735 a	0.969 b	1.066 b
Fruit matured / flower					
Bryce Canyon	0 a	0.009 a	0.071 a	0.769 b	0.980 b
Canyon Mtns	0.025 a	0.026 a	0.219 b	0.814 c	0.978 c
Thoreau	0.067 a	0 a	0.139 a	0.722 a	2.756 a
Fairview	0.047 a	0.007 a	0.189 a	0.733 b	0.840 b
4-population means	0.035 a	0.010 a	0.158 a	0.760 b	1.388 c
3-population means	0.024 a	0.014 a	0.163 b	0.772 c	0.932 d
Filled seed / flower					
Bryce Canyon	0 a	0 a	0.072 a	0.737 b	0.922 b
Canyon Mtns	0.021 a	0.026 a	0.187 a	0.758 b	0.927 b
Thoreau	0.033 a	0 a	0.101 a	0.562 a	2.410 a
Fairview	0.047 a	0.005 a	0.127 a	0.711 b	0.720 b
4-population means	0.025 a	0.008 a	0.125 a	0.692 b	1.245 c
3-population means	0.023 a	0.010 a	0.132 a	0.735 b	0.856 b

TABLE 3. Maternal population means across all pollination treatments for fruit and seed characters. Means followed by different letters indicate significant differences among populations based on least-squares means with an adjusted significance level of 0.05.

	Bryce Canyon	Canyon Mtns.	Fairview	Thoreau	Attained significance
Fruit length (mm)	14.0 a	14.5 a	14.5 a	18.9 b	$P < 0.0001$
Seed weight (g)	0.029 a	0.026 a	0.026 a	0.016 b	$P < 0.0001$

respectively), indicating that bagging did have an effect on overall pollination success.

Interaccessional Crosses

There were no significant differences in the numbers of fruits or seeds produced by intra- or interaccessional crosses of the 3 core populations, although same-accession crosses gave consistently higher numbers. Artificial crosses with *P. stansburiana* were consistently lower, averaging 39.2% fruit set and 37.4% good seed per flower as compared with 54.4% and 54.0% for same-accession crosses ($P = 0.1060$ and 0.0983 , respectively). Interaccessional crosses were intermediate, averaging 48.3% fruit set and 48.2% good seed. Intra- and interaccessional crosses, as well as crosses with *P. stansburiana*, were essentially equal for the Thoreau population ($P = 0.9008$).

Maternal population had a significant effect on fruit and seed characters. Thoreau plants

averaged longer fruits and lighter seeds ($P < 0.0001$) than the other 3 maternal populations (Table 3). There was also significant variation among individual maternal plants, both in reproductive success and fruit and seed characteristics. Pollen population had no significant effect, although fruits and seeds produced using *P. stansburiana* pollen were the longest and lightest, respectively. No significant differences were found among individual pollen donors.

DISCUSSION

Antelope bitterbrush appears to be largely self-incompatible. Blauer et al. (1975) reported only 4 seeds produced on 17 bagged branches over a 4-year period. This low percentage agrees with our 1990 data, where selfing rates ranged from a low 0.05% for the Bryce Canyon population to 1.6% for the Thoreau population.

Bag-only and emasculation treatments of 1989 similarly produced fruit at an average rate of 1%. These were the data used in our initial report (Pendleton and McArthur 1995). In contrast, selfing rates based on bags to which self pollen had been added varied from 10% for the Thoreau population to over 19% for Canyon Mountains (Table 2), indicating a certain amount of self-compatibility. However, it is likely that some outcross pollen was introduced inadvertently during mass pollination in 1989: a steady rain the week before pollination commenced had damaged a few of the bags (which were subsequently repaired), and for this reason, we question the 1989 data and believe the 1990 data to be a more reliable indicator of breeding system. In any case, selfing rates from controlled self-pollinations undoubtedly overestimate actual selfing rates in field populations. Studies have shown that outcross pollen can outcompete self pollen through faster germination and growth (e.g., Weller and Ornduff 1977, Eckert and Allen 1997), a phenomenon known as cryptic self-incompatibility. Regardless of the geitonogamy debate, the low amount of seed produced by the emasculation (apomixis) and the bag-only (autogamy) treatments indicates that flowers lack the means to self-pollinate autogamously and require some agent, either wind or animal, to effect pollination. The hybrid Thoreau population (*P. tridentata* $\times$ *P. stansburiana*) seems particularly dependent on insects for pollination, having low rates of both self- and wind-pollination, despite the higher number of ovules per flower.

A number of insects visit the flowers of antelope bitterbrush. Bees, wasps, and other insects have been reported (Blauer et al. 1975). We also noted a number of these, including many bumblebees, visiting flowers in the common garden. Undoubtedly, insects accomplish the majority of the pollination of bitterbrush flowers. However, some pollination by wind (ambophily) is possible when shrubs are closely spaced. Blauer et al. (1975) noted synchronous flowering over the whole plant, which allowed for mass pollination of bagged branches. Stanton (1959) also reported that bitterbrush plants within a given population flowered simultaneously. Simultaneous flowering, both within individual bushes and within populations is characteristic of wind-pollinated plants (Whitehead 1969). Russell and others (1998) presented

evidence for at least some level of successful wind pollination in *Cercocarpus ledifolius*, another rosaceous shrub or small tree closely related to *Purshia* (Potter et al. 2007). Both shrubs occur in low-structured habitats with infrequent precipitation, low humidity, and frequent winds, conditions conducive for wind pollination (Culley et al. 2002). Another semi-arid rosaceous shrub, *Coleogyne ramosissima*, is exclusively wind-pollinated while showing evidence of ancestral insect pollination—showy yellow sepals and the occasional presence of petals or 2 fruits per flower (Pendleton and Pendleton 1998). Our study also hints at the possibility of among-population differences in degree of wind-pollination. In contrast to the other 3 populations, Fairview plants showed no reduction in the amount of seed produced through wind as compared to open-pollination. Further study would be needed to substantiate among-population differences in relative rates of wind and insect pollination of bitterbrush.

Maternal parent had considerable effect on reproductive success measures, as well as fruit and seed characteristics. This was true at both the population and the individual plant level. Maternal plants of the hybrid Thoreau population (*P. tridentata* $\times$ *P. stansburiana*) produced fruits and seeds more similar in morphology to cliffrose than to the other bitterbrush populations. Seed weight and fruit length also varied among individual maternal plants. In general, studies have found that maternal plants exhibit the greatest control over seed size and other seed attributes (e.g., Antonovics and Schmitt 1986, Andersson 1990, Schlichting and Devlin 1992). This is not unexpected given that most of the fruit and seed mass is derived from maternal tissue. Maternal effects include both genetic and environmental components.

The same studies have reported small but consistent paternal effects on seed characteristics. In antelope bitterbrush, both maternal and paternal effects have been found to control seed germination (Meyer and Pendleton 2000). Again, paternal effects were small in comparison with maternal control. In this study, we found no significant effects of pollen parent population on either reproductive success or seed weights. Seed weights of antelope bitterbrush are reported to vary over 9-fold, with much of the variation occurring within individual shrubs (Krannitz 1997). We did find some evidence of paternal influence on fruit

lengths. Cliffrose sired the longest fruits of any pollen parent (14.6 mm vs. 14.2–14.3 mm), although this difference was not significant. Individual pollen parents also varied in length of fruits sired. Lengths of fruit sired by the 2 CM pollen donors were quite different, one siring very short fruits while the other sired fruits as long as those sired by cliffrose pollen.

Populations of bitterbrush exhibit considerable interfertility, as well as substantial hybridization with its congeners (Stutz and Thomas 1964, Blauer et al. 1975, Koehler and Smith 1981, Meyer and Pendleton 2000, Baggs and Maschinski 2001). In this study, intrapopulation crosses were only slightly more successful than interpopulation crosses. Artificial crosses using cliffrose as the pollen donor had lower success rates but still averaged around 38%. Some of the lowered success rate of interpopulation crosses may be due to slight differences in the timing of flower opening, although we tried to mitigate this possibility by inserting pollen on more than one occasion when indicated.

The interfertility of species in the *Purshia* complex has led to debate as to appropriate taxonomy of the group. The genus *Purshia* is apparently derived from the more ancestral *Cowania*: McArthur et al. (1983) made a strong argument for ancestral *Cowania*, citing its Madro-Tertiary center of distribution, primitive traits, and close affinity to *Cercocarpus*, a widespread genus of Madro-Tertiary origin as well. They theorized that current hybridization between the genera was a result of recent contact following evolution in isolation. Molecular work by Jabbes (2000) confirms that *Purshia* was derived from *Cowania*. Jabbes' phylogenetic analysis of ITS sequences resulted in 3 clades. One consisted of *Purshia tridentata*, *P. glandulosa*, and putative hybrids. A second consisted of 2 *Cowania* species: *C. ericifolia*, and *C. plicata*. The third was comprised of *C. mexicana*, *C. subintegra*, and *C. stansburiana* (currently classified as *P. stansburiana*). The clustering of *P. stansburiana* with other *Cowania* species argues one of two things. Either *Purshia stansburiana* should revert to *Cowania stansburiana*, or the entire group should be considered congeneric. In addition to morphological differences between *P. tridentata* and *P. stansburiana* noted in the work of McArthur et al. (1983), our data indicate a difference in pollination system. Cliffrose has a number of characteristics common to insect-pollinated plants,

including multiple carpels per flower, low within- and among-plant synchrony of flowering, and larger, more fragrant flowers (Blauer et al. 1975, Faegri and van der Pijl 1979). Antelope bitterbrush, while largely animal pollinated, exhibits characteristics of a mixed-pollination system, having single (sometimes 2) carpels, smaller flowers, synchronous flowering within the population, and a tendency to grow in patches. This mixed approach is probably more common in generalist pollination systems than previously thought (Culley et al. 2002) and may be advantageous in arid conditions with highly variable precipitation. Few studies have examined the breeding systems of important western wildland shrubs (McArthur 1989, Pendleton et al. 1989). This report enhances our understanding of one such shrub group.

ACKNOWLEDGMENTS

Thanks are extended to Susan Garvin for technical assistance in data collection and to 2 anonymous reviewers for helpful comments and suggestions that strengthened the manuscript.

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Received 13 September 2011

Accepted 13 February 2012