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REPRODUCTION AND DEMOGRAPHY OF *TOWNSENDIA APRICA* (ASTERACEAE), A RARE ENDEMIC OF THE SOUTHERN UTAH PLATEAU

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ABSTRACT.—*Townsendia aprica* (Asteraceae: Astereae), a rare pulvinate perennial of the Southern Utah Plateau, was listed as threatened under the U.S. Endangered Species Act in 1985. Here we report on the reproductive biology and pollination of this little-known species and provide an estimate, for a single site-year, of size-specific reproductive effort. Last Chance townsendia appears a short-lived perennial that begins reproducing in its 2nd year (1.5–2.0 cm diameter). Maximum reproductive effort is attained with the 2.5–4.0 cm diameter size class: 38% of these plants produced 84% of the flower heads. Few plants survived past the 4-cm size class. The species is primarily self-incompatible: neither autogamous nor geitonogamous breeding system treatments produced a significant number of achenes. Unlike some populations of some congeners, the Ivie Creek population was not apomictic. Outcrossing is the primary means of reproduction and native solitary bees are the most important pollinators. Paramount are several species in the genus *Osmia,* and the ground-nesting species *Synhalonia fulvitarsis,* which nests among the *T. aprica* plants. *Synhalonia fulvitarsis* also visits a contemporaneous blooming phlox (*P. austromontana*), which may facilitate pollination of the rare townsendia. The *Townsendia-Phlox-Synhalonia* interaction may represent another example of why we must consider communities rather than individual species in our conservation efforts.

Key words: Townsendia aprica, *rare plant, reproduction, breeding system, pollinator, conservation, demography, Asteraceae.*

Plant taxa may be rare for many anthropogenic or natural reasons (Fiedler and Ahouse 1992). Certain causes of rarity may be mitigated through changes in land management policies; e.g., altering grazing schedules or restricting off-road vehicle use may improve rare plant reproduction, recruitment, and recovery. Conversely, the plight of other rare plants, e.g., edaphic specialists whose rarity is due to disappearance of substrate, may be irremediable by changes in management protocol. Only additional information on rare plant characteristics will enable informed decisions on how best to allocate scarce resources for conservation; descriptive studies are a first step to realistic management decisions (Schemske et al. 1994).

Some rare species, such as *Townsendia aprica* (Last Chance townsendia), a threatened perennial composite of the Southern Utah Plateau region, may be at risk because of characteristics connected with reproduction and pollination. First, like other rare species, Last Chance townsendia may have difficulty attracting density-dependent, high-energy, and nutrient-demanding pollinators such as bees to its flowers (Jain 1976, Kearns et al. 1998, Tepedino 2000). Second, Last Chance townsendia blooms in early spring when frequent harsh and changeable weather presents problems for plants that depend on exothermic insects to move their pollen (Macnair et al. 1989). Third, some congenerics of *T. aprica* are apomictic, and Stebbins (1950) and Beaman (1957) have suggested that such agamic complexes are unlikely to long endure or to give rise to new taxa. Such considerations are of general import in elucidating correlates of rarity and in providing specific information needed by land managers.

Here we describe the breeding system and identify important flower visitors of this rare Utah endemic. We also provide an estimate, for 1 population in a single year, of size-specific reproductive effort as measured by flower number.

MATERIALS AND METHODS

Species Description

Townsendia aprica was listed as threatened under the U.S. Endangered Species Act in 1985.

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Thirteen occurrences were initially recorded; 38 more have now been discovered in the same 3 central Utah counties: Emery, Sevier, Wayne. The species occurs in small, barren openings of pinyon-juniper interspersed with salt-desert shrubs in soil substrates that tend to be nonuniform (U.S. Fish and Wildlife Service 1993).

Last Chance townsendia plants, like other members of the genus (Reveal 1970, Shultz and Holmgren 1980), are acaulescent, pulvinate, and have one to several rosettes, each of which may support a heterogamous-radiate flower head (Mani and Saravanan 1999). Heads are composed of apricot-colored ray florets (yellow-orange when fresh, aging to cream or even white) that are female, and disc florets that are hermaphrodites. The florets open centripetally beginning with ray flowers; thus each head is protogynous.

In contrast, hermaphrodite disc florets are protandrous, with the initial male stage lasting from a few hours to a day or more, depending upon the temperature. The anther column is thigmotactic and aids in pollen presentation. When touched, the column retracts, thus forcing the egress of pollen like toothpaste from a tube. The female stage may last from a few hours (if pollinated immediately) to a few days. The stigmatic lobes of unisexual ray flowers separate and spread fully, but the lobes of some disc flowers remain attached at the tip (and sometimes along their full length) and never completely separate (personal observations).

Data Collection

Data were collected on the population structure, reproductive biology, and pollination of Last Chance townsendia from 1988 to 1991 at 2 sites in the large upper Last Chance Creek population. In 1989 we constructed a demographic profile of plants at the Ivie Creek site by randomly selecting 200 plants, measuring each cushion at its widest diameter, and counting the number of flower heads. With the data we constructed a size-frequency distribution and related size to reproductive potential.

In 1990 we used 24 plants from the Ivie Creek population to determine whether the florets were capable of seed production without receiving outcrossed pollen. We chose only plants with single heads of comparable phenology. Twelve plants were caged before any florets opened, and 12 were unmanipulated. Plants were marked with a numbered metal tag that was nailed into the substrate. Chicken wire cages covered with pliable 1-mm-mesh nylon excluded all but the smallest insects; cages were nailed into the substrate to anchor them during the frequent high winds. Mature seed heads were collected and returned to the lab, where numbers of ray and disc florets and filled achenes were counted. The Wilcoxon nonparametric paired-rank test was used to compare percent florets with filled achenes.

In 1991 we used plants at Ivie Creek to compare achene production from self- and outcrossing treatments (geitonogamy and xenogamy, respectively). We also replicated our autogamy and agamospermy treatments from 1990 to confirm our results. To conduct these experiments, we caged 25 plants with exactly 3 heads per plant and identified them as before. In addition, each head was marked with an identifying color of nontoxic paint on the involucral bracts signifying the treatment to be received. All florets, ray and disc, of 2 heads of each plant received 1 of the following treatments: autogamy/agamospermy (unmanipulated), geitonogamy (receptive stigmas pollinated with fresh pollen from other florets on the same plant), xenogamy (receptive stigmas pollinated with fresh pollen from florets on another plant). Thus, each plant had 1 head in each treatment. This procedure was adopted because of the small size and crowding of the florets and the difficulty of marking and pollinating them individually. Care was taken to alternate the sequence of treatments among plants so as to avoid any effect of pollination priority. We did not test for the possibility that *T. aprica* is a pseudogamous apomict because all known apomicts in the genus and most in the Asteraceae are diplosporic, while pseudogamic apomicts are predominantly aposporic (Beaman 1957, Nygren 1967).

As experimental plants were chosen, we first selected the closest plant with a head at the same phenological stage. This uncaged head was marked as an open-pollinated control to assess pollinator-limitation; it was later collected for comparison of seed production with the xenogamy treatment of the experimental plant. Again we compared percent filled achenes per floret per head using nonparametric tests: the Wilcoxon rank test, the Mann-Whitney test

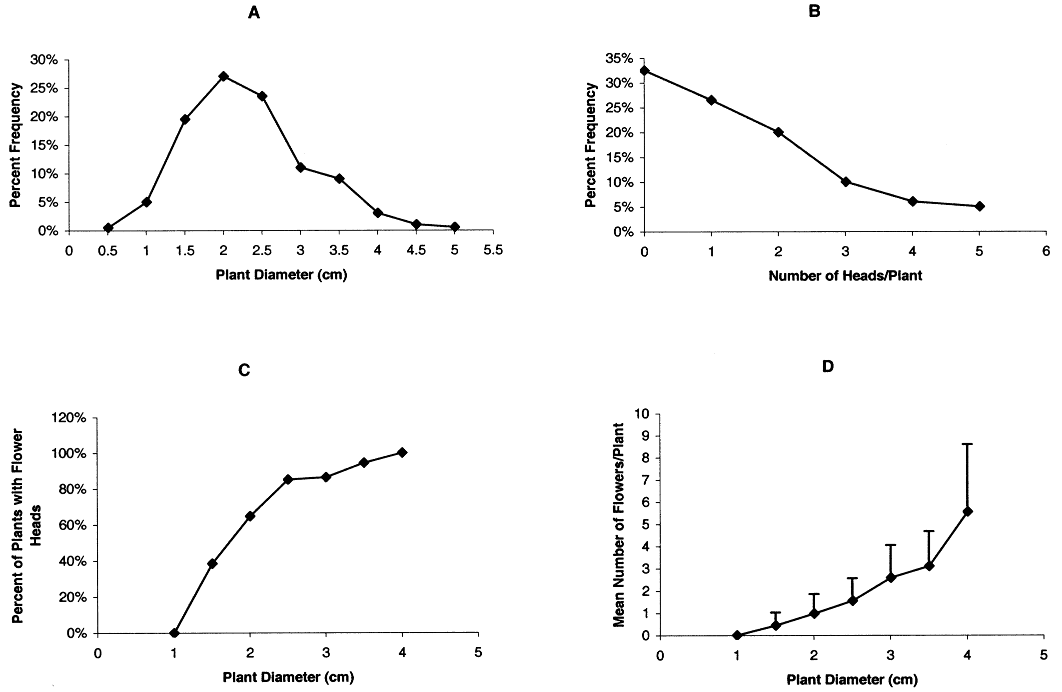

Fig. 1. Measures of size and number of flower heads produced per plant of *Townsendia aprica* at the Ivie Creek study site in central Utah: A, percent frequency distribution of plant size; B, percent frequency distribution of number of heads per plant; C, percent of plants with ≥ 1 flower head by plant size; D, mean number of heads per plant by plant size (solid line; upper *s* shown); percent of total recorded flower heads produced by each size class (broken line).

for unpaired comparisons, or the Friedman 2-way ANOV rank test (Conover 1971).

In 1988 and 1989 we made single-day collections from the flowers of populations along upper Last Chance Creek and at Sage Hole, Sevier County. In 1991 few collections were made because of frequent inclement weather and the demands of conducting breeding system treatments and the pollinator-limitation experiment.

RESULTS

Cushions of *T. aprica* ranged in diameter from 0.5 cm to 5.0 cm (mode = 2.0 cm, Fig. 1a). Plants were concentrated in the smaller size classes suggesting a young and healthy population: over 75% were in the 0.5–2.5 cm size classes; few exceeded 4.0 cm.

Plants produced up to 10 heads. Although the modal head number was 0, most plants (67.5%) produced 1 or more heads (Fig. 1b). Plants began producing heads with the 1.5-cm size class (Fig. 1c); flower production increased with increasing size (Fig. 1d). There was a highly significant positive correlation between mean heads per plant and plant diameter ($P = 0.003$, $t = 6.4$, df = 6, $r^2 = 0.91$). Most plants >2 cm produced ≥1 head. At 3 cm, plants averaged >2 heads; the few plants that grew to 4 cm produced the most heads per plant, averaging 6. Most heads (about 84% of the total produced) were produced by the 38% of plants in the 2.5–4.0 cm size category (Fig. 1d).

Results from preliminary experiments showed that achenes are not produced unless the receptive stigmas of florets receive pollen transported by insects or perhaps by wind; i.e., flowers are neither autogamous or agamospermous. In comparison, 42.6% of ray flowers and 45.5% of disc flowers on open-pollinated heads produced filled achenes. Disc flowers produced significantly more achenes than did ray flowers (Wilcoxon test, $P = 0.01$) but this was due to the greater average number of disc flowers than ray flowers (Wilcoxon test, $P < 0.02$; Table 1).

TABLE 1. Mean (*s*) florets, achenes, and percent achenes per floret for ray and disk flower heads of caged and open *Townsendia aprica* in central Utah. $N = 12$.

	Ray			Disk		
	Florets	Achenes	%	Florets	Achenes	%
OPEN						
mean	13.0	5.5	42.6	22.6	9.3	45.4
s	2.0	3.6	27.9	7.0	5.0	26.7
min	10	0	0	13	1	4.6
max	18	13	92.9	36	17	77.3
CAGED						
mean	12.5	0	0	21.3	0	0
s	4.2	—	—	9.9	—	—
min	7	—	—	4	—	—
max	20	—	—	35	—	—

TABLE 2. Mean (*s*) florets, achenes, percent achenes per floret, and sample size (*N*) of *Townsendia aprica* heads subjected to autogamy/agamospermy (AA), geitonogamy (G), xenogamy (X), or open (O) pollination treatments.

	Ray				Disk			
	Florets	Achenes	%	*N*	Florets	Achenes	%	*N*
AA	11.3 (2.4)	0.9 (1.9)	6.4 (12.9)	19	23.8 (9.5)	1.1 (3.6)	2.4 (7.4)	19
G	12.5 (3.7)	1.0 (2.6)	6.0 (14.7)	20	25.8 (7.1)	0.7 (1.2)	2.3 (4.2)	20
X	13.0 (3.9)	4.6 (3.7)	34.9 (25.2)	20	24.3 (8.6)	12.6 (5.4)	52.3 (15.1)	20
O	11.3 (2.6)	3.1 (2.5)	26.2 (16.7)	11	25.8 (9.3)	11.4 (7.0)	41.5 (20.0)	11

Our 2nd breeding system experiment compared reproductive success of self- and cross-pollinated florets, geitonogamy and xenogamy treatments, respectively. Our results for both ray and disc flowers showed that outcrossed pollen produces maximal achene production: the xenogamy treatments had significantly greater percent seed set than did the geitonogamy and autogamy/agamospermy treatments, and there was no significant difference between the latter 2 (Table 2; Friedman tests, both $P < 0.0001$). Also, we found no difference between disc and ray flowers in percent seed set due to autogamy/agamospermy or geitonogamy (Wilcoxon tests, both $P > 0.15$), but in the xenogamy treatment, disc flowers produced significantly greater percent achenes than did rays (Wilcoxon test, $P = 0.04$).

We also examined the likelihood that achene production in *T. aprica* was limited by a dearth of pollinators. Comparisons of percent seed set between open-pollinated heads and experimentally cross-pollinated heads revealed no significant differences for ray or disc flowers (Table 2; Mann-Whitney tests, both $P > 0.10$).

We captured 15 species of bees in 4 families visiting the flowers of *T. aprica* in 3 site-years (Table 3). The genus *Osmia* was represented by 9 species, all in small numbers. Most abundant were members of the anthophorid species *Synhalonia fulvitarsis,* which we found nesting in the ground among the *T. aprica* plants at Ivie Creek. In 1991 many more *S. fulvitarsis* and other bee species, as well as assorted dipterans, were seen on the flowers than we were able to capture (see Methods).

DISCUSSION

Although it is uncommon for size and age to be closely correlated in plant species (Hutchings 1986), our data suggest that *T. aprica* defies this rule (Fig. 1). *Townsendia aprica* appears a short-lived perennial that begins blooming with a single head in the 2nd year as diameter size of 1.5–2.0 cm diameter is reached. No plant <1.5 cm diameter flowered, and relatively few of the 2-cm modal size class produced flower heads. Because maximum reproduction is not achieved until later in life, it is essential that populations be managed to ensure the persistence of plants to the larger size classes.

TABLE 3. Bees captured on the flowers of Last Chance townsendia in 3 years at the Ivie Creek (5/2/89, 1991) and Sage Hole (5/12/88) sites in central Utah. Ivie Creek sites noted by $^{\mathrm{IC,}}$ Sage Hole by $^{\mathrm{SG}}$. Species also collected foraging on *Phlox austromontana* noted by *. Species that nest in wood substrates noted by $^{\mathrm{W}}$.

Family Species
Apidae
Ceratina nanula$^{\mathrm{IC, SH, W}}$
Nomada sp.$^{\mathrm{IC*}}$
Synhalonia fulvitarsis $^{\mathrm{IC*}}$
Halictidae
Lasioglossum (*Evylaeus*) sp.$^{\mathrm{IC*}}$
Megachilidae
Dioxys pomonae$^{\mathrm{IC}}$
Osmia coloradensis$^{\mathrm{IC, W}}$
O. gaudiosa$^{\mathrm{IC, SH, W*}}$
Megachilidae (continued)
O. kincaidii$^{\mathrm{SH, W}}$
O. pusilla$^{\mathrm{IC}}$
O. sanrafaelae$^{\mathrm{IC, W*}}$
O. sladeni$^{\mathrm{SH*}}$
O. vandykei$^{\mathrm{SH*}}$
O. (Acanthosmioides) sp.$^{\mathrm{IC}}$
O. (Melanosmia) sp.$^{\mathrm{SH*}}$
Stelis pavonina$^{\mathrm{IC}}$

Townsendia aprica illustrates how determining method(s) of reproduction of rare plants can aid conservation objectives. Stebbins (1950) argued that plant species that reproduced agamically were more likely to be evolutionary dead ends. Obligate apomixis is known from at least 12 of 21 species of *Townsendia* (Beaman 1957). As a perennial of higher elevations (>2000 m), *T. aprica* also fits an apomictic profile. All known *Townsendia* taxa with apomictic populations also have sexual populations. If Stebbins (1950) is correct, then protecting apomictic populations of *T. aprica* would be of slightly lower priority than protecting sexual populations. Thus, the Ivie Creek population merits conservation priority. Until the mode of reproduction is examined for other *T. aprica* populations, land managers should assume that all populations reproduce sexually and accord them equal status. Finally, we do not propose the sacrifice of any extant apomictic populations. All populations of an imperiled species are of value; apomicts, for example, are superior colonizers because they can reproduce unassisted.

While we found no evidence for apomicty in the Ivie Creek population, we commonly found unsplit stigmas in disc flowers. These disc flowers, particularly at the center of the capitulum, may be functional males, and heads may be developing toward functional monoecy. This phenomenon is known in other composites where it is usually indicated by a notched style (Burtt 1977, Mani and Saravanan 1999). Other populations should be surveyed for this character.

Our breeding system experiments showed that the Ivie Creek population of *T. aprica* is predominantly outcrossed: achene production in all selfing treatments was very low and may have resulted from slight contamination of some heads in the 2nd year. Stiff winds may move some pollen, but pollen is unlikely to adhere to receptive stigmas because wind also coats the stigmatic surface with dirt. Hand-applied pollen would not adhere to dirt-covered stigmas. The habit of the ray petals folding over and covering the disc flowers at night and in inclement weather may partially shield stigmas from clogging with dirt and from receiving pollen.

The prime movers of *T. aprica* pollen are native solitary bees (Table 3). Native bees are also important to the success of many other rare plant species in the western United States (Tepedino 2000). The activity of these insects is inhibited by inclement spring weather. Cold, rain, snow, and wind can greatly restrict the time that bees have to forage on and pollinate flowers. Inclement weather also kills pollen, slows development, and may vitiate female reproduction (Frankel and Galun 1977). For example, studies in 1991 began on 11 May. Inclement weather during 5 of the initial 9 days prohibited pollinator activity and many florets likely expired without producing achenes.

The most abundant species to visit the flowers was the early spring bee *Synhalonia fulvitarsis,* which also nested in the ground among *T. aprica* and *Phlox austromontana* plants. Nine species of mason/leafcutter bees in the genus *Osmia* were also captured and observed. At least 4 of these *Osmia* species, and *Ceratina nanula,* nest in holes in wood (Hurd 1979, F.D. Parker unpublished); their numbers might be augmented by the use of trap-nests (Krombein 1967). Supplying trap-nests would be especially advisable if achene production were limited by pollinator scarcity. Although we found no indication of pollinator limitation (Table 2), this could quickly change because bees are readily and subtly victimized by human activity. Then, we might need to take steps to preserve bees along with the plants they service (Tepedino et al. 1997).

Of especial interest was the commonness with which bees that visited *T. aprica* also visited the contemporaneously blooming *Phlox austromontana* (several species of *Osmia, S. fulvitarsis*; Table 3). Interestingly, *S. fulvitarsis,* although usually a species that visits a variety of flowering plant species (Hurd 1979), has also been found closely associated with another species of *Phlox* in Wyoming (Tepedino 1979). Perhaps the presence of *P. austromontana* facilitates (Thomson 1978, Rathcke 1983) the pollination of the rare *T. aprica* as has been suggested for other rare plant species (Geer et al. 1995). Studies should investigate the association between these 2 plant species and *S. fulvitarsis.* For example, is *T. aprica* achene production higher in the presence of *P. austromontana,* and can this be related to increased visitation by *S. fulvitarsis*?

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