



Comparative Reproductive Biology of Two Alpine Primrose Species

J. Miller; M. Litvak; S. Kelso; A. Vargo

Arctic and Alpine Research, Vol. 26, No. 3. (Aug., 1994), pp. 297-303.

Stable URL:

<http://links.jstor.org/sici?&sici=0004-0851%28199408%2926%3A3%3C297%3ACRBOTA%3E2.0.CO%3B2-4>

Arctic and Alpine Research is currently published by The Regents of the University of Colorado, a body corporate, contracting on behalf of the University of Colorado at Boulder for the benefit of INSTAAR.

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/about/terms.html>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/journals/regentsINSTAAR.html>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

The JSTOR Archive is a trusted digital repository providing for long-term preservation and access to leading academic journals and scholarly literature from around the world. The Archive is supported by libraries, scholarly societies, publishers, and foundations. It is an initiative of JSTOR, a not-for-profit organization with a mission to help the scholarly community take advantage of advances in technology. For more information regarding JSTOR, please contact support@jstor.org.

Comparative Reproductive Biology of Two Alpine Primrose Species

J. Miller, M. Litvak,*

S. Kelso,† and A. Vargo

Department of Biology, Colorado College, Colorado Springs, Colorado 80903, U.S.A.

*Present address: Department of Environmental, Population, and Organismic Biology, University of Colorado, Boulder, Colorado 80309, U.S.A.

†Corresponding Author.

Abstract

Primula angustifolia and *Primula parryi* are common alpine primroses in Colorado. We examined the reproductive biology of these species to determine (1) if they were fully distylos, (2) what differences in pollinators and in reproductive allocation and success might exist between the species, and (3) whether reproduction was limited by pollen availability during the period of study. We found both taxa to be fully distylos. *Primula parryi* has numerous, diverse pollinators, a high seed/ovule ratio, and high fecundity. *Primula angustifolia* has fewer, less diverse pollinators, lower seed/ovule ratios, and lower fecundity. The greater reproductive success of *P. parryi* may reflect its inflorescence structure and supply of attractants and rewards. Reproduction in both species appears to be limited to some extent by pollen availability, although more so in *P. parryi* than in *P. angustifolia*. These results demonstrate while distyly, with obligate outcrossing and reliance on insect pollen vectors, can be a viable reproductive strategy even in a severe environment, it functions differently even in closely related species and understanding individual pollination systems should be a focus for research on other distylos species.

Introduction

The reproductive biology of the genus *Primula* L. (Primulaceae) first became known through the investigations of Charles Darwin (1877) on distyly. This floral dimorphism occurs in some 24 families of flowering plants (Ganders, 1979), but is best documented in *Primula*. In this genus, the “pin” morph is characterized by a long style, prominent stigmatic papillae, stamens located low in the corolla tube, and small pollen grains; the “thrum” morph has a short style, short stigmatic papillae, stamens located high in the corolla tube, and larger pollen grains. Strong intramorph incompatibility is coupled with the morphological differences: pin morphs can only be fertilized by pollen from thrum morphs, and vice versa. Consequently, distylos primulas are obligate outcrossers that require external pollen vectors.

Although the morphological, genetic, biochemical, and evolutionary origins of distyly have been the subject of much scrutiny (e.g., Veuilleumier, 1967; Charlesworth and Charlesworth, 1979; Ganders, 1979; Barrett, 1990, 1992; Richards, 1993), little experimental work on natural pollination in *Primula* has been done, and this only on species found in temperate latitudes at low elevations (e.g., Knuth, 1909; Christy, 1922; Woodell, 1960; Schou, 1983; Campbell et al., 1986). The question of how distyly functions in an environment where low temperatures, wind, and cloud cover can put different constraints on insect pollinators (Macior, 1974; Moldenke and Lincoln, 1979; Arroyo et al., 1982; Levesque and Burger, 1982; Kevan and Baker, 1983) has never been addressed. In arctic *Primula* species, it is common (although not universal) to see a change in breeding system from distyly to homostyly and at least facultative autogamy (Hultgård, 1990; Kelso, 1991, 1992; Mazer and Hultgård, 1993). In the Plumbaginaceae, another usually distylos species, *Armeria maritima* (Mill.) Willd., has also replaced distyly with homostyly and concomitant self-fertility in the tundra portion of its range (Baker, 1966; Vekemans et al., 1990).

Our study focused on how distyly functions in an alpine tundra. The study species were the two perennial primroses *Primula parryi* Gray and *P. angustifolia* Torrey. *Primula parryi* is broadly distributed through the Rocky Mountains from Montana to Arizona between 3000 and 4300 m. It is relatively large statured (usually 15–40 cm high), with a basal rosette of broad leaves and a many-flowered inflorescence (Fig. 1A). In contrast, *P. angustifolia* is limited to the alpine zone of Colorado and northern New Mexico, usually growing above 3300 m. It is a smaller plant, less than 10 cm high, with a one to two-flowered inflorescence and short, narrow leaves (Fig. 1B). Our objectives were as follows: (1) to determine if *P. parryi* and *P. angustifolia* were fully distylos, with all the manifestations of the syndrome as documented in other *Primula* species, (2) to identify pollen vectors of both species and to determine the differences in their abundance and reliability, and (3) to determine if female reproductive success, as measured by annual seed set, is limited by pollination in either or both of these species.

Materials and Methods

We conducted our study during the summers of 1988, 1990, and 1991 at the Mountain Research Station of the University of Colorado. The study site was located on Niwot Ridge, 40 km northwest of Boulder in the Front Range. Study plots were at 3800 and 3700 m for *P. parryi* and *P. angustifolia*, respectively. We chose nearly adjacent populations to reduce any effects of elevational differences in pollinator faunas. Populations of the two species bloom at different times during the summer, so it was possible to assess pollinators associated with each species separately. Studies on *P. angustifolia* were conducted in early to mid-June, and those on *P. parryi* throughout July and August.

ASSESSMENT OF DISTYLY

To determine if both species were fully distylos, we examined several aspects of the syndrome characteristic for *Pri-*

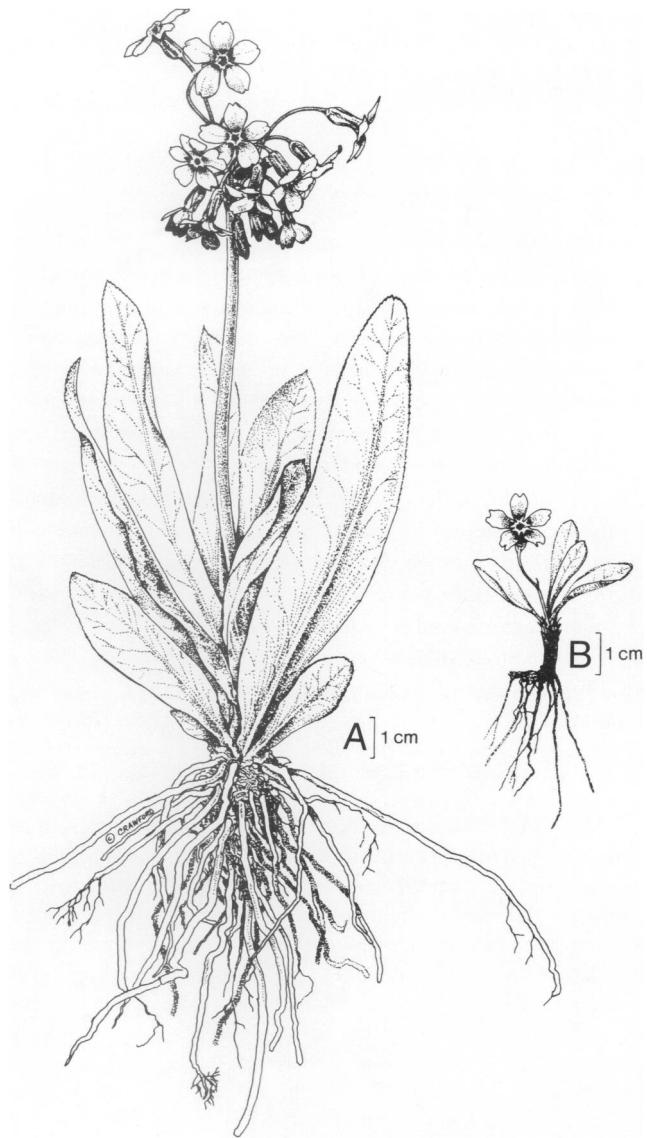


FIGURE 1. Comparative morphology of (A) *Primula parryi* and (B) *P. angustifolia*.

mula: (1) style and anther position, (2) pin and thrum pollen size dimorphism, (3) dimorphism of stigmatic papillae length, and (4) autogamy as a measure of intramorph incompatibility. Style/anther positions were assessed visually and pollen and stigmas were observed under scanning electron microscope. Autogamy was assessed using insect exclosures made from wooden frames covered with fine mesh cloth which allowed light and wind, but no flying insects, to pass through. Exclosures were constructed when flowers were in the young bud stage. Control plants were left uncovered. Seeds were counted approximately 1 mo after exclosures were constructed. Exclosure experiments were repeated in two different growing seasons: 1988 and 1990 for *P. angustifolia*, and 1988 and 1991 for *P. parryi*.

POLLEN AUGMENTATION

To determine if female reproductive success was a function of pollination, we artificially pollinated flowers by removing an unquantified amount of pollen from thrum anthers and transferring it to pin stigmas using the ball-tip of an insect pin. The reciprocal transfer was not performed due to the probability of

flower damage when reaching thrum stigmas and pin anthers which are inserted low in a narrow corolla tube. We used two control groups: one was mock pollinated by touching the pin stigma without pollen transfer and the other was not pollinated at all. We performed the mock pollination to test for differences in seed set due to manipulation rather than pollen transfer. The experiment included three replicates of three plots each. Each plot contained 25 pin flowers that were pollen-augmented, 25 that were mock pollinated, and 25 left as controls. Augmentation and mock pollination were repeated a total of three times per flower on 25 plants over a 3-d period.

REPRODUCTIVE ALLOCATION AND SUCCESS

We measured flower diameter (the distance across the limb of the corolla) and flowers/plant on samples of each species. In addition, we measured duration of anthesis for naturally pollinated flowers and total flowering duration of individual plants. The latter corresponded exactly to flower anthesis in our sample of *Primula angustifolia*, since all individuals had a single flower. We scored presence or absence of scent and nectar volume at several different times of day between 0600 and 1800. Nectar was sampled by inserting a microhematocrit capillary tube 75 (± 0.2) mm long (I.D. 1.1–1.2 mm) into the corolla tube of one flower of each of 15 pin and 15 thrum plants. Amounts were recorded as abundant (>1 cm liquid), slight (<1 cm liquid), or absent (no liquid apparent).

Seed set/capsule was measured using one capsule from 50 individuals of each species. Because of the multiflowered inflorescence in *Primula parryi*, it was necessary to select representative capsules on each plant using visual criteria of apparently average size and fullness. Percent seed set in each species was calculated as mean seed set/mean ovule number. As a measure of the mean seed size in each species, the counted seeds were measured to the nearest 0.5 mm using an optical micrometer in a dissecting microscope.

INSECT POLLINATORS

We collected insect visitors on 22 plots of 1 m² containing an average of 167 plants each for *P. angustifolia* and on 14 plots of 1 m² with an average of 104 individuals each for *P. parryi*. Insect visitors were collected during 30-min intervals throughout the period of anthesis, for a total of 20.5-h for *P. angustifolia* and 42-h for *P. parryi*. Insect pollen loads were removed by swabbing entire insects with fuchsin gel (Beattie, 1971), then melting the gel onto slides for observation (Kearns and Inouye, 1993). Individual grains and morph type could be distinguished easily under the microscope. Additional observations of pollen load were made by sputter-coating body segments or entire insects with gold and viewing under a scanning electron microscope.

We also used exclosures to examine the effect of short-term exposure to pollinators for both species. Twenty-five individuals each of *P. parryi* and *P. angustifolia* were covered in young bud stage. Once flowers opened, the exclosures were removed for a 24-h period of clear weather, then covered again and left to develop capsules.

Results

DISTYLY AND POLLEN AUGMENTATION

Both *Primula angustifolia* and *P. parryi* appear to be functionally distylous. Of the approximately 2000 individuals of each

TABLE 1

Elements of female reproductive success in *Primula angustifolia* and *P. parryi*

	No. flowers sampled	No. setting seed	% Seed set
<i>Primula angustifolia</i>			
Exclosure			
1988	44	0	0.00
1990	20	0	0.00
Control			
1988	43	32	74.42
1990	20	17	85.00
24-h exposure			
1990	22	1	4.50
Seeds/capsule ^a for 24-h exposure = 22			
<i>Primula parryi</i>			
Exclosure			
1988	53	2	0.04
1991 ^b	50	1	0.02
Control			
1988	52	38	73.08
1991 ^b	50	50	100.00
24-h Exposure			
1991 ^b	10	10	100.00
Mean seeds/capsule for 24-h exposure = 178.3 (SD = 72.7)			

^a Excluding individuals with zero seed set from the 24-h exposure.

^b Seed set in 1990 could not be surveyed due to late season damage from elk.

species surveyed in the field, all had distinct pin/thrum morphology. Mean pin pollen diameter was 15.0 μm ($n = 150$, SD = 1.6) in *P. angustifolia* and 14.4 μm ($n = 150$, SD = 1.7) in *P. parryi*. As expected, mean thrum pollen diameter was larger: 22.6 μm ($n = 150$, SD = 1.8) in *P. angustifolia*, and 21.8 μm ($n = 150$, SD = 1.5) in *P. parryi*. Microscopic examination indicated that pin/thrum dimorphism was present in stigmatic papillae length. Autogamy was virtually nonexistent: only a few individuals of *P. parryi* set seed under exclosures and no individuals of *P. angustifolia* set seed when insect visitation was prevented (Table 1).

The effectiveness of only 24 h of exposure to pollinators differed between the two species (Table 1). Among 22 individuals of *Primula angustifolia*, only one flower set seed with 22 seeds/capsule (seed set 4.5%). Three of the original 25 study plants were lost to herbivory. For *P. parryi*, however, mean seed set of 10 flowers on 7 plants was dramatically higher: 178.3 seeds/capsule (SD = 72.7), for seed set of 100%. Eighteen of the original 25 study plants were lost to herbivory.

Augmented pollination increased seed set significantly in *Primula parryi* but only marginally in *P. angustifolia* (Table 2). Although we observed some differences between populations, seed set in naturally pollinated populations of both species always had lower mean seed set than populations with augmented pollination. We found no significant difference in seed set between mock and naturally pollinated plants.

COMPARATIVE REPRODUCTIVE ALLOCATIONS

Female reproductive success differs between the two species, and may at least in part, be a function of their different

TABLE 2

Pollen augmentation in *Primula angustifolia* and *P. parryi*: mean seed set/capsule

Popu-lation	Augmented pollen	Mock pollination	Control
<i>Primula angustifolia</i>			
1	9.2 (SD = 4.0) <i>n</i> = 19	7.9 (SD = 6.5) <i>n</i> = 24	7.4 (SD = 8.0) <i>n</i> = 21
2	17.4 (SD = 12.7) <i>n</i> = 22	13.9 (SD = 7.1) <i>n</i> = 16	3.7 (SD = 7.4) <i>n</i> = 19
3	11.7 (SD = 11.0) <i>n</i> = 21	9.1 (SD = 8.5) <i>n</i> = 22	7.2 (SD = 6.7) <i>n</i> = 22
Total	12.9 (SD = 10.6) ^a <i>n</i> = 62	10.0 (SD = 8.5) <i>n</i> = 62	9.3 (SD = 7.9) ^a <i>n</i> = 62
<i>Primula parryi</i>			
1	212.0 (SD = 77.2) <i>n</i> = 25	174.8 (SD = 49.0) <i>n</i> = 25	166.2 (SD = 58.0) <i>n</i> = 25
2	203.7 (SD = 59.2) <i>n</i> = 25	164.8 (SD = 51.1) <i>n</i> = 25	168.9 (SD = 69.3) <i>n</i> = 25
Total	207.8 (SD = 68.2) ^b <i>n</i> = 50	169.8 (SD = 49.8) <i>n</i> = 50	163.8 (SD = 63.2) ^b <i>n</i> = 50

^a Student-Newman-Keuls 1-way ANOVA shows pollen augmentation yields marginally higher seed set. ($F = 2.90$; $p < 0.057$; $R^2 = 0.031$). There is no significant difference in seed set between control and mock pollinated plants.

^b Student-Newman-Keuls 1-way ANOVA shows pollen augmentation yields significantly higher seed set than either of the other treatments ($F = 7.33$; $p < 0.0009^{***}$; $R^2 = 0.091$). There is no significant difference in seed set between control and mock pollinated plants.

morphologies and reproductive allocations (Table 3). *Primula parryi* has more and larger flowers than *P. angustifolia*; because these bloom asynchronously in basipetal maturation, any individual plant remains available to pollinators for nearly three times as long. Floral attractiveness also differs: *P. parryi* flowers have a characteristic strong odor and abundant nectar, while *P. angustifolia* has virtually no scent and little nectar. Not only does *P. parryi* have greater investment in reproductive structures and rewards than *P. angustifolia*, but in vegetative ones as well. *Primula parryi* produces a large root extending several decimeters into the soil, whereas *P. angustifolia* produces a minimal root only a few centimeters deep. *Primula parryi* also produces more than ten times as much leaf tissue as *P. angustifolia*.

INSECT POLLINATORS

We collected 68 individuals from 8 orders and 15 families visiting *Primula angustifolia*, but we could document *Primula* pollen on only a few of them (Table 4). The primary pollinator in 1990 was in the Halictidae, but in 1991, nine *Bombus* queens were observed visiting during a period of 5-d; these carried abundant *Primula* pollen and thus could be primary pollinators for that year.

We collected 286 individuals from 3 orders and 14 families on *Primula parryi*, most of which carried at least some *Primula* pollen (Table 5). The most abundant visitor was *Bombus balteatus*, and all individuals surveyed carried *Primula* pollen. A total of nine different species of *Bombus* were collected on *P. parryi*. We also observed hummingbirds visiting on several occasions, although we were not able to assess pollination since these were not collected.

TABLE 3
Comparative morphology and reproduction of Primula angustifolia and P. parryi

	<i>Primula angustifolia</i>	<i>Primula parryi</i>
Anthesis	early June	July-early September
Mean no. days/flower	7.0 (<i>n</i> = 28, SD = 0.8)	6.7 (<i>n</i> = 39, SD = 1.1)
Mean no. days/plant	7.0 (<i>n</i> = 28, SD = 0.8)	21.2 (<i>n</i> = 39, SD = 1.8)
Mean no. flowers/inflorescence	1.0 (<i>n</i> = 400, SD = 0.0)	13.6 (<i>n</i> = 103, SD = 3.5)
Mean corolla diameter (cm)	1.6 (<i>n</i> = 50, SD = 0.3)	2.3 (<i>n</i> = 50, SD = 0.5)
Mean corolla tube length (cm)	0.8 (<i>n</i> = 23, SD = 0.2)	1.2 (<i>n</i> = 50, SD = 0.2)
Mean plant height (cm)	1.6 (<i>n</i> = 23, SD = 1.0)	16.6 (<i>n</i> = 50, SD = 7.6)
Scent	Weak to absent	Consistently strong
Nectar	Little to absent	Abundant
Mean seed diameter (mm)	1.0 (<i>n</i> = 50, SD = 0.2)	1.7 (<i>n</i> = 50, SD = 0.2)
Mean no. ovules/flower	39.3 (<i>n</i> = 58, SD = 10.4)	295.1 (<i>n</i> = 58, SD = 49.8)
Mean no. seeds/capsule	9.3 (<i>n</i> = 50, SD = 7.8)	167.6 (<i>n</i> = 50, SD = 63.2)
Mean percent seed set	23.7	56.8

Discussion

DISTYLY

We find no evidence that *Primula parryi* and *P. angustifolia* lack any component of distyly as documented in other species of *Primula*. Since there is no indication in the substantial literature now available that self-infertility in primroses is any stronger than intramorph infertility, the lack of autogamy that we observed probably is a reliable indicator of intramorph infertility. The low seed set we found in a few individuals of *P. parryi* under exclosures (Table 1) probably represents *Bombus* visitation to unopened buds (which we observed on several occasions) before exclosures were in place. Similar seed set for *Primula parryi* was recorded by Macior (1974). Neither *Primula parryi* nor *P. angustifolia* show any tendency towards vegetative reproduction, and we conclude that both rely on seed production for recruitment and depend on insect pollinators for reproduction. While work from a variety of locations now seems to indicate clearly that temperate alpine plants are predominantly entomophilous and outcrossed (Moldenke and Lincoln, 1979; Arroyo et al., 1982; Totland, 1993), little is known about how extensive obligate outcrossing and incompatibility systems are in different alpine species. Distyly, with both self and intramorph incompatibility, would appear to be risky in a restricted flowering season. However, the broad distributions and local abundance of these two species indicate that obligate outcrossing can indeed be functional in a tundra environment, and is perhaps more common than previously realized.

POLLINATORS

Environmental conditions that impose restrictions on pollinator activity may be overcome by attracting effective and/or diverse pollinators. Our results from short-term exposure suggest that a few, or perhaps a single, visit from a pollinator may be sufficient for seed set in these species. In particular, bees (*Bombus* spp.) were heavily laden with *Primula* pollen, and appear to be important pollinators for *Primula parryi*, and probably *P. angustifolia* as well, at least in some years. In spite of their sensitivity to cool temperatures and high energetic requirements (Heinrich, 1973; Arroyo et al., 1982; Levesque and Burger, 1982), *Bombus* species can be effective alpine pollinators due to their large body size that enables them to fly in windy conditions, hairy bodies, and foraging patterns (Moldenke and Lincoln, 1979; Levesque and Burger, 1982; Kevan and Baker,

1983). Work in other alpine zones has shown that Lepidopterans are frequently important pollinators at high elevations (Arroyo et al., 1982). Although we found Lepidopterans visiting *Primula angustifolia*, none carried any *Primula* pollen. In contrast, 5 different taxa were collected on *P. parryi*, including 13 individuals of *Colias meadii*, which we did document to carry pollen. Lepidopterans have a long proboscis that can easily reach nectar at the base of a long corolla tube like that found in primulas. Because they tend to fly longer between flower visits than bees do (Schmitt, 1980), a few Lepidopteran visits to a population might increase pollen flow between the more widespread individuals. Dipterans are also thought to be common tundra pollinators (Levesque and Burger, 1982; Totland, 1993), if somewhat unreliable due to irregular foraging patterns (Faegri and van der Pijl, 1979). However, Kevan (1972) suggested that flies may be relatively good tundra pollinators due to flower constancy in the compressed growing season. Syrphid flies were abundant on both species. Three different species of Syrphidae carried pollen of *Primula angustifolia*; the most abundant of these was *Epistrophe solalis*. While *P. parryi* was also visited by Syrphids, none of the individuals of the most abundant species, *Syrphus lapponicus*, carried any *Primula* pollen. Most of the additional taxa collected on *Primula angustifolia* may be visitors or only occasional pollinators. Members of the families Collembola, Psocoptera, and Thysanoptera are extremely small and probably not able to transport pollen effectively. While Anthomyiidae were visitors to both species, only a few individuals found on *P. parryi* and none found on *P. angustifolia* carried any pollen. They do not appear to be efficient pollen vectors for either species.

LIMITATIONS ON FEMALE REPRODUCTIVE SUCCESS

Our observations suggest that reproduction in both of these species appears to be limited to some extent by pollination. Given the lesser visitation and lower seed set in *Primula angustifolia*, we expected to find that augmented pollen availability would increase seed set significantly, and that *P. parryi* would exhibit less response. However, just the opposite occurred (Table 2). While some of this response may be attributable to the greater ease of transferring pollen to the larger flowers and exposed stigmas of *Primula parryi*, R^2 values show that less than 10% of the variation between the treatments can be attributed to increased pollen availability. Likewise, only a small percentage of

TABLE 4

Insect visitors to *Primula angustifolia*

Taxon	No. of specimens
Diptera (Flies)	
Anthomyiidae	
Anthomyiinae	
<i>Paregle cinerella</i>	17
Unidentified sp.	4
Unidentified sp.	1
Unidentified sp.	1
Unidentified sp.	1
Syrphidae	
<i>Epistrophe solalis</i> ^a	5
<i>Melanostoma</i> sp.	1
<i>Eristalis</i> sp.	3
Unidentified sp.	1
<i>Syrphus</i> sp.	1
Scatophagidae ^a	1
Unidentified	2
Hymenoptera (Bees, Wasps, Ants)	
Apidae	
<i>Bombus balteatus</i> ^a	1
<i>Bombus sylvicola</i> ^a	1
<i>Bombus melanopygus</i>	1
<i>Bombus</i> sp. ^a	7
Halictidae ^a	4
Ichneumonidae	
<i>Cryptus</i> sp.	1
Tenthredinidae ^a	1
Eulophidae	1
Lepidoptera (Butterflies, Moths)	
Pieridae	
<i>Pieris occidentalis</i>	2
Homoptera (Leafhoppers)	
Cicadellidae	
Cicadellinae	
<i>Cicadella</i> sp.	1
Hemiptera (True bugs)	
Lygaeidae ^a	2
Thysanoptera (Thrips)	6
Pscoptera (Booklice & Barklice)	
Pseudocaeciliidae ^a	1
Collembola (Springtails)	
Sminthuridae ^a	1

^a Some specimens documented as carrying *Primula* pollen. Specimens were identified using reference collections at Colorado College and the University of Colorado at Boulder, and texts of Cole (1969), Borror and White (1970), Bryon (1980), Ferris and Brown (1980), and Borror et al. (1980). Voucher specimens are at Colorado College.

increased seed set in *P. angustifolia* can be attributed to increased pollen. This indicates that seed set is a function of more than just pollen availability; in particular, soil nutrients may be critical as well. Although *Primula parryi* and *P. angustifolia* grow on Niwot Ridge at similar elevations, they have very different habitats: *P. parryi* grows in bogs rich in organic material and *P. angustifolia* grows in moist mineral soil. Since reproduction in perennials can ultimately be affected by primary produc-

TABLE 5

Insect visitors to *Primula parryi*

Taxon	No. of specimens
Diptera (Flies)	
Anthomyiidae	
Anthomyiinae	
<i>Hylemya</i> sp.	2
Unidentified sp. ^a	3
Muscidae	
<i>Musca</i> sp.	1
Syrphidae	
<i>Syrphus lapponicus</i>	14
<i>Syrphus</i> sp. 1	1
<i>Syrphus</i> sp. 2	1
<i>Syrphus</i> sp. 3	1
<i>Syrphus</i> sp. 4	2
<i>Chrysotoxum ventricosum</i>	4
<i>Chrysotoxum</i> sp. ^a	1
<i>Melanostoma</i> sp.	1
<i>Scaeva</i> sp.	2
<i>Eristalis hirtus</i>	1
<i>Pipiza</i> sp. ^a	2
<i>Didea</i> sp. ^a	1
<i>Epistrophe</i> sp. ^a	1
Unidentified sp.	1
Tabanidae	
<i>Hybomitra sonomensis</i> ^a	1
Scatophagidae ^a	2
Calypratae ^a	1
Hymenoptera (Bees, Wasps, Ants)	
Apidae	
<i>Bombus balteatus</i> ^a	161
<i>Bombus balteatus</i> ^a (male)	10
<i>Bombus sylvicola</i> ^a	27
<i>Bombus terricola occidentalis</i> ^a	6
<i>Bombus melanopygus</i> ^a	7
<i>Bombus flavifrons</i> ^a	4
<i>Bombus nevadensis</i> ^a	1
<i>Bombus frigidus</i> ^a	2
<i>Bombus bifarius</i> ^a	3
<i>Bombus appositus</i> ^a	2
Adrenidae ^a	1
Tenthredinidae	1
Megachilidae	1
Lepidoptera (Butterflies, Moths)	
Pieridae	
<i>Colias meadi</i> ^a	13
Lycaenidae	
<i>Lycaena cupreus</i>	1
Hesperiidae	
<i>Polites draco</i>	1
Argynninae	
<i>Speyeria eurynome</i> ^a	1
<i>Boloria napaea</i> ^a	1

^a Some specimens documented as carrying *Primula* pollen. Specimens were identified using reference collections at Colorado College and the University of Colorado at Boulder, and texts of Cole (1969), Borror and White (1970), Bryon (1980), Ferris and Brown (1980), and Borror et al. (1980). Voucher specimens are at Colorado College.

tivity and nutrient reserves (Chapin, 1980; Chapin et al., 1990), these substrate differences may be important contributors to seed output. The massive root system of *Primula parryi* far exceeds that of *P. angustifolia*; consequently, the former species may have more stored resources upon which to draw. *Primula angustifolia* may be reproducing at capacity given the available nutrients in the soil or stored in belowground tissues.

DIFFERENCES BETWEEN SPECIES

By all of our measures, *Primula parryi* is an extremely "successful" species: high production of biomass and reproductive structures, abundant chemical attractants, high rates of visitation from diverse insect taxa, high seed set, high population numbers, and a wide distribution. In contrast, *P. angustifolia* has much less biomass, fewer reproductive structures and attractants, low rates of visitation from relatively few insect taxa, and a more restricted distribution. However, although it may appear to be reproductively marginal in comparison to the fecund *P. parryi*, *P. angustifolia* should also be considered reproductively "successful." Within its more narrow geographic range, the species is relatively common, populations are generally large, and even in a season of apparently low insect visitation, nearly one quarter of the ovules developed into seeds.

The differences between these two species highlight the different ways in which distyly can function. In general, an inflorescence with few, smaller flowers may be less attractive to pollinators than a large, multiflowered one (Faegri and van der Pijl, 1979; Galen, 1989). Any *Primula parryi* individual is available to foraging pollinators for a relatively long period of time. The ability of *P. parryi* to offer rewards to insects undoubtedly also influences its ability to garner more abundant and more diverse insects. *Primula angustifolia* may compensate for its inconspicuous inflorescence by a tendency to grow in clumps with an average of seven individuals. The clumps probably result from germination of a single capsule in situ, and thus would represent close relatives. The cost of individual competition may be overcome by the advantages of an increased floral display to attract the attention of pollinators (Waser, 1983). In addition, the early phenology of *Primula angustifolia* may affect its certainty for pollination. In comparison to mid-July (the period of anthesis for *P. parryi*), there are relatively few species flowering in early June in synchrony with *P. angustifolia*. If competition for pollinator attention is not a critical factor for *P. angustifolia*, costly attractants would be a less essential investment.

Conclusions

Although short-term reproductive studies of perennial species must be viewed with caution, this comparative study suggests that distyly is indeed viable on the tundra but that it may work differently in different species. Many case studies have pointed out all too well that loss or change in pollinator faunas can have catastrophic effects on local plant species (Kevan and Baker, 1983; Hafernik, 1992). Although neither of our study species are currently threatened, the population viability and long-term outlook for other related rare distylous primulas in the Great Basin and southern Rockies is of considerable concern (Kelso, unpublished). We suggest that distyly and other such reproductive systems entailing obligate plant-pollinator relationships have ecological and conservation implications at both the species and the community level, and are worthy of further attention in tundra environments.

Acknowledgments

We are grateful for the help and suggestions of the following: C. Galen, D. Inouye, C. Kearns, D. McGuire, N. Waser, an unidentified reviewer, the Mountain Research Station of the University of Colorado (facilities funded under NSF DIR 8912249), and the Howard Hughes Medical Institute (for providing a grant to the Department of Biology at Colorado College).

References Cited

- Arroyo, M. T. K., Primak, R., Armesto, J., 1982: Community studies in pollination ecology in the high temperate Andes of Central Chile. I. Pollination mechanisms and altitudinal variation. *American Journal of Botany*, 69: 82-97.
- Baker, H. G., 1966: The evolution, functioning, and breakdown of heteromorphic incompatibility systems. I. The Plumbaginaceae. *Evolution*, 20: 349-368.
- Barrett, S. C. H., 1990: The evolution and adaptive significance of heterostyly. *Trends in Ecology and Evolution*, 5: 144-148.
- Barrett, S. C. H., 1992: *Evolution and Function of Heterostyly. Monographs on Theoretical and Applied Genetics*, 15. New York: Springer-Verlag. 279 pp.
- Beattie, A. J., 1971: A technique for the study of insect-born pollen. *Pan Pacific Entomologist*, 47: 82.
- Borror, D. J. and White, J. D., 1970: *A Field Guide to the Insects of America North of Mexico*. Boston: Houghton Mifflin. 402 pp.
- Borror, D. J., Triplehorn, C. A., and Johnson, N. F., 1980: *An Introduction to the Study of Insects*. Philadelphia: Saunders Publishing. 875 pp.
- Bryon, P. A., 1980: On the ecology and systematics of Colorado bumblebees. PhD dissertation, University of Colorado, Boulder. 193 pp.
- Campbell, C. S., Famous, N. C., and Zuck, M. G., 1986: Pollination ecology of *Primula laurentiana* (Primulaceae) in Maine. *Rhodora*, 88: 253-260.
- Chapin, F. S. III, 1980: The mineral nutrition of wild plants. *Annual Review of Ecology and Systematics*, 11: 233-260.
- Chapin, F. S. III, Schulze, E.-D., and Mooney, H. A., 1990: The ecology and economics of storage in plants. *Annual Review of Ecology and Systematics*, 21: 423-447.
- Charlesworth, B. and Charlesworth, D., 1979: A model for the evolution of distyly. *American Naturalist*, 114: 467-498.
- Christy, M., 1922: The pollination of the British Primulas. *Botanical Journal of the Linnaean Society*, 46: 105-139.
- Cole, F. R., 1969: *The Flies of Western North America*. Berkeley: University of California Press. 693 pp.
- Darwin, C., 1877: *The Different Forms of Flowers on Plants of the Same Species*. London: John Murray. 352 pp.
- Faegri, K. and Van der Pijl, L., 1979: *The Principles of Pollination Biology*. 2nd ed. London: William Clowes. 244 pp.
- Ferris, C. D. and Brown, F. M., 1980: *Butterflies of the Rocky Mountain States*. Norman: University of Oklahoma Press. 442 pp.
- Galen, C., 1989: Measuring pollinator-mediated selection on morphometric floral traits: bumblebees and the alpine sky pilot, *Polemonium viscosum*. *Evolution*, 43: 882-890.
- Ganders, F., 1979: The biology of heterostyly. *New Zealand Journal of Botany*, 17: 607-635.
- Hafernik, J. E., Jr., 1992: Threats to invertebrate biodiversity: implications for conservation strategy. In Fiedler, P. L. and Jain, S. K. (eds.), *Conservation Biology*. New York: Chapman and Hall, 172-195.
- Heinrich, B., 1973: Energetics of the bumblebee. *Scientific American*, 228: 96-102.
- Hultgård, U.-M., 1990: Polyploidy and differentiation in N. European populations of *Primula* subgenus *Aleuritia*. *Sommerfeltia*, 11: 117-135.
- Kearns, C. A. and Inouye, D. W., 1993: *Techniques for Pollination Studies*. Princeton: Princeton Scientific. 224 pp.

- nation Biologists. Niwot: University Press of Colorado. 583 pp.
- Kelso, S., 1991: Taxonomy of *Primula* sects. *Aleuritia* and *Armerina* in North America. *Rhodora*, 93: 67-99.
- Kelso, S., 1992: The genus *Primula* as a model for evolution in the Alaskan flora. *Arctic and Alpine Research*, 24: 82-87.
- Kevan, P. G., 1972: Insect pollination of high arctic flowers. *Journal of Ecology*, 60: 831-847.
- Kevan, P. G. and Baker, H. G., 1983: Insects as flower visitors and pollinators. *Annual Review of Entomology*, 28: 407-453.
- Knuth, P., 1909: *Handbook of Flower Pollination*. Volume 3. Transl. J. R. Ainsworth Davis. Oxford: Oxford University Press, 58-81.
- Levesque, C. M. and Burger, J. F., 1982: Insects (Diptera, Hymenoptera) associated with *Minuartia groenlandica* (Caryophyllaceae) on Mount Washington, New Hampshire, U.S.A. and their possible role as pollinators. *Arctic and Alpine Research*, 14: 117-124.
- Macior, L. W., 1974: Pollination ecology of the Front Range of the Colorado Rockies. *Melanderia*, 15: 1-59.
- Mazer, S. J. and Hultgård, U.-M., 1993: Variation and covariation among floral traits within and among four species of northern European *Primula* (Primulaceae). *American Journal of Botany*, 80: 474-485.
- Moldenke, A. R. and Lincoln, P. G., 1979: Pollination ecology in montane Colorado: a community analysis. *Phytologia*, 42: 349-379.
- Richards, A. J., 1993. *Primula*. Portland, Oreg.: Timber Press. 299 pp.
- Schmitt, J., 1980: Pollinator foraging behavior and gene dispersal in *Senecio* (Compositae). *Evolution*, 34: 934-943.
- Schou, O., 1983: The distyly in *Primula elatior* (L.) Hill (Primulaceae), with a study of flowering phenology and pollen flow. *Botanical Journal of the Linnaean Society*, 86: 261-274.
- Totland, Ø., 1993: Pollination in alpine Norway: flowering phenology, insect visitors, and visitation rates in two plant communities. *Canadian Journal of Botany*, 71: 1072-1079.
- Vekemans, X., Lefebvre, C., Belalia, L., and Meerts, P., 1990: The evolution and breakdown of the heteromorphic incompatibility system of *Armeria maritima*, revisited. *Evolutionary Trends in Plants*, 4: 15-23.
- Vuilleumier, B. S., 1967: The origin and evolutionary development of heterostyly in the angiosperms. *Evolution*, 21: 210-226.
- Waser, N. M., 1983: The adaptive nature of floral traits: ideas and evidence. In Real, L. (ed.), *Pollination Biology*, New York: Academic Press, 242-277.
- Woodell, S. R. J., 1960. What pollinates primulas? *New Scientist*, 8: 568-571.

Ms submitted July 1993