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Reproductive biology of Erythronium grandiflorum Pursh varieties grandiflorum and candidum (Piper) Abrams (Liliaceae)

Jane K. Fritz-Sheridan
The University of Montana

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REPRODUCTIVE BIOLOGY OF ERYTHRONIUM GRANDIFLORUM PURSH VARIETIES

GRANDIFLORUM AND CANDIDUM (PIPER) ABRAMS (LILIACEAE)

by

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B. S., Michigan State University, 1972
M. S., University of Montana, 1981

Presented in partial fulfillment of the requirements for the degree of

Master of Arts

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Approved by

Chairman, Board of Examiners

Dean, Graduate School

Date
ABSTRACT

Fritz-Sheridan, Jane K., M. A., December 1986
Botany

Reproductive Biology of Erythronium grandiflorum Pursh varieties grandiflorum and candidum (Piper) Abrams (Liliaceae) (58 pages)

Director: David E. Bilderback

This four-year (1982-1986) study compared the pollination biology and cytology of a relatively rare taxon, Erythronium grandiflorum Pursh var. candidum (Piper) Abrams, with that of a geographically widespread sister taxon, E. grandiflorum var. grandiflorum, in the Pacific Northwest. Breeding studies were used to study the reproductive systems of the taxa, to test for interfertility between them, and to seek abnormalities in the breeding system of the rare taxon that might account for its relative rarity. Chromosomes were counted in both taxa and in hybrids from artificial crosses. Ranges of the two taxa were determined from field studies and herbarium specimens. Although the ranges of the taxa overlap in part, populations are usually allopatric. Phenological factors are probably minor in preventing cross-pollination between the taxa. Both taxa are protogynous obligate outcrossers pollinated by bees. Seed production apparently is not pollinator-limited. The two taxa are interfertile only when individuals from allopatric populations are artificially crossed, and thus should be considered two biological species. When the taxa overlap in floral phenology in sympatric populations, they exhibit reciprocal incompatibility. Such incompatibility between closely-related perennial species is unusual. It may have arisen via natural selection in mixed populations. Alternatively, if populations of each taxon vary with regard to their incompatibility alleles, they may have acquired their fertility barriers by chance before populations of the two taxa came into contact with each other.
ACKNOWLEDGEMENTS

I would like to express special thanks to Jerrold I. Davis for his guidance and critical comments on several drafts, and to David E. Bilderback for his support and suggestions on the research and on the final draft. I would also like to thank the other members of my committee, James R. Habeck, Charles N. Miller, and David Alt, for their advice and comments. I thank Meredith A. Lane for review of an earlier draft, and Alexander F. Motten and Peter Bernhardt for suggestions on the improvement of the manuscript.

Curators of several herbaria graciously loaned specimens for this study. Robert D. Pfister gave permission to use a study site at the Lubrecht Experimental Forest, and Cliff MartinKa and Robert C. Haraden authorized my use of a study site at Glacier National Park. Martha Apple provided field assistance. Terry Griswold of the University of Utah identified the insects. I am especially grateful to Richard P. Fritz-Sheridan for field assistance and encouragement throughout this project.

This research was supported by the Five Valleys Chapter of the National Audubon Society, Sigma Xi, and a Bertha Morton Scholarship administered by the University of Montana Graduate School.
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INTRODUCTION

The protection and management of rare plant species is impossible without a clear understanding of their biology. There are different degrees and kinds of rarity, and certainly there is no one cause of it. Suggested causes have been youth, senescence, lack of success, genetic depletion, and narrow ecological tolerances of the taxon (Drury, 1980), but none of these explanations is all-encompassing, because of numerous and complex factors (Stebbins, 1980). For example, limited genetic variability and ecological amplitude may suggest that a species is newly derived, but other explanations are possible. The species may have gone through a genetic bottleneck (e.g., population restriction during glaciation). Steep ecological gradients surrounding populations may reduce the environmental variation at population sites. The ability of the plants to disperse propagules to a suitable habitat may be limited. As a result, Stebbins (1980) concluded that the rarity of a species can not be correlated consistently with its amount of within-population genetic variation. Likewise, while most rare and localized species occur in ecological islands, a correlation is foiled because other species in these islands may be widespread. Nor are historical correlations consistent, because "rare and localized species can be either young, ancient, or of an intermediate age" (Stebbins, 1980). Thus, the cause of the rarity of a species must be sought by using a synthetic approach in which ecological, genetic, and historical factors are considered and their interactions elucidated (Drury, 1980; Stebbins,
Studies that compare a rare plant taxon with a closely related non-rare species provide important contributions toward understanding rare species. Once compiled for many groups of plants, comparative data will better enable us to "judge whether the traits of rare plants are unique to them or are some random sample of plant traits in general and unrelated to the rare state" (Rabinowitz, 1981). This study compared the pollination biology and cytology of a rare taxon, Erythronium grandiflorum Pursh var. candidum (Piper) Abrams, with that of the closely related and widespread E. grandiflorum var. grandiflorum. These taxa lend themselves well to such a comparative study; variety grandiflorum (GRAN) is geographically widespread in the Rocky Mountain region and occupies a wide variety of habitats, and variety candidum (CAND) is restricted both geographically and apparently ecologically.

The genus Erythronium has never been monographed in its entirety, and its western North American species were last monographed by Applegate (1935). Unresolved taxonomic and phylogenetic relationships within the genus are exemplified by the different classification of CAND by various authors (e.g., Purdy, 1904; Piper, 1914; Abrams, 1923; St. John and Jones, 1929; Davis, 1946; Hitchcock, 1969).

The yellow-flowered perennial herb GRAN occurs from southern British Columbia to Colorado and California (Munz and Keck, 1968; Hitchcock, 1969). Its habitat ranges from semi-dry montane valleys to snowbank edges in alpine meadows at about 3700 m elevation. Characters used to distinguish GRAN from CAND have been yellow tepals 20-35 mm long and 4-7 mm wide, yellow, red, or white anther color, and capsules 30 mm
long and 10 mm in diameter (Applegate, 1935; Hitchcock, 1969). Previous chromosome counts for *Erythronium grandiflorum* var. *pallidum* (a white-anthered form of GRAN, according to Hitchcock, 1969) were \(2n = \text{ca. 24}\) (Cave, 1970) and \(n = 12\) (Smith, 1955).

CAND is a relatively rare taxon that occurs as disjunct populations in comparatively small areas of western Montana, northern Idaho, and eastern Washington. CAND has been observed in montane valleys and hillsides at elevations up to about 2154 m, but usually below 1415 m. The taxon differs from GRAN in having white tepals 35-45 mm long and 10-12 mm wide, and capsules 50 mm long and 15 mm in diameter (Applegate, 1935). Although Applegate (1935) described the anthers as white, the taxon also has yellow and red anthers, as in GRAN. Prior to this study, the chromosome number of CAND was unreported.

Vegetative propagation of many *Erythronium* species of eastern North America (*E. americanum* Ker., *E. albidum* Nutt., *E. propullans* Gray, *E. rostratum* Wolf, and *E. umbilicatum* subsp. *monostolum* Parks and Hardin) has been well-documented (e.g., Blodgett, 1900; Parks and Hardin, 1963; Holland, 1974; Banks, 1980; Morley, 1982). Of *Erythronium* species in western North America, only *E. multiscapeoidem* (Kell.) Nels. and Kenn. produces runners (Purdy, 1904; Applegate, 1935). In other western species and in *E. japonicum* (L.) Decne of Japan, offset bulbs occasionally form within the sheath of the bulb, but probably only after injury (Purdy, 1904; Kawano, 1982). Field observations of 230 GRAN and 255 CAND plants confirm that this is also the case with *E. grandiflorum*. Therefore, breeding experiments are uncomplicated by geitonogamous crosses from flowers in the same clump.
This study accomplished several goals. First, breeding studies were conducted in 1982-1984 to characterize the reproductive systems of the taxa, and to test for interfertility between CAND and GRAN at both allopatric and sympatric sites. A second objective was to determine whether any aspect of the breeding system of CAND (e.g., failure to attract pollinators, low fertility, dependence on sexual reproduction, or interaction with GRAN) might contribute to its relative rarity as compared to GRAN. Third, chromosomes were counted in germinated seeds of both taxa and of hybrids from artificial crosses to determine whether karyological differences between the taxa might restrict the sexual reproduction of CAND. Fourth, the ranges of the two taxa were determined from herbarium specimens and field observations.

Field studies revealed that although the two taxa are sympatric within the range of CAND, mosaic populations including both taxa rarely occur. Allopatric populations of the two taxa usually are separated by at least several kilometers, although site elevations may be identical. Both taxa are obligate outcrossers. In the populations studied, the taxa are interfertile only when individuals from allopatric populations are artificially crossed. Pollinators for both taxa are *Bombus bisarius* Cresson, *Apis mellifera* Linn., and *Andrena nigrihirta* (Ashmead). Both taxa have $2n = 24$ chromosomes, but hybrids exhibit $2n = \text{ca. } 22-26$ and, in some cases, putative connections between the chromosomes.
MATERIALS AND METHODS

Study sites

Both GRAN and CAND were collected at numerous sites throughout the known range of CAND. These locations as well as those from herbarium sheets from several herbaria (US, NY, MO, WTU, WS, UC, ORE, OSC, IDS, ID, MONTU and MRC) were used to prepare a distribution map of both taxa (Fig. 1). Flowering dates for the two taxa were compiled to determine phenological overlap.

All pollination studies were conducted in western Montana. In 1982, allopatric GRAN and CAND populations approximately 43 km apart were studied. The CAND site was located beside Rice Ridge Road, about 0.2 km E of Montana Highway 83, 2.5 km N of the town of Seeley Lake, T17N, R15W, SW1/4 sec. 27, Missoula Co. at an elevation of 1335 m (Fig. 1, d). No other species were in anthesis on 1 May at the commencement of the experiments. The GRAN site was across the road from the entrance to the University of Montana Forestry School’s Lubrecht Experimental Forest on Montana Highway 200, T13N, R15W, NW1/4 SE1/4 sec. 11, Missoula Co., at an elevation of 1336 m (Fig. 1, c). Ranunculus glaberrimus Hook. and Anemone nuttalliana DC. were also in anthesis at the time of the pollination experiments.

The 1983 study sites also were allopatric. CAND was studied 2.9 km W of the bridge over the outlet of Placid Lake, T16N, R15W, N1/2 sec. 32, Missoula Co., along the south side of the Placid Lake road, at an elevation of 1330 m (Fig. 1, a). GRAN was studied at Lubrecht
Experimental Forest, about 100 m E of the entrance from Highway 200, T13N, R15W, SE1/4 sec. 11, Missoula Co. (Fig. 1, c). Pollination experiments began on 6 May.

In 1984, CAND and GRAN were studied at two sympatric sites, where CAND and GRAN were interspersed and both taxa bloomed at the same time. One site was between Owl Creek and the Placid Lake road, 2.7 km W of Montana Highway 83, T16N, R15W, NW1/4 sec. 27, Missoula Co., at an elevation of 1346 m (Fig. 1, b). The mixed population covered approximately 2750 m². Plants were hand-pollinated between 5 and 11 May. At the other site, 0.5 km NW of the Logging Creek Campground on the northeast side of the North Fork Road in Glacier National Park (elevation 1047.5 m), T34N, R20W, SE1/4 sec. 17, plants were pollinated on 19 May (Fig. 1, e). The mixed population covered approximately 5500 m².

Pollinating insects were observed at five locations. Site 1: CAND was observed along the east side of Montana Highway 83, across the road from the Tamarack Lodge, 4.2 km N of the town of Seeley Lake, T17N, R15W, NE1/4 sec. 28, Missoula Co., at an elevation of 1314 m. Site 2: CAND was observed at Big Larch Campground, on the west side of Montana Highway 83, 0.8 km N of the town of Seeley Lake, T17N, R15W, S1/2 sec. 34, Missoula Co. Site 3: a mixed population of GRAN and CAND was observed at the terminus of the road at Hidden Lake, T16N, R16W, SE1/4 NW1/4 sec. 13, Missoula Co. (approximately 4.2 km NW of Placid Lake). Site 4: a CAND population was studied directly adjacent to the mixed population at Owl Creek as described above. Site 5: GRAN was observed at the Pattee Canyon Picnic Area, 10 km SE of Missoula, T12N, R19W,
Breeding studies

During the spring of 1982, breeding studies of CAND tested for self-fertilization with and without manual aid, agamospermy, and cross-fertilization with GRAN. For both taxa normal seed set was determined. Procedures followed Bell (1974). As each plant had only 1 flower, the number of plants equaled the number of flowers used in each treatment. The treatments were as follows:

Unbagged and open-pollinated: Twenty-five plants of each taxon were tagged but otherwise not manipulated. This group demonstrated levels of normal seed set.

Bagged and self-pollinated: Forty CAND floral buds were enclosed in nylon net bags to exclude pollinators, and later, during anthesis, hand-pollinated with self-pollen and re-bagged. Seed set in this group indicated the degree to which the flowers were self-compatible and/or produced apomictic seeds as a result of stimulation by pollen tube secretions.

Bagged and not manipulated: Twenty-five CAND floral buds were bagged and otherwise not manipulated. Seed production in this group indicated the degree to which the flowers naturally self-fertilized.

Bagged and emasculated: Twenty-five CAND floral buds were emasculated to prevent self-pollination, bagged, and otherwise not manipulated. The level of seed production in this group indicated the degree to which agamospermy occurred.
Bagged - reciprocal crosses: Reciprocal crosses were made between CAND and GRAN. Twenty-five GRAN flowers were emasculated in the bud, immediately cross-pollinated with pollen from anthers of CAND, and bagged. The method used to cross-pollinate CAND flowers with GRAN pollen was identical, except that the flowers were emasculated and bagged in the morning, and cross-pollinated and re-bagged 6 1/2 hr later.

To insure that pollen had not been transferred too early during cross-pollination before repeating the experiments in 1983, the timing of the onset of stigma receptivity was determined. The study site was along the E side of Huckleberry Road, 0.8 km S of Pattee Canyon Road, Missoula. On 18 April 1983, 6 GRAN flowers were emasculated, cross-pollinated, and caged at the bud stage, approximately 1 day before anthesis. The procedure was repeated with CAND flowers on 5 May 1984 at the Owl Creek pollination study site (described above), except that the flowers were not emasculated. One day after cross-pollination and before anther dehiscence in CAND, flowers were excised, placed in an ice chest to maintain ambient air temperature, and returned to the lab. The next morning, approximately 36 hr after pollination, the styles were hand-sectioned longitudinally, stained with aceto-orcein to improve visibility of pollen tubes, examined microscopically for pollen tube growth, and photographed.

In 1983, breeding studies included all treatments for GRAN as well as CAND. Within-population cross-pollination was added for comparison with the open-pollinated group and to determine whether seed set is
pollinator-limited. That is, significantly greater seed set in this treatment than in the open-pollinated group would indicate that under natural conditions, pollinators limit seed production due to their insufficient numbers or effectiveness, or to transfer of incompatible pollen. Twenty-five flowers of each taxon were tested in each treatment. Flowers were pollinated in the bud approximately one day before the buds opened, and caged. Cages constructed from plastic window screen and heavy wire were used for all caged treatments.

The 1984 studies repeated the procedures of 1983, except that the tests for self-fertilization and agamospermy were omitted since no seeds had resulted from these treatments in 1982 or 1983. At Owl Creek, CAND plants were caged in the bud on 28 April, and each flower was pollinated on 5, 9, or 11 May. Some flowers were pollinated in the bud, and some after the flowers opened. Twenty-five plants were tested in each treatment. At Logging Creek, GRAN flowers were caged in the bud on 12 May, and pollinated on 19 May. Some of the flowers were in bud, and some were open. Twenty plants were tested in each treatment.

Because self-pollination produced no seeds, plants were tested in 1984 to determine whether self-pollen grows within the styles. CAND plants at the Owl Creek pollination study site were caged at the bud stage on 5 May 1984, then self-pollinated by hand at anthesis on 9 and 11 May. These flowers were excised on 11 May and placed in plastic bags until the next day, when they were placed in an ice chest until they were returned to the lab on 14 May. The styles were then immediately hand-sectioned longitudinally, stained with aceto-orcein, and examined microscopically for pollen tube growth. The same procedure was followed
with GRAN in 1986 beside the E side of Huckleberry Road, 0.9 km S of Pattee Canyon Road, Missoula. Floral buds were caged on 9 May and flowers were self-pollinated on 14 May.

In 1982, cages were removed after the tepals dropped off the flowers. Developing fruits were collected on 12 May, 10 - 20 days after pollination. At this stage of development, ovules were either plump or withered. Plump ovules were considered to be developing ovules. In 1983 and 1984, plants remained caged until approximately 2 months after pollination, at which time the fruits were placed in glassine or manila envelopes to dry and dehisce. In some instances, fewer than 25 fruits per treatment were harvested due to herbivory on uncaged plants or loss due to unknown causes.

Seeds that resulted from the control treatments and from the intertaxon crosses between CAND and GRAN from allopatric sites in 1983 were planted at the University of Montana Experimental Garden on 30 August 1983. Surviving plants were counted on 17 April 1984, 28 April 1985, and 16 May 1986.

Pollinator observations

Insect visitors were observed and collected from Erythronium and co-blooming species during the flowering seasons of 1982 and 1986. Dates, times of day and locations of observations are listed in Table 1. Pollinator behavior was noted in a field notebook, and, when possible, pollinators were photographed. Several collecting jars were used so that only one insect at a time occupied each jar. Thus, contamination of pollen from one insect onto another was minimized. Microscope
slides of pollen loads mounted in glycerine jelly were prepared. Pollen was evenly dispersed on each slide by stirring with a dissecting needle. These slides were compared to slides of *Erythronium grandiflorum* pollen to determine insect fidelity. If fewer than 100 pollen grains were present on a slide, all were counted; if more than 100 were present, only 100 grains from a randomly-selected location on the slide were counted. An insect was considered to be a pollen carrier of *Erythronium* if its pollen slide contained at least 20 *Erythronium* pollen grains.

**TABLE 1.** Locations, dates and times of pollinator observations. Site locations are described in the text.

<table>
<thead>
<tr>
<th>Date</th>
<th>Time</th>
<th><em>Erythronium</em> spp.</th>
<th>Temp. (C)</th>
<th>Location</th>
</tr>
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<tr>
<td>25 Apr 1982</td>
<td>15:00-16:30</td>
<td>CAND</td>
<td>20</td>
<td>site 1</td>
</tr>
<tr>
<td>8 May 1982</td>
<td>9:00-19:30</td>
<td>CAND</td>
<td>3-14</td>
<td>site 2</td>
</tr>
<tr>
<td>9 May 1982</td>
<td>8:00-11:00</td>
<td>CAND</td>
<td>3-6</td>
<td>site 2</td>
</tr>
<tr>
<td>17 May 1982</td>
<td>15:00-17:00</td>
<td>GRAN and CAND</td>
<td>-</td>
<td>site 3</td>
</tr>
<tr>
<td>22 May 1982</td>
<td>7:30-15:30</td>
<td>CAND</td>
<td>8-24</td>
<td>site 4</td>
</tr>
<tr>
<td>3 May 1986</td>
<td>11:30-16:00</td>
<td>GRAN</td>
<td>13</td>
<td>site 5</td>
</tr>
<tr>
<td>6 May 1986</td>
<td>14:30-17:00</td>
<td>CAND</td>
<td>11</td>
<td>site 4</td>
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<tr>
<td>8 May 1986</td>
<td>13:00-16:00</td>
<td>GRAN</td>
<td>11</td>
<td>site 5</td>
</tr>
<tr>
<td>10 May 1986</td>
<td>7:00-17:00</td>
<td>GRAN and CAND</td>
<td>3-9</td>
<td>site 3</td>
</tr>
<tr>
<td>18 May 1986</td>
<td>14:30-17:00</td>
<td>GRAN</td>
<td>18-21</td>
<td>site 5</td>
</tr>
<tr>
<td>19 May 1986</td>
<td>14:00-17:00</td>
<td>GRAN</td>
<td>25</td>
<td>site 5</td>
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**Pollen viability**

Pollen viability was determined by staining in cotton blue in lactophenol (Dickison and Bell, 1974). One pollen slide was prepared for each of three to five flowers per population. Five populations of each taxon were sampled (Table 2). At least 100 pollen grains per slide were examined. Voucher specimens were deposited at MONTU.
TABLE 2. Collections used for pollen viability. Collections of the author except where noted.

<table>
<thead>
<tr>
<th>Collection</th>
<th>Location</th>
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<tr>
<td>E. grandiflorum var. grandiflorum</td>
<td>IDAHO: Idaho Co., 54; Kootenai Co., 29</td>
<td></td>
</tr>
<tr>
<td></td>
<td>MONTANA: Glacier National Park, 46; Powell Co, 4</td>
<td></td>
</tr>
<tr>
<td></td>
<td>WASHINGTON: Pend Oreille Co., 27</td>
<td></td>
</tr>
<tr>
<td>E. grandiflorum var. candidum</td>
<td>IDAHO: Kootenai Co., 20</td>
<td></td>
</tr>
<tr>
<td></td>
<td>MONTANA: Glacier National Park, 47; Beaverhead Co., Jerrold J Davis 386; Missoula Co., 6</td>
<td></td>
</tr>
<tr>
<td></td>
<td>WASHINGTON: Pend Oreille Co., 24</td>
<td></td>
</tr>
</tbody>
</table>

Cytology

Chromosome numbers for GRAN and CAND were determined from mitotic preparations of root tips from germinating seeds collected in the field (Table 6). Vouchers representing these collections were deposited at MONTU. Seed germination required 100 days of cold stratification (Pelton, 1956). Root tips were excised from germinated seeds stored in 70% ethanol at OC. Root tips were then hydrolyzed in HCl:95% ethanol (1:1) in a depression dish for five minutes (Löve and Löve, 1975). After rinsing briefly in water, standard acetocarmine squash technique was followed (Smith, 1974). Iron deepened the stain, but heating was unnecessary. Five cells were observed from each root tip slide. A slide was prepared for each of one or two plants per population, and four populations of each taxon were sampled. A total of 70 cells were observed. One slide was prepared for each of two hybrid seeds, each from a different plant, that resulted from artificial crosses, and 20 cells were observed in all. Chromosomes were examined with an Olympus BHS microscope, photographed, and documented with a drawing tube.
RESULTS

Geography and phenology

GRAN ranges from southern British Columbia to Colorado and California, whereas CAND ranges from western Glacier Park south to Big Hole Pass, Beaverhead Co., Montana, and west to the Pend Oreille River valley and isolated buttes near Pullman, Washington (Fig. 1). CAND and GRAN populations at similar elevations in a given geographical region flower at the same time. Both taxa begin blooming in late March or early April at the lowest elevations (e.g., south of Coeur d'Alene Lake, Idaho, 710 m), mid-April to early May at mid-elevations (e.g., Seeley Lake, Montana, 1335 m), and June to July at high elevations (e.g., CAND: late June at Big Hole Pass, MT, 2246 m; GRAN: mid-July at Cameron Pass, CO, 3477 m).

At a given location, floral buds are present for about three weeks. In both taxa, the pendulous buds begin to open about three to six days after plants emerge aboveground. Stigmatic lobes are slightly reflexed even in bud, and pollen grains will adhere to the stigmatic papillae. Flowers are protogynous, as evidenced by pollen tube growth in the styles of pistils prior to anthesis. Protogyny is weak, however, as anthers usually begin to dehisce within about 2 hr of tepal opening. Stigmas remain receptive in both taxa during anthesis, as evidenced by tube growth of self-pollen in the styles. The first three anthers to dehisce in a flower lie opposite the outer whorl of tepals (sepals) and have relatively short filaments. As the anthers dehisce acropetally,
Fig. 1. Distribution of *Erythronium grandiflorum* vars. *grandiflorum* and *candidum*. Variety *grandiflorum*: squares. Variety *candidum*: circles. Sympatric populations: triangles. Open symbols designate study sites described in the text.
they decrease to less than half their original length. As dehiscence is completed, the tip of the anther, originally at about the same level as the stigma lobes, is no longer near the stigma. Deposition of self-pollen is thus at least partially prevented by mechanical means. The other three anthers with longer filaments then dehisce in a similar manner within 24 hr of tepal opening, and some self-pollen may be deposited on the receptive stigma. In warm weather, all pollen is dispersed within 60 hr of bud opening. Flowers may close partially at night, particularly during cold weather. Tepals remain reflexed for about seven to 10 days, depending on weather conditions. Three weeks after fertilization of hand-pollinated flowers, fruits are enlarging and upright. After four weeks, fruits are about 2 cm long, and mature by eight weeks. Fruits dehisce at maturity about two months after pollination, and seeds fall to the ground gradually as the fruits are shaken by wind or other disturbances.

Pollination studies

In field studies, self-pollen grew the full length of CANO styles and only partially down GRAN styles (perhaps in part due to cold weather). Nonetheless, in all populations tested, both taxa were obligate outcrossers, producing no seeds via self-pollination or agamosperous apomixis. Treatments for self-compatibility, mechanical autogamy, and agamospermy were therefore omitted from Table 3. Although hand-pollinated flowers examined microscopically revealed numerous pollen tubes growing in the styles, within-taxon manual crosses did not yield more seeds than did the unmanipulated group. In fact, they produced fewer seeds (Table 3, Open-pollinated vs. Within Taxon
Crosses). Although plants at Owl Creek were hand-pollinated on three different dates (5, 9, or 11 May, 1984), the only plants that set seeds were pollinated on 9 May (Table 3, Within Taxon Crosses). Numbers of developing ovules per fruit collected 10 - 20 days after pollination in 1982 were higher than numbers of mature seeds per fruit collected two months after pollination in 1983 and 1984 (Table 3, Open-pollinated). Reciprocal cross-pollination between GRAN and CAND resulted in seed set only when the plants that were crossed came from populations distant both from each other and from sympatric populations (Table 3, Reciprocal Cross Pollination, 1982 and 1983). Plants from sympatric sites produced some fruits (enlarged ovaries after two months) when GRAN pollen pollinated CAND pistils, but set no fully developed seeds from either type of reciprocal cross (Table 3, Reciprocal Cross Pollination, 1984).

Figure 2 depicts the germination and subsequent three year survivorship of seeds from the 1983 pollination studies planted at the University of Montana experimental garden. Although only 20% of the seeds from the CAND x CAND crosses germinated (Fig 2), these crosses produced more than twice as many seeds per plant as any other treatment (Table 3), and yielded three times as many surviving seedlings per plant treated as did GRAN x GRAN by May 1986. For all treatments, seed mortality was highest during the first winter. Once the seeds germinated, the seedling numbers remained relatively constant.
### TABLE 3. Pollination study results. Treatments are described in text.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Crosses</th>
<th>Open Pollinated</th>
<th>Reciprocal Cross</th>
<th>Within Taxon</th>
<th>Crosses</th>
<th>Open Pollinated</th>
<th>Reciprocal Cross</th>
<th>Within Taxon</th>
</tr>
</thead>
<tbody>
<tr>
<td>Allopatric Populations</td>
<td>1982a</td>
<td>1983b</td>
<td>Sympatric Populations</td>
<td>1984</td>
<td>Owl Creek</td>
<td>Logging CR.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cand</td>
<td>XPLS w/FRUIT</td>
<td>28.0 (n:25)</td>
<td>32.0 (n:18)</td>
<td>27.3 (n:22)</td>
<td>63.2 (n:19)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Avg $ SDS/PL</td>
<td>12.72 ovules</td>
<td>9.72</td>
<td>2.60</td>
<td>12.37</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Gran</td>
<td>XPLS w/FRUIT</td>
<td>67.9 (n:28)</td>
<td>20.0 (n:24)</td>
<td>4.8 (n:21)</td>
<td>25.0 (n:20)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Avg $ SDS/PL</td>
<td>34.43 ovules</td>
<td>2.67</td>
<td>1.90</td>
<td>2.10</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cand x gran</td>
<td>XPLS w/FRUIT</td>
<td>18.2 (n:22)</td>
<td>36.0 (n:25)</td>
<td>26.1 (n:23)</td>
<td>20.0 (n:20)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Avg $ SDS/PL</td>
<td>Not det'd</td>
<td>4.68</td>
<td>0.0</td>
<td>0.0</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Gran x cand</td>
<td>XPLS w/FRUIT</td>
<td>21.7 (n:22)</td>
<td>4.20 (n:24)</td>
<td>0.0 (n:23)</td>
<td>0.0 (n:20)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Avg $ SDS/PL</td>
<td>Not det'd</td>
<td>0.38</td>
<td>0.0</td>
<td>0.0</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cand</td>
<td>XPLS w/FRUIT</td>
<td>12.0 (n:25)</td>
<td>8.3 (n:24)</td>
<td>26.3 (n:19)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Avg $ SDS/PL</td>
<td>2.16</td>
<td>1.63</td>
<td>5.45</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Gran</td>
<td>XPLS w/FRUIT</td>
<td>15.0 (n:25)</td>
<td>4.2 (n:24)</td>
<td>5.0 (n:20)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Avg $ SDS/PL</td>
<td>2.68</td>
<td>1.71</td>
<td>0.90</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

- **a** In 1982, fruits with developing ovules were collected on 12 May, 10 - 20 days after pollination.
- **b** In 1983 and 1984, nature or almost nature seeds were collected approximately 2 months after pollination.
- **c** These plants were randomly collected at the time of fruit collection; thus, the percentage of plants with enlarged ovules may have been overrepresented (i.e., these plants were more easily located than those senesced plants without developing fruits).
- **d** All but one of these plants were left to develop seeds; however, at collection time, no fruits were found. They may have failed to develop, been eaten, or already dehisced. Twenty-two ovules were developing in the 1 Cand x Gran fruit that was examined. By contrast, the average numbers of developing ovules for only successful open pollinated plants were 46 ovules for Cand (n:7) and 51 ovules for Gran (n:19).
- **e** This experiment was not conducted in 1982.

**NOTE:** AVG $ SDS/PL (average number of seeds per plant) includes plants with seed set of 0.
Fig. 2. Seed germination and subsequent seedling survivorship. Seeds were planted in August, 1983, and germinated in March, 1984. CAND x CAND (triangles): 18 plants, 175 seeds recovered, 88 seeds planted. GRAN x GRAN (circles): 25 plants, 64 seeds recovered, 31 seeds planted. CAND♀ x GRAN♂ (inverted triangles): 25 plants, 117 seeds recovered, 57 seeds planted. GRAN♀ x CAND♂ (squares): 24 plants, 9 seeds recovered, 5 seeds planted.
Pollinator observations

During 52 hr of observation, 43 bee pollinators were observed and 21 collected (Table 4). Pollen loads of bees are summarized in Table 5, and pollinator behavior is recorded in Appendix A. Apparent pollinators observed for both GRAN and CAND were Bombus bisarius Cresson, Apis mellifera Linn., Andrena nigrihirta (Ashmead), and Melittid bees (the latter on CAND only). Apparent pollinators were those visitors that, while gathering nectar and/or pollen, came into bodily contact with both stigmas and anthers of Erythronium flowers. Other visitors, such as the halictid bee Evylaeus spp., a meloid beetle, midges, and spiders, appeared to be ineffective pollinators.

Bumble bees, honey bees and melittid bees appeared to respond to corolla color and/or odor, as they flew directly from flower to flower. They generally landed on the stamens, and often held onto the tepals with some of their legs. A bee faced the tepal bases and systematically gathered nectar from each tepal, encircling the gynoecium. In doing so, the bee gathered pollen sternotribically and on the legs, and also brushed its body against the stigmatic lobes. Red pollen was seen on stigmas of flowers producing white pollen following bee activity at allopatric populations. Andrena nigrihirta individuals were too small to brush against the anthers while collecting nectar at the tepal bases, so after nectar gathering was completed, the andrenids collected pollen directly from the anthers. In so doing, their bodies contacted the stigma lobes.

Early in the season, E. grandiflorum was the only plant species blooming within its habitat. Pollinators, by necessity, exhibited
floral constancy as reflected by their pollen loads and observed behavior (Appendix A). As other species came into bloom, bumble bees ignored *Erythronium*, and visited other species such as *Arctostaphylos uva-ursi* and *Dodecatheon conjugens* (Appendix A). Late in the flowering season, honey bees and andrenid bees pollinated GRAN, and melittid bees pollinated CAND at the populations observed (Appendix A).

TABLE 4. Summary of observation hours and collections of pollinators

<table>
<thead>
<tr>
<th>Erythronium spp. present</th>
<th>Hours of observation</th>
<th>No. of bees observed</th>
<th>No. of bees collected</th>
</tr>
</thead>
<tbody>
<tr>
<td>GRAN</td>
<td>13.0</td>
<td>on GRAN: 15</td>
<td>10</td>
</tr>
<tr>
<td></td>
<td></td>
<td>on other spp.: 8</td>
<td>2</td>
</tr>
<tr>
<td>CAND</td>
<td>26.0</td>
<td>on CAND: 9</td>
<td>5</td>
</tr>
<tr>
<td></td>
<td></td>
<td>on other spp.: 6</td>
<td>2</td>
</tr>
<tr>
<td>mixed pop.</td>
<td>13.0</td>
<td>on both: 1</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td></td>
<td>on GRAN &amp; other spp.: 1</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td></td>
<td>on other spp.: 3</td>
<td>0</td>
</tr>
<tr>
<td>Total</td>
<td>52.0</td>
<td>43</td>
<td>21</td>
</tr>
</tbody>
</table>
**TABLE 5. Pollen loads of bees collected on *Erythronium grandiflorum* and coblooming species**

<table>
<thead>
<tr>
<th>bee species (n)</th>
<th>no. grains counted</th>
<th>% <em>Erythronium</em> grains</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>on GRAN</td>
<td></td>
</tr>
<tr>
<td><em>Apis mellifera</em> (6)</td>
<td>100, 59, 100, 100, 100, 100</td>
<td>88 (sd: 25, range: 37-100)</td>
</tr>
<tr>
<td><em>Bombus bisarius</em> (1)</td>
<td>57</td>
<td>98</td>
</tr>
<tr>
<td><em>Andrena nigrihirta</em> (2)</td>
<td>100, 100</td>
<td>100</td>
</tr>
<tr>
<td><em>Erytlaeus spp.</em> (2)</td>
<td>0, 7</td>
<td>0, 29</td>
</tr>
<tr>
<td></td>
<td>on CAND</td>
<td></td>
</tr>
<tr>
<td><em>Bombus bisarius</em> (1)</td>
<td>100</td>
<td>100</td>
</tr>
<tr>
<td><em>Andrena nigrihirta</em> (1)</td>
<td>100</td>
<td>100</td>
</tr>
<tr>
<td><em>Melittid</em> (3)</td>
<td>100, 100, 100</td>
<td>100</td>
</tr>
<tr>
<td></td>
<td>on GRAN and CAND</td>
<td></td>
</tr>
<tr>
<td><em>Bombus bisarius</em> (1)</td>
<td>57</td>
<td>89</td>
</tr>
<tr>
<td></td>
<td>on <em>Arctostaphylos uva-ursi</em></td>
<td></td>
</tr>
<tr>
<td><em>Bombus bisarius</em> (2)</td>
<td>5, 3</td>
<td>40, 0</td>
</tr>
</tbody>
</table>

*a No pollen was present.
*b These bees were lost before their genus could be determined.

**Pollen viability**

Mean pollen viability was 92.8% (s.d. = 10.04, range = 56.5 - 98.0) for GRAN and 91.6% (s.d. = 10.54, range = 63.0 - 100.0) for CAND.

**Cytology**

Chromosome counts of $2n = 24$ for GRAN agreed with those of $n = 12$ (Smith, 1955) and $2n = ca. 24$ (Cave, 1970); CAND also had $2n = 24$ chromosomes (Table 6). No variation in chromosome number was observed in either GRAN or CAND. Seeds from pistillate CAND x staminate GRAN
crosses exhibited variable counts of $2n = \text{ca.} 22-26$ within an individual root tip (Table 6), with putative connections between some chromosomes in some cells (Fig. 3).

**TABLE 6.** New chromosome counts in *Erythronium grandiflorum*. All collections of the author.

<table>
<thead>
<tr>
<th>Variety</th>
<th>Count</th>
<th>Location</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>E. grandiflorum var. grandiflorum</em></td>
<td>$2n = 24$</td>
<td>Glacier National Park, 135; Missoula Co., 125, 126, 129.</td>
</tr>
<tr>
<td><em>E. grandiflorum var. candidum</em></td>
<td>$2n = 24$</td>
<td>Glacier National Park, 136; Missoula Co., 127, 128, 133.</td>
</tr>
<tr>
<td>Pistillate <em>E. grandiflorum var. candidum</em> x Staminate <em>E. grandiflorum var. grandiflorum</em></td>
<td>$2n = \text{ca.} 22-26$</td>
<td>Missoula Co., 22A.</td>
</tr>
</tbody>
</table>
Fig. 3. Root tip chromosomes of pistillate CAND x staminate GRAN. Arrows indicate putative chromosomal connections. A. $2n = 24$. B. $2n = 25$. Scale = 10 $\mu$m.
**DISCUSSION**

**Geography and phenology**

If *Erythronium grandiflorum* vars. *grandiflorum* and *candidum* were completely allopatric, gene flow would be prevented. Such spatial isolation could provide a setting for subsequent genetic differentiation between the taxa. Spatial isolation is not complete at present, however, as a few sympatric populations do exist. The amount of spatial isolation between the taxa during the past is unknown, but certainly ranges of plant species have changed continually during and since the Pleistocene (Mehringer, 1985 and references within). External barriers such as phenology and geography would break down during such periods of frequent change. At sites of previous glaciation, present distribution patterns of both taxa reflect migration into those sites. Seed dispersal by the plant does not seem to play an important role in range expansion, and its apparent ineffectiveness may help to keep the two taxa geographically isolated. Although it has not been observed, animal activity may aid in seed dispersal. Since the plants are edible, and the Montana Salish Indians are known to have occasionally eaten the bulbs of GRAN (Hart, 1976), it is possible that people have played a role in the migration of the taxa.

Gene flow between taxa can be temporally prevented if they bloom at different times of day or on different days. Field studies indicated that GRAN and CAND are in anthesis at the same time, so temporal isolation is probably not an effective mechanism in these taxa.
Cytology

Related taxa with different chromosome numbers may produce hybrids, yet taxa with the same chromosome number commonly fail to cross (Grant, 1981); thus a common chromosome number does not insure, nor is it a prerequisite of, hybrid formation. Root tips of GRAN and CAND consistently exhibited $2n = 24$ chromosomes, yet each individual in the small sample of their hybrids exhibited variable chromosome numbers. As chromatids could be seen in each chromosome, high aneuploid chromosome counts did not result from early centromere division. Likewise, the counts lower than the diploid number are also unexplained. While roots often vary in chromosome number, it is interesting that in these taxa this phenomenon was observed only in hybrids. It is also unknown why apparent connections between chromosomes would form in mitotic material, since there is no pairing of homologous chromosomes during mitosis.

Pollination studies

Table 7 compares some pollination characteristics of seven species of Erythronium. GRAN, CAND and E. umbillicatum are protogynous. All other reported species are protandrous, although the protandry in E. japonicum is weak. Pollen viability for GRAN and CAND is similar to that of E. japonicum (Utech and Kawano, 1975), the only other obligately outcrossing species of the genus that has been tested for pollen viability.
### TABLE 7: Comparison of several Erythronium species

<table>
<thead>
<tr>
<th>E. albium</th>
<th>E. propius</th>
<th>E. americanum</th>
<th>E. umbilicatum ssp. umbilicatum</th>
<th>E. japonicum</th>
<th>E. grandiflorum var. grandiflorum</th>
<th>E. grandiflorum var. candidum</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>REFERENCE</strong></td>
<td>Banks, 1980</td>
<td>Banks, 1980</td>
<td>Bernhardt, 1977</td>
<td>Notten, 1983</td>
<td>Karano and Nagai, 1982 (except where noted)</td>
<td>this paper except where noted</td>
</tr>
<tr>
<td><strong>DICHOGAMY</strong></td>
<td>protandrous (also Schemke et al., 1978)</td>
<td>protandrous</td>
<td>weakly protogynous (Hollen, 1986)</td>
<td>weakly protandrous</td>
<td>weakly protandrous</td>
<td>weakly protogynous</td>
</tr>
<tr>
<td><strong>BREEDING SYSTEMS</strong></td>
<td>facultatively outcrossing</td>
<td>outcrosser, but didn't test for manual aid</td>
<td>facultatively outcrossing</td>
<td>outcrosser, but didn't test for manual aid</td>
<td>obligate outcrosser (also reported as facultative outcrosser - A. Snow, pers. comm. in Thomson and Straiton, 1985)</td>
<td>obligate outcrosser</td>
</tr>
<tr>
<td><strong>CHROMOSOME NUMBERS</strong></td>
<td>n = 22 (Smith, 1955)</td>
<td>2n = ca. 44 (Smith, 1955; Parks and Hardin, 1963)</td>
<td>2n = 24 (Parks and Hardin, 1963)</td>
<td>2n = 24 (Utech and Karano, 1975)</td>
<td>2n = 48 (this paper)</td>
<td>2n = 24</td>
</tr>
<tr>
<td><strong>STAINABLE POLLEN</strong></td>
<td>57.3%</td>
<td>37.2X</td>
<td>---</td>
<td>---</td>
<td>95.3% / 96.2%1 (Utech and Karano, 1975)</td>
<td>92.8%</td>
</tr>
<tr>
<td><strong>POLLEN: OVALE</strong></td>
<td>966:1</td>
<td>767:1</td>
<td>---</td>
<td>---</td>
<td>4800:1</td>
<td>---</td>
</tr>
<tr>
<td><strong>POLLEN LIMIT?</strong></td>
<td>results varied depending on pollen source distance</td>
<td>didn't hand-pollinate for comparison</td>
<td>no</td>
<td>yes</td>
<td>no</td>
<td>no</td>
</tr>
</tbody>
</table>

1*95.3% of pollen grains stained with aceto-carmine; 96.2% of pollen grains germinated on agar medium.*
GRAN and CAND are similar in compatibility to the other species studied; all are outbreeders, either obligate or facultative. Since self-pollen tubes grew the full length of CAND styles and partway down GRAN styles, the observed self-incompatibility is not sporophytic, but rather gametophytic, ovular or post-zygotic. Ovular and post-zygotic incompatibility systems are usually considered rare, but occur in many species of tropical trees in Costa Rica (Bawa et al., 1985 and references within). The styles of Erythronium are hollow (i.e., lack transmission tissue), as are the styles of most species having the incompatibility reaction localized in the ovules (de Nettancourt, 1977; Linskens, 1975 and references therein).

Since within-taxon manual crosses did not produce more seeds than did the controls, seed production apparently is not pollinator-limited. Similar conclusions were reached by Motten (1983) for E. umbilicatum (Table 8). Banks' (1980) results for E. albidum were variable, depending on the distance of the pollen source. Conversely, Kawano and Nagai (1982) and Schemske et al. (1978) found E. japonicum and E. albidum, respectively, to be pollinator-limited in seed production. However, Schemske et al. (1978) also found that the importance of pollinator limitation is offset if abortion of fertilized ovules is relatively great. Comparison of my 1982 pollination results with those of 1983 and 1984 (Table 3) indicates that high ovule abortion may occur in E. grandiflorum. In fact, at a dry site where CAND individuals bloomed very early in the season (25 April 1982), and where bumble bee pollinators were active, no fruits were set at all. Stephenson (1981) indicates that in many species, pollination does not limit fruit set.
The fact that all hand-pollinated plants that set seed at Owl Creek were pollinated on the same day provides further evidence that seed set is limited by some factor other than pollination. Since plants that were receptive on the different days matured at different times, they may have experienced different environmental conditions that in turn may have affected seed set.

Extensive field study throughout the known range of CAND has shown that CAND and GRAN populations are usually allopatric, even where the ranges of the taxa overlap. Although geographic barriers and reproductive barriers may work separately, they may also work in concert. Lewis (1961, 1966) has shown that in some annual species reproductive barriers can maintain geographic isolation by mutual competitive exclusion from contact zones. *Clarkia biloba* and its derivative *C. lingulata*, for example, are unable to grow together in experimentally mixed populations. The species in lower frequency at a given site produces a higher proportion of hybrids. Consequently, its own relative frequency is reduced and it is eventually eliminated from the site. Lewis cited the relationship between *Lasthenia fremontii* (Asteraceae) and *L. conjugens* as another example. Although these species grow in comparable ecological sites close to one another, they do not grow sympatrically. While they hybridize in cultivation, the hybrids have low fertility (Lewis, 1966). Lewis predicted that such interfertile species would continue to mutually exclude each other from contact zones until such time as selection for reproductive isolation (cf. Grant 1981) occurred; then the species could coexist at a given site. He provides an example involving *Clarkia williamsonii* and
Ç. speciosa. Interspecific crosses between plants in the area where the species are sympatric produce no offspring; otherwise they are interfertile (Lewis, 1966).

Reciprocal cross pollination experiments between CAND and GRAN revealed that the taxa can cross and produce viable seeds only if the plants that are crossed come from allopatric populations that are distant both from each other and from sympatric populations (Table 3, Reciprocal Cross Pollination). Thus, these results, at least at the sympatric sites, are contrary to the well-documented generalizations (Grant, 1981) that 1) closely related perennial herbaceous species are usually isolated by external factors (ecological, seasonal, ethological or mechanical), and 2) such species hybridize naturally if external barriers break down. Rather, in this case, internal barriers may have developed via selection for ethological or incompatibility barriers (Grant's "selection for reproductive isolation") in contact zones between GRAN and CAND (cf. Lewis, 1961, 1966). These results are significant because it is generally believed that selection for ethological or mechanical barriers is relatively ineffective in long-lived perennial plants (Grant, 1981). While Grant (1981, p. 179) states that "some perennial herbs probably approach annuals in their responsiveness to selection for isolation", he cites only one example. This ineffectiveness might explain why only a few sympatric populations of GRAN and CAND have been located, i.e., only rarely has reproductive isolation occurred to prevent mutual exclusion from a sympatric site. Perhaps biological barriers arose in populations where the taxa were represented in approximately equal proportions. In such a case, each
taxon would have an equal probability of wasting gametes to hybrid formation, and conceivably an equilibrium might be maintained long enough for incompatibility barriers to develop between the taxa. Alternatively, it is possible that different populations of both CAND and GRAN vary with regard to their incompatibility alleles. The above-mentioned scenario would be the same, except that incompatible sympatric populations would have acquired their fertility barriers by chance before populations of the two taxa came into contact with each other. Since GRAN has a much wider range than CAND, mutual competitive exclusion may prevent the expansion of the range of CAND.

Both taxa were visited by bee pollinators at allopatric sites during appropriate weather conditions. Open-pollinated CAND flowers produced more seeds than did GRAN at all three sites in 1983 and 1984, although when manually crossed, CAND produced slightly fewer seeds in two cases out of three (Table 2). Survivorship of CAND seedlings is comparable to that of GRAN (Fig. 3). Thus, the distribution of CAND is not limited by failure to attract pollinators, low fertility, or differential seedling survivorship.

Since individuals of *Erythronium* species can take at least 8 years to reach a reproductive state (Kawano et al., 1982), the question still remains as to whether the viable seeds produced by intertaxon crosses of CAND and GRAN from allopatric sites in 1983 (Fig. 2) will produce fertile plants. Chromosome numbers in these seeds are variable (Fig. 3), so karyological differences that would interfere with meiosis may well exist between the taxa. At any rate, these seeds were produced by crossing individuals that were geographically too distant from each
other to cross-pollinate in nature. Therefore, geographic separation between most populations of GRAN and CAND remains an important reproductive isolating barrier for those populations that have not yet developed internal barriers to hybridization.

**Biological species**

Individuals that can interbreed in nature are members of the same biological species (Mayr, 1982). Gene flow between CAND and GRAN apparently does not occur, because the taxa either are allopatric or are reproductively isolated biologically where they are sympatric. It appears, then, that CAND and GRAN are two biological species.

This hypothesis could be further tested by searching for hybrids in sympatric populations. If hybrids are produced in nature, some intermediacy of chemical or morphological characters should be apparent. Preliminary phytochemical analyses (Fritz-Sheridan, unpublished data) distinguished flavonoid and carotenoid differences between the taxa. Once each taxon is characterized, plants with hybrid traits can be sought via morphological measurements, chromatography, and electrophoresis of enzymes. These data will also facilitate the determination as to whether GRAN and CAND should be considered as two taxonomic species.
Each entry includes: bee species, collection number if collected, location (O C = Owl Creek, P C = Pattee Canyon Picnic Area), date, time, air temperature, observations, (number of pollen grains from bee counted, % Erythronium pollen).

On GRAN:

Apis mellifera GRAN 141-A P C 5/3/86 11:30 13C flew to 7 GRAN flowers, legit. pollinating position (100, 100%)

Bombus spp. GRAN P C 5/3/86 14:00 13C


Bombus spp. GRAN P C 5/3/86 15:02 13C flew to 3 GRAN flowers.

Apis mellifera GRAN 142-A P C 5/3/86 15:14 13C flew to 2 GRAN flowers (59, 37%)

Bombus bisarius GRAN 142-B P C 5/3/86 15:24 13C flew to 2 GRAN flowers (57, 98%)

Andrena nigrihirta GRAN 151-A P C 5/18/86 14:57 21C flew to 5 GRAN flowers. At each flower, collects copious amount of pollen, and in so doing occasionally comes into contact with stigmas with legs or abdomen. Then collects nectar ((100, 100%)

Andrena spp. GRAN P C 5/18/86 15:37 18C flew to one GRAN flower, collected pollen in legitimate position, then nectar.

Evylaeus spp. GRAN 151-B P C 5/18/86 15:57 18C robbed nectar from four GRAN flowers (7, 29%)

Apis mellifera GRAN 151-C P C 5/18/86 16:21 18C collecting nectar on 4 flowers in legitimate pollinating position: hanging onto anthers, in contact with stigmas at times. Petals beginning to wilt (100, 93%)

Apis mellifera GRAN 152-A P C 5/19/86 14:40 25C visited 6 GRAN flowers, collecting pollen and nectar simultaneously in legitimate pollinating position (100, 100%)

Andrena nigrihirta GRAN 152-B P C 5/19/86 14:40 25C flew into net during collection of 152-A. activity uncertain, but pollen load suggests pollen collection (100, 100%)
Apis mellifera GRAN 152-C P C 5/19/86 15:17 25C visited 30
GRAN flowers in 3 minutes (ave. = 6s/fl), actively collecting
nectar in legitimate pollinating position. Photographed (100,
100%)

Apis mellifera GRAN P C 5/19/86 15:57 25C visited 17 GRAN
flowers in 7 minutes, spending 3 - 47 sec. at each flower. Usually
landed on flower hanging onto anthers, but then immediately rotated
around to hang onto petals. May have effected some cross-
pollination.

Apis mellifera GRAN 152-D P C 5/19/86 25C visited 12 GRAN
flowers in 2 minutes. Collecting nectar in legitimate pollinating
position. Photographed (100, 100%)

On other species at GRAN sites:

Bombus spp. 141-B P C 5/3/86 12:07 13C flew to 5
Arctostaphylos uva-ursi plants, ignoring GRAN (5, 40%)

Bombus spp. P C 5/3/86 12:10 13C on Dodecatheon

Bombus spp. P C 5/3/86 12:12 13C on Arctostaphylos

Bombus bisarius 141-C P C 5/3/86 12:16 13C flew to 5
Arctostaphylos plants (3, 0%)

Bombus spp. P C 5/3/86 12:23 13C on Arctostaphylos

Bombus spp. P C 5/3/86 12:28 13C on Arctostaphylos

Bombus spp. P C 5/3/86 14:53 13C appears to be looking for
Arctostaphylos flowers, ignoring GRAN.


On CAND:

Bombus bisarius Coll. A Tamarack Lodge 4/25/82 15:17 20C visited
14 CAND flowers, collecting nectar and pollen in legitimate
pollinating position. ave. = 17s/fl, s.d.=10, range=5-42s. (100,
100%)

Andrena nigrihirta CAND Coll. B Tamarack Lodge 4/25/86 16:10 20C
collected nectar, then crawled around on anthers, collecting pollen
on abdomen (100, 100%)

Bombus spp. CAND O C 5/22/82 10:04 17C visited 2 CAND flowers
very briefly.
Melittid bee CAND 15-A O C 5/22/82 11:20 20C collecting pollen from CAND, scopae loaded (100, 100%)

Melittid bee CAND 15-B O C 5/22/82 11:30 20C collecting nectar from CAND, scopae loaded (100, 100%)

Melittid bee CAND 15-C O C 5/22/82 11:35 20C collecting pollen from CAND, scopae loaded (100, 100%)

Apis mellifera CAND O C 5/22/82 11:46 20C visited one CAND flower.

2 Melittid bees CAND O C 5/22/82 12:40 23C visiting CAND flowers.

On other species at CAND sites:


Bombus spp. O C 5/22/82 12:40 23C visiting only Dodecatheon flowers.

Bombus spp. O C 5/22/82 13:00 23C on Dodecatheon

Bombus spp. 15-D O C 5/22/82 13:20 23C on Dodecatheon

Bombus spp. 15-E O C 5/22/82 15:00 23C on Dodecatheon

On Erythronium at mixed site:

Bombus bisarius Hidden L. 12-A 5/17/82 15:12 visited 1 GRAN, 2 CAND, then 1 GRAN flowers (57, 89%)

Evylaenus spp. GRAN 12-B Hidden L. 5/17/82 15:18 visited GRAN and Claytonia lanceolata (no pollen on slide)

On other species at mixed site:

Bombus spp. Hidden L. 5/10/86 13:30 9C visited 2 Arctostaphylos flowers, few of which are in bloom yet.

Bombus spp. Hidden L. 5/10/86 14:48 8C on Taraxacum

Appendix B. Exsiccatae

Erythronium grandiflorum Pursh var. candidum (Piper) Abrams

UNITED STATES: IDAHO: BENEWAH CO.: Along St. Joe River 2 miles east of St. Maries, 23 March 1941, Christ 12039 (ID, WS); Open woods near Chatcolet, 12 May 1928, Warren 891 (WS); Sunny thicket, Lovell, 2600 ft., Jones, Ransom, & Ridout 3730 (WS); Near CCC Camp Chatcolet, Heyburn State Park, 19 April 1937, Gleason 133 (WS); One mile south of Plummer, 24 April 1949, Baker 5710 (ID); St. Maries, 7 April 1933, Rust 2123 (ID); Summit of Plummer Butte southeast of Plummer, 17 May 1961, Baker 16117 (ID); Garnet road 8 miles north of St Maries along Highway 3, 22 April 1984, Fritz-Sheridan 31 (MONTU); One mile south of Emida, 21 April 1940, M. & R.P. Ownbey 2021 (WS, IDS, ORE, UC); St. Maries River Valley along Idaho State Hwy. 3 near Adams 8 mi. northwest of Clarkia, S5, T43N, R1E, 2700 ft., 6 May 1972, Stickney 2605 (ID). KOOTENAI CO: Wooded slope 5 mi. south of Worley, 23 April 1951, Torrell 29 (ID); Cut-over pine woodland, Worley, 2700 ft., 21 March 1926, St. John, English, Jones, Ransom, & Ridout 3719 (UC); Between Ford and Worley, 28 April 1931, Applegate 6711 (UC); Cut-over Ponderosa pine forest west of Worley, 19 April 1946, Daubenmire 462 (WS); 15 mi. south of Cour d’Alene on Hwy. 95, 22 April 1984, Fritz-Sheridan 30 (MONTU); 14 mi. north of St. Maries along Hwy. 3, 22 April 1984, Fritz-Sheridan 32 (MONTU); Cut-over woodland, 3 mi. east of Worley, 3 July 1927, St. John 10128 (WS); Wooded area along stream, 3 mi. west of Worley, 15 May 1927, Kienholz
19 (WS); Ponderosa pine forest over lake, south slope Coeur d'Alene Lake across from Harrison, T47N, R4W, sec. 2 S 1/2 Sw 1/4 Sw 1/4, 2300 ft., 8 April 1976, Lamberts s.n. (WS); 5 mi. north of Worley, 11 April 1957, Baker 14786 (ID); Type locality, 3 mi. east of Worley, 25 April 1926, St. John, Gessell, Jones, Ridout, & Woods 4255 (WS); Abundant in open fields and in yellow pine woods, 2 mi. north of Plummer, 28 April 1931, Applegate 6713 (IDS); 7 mi. east of Harrison on Harrison flats, 23 March 1941, Christ 12038 (IDS); Cataldo hillsides, 25 April 1932, Christ 1384 (ID); Near Worley, 15 April 1951, Mohan s.n. (ID); 1 mi. south of Worley, 11 April 1957, Baker 14782 (ID). LATAH CO.: Along a rocky ridge on the summit of Bald Mtn., T43N, R2W, 19 May 1956, Richards 39 (ID); T41N, R3W, 12 May 1928, Ainaly s.n. (WS); Cool coniferous woods, T41N, R3W, 12 May 1928, Van Amburg s.n. (WS); 6 mi. northwest of Deary on Harvard road, 21 May 1943, Christ 14025 (ID); 6 mi. northwest of Deary, 2 May 1954, Baker 11393 (ID). MONTANA: BEAVERHEAD CO.: Bull Creek, Beaverhead National Forest, in wet clearing, T 5 S, R 13 W, Sec. 31, NE 1/4, Se 1/4, 7300 ft., 22 June 1984, Bump s.n. (MONTU). GLACIER NATIONAL PARK: Shaded site, dense overstory, along inner road from West Glacier to Polebridge, 10 mi. north of West Glacier, 25 May 1979, Belhler 61 (MONTU). LINCOLN CO.: ca. 2 mi. southeast of Libby, Dunn Creek watershed, Salish Mts., T 30 N, R 29 W, NW 1/4 sec. 2, 3200 ft., 23 May 1981, Pedersen 165 (MRC). MISSOULA CO.: Placid Lake, 14 May 1933, Thieme 1570 (MONTU); Wooded margins along Highway 93 just
north of Seeley Lake, Near Ranger Station, ca. 4000 ft., 25 April 1981, Lesica 1388 (MONTU). WASHINGTON: PEND OREILLE CO.: Tiger, 29 April 1925, Hupp s.n. (WS); Along the Pend Oreille River Valley from about Lost Creek north to just south of Ione, 16 April 1967, Layser 16 (WS); Dry Canyon, 10 mi. north of Ruby, 5 June 1926, Hagenmeyer s.n. (WS); In hard clay soil across Pend Oreille River from Dalkene, 11 May 1923, Spranque s.n. (WS); Woods, Dry Canyon, Molybdenite Mt., Kaniksu Forest, T37N, R44E, 16 May 1925, St. John, Pickett, Davison, & Warren 3741 (WS); Molybdenite Mt., 16 May 1926, St. John, Pickette, Davison, & Warren 7132 (WS); 42 mi. north of Newport along Hwy. 20, 21 April 1984, Fritz-Sheridan 24 (MONTU); 61 mi. north of Newport along Hwy. 20, 21 April 1984, Fritz-Sheridan 25 (MONTU); 51 mi. north of Newport along Hwy. 20, 21 April 1984, Fritz-Sheridan 26 (MONTU); 40 mi. north of Newport along east side of Hwy. 20, 21 April 1984, Fritz-Sheridan 23 (MONTU). SPOKANE CO.: Without location, April 1891, Suksdorf 2001 (WS); Waverly, 19 April 1928, Snyder s.n. (WS); North of Freeman, 5 May 1929, Cook s.n. (WS). WHITMAN CO.: Open moist slopes, Steptoe Butte, 7 May 1950, Baker 6554 (WS, ID); Grassy south slope of Steptoe Butte, halfway up, 3000 ft., arid transition life zone, 13 April 1935, Constance, Dillon, & Rollins 1031 (NY, UC).

Erythronium grandiflorum var. grandiflorum Pursh

CANADA: ALBERTA: Waterton Lakes National Park, open mountain meadows near snow banks, trail to Bertha Lake, Hudsonian Zone, 5900 ft., 18 July 1953, Breitung 16258 (NY); Waterton Lakes
between R. Florida and R. Pinos, 25 June, **Brandegee 1056** (NY).

**LARIMER CO.**: Cameron Pass, 11,500 ft., 14 July 1896, **Baker s.n.** (NY); Cameron Pass above timberline, 1 August 1899, **2461** (NY).


**SAGUACHE CO.**: Buffalo Pass Park Range, 10,000 ft., 13 August 1898, **Shear 3864** (NY).

**SUMMIT CO.**: Arapahoe Peak, moist soil, 10,700 ft., 29 July 1918, **Clokey 3145** (NY).

**IDAHO**: **ADA CO.**: Boise, 24 May 1934, **Christ 4639** (NY).

**ADAMS CO.**: Frequent on north-facing slope at edge of snowbank in *Pinus contorta* and *P. flexilis*, Kinney Point 8 mi. north of Cuprum, 14 July 1953, **Holmgren & Tillett 9593** (NY); Starkey, on hillside along Weiser River, 12 May 1938, **Christ 9200** (NY); Placer Basin, north of Bear, 30 May 1940, **Christ 11059** (NY).

**BANNOCK CO.**: 12 mi. southwest of Portneuf, in aspen groves on upper slopes of Scout Mt., 8 July 1950, **J. H. Christ & C. B. Christ 19927** (ID).

**BEAR LAKE CO.**: In moist meadows and black sagebrush flats, 1 mi. below Bloomington Lake. Scattered spruce subalpine fir and lodgepole pine flats.

Bear River Range, northern Wasatch Mts., 7500 ft., 21 June 1958, **Kruckeberg 4511** (NY); Copenhagen Basin, 8200 ft., 16 June 1959, **Cottam, Anderson, Rowland, & Ream 15523** (RSA); 13 mi. west of Bloomington, on Bloomington Peak in the Bear River Range, 10 July 1949, **J. H. & C. B. Christ 18801** (NY); 13 mi. west of Bloomington, at Bloomington Lake in the Bear River Range, 9 July 1949, **J. H. & C. B. Christ 18739** (NY).

**BENEWAH CO.**: In alpine
meadows, 24 June 1934, Christ 4881 (NY); Plummer, 12 May 1934, Christ 3830 (NY). BOISE CO.: Garden Valley, 26 May 1933, Christ 6406 (NY). BONNER CO.: Hope, Warren Island, open woods, 5 April 1914, Dunkle 13895 (NY); Hope, 18 April 1928, Christ 10 (NY); Dover, by S. I. Bridge, in valley along Pend Oreille River, 16 April 1931, Christ 957 (NY); Dover, at S. I. Bridge. In valley along Pend Oreille River, 16 April 1931, Christ 956 (NY); Hope, Warren Island, open woods, 5 April 1914, Dunkle s.n. (ID); About 3 mi. north of Hope, 27 April 1931, Applegate 6703 (RSA). BOUNDARY CO.: Snowy Top, in draw below peak, W. B. Schroeder, 15 July 1934, Christ 6002 (NY); Continental Mt., 25 mi. west of Porthill, near banks of receding snow on peak, 12 July 1932, Christ 1685 (NY). CLEARWATER CO.: 2 mi. east of Orofino on gravelly canyon outwash, 30 May 1937, Christ 7370 (NY); Bertha Hill 12 mi. north of Headquarters, 24 May 1941, Christ & Ward 12066 (NY); 11 mi. east of Elk River, 23 May 1941, Christ & Ward 12128 (NY); Open grassy flat, summit Nez Perce grade, south of Orofino, 19 April 1953, Baker 10040 (ID); Between Pierce and Bungalow, s.d., Davis 279 (NY). CUSTER CO.: Wet meadow of divide at head of Morgan Creek (empties into Salmon River ca. 10 mi. north of Challis), 29 June 1944, Hitchcock & Muhlick 9403 (NY). ELMORE CO.: Trinity Mt., west of Rocky Bar, 14 July 1944. Christ 1419 (NY). FREMONT CO.: About 14 mi. north of Mack's Inn, 16 July 1949, J. H. & C. B. Christ 18999 (NY); About 14 mi. north of Mack's Inn, 16 July 1949, J. H. & C. B. Christ 18997 (NY); Sawetelle, with
lodgepole pine on mountainside, 17 July 1934, Christ 5672 (NY);
2 mi. west of Rae, open lodgepole pine woodland, 22 June 1939,
Maguire 17123 (NY); Juniper Hills near St Anthony, 20 June
1919, Quayle 89 (NY); Continental divide near Henery’s Lake,
21 June 1899, A. Nelson & E. Nelson 5480 (NY). IDAHO CO.: In
boulder-strewn (granitic) flat among scattered conifers along
French Creek, 2 mi. south of Salmon River, 20 mi. east of Riggins,
T24N, R3E, 21 April 1950, Cronquist 6189 (NY, ID);
Whitebird Summit, dry soil, 7 May 1947, Davis s.n. (RSA);
Brush slope below Patrol Point on Pilot Knob, S28, T30N, R6E, 6900
ft., 13 July 1947, Elwood 42 (NY); Whitebird, s.d., Christ
3125 (NY); Whitebird, open places in woods, s.d., Christ
3131 (NY); Crest of Whitebird Hill on open hillside, 16 May
1937, Christ & Ward 7315 (NY); Meadow east side of Hwy. 95,
5.9 mi. south of Grangeville, ca. 1.5 mi. north of Whitebird
Summit, 15 April 1973, Henderson 867 (ID); Among snow and
rocks, Moe Peak, T32N, R15E, S26, 8078 ft., 4 July 1928, Baker
s.n. (WS); East fork of Pappoose Creek (near Lochsa River) west
of Powell Ranger Station, 6 June 1963, Baker 16337 (ID); Moist
shady meadow, Twin Buttes Meadow, T32N, R14E, 6000 ft., 2 July
1928, Baker s.n. (WS); 29 mi. southeast of Elk City, 15 July
1951, Christ 51588 (ID); Below summit of Elk Mountain, 15
Agust 1954, Baker 12602 (ID); Lowell, 6 May 1932, Scott
s.n. (ID); Heaven’s Gate, Seven Devil Mountains, S32, T24N, R1W,
12 July 1950, Jones 205 (NY); French Creek Divide north of
Burgdorf, 29 May 1940, Christ 11022 (NY). KOOTENAI CO.: Near
Spirit Lake, s.d., Christ 3126 (NY); Hauser Lake, between junction and lake, with yellow pine, 14 April 1930, Christ 10818 (NY); Hauser Lake, between junction and lake in yellow pine timber, 14 April 1940, Christ 10817 (NY); Hauser Lake, between junction and lake, 14 April 1940, Christ 10819 (NY); 25 mi. south of Newport on Hwy. 41, 22 April 1984, Fritz-Sheridan 28 (MONTU); 8 mi. south of Coeur d'Alene on Hwy. 95, 22 April 1984, Fritz-Sheridan 29 (MONTU); Mica Flats southwest of Coeur d'Alene in wheat field, 21 April 1940, Christ 10862 (set of six) (NY). LATAH CO.: 6 mi. south of Troy, 16 April 1937, Christ & Ward 6727 (NY); Hillside above Robinsons Lake 4 mi. east of Moscow, 26 April 1949, Baker 5725 (NY); Along Potlach River 6 mi. above Kendrick, 23 March 1941, Rogers 762 (NY); Moscow, 6 April 1900, Abrams 539 (NY); One mi. west of Kendrick, 31 March 1940, M. Ownbey & R. P. Ownbey 2009 (NY). LEMHI CO.: Red Rock and Salmon City, 9-10,000 ft., 10 June 1896, Kemp s.n. (NY); Under lodgepole pines at summit of Moccasin Creek, Salmon Mts., 1 July 1946, Hitchcock & Muhlick 14292 (MO); Near top of Quartzite Mt., Yellowjacket Mts., 30 June 1946, Hitchcock & Muhlick 14208 (MO); Without location, June 1934, Christ 6104 (NY); Mt. Baldy, wet subalpine slopes, 8000 ft., 1 July 1920, E. B. Payson & L. B. Payson 1862 (NY). LEWIS CO.: Head of Wilson Canyon, top of Kamiah grade, Yellow Pine woods, near and west of Kamiah, the type station, 3 May 1931, Applegate 6755 (NY); Open forest Ponderosa pine zone north of Whitebird, 1 May 1937, Daubenmire 3785 (NY). NEZ PERCE CO.: Craig Mts., 15
May 1934, Christ 4247 (NY); Common on Craig Mts., vicinity of Lake Waha, 20 May 1892, Sandberg 362 (US); Common on Craig Mts., vicinity of Lake Waha, 20 May 1892, Sandberg 202 (NY); 5 1/4 mi. up highway from Culdesac, 17 April 1933, Baker 7400 (RSA). ONEIDA CO.: In less of crest of divide of the Malad Range in a maple thicket, 9 1/2 mi. southeast of Malad, 6 July 1950, Christ 19809 (ID). PAYETTE CO.: Payette, s.d., Christ 3128 (NY). SHOSHONE CO.: 5 mi. north of Wallace, about 4000 ft., 22 April 1979, Beehler 75 (MONTU); Striped Peak, 9 July 1951, Christ 51-405A (ID); Open woods Crater Lake Campground, St Joe National Forest, 19 mi. east of Clarkia, 20 July 1958, Baker 15378A (ID); Breezy Point, about 16 mi. south of Avery, 27 July 1947, Christ 17005 (NY). VALLEY CO.: McCall, 15 June 1933, Christ 6457 (NY); McCall, 16 May 1935, Tucker 406 (NY); 1 mi. north of McCall on cut-over land near Payette Lake, 15 May 1931, Christ & Ward 7231A (NY); 1 mi. north of McCall on cut-over land near lake, 15 May 1937, Christ & Ward 7231 (NY); Boggy soil near summit of divide between Cascade and Warm Lake, 26 June 1946, Hitchcock & Muhlick 14029 (MD); Moist places near summit between New Meadows and McCall, 12 May 1939, Cronquist 1196 (NY); Dry woods Pearl Creek, near Upper Payette Lake, 7100 ft., 11 July 1969, Munz & Davidson 19167 (RSA). IDAHO-WYOMING BOUNDARY: TETON CO. - TETON CO. BOUNDARY: Summit of the Continental Divide, Targhee Pass, Lodgepole pine forest, 22 June 1930, Applegate 6362 (ID). MONTANA: BEAVERHEAD CO.: Open avalanche area on Cole Creek, ca. 1 mi. above Red Rock Pass Road,
7400 ft., 20 June 1979, Lowry 2113 (MONTU); Very wet slope above Ajax Lake, Bitterroot Range, 23 July 1945, Hitchcock & Muhlick 12665 (NY, MO); Along road 1 mi. above Reservoir Lake, Beaverhead National Forest, 6700 ft., 26 May 1937, Munson B-7 (NY, MO); In fine soil near snow bank on high limestone ridge connecting Sheep and Black Lion Mts., Pioneer Mts., ca. 9000 ft., 30 July 1945, Hitchcock & Muhlick 12951 (OSC, MO); Wet meadow ca. 15 mi. west of Wisdom on Gibbonsville Pass Road, 22 June 1944, Hitchcock & Muhlick 9213 (NY, US, MO); Moist slope near snow at Oreamnos Lake, head of Pintlar Creek, Anaconda Range, 27 July 1945, Hitchcock & Muhlick 12732 (MO); Gibbons Pass, 1 May 1935, Rose 100A (MONTU). BROADWATER CO.: Belt Mts., in rich soil and by open stream banks in the mountains, 28 June 1885, Anderson 8162 (NY). DEERLODGE CO.: Storm Lake Pass, Continental Divide, Anaconda Mts., 21 July 1946, Hitchcock & Muhlick 14850 (MO); Anaconda, 1 June 1892, Kelsey s.n. (NY). FLATHEAD CO.: Coram, 12 May 1937, Bachert s.n. (MONTU); Mt. Aeneas, Swan Range, 2000 m, 16-18 July 1948, Harvey 3229 (MONTU). GALLATIN CO.: Spanish Basin, Madison Range, 6000 ft., 9 July 1896, Flocman 347 (NY); Spanish Peaks, Madison Range, 7-8000 ft., 14 July 1896, Flocman 346 (NY); Spanish Basin, 6500 ft., 1 July 1897, Rydberg & Bessey 3872 (NY); Bozeman, June 1900, Chesnut & Jones 318 (NY); Bridger Mts., 7000 ft., 18 June 1897, Rydberg & Bessey 3870 (NY); Bridger Mts., 7000 ft., 15 June 1897, Rydberg & Bessey 3869 (NY); Bridger Mts., 7000 ft., 18 June 1897, Rydberg & Bessey 3871 (NY). GLACIER
NATIONAL PARK: Rock ledge near north fork of Reynolds Creek, Logan Pass, 6600 ft., 18 July 1956, Sammons 413 (MONTU); Avalanche Lake, 20 June 1969, Mooar 10342 (MONTU); Slope below Grinnell Glacier, 6000 ft., 28 July 1933, Hitchcock 1992 (MONTU); Sperry Glacier, 4 July 1922, Christ 1334 (NY). GRANITE CO.: Skalkaho Pass, 7200 ft., 7 July 1946, Hitchcock & Muhlick 14467 (MO); Garnet, 6600 ft., 23 June 1924, Mearyfield 14 (MONTU).

JEFFERSON CO.: Deerlodge, May 1888, TrapLageu s.n. (NY). LAKE CO.: Swan Lake, 2 June, Elrod s.n. (MONTU); Mollman Pass, Mission Mts., 7 July 1948, Reynolds 102 (MONTU); Near Biological Station on Flathead Lake, 23 April 1933, Hitchcock 1513 (MONTU); Cliffs high above and southeast of McDonold Lake, Mission Range, 12 July 1948, Hitchcock 18285 (NY). LEWIS AND CLARK CO.: Scapegoat Mt., 7300 ft., 9 July 1975, Craighead 124 (MONTU); In the vicinity of Helena, s.d., Kelsey s.n. (NY).


MINERAL CO.: Stark Mt., Ninemile Divide 7 1/2 air mi. northwest of Alberton, 7349 ft., 12 July 1971, Vincent 488 (MONTU); On
ridge above Dominion Creek Valley, western Bitterroot Mts., 27 July 1971, Mooar 13845 (MONTU); Haugen, Dry Creek, 25 April 1932, Christ 1389 (NY). MISSOULA CO.: Near Masse Creek Trail, Seeley Lake-Jacko Road, 2 June 1952, Harvey 4945 (MONTU); Blackfoot Valley, 30 mi. from Bonner, 3600 ft., 13 May 1933, Hitchcock 1557 (MONTU); Along banks of Deer Creek, 27 April 1968, Mooar 6685 (MONTU); Wooded gulch 3 mi. north of Missoula, 30 April 1938, Trump 3 (OSC); West of Upper Holland Lake, Flathead Range, Flathead National Forest, 15 July 1948, Hitchcock s.n. (ID); North-facing slope of Pattee Canyon, 1450 m, 3 July 1979, Crane (Keller) 452 (MONTU); Top of Mt. Stewart, 9 July 1946, Hitchcock & Muhlick 14557 (NY); Rattlesnake River, 3300 ft., 1 May 1897, Elrod & assistants 25 (NY); Old Sentinel Mountain near Missoula, 12 June 1901, MacDougal 158 (NY); Swamplake soil 1/2 mi. west of Upper Holland Lake, Flathead Range, Flathead National Forest, 15 July 1948, Hitchcock 18459 (NY). PARK CO.: Bozeman Pass, 5 July 1883, Canby 323 (NY); Livingston, 20 May 1901, Scheuber s.n. (NY); 1901, Scheuber 81 (NY); Jardine Bear Gulch, 22 June 1902, Mearns 1288 (NY). POWELL CO.: Ovando Mts., 24 May 1931, Young s.n. (MONTU). RAVALLI CO.: At the upper pond meadows above Chaffin Lakes, Chaffin Lakes Basin, 8400 ft., 7 August 1971, Lackschewitz 3178 (MONTU); North slope above Wyant Lake, Canyon Lakes Basin, 8100 ft., 21 August 1971, Lackschewitz 3311 (MONTU); Skalkaho Road to Crooked Creek and up to pass, 1 July 1968, Mooar 8900 (MONTU). SANDERS CO.: Harry Creek above

Watkins & Dunn 108 (NY). WALLOWA CO.: Rocky hillside at Hat Point, 26 June 1946, Murphy 57 (NY); Above Joseph Creek near Flora, 4200 ft., 1 June 1933, Sprague s.n. (OSC); Moist grassy Ponderosa woods near the river, Imnaha River Road, Blackhorse Camp, R48E, T5S, S6, 4000 ft., 10 June 1963, Mason 6005 (OSC); R4E, T3N, S9, profuse with Ponderosa Pine, and Service, in moist open glade, 4200 ft., 18 May 1956, Ferguson 41 (OSC); 9 mi. east of Imnaha, Wallowa Mts., 6 June 1952, Baker 9073 (ID). WASCO CO.: Moist slopes under oaks, near Rowena, 18 April 1935, Thompson 11366 (NY). WHEELER CO.: Open ponderosa pine woods at summit about 15 mi. northeast of Spray, Twp 75, R25E, 14 May 1950 Cronquist 6335 (NY); Near Fossil, 5 May 1930, Leach 19365 (OSC); Open rocky slopes in ponderosa pine area, summit of the Ochoco Mts., about 26 mi. northeast of Paulina, T14S, R24E, S8, 5700 ft., 19 June 1953, Cronquist 7228 (NY).

UTAH: CACHE CO.: Brigham, 23 April 1890, Jones s.n. (NY).

MILLARD CO.: 5 mi. east southeast of Fillmore, Fillmore district, Pavant Mts. 6600 ft., 25 April 1978, Welsh 16434 (NY). RICH CO.: Hills near Bear Lake, 18 June 1932, Williams & Pierson 642 (NY). SALT LAKE CO.: In vicinity of Salt Lake City, 6-8000 ft., 19 April 1884, Leonard 10 (NY); Brighton, Big Cottonwood Canyon, 8 June 1920, Garrett 2907 (NY); East of Brighton Guard Station, Big Cottonwood Canyon, Engelmanns spruce-quaking aspen association, loam soil and west facing slope, 1 July 1962, Eyre 41 (NY); Big Cottonwood Canyon, between Silver Lake and the summit of Mt. Majestic, 28 June 1905, Rydberg & Carlton 6367
(NY); Big Cottonwood Canyon, below Silver Lake, 29 June 1905, Rydberg & Carlton 6506 (NY). SANPETE CO.: Woods and open slopes in the mountains, Subalpine meadow with clumps of Engleman spruce, clay soil, Manto Canyon, Manto-lasal National Forest, 10,000 ft., 10 July 1971, Fitz s.n. (OSC). TOOELE CO.: 8 mi. southwest of Vernon, in gravelly loam with Amelanchier, 1 May 1936, Rigby & Levi s.n. (NY). UTAH CO.: East slope of Mt. Timpanogos, near Provo, Wasatch Mts. edge of snow, 12 June 1933, Applegate 8428 (NY); Provo, Wasatch Mts., 16 June 1902, Goodding 1131 (NY). WASHINGTON: ASOTIN CO.: Partly shaded, rocky, organic soil, among Abies and Pseudotsuga, along west fork of Cottonwood Creek, about 1 mi. above the forks, southwest of Anatone, T7N, R44E, S15, 30 April 1949 Cronquist 5747 (NY, RSA); 12 mi. west of Anatone, dirt road cut through forest of yellow pine-Douglas fir, in clearing, basalt, 3 June 1970, Cox, Dunn, & Fleak 1854 (NY). CHELAN CO.: Rocky woods northern base of Blewett Pass, 18 April 1931, Thompson 5998 (US); Jolly Mt. (Mt. Stewart area), Wenatchee, 1 July 1933, Easton s.n. (OSC); Leavenworth winter sports area, Leavenworth, 2500 ft., 10 April 1937, Handy s.n. (MONTU); Forested slopes in Brender Canyon, 5 mi. west of Cashmere, 17 April 1946, Ward 231 (NY); West side of Chumstick Mt. near top, ca. 12 mi. north of Cashmere, near snowbank, Wenatchee Mts., 15 June
1948, *Hitchcock* 17284 (NY, RSA); Forest along Nason Creek, about 2 mi. southeast of Lake Wenatchee, 4 May 1946, *Ward 332* (NY).


*GARFIELD CO.*: Duff under yellow pine ca. 15 mi. south of Pomeroy in Blue Mountains, 4800 ft., 25 May 1944, *Hitchcock & Muhlick 8294* (NY).


*KITTITAS CO.*: In woods at Fish Lake, 13 July 1954, *Hitchcock 20260* (NY).

*KLICKITAT CO.*: In brush, Bingen, 2 April 1907, 25 May 1907, *Suksdorf 5908* (NY);

In forest edge on the mountain at Bingen, 12 April 1906, 21 May 1906, *Suksdorf 5536* (NY);


*PEND OREILLE CO.*: 23 mi. south of Lone Bridge on Hwy. 20, 21 April 1984, *Fritz-Sheridan 27* (MONTU).

*STEVENS CO.*: Sandy loam in Ponderosa pine forest along Columbia River 3 mi. above mouth of Spokane River, below 1290 ft., 5 April 1940, *Rogers, Boothroyd, Meyer, & Ownbey 260* (NY).

*WHITMAN CO.*: On bank of Union Creek, 6 mi. west of Pullman, 6 April 1922, *Parker 341* (OSC);

Pullman, 25 April 1894, *Piper s.n.* (NY); Perianth lemon-yellow, anthers mahogany-red; grassy northeast slope, Arid Transition Zone, Alomota road 6 mi. southeast of Colfax, 2000 ft., 13 April 1935, *Constance, Dillion, & Rollins 1036* (NY).

*YAKIMA CO.*: Mt. Adams, Bird Creek Meadows, 24 July 1935, *Langdon 23*


