THE BIOSYSTEMATICS OF ERYTHRONIUM PROPULLANS GRAY AND
SYMPATRIC POPULATIONS OF ERYTHRONIUM ALBIDUM NUTTALL (LILIACEAE)

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ABSTRACT

A biosystematic comparison of Erythronium propullans and sympatric populations of E. albidum was conducted to clarify the relationships of these two species. E. propullans is endemic to southeastern Minnesota, while E. albidum is common and widespread throughout the eastern United States, including southeastern Minnesota. The morphology, geography, cytology, ecology, and reproductive biology of each species were investigated. Populations of E. albidum and E. propullans within Rice and Goodhue Counties, Minnesota, were utilized in the study.

A morphological analysis of six characters indicated that E. albidum and E. propullans are morphologically distinct species, and that three size classes of plants exist: E. propullans, depicted as a dwarfed E. albidum, an intermediate size class, and E. albidum. The intermediate size class suggested that E. albidum and E. propullans hybridize to form fertile offspring. The rarity of the hybrid further suggested that some reproductive isolation between the two species exists. The pollen-ovule ratio, protandry, and the dimorphic stamens of E. propullans and E. albidum suggest that both species are facultatively outcrossing. Breeding experiments demonstrated that E. albidum is facultatively outcrossing and able to produce seed when crossed with E. propullans. Self-fertilization in E. albidum required a physical mechanism to transfer pollen from the anther to the stigma. E. propullans, however, produced seed only when crossed with E. albidum. Pollen was found to be effectively transferred either between clones of E. albidum or E. propullans by Andrena carlini CK11, a solitary oligoleotic bee whose pollination behavior was well suited to the flowers of both species. Visits by this insect were primarily to E. albidum flowers. The reproductive evidence questions the validity of the specific ranking given to Erythronium propullans as suggested by its morphology. The restricted range, the relative sterility, and the ploidy level of E. propullans suggest it is a relatively young species of recent origin derived from E. albidum. The inability of E. propullans to reproduce with itself, and a natural low level of seed production in this species, further suggested that populations are maintained exclusively by vegetative reproduction. The lack of input of genetic variability by sexual processes indicates that E. propullans will not adapt to drastically changing environments. Unless critical habitat is preserved, the populations are likely to be extirpated in the near future, resulting in the extinction of E. propullans.
ACKNOWLEDGEMENTS

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INTRODUCTION

*Erythronium propullans* Gray (Liliaceae), the Miniature or Minnesota Trout Lily, is a vernal, herbaceous geophyte which occurs only in two counties of southeastern Minnesota. There are three striking peculiarities of *E. propullans* relative to other species of *Erythronium*: a diminutive size, an irregular number of perianth parts (4, 5, or 6), and a unique manner of vegetative reproduction. *E. propullans* is most similar to *E. albium* Nuttall, the White Trout Lily, which occurs abundantly within deciduous forests throughout eastern North America. *E. albium* occurs sympatrically with all populations of *E. propullans*.

The goal of this study was to better define the relationships between *E. propullans* and *E. albium* by making a biosystematic comparison of the two species. Investigations were conducted on aspects of morphology, geography, cytology, ecology, and reproductive biology. The rarity and potential human impact of *E. propullans* made this study timely. The data acquired from this study will be of value in evaluating the status of populations and critical habitat, to aid in the recovery of stressed populations, and to implement stewardship plans that will help insure its persistence.
LITERATURE REVIEW

Taxonomy

The genus *Erythronium* extends throughout the northern temperate regions of the world. The greatest species diversity of *Erythronium* occurs in western North America (Applegate, 1935). In eastern North America, the species are separated by flower color into a yellow group of five taxa (Parks and Hardin, 1963) and a white group of three taxa. The white group is composed of *E. propullans* Gray, *E. albidum* Nutt. and *E. mesochoreum* Knerr. *E. albidum* has the largest geographic range (Fig. 1) extending from Ontario and Minnesota southward through Kentucky, Arkansas, Oklahoma, and Texas, and eastward to Pennsylvania. *E. mesochoreum* is known from Iowa, Missouri, eastern Nebraska, eastern Kansas, Oklahoma and Texas. *E. propullans* is known only from southeastern Minnesota.

Asa Gray, who first described *E. propullans* in 1871, cited three distinguishing features of *E. propullans* to warrant its specific ranking: (1) the small flower size, one-half the length of the *E. albidum* flower, (2) the origin of a lateral offshoot or runner just below the base of the leaves rather than from the base of the bulb as in *E. albidum*, and (3) the color of the flower which he described as bright pink or rose. Rösendahl (1919) described the variation in perianth parts, a fourth distinguishing feature of *E. propullans*. The flowers have either 4, 5, or 6 stamens and petals. Variations in the number of perianth parts has not
Fig. 1. Range of distribution of *E. albidum*, *E. mesochoreum* and *E. propullans*. 
been reported in other species of the genus. Stamen dimorphism is common in Erythronium (Applegate, 1935; Graff, 1916; Meads, 1893; Pickett, 1917; Utech and Kawano, 1975a; 1975b), including E. albidum, E. mesochoreum, (Robertson, 1966) and E. propullans (Rosendahl, 1919).

E. mesochoreum is morphologically similar to E. albidum and was regarded as a variety of E. albidum (Knerr, 1891a; 1891b; Rickett, 1937; Robertson, 1966). The morphological, ecological, and chromosomal differences between the two species as described by Ireland (1957) and Robertson (1966) are listed in Table 1.

Cytology

The base chromosome number of the genus Erythronium (X=11 or 12) was established by Utech and Kawano (1976). The yellow Erythronium species of the eastern United States are represented by diploid (2N=24) and tetraploid (2N=48) species (Haque, 1961; Parks and Hardin, 1963). Polyploid sequence also occurs within the white flowering taxa: 2N=22 in E. mesochoreum (Ireland, 1957; Robertson, 1966) and 2N=44 in E. albidum (Cave, 1966; Cooper, 1939; Ireland, 1957; Robertson, 1966; Smith, 1955). The chromosome number of E. propullans has not been reported.

Life History

Several aspects of the life history of E. albidum, with emphasis on vegetative reproduction, have been investigated by Blodgett (1894; 1900; 1910) and Schaffner (1901). Being a vernal species, the shoots first emerge in March or early April. By the time the forest canopy has formed, approximately the first of June, the leaves of Erythronium are well into senescence. The above-ground life cycle is therefore begun and completed.
Table 1. Characteristics comparing *E. albidum* and *E. mesochoreum* (from Ireland, 1957, and Robertson, 1966)

<table>
<thead>
<tr>
<th>Characteristic</th>
<th><em>E. albidum</em></th>
<th><em>E. mesochoreum</em></th>
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<tr>
<td>flower length</td>
<td>2.6-3.0 cm</td>
<td>2.7-3.3 cm</td>
</tr>
<tr>
<td>perianth shape</td>
<td>completely reflexed</td>
<td>usually straight, sometimes reflexed</td>
</tr>
<tr>
<td>leaf width (flowering plant)</td>
<td>1.0-2.5 cm</td>
<td>1.0-2.0 cm</td>
</tr>
<tr>
<td>leaf traits</td>
<td>usually flat and mottled</td>
<td>usually conduplicate and nonmottled</td>
</tr>
<tr>
<td>propagation of 1-leaved forms</td>
<td>1 or 2 runners</td>
<td>1 dropper</td>
</tr>
<tr>
<td>habitat preference</td>
<td>shaded ravines and moist woods</td>
<td>prairies, pastures, dry woods</td>
</tr>
<tr>
<td>haploid chromosome number</td>
<td>22</td>
<td>11</td>
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within a two month period.

**Vegetative Reproduction**

During the flowering phenophase of *E. albidum* (late April or early May) one to three runners up to 20 cm long form from the base of the non-flowering individuals. Occasionally, one runner forms at the base of the flowering plants. One new bulb is formed at the apex of each runner. If runners are not formed, then new bulbs are formed adjacent to the parent bulb in the flowering and non-flowering plants. If bulbs are not formed, the persistence of that individual is terminated. Vegetative persistence of *E. mesochoreum* by bulb multiplication is similar to that of *E. albidum*. The short runners of *E. mesochoreum* are called "droppers" (Ireland, 1957). *E. mesochoreum* produces "droppers" each year, while *E. albidum* produces "droppers" only from first year bulbs.

In flowering plants of *E. propullans*, the runner originates not from the base of the bulb of the parent plant, but from the sheathed petiole below the leaf bases at a distance above the bulb (Gray, 1871; Blodgett 1909). The runner pushes out from the leaf sheath, elongates, and produces a new bulb at its terminus. One-third of the vascular bundles below the point of stolon origin continue up the flowering stalk (Blodgett, 1909). The remaining two-thirds of the bundles enter into the runner. According to Blodgett (1909), this diversion of vascular tissue from the flower stalk results in the dwarfed size of the *E. propullans* flower. In the non-flowering *E. propullans* individuals, the formation of runners and bulbs is identical to that of the non-flowering *E. albidum* individuals. The production of up to three new bulbs each year by each parent plant results in populations of *E. albidum* and *E. propullans* with extensive, dense clones.
E. albidum bulbs present at the end of the fruiting season remain dormant until the latter part of October when leaves and flower buds differentiate within the subterranean bulb (Blodgett, 1894). The bulb ceases further development and overwinters until the following spring.

**Sexual Reproduction**

E. albidum plants occur in two forms: the single-leaved, non-flowering form, and the two-leaved, flowering form. Because the bulbs of the flowering plants were usually larger in size and deeper in the soil than the bulbs of the non-flowering plants, Blodgett (1900) suggested that flowering was dependent on the bulb attaining the "necessary vigor, depth, and size". He estimated that a minimum of five years was required for a seed to become a mature plant capable of flowering.

Studies to determine the level of apomixis, the degree of compatibility or the success of experimental hybridization have yet to be performed in any Erythronium species. A relationship between pollen-ovule ratios and breeding systems has been investigated by Cruden (1977); this technique has not been attempted for any species of Erythronium.

Pollinators have been surveyed only for E. mesochoreum and E. japonicum (a Japanese species). Utech and Kawano (1975a) described the pollination behavior of Xylocopa appendiculata circumvolans (a bumble bee). This insect was well suited to the flower of E. japonicum and effectively transferred pollen between clones. An ethological study of Andrena erythronii Ckll. by Michener and Rittenmeyer (1956) established that this insect gathered pollen of E. mesochoreum, however, no reference was made to the efficiency of Andrena erythronii as a vector of pollen transfer. The ecology and pollination behavior of solitary bees, including Xylocopa and
Andrena, has been reviewed by Linsley (1958) and Faegri and van der Pijl (1971).

The fruits of *E. albidum* develop during the latter part of May corresponding with the closing of the forest canopy. At this time, the leaves begin to senesce. By the end of July, the runners, parent bulbs, and fruits are gone, leaving only new bulbs and seeds to continue the life cycle the following spring. The annual seed crop of *E. albidum* averages only two seeds per flowering plant (Struik, 1957). Sernander (1906) noted that an outgrowth (caruncle) present on the seed of *E. denscanis* is utilized as a food source by ants which harvest and disperse the seeds. This phenomenon was reviewed by Gates (1943).

Prior investigations elucidating the biology of *Erythronium* provides minimal information concerning *E. propullans*, perhaps the most intriguing species within the genus. Many questions remain to be answered. What was the origin and subsequent evolution of *E. propullans*? Why is its present distribution so limited? What is its relationship to *E. albidum* and *E. mesochoreum*? Why is *E. propullans* dwarfed? What can be done to insure the persistence of its populations? To answer these questions, a field study was designed that would elucidate the morphology, geography, cytology, ecology, and reproductive biology of *E. propullans* and sympatric populations of *E. albidum* as a comparative standard.
STUDY SITE DESCRIPTION

Regional Description

All documented populations of *E. propullans* are located in Rice and Goodhue Counties of southeastern Minnesota (Fig. 2). The two county area is dissected by the Cannon River, the Straight River, the Little Cannon River, and the headwaters of the North Zumbro River. Populations of *E. propullans* occur in small ravine systems connected to each of these rivers. The bedrock of each valley is predominately St. Peter Sandstone; overlying alluvial soils are loamy and well drained (Carlson *et al.*, 1975).

Glacial till deposits of pre-Wisconsin glaciation persist in Rice and Goodhue Counties. Two Wisconsin morainal ridges, one east and one west of Faribault, Rice County, are evident. According to Wright's (1956) interpretation of Wisconsin glaciation in Minnesota, the eastern Bemis moraine represents the extent of movement of the Des Moines ice lobe during the Cary substage of glaciation; the western Altamont Moraine was formed during the retreat of the Des Moines lobe during the later Mankato substage. Populations of *E. propullans* exist adjacent to, but outside the area of Wisconsin glaciation (Fig. 3).

The floristic province in which *E. propullans* occurs is the "Big Woods" of Minnesota (Daubenmire, 1936), a mesic hardwood forest dominated by sugar maple, basswood, and elm. Prior to human settlement, "Big Woods" type vegetation in Minnesota extended from Rice and Le Sueur Counties in the southeast to Mahnomen County in the northwest (Fig. 4). The present distribution of *E. propullans* and the pre-settlement extent of "Big Woods"
Fig. 2. Distribution of *E. propullans* in Rice and Goodhue Counties, Minnesota.
documented *E. propullans* populations
Fig. 3. Distribution of *E. propullans* near the terminus of the Des Moines lobe at the Bemis moraine formed during the Cary Phase of Wisconsin glaciation (adapted from Wright, 1955).
Fig. 4. Major presettlement floristic provinces in Minnesota and location of E. propullans populations (adapted from Marschner, 1930).
in Rice and Goodhue Counties is shown in Fig. 5; prairie and oak savannah comprise most of the remaining vegetation. The "Big Woods" type vegetation that exists today is evident only in Nerstrand State Park, Rice County, and along ravines and river bottoms. The latter is typically too steeply sloped to develop for agricultural or commercial purposes.

Locality Descriptions

The descriptions of the five sites utilized in this study are individually discussed.

Site I

Site I (Fig. 6) was located in Goodhue County, approximately two miles west of Kenyon (T109N, R18W, Sec. 8) in an open, disturbed woods. This site lies directly adjacent to the North Zumbro River and has a slope of less than 5° from the midstream bed. The soil is loamy, and leaf litter, although not present everywhere, often formed a layer of 2 cm or more.

This site was disturbed by three factors: grazing by farm animals, nearby railroad construction, and the loss of canopy cover and leaf litter by the death of elm trees. The latter might be the most significant disturbance as the canopy cover and leaf litter strongly influence the environment at ground level. The vegetation of Site I is becoming dominated by grasses, Urtica dioica, and Laportea canadensis. Only four small clones of E. propullans, each occupying no greater than 20 square meters, were observed at this site in 1977 and 1978.

The ground-cover species associated with E. propullans and E. albidum at Site I were Anemonella thalictroides, Asarum canadense, Claytonia virginica, Hepatica acutiloba, Trillium nivale, and Viola spp. The predominate species at ground level was Erythronium albidum. It formed several
Fig. 5. Extent of "Big Woods" type vegetation and distribution of *E. propullans* populations in Rice and Goodhue Counties, Minnesota (adapted from Marschner, 1930).
documented populations of *E. propullans*
Fig. 6. Location of study sites in Rice and Goodhue Counties, Minnesota.
dense clones that almost made a continuous mat from the river bank to the margin of the woods, approximately 20 meters.

Woody species at this site included *Acer negundo*, *Acer saccharum*, *Crataegus* sp., *Ostrya virginica*, *Prunus serotina*, *Prunus virginica*, *Quercus alba*, *Quercus macrocarpa*, *Quercus palustris*, *Tilia americana*, *Ulmus americana* (standing dead), and *Xanthoxylum americanum*.

**Site II**

Site II (Fig. 6) was located in Faribault, Rice County, in a rich woods just north of Shattuck Preparatory School (T110N, R20W, Sec. 29). This site was situated on the steep slopes (26° from midstream bed) of a ravine above an intermittent stream which drained into the Straight River. The soil was loamy, well drained, and covered with an abundance of leaf litter.

The elm trees at this and all subsequent sites were not diseased in 1977. Some refuse deposited over several years has accumulated in the ravine at this site.

Herbaceous species associated with *E. propullans* and *E. albidum* included *Anemonella thalictroides*, *Asarum canadense*, *Claytonia virginica*, *Dentaria laciniata*, *Dicentra canadensis*, *Dicentra cucullaria*, *Hepatica acutiloba*, *Sanguinaria canadensis* and *Viola* spp. Clones of *E. albidum* occurred abundantly on the north and south facing slopes of the ravine. *E. propullans* was restricted to the north facing slope with the exception of one small clone that occurred near the south bank of the stream.

Woody species within this site were *Acer saccharum*, *Alnus alterifolia*, *Celtis occidentalis*, *Prunus virginiana*, *Tilia americana*, *Ulmus americana*, and *Xanthoxylum americanum*. 
Site III

Site III (Fig. 6) was located in Faribault, Rice County, in a woods 0.5 miles north of the Wilson Center School (2.5 miles north of Site II), on the north facing slope of a ravine draining into the Cannon River (T11ON, R20W, Sec. 20). The slope from the midstream bed was 18.5°. The soil was loamy and well drained with an abundant covering of leaf litter.

This particular woods was the least disturbed of all sites. *E. albidum* clones were scattered on the north facing slope and toward the periphery of the woods (an alfalfa field enclosed much of the wooded area). On the north facing slope, *E. propullans* was more abundant than *E. albidum*.

The associated ground cover species included *Anemonella thalictroides*, *Asarum canadense*, *Claytonia virginica*, *Dentaria laciniata*, *Dicentra canadensis*, *Dicentra cucullaria*, *Hepatica acutiloba*, *Sanguinaria canadensis*, and *Viola spp.*

Woody species within this site were *Acer saccharum*, including many seedlings, *Fraxinus americana*, *Fraxinus pennsylvanica* var. *subintegerrima*, *Prunus virginiana*, *Tilia americana*, *Ulmus americana*, and *Ulmus rubra*.

Site IV

Site IV (Fig. 6) was located in Faribault, Rice County, in a rich woods behind St. Mary's School (type locality of *E. propullans*), 1 mile south of Site II (T11ON, R20W, Sec. 31). The slope was 24° from the midstream bed and soil was loamy, well drained and covered with leaf litter. The stream below the ravine drained into the Straight River. Although *E. albidum* grew abundantly on north and south facing slopes, only one small clone (approximately one square meter in area) of *E. propullans* was found on the north facing slope.
The same woody and herbaceous species as those found at Site II were observed here. The accumulation of human refuse was conspicuous at this site.

Site V

Site V (Fig. 6) was located 4 miles north of Site II, just outside the Faribault city limits in a disturbed woods adjacent to the Cannon River (T11ON, R20W, Sec. 20). The slope was 20° from the midstream bed. This site was unique in that a small clone composed of approximately 25 individuals was observed to be intermediate in size between *E. propullans* and *E. albidum*.

One large clone of *E. propullans*, approximately 35 x 8.5 meters, was present with several *E. albidum* plants interspersed throughout the clone. Although *E. propullans* grew abundantly on the slope, they were absent on the adjacent flood plain area grazed by cattle. A few *E. albidum* were found on the flood plain, however. The same woody and herbaceous species as those found at Site II and IV were observed at Site V.
METHODS AND MATERIALS

Morphology

Morphological characteristics of *E. albidum* and *E. propullans* were analyzed by measuring live flowering plants and by inspecting herbarium specimens to numerically define and compare the two species. The herbarium specimens which were examined are listed in Appendix I. The following five characters were measured: (1) flower length, (2) peduncle length, (3) length and width of the larger leaf of the flowering plant, (4) leaf length - peduncle length ratio and (5) distance from the peduncle apex to the point of runner origin on the stem (*E. propullans*). Approximately 200 *E. propullans* and *E. albidum* plants from Sites I, II, III, and V were measured. A Student's t-test was performed for each character to distinguish significant differences between the taxa. Non-flowering plants were not measured because of the difficulty encountered in assigning these to either species. Single-leaved forms of *E. propullans* and *E. albidum* are similar in shape and are difficult to distinguish.

Cytology

Chromosome preparations were obtained according to the method outlined by Mitra (1965). Actively growing runner tips of *E. propullans* were gathered in the field and treated for four hours in a 1:1 mixture of 0.003 M aqueous 8-hydroxyquinoline and saturated aqueous solution of alpha-bromo-naphthalene to obtain straight and well spread chromosomes. Runner tips
were stained in a 9:1 mixture of 1% aceto-orecin and 1N HCl heated over an alcohol burner, and then squashed. Preparations were microscopically examined at 1000x using a Leitz Dialux photomicroscope. Photographs were taken using Kodak Panatomic X film.

Chromosome counts from microspore mother cells were not attempted. Microsporogenesis occurs within the subterranean bulb of _E. propullans_ in the fall, and only in those bulbs that are destined to become flowering individuals. The uncertainty in the timing and choice of bulbs would result in too many bulbs being destroyed to justify their use in this method.

**Demographics and Phenology**

Clones of _E. propullans_ at each study site were assessed for three factors: (1) area of clone, (2) number of non-flowering plants, and (3) number of flowering plants per 0.25 m².

Phenological data on flowering and insect activity were recorded, particularly the relationship between ambient temperature and the daily opening and closing of the flowers, the presence of insects, and the annual duration of the flowering interval.

**Pollen and Ovule Production**

Eighteen flowers of _E. albidum_ and 26 flowers of _E. propullans_ with undehisced anthers were gathered among the sites where breeding experiments were conducted to determine pollen and ovule production in both species. A total pollen count was obtained by rupturing one anther from each flower in warmed glycerine jelly to release the pollen, and by staining them with methylene green (Radford, Dickison, Massey and Bell, 1974). The number of ovules per flower was also recorded.
A staining procedure was used to determine pollen viability (actual germination of pollen grains was not performed). One anther from each of 37 *E. propullans* and 21 *E. albidum* flowers between 1977 and 1978 were collected from among all sites where breeding experiments were conducted. The pollen grains of each anther were stained with 1% aniline blue in lactophenol (Swanson and Sohmer, 1975), with a minimum of 500 grains scored per plant. Pollen was recorded as stainable pollen, unstainable pollen, or micropollen.

**Pollen-Ovule Ratios**

The pollen-ovule ratios of *E. albidum* and *E. propullans* were determined by multiplying the total number of pollen grains per anther by the number of anthers per flower, and by dividing this value by the number of ovules per flower.

**Vectors of Pollen Transfer**

The search for pollinators was conducted throughout the flowering phenophase of *Erythronium* in 1977 and 1978. All of the types of insects that visited *E. propullans* and *E. albidum* between the hours of 9:00 am and 4:00 pm were collected. After preliminary sorting, specimens were sent to experts for specific determinations of verifications. Extensive observations were recorded on pollinator activity and flower morphology in relation to pollination.

**Breeding Studies**

Pollination experiments were conducted to determine the propensity of *E. propullans* and *E. albidum* for apomixis, self-compatibility, and
hybridization. Sites I, II, and IV in 1977 and Sites I, II, and III in 1978 were utilized for this purpose (Site IV was not used in 1978 because of the scarcity of E. propullans at this site). The rationale and design for each treatment is described in each of the following subsections.

Treatment I: Propensity for Apomictic Reproduction

In both species, agamospermy (production of seed without pollen) was to be detected by removing all stamens (undehisced) prior to anthesis. Any possibility for chance cross pollination was assured by enclosing the emasculated flowers within glassine bags. Seeds produced under these conditions would establish the level of apomictic reproduction. In 1977 and 1978, 39 E. propullans and 40 E. albidum flower buds representing all sites utilized were treated this way.

Treatment II Propensity for Self-fertilization

Selected flower buds of E. propullans and E. albidum were enclosed in glassine bags prior to anthesis. The pollen available to that flower, therefore, belonged only to that plant. In 1977, no further treatment was given. In 1978, the bags were removed during anthesis, and the anthers were rubbed against the stigmatic surface of the pistil either before or after the stigmatic surface of the pistil had fully expanded. The bags were then replaced. The production of seeds by these plants in 1977 would demonstrate the level of self-fertilization evident in plants not visited by pollinators. The production of seeds by these plants in 1978 would demonstrate the level of self-compatibility in the species. In 1977 and 1978, 43 E. propullans and 48 E. albidum, representing all sites utilized, were treated this way.

Treatment III: Crosses Within Clones

Prior to anthesis, all stamens were removed from flowers of E. pro-
pullans and *E. albidum*. The emasculated flowers were then enclosed in glassine bags. Pollen of that species from flowers within the same clone was introduced onto the stigmatic surface, and the glassine bags were replaced. Seed production in plants treated in this manner would indicate the level of self-compatibility of pollen for different flowers in the same clone. In 1977 and 1978, 29 *E. propullans* and 32 *E. albidum* were treated this way.

**Treatment IV: Crosses Between Clones Within the Same Study Site**

Prior to anthesis, flowers were emasculated and enclosed in glassine bags. Pollen from a flower of that species from a distant clone within the same site was later introduced onto the stigma. Seed production levels from this treatment when compared to levels in Treatment III would establish whether seed production is enhanced by pollen transfer between clones. In 1977 and 1978, 21 *E. propullans* and 21 *E. albidum* flowers were treated in this manner.

**Treatment V: Interpopulational Crosses**

Flowers were emasculated and enclosed prior to anthesis. When the stigma was fully expanded, pollen of the same species from plants that occurred at another site was introduced onto the stigma. The glassine bags were then replaced. Seed production in this experimental group when contrasted with Treatment IV would indicate the level of seed production that a maximally outcrossing system could produce. In 1977 and 1978, 31 *E. propullans* and 43 *E. albidum* flowers were treated this way.

**Treatment VI: Crosses Between *E. propullans* and *E. albidum***

Flowers of both species were emasculated and enclosed prior to anthesis. Pollen from *E. propullans* was introduced onto the expanded *E. albidum* stigma; pollen of *E. albidum* was introduced onto the *E. propullans*
stigma. Seed production within this group would suggest the extent to which gene flow might be possible between the two species. In 1977 and 1978, a total of 49 *E. propullans* and 30 *E. albidum* were included in this experimental group.

**Treatment VII: Natural Level of Seed Production**

A total of 52 *E. propullans* and 43 *E. albidum* plants, representing all sites utilized in the breeding studies in 1977 and 1978, were selected and marked. This control group established normal levels of seed production in each species. The annual seed crop per flower of *E. propullans* and *E. albidum* was determined by dividing the total number of seeds obtained from each species by the number of flowering plants selected within this control group.

Reciprocal crosses between the pollen donating clone and the pollen recipient clone were performed for Treatments III, IV, V, and VI. Several individuals from different areas of a site were used as pollen donors to obtain a true indication of the population as a whole. Hand pollination was carried out only when the stigma had fully expanded, approximately three to five days following anthesis of the flower bud. When fully expanded, the stigmatic surface was well exposed and was covered with many minute hairs which facilitated lodging of pollen. To facilitate retrieval of the fruit, the glassine bags were stapled to tongue depressors which were secured in the ground (Fig. 7). Fruits were harvested five weeks after hand pollination and were allowed to sit for five days until the capsules dried and split, releasing the seeds for counting. At the time of harvest, the peduncle and fruit were prostrate on the ground (unless supported by a tongue depressor) with the peduncle unattached from the remainder of the plant. Although the fruit and most of the peduncle were
Fig. 7. Bagged *E. propullans* flowers after treated for one of the various crosses.
green at the time of harvest, the fruit had to be retrieved at that time or lost to decay.
RESULTS

Morphology

The range of variation in the five characters measured for E. albidum is large within each site (Table 2). Variability in E. albidum more than likely represents the ecotypic differences between individuals. For example, at Site I where the length of the flower ranged from 1.5 to 3.2 cm, smaller flowers were observed growing in grassy, matted areas.

The range of E. propullans measurements was considerable at Sites II and III (Table 3). Many of these E. propullans plants had measurements approaching that obtained from the intermediate size class (Table 4) and larger than the population means or ranges of E. propullans at other sites (Sites I and IV). These plants may represent the hybridization of an intermediate or hybrid class and E. propullans.

At all sites, significant size differences between E. propullans and E. albidum were evident (Table 4). The average length of the E. albidum flower, 2.78 cm, was more than twice the average length of the E. propullans flower. The range in flower length did not overlap between both species. Size differences were also apparent in the mean length of the peduncle, 6.48 cm in E. propullans and 12.25 cm in E. albidum, and in the mean length and width of the leaf, 9.06 cm x 2.02 cm in E. propullans as compared to 12.25 cm x 2.3 cm in E. albidum. As the mean leaf length to peduncle length ratio was 1.5:1 in E. propullans, the height of the flower is consistently shorter than the height of the leaf. In E. albidum, the
### Table 2. Comparison among sites of 5 morphological characters analyzed in *E. albidum*.

<table>
<thead>
<tr>
<th>Site</th>
<th>Flower length</th>
<th>Peduncle length</th>
<th>Leaf length</th>
<th>Leaf:peduncle</th>
<th>Leaf width</th>
</tr>
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<td>Site I</td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
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<td>10.5-17.8 cm</td>
<td>.82-1.25:1</td>
<td>1.3-2.8 cm</td>
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</tr>
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Table 3. Comparison among sites of 5 morphological characters analyzed in E. propullans.

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<tr>
<th>Site</th>
<th>flower length</th>
<th>peduncle length</th>
<th>leaf length</th>
<th>leaf:peduncle</th>
<th>leaf width</th>
<th>distance¹</th>
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<td></td>
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<td>5-11.4 cm</td>
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¹Distance from origin of stem offshoot to the apex of the peduncle
Table 4. Comparison of morphological characters between *E. propullans*, the intermediate size class and *E. albidum*.

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<tr>
<th></th>
<th>flower length</th>
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<th>leaf length</th>
<th>leaf:peduncle</th>
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</tr>
<tr>
<td>sample size</td>
<td>106</td>
<td>106</td>
<td>106</td>
<td>106</td>
<td>106</td>
<td>90</td>
</tr>
<tr>
<td>standard deviation</td>
<td>.214</td>
<td>1.462</td>
<td>1.626</td>
<td>.281</td>
<td>.336</td>
<td>2.117</td>
</tr>
<tr>
<td>range</td>
<td>.8-1.5 cm</td>
<td>3.9-10.6 cm</td>
<td>4-13 cm</td>
<td>1.06-2.52:1</td>
<td>1.2-2.8 cm</td>
<td>6-14.4 cm</td>
</tr>
</tbody>
</table>

| Intermediate size class |               |                 |             |               |            |             |
| mean                     | 1.9 cm        | 9.78 cm         | 11.74 cm    | 1.2:1         | 2.11 cm    | 13.31 cm    |
| sample size              | 12            | 12              | 12          | 12            | 12         | 12          |
| standard deviation       | .141          | .810            | 1.682       | .152          | .343       | 1.458       |
| range                    | 1.6-2.1 cm    | 8.6-11.3 cm     | 9.3-13.9 cm | .93-1.35:1    | 1.7-2.9 cm | 10.8-14.8 cm |

| **E. albidum** |               |                 |             |               |            |             |
| mean           | 2.78 cm       | 12.25 cm        | 12.22 cm    | 1:1           | 2.32 cm    |             |
| sample size    | 85            | 85              | 85          | 85            | 85         |             |
| standard deviation | .358         | 1.485           | 1.423       | .103          | .422       |             |
| range          | 1.5-3.6 cm    | 8.8-15.2 cm     | 9.4-17.8 cm | .74-1.3:1     | 1.7-4 cm   |             |

$^1$distance from the origin of the stem offshoot to the apex of the peduncle
two are approximately of equal heights. Based on these measurements, the two taxa are quite distinct as to the relative size of their above ground parts, and may be readily distinguished without noting the presence or absence of a lateral offshoot.

Three size classes of plants were evident from the numerical analysis of each of the four indices (flower length, peduncle length, length of the leaf, and the ratio of the leaf length to the peduncle length). The largest of the three classes was *E. albidum* with a bulb offshoot. The smallest size class was *E. propullans* with a lateral stem offshoot. The intermediate size class encountered at Site V (approximately 25 individuals) was found to be significantly different from the *E. propullans* and *E. albidum* size classes in each of the four indices (Table 4 and Figs. 8 and 9). The intermediate size class has a mean flower length of 1.9 cm, a mean peduncle length of 9.78 cm, a mean leaf length - peduncle length ratio of 1.2:1, and a mean distance of 13.31 cm from the point of runner origin on the stem to the apex of the peduncle. Morphologically, the intermediate size class with a stem offshoot (Fig. 10) and a flower size approaching that of *E. albidum* is difficult to assign to either taxa (*E. albidum* or *E. propullans*). The flowering intermediate individuals were observed to form fruit and produce normal seeds (Fig. 11). The flower color of each of the three size classes was white. The "bright pink or rose" *E. propullans* flowers as described by Gray (1871) were not encountered in this study.

Cytology

All chromosome counts taken from mitotically dividing cells within the runner tip of *E. propullans* were in the low 40's, suggesting that
Figs. 8-9. Fig. 8, an E. propullans, intermediate sized, and E. albidum flowering individual. Fig. 9, the flower of E. albidum (top) the intermediate size class, and E. propullans.
Figs. 10-11. Fig. 10, the lateral stem offshoots of plants of the intermediate size class. Fig. 11, the fruit of *E. aibidum* (left), the intermediate size class, and *E. propullans* (right).
E. propullans, like E. albidum, is a tetraploid species. An exact chromosome number was not obtained in any of the preparations due to artifacts and the clumping of the chromosomes. The best chromosome preparation is illustrated in Fig. 12.

Demographics and Phenology

Contiguous clones of E. albidum form extensive mats of ground cover (Fig. 13). This phenomenon was not evident for E. propullans at any site. The largest clone of E. propullans observed, 393.5 square meters, was located at Site 5 (Table 5). In general, E. propullans (as compared to E. albidum) tends to occur as relatively small, isolated aggregations of clones.

The density of plants in E. propullans clones ranged from 38 to 212 plants per 0.25 m² (Table 5). The percent of flowering plants as compared to non-flowering plants ranged from 1.1 to 22.9% (2 to 32 flowering plants per 0.25 m²). This density reflects the manner and mode of vegetative reproduction. Each fertile flowering plant produces one or two new bulbs each year, and the sterile, non-flowering plants produce two or three new bulbs each year. Therefore, high population densities of young sterile plants could be expected.

The normal blooming interval of Erythronium in southern Minnesota is between the last two weeks of April and the first two weeks of May. In 1977, the first Erythronium blossoms opened the 13th of April, and in 1978, the first flowers began blooming on the 20th of April. In 1976, Minnesota recorded a severe summer and winter drought which diminished the number of E. propullans individuals in many populations the following 1977 spring season. In the spring of 1978, E. propullans was more abundant and new
Fig. 12. Chromosomes of *E. propullans.*
Fig. 13. A typical population of *E. albidum* showing its dominance as a ground cover species in early spring.
Table 5. Number of flowering and non-flowering individuals of *E. propullans* within a .25 m² area, with the approximate area each respective clone occupies.

<table>
<thead>
<tr>
<th>Site:</th>
<th>I</th>
<th>II</th>
<th>III</th>
<th>IV</th>
<th>V</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Number of non-flowering individuals</td>
<td>35</td>
<td>82</td>
<td>125</td>
<td>70</td>
<td>125</td>
</tr>
<tr>
<td>2. Number of flowering individuals</td>
<td>3</td>
<td>2</td>
<td>15</td>
<td>16</td>
<td>13</td>
</tr>
<tr>
<td>3. % flowering individuals</td>
<td>8.6%</td>
<td>2.4%</td>
<td>12%</td>
<td>22.9%</td>
<td>10.4%</td>
</tr>
<tr>
<td>4. Area of clone (square meters)</td>
<td>11.88</td>
<td>17.2</td>
<td>1.32</td>
<td>6.48</td>
<td>290.5</td>
</tr>
</tbody>
</table>
populations were located at this time.

The daily opening and closing of flowers corresponded with diurnal temperature fluctuations during favorable weather conditions. In 1978, the *E. propullans* and *E. albidum* petals did not assume their fully reflexed positions until the afternoon hours (between 12:30 pm and 1:30 pm or later if on a north facing slope) when the ambient temperature was at least 12°C. The optimum interval of insect activity (including pollinators) also began after 12:30 to 1:30 pm. During inclement weather conditions (rain or low ambient temperatures), the flowers remained closed and pollinator activity ceased.

**Pollen and Ovule Production**

Pollen productivity in *E. albidum* was six to eight times greater than in *E. propullans* (Table 6). In *E. propullans*, the mean number of pollen grains per anther was 953 compared to 5,596 in *E. albidum*. The mean number of pollen grains per flower was 4,184 in *E. propullans* and 33,575 in *E. albidum*. *E. albidum* has an average of 36 ovules per flower as compared to only 5.3 in *E. propullans*.

The mean percent stainable pollen in *E. propullans* (37.23%) was much lower than that obtained for *E. albidum* (57.3%, Table 7). In *E. propullans* this value never exceeded 50% in any individual while in *E. albidum* this value always exceeded 50%. The percent micropollen was low in both species, with a mean of 0.8% in *E. propullans* and 3.3% in *E. albidum* (Table 8).

**Pollen-Ovule Ratios**

The pollen-ovule ratio of both species is similar although pollen productivity is much higher in *E. albidum*. A mean ratio of 767:1 in *E. pro-
Table 6. Pollen and ovule production and pollen-ovule ratios of *E. propullans* and *E. albidum*.

<table>
<thead>
<tr>
<th></th>
<th>pollen/anther</th>
<th>pollen/flower</th>
<th>ovules/flower</th>
<th>P:O</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>E. propullans</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>mean</td>
<td>953</td>
<td>4,194</td>
<td>5.32</td>
<td>767:1</td>
</tr>
<tr>
<td>sample size</td>
<td>26</td>
<td>26</td>
<td>26</td>
<td>26</td>
</tr>
<tr>
<td>standard deviation</td>
<td>370</td>
<td>2,310</td>
<td>1.17</td>
<td>261.3</td>
</tr>
<tr>
<td>range</td>
<td>467-1,872</td>
<td>1,862-11,232</td>
<td>2-8</td>
<td>374-1,310:1</td>
</tr>
<tr>
<td><strong>E. albidum</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>mean</td>
<td>5,596</td>
<td>33,575</td>
<td>35.9</td>
<td>965:1</td>
</tr>
<tr>
<td>sample size</td>
<td>18</td>
<td>18</td>
<td>18</td>
<td>18</td>
</tr>
<tr>
<td>standard deviation</td>
<td>1,339</td>
<td>8.037</td>
<td>7.7</td>
<td>176.5</td>
</tr>
<tr>
<td>range</td>
<td>2,205-7,836</td>
<td>13,230-47,016</td>
<td>24-43</td>
<td>427-1,200:1</td>
</tr>
</tbody>
</table>
Table 7. Percent stainable, unstainable and micropollen in *E. propullans* and *E. albidum*.

<table>
<thead>
<tr>
<th></th>
<th>mean</th>
<th>sample size</th>
<th>standard deviation</th>
<th>range</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>E. propullans</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>% stainable pollen</td>
<td>37.23%</td>
<td>37</td>
<td>9.04</td>
<td>17-50%</td>
</tr>
<tr>
<td>% unstainable pollen</td>
<td>61.98%</td>
<td>37</td>
<td>8.91</td>
<td>50-82%</td>
</tr>
<tr>
<td>% micropollen</td>
<td>.8%</td>
<td>37</td>
<td>.94</td>
<td>.1-2.7%</td>
</tr>
<tr>
<td><strong>E. albidum</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>% stainable pollen</td>
<td>57.30%</td>
<td>21</td>
<td>3.61</td>
<td>52-64%</td>
</tr>
<tr>
<td>% unstainable pollen</td>
<td>39.5%</td>
<td>21</td>
<td>3.69</td>
<td>34-46%</td>
</tr>
<tr>
<td>% micropollen</td>
<td>3.3%</td>
<td>21</td>
<td>1.70</td>
<td>1-7.5%</td>
</tr>
</tbody>
</table>
pullans and 966:1 in E. albidum was obtained. The range of pollen-ovule ratios between individuals in both species was broad (Table 6).

Based upon a pollen-ovule ratio index (Cruden, 1976; 1977), the breeding system of E. propullans and E. albidum is predicted as facultative xenogamy, i.e., each species is self-compatible and adapted for outcrossing. Cruden's pollen-ovule ratio for facultative xenogamy is 796:1 (plus or minus a standard error of 88). The next highest category is xenogamy, with a pollen-ovule ratio of 5859:1 (plus or minus a standard error of 935.5).

Observations of Floral Biology

The flower of E. albidum consists of two whorls of petals, three inner and three outer, with one stamen attached opposite each petal (Fig. 14). At full anthesis of the flower, the petals reflex to form a pendent, bell-shaped flower (Figs. 15 and 16). The flowers reflex, as previously mentioned, at approximately noon as the ambient temperature increases, and remain reflexed until early evening when the flowers close in conjunction with loss of sunlight and decreasing temperatures. In a single day, when climatic conditions are favorable, the flowers are available for pollination by bees or other diurnal insects for a maximum of approximately six hours.

E. propullans flowers likewise consist of two whorls of petals. Each whorl, however, is composed of either two or three petals, so that the flowers are either 4, 5, or 6-merous (Figs. 17-19). The stamens, which are attached opposite to the petals, are equal in number to the number of petals. In any E. propullans clone, any combination of 4, 5, or 6-merous flowers exists. The timing of the opening and closing of the E. propullans
Figs. 14-16. Fig. 14, *E. propullans* (left) and *E. albidum* flowers showing the inner and outer whorl of petals and stamens. Fig. 15, stamen dimorphism in *E. albidum*, the shorter whorl dehiscing prior to the longer inner whorl. Fig. 16, stamen dimorphism in *E. propullans*. 
Figs. 17-19. Fig. 17, *E. propullans* flower showing 4-merous condition. Fig. 18, *E. propullans* flower showing 5-merous condition. Fig. 19, *E. propullans* flower showing 6-merous condition.
flower is identical with that of *E. albidum*.

Stamen dimorphism occurs in both *E. propullans* and *E. albidum*; the stamens attached to the outer whorl of petals are shorter than those attached to the inner whorl (Figs. 15 and 16). As the flower opens for the first time, the stamens of the shorter outer whorl begin to dehisce. All pollen is exposed within two hours following the initial splitting of the anther. The taller inner whorl of anthers dehisce from several hours to one day after dehiscence of the outer whorl. Although pollen may be observed on the anthers for three days following initial dehiscence, a sudden spring shower was observed to wash all pollen from an anther in a matter of minutes. The stigmas of both *E. albidum* and *E. propullans* spread three to five days after the shorter whorl of anthers dehisce. In *E. albidum*, the stigma spreads into three distinct lobes, while in *E. propullans*, the stigmatic surface merely expands to expose numerous minute hairs (the lobing of the stigmas evident in *E. albidum* is not pronounced in *E. propullans*). Each species is therefore protandrous, as pollen is shed before the stigmatic surface spreads to facilitate pollen lodging.

Floral nectaries were observed in *E. albidum*. The nectar was sweet to taste. Although nectar was not detectable in *E. propullans*, the nectar-gathering behavior of many bees on *E. propullans* flowers suggested that nectar was present.

Observations on Pollinator Biology

The emergence of many miner bees, bumble bees and other insects was synchronous with the opening of *Erythronium* flowers. The majority of visits to *Erythronium* blossoms were made by the miner bee, *Andrena carlini* Ckll. (Fig. 20), although one bumble bee (*Bombus bimaculatus* Cresson) was observed
Figs. 20-21. Fig. 20, *Andrena carlini* Ckll. Fig. 21, *Andrena carlini* entering an *E. albidum* blossom.
to visit an *E. albidum* flower. *Andrena carlini* were observed to collect nectar and pollen and mate on both *E. albidum* and *E. propullans* flowers.

The nectar gathering behavior of *A. carlini* was similar in the *E. albidum* and *E. propullans* flowers. The bee approached the flower from the rear, landed on the back of the flower, and crawled down between the reflexed petals into the flower (Fig. 21). The bee then somersaulted, holding onto the anthers with its legs. Because of the small size of *E. propullans*, the bee stabilized itself by hanging onto the petals, as well as the anthers, with its legs (Figs. 22 and 23). The bee then crawled upward into the base of the pendant flower (between the petals and the anthers) and began to systematically collect nectar from each petal, eventually circling the entire pistil. While gathering nectar, it pushed the anthers away from its body and in contact with the stigma. After emerging from the *E. albidum* flower, a considerable amount of pollen was observed on the ventral surface of the bee. Comparatively less pollen was observed on bees emerging from *E. propullans* flowers. Several *A. carlini* were observed to visit *E. albidum* flowers to gather pollen only. In this case, the bee oriented itself away from the base of the flower and clung onto the anthers and filaments with its front two pair of legs, freeing its two rear legs to collect pollen. Four pollen packets (two on each of the rear legs) were observed on the pollen-gathering bees (Fig. 24).

Up to ten *A. carlini* were observed collecting nectar within a single clone of *E. albidum* or *E. propullans*. Each visit to each flower lasted from five to twenty-five seconds in *E. propullans* and up to 30 seconds in *E. albidum*. Showing consistency to either species, a single bee visited up to five flowers within a clone before moving on to another clone.

Where clones of *E. propullans* and *E. albidum* grew adjacent to each
Figs. 22-23. *Andrena carlini* collecting nectar from *E. propullans* blossoms.
Figs. 24-25. Fig. 24, Andrena carlini with pollen sacs on rear legs. Fig. 25, Bombylius major collecting nectar from E. albidum.
other, Andrena carlini consistently passed up the E. propullans flowers in favor of E. albidum flowers. In areas where clones of E. propullans were extensive (as in Site III), A. carlini regularly visited the E. propullans flowers at the exclusion of E. albidum. E. propullans competed with Claytonia virginica and Dentaria laciniata for the pollinator Andrena carlini. Where all four plant species grew in close proximity, E. albidum was visited most frequently by Andrena carlini. Pollinator activity was equally divided between plant species at sites where E. propullans and Dentaria laciniata, E. propullans and Claytonia virginica, or E. propullans, Dentaria laciniata, and Claytonia virginica occurred. The pollen load from a pollen gathering Andrena carlini was composed of 93% Erythronium pollen (of a total of 9,015 pollen grains), suggesting that A. carlini is constant for a particular type of plant.

Other insects visiting the Erythronium flowers included Coleopterans Asclera ruficollis Say (Oedomeridae) and Hippodroma sp. (Coccinellidae), Dipterans, Bombylius major L. (Bombyllidae, Fig. 25) and Scatophaga stercoraria L. (Anthomyiidae), and Hymenopterans, Dialictus sp. (Halicictidae), Nomada bella Cresson, Nomada sp. (Anthophoridae), and Priocnemis minorata Banks (Pompilidae). Visits to Erythronium flowers by these insects were erratic and infrequent compared to Andrena carlini.

Breeding Studies

The results from each pollination treatment, as outlined in the Methods and Materials section, is discussed separately.

Treatment I: Propensity for Apomictic Reproduction

Neither the E. propullans nor E. albidum flowers that were emasculated in 1977 or 1978 produced fruit of seed (Tables 8 and 10). Apomictic repro-
Table 8. Comparison of data between the sites utilized in 1977 and 1978 measuring the occurrence of apomixis in *E. propullans* and *E. albidum*.

<table>
<thead>
<tr>
<th></th>
<th>Site I</th>
<th>Site II</th>
<th>Site III</th>
<th>Site IV</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>E. propullans - 1977</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>number bagged/number retrieved</td>
<td>15/15</td>
<td>7/7</td>
<td></td>
<td></td>
<td>22/22</td>
</tr>
<tr>
<td>% with fruit</td>
<td>0%</td>
<td>0%</td>
<td></td>
<td></td>
<td>0%</td>
</tr>
<tr>
<td><strong>E. propullans - 1978</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>number bagged/number retrieved</td>
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<td>6/6</td>
<td>5/5</td>
<td></td>
<td>17/17</td>
</tr>
<tr>
<td>% with fruit</td>
<td>0%</td>
<td>0%</td>
<td>0%</td>
<td></td>
<td>0%</td>
</tr>
<tr>
<td><strong>E. albidum - 1977</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>number bagged/number retrieved</td>
<td>14/14</td>
<td></td>
<td>1/1</td>
<td></td>
<td>15/15</td>
</tr>
<tr>
<td>% with fruit</td>
<td>0%</td>
<td></td>
<td>0%</td>
<td></td>
<td>0%</td>
</tr>
<tr>
<td><strong>E. albidum - 1978</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>number bagged/number retrieved</td>
<td>10/10</td>
<td>10/8</td>
<td>5/5</td>
<td></td>
<td>25/23</td>
</tr>
<tr>
<td>% with fruit</td>
<td>0%</td>
<td>0%</td>
<td>0%</td>
<td></td>
<td>0%</td>
</tr>
</tbody>
</table>
duction, if it occurs at all, must occur at an incidence so rare that it could not be detected with the sample sizes employed in this study. These results suggest that pollen is required to facilitate seed set.

**Treatment II: Propensity for Self-fertilization**

No fruit or subsequent seed development occurred in the *E. propullans* flowers that were self-pollinated in 1977 or 1978 (Tables 9 and 10). In *E. albidum*, no fruit or seed was produced by plants that were treated for self-fertilization in 1977. In 1978, however, 50% of those flowers treated for self-fertilization produced fruit, with an average of 2.33 seeds per fruit (Table 9). Pollen was not manually rubbed on the stigma in 1977 as it was in 1978. The two year data suggests that without physical assistance, pollen cannot be transferred to the stigma. Further, seed set in *E. albidum* was highest when plants were pollinated shortly after the dehiscence of the anther and prior to the spreading of the stigmas, as they were at Site III. At Sites I and II, where seed production was lower, the flowers were pollinated when the stigmas were spread and the pollen from three to four days old. Collectively, the data indicates that either the proper age of the pollen or the receptivity of the stigma, plus a physical mechanism to transfer pollen, are required for *E. albidum* flowers to produce seed when self-pollinated. If *E. propullans* is self-compatible, it is at an incidence so rare that it could not be demonstrated with the sample sizes employed.

**Treatment III: Crosses Within Clones**

In 1977 and 1978, no fruit or seed set was found in *E. propullans* plants crossed with pollen from flowers of the same clone (Tables 11 and 12). *E. albidum* flowers crossed with a flower of the same clone in 1977 and 1978 resulted in 40% of all plants producing fruit and a mean of 4.2
Table 9. Comparison of data between the sites utilized in 1977 and 1978 measuring the occurrence of self-fertilization in *E. propullans* and *E. albidum*.

<table>
<thead>
<tr>
<th></th>
<th>Site I</th>
<th>Site II</th>
<th>Site III</th>
<th>Site IV</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>E. propullans - 1977</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>number bagged/number retrieved</td>
<td>7/7</td>
<td>15/15</td>
<td></td>
<td></td>
<td>22/22</td>
</tr>
<tr>
<td>% with fruit</td>
<td>0%</td>
<td>0%</td>
<td></td>
<td></td>
<td>0%</td>
</tr>
<tr>
<td><strong>E. propullans - 1978</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>number bagged/number retrieved</td>
<td>5/5</td>
<td>9/9</td>
<td>6/6</td>
<td></td>
<td>20/20</td>
</tr>
<tr>
<td>% with fruit</td>
<td>0%</td>
<td>0%</td>
<td>0%</td>
<td></td>
<td>0%</td>
</tr>
<tr>
<td><strong>E. albidum - 1977</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>number bagged/number retrieved</td>
<td></td>
<td>17/17</td>
<td></td>
<td>5/5</td>
<td>22/22</td>
</tr>
<tr>
<td>% with fruit</td>
<td>0%</td>
<td></td>
<td>0%</td>
<td></td>
<td>0%</td>
</tr>
<tr>
<td><strong>E. albidum - 1978</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>number bagged/number retrieved</td>
<td>10/8</td>
<td>10/6</td>
<td>6/6</td>
<td></td>
<td>26/20</td>
</tr>
<tr>
<td>% with fruit</td>
<td>25%</td>
<td>33%</td>
<td>100%</td>
<td></td>
<td>50%</td>
</tr>
<tr>
<td>mean number of seeds/fruit</td>
<td>1</td>
<td>2.5</td>
<td>2.7</td>
<td></td>
<td>2.33</td>
</tr>
<tr>
<td>range of seeds/fruit</td>
<td>1</td>
<td>4-6</td>
<td>1-4</td>
<td></td>
<td>1-6</td>
</tr>
</tbody>
</table>
Table 10. Summary of results from treatments to determine apomixis and self-fertilization within *E. propullans* and *E. albidum* in 1977 and 1978.

<table>
<thead>
<tr>
<th></th>
<th>apomixis</th>
<th>self-fertilization</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>E. propullans</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>number bagged/number retrieved</td>
<td>39/39</td>
<td>43/43</td>
</tr>
<tr>
<td>% with fruit</td>
<td>0%</td>
<td>0%</td>
</tr>
<tr>
<td><strong>E. albidum</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>number bagged/number retrieved</td>
<td>40/38</td>
<td>26/20(^1)</td>
</tr>
<tr>
<td>% with fruit</td>
<td>0%</td>
<td>50%(^1)</td>
</tr>
<tr>
<td>mean number of seeds/fruit</td>
<td></td>
<td>2.33(^1)</td>
</tr>
<tr>
<td>range of seeds/fruit</td>
<td></td>
<td>1-6(^1)</td>
</tr>
</tbody>
</table>

\(^1\) *E. albidum* 1978 data only
Table 11. Comparison of data between the sites utilized in 1977 and 1978 measuring the success of intraspecific crosses in *E. propullans* and *E. albidum*.

<table>
<thead>
<tr>
<th></th>
<th>Site I</th>
<th>Site II</th>
<th>Site III</th>
<th>Site IV</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>E. propullans - 1977</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>number bagged/number retrieved</td>
<td>3/3</td>
<td>10/10</td>
<td></td>
<td></td>
<td>13/13</td>
</tr>
<tr>
<td>% with fruit</td>
<td>0%</td>
<td>0%</td>
<td></td>
<td></td>
<td>0%</td>
</tr>
<tr>
<td><strong>E. propullans - 1978</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>number bagged/number retrieved</td>
<td>5/4</td>
<td>6/6</td>
<td>5/5</td>
<td></td>
<td>16/15</td>
</tr>
<tr>
<td>% with fruit</td>
<td>0%</td>
<td>0%</td>
<td>0%</td>
<td></td>
<td>0%</td>
</tr>
<tr>
<td><strong>E. albidum - 1977</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>number bagged/number retrieved</td>
<td></td>
<td>16/16</td>
<td></td>
<td></td>
<td>16/16</td>
</tr>
<tr>
<td>% with fruit</td>
<td></td>
<td>31%</td>
<td></td>
<td></td>
<td>31%</td>
</tr>
<tr>
<td>mean number of seeds/fruit</td>
<td></td>
<td>3.6</td>
<td></td>
<td></td>
<td>3.6</td>
</tr>
<tr>
<td>range of seeds/fruit</td>
<td></td>
<td>1-7</td>
<td></td>
<td></td>
<td>1-7</td>
</tr>
<tr>
<td><strong>E. albidum - 1978</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>number bagged/number retrieved</td>
<td>5/2</td>
<td>5/5</td>
<td>6/2</td>
<td></td>
<td>16/9</td>
</tr>
<tr>
<td>% with fruit</td>
<td>0%</td>
<td>60%</td>
<td>100%</td>
<td></td>
<td>56%</td>
</tr>
<tr>
<td>mean number of seeds/fruit</td>
<td></td>
<td>4.7</td>
<td>8</td>
<td></td>
<td>6</td>
</tr>
<tr>
<td>range of seeds/fruit</td>
<td></td>
<td>2-8</td>
<td>4-12</td>
<td></td>
<td>2-12</td>
</tr>
</tbody>
</table>
Table 12. Summary of results from treatments to determine success of intraclonal crosses in *E. propullans* and *E. albidum* in 1977 and 1978.

<table>
<thead>
<tr>
<th></th>
<th><em>E. propullans</em></th>
<th><em>E. albidum</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>number bagged/number retrieved</td>
<td>29/29</td>
<td>32/25</td>
</tr>
<tr>
<td>% with fruit</td>
<td>0%</td>
<td>40%</td>
</tr>
<tr>
<td>mean number of seeds/fruit</td>
<td></td>
<td>4.2</td>
</tr>
<tr>
<td>range of seeds/fruit</td>
<td></td>
<td>1-12</td>
</tr>
</tbody>
</table>
seeds per fruit (Tables 11 and 12). These results indicate that intraclonal hybridization in E. propullans is not likely to produce seeds. In E. albidum, the similar levels of seed production of self-fertilized flowers (Treatment II) and intraclonal hybridization reflects the genetic uniformity of all E. albidum plants within a clone.

Treatment IV: Crosses Between Clones Within the Same Study Site

In 1977 and 1978, no seeds were produced in those E. propullans flowers that were crossed with pollen from another clone within the same site (Tables 13 and 14). During the same two years, 63% of the E. albidum similarly treated produced fruit with a mean of 12.5 seeds per fruit (Tables 13 and 14). In E. albidum, these results in addition to the results from Treatments II and III indicate that the percentage of seed set increases as the distance of the pollen source increases. Interclonal hybridization in E. propullans is not likely to produce seeds.

Treatment V: Interpopulational Crosses

No fruit or seeds were formed in the E. propullans flowers crossed with a member from different sites in 1977 or 1978 (Tables 15 and 16). In E. albidum, 63% of the plants so treated in 1977 and 1978 formed fruit with an average of 9 seeds per fruit (Tables 15 and 16). The level of fruit and seed set in E. albidum for this treatment is similar to that noted in Treatment IV. The range in the number of seeds produced from site to site was large, from a mean of 5.5 seeds at Site II in 1978, to a mean of 18 seeds at Site I in 1978 (Table 15). These results indicate that in E. albidum, the highest levels of seed set are a result of outcrossing, and that a vector is required to transfer pollen from site to site. If E. propullans is capable of setting seed from outcrossing, it is at levels so low that it was not detected.
Table 13. Comparison of data between sites measuring the success of interclonal crosses in *E. propullans* and *E. albidum* in 1977 and 1978.

<table>
<thead>
<tr>
<th></th>
<th>Site I</th>
<th>Site II</th>
<th>Site III</th>
<th>Site IV</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>E. propullans - 1977</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>number bagged/number retrieved</td>
<td>8/8</td>
<td>3/3</td>
<td></td>
<td></td>
<td>11/11</td>
</tr>
<tr>
<td>% with fruit</td>
<td>0%</td>
<td>0%</td>
<td></td>
<td></td>
<td>0%</td>
</tr>
<tr>
<td><strong>E. propullans - 1978</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>number bagged/number retrieved</td>
<td>5/5</td>
<td>5/5</td>
<td></td>
<td></td>
<td>10/10</td>
</tr>
<tr>
<td>% with fruit</td>
<td>0%</td>
<td>0%</td>
<td></td>
<td></td>
<td>0%</td>
</tr>
<tr>
<td><strong>E. albidum - 1977</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>number bagged/number retrieved</td>
<td>11/11</td>
<td></td>
<td></td>
<td></td>
<td>11/11</td>
</tr>
<tr>
<td>% with fruit</td>
<td>64%</td>
<td></td>
<td></td>
<td></td>
<td>64%</td>
</tr>
<tr>
<td>mean number of seeds/fruit</td>
<td>8.1</td>
<td></td>
<td></td>
<td></td>
<td>8.1</td>
</tr>
<tr>
<td>range of seeds/fruit</td>
<td>1-13</td>
<td></td>
<td></td>
<td></td>
<td>1-13</td>
</tr>
<tr>
<td><strong>E. albidum - 1978</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>number bagged/number retrieved</td>
<td>5/5</td>
<td>5/5</td>
<td></td>
<td></td>
<td>10/10</td>
</tr>
<tr>
<td>% with fruit</td>
<td>0%</td>
<td>60%</td>
<td></td>
<td></td>
<td>30%</td>
</tr>
<tr>
<td>mean number of seeds/fruit</td>
<td>17.7</td>
<td></td>
<td></td>
<td></td>
<td>17.7</td>
</tr>
<tr>
<td>range of seeds/fruit</td>
<td>14-22</td>
<td></td>
<td></td>
<td></td>
<td>14-22</td>
</tr>
</tbody>
</table>
Table 14. Summary of results from treatments to determine success of inter-clonal crosses in *E. propullans* and *E. albidum* in 1977 and 1978.

<table>
<thead>
<tr>
<th></th>
<th><em>E. propullans</em></th>
<th><em>E. albidum</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>number bagged/number retrieved</td>
<td>21/21</td>
<td>21/21</td>
</tr>
<tr>
<td>% with fruit</td>
<td>0%</td>
<td>47%</td>
</tr>
<tr>
<td>mean number of seeds/fruit</td>
<td>12.5</td>
<td>3-23</td>
</tr>
<tr>
<td>range of seeds/fruit</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 15. Comparison of data between the sites utilized in 1977 and 1978 measuring the success of inter-populational crosses in *E. propullans* and *E. albidum*.

<table>
<thead>
<tr>
<th></th>
<th>Site I</th>
<th>Site II</th>
<th>Site III</th>
<th>Site IV</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>E. propullans - 1977</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>number bagged/number retrieved</td>
<td>12/12</td>
<td></td>
<td></td>
<td></td>
<td>12/12</td>
</tr>
<tr>
<td>% with fruit</td>
<td>0%</td>
<td></td>
<td></td>
<td></td>
<td>0%</td>
</tr>
<tr>
<td><strong>E. propullans - 1978</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>number bagged/number retrieved</td>
<td>6/5</td>
<td>8/5</td>
<td>5/5</td>
<td></td>
<td>19/15</td>
</tr>
<tr>
<td>% with fruit</td>
<td>0%</td>
<td>0%</td>
<td>0%</td>
<td></td>
<td>0%</td>
</tr>
<tr>
<td><strong>E. albidum - 1977</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>number bagged/number retrieved</td>
<td></td>
<td>8/8</td>
<td>8/8</td>
<td></td>
<td>16/16</td>
</tr>
<tr>
<td>% with fruit</td>
<td>87.5%</td>
<td>62%</td>
<td>75%</td>
<td></td>
<td></td>
</tr>
<tr>
<td>mean number of seeds/fruit</td>
<td>6.1</td>
<td>7</td>
<td>6.4</td>
<td></td>
<td></td>
</tr>
<tr>
<td>range of seeds/fruit</td>
<td>1-24</td>
<td>2-15</td>
<td>1-24</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>E. albidum - 1978</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>number bagged/number retrieved</td>
<td>8/7</td>
<td>14/10</td>
<td>5/5</td>
<td></td>
<td>27/22</td>
</tr>
<tr>
<td>% with fruit</td>
<td>14%</td>
<td>60%</td>
<td>100%</td>
<td></td>
<td>54.5%</td>
</tr>
<tr>
<td>mean number of seeds/fruit</td>
<td>18</td>
<td>5.5</td>
<td>17.2</td>
<td></td>
<td>11.4</td>
</tr>
<tr>
<td>range of seeds/fruit</td>
<td>18</td>
<td>3-11</td>
<td>14-20</td>
<td></td>
<td>3-20</td>
</tr>
</tbody>
</table>
Table 16. Summary of results from treatments to determine the success of interpopulational crosses in *E. propullans* and *E. albidum* in 1977 and 1978.

<table>
<thead>
<tr>
<th></th>
<th><em>E. propullans</em></th>
<th><em>E. albidum</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>number bagged/number retrieved</td>
<td>31/27</td>
<td>43/38</td>
</tr>
<tr>
<td>% with fruit</td>
<td>0%</td>
<td>63%</td>
</tr>
<tr>
<td>mean number of seeds/fruit</td>
<td></td>
<td>9</td>
</tr>
<tr>
<td>range of seeds/fruit</td>
<td></td>
<td>1-24</td>
</tr>
</tbody>
</table>
Treatment VI: Crosses Between E. propullans and E. albidum

In 1977, 0% of the E. propullans plants crossed with E. albidum produced seeds. In 1978, however, 20% of E. propullans produced fruit with a mean of 1.16 seeds per fruit (Tables 17 and 18). The discrepancy in results is probably due to the drought conditions of 1977 which made this an atypical season and may have had an influence on the ability of E. propullans to produce seeds. In E. albidum, 73% of those plants in 1977 and 1978 crossed with E. propullans pollen produced seeds with an average of 7.7 seeds per fruit (Tables 17 and 18). The high levels of seed set evident from interspecific hybridization between E. albidum and E. propullans indicate that gene flow between the two species may be possible. The fact that seeds were set in E. propullans only when E. albidum pollen was crossed onto the stigma raises some questions as to the extent of distinctness of these species.

Treatment VII: Natural Level of Seed Production

Among the E. propullans plants selected as controls, 15% produced fruit with a mean of 1.3 seeds per fruit in 1977 and 1978 (Tables 19 and 20). Of the E. albidum control plants selected in 1977 and 1978, 69% produced fruit averaging 5.8 seeds per fruit (Tables 19 and 20). This suggests that in nature, less than one-fourth of all E. propullans and about two-thirds of all E. albidum flowering plants produce seeds and fruit. The annual seed crop among all study sites averaged 0.3 seeds per flowering plant per year in E. propullans and four seeds per flowering plant per year in E. albidum. Based upon the evidence established in Treatments I-VI, seed production in E. propullans in nature is probably a result of pollen transfer from E. albidum rather than from E. propullans flowers. The natural level of seed set in E. albidum (5.8 seeds per fruit) is close to
Table 17. Comparison of data between sites measuring the success of interspecific hybridization between *E. propullans* and *E. albidum* in 1977 and 1978.

<table>
<thead>
<tr>
<th></th>
<th>Site I</th>
<th>Site II</th>
<th>Site III</th>
<th>Site IV</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>E. propullans - 1977</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>number bagged/number retrieved</td>
<td>15/15</td>
<td>13/12</td>
<td>14/14</td>
<td>34/30</td>
<td></td>
</tr>
<tr>
<td>% with fruit</td>
<td>0%</td>
<td>8%</td>
<td>36%</td>
<td>20%</td>
<td></td>
</tr>
<tr>
<td>mean number of seeds/fruit</td>
<td>2</td>
<td>1</td>
<td>1.16</td>
<td>1-2</td>
<td></td>
</tr>
<tr>
<td>range of seeds/fruit</td>
<td>2-14</td>
<td>1-24</td>
<td>1.25</td>
<td>3-10</td>
<td></td>
</tr>
<tr>
<td><strong>E. albidum - 1977</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>number bagged/number retrieved</td>
<td>8/8</td>
<td>14/8</td>
<td></td>
<td>22/14</td>
<td></td>
</tr>
<tr>
<td>% with fruit</td>
<td>75.5%</td>
<td>66.6%</td>
<td>66.6%</td>
<td>66.6%</td>
<td></td>
</tr>
<tr>
<td>mean number of seeds/fruit</td>
<td>17.25</td>
<td>5.5</td>
<td>10.25</td>
<td>3-10</td>
<td></td>
</tr>
<tr>
<td>range of seeds/fruit</td>
<td>13-20</td>
<td>3-11</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 18. Summary of results from treatments to determine success of interspecific hybridization between *E. propullans* and *E. albidum* in 1977 and 1978.

<table>
<thead>
<tr>
<th></th>
<th>E. propullans</th>
<th>E. albidum</th>
</tr>
</thead>
<tbody>
<tr>
<td>number bagged/number retrieved</td>
<td>49/45</td>
<td>30/22</td>
</tr>
<tr>
<td>% with fruit</td>
<td>20%</td>
<td>73%</td>
</tr>
<tr>
<td>mean number of seeds/fruit</td>
<td>1.16</td>
<td>7.7</td>
</tr>
<tr>
<td>range of seeds/fruit</td>
<td>1-2</td>
<td>1-20</td>
</tr>
</tbody>
</table>

*E. propullans* 1978 data only.
Table 19. Comparison of data between sites measuring the natural level of seed production in *E. propullans* and *E. albidum* in 1977 and 1978.

<table>
<thead>
<tr>
<th></th>
<th>Site I</th>
<th>Site II</th>
<th>Site III</th>
<th>Site IV</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>E. propullans - 1977</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>number bagged/number retrieved</td>
<td>7/7</td>
<td>10/10</td>
<td>17/17</td>
<td>5.8%</td>
<td></td>
</tr>
<tr>
<td>% with fruit</td>
<td>0%</td>
<td>10%</td>
<td>1</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>mean number of seeds/fruit</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>range of seeds/fruit</td>
<td>1-3</td>
<td>1-3</td>
<td>1-3</td>
<td>1-3</td>
<td></td>
</tr>
<tr>
<td><strong>E. propullans - 1978</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>number bagged/number retrieved</td>
<td>10/10</td>
<td>12/10</td>
<td>14/14</td>
<td>36/34</td>
<td></td>
</tr>
<tr>
<td>% with fruit</td>
<td>0%</td>
<td>30%</td>
<td>36%</td>
<td>17.6%</td>
<td></td>
</tr>
<tr>
<td>mean number of seeds/fruit</td>
<td>1.66</td>
<td>1</td>
<td>1.33</td>
<td>1-3</td>
<td></td>
</tr>
<tr>
<td>range of seeds/fruit</td>
<td>1-3</td>
<td>1-3</td>
<td>1-3</td>
<td>1-3</td>
<td></td>
</tr>
<tr>
<td><strong>E. albidum - 1977</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>number bagged/number retrieved</td>
<td>8/8</td>
<td>5/5</td>
<td>13/13</td>
<td></td>
<td></td>
</tr>
<tr>
<td>% with fruit</td>
<td>62.5%</td>
<td>80%</td>
<td>69.2%</td>
<td></td>
<td></td>
</tr>
<tr>
<td>mean number of seeds/fruit</td>
<td>3.6</td>
<td>3.7</td>
<td>3.66</td>
<td></td>
<td></td>
</tr>
<tr>
<td>range of seeds/fruit</td>
<td>1-6</td>
<td>1-5</td>
<td>1-6</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>E. albidum - 1978</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>number bagged/number retrieved</td>
<td>10/10</td>
<td>10/10</td>
<td>10/9</td>
<td>30/29</td>
<td></td>
</tr>
<tr>
<td>% with fruit</td>
<td>70%</td>
<td>70%</td>
<td>66.6%</td>
<td>69.8%</td>
<td></td>
</tr>
<tr>
<td>mean number of seeds/fruit</td>
<td>9.6</td>
<td>4.5</td>
<td>6.5</td>
<td>6.8%</td>
<td></td>
</tr>
<tr>
<td>range of seeds/fruit</td>
<td>5-12</td>
<td>1-7</td>
<td>2-11</td>
<td>1-12</td>
<td></td>
</tr>
</tbody>
</table>
Table 20. Summary of results determining the natural level of fruit and seed set of *E. propullans* and *E. albidum* in 1977 and 1978, plus the annual seed crop of each species.

<table>
<thead>
<tr>
<th></th>
<th><em>E. propullans</em></th>
<th><em>E. albidum</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>number marked/number retrieved</td>
<td>53/53</td>
<td>43/42</td>
</tr>
<tr>
<td>% with fruit</td>
<td>15%</td>
<td>69%</td>
</tr>
<tr>
<td>mean number of seeds/fruit</td>
<td>1.3</td>
<td>5.8</td>
</tr>
<tr>
<td>range of seeds/fruit</td>
<td>1-3</td>
<td>1-12</td>
</tr>
<tr>
<td>estimated annual seed crop</td>
<td>.3/flowering indiv.</td>
<td>4/flowering indiv.</td>
</tr>
</tbody>
</table>
the values obtained from intraclonal crosses, suggesting that pollinators are effective in transferring pollen within clones of *E. albidum.*

**Seed Dispersal**

The outgrowth present on both the *E. propullans* and *E. albidum* seeds is illustrated in Fig. 26. This structure has been suggested as a means to attract ants, which would then disperse the seeds as they carried them back to their nests (Gates, 1943). Ants placed among the *E. albidum* and *E. propullans* seeds fed upon the outgrowth when it was macerated. However, the ants did not move or carry seeds at any time during a one week interval. Because the ants were removed from their nest and placed in an artificial environment, their behavior may not be indicative of how they behave in nature.
Fig. 26. Seeds of *E. propullans* (left) and *E. albidum* (right) showing the outgrowth present on each of the seed coats.
DISCUSSION

Morphology

Three size classes of plants are distinguishable based on the morphological analysis of *E. propullans* and *E. albidum*. The differences in the size classes are significant for the six characters measured (Table 21). The intermediate size class may represent fertile hybrid plants from the crossing of *E. albidum* and *E. propullans*. Some of the *E. propullans* size class were significantly closer to the population means of the intermediate size class, suggesting that these plants may be backcrosses of the hybrids to the *E. propullans*. The relative rarity of the intermediate plants further suggests that the intermediates are not frequently formed. The putative hybrid which is suggested from the morphological analysis will require chemotaxonomic investigations to further define the origin of this taxa. Morphologically, *E. albidum* and *E. propullans* (depicted as a dwarfed *E. albidum*) are two distinct species. The characteristics of the three species of the white-flowering *Erythronium* of eastern North America (*E. propullans, E. albidum, and E. mesochoreum*) are compared in Table 22.

Demographics and Phenology

Within Rice and Goodhue Counties, populations of *E. propullans* and *E. albidum* grow in relatively undisturbed, climax, maple-basswood forests
Table 21. Comparison between *E. propullans*, the intermediate size class and *E. albidum* for 6 morphological characters.

<table>
<thead>
<tr>
<th></th>
<th><em>E. propullans</em></th>
<th>intermediate size class</th>
<th><em>E. albidum</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>mean flower length</td>
<td>1.19 cm</td>
<td>1.90 cm</td>
<td>2.78 cm</td>
</tr>
<tr>
<td>mean peduncle length</td>
<td>6.48 cm</td>
<td>9.78 cm</td>
<td>12.25 cm</td>
</tr>
<tr>
<td>mean leaf length</td>
<td>9.06 cm</td>
<td>11.74 cm</td>
<td>12.22 cm</td>
</tr>
<tr>
<td>leaf-peduncle ratio</td>
<td>1.5:1</td>
<td>1.2:1</td>
<td>1:1</td>
</tr>
<tr>
<td>mean leaf width</td>
<td>2.02 cm</td>
<td>2.11 cm</td>
<td>2.32 cm</td>
</tr>
<tr>
<td>distance(^1)</td>
<td>11.24 cm</td>
<td>13.31 cm</td>
<td></td>
</tr>
</tbody>
</table>

\(^1\) distance from the origin of the stem offshoot to the apex of the peduncle
Table 22. Comparison of the morphology, ecology and chromosome number of *E. propullans*, *E. albidum*, and *E. mesochoreum*.

<table>
<thead>
<tr>
<th></th>
<th><em>E. propullans</em></th>
<th><em>E. albidum</em></th>
<th><em>E. mesochoreum</em>¹</th>
</tr>
</thead>
<tbody>
<tr>
<td>flower length</td>
<td>.8-1.5 cm</td>
<td>1.5-3.6 cm</td>
<td>2.1-4.3 cm</td>
</tr>
<tr>
<td>perianth shape</td>
<td>completely reflexed</td>
<td>completely reflexed</td>
<td>usually straight</td>
</tr>
<tr>
<td>leaf width</td>
<td>1.2-2.8 cm</td>
<td>1.7-4 cm</td>
<td>1-2 cm</td>
</tr>
<tr>
<td>leaf traits</td>
<td>mottled</td>
<td>mottled</td>
<td>usually nonmottled</td>
</tr>
<tr>
<td>lateral stem offshoot</td>
<td>present</td>
<td>absent</td>
<td>absent</td>
</tr>
<tr>
<td>propagation of 1-leaved forms</td>
<td>1 to 3 runners</td>
<td>1 to 3 runners</td>
<td>1 dropper</td>
</tr>
<tr>
<td>habitat preference</td>
<td>shaded ravines</td>
<td>shaded ravines</td>
<td>prairies, pastures, dry woods</td>
</tr>
<tr>
<td>diploid chromosome number</td>
<td>low 40's</td>
<td>44</td>
<td>22</td>
</tr>
</tbody>
</table>

¹*E. mesochoreum* data taken from Ireland (1957) and Robertson (1966).
adjacent to rivers or streams. In general, *E. albidum* grows abundantly on south facing slopes while *E. propullans* is usually restricted to north facing slopes of ravines.

Individual clones of *E. albidum* are generally larger in area than *E. propullans* clones. *E. propullans* clones, although quite dense (up to 720 plants per square meter), are scattered and isolated as compared to clones of *E. albidum*. This suggests that *E. albidum* is more aggressive than *E. propullans* in colonization. In forests that have been recently disturbed (as Site I), the population of *E. albidum* is extensive. In the *E. propullans* populations, however, the area and number of individual plants per clone is declining, although the number of clones is stable. Because *E. propullans* is unable to thrive in disturbed areas, efforts to maintain suitable habitat should give careful consideration to the successional stage of the forest. Other herbaceous plants, such as *Trillium nivale*, *Dentaria laciniata*, *Hepatica acutiloba*, and *Dicentra cucullaria*, may serve as indicators of appropriate habitat in which *E. propullans* may grow.

The phenology and life cycle of *E. propullans* and *E. albidum* are similar. Both species emerge, flower, initiate runner growth, form fruit, and senesce synchronously. Because *E. albidum* and *E. propullans* are vernal species which complete their above ground life cycle in a limited amount of time, staggered blooming periods which could insure minimal hybridization and backcrossing does not occur. Phenological isolation, which might strengthen reproductive isolation between the two species, therefore, does not exist. The ability of *E. albidum* and *E. propullans* to remain morphologically distinct, with the exception of a few intermediate plants, suggests, however, that some degree of reproductive isolation must exist between the two species.
Reproductive Capacity

The capacity for sexual reproduction is greater in *E. albidum* than in *E. propullans*. The amount of pollen produced per *E. albidum* flower was six to eight times greater than that produced by *E. propullans*. An average of 57% of *E. albidum* pollen was stainable as compared to only 37% in *E. propullans*. The average *E. albidum* flower has 36 ovules, *E. propullans* has only 5.3. The contrast in reproductive capacity is further reflected in the results from the experimental control group. The average annual seed crop of *E. albidum* is 4 seeds per flowering plant, and only 0.3 seeds per flowering individual in *E. propullans*.

The pollen-ovule ratio may be used to predict the breeding system of a particular plant. This prediction is based on the premise that the ratio increases as the plant progresses from a self-pollinating (autogamous) situation to an outcrossing (allogamous) situation (Cruden 1976; 1977). An outcrossing index devised by Cruden (1977) utilizes pollen-ovule ratios as indicators of breeding systems and correlates pollen-ovule ratios with successional stages of habitat. Using this index, both *E. propullans* and *E. albidum* would be predicted to be facultatively xenogamous species (outcrossing and regularly self-compatible) and exist in late successional stage habitats (habitat undisturbed) and flower when pollinators are unreliable (early vernal insects). The *E. albidum* reproductive strategy is correctly predicted, however, *E. propullans* is extremely xenogamous, producing seeds only when crossed with *E. albidum*.

Vectors of Pollen Transfer

*E. albidum* and *E. propullans* are bell-shaped blossoms, typically suited to a "crawling-in" behavior of bees (Faegri and van der Pilj, 1971).
Both species were visited primarily by *Andrena carlini* Ckll., small solitary bees which were observed to transfer pollen between clones of both species.

According to Linsley (1958) members of the genus *Andrena* are oligolectic bees, i.e., they display flower specificity and constancy and are physiologically synchronized with the blooming period of the plants they visit. The significance of oligolecty in bees is (1) that it reduces competition for flowers between species of bees, and (2) that it insures more efficient pollination of the plant species. Linsley notes one drawback of oligolecty. The bee species may become locally extinct when an appropriate pollen source is lacking and the bee species is unable to adapt to alternate pollen sources.

This type of plant-pollinator relationship has been exemplified in the pollination case studies conducted within the genus *Erythronium* (Michener and Rittenmeyer, 1956; Utech and Kawano, 1976a). *Andrena carlini*, the pollinator of *Erythronium albidum* and *E. propullans*, was observed to be largely dependent of *Erythronium* for pollen, although it was also observed to collect nectar from *Dentaria laciniata* and *Claytonia virginica*. Whereas *Erythronium albidum* and/or *E. propullans* may be necessary for the survival of this bee, the absence of *Andrena carlini* would certainly exclude the only reliable vector for the transfer of pollen for *E. albidum* and *E. propullans*.

The pollination and foraging behavior of *Andrena carlini* is well suited to both the *E. albidum* and *E. propullans* flower, even though *E. propullans* is much smaller in size. Sufficient amounts of pollen adhere to the ventral surface of the insect, promoting the transfer of pollen from clone to clone. The preference of *Andrena carlini* for *E. albidum* probably
reflects the larger size and conspicuousness of the flower as well as the relative abundance of pollen and nectar, giving *E. albidum* a competitive edge for pollinators over *E. propullans*. However, where large clones of *E. propullans* occurred with few *E. albidum* evident, the pollinator visited *E. propullans* flowers at the exclusion of *E. albidum*. This suggests that the bees are under strong resource allocation regimes.

**Breeding Studies**

Collectively, the results for the breeding experiments indicate that seed production in *E. albidum* is highest with an outcrossing system (Table 23). When flowers were exposed to their own pollen or from pollen within the same clone, far fewer seeds were produced than if pollinated either with pollen from another clone within the same site or from another site. *E. albidum* is facultatively outcrossing, adapted for outcrossing but able to self-fertilize, as predicted from its pollen-ovule ratio.

Seed production in *E. albidum* by self-fertilization was found to be most successful when the pollen of *E. albidum* reached the stigma within 24 hours after the anthers dehisced. In 1978, when flowers were bagged and hand-pollinated, 50% produced fruit with a mean of 2.3 seeds per fruit. In 1977, when bagged flowers were not hand pollinated, fruit and seeds did not form, suggesting that some physical mechanism is required for the pollen to reach the stigma. Two such mechanisms were observed. First, the foraging activity of *Andrena carlini* often bent the style and stigma toward the anther making contact with it. Second, the daily opening and closing of the flower brought the stigma in close proximity to and often touching the outer longer whorl of anthers. The latter mechanism can be of significance to *E. albidum* as it can then produce seeds by self-fert-
Table 23. Summary of results obtained from breeding experiments in *E. propullans* and *E. albidum*.

<table>
<thead>
<tr>
<th></th>
<th>INBREEDING</th>
<th>OUTCROSSING</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>apomixis</td>
<td>selfing</td>
</tr>
<tr>
<td><em>E. albidum</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td>% with fruit</td>
<td>0%</td>
<td>50%&lt;sup&gt;1&lt;/sup&gt;</td>
</tr>
<tr>
<td>mean number of seeds/fruit</td>
<td>2.33&lt;sup&gt;1&lt;/sup&gt;</td>
<td>4.2</td>
</tr>
<tr>
<td>range of seeds/fruit</td>
<td>1-6&lt;sup&gt;1&lt;/sup&gt;</td>
<td>1-2</td>
</tr>
<tr>
<td><em>E. propullans</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td>% with fruit</td>
<td>0%</td>
<td>0%</td>
</tr>
<tr>
<td>mean number of seeds/fruit</td>
<td>1.66</td>
<td>1.3</td>
</tr>
<tr>
<td>range of seeds/fruit</td>
<td>1-2</td>
<td>1-3</td>
</tr>
</tbody>
</table>

<sup>1</sup>1978 data only
ilization even if pollinators are not present. However, the traits of protandry and stamen dimorphism limits the extent to which *E. albidum* can produce seeds from this mechanism.

The results of crosses between the two species were striking: *E. albidum* readily produces seeds with pollen of *E. propullans*; *E. propullans* is only capable of producing seeds when pollinated with *E. albidum*. The lack of seed production by *E. propullans* when pollinated by *E. propullans* suggests that *E. propullans* cannot produce additional plants by sexual reproduction. The scarcity of hybrid plants (of the intermediate size class) may be a result of pollinator constancy or a result of high mortality of seeds of hybrid origin. Viability of seeds, progeny survivorship and eventual recruitment, particularly of individuals produced by interspecific hybridization, needs additional investigation.

Evolutionary Relationships

The pattern of distribution in the white *Erythronium* of eastern North America where the tetraploid species are distributed north of the diploid species, is similar to that reported by Parks and Hardin (1963) for the yellow *Erythronium* species of eastern North America. They hypothesized that the yellow tetraploid, *E. americanum* with a diploid chromosome number of 48, is an allotetraploid formed by the natural hybridization of two diploid species, *E. rostratum* (*2N=24*) and *E. umbilicatum* (*2N=24*). Hybridization probably took place in Alabama (the region with the most yellow-flowering species of *Erythronium*) during the Pleistocene Epoch; the tetraploid then migrated northward following the retreat of glaciation to its present distribution (Parks and Hardin, 1963).

Similarly, this scenario might be applied to the white flowering taxa.
Although only one diploid species of the white *Erythronium* group has been found, tetraploidy (perhaps autotetraploidy of *E. mesochoreum* or hybridization and allotetraploidy of *E. mesochoreum* and an unknown diploid species) might also have occurred in the southern United States during Pleistocene glaciation, with subsequent northward migration of the tetraploid (now *E. albidum*) following deglaciation. Speciation to form *E. propullans* probably occurred after glacial ice had disappeared from the Minnesota-Wisconsin area. The restricted range of *E. propullans* more than likely indicates a recent origin of *E. propullans* rather than a reduction of a formerly large range by the Wisconsin glaciation.

The reproductive compatibilities of *E. albidum* and *E. propullans* suggests that *E. propullans* was derived from *E. albidum*. The possibility of *E. propullans* being some sort of rare genetic form of *E. albidum* which has persisted solely be vegetative reproduction, cannot be omitted. Such a view would lead one to consider *E. propullans* as an incipient species that has not yet overcome its sterility barrier (Stebbins, 1971).

**Species Persistence**

Because *E. propullans* is maintained exclusively by vegetative reproduction, all progeny are presumably genetically identical. If indeed the entire species is genetically uniform, then the inability of *E. propullans* to successfully breed intraspecifically may be explained by suggesting that the entire species is one self-incompatible clone distributed in space. To test this hypothesis, chemotaxonomic techniques, particularly isozyme analysis, are being applied to determine the extent of genetic variability within *E. propullans*, a factor of importance to the persistence of rare plants (Stebbins, 1942).
A natural low seed set in *E. albidum* appears to be the rule. The persistence of *E. propullans* is insured by the multiplication of bulbs in lieu of reproduction by seeds. Critical seed characteristics are transferred to the bulbs, such as (1) the ability to store starch during spring growth, (2) the ability to provide protection for the developing shoot within, and (3) the ability to overwinter and endure freezing temperatures. The emphasis on bulb reproduction may be viewed as a successful adaptation for ephemeral, vernal sporophytes. For example, bulb formation does not rely upon pollinators which are unreliable in early spring. The production of bulbs in spring insures that successful combinations will be perpetuated and any genetic heterozygosity will not be diminished by repeated inbreeding of relatively isolated populations. However, the production of seeds by sexual reproduction; whether by recombination or introgression, is the only means by which new genetic combinations may be introduced into the population. The low levels of seed production, particularly evident in *E. propullans*, might reduce the prospects for long-term survival of the species. Lacking continual input of genetic variability into the population of mature plants, the species may be slow to adapt to changing environments or to colonize new habitats. An entire population or the species could be eradicated if the environment were to change drastically. The "Big Woods" maple-basswood forest in which *E. propullans* thrives is but a remnant of its original post-glacial range. This restrictiveness of "Big Woods" is continuing today under the pressures brought on by agricultural and urban development. Therefore, the persistence of this species is in doubt. The species will become extinct unless its critical habitat is protected.
CONCLUSIONS

Erythronium propullans Gray is a vernal species found only in remnant "Big Woods" maple-basswood forests within Rice and Goodhue counties, Minnesota. E. albidum Nutt. grows sympatrically with all documented populations of E. propullans. The two species are morphologically distinct based on size and mode of vegetative reproduction, and are able to hybridize and produce fertile offspring as suggested from the presence of a fertile intermediate sized class. E. propullans has a diploid chromosome number in the low 40's.

Both E. propullans and E. albidum were pollinated by Andrena carlini Ckll., an oligolectic solitary bee, which was observed to transfer pollen between either clones of E. albidum or E. propullans. The pendant-shaped blossoms of E. albidum and E. propullans were well suited to its pollination behavior. Both species are protandrous and have dimorphic stamens to promote outcrossing. The pollen-ovule ratio and breeding experiments conducted within the species indicate that E. albidum is facultatively outcrossing and able to produce seed when crossed with E. propullans. E. propullans, however, is xenogamous, not self-compatible and able to produce seed only when crossed with E. albidum. A low reproductive capacity, a low level of natural seed production, and an inability to sexually reproduce with members of its own species, suggests that the persistence of E. propullans is maintained only by the multiplication of bulbs.
Of the two species, *E. propullans* is less abundant in number of individuals per clone and number of clones per site. This, coupled with the possibility of agricultural or urban development within its populations, and the lack of input of genetic variability required to adapt to a drastically changed environment, foretells the extirpation of its populations. Unless its critical habitat is protected, *E. propullans* is quite likely to become extinct.
LITERATURE CITED


Appendix 1. *E. propullans* herbarium specimens examined.

Minnesota, Rice County, Faribault (type locality), St. Mary's Preparatory School: May 1871, Hedges sn. (G) TYPE SPECIMEN, duplicate at NY; F. S. Beane sn. (MIN); May 1944, K. Orwig sn. (G, MIN); 7 May 1953, Rosendahl, Mayla, Jalm and Dobies 7962 (MIN). Shattuck Preparatory School, Faribault: 22 April 1977, Banks 333, 334, 340, 341, 342, 345, 347 (UWL).

Faribault: May 1890, F. S. Beane sn. (MIN, PH); 28 April 1903, C. C. Camp (G); 1872, Darlington (NY); May 1874, S. A. Darlington sn. (MO, PH); Darlington sn. (NY); M. Hedges and S. A. Darlington sn. (G, NY); May 1880, I. Martindale sn. (NY); 1891, Patterson sn. (MO); May 1890, J. H. Sandberg sn. (F, MIN, MO, NY, PH); May 1890, J. H. Sandberg 4917 (NY); May 1894, J. H. Sandberg sn. (F, G, MICH, MO, NY, PH). Rice County: May 1891, G. B. Aiton sn. (F, MIN, MO, NY); 14 May 1961, T. Morley 960 (MIN); 3 May 1964, T. Morley 1041 (MIN); J. H. S. sn. (MIN).

Minnesota, Goodhue County, Kenyon: 30 April 1975, Banks 73, 76 (UWL); 17 April 1946, J. W. Moore and N. L. Huff 18443 (G, MIN); 6 May 1945, C. O. Rosendahl 7722 (MIN, MO); 6 May 1975, Sohmer 9738, 9767 (UWL); 10 May 1975, Sohmer 9769, 9770 (UWL). Cannon Falls: April 1895, G. B. Aiton (MIN, NY); E. O1 Rosendahl, E. E. Dutton and E. T. Nielsen 2934 (MIN); 10 May 1919, C. O. Rosendahl and F. K. Butler 3786 (MIN); 3 May 1918, C. O. Rosendahl and F. K. Butler 3451 (G, MIN, NY); J. L. Scofield 1015 (MIN). Zumbrota: May 1892, A. L. Ballard (G, MIN, NY).

Minnesota: Darlington sn. (MIN).