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POLLINATION AND SEED PRODUCTION IN *XEROPHYLLUM TENAX* (MELANTHIACEAE) IN THE CASCADE RANGE OF CENTRAL OREGON[1]

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Xerophyllum tenax is a mass-flowering, nectarless herb in which self-pollination is unavoidable as anthers shed pollen onto the three, receptive stigmatic ridges attached to each pistil within a few hours after expansion of the perianth. We compared the pollination system with reproductive success in this species through controlled, hand-pollination experiments. Ovaries of flowers sampled from unbagged inflorescences were visited by pollen-eating flies (primarily members of the family Syrphidae), beetles (primarily *Cosmosalia* and *Epicauta* spp.), and small bees, and produced normal-sized capsules and mature seeds. Ovaries of flowers from inflorescences bagged to prevent insect pollination produced small capsules containing undeveloped or no seeds. Epifluorescence analyses suggest that 0.95 of the uncovered flowers are cross-pollinated by insects with pollen tubes penetrating style and ovary tissue. Flowers show a "leaky" but early-acting self-incompatibility system. While hundreds of pollen tubes germinate on each stigmatic surface following self-pollination, few pollen tubes penetrate the stigmatic surface and none penetrate the ovary. In contrast, when stigmas are cross-pollinated by hand with pollen from a second inflorescence pollen tubes were seen penetrating style and ovary. Self-incompatibility in *X. tenax* parallels that of some species of *Trillium*, a sister genus within the Melanthiaceae.

Key words: beargrass; Melanthiaceae; pollen; pollination; seed production; self-incompatibility; *Xerophyllum tenax*.

Xerophyllum tenax (Pursh.) Nutt. is an evergreen perennial monocot of montane forests in the Pacific Northwest with long fibrous leaves. In openings the long-lived plants often grow large with multiple shoots of which one or two may produce an inflorescence. The species is not only a significant component of subalpine ecosystems, it is of cultural and commercial importance in the region (Lobb, 1990). Although forest management practices as well as extensive commercial harvest may be affecting the species' reproduction, growth, and survival (Dimock, 1981; Mosley, 2000), little knowledge exists of its reproductive ecology (Bradley, 1984). While the floral phenology and flowering pattern of its inflorescence have been described (Long, 1981; Utech, 1978; Maule, 1959) its pollination ecology, self-isolation mechanisms (sensu Bernhardt and Thien, 1987), and rates of fruit and seed set remain largely anecdotal.

Xerophyllum tenax (beargrass or Indian basket grass) is of cultural and economic importance in northwestern North America (Vance et al., 2001). To Native American basket weavers of California and the Pacific Northwest, *X. tenax* historically was and continues to be a valued plant (Turner, 1998; Rentz, 2003). Leaves are carefully selected, gathered and dyed for use in basketry (Lobb, 1990; Moerman, 1998). Burning off areas where beargrass grows continues to be a traditional practice used to produce the pliable and less pigmented leaves preferred for basketry (Rentz, 2003). The management and protection of these resources are supported by the USDA Forest Service on lands under their jurisdiction (Vance et al., 2001). In recent years beargrass leaves have grown in commercial value and are harvested for the floral industry. These leaves are sold to processors for export as raw material to Asian and European markets for dried floral crafts and decorations. The market potential has been estimated for thousands of tons of leaves at over $US 1 million (Blatner and Schlosser, 1998). Illegal harvest has been extensive and damaging as flowering shoots are often destroyed. In one year over 100 tons of illegally harvested leaves were confiscated from the Willamette National Forest (Mosley, 2000). Interpreting the floral biology of *X. tenax* is necessary to understand its conservation and to develop appropriate management of this species.

Furthermore molecular analyses have changed the morphologically based interpretation of the phylogeny of the monocotyledons in general and *Xerophyllum* and its allied genera in particular. Rudall et al. (2000) maintain *Xerophyllum* within the Liliales but their strict consensus tree now places this genus within the family Melanthiaceae. Genera placed within the Melanthiaceae s.s. are synapomorphic for dorsal composite vascular bundles in their flowers, a pollen grain with an operculate sulcus and the presence of *Veratrum*-type alkaloids. However, while *Xerophyllum* spp. bear many small, whitish flowers on a much elongated, racemose-paniculate inflorescence, this genus is not a sister of *Veratrum* and *Zigadenus* with similar modes of floral presentation. Instead, *Xerophyllum* is a sister genus of *Paris* and *Trillium*. In these two genera the short flowering shoot usually terminates in a large but solitary and often sessile flower. Recent work by Sage et al. (2000) has also found an early acting, stigmatic self-incompatibility in *Trillium* spp. This self-incompatibility mechanism is rare in the monocotyledons in general and is currently restricted to lineages in only four other families. Consequently additional

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work on the floral biology of *Xerophyllum* is also required to compare phenotypic characters between this taxon and its sister genera to determine the divergence of pollination mechanisms and breeding systems within this lineage.

MATERIALS AND METHODS

Study species—*Xerophyllum tenax* (Melanthiaceae) is a perennial, acaulescent, monocot that grows in cool, coniferous forest communities in the subalpine zone of northwestern North America. In the western hemlock zone of the Cascade Mountains it is often a dominant component of the understory. There it grows on rocky shallow soils in association with hemlock and true firs where the forb layer may often be depauperate (Franklin and Dyrness, 1973). *Xerophyllum tenax* consists of a short rhizome and tightly connected shoots. Each vegetative shoot of *X. tenax* arises from a basal meristem, producing grass-like, keeled, rigid leaves with a life span of several years (Bradley, 1984). In openings the long-lived plants may become large with multiple shoots of which one or two may produce an inflorescence. The onset or length of flowering at different locations varies with differences in seasonal temperatures, aspect, and elevation (Long, 1981). In the Oregon Cascades flowering may be initiated as early as April and continue into August. Flowering is often most prevalent in plants growing in forest openings created by disturbance such as wildfire; however, flowering becomes less frequent and may disappear altogether as the forest canopy recloses (Maule, 1959; Simpson, 1990).

Floral morphology—The inflorescense is a mass-flowering terminal raceme of small, white to cream-colored flowers on pedicels 2–5 cm long maturing successively from the bottom to the top (Maule, 1959). The flowering phase is initiated when an inflorescence elongates on an axis that may extend as high as 15 dm. The lower flowers have distinctive bracts that become reduced in length and adnate to the pedicels of the upper flowers. The flower pedicels become elongate and erect at maturity, so that midway through the flowering season, the raceme appears as a conical or cylindrical cluster of opened flowers topped by unopened floral buds. Each flower consists of six oblong to ovate tepals without basal glands. We detected a distinct odor (see Floral attractants and rewards under RESULTS) when the majority of the flowers in the raceme were open. The gynoecium is tricarpellate with three free, recurved styles. The carpels are unilocular, each carpel having a maximum of four ovules (Utech, 1978). The capsule is ovoid, acute, and about 5–7 mm long and it undergoes loculicidal dehiscence when seeds mature in late summer. After the capsule dehisces and seed has been released, the shoot senesces (Hitchcock and Cronquist, 1978; Utech, 1978).

Study sites and design—Two similar but geographically separated sites were selected for the experimental pollination study series and for the observation/collection of insect pollinators. A third site not used for experimentation was used only to collect pollinating insects. These three sites are in the central Cascade Range of Oregon on the USDA Forest Service, Willamette National Forest. The plant association at these sites is *Abies amabilis/Rhododendron macrocarpum/Xerophyllum tenax*. At all sites flowering occurs usually from late May through early July. The first experimental study site, at about 1020 m elevation, is on a shallow slope of the Hackleman Creek drainage within 100 m of the road. The coniferous stand had been logged on part of the site in the early 1990s and trees were scattered in clumps on grassy openings. The second experimental site is situated on a shallow slope of Camp Creek drainage at about 1120 m elevation and also logged in the early 1990s. Removal of a part of the overstory at both sites created sufficiently large openings that favored *X. tenax* flowering. These two sites were about 13 km apart in order to ensure that separate populations were being sampled. The third site, used exclusively for insect collection, was Browder Ridge at about 1350 m elevation where the coniferous overstory was also removed in the early 1990s.

The controlled pollination study was carried out on the two widely separated sites noted above. Four treatments were applied to 24 independent plants selected at each site and randomly assigned. Treatment descriptions follow. (1) Self: stigmas of tagged flowers on re-bagged inflorescences received no additional pollen. (2) Open: stigmas of tagged flowers that opened that morning on unbagged inflorescences were exposed to insect pollinators for 24 h. (3) Short-distance hand cross-pollination (SDP): stigmas of bagged inflorescences received pollen from a solitary inflorescence of a neighboring plant within the same population. (4) Long-distance hand cross-pollination (LDP): stigmas of bagged inflorescences received pollen from a solitary inflorescence of a plant from a disjunctive population at the other site (13 km).

Insect identification and observations of floral development and scent occurred during two flowering seasons from 2001 through 2002. The hand cross- and self-pollination study occurred during flowering season of 2002. Micrographs were taken from collections made in 2001 and 2002.

Flower and floral forager observations—Individual flowers on inflorescences were labeled with jeweler's tags and observed while wearing optical glass magnifiers (Opti Visor). Insect foraging behavior was recorded for 2 d in early July 2000, and 3 d in late June 2001 and 2002, representing approximately 22 h of observation. Optical glass magnifiers made it possible for the observer to note whether the forager contacted the stigmas and the anthers while foraging.

To determine whether visitors carried significant quantities of pollen of *X. tenax* (>25 grains/insect) insects observed foraging on flowers and/or manipulating floral organs with their legs or mouth parts were collected in butterfly nets and killed in jars poisoned with fumes of ethyl acetate on each observation day. Removal, staining, mounting, identification, counting and recording of individual pollen grains carried on insect bodies followed Bernhardt and Weston (1996). We used Calberla's fluid (Ogden et al., 1974) to stain the exine of the pollen walls with basic fuchsin. Insect body length was recorded by measuring the body from its labrum to the apex of the abdomen prior to pinning. Pinned specimens were sent for identification and vouchers were deposited in respective collections: Coleoptera (J. Chemsak, Division of Insect Biology, University of California, Berkeley, California, USA), Diptera (F. C. Thompson, Entomology Division, Smithsonian, Washington, D.C., USA) and Hymenoptera (C. D. Michener; Snow Entomological Museum, Kansas State University, Lawrence, Kansas, USA).

Pollination experiments—Twenty-four flowering plants were randomly assigned to the Open, Self, short-distance cross-pollination (SDP), and long-distance hand cross-pollination (LDP) treatments at each site in late May–early June 2002. For all treatments except the Open treatment, an inflorescence on each plant was isolated in a nylon mesh bag before the flower buds opened.

For determining natural rates of successful pollination Open-treated (unbagged) flowers (each sampled within 24 h of anthesis) were collected from inflorescences at both experimental sites every second day over a 10-d period during mid-June (at peak flowering). For the Self, SDP, and LDP treatments, bags were removed every day and 3–6 flowers were sampled from each inflorescence on their first day of anthesis, hand-pollinated and then labeled with jeweler's tags. Hand-pollinations were made at this time with the aid of an optical glass binocular magnifier, but pollen was applied to the stigmatic surfaces until it was visible to the naked eye. These treatments required re-bagging the inflorescence for an additional 24 h prior to harvesting, fixing, and preserving whole flowers. Pollination success was determined by the numbers of pollen tubes in pistils that penetrated the micropyles of ovules. All flowers were too small to emasculate prior to hand-pollination so the SDP and LDP treatments represent "cross-pollen enhancements" as in Lipow et al. (2002).

Collected flowers were fixed in a 3 : 1 glacial acetic acid : 95% ethanol solution for 2 h before decanting the fixative and storing flowers in 70% ethanol. Individual flowers were softened in a 5% aqueous solution of sodium sulphite at room temperature for 24 h. Each pistil was then excised and taken through three consecutive baths of distilled water. Each washed pistil was placed on its own glass slide, the styles were teased apart with forceps or dissecting probes, and then the entire organ was spread and squashed in 2–3 drops of decolorized aniline blue, labeled, and refrigerated a minimum of 7 d. To view pollen tubes in the pistil under epifluorescence we used a Carl

peduncle, beginning with flowers in the basal portion of the raceme and progressing acropetally so that the same inflorescence may have receptive flowers for up to 2 wk.

The ovary swells within 3–4 d following the withering of the perianth and the androecium. These ovaries remained on the infructescence whether or not they contained seeds. As the ovaries matured into fruits, the capsules of the nonpollinated flowers that presumably had no developing seed appeared appreciably smaller in size than those containing seeds (see section *Fruit and seed set* below).

Floral attractants and rewards—Perianth segments and pistils were white to the human eye, while dehiscent anthers released yellowish, cream-colored pollen. Ovaries commonly turned pink-burgundy purple after the perianth and androecium withered or when the outer whorls were dried by excessive heat.

Scent was variable. In three inflorescences sampled in the field, the floral odor was sweet and agreeable; to the second author it was reminiscent of cultivated lilacs (*Syringa*). In the remaining 12 inflorescences the odor was musty-acrid. Flowers were removed from eight inflorescences at random and placed in a clean, capped glass vial. The lid was removed and the accumulated odor was described at 5-, 10-, and 30-min intervals. Musty-acrid notes dominated with undertones of sweet notes. The odor of these bottled flowers most resembled cultivated privet (*Ligustrum*). Floral nectar was not detected at any stage in the floral life-span.

Foraging insects and their pollen loads—Prospective pollinators represented three insect orders and varied considerably in size, yet almost all foragers examined carried the pollen of *X. tenax* (Table 1). Taxa within the order Diptera (true flies) provided the most numerous and diverse group of foragers. Flies represented six families, but the majority of identified taxa (0.91) belonged to the family of hover flies (Syrphidae). Hover flies were observed probing the stamens and style arms with their probosces while they foraged. These insects remained on an inflorescence for only a few seconds before flying to a second inflorescence. A total of 17 fly specimens were measured with lengths varying from 8 mm (e.g., *Parasyrphus relictus*) to 17 mm (*Laphria* sp.). The male-to-female sex ratio of collected hover flies visiting *X. tenax* was low. Of 69 hover flies evaluated, 0.277 were males. Only one specimen of *Cheilosia hoodiana* (Syrphidae), the most commonly collected fly, was a male.

Flower-visiting beetles (Coleoptera) were represented by four families (Table 1). Beetles carried the pollen of *X. tenax* as they grazed on whole anthers but were also observed to place their heads into the shallow floral cup touching the style arms with their legs and mouth parts. *Cosmosalia chrysocoma* (Cerambycidae) was the most commonly observed species at both sites and was observed flying from inflorescence to inflorescence. However, individual beetles, particularly *C. chrysocoma*, would remain on the same inflorescence for >1 h. On 21 June, 2001, at the Browder Ridge site, we observed *Epicauta* spp. flying from *X. tenax* to flowers of *Ceanothus velutinus* to drink nectar. A total of 33 beetles were measured, ranging in length from 9 mm (e.g., *Anastranglia laetifica*) to 16 mm (e.g., *Cosmosalia chrysocoma*). Of 50 beetle specimens in which gender was identified, 0.64 were males but only two of the 25 specimens of *Cosmosalia chrysocoma* were females.

TABLE 1. Pollen load analyses of insects collected on flowers of *Xerophyllum tenax*.

Insect taxon	Pollen load		
	X. tenax only	*X. tenax* + other species	No pollen
Coleoptera			
Cerambycidae			
Anastrangalia laetifica	2	1	0
Cosmosalia chrysocoma	18	7	0
Leptaura propinqua	1	0	0
Cleridae			
Trichodes ornatus	2	3	0
Meloidae			
Epicauta sp.	12	0	1
Scarabaeidae			
Dichelonyx backi	2	0	0
Diplotaxis sp.	1	0	0
Subtotals	38	11	1
Diptera			
Acroceridae			
Eulonchus sp.	1	0	0
Asilidae			
Laphria sp.	0	0	1
Bombyllidae			
Conophorus sp.	1	0	0
Calliphoridae			
Calliphora vomitoria	1	0	0
Tachinidae			
Tachina sp.	0	1	0
Syrphidae			
Cheilosia hoodiana	20	0	1
Chrysotoxum fasciatum	4	0	1
Eriozona laxa	3	0	0
Eupeodes aberrantis	1	0	1
E. lapponicus	2	1	0
Hadromyia crawfordi	1	0	0
H. pulcher	1	0	0
Melangyna triangulifera	1	0	0
Parasyrphus relictus	18	1	0
Sericomyia chalopyga	1	0	0
Syritta pipiens	1	0	0
Syrphus opinator	5	1	0
S. ribesii	3	2	0
Subtotals	61	5	3
Hymenoptera			
Andrenidae			
Andrena nivalis	0	1	0
A. vicina	1	1	0
Apidae			
Apis mellifera	1	0	0
Bombus fernaldi	0	1	0
Halictidae			
Halictus rubicundus sp.	0	1	0
Lasioglossum athabascense	1	1	0
L. sp. 1 (*Dialictus*)	1	0	0
L. sp. 2 (*Dialictus*)	2	0	0
L. sp. (*Evylaeus*)	1	1	0
Megachilidae			
Coelioxys sp.	1	0	0
Megachile vidua	0	1	0
Subtotals	8	6	0
Grand totals	110	23	5

TABLE 2. Mean number of pollen tubes and 95% confidence intervals (CI) in style and ovary of self-pollinated *Xerophyllum tenax* flowers (Self), open-pollinated flowers (Open), flowers mechanically cross-pollinated with flowers from nearby plants (Short-distance cross), and flowers mechanically cross-pollinated with flowers from a different population separated by 13 km (Long-distance cross). Different letters denote significant differences between treatments (Kolmogorov-Smirnov test $P \leq 0.01$).

Treatment	*N*	Mean	CI
Style			
Self	62	3.79[a]	[2.17, 5.37]
Open	106	8.21[b]	[6.10, 10.32]
Short-distance cross	51	24.00[c]	[18.73, 29.25]
Long-distance cross	55	16.58[c]	[11.03, 16.14]
Ovary			
Self[1]	62		
Open	106	1.52[a]	[0.72, 2.32]
Short-distance cross	51	19.49[b]	[14.70, 24.20]
Long-distance cross	55	14.96[b]	[10.64, 19.29]

[1] No analysis performed as there were no pollen tubes detected in ovary.

proximately 4 tubes and no tubes were found in their ovaries (Table 2). Furthermore, the majority of these pollen tubes showed some form of aberrant growth in their styles, either developing excessive deposits of callose at their tips and/or forming short "corkscrews" or tubes that grew backwards forming geometric patterns (Fig. 2B). We reject the null hypothesis that pistils of flowers that were bagged but not hand-pollinated contained the same number of tubes in their styles and ovaries as those pistils that were bagged and hand cross-pollinated (Table 2).

There was a greater number of penetrating pollen tubes in the stigmas and ovules of pistils that received SDP and LDP (Fig. 2C, D) than those counted in Open or Self treatments (Fig. 2A, B). In styles and ovaries of pistils that received the SDP treatment, the mean number of penetrating pollen tubes were approximately 24 and 20 tubes, respectively. In styles and ovaries of pistils that received the LDP treatment the mean numbers of penetrating pollen tubes were approximately 17 and 15 tubes, respectively. No significant difference was detected in mean number of pollen tubes counted in styles or ovaries between the SDP- and the LDP-treated pistils (Table 2).

Fruit and seed set—Observations of the infructescences and fruits at both sites showed distinct differences between those that developed from flowers that were naturally pollinated (Open) and those bagged (Self). Although there was no significant difference in the number of flowers per inflorescence, we detected a significant difference in mean length between bagged and unbagged infructescences at both sites (Table 3). The size of infructescence may be a function of capsule development as the open pollinated flowers on the (Open) treated inflorescences produced larger, but not significantly more capsules (Table 3). We observed that development was arrested in capsules sampled from bagged inflorescences. Those found to be ≤1 mm in length were not included in any capsule analysis as they were obviously undeveloped capsules. Even with this exclusion of undeveloped capsules, the analysis indicated that there was no significant difference detected in the mean capsule-to-flower ratio among the bagged and unbagged flowers (Table 3).

At both sites, the fruit that developed from the bagged flowers, (autogamy) were significantly smaller in size (based on measured capsule length) than those of the open-pollinated flowers. The capsules from the open-pollinated flowers had a significantly higher rate of filled seed compared to those from the bagged inflorescences (Table 3). The number of filled seed per capsule was related to capsule length which ranged from 1.6 to 7.2 mm. Capsules appeared to expand to accommodate the number of developing seed, which was high as 12 seeds. Length was directly related to number of filled seed (adjusted $R^2 = 0.65$, $P < 0.001$), where the model ($Y = 3.75 + 0.248X$) predicted that capsule <4.0 mm would have a high probability of no or few filled seed. The mean number of filled seed per capsule was 7.06 and 0.94 seeds at the Hackleman Creek site, and 6.63 and 0.18 seeds at the Camp Creek site for Open- and Self-treated flowers, respectively (Fig. 3). The mean filled seed per capsule of the bagged flowers was an order of magnitude lower than that of the open-pollinated flowers indicating almost complete lack of ovule development in flowers prohibited from cross-pollination. The effect was not absolute as a few capsules developed from flowers that were inside the nylon bags, and contained filled seeds. Excision of those capsules revealed seeds that were fewer in number, smaller in size, and predominantly empty. The mean number of empty seeds per capsule was 0.03 and 0.30 seeds at the Hackleman Creek site, and 0.08 and 0.23 seeds at the Camp Creek site for Open- and Self-treated flowers, respectively (Fig. 3). In the capsules of the open-pollinated flowers, empty seeds contributed to <1% of the total number of seeds, whereas in capsules of the flowers receiving no cross-pollination, empty seeds contributed to ≥50% or more of the total. Either total lack of any pollen reaching the anthers or autogamy was possible for flowers that had been bagged. It is likely no seed (or capsule) development occurred if there was no pollination and aborted development occurred with autogamy.

DISCUSSION

In the absence of floral nectar, *X. tenax* is restricted to guilds of pollinators that consume pollen as a primary reward, but it

TABLE 3. Differences between treatments of bagged (Self) and unbagged for natural insect pollination (Open) inflorescences collected from *Xerophyllum tenax*. Significant differences between treatments in mean inflorescence length and mean number of flowers per inflorescence by Tukey's HSD; the Kruskal-Wallis test was also used for detection of significant difference between treatments in mean capsules per flower at $P = 0.05$. Significant difference between treatments is indicated by different letters. Data are presented as means (± 1 SD).

Site	Inflorescence length (cm)		No. flowers per inflorescence		No. capsules per flower	
	Open	Self	Open	Self	Open	Self
Camp Creek	51.3[a]	35.4[b]	276.8[a]	240.4[a]	0.952[a]	0.686[a]
N = 11	(10.3)	(12.8)	(82.2)	(93.3)	(0.070)	(0.259)
Hackleman Creek	61.5[a]	36.8[b]	296.3[a]	282.5[a]	0.907[a]	0.883[a]
N = 12	(13.4)	(11.2)	(87.9)	(69.3)	(0.146)	(0.168)

et al., 2000). As a few bagged flowers of *X. tenax* set seeds in the absence of cross-pollen, early-acting SI may be "leaky," a feature common to other, unrelated taxa with early-acting systems (Richards, 1997). A less likely possibility is that these two populations of *X. tenax* show a small but persistent rate of agamospermy.

This means that while short-tongue flies and beetles are indicative of a "mess and soil" mode of pollination as described by Faegri and van der Pijl (1979), our pollen tube analyses suggest at least that some members of these orders are fairly efficient agents of cross-pollination. Most vectors must transfer a minimum of 1–8 viable grains of pollen from one plant to a minimum of one flower on a second genet within 24 h after the flower buds first open as almost 95% of all insect-pollinated pistils contained at least eight normal, penetrating tubes. While less than two tubes penetrated ovules within 24 h, we must remind ourselves that the tubes in the styles showed normal development and probably represented more than one insect visit several hours apart. These tubes would have probably reached the ovary had each one been allowed to grow the full 24 h as in the case of both sets of single-deposition, manually manipulated cross-pollinations. As all flowers were harvested 24 h after the perianth expanded our results reflect insect visitations limited to the first 25–33% of the actual floral lifespan.

Technically, *X. tenax* cannot be labeled as a "pollen-limited" species either, because even the stigmatic ridges of bagged flowers remain liberally coated with grains due to mechanical or wind-driven self-pollination. However, due to the early-acting self-incompatibility system relatively few adhering grains produce tubes that penetrate pistil tissue. Although insects transport pollen between compatible genets, pollen tube and fruit and seed set analyses show clearly that they don't deposit enough compatible grains to fertilize every ovule in the *same* ovary. This may also be because some insect pollinators are likely to transfer additional incompatible grains as they visit more than one flower in succession on the same inflorescence. Therefore this geitonogamous transfer of grains may decrease the effectiveness of an insect's cross-pollination service. Cross-pollinations made by hand from single sires selected from presumably different genets result in far more pollen tubes penetrating ovules than the vast majority of cross-pollinations perpetuated by insects. Consequently this species may be described as "compatible-pollen limited" for, although this plant is a copious pollen producer and attracts many vectors that cross-pollinate, in 95% of all flowers seed set remains relatively low.

The species is further limited by a fairly substantial light requirement to produce the large racemes. It is adapted to the variation and unpredictability of climate in late May and early June in its montane habitat by producing an inflorescence with many flowers that open sequentially over the span of several weeks. Despite that flowering trait, we observed at one site almost all flowers damaged by a late frost. In addition, flowers are browsed presumably by large ungulates (Young et al., 1939; Simpson, 1990). As long as a population remains intact, plants within a population maintain their genetic structure through rhizomatous regeneration and growth. However, if a population is reduced in number by severe fire (Bradley, 1984) or other disturbances that would displace whole plants, this study suggests that demographic recovery through outcrossing may be slow. Seeds do not germinate readily in cultivation and have long stratification requirements (Smart and Minore, 1977), so it is unlikely that hand-planting seedlings currently represents a feasible technology. The rhizomatous habit may maintain individual genets particularly when environmental conditions do not favor flowering. However, after natural disturbance such as fire, *X. tenax* with an incompatibility system and copious pollen production as an attractant can ensure sufficient outcrossing to effect gene flow and remixing of alleles. In addition, by providing food that attracts numerous and diverse pollinators, *X. tenax* is assuming an important functional role in a montane pollinator system.

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