

FROM FLOWERING TO DISPERSAL: REPRODUCTIVE
ECOLOGY OF AN ENDEMIC PLANT,
ASTRAGALUS AUSTRALIS VAR. *OLYMPICUS* (FABACEAE)¹

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Astragalus australis var. *olympicus* is an endemic plant of the Olympic Mountains, Washington. It is considered a Species of Concern by the U.S. Fish and Wildlife Service. This study focused on the reproductive biology of the plant from flower production through seed germination to identify possible weak points that might contribute to its rarity and impede its conservation. Most plants produced a large mean number of flowers and ovules (314.8 and 4106, respectively), but relatively few of these formed fruits and seeds (25.8 and 3.8%, respectively). In decreasing importance, ovules in fruits were lost to predation, seed abortion, and lack of fertilization. The percentages of these fates differed among sites and years. Excluding pollinators by bagging flowers reduced fruit set by ~50%, but seed set per fruit and seed mass were unaffected. Germination was affected by scarification, temperature, and moisture availability. About 11% of seeds damaged by predispersal seed predators (weevil larvae) remained viable and were released from dormancy. I hypothesize that predispersal seed predation (over 80% at one site) has a negative effect on population growth. Conservation of this species could benefit from improved fruit set and decreased seed predation.

Key words: *Astragalus australis* var. *olympicus*; endangered species; conservation; Fabaceae; ovule fate; pollination; seed predation; *Tychius*; spatio-temporal variability.

Knowledge of reproduction is crucial to our understanding of the causes of rarity and for conservation of rare plant taxa (e.g., Drury, 1974, 1980; Harper, 1979; Ayensu, 1981; Kruckeberg and Rabinowitz, 1985). Herbaceous perennials that do not reproduce vegetatively depend on seeds to recruit new individuals into populations. In order for new plants to establish in a population, flowers must be pollinated to form fruits, ovules must be fertilized, sustained with nutrients, and escape predation to form viable seeds, and seeds must be dispersed to suitable substrates for growth, where they must germinate. Any weak link or break in this chain of events curtails a plant's ability to reproduce and, if constant over space and time, may contribute to a species' rarity and impede its conservation.

Many workers have investigated single or combined components of the reproductive ecology of rare plants, such as flowering frequency and vegetative reproduction (Morely, 1982), pollination (Macior, 1978; Karron, 1987; Deyrup and Menges, 1997), breeding system (Planisek, 1983; Karron, 1989), seed predation (Gisler and Meinke, 1997), seed germination (Baskin and Quarterman, 1969; Baskin and Baskin, 1979, 1997; Halse, 1988; Jacobs, 1993; Clark, Ingersoll, and Finley, 1997; Florance, 1997), breeding system and germination (Clampitt, 1987; Menges, 1995), and seed production and predation (Menges,

Waller, and Gawler, 1986). However, few studies of rare plants describe the limits to reproduction at all stages from flower production through dispersal of germinable seed (Massey and Whitson, 1980; but see Crowder, 1978; Pavlik, Ferguson, and Nelson, 1993). The goal of this study was to describe the reproductive ecology of *Astragalus australis* (L.) Lam. var. *olympicus* Isely, a local endemic of the Olympic Mountains, Washington (Buckingham et al., 1995), from flowering to seed dispersal to increase baseline information on its biology and identify deficiencies in its capacity to reproduce.

Astragalus australis var. *olympicus* is a Species of Concern with the U.S. Fish and Wildlife Service, and is considered by the Washington Natural Heritage Program to be threatened (WNHP, 1997). Only ~4000 individuals in five populations are known (Sheehan and Kaye, 1986). Plants occur on gravelly subalpine slopes from 1450 to 1800 m where vegetative cover is typically sparse, revealing bedrock and mineral soil. Associated species include *Allium crenulatum*, *Crepis nana* ssp. *ramosa*, *Festuca idahoensis* var. *oregona*, *Geum triflorum* var. *turbinatum*, *Lomatium martindalei* var. *flavum*, and *Phlox diffusa* var. *longistylis*, among others (Kaye, 1989). The high ridges and mountain tops where the plant typically grows are free of snow in early spring.

Despite its rarity, conservation status, and location inside a National Park, little information is available on the reproductive ecology of *Astragalus australis* var. *olympicus*. It is a long-lived, herbaceous perennial that holds its overwintering buds just below the soil surface (Kaye, 1989). The species does not reproduce vegetatively (personal observation), which is typical of most *Astragalus* species (Barneby, 1964). Timing of germination in the field is unknown. Depending on the year and location, plants usually begin to bloom in early June and peak in late June. By mid-July, most plants are past flowering. A

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few fruits dehisce as early as late July while still on the plant, but most seed dispersal occurs in September after fruits have fallen. The seeds lack appendages attractive to animals, but some remain attached to dehisced and fallen fruits that can be wind-blown several metres and perhaps farther (personal observation). Seed production and insect seed predators were observed in 1981 at a few sites, and the identity of the predators was tentatively suggested as “possibly bruchid beetles” (Buckingham, 1981).

The objective of this research was to describe the reproductive ecology of *Astragalus australis* var. *olympicus* at various stages from flower production to seed germination. Specifically, I attempted to answer these questions: Do plants produce flowers, fruits, and seeds at all sites? Are potential insect pollinators present, and do plants self-pollinate without them? Do pollinators and/or resources limit reproduction? What percentage of ovule loss in fruits can be attributed to lack of fertilization, seed abortion, and/or predispersal predation? What organism (or organisms) are responsible for predispersal seed predation? Do seeds possess highly specific germination requirements? I performed field observations at three sites and controlled experiments to address these questions.

MATERIALS AND METHODS

Study sites—*Astragalus australis* var. *olympicus* is confined to five population clusters within a 4 × 21 km east-west belt in the northeastern Olympic Mountains, Clallam County, Washington. Three subpopulations, each with several hundred plants, were selected to represent the known ecological and geographic breadth of the taxon: Hurricane Hill (47°59'50" N, 123°32'56" W) at 1460 m, the westernmost population; Mount Angeles (48°00'30" N, 123°27'30" W) at 1650 m, a population near the distribution center; and Blue Mountain (47°57'17" N, 123°15'30" W) at 1770 m, a high-elevation eastern population.

Fruit set and ovule fate—Twenty-five plants were chosen at random from each population in August of 1987 and 1988, when fruits were nearly mature. One raceme on each plant was selected at random and covered with a nylon mesh bag so that dispersed fruits were captured as they fell. Bags were collected in early September of 1987 and 1988 before pods dehisced. The number of racemes, flowers, and fruits were counted on each plant in 1988 only. I determined flower initiation by counting the number of pedicel scars on each rachis. In 1988, five additional individuals were selected at random in each population and included in counts of total raceme, flower, and fruit production per plant. Loss of bags reduced harvest sample sizes to 18 plants at Blue Mountain and 24 at Hurricane Hill in 1987.

Five pods, or less if fewer matured, were randomly selected from each harvested raceme. Pods were opened and examined under a dissecting microscope. Unfertilized ovules in *Astragalus* (Karron, 1989) and other legumes (Cooper and Brink, 1940; Schaal, 1980) are distinguishable in mature fruits as unexpanded, membranous ovules. Ovules were counted and scored into four categories: filled seed, if fully developed and plump; depredated, if any tissue was eaten; aborted seed, if the seed coat was shriveled; and unfertilized, if ovules were <0.5 mm in diameter and membranous. Some fertilized ovules may have aborted without expanding first. Therefore, the percentage of aborted seeds may have been underestimated and the percentage of unfertilized ovules may have been overestimated. In 1988, depredated seeds were classified according to the volume of seed tissue removed: <5, 5–25, and >25%.

I used one-way analysis of variance (ANOVA) to test for a site effect on number of inflorescences, flowers, mature fruits, ovules, filled seeds,

and percentage fruit set per plant in 1988. Ovules per plant were calculated by multiplying the number of flowers on a plant by the mean number of ovules per fruit on that plant. Similarly, the number of seeds per plant was calculated as the product of the number of fruits and mean seeds per fruit on each plant. Before analysis, all data were transformed to meet the assumptions of ANOVA and linear regression. Data for number of flowers, fruits, and racemes per plant and number of ovules per plant were square-root transformed, and seeds per fruit were log-transformed. The arcsine square-root transformation (Sokal and Rohlf, 1981) was applied to percentage of filled seed, depredated seed, aborted seed, and unfertilized ovules per pod, and percentage fruit set per plant.

Nested ANOVA (SAS, 1985: general linear model) was used to test for site and year effects on percentage of ovules per fruit producing good seed, depredated seeds, aborted seeds, and unfertilized seeds after arcsine square-root transformation. The seed-predation data for Hurricane Hill were omitted from the nested ANOVA because seed predation was so infrequent there that the data were neither normal nor homoscedastic, even after transformation. Tukey's Honest Significant Difference (HSD) multiple range test (STSC, 1987) was applied to all one-way ANOVAs in which *F* was significant ($P \leq 0.05$). I used linear regression to test for an association of percentage seed set (filled + damaged seed) with number of fruits produced per raceme, and number of fruits per plant with number of flowers per plant.

Pollination—A pollinator-exclusion experiment (Kearns and Inoué, 1993) was conducted to determine whether insect pollinators were necessary for fruit and seed production. Twenty reproductive plants with over ten inflorescences each were randomly selected in early July of 1988 (a late year for flowering) from near the center of the Blue Mountain summit population. On each plant, two inflorescences in bud (all flowers unopened and therefore unvisited by pollinators) were randomly selected. One was covered with a fine-mesh nylon bag to exclude insect pollinators and the second served as an open-pollinated control. Controls were not manipulated while in bud or flower. After fruits were initiated, controls were covered with the same material as the bagged inflorescences to capture pods as they dispersed from the rachis. All inflorescences were harvested in late August of 1988. Loss of bagged inflorescences to vandalism and animals reduced the total paired sample size to 15.

Percentage fruit set, average percentage seed set, and average seed mass were determined for each inflorescence. To account for greater seed predation in controls, I assumed that damaged seeds would have formed normal seeds had they not been eaten. This assumption is supported by the fact that eggs of seed predators do not hatch until developing seeds are nearly full size. I used a paired *t* test to test the null hypothesis that there was no difference between treatments. Seed mass data were log-transformed prior to analysis.

Insect visitors to flowers were collected, when possible, at each site. No effort was made to quantify pollinator efficiency. Instead, to establish the presence of potential pollinators, the identity and ability of insect visitors to work the legume floral mechanism (Green and Bohart, 1975; Faegri and van der Pijl, 1979) were observed.

Predispersal seed predators—Several *Astragalus australis* var. *olympicus* plants at each population were inspected at peak flowering to observe and catch adult insects laying eggs in buds, flowers, and newly initiated fruits. Representatives of all insects found feeding on any plant part were collected. To determine whether adult insects observed ovipositing on *A. australis* var. *olympicus* were the same species as the larvae observed eating seeds, the larvae were reared. Seven infructescences with five to ten pods each were collected at Blue Mountain in mid-July of 1987, when larval seed predators were abundant in pods. Each group of fruits was placed on the surface of fine gravel in a foam cup, left at room temperature until October 1987, then refrigerated at

TABLE 1. Mean \pm 1 SE inflorescence, flower, fruit, ovules, and seed production per plant and percentage fruit set in 1988 at three populations. Values in rows followed by different superscripts differed at $\alpha = 0.05$ (Tukey's HSD). Ovule means were not compared because there was no site effect in ANOVA. Data were transformed for ANOVA (see text).

	Population			Mean	df	F	P
	Blue Mountain	Mount Angeles	Hurricane Hill				
Inflorescences	21.5 \pm 4.7 ^a	28.2 \pm 2.6 ^b	13.3 \pm 2.5 ^a	20.7 \pm 1.9	2, 91	8.55	<0.0001
Flowers	308.9 \pm 85.5 ^{ab}	406.3 \pm 47.2 ^a	239.3 \pm 50.9 ^b	314.8 \pm 36.2	2, 91	4.98	0.009
Fruits	32.8 \pm 8.8 ^a	49.5 \pm 8.5 ^{ab}	82.76 \pm 15.8 ^b	56.2 \pm 6.9	2, 91	3.53	0.033
Ovules	3993 \pm 1122	4043 \pm 569	4282 \pm 862	4106 \pm 508	2, 72	0.53	0.59
Seeds	50.3 \pm 16.1 ^a	58.5 \pm 30.7 ^a	355.0 \pm 99.4 ^b	154.6 \pm 35.1	2, 72	17.36	<0.0001
% fruit set	15.9 \pm 3.4 ^a	13.9 \pm 1.7 ^a	45.1 \pm 4.5 ^b	25.8 \pm 2.0	2, 91	20.65	<0.0001

7°C until March of 1988. At this time, the pods and gravel were inspected for larvae and adults.

To determine whether the seed predator found on *A. australis* var. *olympicus* was host specific or present on other legumes, additional fruits of all legume species growing near the study sites were inspected in 1987 and 1988.

Germination—Two germination experiments were conducted to assess the viability and germination requirements of *Astragalus australis* var. *olympicus* seeds. Separate experiments were conducted to test (1) the effect and interaction of moisture availability and temperature on germination, and (2) the effect of predation class and scarification on germination. All seeds used in experiment 1 were collected at Blue Mountain and Mount Angeles in 1987, stored in paper envelopes at 7°C, pooled, and used within 9 mo of collection. Seeds for experiment 2 came from the seed predation sampling at Blue Mountain and Mount Angeles in 1988.

Previous studies (Kaye, 1997) indicate that most seeds of this species require scarification to germinate, and once scarified they germinate equally well under fluorescent light or darkness. Therefore, all seeds were scarified before testing, except where otherwise noted. Seeds were placed on 5 \times 5 cm cellulose germination pads ("Kimpak") moistened with distilled water (except in experiment 1) in 10-cm petri plates. Germinators with 8 h of fluorescent light were used, and petri plate positions were rotated on the shelves every second day.

In experiment 1, three constant temperatures (5°, 15°, and 25°C) and one alternating temperature (15°/25°C) were combined with four osmotic potentials (0, -0.5, -1.0, and -1.5 MPa) in a 4 \times 4 factorial design. Osmotic potential was included as a factor because it affects moisture availability to seeds, and can be used to emulate a moisture gradient. Solutions with the above osmotic potentials were prepared by dissolving appropriate amounts of polyethylene glycol (PEG 8000) in distilled water following the procedure of Michel (1983). Seeds were placed on germination pads, each saturated with 15 cm³ of solution. Three replicates (or pseudoreplicates, because they were placed in the same germinator) of 20 seeds each were allotted to each treatment. The number of germinated seeds was counted daily for 2 wk to determine days to 50% of maximum germination (a measure of rate independent of the total number that germinate) and total germination. Germination was defined as emergence of the radical 1 mm from the seed coat.

Experiment 2 used six replicates (or pseudoreplicates) of 50 seeds from each predation class (<5, 5–25, and >25% eaten). For comparison to depredated seeds, equal replicates of nondamaged scarified and unscarified seeds were included. After 2 wk, I counted the number of living seedlings with intact radicles, which I defined as viable. The fraction of seeds scored as "depredated" that were actually viable was estimated by multiplying the proportion of seeds scored as damaged in each predation class by the percentage viability of each predation class, and summing:

percentage viable

$$= [(Pd_{<5\%} \times Pv_{<5\%}) + (Pd_{5-25\%} \times Pv_{5-25\%}) + (Pd_{>25\%} \times Pv_{>25\%})] \times 100$$

where Pd equals the proportion damaged and Pv the proportion viable in each predation class.

All germination counts were converted to percentages before analysis. No transformations were necessary to meet the assumptions of ANOVA. In experiment 1, two-way ANOVA was used to test for osmotic potential and temperature effects and interactions of these factors. Tukey's HSD test was used to compare means. In experiment 2, one-way ANOVA was used to test for a predation class or scarification treatment effect, and means were compared with a protected LSD multiple range test (STSC, 1987).

RESULTS

Fruit set and ovule fate—Plants produced flowers and seeds at each site, but there were significant site effects on inflorescence, flower, fruit, and seed production, and fruit set per plant in 1988 (Table 1). Although plants at Hurricane Hill produced the fewest racemes and flowers, they yielded the most fruits, most seeds, and highest fruit set (Table 1). Conversely, Mount Angeles plants produced the most racemes and flowers, but only intermediate numbers of fruits, the fewest seeds, and lowest fruit set (Table 1).

Within fruits, there were also significant site-to-site differences in percentage of ovules producing filled seed ($F_{2,138} = 24.62$, $P = 0.0009$), depredated seed ($F_{1,90} = 6.65$, $P = 0.011$), aborted seed ($F_{2,138} = 40.78$, $P < 0.0001$), and unfertilized ovules ($F_{2,138} = 17.02$, $P < 0.0001$), but differences between 1987 and 1988 were detected only in filled seed ($F_{1,138} = 11.67$, $P < 0.0001$) and depredated seed ($F_{1,90} = 24.73$, $P < 0.0001$). Fruits at Hurricane Hill lost the highest percentage of seeds to lack of fertilization and seed abortion, but maintained the highest seed set, presumably because of extremely low predispersal seed predation (Fig. 1).

Seed predation at Blue Mountain and Mount Angeles claimed the largest percentage of ovules in both years (39.3% in 1987 and 60.9% in 1988 at Blue Mountain, 28.4% in 1987 and 49.2% in 1988 at Mount Angeles), suggesting that seed predation is a more significant limiting factor to seed production than are seed abortion and lack of fertilization at these sites (Fig. 1). In contrast, very few seeds were eaten by predispersal seed predators at Hurricane Hill. In the absence of appreciable seed predation, the greatest loss of ovules at Hurricane Hill was

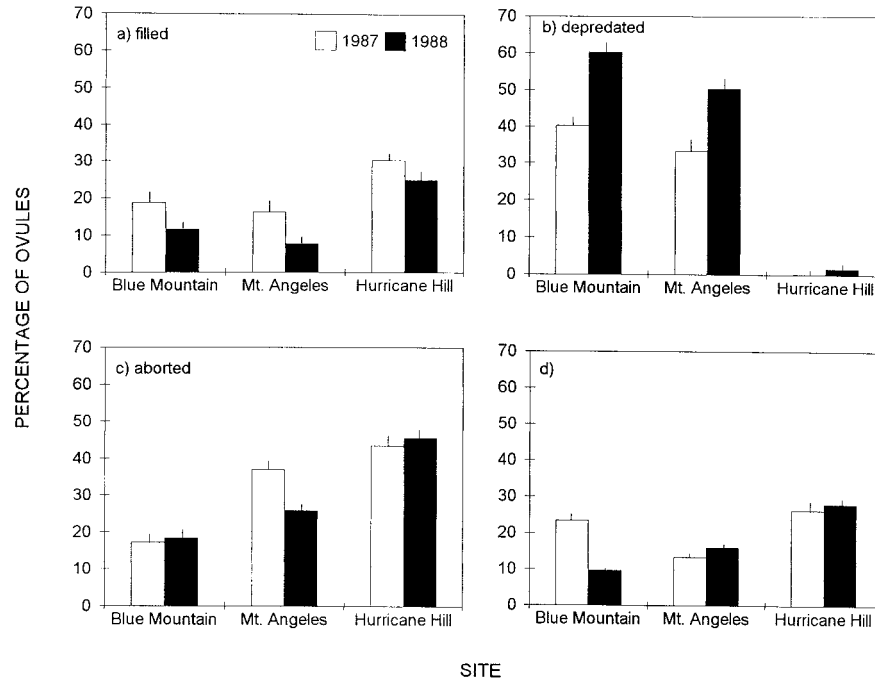


Fig. 1. Ovule fates at Blue Mountain, Mount Angeles, and Hurricane Hill in 1987 and 1988. Percentage of ovules (mean + 1 SE) yielding (a) filled seed, (b) depredated seed, (c) aborted seed, and (d) unfertilized ovules.

to seed abortion. Ovule loss due to lack of fertilization was almost always the smallest component over all sites both years, with the exception of Blue Mountain in 1987, when unfertilized ovules exceeded aborted seeds (Fig. 1).

The number of fruits matured per plant was strongly and positively associated with the number of flowers per plant at Blue Mountain ($r^2 = 0.82, P < 0.0001$), Hurricane Hill ($r^2 = 0.90, P < 0.0001$), and weakly correlated at Mount Angeles ($r^2 = 0.21, P = 0.011$). When all sites were pooled the correlations were modest, but highly significant ($r^2 = 0.59, P < 0.0001$). The regression for mean number of fruits per inflorescence with seed set per fruit was significantly negative only when all sites were pooled ($r^2 = 0.41, P < 0.0001$), not within sites ($0.35 > r > -0.36, P > 0.05$).

Pollination—Fruit set was significantly reduced ($t_{14,0.05}$

$= 2.74, P = 0.016$), but seed set per fruit was not significantly affected ($t_{14} = -0.23, P = 0.82$) when insect pollinators were excluded from inflorescences at Blue Mountain. Also, there was no treatment effect on seed mass ($t_{12} = -0.56, P = 0.58$). Even though bagging lowered mean fruit set by almost half, from 23.3 to 12.2%, some fruits were formed in the absence of pollinators. Seed set per fruit and seed mass were unchanged (Fig. 2).

Insects capable of tripping the floral mechanism of *Astragalus australis* var. *olympicus* were present at Blue Mountain and Mount Angeles. I made no observations of insects at the Hurricane Hill site when plants were in peak bloom. Bumble bees (*Bombus appositus*, *B. bifarius nearcticus*, and *B. occidentalis occidentalis*) and a solitary bee (*Osmia* sp.) were the dominant flower visitors at Blue Mountain, and one tachinid fly was also collected.

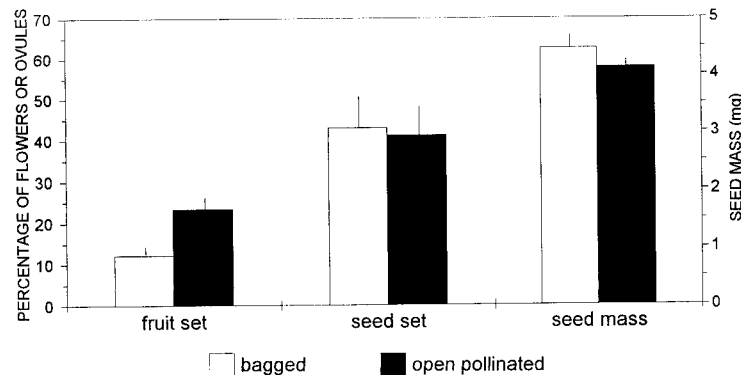


Fig. 2. Percentage fruit and seed set and seed mass in bagged vs. open-pollinated inflorescences (mean + 1 SE) of *Astragalus australis* var. *olympicus* at Blue Mountain.

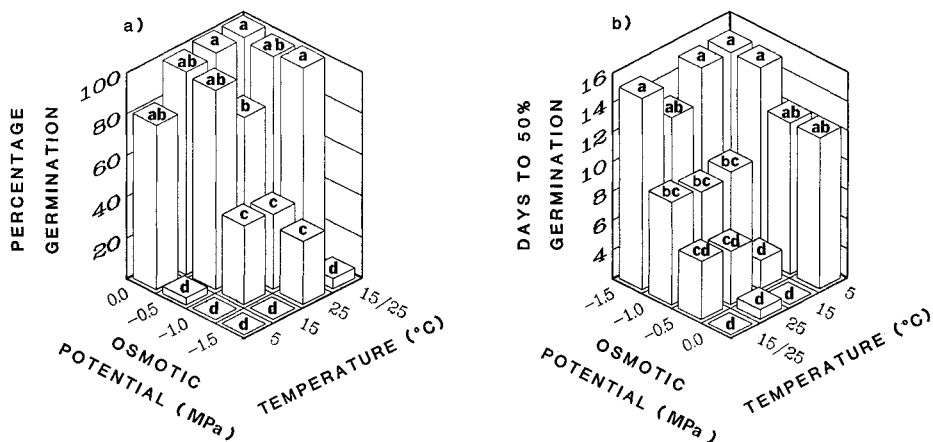


Fig. 3. Effects of osmotic potential and temperature on (a) percentage germination and (b) days to 50% of maximum germination. Axis directions are reversed in (b) so that all bars can be seen. Bars with the same letter do not differ at the 95% level of probability. Two-way ANOVA indicated a significant osmotic potential \times temperature interaction.

At Mount Angeles, only solitary bees (*Anthidium tenuiflorae* and *Megachile melanophaea calogaster*) were observed. Based on limited observations, ~ 6 h at each site, I found no overlap in species composition between populations. All visitors except the tachinid fly could manipulate the flowers.

Predispersal seed predators—Only one species of adult insect, a weevil (*Tychius* sp.), was common on buds, flowers, and immature fruits of *Astragalus australis* var. *olympicus* in the spring of 1987. Other insects were encountered infrequently, such as the lygaeid bug *Lopidea* sp. and a pyralid caterpillar, which was apparently responsible for the minimal predispersal seed predation at Hurricane Hill. Larvae reared from fruits produced adult *Tychius* weevils only. The weevil larvae apparently pupate in the soil beneath the host plants because all reared adults were found in small rock cases in the gravel, not in the fruits.

The weevil found on *Astragalus australis* var. *olym-*

picus was also observed on *Oxytropis campestris* and *O. viscida*. The fruits of other members of the Fabaceae contained different predispersal seed predators. *Lupinus latifolius* var. *subalpinus* and *Hedysarum occidentale* hosted larvae of muscoid flies, and *Lathyrus nevadensis* suffered losses from a tortricid caterpillar.

Germination—*Astragalus australis* var. *olympicus* seeds germinated over a variety of temperatures and osmotic potentials. Moisture availability and temperature significantly affected percentage germination ($F_{3,32} = 263.91$, $P < 0.0001$ and $F_{3,32} = 143.40$, $P < 0.0001$, respectively) and days to 50% germination ($F_{3,32} = 161.25$, $P < 0.0001$ and $F_{3,32} = 64.37$, $P < 0.0001$, respectively), and there was a significant moisture \times temperature interaction for both response variables ($F_{9,32} = 29.61$, $P < 0.0001$ and $F_{9,32} = 14.14$, $P < 0.0001$, respectively). At 5°C, even a moderate decrease in osmotic potential drastically reduced germination percentage (Fig. 3a) but not rate (Fig. 3b). At higher temperatures, more seeds germinated faster at high water potentials (Figs. 3a, b). Peak germination percentage occurred at 15°/25°C alternating temperatures and at 0.0 MPa osmotic potential (distilled water). Germination was fastest at 15°C constant temperature and 0.0 MPa. In general, total germination and rate decreased as water potential and temperature decreased.

The effect of seed predation on germination depended on the amount of seed tissue eaten. A small amount of tissue removal (<5%) appeared to satisfy the scarification requirement of some seeds, but most seeds with larger amounts of tissue removed (5–25% and >25%) were killed (Fig. 4). The seed predation percentages reported for Blue Mountain and Mount Angeles, therefore, overestimated the percentage of ovules killed.

The fraction of seeds scored as depredated that were actually viable was 11.2%, based on estimates of the viability of seeds in each damage class. Of all seeds damaged by weevils in 1988, 6.7% were in the <5% class, and 92.2% of these were viable; 10.4% were in the 5–25% class, and 28.3% were viable; and 82.8% were in the >25% tissue removal class, and 2.5% were viable.

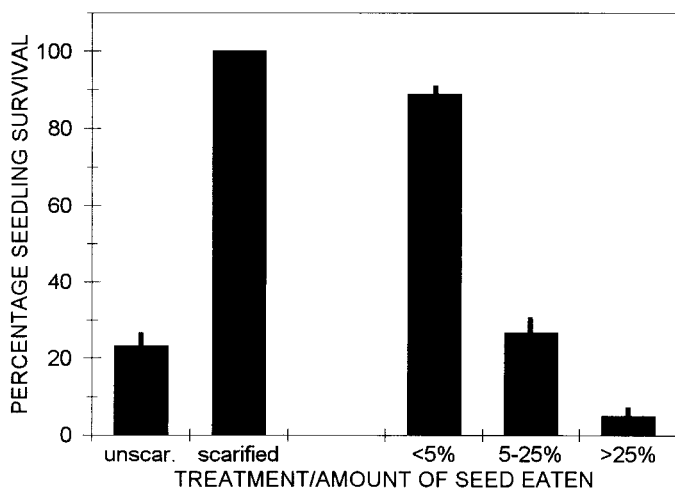


Fig. 4. Effects of predation intensity and scarification on seedling survival after 2 wk (mean \pm 1 SE). See text for explanation of predation classes. All means differed at the 95% level of probability.

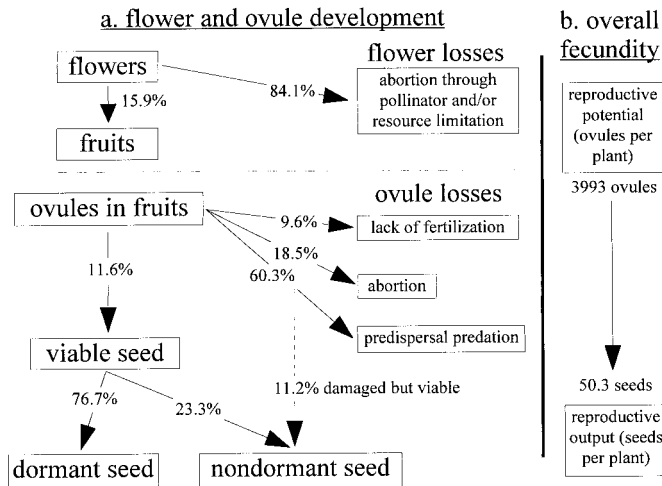


Fig. 5. Flow charts of (a) flower and ovule development describing avenues of observed reproductive losses and successes for *Astragalus australis* var. *olympicus*, and (b) overall fecundity enumerating the number of ovules on an average plant that mature into viable seeds. The dashed arrow indicates a pathway in which a portion of damaged seeds are released from dormancy and remain viable. Values shown with arrows are example data from Blue Mountain (1988) and are derived from Table 1, Figs. 2 and 4, and the text.

The distribution of 1988 predation intensities did not differ significantly between Blue Mountain and Hurricane Hill ($P > 0.14$ in t tests). Therefore, ~11% of all seeds scored as depredated at both sites in 1988 (and probably 1987) were viable. These seeds were also released from water-impermeable seed dormancy.

DISCUSSION

Limits to fruit and seed production—*Astragalus australis* var. *olympicus* plants have considerable reproductive potential. But in spite of the fact that an average plant produced over 300 flowers and 4100 ovules, fewer than 60 fruits and 150 seeds per plant matured in 1988. Using flow charts (Fig. 5) to integrate information from different parts of this study illustrates the reproductive path from flowers to seeds: plants lost most of their reproductive potential through abortion of flowers. Ovule loss in fruits was dominated by weevil damage at two sites, followed by seed abortion, then lack of fertilization. Seed abortion also exceeded lack of fertilization where weevils were absent (Hurricane Hill). Seed viability was near 100% and the majority were dormant, although a small percentage germinated readily and some weevil-damaged seeds were viable.

Production of more flowers than fruits and more ovules than seeds has been associated with insufficient pollination, resource limitation, selective abortion of fruits and seeds, and predation (Stephenson, 1981). Plants that produce more flowers than fruits may have been selected to do so because large floral displays attract pollinators, allow plants versatility in the face of variable pollinator and resource availability, and/or improve male fitness of hermaphroditic flowers (Stephenson, 1981; Sutherland, 1986). There was a significant linear relationship between the number of flowers and number of fruits per *Astragalus australis* var. *olympicus* plant at each site and when

all sites were pooled, which is consistent with the pollinator and resource limitation hypotheses. Larger floral displays should mature more fruits because they attract more pollinators and represent larger energy investments in reproduction (Udovic, 1981). For example, as young *Yucca whipplei* fruits compete for limited resources many abort and a nearly constant proportion of flowers result in fruits (Udovic and Aker, 1981). Campbell (1987) has shown that pollinators, at least, limit fruit production in *Veronica cusickii* near my study sites. My data were insufficient to test these hypotheses, but they suggest that both pollinators and resources limited fruit set in *A. australis* var. *olympicus*.

Once a flower is pollinated and a fruit is initiated, however, resource availability may limit seed production within that fruit. Abortion of developing seeds of *Astragalus australis* var. *olympicus* accounted for about one-third of ovule losses from fruits in 1987 and 1988 at all sites combined. Studies of nonrandom abortion in other legumes suggest that resources limit seed production more often than pollinator availability or genetic quality (Lee and Bazzaz, 1982, 1986; Hossaert and Valero, 1988), although it is not known whether this is generally true. In my study, a negative correlation between the number of fruits matured per raceme and seed set per fruit suggests that resources limited seed set, although this correlation was significant only with all sites pooled rather than within each site. An insufficient amount of resources divided among an increasing number of fruits may have caused each fruit to mature fewer seeds. A controlled experiment is needed to confirm this hypothesis. Water, especially, may have been limiting because of the gravelly substrate and summer drought typical of *A. australis* var. *olympicus* habitat.

Predispersal seed predation in *Astragalus australis* var. *olympicus* was locally intense, damaging 36 and 55% of ovules in 1987 and 1988, respectively, at Blue Mountain and Mount Angeles combined; it was almost nil at Hurricane Hill, however, showing that it can fluctuate widely through both space and time. It is unknown why seed weevils were missing at the Hurricane Hill population, but the relatively low elevation of this site, lack of *Oxytropis* species as alternate hosts (personal observation), or chance could have contributed to its absence. Predation levels exceeded 80% of developed, nonabortive ovules at Blue Mountain in both years. These predation intensities and variations are not unusual in more common *Astragalus* species (Green and Palmblad, 1975; Youtie and Miller, 1986). In fact, some amount of seed predation may be the norm in widespread seed-producing plants (Auld, 1983), including those in alpine areas (T.N. Kaye, personal observation). However, heavy seed predation in *A. australis* var. *olympicus* is inconsistent with the hypothesis that rarity may be an escape from predation (Feeny, 1976; Landa and Rabinowitz, 1983). On the other hand, rarity may take many forms (Rabinowitz, 1981), and a patchy but locally abundant distribution (as in *A. australis* var. *olympicus*) may make a taxon more susceptible to predation than a sparse distribution, because larger populations of host-specific (and some generalist) seed predators can be supported (Menges, Waller, and Gawler, 1986).

Common plants may encounter predation more often

and thus invest more energy in chemical defenses than rare plants (Menges, Waller, and Gawler, 1986). Predispersal seed predation can limit plant recruitment (Louda, 1982, 1983) and may contribute to the local rarity of some species (Greig-Smith and Sagar, 1981). Harper (1981) speculates that host-specific herbivores do not threaten their hosts with extinction because predator and prey remain in equilibrium. *Tychius* larvae were found in fruits of two native species of *Oxytropis*, a genus closely related to *Astragalus*, but not in any other adjacent legumes, suggesting that the weevil is neither a generalist nor completely host-specific. Whether or not predispersal seed predation affects recruitment in *A. australis* var. *olympicus* populations is unclear, but it seems unlikely to drive *A. australis* var. *olympicus* to extinction because some sites and years partially escape seed damage. Pollinator and resource availability probably interact to limit fruit set, but once fruits are initiated, the limitations to seed production appear to rank in this order: predispersal seed predation (if weevils are present) > resources (water?) > pollinators.

Breeding system—Bumble bees and solitary bees were the most common visitors to *Astragalus australis* var. *olympicus* flowers at Blue Mountain and Mount Angeles. These are typical pollinators of rare and common species of *Astragalus* (Green and Bohart, 1975; Karron, 1987) and other alpine legumes (Shaw and Taylor, 1986). They were capable of tripping the floral mechanism and were relatively faithful to *A. australis* var. *olympicus* (personal observation). Curiously, none of the insect visitors observed at Blue Mountain were seen at Mount Angeles, and vice versa, despite the fact that observations were conducted at the same time of year. Differences in elevation and habitat in and adjacent to the *Astragalus* populations or inadequate observations may account for this.

Exclusion of insect pollinators from *Astragalus australis* var. *olympicus* inflorescences reduced fruit set per inflorescence, but not seed set per fruit or seed mass, suggesting that plants are typically outcrossed, but genetically self-compatible. A mechanical barrier, not a genetic one, may have interfered with self-pollination. Peristigmatic hairs, for example, block self-pollination in other genetically self-compatible legumes, such as lupines (Juncosa and Webster, 1989). A mechanical barrier that failed occasionally could allow adequate pollination for full seed set while still reducing fruit set and produce the pattern observed in this study. Stebbins (1957) asserts that rare plants are likely to be self-compatible. This may be true for *Astragalus*, where some common species are self-incompatible (Green and Bohart, 1975) and their rare congeners set selfed seed freely (Karron, 1989). Inbreeding depression in seedlings was not tested in *A. australis* var. *olympicus*, but it limits their growth in other rare *Astragalus* (Karron, 1989).

Self-compatibility may be the result of natural selection during repeated population bottlenecks (or pollinator failures). When population sizes are small (or gene flow is reduced), genetic load may be largely eliminated, thus reducing inbreeding depression (Lande and Schemske, 1985; Schemske and Lande, 1985) and increasing self-compatibility. Therefore, self-compatibility in *Astragalus australis* var. *olympicus* is consistent with the theory that

small populations survived in the Olympic Mountains in Pleistocene glacial refugia (Buckingham et al., 1995) and suggests that the taxon might be able to survive future bottlenecks.

Germination—Seeds of *Astragalus australis* var. *olympicus* did not possess highly specific germination requirements. Percentage and rate of germination generally decreased with decreasing temperature and moisture availability, but some seeds were able to germinate even near environmental extremes. Germination percentage and rate at 25°C and -1.5 MPa were similar to those recorded for *Sarcobatus vermiculatus* (Romo and Edelman, 1985), a halophyte. At low water potentials (-1.0 to -1.5 MPa), percentage germination of *A. australis* var. *olympicus* was greater than in one (Everitt, 1983) but less than in two other (Redente, 1982; Everitt, 1983) common legumes. In the presence of adequate moisture, seeds of *A. australis* var. *olympicus* germinated well at all temperatures tested, even 5°C, despite Amen's (1966) observation that alpine seeds generally fail to germinate below 10°C.

Most *Astragalus australis* var. *olympicus* seeds required scarification of the seed coat to break dormancy, a trait common in this genus (Baskin and Quarterman, 1969) and many other legumes (e.g., Rolston, 1978; Grime et al., 1981; Baskin and Baskin, 1988). A variety of phenomena may scarify seeds naturally, such as damage by insects, ingestion by mammals or birds, frost heave, solifluction, wind (Amen, 1966), and even invasion by fungal hyphae (Gogue and Emino, 1979). Some *A. australis* var. *olympicus* seeds attacked by weevil larvae were not killed, but scarified and left alive, so that ~11% of all seeds eaten by larvae were released from dormancy and produced healthy seedlings in a germinator. Predispersal seed scarification has not been reported previously. It may or may not be beneficial to seedling recruitment. Early release from dormancy might confer an advantage on some individuals by allowing them to germinate and begin growth early, improving their competitive ability (Harper, 1977). The same process, however, might put those individuals at a disadvantage by causing them to germinate under environmental conditions that do not favor seedling survival, a situation perhaps normally avoided by dormant seeds (Harper, Lovell, and Moore, 1970; Rolston, 1978; Kaye, 1997). The majority of germination of normal seeds of this species probably occurs in spring, after seeds have been scarified and temperatures have increased.

Conclusion—All reproductive processes, from flowering to germination, functioned adequately to allow dispersal of germinable seed into *Astragalus australis* var. *olympicus* populations, but ovule fate had significant spatial and temporal variation. The weakest points in the sequence from anthesis to dispersal appeared to be flower abortion and locally intense predation by weevil larvae. Where weevils were absent, however, abortion was the most common ovule fate. Limitations to seed production in any single year are unlikely to lead to permanent reproductive failure in this taxon, given that most individuals are iteroparous and long lived; 78–80% of individuals mapped at three sites in 1987 were still present in

1991 (unpublished data). I hypothesize that predispersal seed predation has a negative effect on population growth during years of intense seed loss. Some *A. australis* var. *olympicus* populations occupy habitats prone to rock slides and frequent surface disturbances by introduced mountain goats (Kaye, 1989; Schreiner et al., 1994). Therefore, seed production is crucial for replacement of individuals within disturbed populations and dispersal to new sites. Conservation strategies for this rare taxon should evaluate factors that reduce fruit set, damage to seeds and established plants (e.g., weevils and goats, respectively), and restrict seedling recruitment. Other factors not considered here, but that are important for successful reproduction, such as postdispersal seed predation and availability of safe sites, may limit recruitment after the predispersal stages.

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