

AN ABSTRACT OF THE THESIS OF

Thomas N. Kaye for the degree of Master of Science in
Botany and Plant Pathology presented on December 19, 1989

Title: Autecology, Reproductive Ecology, and Demography of
Astragalus australis var. *olympicus* (Fabaceae)

Redacted for privacy

Abstract approved: _____

Kenton L. Chambers

The goal of this study was to gather information on the autecology, reproductive ecology, and population dynamics of *Astragalus australis* var. *olympicus* as a baseline for conservation strategies and to help explain its restricted range. Approximately four thousand individuals occurred in four known population centers in the Olympic Mountains, Olympic National Park, Clallam County, Washington. The populations were restricted to plant communities on calcareous substrates largely on southeast to southwest slopes above 1450 m. *A. australis* var. *olympicus* was absent from surrounding non-calcareous soils. Several characteristics of the physical environment and competition with associated plants influenced its distribution within calcareous sites. The relative importance of the physical environment and competition differed between plant community-types.

Most plants produced a large number of flowers and ovules, but relatively few of these formed fruits and seeds. In decreasing importance, ovules in fruits were lost to predation, seed abortion, and lack of fertilization. The absolute percentages of these fates differed from site to site and year to year. Excluding insects by

bagging flowers significantly reduced fruit set, but seed set per fruit was unaffected. After seeds were scarified to relieve dormancy, germination was sensitive to temperature and moisture availability, but some seeds germinated at environmental extremes. About 11% of the seeds damaged by predispersal seed predators (weevil larvae) remained alive and were released from dormancy.

Population sizes declined at three sites from 1985 to 1988, and a transition matrix model based on the 1987-88 transitions between seedling, vegetative, and reproductive life history stages projected this decline to continue. Therefore, further monitoring is warranted. Seedling survival was low and populations were dominated by reproductive individuals. Predispersal seed predation, damage by introduced mountain goats, and drought may have contributed to the observed decreases in population sizes. Historical reasons and an affinity for calcareous substrates seem to explain the rarity of the taxon, but minimal reproduction and slow or negative population growth may help maintain its restricted range and low numbers.

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Autecology, Reproductive Ecology, and Demography
of Astragalus australis var. olympicus (Fabaceae)

by

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AUTECOLOGY, REPRODUCTIVE ECOLOGY,
AND DEMOGRAPHY OF
ASTRAGALUS AUSTRALIS VAR. OLYMPICUS (FABACEAE)

CHAPTER I: INTRODUCTION

Astragalus australis (L.) Lam. var. olympicus Isley is a rare plant endemic to the Olympic Mountains, Washington, a phytogeographically isolated region distinguished by a number of endemic and disjunct taxa. About 4000 A. australis var. olympicus individuals are known, all within the boundaries of Olympic National Park (Sheehan and Kaye 1986). The plant is considered threatened by the Washington Natural Heritage Program, and is a Category 1 candidate for the federal endangered species list (U. S. Fish and Wildlife Service 1985). The impact of grazing and wallowing by introduced Mountain Goats (Oreamnos americanus) on subalpine vegetation has caused much concern in Olympic National Park (Pfitsch et al. 1983, Pfitsch 1985, Olympic National Park 1987). The presence of introduced mountain goats in A. australis var. olympicus habitat, a desire to meet any future crises concerning this plant with a sound knowledge of its biology, and a recognition that rare organisms may require management for their survival even in non-crisis times provided the incentive for this study.

Taxonomy--In 1900, A. D. E. Elmer collected what was to become the type specimen of Astragalus australis var. olympicus from the "Olympic Mountains, Clallam County" (Elmer 2531). Two years later,

John Storrs Cotton published a description of A. olympicus based on this specimen (Cotton 1902). However, this name had already been applied to two species, one in Greece (Pallas 1800) and the other in Armenia (Bunge 1869), so Jones (1923) legitimately substituted A. cottonii ("A. cottoni") for A. olympicus in his revision of the genus. At this time it was clear to Jones that A. cottonii was closely related to A. aboriginum Richards., a species distributed in North America from arctic Alaska through the Rockies to Utah, and as far east as Gaspé County, Quebec. Astragalus aboriginum, however, is related to A. australis (L.) Lam. of Eurasia. Together they form a circumboreal complex that reaches across North America, Siberia, Mongolia, and northern Asia into the Carpathians, Alps, Apennines, and Pyrenees (Komarov 1946, Barneby 1964). In his monumental Atlas of North American Astragalus, Barneby (1964) welcomed Polunin's (1959) move to combine arctic forms of A. aboriginum with A. australis, and he agreed with Jones (1923) that A. cottonii might not be sufficiently different from A. aboriginum to deserve a specific rank, but he postponed nomenclatural changes until the taxonomy of the whole circumboreal complex was stable. Recently, all North American A. aboriginum were transferred to A. australis var. glabriusculus, except for A. cottonii, which was given the varietal designation A. australis var. olympicus (Isely 1983, 1984), placing it close to A. australis and returning to it Cotton's (1902) original epithet. The complete synonymy of the taxon is listed below:

Astragalus olympicus Cotton (1902) non Pallas (1800) nec Bunge
(1869);

A. cottonii Jones (1923);

Atelophragma cottonii (Jones) Rydberg (1928);

Astragalus australis (L.) Lam. var. olympicus (Cotton) Isely
(1983).

Distribution and phytogeography--There are four known population centers for Astragalus australis var. olympicus, each with one or more scattered subpopulations: Blue Mountain, Mount Angeles, Unicorn Peak, and Hurricane Hill (Fig. I.1). These populations lie in the northeastern corner of the Olympic Mountains, a key region in the phytogeographic history of the Olympic Mountains. Several of the ridges and peaks in this area may have served as glacial refugia for plants during Fraser glaciation and earlier Pleistocene glaciations (Buckingham, in prep.). The refugia were probably only one group in a series along the northern Pacific Coast of North America, including parts of Vancouver Island (Ogilvie and Ceska 1984). The Olympic Peninsula is bordered by the Pacific Ocean to the west, the Strait of Juan de Fuca to the north, and Hood Canal and Puget Sound on the east, while the Chehalis River flows westward along its southern front. Isolated by ice or water and inoculated with a refugial flora, the Olympic Mountains are now habitat for a legacy of over ten endemic plant species and varieties, and several disjunct taxa (Buckingham and Tisch 1979).

How Astragalus australis var. olympicus, or its precursor, reached the Olympic Mountains is an open question. The endemic and disjunct flora of the Olympic Mountains show affinities to circumboreal, eastern North American, western North American, and Coast Range balds

floras, indicating that past climate changes and migration routes were diverse (Buckingham in prep.). A. australis var. olympicus is similar in many respects to A. australis var. glabriusculus in the Rockies, but it has inflated seed pods only approached by some Alaskan forms of A. australis sensu lato (Barneby 1964, Isely 1983). Whether A. australis var. olympicus arose from northern or eastern stock is uncertain, but it seems likely that it reached the Olympic Peninsula through migration during a cool glacial period (Barneby 1964) as an off-shoot after the Eurasian progenitor entered North America through Beringia. The distributions of A. australis and Oxytropis viscida (also present in the Olympics and of Eurasian kinship) in America are so alike in their wide but interrupted ranges that Barneby (1964) suspects they followed similar migration routes at similar times, even yielding named or aberrant taxa in the same areas. O. viscida in the Olympic Mountains is deviant, but it has not been named as a distinct taxon (Buckingham and Tisch 1979).

Speciation through vicariance and reproductive isolation, rather than through long distance dispersal and isolation, is common in montane floras (Hickman 1968, Favarger 1972, Ives 1974, Stebbins 1982).

Astragalus australis var. olympicus may represent a relictual population of A. australis that existed in the Olympics in the Pleistocene, remained in refugia during glacial advances, and was stranded in suitable habitats as the climate subsequently changed and adjoining populations receded. Today it is a minor component of a "subalpine prairie association" concentrated in the northeast Olympics that is floristically more similar to the arid transition

zone of eastern Washington than the characteristic subalpine meadows of the Olympic and Cascade Mountains (Jones 1936, p. 26). It is restricted entirely to calcareous substrates (derived from sea-floor sediments [Tabor 1975]), a phenomenon common in A. australis throughout North America (personal observation of herbarium specimens, and Barneby 1964).

Mountain goats--Approximately twelve mountain goats were introduced to the Olympic Mountains in the 1920s, apparently to initiate a huntable population. However, Olympic National Park was created in 1938, and the goats have been protected from hunting ever since (Olympic National Park 1987). A recent goat census (Houston et al. 1986) of the Olympic Mountain Range over 1520-m estimated there to be 1175 ± 171 (S.E.) animals, and the National Park Service, considering the goats to be exotic species, has initiated an aggressive removal program to eliminate goats from the Park interior and reduce goat densities along the boundaries of the Park (Olympic National Park 1987).

Study goals--A knowledge of several facets of a species' biology may be the key to rare plant conservation (Massey and Whitson 1980). The goal of this study is to provide baseline information on the distribution and biology of Astragalus australis var. olympicus in Olympic National Park. In chapter II, the position of A. australis var. olympicus within local plant communities is described, and the influence of competition and the physical environment on its distribution are investigated through an autecological approach.

Chapter III deals with the reproductive ecology of *A. australis* var. *olympicus* in terms of pollination, fruit and seed set, seed predation, and germination. Population trends are described and modeled in chapter IV. It is hoped that this broad approach will contribute to the effective management of *A. australis* var. *olympicus*, and provide insight into reasons for its rarity.

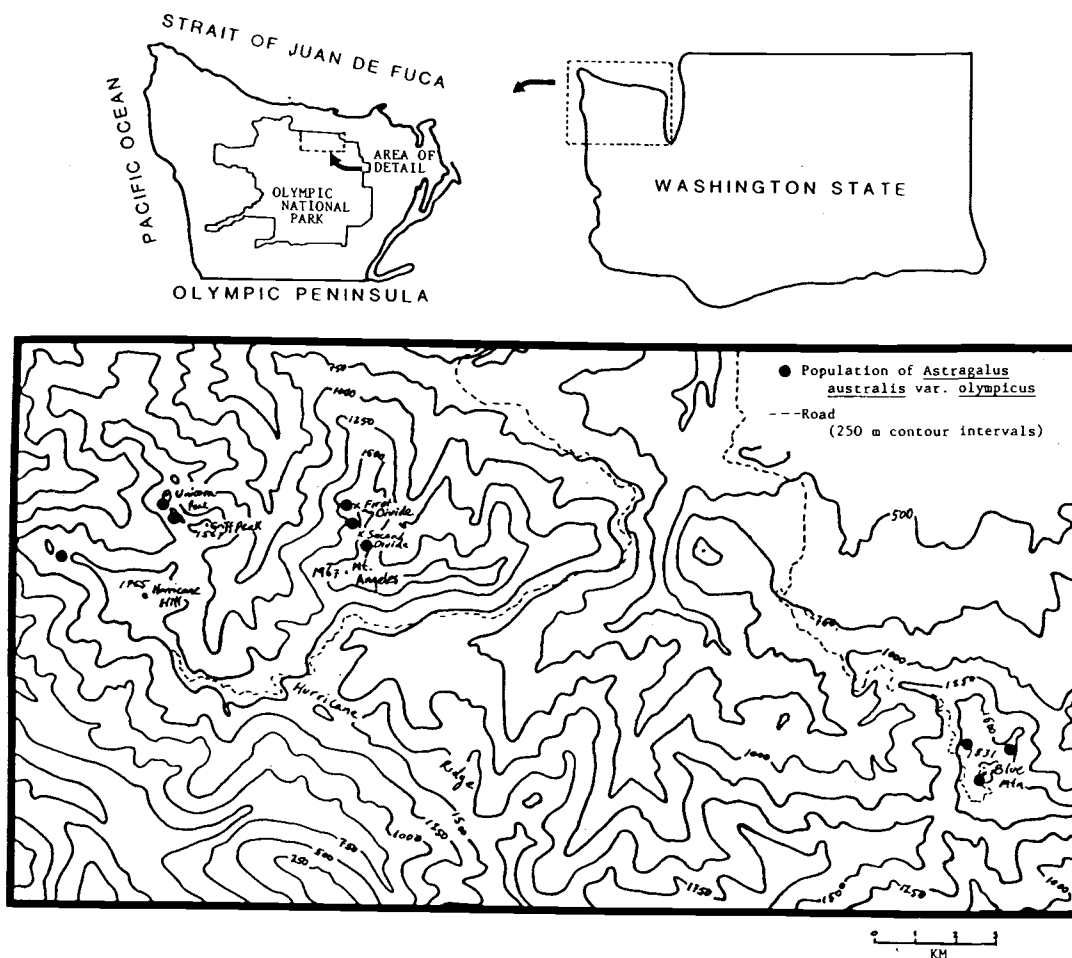


Fig. I.1. Location of *Astragalus australis* var. *olympicus* populations in the Olympic Mountains, Clallam County, Washington.

CHAPTER II

AUTECOLOGY

INTRODUCTION

Rare species often have large but geographically restricted populations (Rabinowitz 1981). The factors that determine population presence, such as a localized soil type or phytogeographic history, may be quite different from those factors that influence plant distribution within a population. Astragalus australis var. olympicus is a rare plant with few locally large populations restricted to calcareous alpine soils in the Olympic Mountains, Washington, an area of physiographic isolation and a center of endemism. The goal of this study was to typify the plant communities where A. australis var. olympicus grew, and determine the effect of interspecific competition and environmental factors on the abundance of this plant within four local populations.

Competition is defined as the tendency of plants to use the same resource, and stress is the sum of the external limits to plant growth (Grime 1979). Alpine plant communities are subject to environmental stresses in the form of low temperatures, a short growing season, abrasive winds, unstable soils, and other factors (Billings 1988). Grime (1979) has suggested that plants adapted to alpine stresses are generally poor competitors because they have low growth rates. However, detectable competition occurs in high elevation areas of the Olympic Mountains, at least in sites with moderate to high productivity (del Moral 1983), despite the short, summer-dry growing season and exposed habitat.

Although plants do interact with each other in some alpine plant communities, the physical environment probably outweighs competition in determining overall community structure, larger-scale plant distributions, and the nature of plant interactions. Alpine and subalpine plant communities in Olympic National Park are distributed according to complex moisture-exposure gradients, soil stability (Belsky and del Moral 1980), topography, snow-melt patterns, soil type, and other factors (Kuramoto and Bliss 1970). Soil creep reduces plant survival (Bell and Bliss 1973), and the distributions of at least six subalpine species are clearly related to the effects of temperature, moisture, and light on photosynthetic rate (Kuramoto and Bliss 1970) at Obstruction Point in the Olympic Mountains.

The present study explored the hypotheses that a) abundance and individual size of Astragalus australis var. olympicus are influenced by competition, and b) its abundance is limited by environmental factors. A set of null hypotheses were tested. These hypotheses were not mutually exclusive. Competition and physical stress may act independently, or, as other workers have shown, the magnitude of competition may be a function of the physical environment (del Moral 1983).

MATERIALS AND METHODS

Study sites--Astragalus australis var. olympicus is confined to four population clusters within a 4 x 21 km east-west belt in the northeastern Olympic Mountains, Clallam Co., Washington (Sheehan and Kaye 1986). Three subpopulations, each with several hundred plants, were selected to represent the known geographic spread of the taxon: Hurricane Hill (47°59'50"N, 123°32'56"W) at 1460 m, the western-most population; Mount Angeles, First Divide (48°00'30"N, 123°27'30"W) at 1650 m, a population near the distribution center; and Blue Mountain, the eastern-most population center. At Blue Mountain two subpopulations were sampled because the population is discontinuous: the south face of the summit (47°57'17"N, 123°15'30"W) at 1770 m, and the northeast buttress (47°57'38"N, 123°15'10"W) at 1700 m.

Transect Sampling--Seventeen transects, five at Blue Mountain summit, four at Blue Mountain northeast buttress, four at Hurricane Hill, and four at Mount Angeles, were sampled. Transects were four meters wide, of various lengths (30 to 120 m), and subjectively positioned to pass through areas of high Astragalus australis var. olympicus abundance to areas unoccupied by A. australis var. olympicus. Three one square meter plots were sampled within a 2 x 4 m sample area at 4 m intervals along the transects. Two plots were consistently sampled on either side of the transect center-line, while the third plot was randomly located within the 2 x 4 m area (Fig. 1).

The percentage of ground covered by mosses, lichens, and each vascular plant species present, including Astragalus australis var.

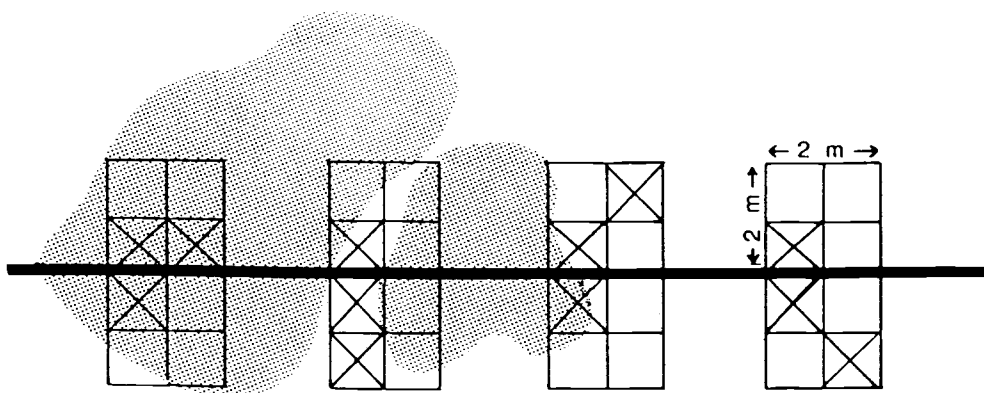


Fig. II.1. A hypothetical segment of a 4 m-wide belt transect passing through an *Astragalus australis* var. *olympicus* population (stippled). Sample areas were positioned at 4 m intervals. Three 1 x 1 m plots were placed in each sample area; two in regular positions and a third at random (crossed).

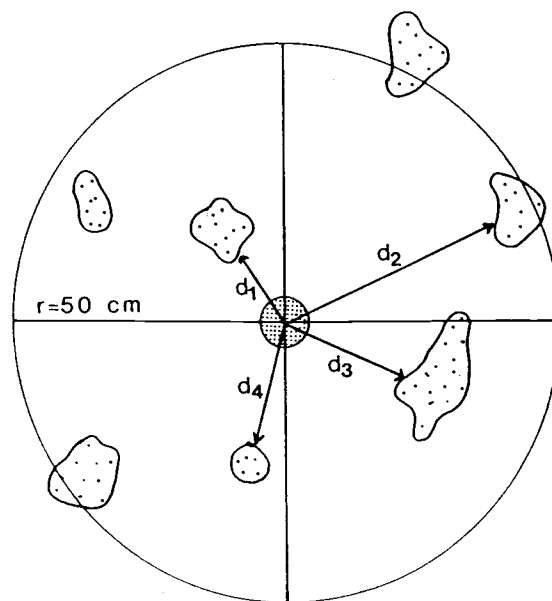


Fig. II.2. The distances to the nearest neighbors in four directions (or quadrants) were measured within 50 cm of each *Astragalus australis* var. *olympicus* individual (stippled area in center) encountered in a plot. The sum of these four distances was calculated as $d_1 + d_2 + d_3 + d_4$.

olympicus, was estimated to the nearest one percent. Cover values less than or equal to 0.1 percent were recorded as "t" and entered as 0.1 percent for analysis. The total number of A. australis var. olympicus plants within the 2 x 4 m sample area was recorded as a measure of density. In addition to plant abundances, the slope, aspect, elevation, and percentage of ground represented by bare mineral soil, litter, rock fragments of 1-5, 5-10, 10-20, and >20 cm, and bedrock were also estimated. A 1 x 1 m quadrat frame gridded with string at 10 cm intervals was used as a visual aid for estimating percentage cover values. The plant cover and soil-surface topography data for each three-plot cluster were averaged into a single sample to reduce the data set prior to analysis.

The neighborhood of each Astragalus australis var. olympicus individual rooted in a plot was described in terms of the identity of, and distance to, the nearest neighbor in four directions within a radius of 50 cm (Fig. 2). The area, height, number of stems, and number of inflorescences of each A. australis var. olympicus individual were recorded.

Plant water potential was measured from Astragalus australis var. olympicus branches at mid-day with a Scholander pressure bomb along four transects at Blue Mountain summit in mid-August, a period of summer drought.

Thirty-one soil pits were subjectively placed to coincide with the major vegetation types of five of the transects, and dug to bedrock

or a maximum depth of one meter. The below-ground structure of Astragalus australis var. olympicus was observed during soil-pit sampling, when possible. Soil samples were taken from each horizon occupied by roots. Gravel (particles >2 mm) was sifted from each sample and weighed. The less than 2 mm fraction was sent to the University of Idaho Analytical Services Lab for analysis of texture (percentage sand, silt, and clay), pH, organic carbon, total nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), manganese (Mn), and cation exchange capacity (CEC).

Community analysis--Two Way Indicator Species Analysis (TWINSpan [Hill 1979]), a classification computer program based on dividing a reciprocal averaging ordination space, was used to define plant community-types consisting of groups of vascular plant cover samples. Of the 107 species encountered, 35 were omitted from the analysis because they occurred at an overall frequency of less than two percent. One sample was omitted because it did not contain plants. One-way analysis of variance (ANOVA) was used to test for a community effect on Astragalus australis var. olympicus size and abundance, and a protected LSD multiple range test was used to compare means. A. australis var. olympicus cover data were transformed by arcsine-squareroot, plant area data were log transformed, and density, number of stems, and number of inflorescences values were squareroot transformed to meet the assumptions of ANOVA.

Tests of null hypotheses: competition--In order to explore the hypothesis that interspecific competition limits Astragalus australis

var. olympicus distribution, I tested the null hypotheses that the average A. australis var. olympicus cover, density, and water potential at each sample were independent of the average total cover of associated vascular plant species. The null hypothesis that average A. australis var. olympicus size was independent of the average sum of the distances to the nearest neighbor in four directions was also tested as an independent approach to detecting competition.

Tests of null hypotheses: physical environment--The hypothesis that Astragalus australis var. olympicus distribution is limited by the physical environment was investigated by testing the null hypotheses that A. australis var. olympicus cover and density were independent of each of 10 soil surface topography characteristics and 14 soil property variables. All hypotheses, including those concerning competition, were tested for all samples pooled, as well as separately for the two largest community-types identified by the TWINSpan analysis. Spearman rank correlation was used to test all hypotheses.

RESULTS

Community analysis--Community classification resulted in seven community-types after seven TWINSpan divisions (Table II.1). Six of these communities contained Astragalus australis var. olympicus. Community-type 1 was dominated by Crepis nana ssp. ramosa, and contained only three other species (an average of 1.75 species per sample), including A. australis var. olympicus at a frequency of 25%.

Table II.1. Species composition of seven plant community-types. A hierarchical classification is shown above the table. Species and communities are listed in ordination sequence determined by TWINSPLAN. Values are mean cover percentages of species in each community-type. $t < 0.1\%$.

	COMMUNITY-TYPE						
	1	2	3	4	5	6	7
(number of samples)	(4)	(18)	(127)	(97)	(10)	(5)	(8)
Species							
<u>Chamaecyparis nootkatensis</u>		t	0.4				52.2
<u>Valeriana sitchensis</u>			t		0.8		0.7
<u>Taxus brevifolia</u>					5.4		0.5
<u>Pachistima myrsenites</u>			t		0.8	0.5	* 1.5
<u>Abies lasiocarpa</u>					43.6		6.9
<u>Pseudotsuga menziesii</u>							
var. <u>menziesii</u>			0.8	1.0	1.9	48.7	
<u>Petrophytum hendersonii</u>		0.6	t		t	0.4	
<u>Saxifraga bronchialis</u>							
var. <u>austromontana</u>		0.2	t			0.2	
<u>Penstemon davidsonii</u>							
var. <u>menziesii</u>		0.6	t			0.2	t
<u>Lomatium martendalei</u>							
var. <u>flavum</u>		t	t	0.2	0.1	0.5	
<u>Campanula piperi</u>		0.2	t		t		t
<u>Arabis holboellii</u>							
var. <u>holboellii</u>			t	t	t		t
<u>Juniperus communis</u>							
var. <u>montana</u>			3.8	0.9	2.7	9.1	
<u>Hedysarum occidentale</u>			0.2	t	0.2		0.2
<u>Viola adunca</u>							
var. <u>adunca</u>		t	t	t			t
<u>Phacelia hastata</u>			0.1				0.1
<u>Eriqeron compositus</u>							
var. <u>qlabratus</u>	t	0.3	0.3	t			4.2
<u>Allium cernuum</u>		t	0.6	0.4	t	t	0.3
<u>Anemone multifida</u>							
var. <u>multifida</u>			t	t	t		
<u>Silene douglasii</u>							
var. <u>douglasii</u>			t	0.6			0.2
<u>Epilobium alpinum</u>							
var. <u>alpinum</u>		t	t	0.1			t
<u>Sitanion hystrix</u>							
var. <u>hystrix</u>			t	0.3	t		

Table II.1 Continued.

	COMMUNITY-TYPE						
	1	2	3	4	5	6	7
<u>Phlox diffusa</u>							
var. <u>longistylis</u>		t	2.1	6.6	t	0.3	
<u>Erysimum arenicola</u>							
var. <u>torulosum</u>		t	t	t	t		
<u>Allium crenulatum</u>		0.9	0.6	t	t	t	
<u>Achillea millefolium</u>							
ssp. <u>lanulosa</u>							
var. <u>alpicola</u>		t	0.7	1.7	t	t	
<u>Astragalus australis</u>							
var. <u>olympicus</u>	0.3	t	1.0	1.0	0.3		0.1
<u>Polypodium amorphum</u>		t	t				
<u>Phacelia sericea</u>							
var. <u>sericea</u>	0.2	t	0.2	0.2			
<u>Penstemon procerus</u>							
var. <u>tolmiei</u>		0.2	t				
<u>Crepis nana</u>							
ssp. <u>ramosa</u>	1.6	t	t				
<u>Polemonium pulcherrimum</u>							
var. <u>pulcherrimum</u>		t	0.3	t			
<u>Artemisia norvegica</u>							
var. <u>saxatilis</u>		t	0.2	t			
<u>Trisetum spicatum</u>			t	t			
<u>Potentilla fruticosa</u>			1.6	t			
<u>Lupinus lepidus</u>							
var. <u>lobbii</u>			t	t			
<u>Artemisia ludoviciana</u>							
var. <u>latiloba</u>			0.2	t			
<u>Agropyron caninum</u>							
ssp. <u>majus</u>							
var. <u>latiglume</u>			t	t			
<u>Oxytropus campestris</u>							
var. <u>gracilis</u>		t	0.1	0.2			
<u>Selaginella densa</u>							
var. <u>scopulorum</u>			0.2	0.3			
<u>Sedum stenopetalum</u>			t	t			
<u>Luina hypoleuca</u>			t				
<u>Eriogonum ovalifolium</u>							
var. <u>nivale</u>			t	t			
<u>Cerastium arvense</u>			t	t			
<u>Carex rossii</u>			t	t			
<u>Campanula rotundifolia</u>			t	0.2			
<u>Viola flettii</u>		t	t				
<u>Vicia americana</u>							
var. <u>truncata</u>			t	0.5			
<u>Antennaria microphylla</u>			t	t			
<u>Stipa occidentalis</u>							
var. <u>minor</u>			t	t			

Table II.1 Continued.

	COMMUNITY-TYPE						
	1	2	3	4	5	6	7
<u>Geum triflorum</u>							
var. <u>campanulatum</u>			t	2.8			
<u>Poa incurva</u>			t	t			
<u>Lathyrus nevadensis</u>							
ssp. <u>lanceolatus</u>							
var. <u>pilosellus</u>			t	0.1			
<u>Festuca idahoensis</u>							
var. <u>oregona</u>		t	1.2	11.2	t		
<u>Eriqeron subtrinervis</u>							
var. <u>conspicuus</u>			0.3	2.5			
<u>Eriophyllum lanatum</u>							
var. <u>lanatum</u>			0.3	2.0			t
<u>Bromus sitchensis</u>							
var. <u>aleutensis</u>			t	1.3			
<u>Symphoricarpos albus</u>							
var. <u>laevigatus</u>				1.3			
<u>Rosa nutkana</u>							
var. <u>nutkana</u>				0.8			
<u>Lonicera ciliosa</u>			t	0.3			
<u>Lomatium dissectum</u>							
var. <u>dissectum</u>				0.2			
<u>Epilobium angustifolium</u>				0.1			
<u>Elymus glaucus</u>							
var. <u>breviaristatus</u>			t	1.9			
<u>Delphinium glareosum</u>			t	t			
<u>Cryptantha intermedia</u>							
var. <u>grandiflora</u>			t	0.2			
<u>Castilleja hispida</u>							
var. <u>hispida</u>			t	t			
<u>Carex phaeocephala</u>			t	0.2			
<u>Carex hoodii</u>				0.2			
<u>Arabis lemmonii</u>							
var. <u>lemmonii</u>				t			
<u>Allium acuminatum</u>				0.1			
<u>Agoseris glauca</u>							
var. <u>monticola</u>			t	0.2			
<u>Lomatium nudicaule</u>			t	1.1			
Frequency (%) of							
<u>A. australis</u>							
var. <u>olympicus</u>	25.0	21.0	66.7	56.7	30.0	0.0	12.5
moss		t	0.3	2.0	0.3	t	t
lichen		t	0.5	1.4	0.2		
Total vascular cover	2	2	16	42	56	62	64
Avg. no. species per sample	1.75	4.1	8.3	14.0	4.8	3.6	3.89

Only four samples comprised this cluster. This was the most depauperate community (average total cover was 2%), with conspicuously high levels of 1-5 cm rock fragments (>45%) and only 0.2% litter (Table II.2). No soil samples were analyzed from this community, which was encountered only at Mount Angeles.

Community-type 2, with 18 samples, represented areas dominated by rock outcrop plants such as Petrophytum hendersonii, Penstemon davidsonii var. menziesii, P. procerus var. tolmiei, and Saxifraga bronchialis var. austromontana (Table II.1). This community had the highest average cover of bedrock (>60%) and slope (34.8°) (Table II.2). Total plant cover was nearly as low as in community 1, but average species richness was much higher (4.1 species per sample). Astragalus australis var. olympicus was present at a frequency of 21%. Soil pH and CEC were the highest for all communities sampled, Ca was greater than the highest calibrated value (24.0+ ueq/100g), and P was the lowest recorded at 0.8 ug/g (Table II.3), reflecting a calcareous parent material and weak soil development. This community was present at both Mount Angeles and Blue Mountain northeast buttress.

The largest number of samples (127) were grouped into community-type 3 (Table II.1), an environmentally heterogeneous cluster with relatively high average species richness (8.3 species per sample), and the highest frequency of Astragalus australis var. olympicus (66.6%). This was an unstable meadow community dominated by Phlox diffusa var. longistylis and Festuca idahoensis var. oregona, with

patches of low woody shrubs such as Juniperus communis var. montana and Potentilla fruticosa. Regions of down-slope moving gravels (scree) were abundant, as indicated by the relatively high levels of 1-5 cm gravel and abundance of scree-adapted plants such as Allium crenulatum, Artemisia spp., and Phacelia hastata. The relatively low total cover of vascular plants (16%) in this community was probably not completely explained by soil movement, but also reflected areas of thin but stable soils. Soil depth averaged only 26 cm (Table II.3), the lowest value except for the rock outcrop community (type 2), and a relatively high percentage of bare soil was exposed (Table II.2). This community was encountered at all sites.

Community-type 4 was the second largest cluster, with 97 samples. This community was similar to type 3, but apparently represented meadows with greater stability, deeper and better developed soils, and higher productivity. Average total vascular cover (42%) and species richness (14.0 species per sample) were the highest of the meadow communities, and again Festuca idahoensis var. oregona and Phlox diffusa var. longistylis dominated (Table II.1). Astragalus australis var. olympicus was present in 56.7% of the samples. Deciduous shrubs such as Symphoricarpos albus var. laevigatus and Rosa nutkana var. nutkana, perennial herbs like Geum triflorum var. turbinatum and Erigeron subtrinervis var. conspicuus, and tall grasses such as Elymus glaucus var. breviaristatus and Bromus sitchensis var. aleutensis combined to produce high total cover values (Table II.1). The abundance of mosses and lichens and lower average cover of rock fragments and bedrock indicated that the soil

Table II.2. Mean (S.E.) percentage bare ground, rock fragments, bedrock, and litter, and slope, aspect, and elevation for each community type.

	COMMUNITY TYPE						
	1	2	3	4	5	6	7
Bare ground (%)	30.9(12.8)	8.6(1.9)	27.7(1.6)	28.6(1.5)	18.7(6.2)	15.9(7.6)	5.7(2.3)
Rock fragments							
1-5cm (%)	45.8(10.5)	20.1(4.5)	33.3(1.6)	17.2(1.5)	18.7(8.9)	11.8(7.5)	12.4(7.1)
5-10cm (%)	3.5(0.9)	3.0(1.0)	4.5(0.3)	2.9(0.3)	1.5(0.7)	1.6(0.6)	3.1(1.5)
10-20cm (%)	0.8(0.4)	2.1(0.8)	2.7(0.2)	1.7(0.2)	0.8(0.3)	1.6(0.8)	2.2(0.9)
>20cm (%)	0.4(0.4)	2.7(1.1)	2.4(0.4)	1.1(0.2)	0.2(0.1)	1.3(0.8)	3.9(2.8)
Bedrock (%)	9.6(9.6)	60.4(7.3)	12.4(2.0)	2.0(0.8)	6.7(6.6)	10.1(9.9)	25.1(13.4)
Litter (%)	0.2(0.1)	2.6(1.7)	4.2(0.6)	12.4(0.9)	29.5(8.8)	21.8(12.0)	36.2(13.6)
Slope (°)	26(3.5)	34.8(3.9)	23.9(0.5)	23.0(0.4)	27.2(1.8)	33.6(9.4)	24.5(0.9)
Aspect	S39°W (9)	S11°W (1)	S3°E (3)	S14°W (2)	S46°W (2)	S35°W (14)	S37°E (15)
Elevation (m)	1655(11)	1661(4)	1689(6)	1549(12)	1625(5)	1548(40)	1827(6)

Table II.3. Soil properties within the rooting zone (mean, S.E.) for communities that received soil sampling. Standard errors are provided only where more than one sample was taken.

Comm- unity- type	No. pits (N)	soil depth (cm)	pH	Org.		P μg/g	K	Ca (-----μeq/100g-----)	Mg	CEC	Mn μg/g	<2mm fraction			
				C (%)	N (%)							Gravel (%)	Sand (%)	Silt (%)	Clay (%)
2	1	10	7.25	0.75	0.12	0.8	0.13	24.0+	2.9	34.5	4.07	42.8	75.1	13.0	11.9
3	20	26 (4)	7.13 (0.10)	0.77 (0.08)	0.16 (0.01)	2.2 (0.1)	0.17 (0.02)	19.3 (0.9)	1.3 (0.2)	18.8 (1.9)	10.88 (1.71)	44.0 (2.3)	71.8 (1.6)	13.2 (1.0)	15.0 (1.0)
4	8	49 (12)	6.89 (0.09)	0.02 (0.12)	0.21 (0.03)	3.2 (0.2)	0.23 (0.02)	15.3 (0.9)	0.9 (0.1)	14.6 (0.9)	30.4 (3.42)	46.3 (5.1)	72.3 (0.9)	10.3 (0.5)	17.4 (0.5)
5	1	75	7.08	0.31	0.09	1.9	0.14	24.0+	1.4	22.0	2.9	50.4	85.7	6.0	8.3
7	1	85	6.83	1.07	0.12	2.2	0.42	19.5	3.15	29.2	22.8	52.1	75.0	13.7	11.3

in this community was more stable than in community-type 3. High levels of N, P, K, Mn, and clays, combined with lower pH and Ca (Table II.3), indicate that soils in community 4 are generally richer in nutrients and may have interacted with plants for a longer period of time than in community 3. This community was absent from Mount Angeles but present at the other sites.

Community-types 5, 6, and 7 each represented clusters dominated by trees. Community-type 5 contained 10 samples, had an average richness of 4.8 species per sample. It was dominated by Abies lasiocarpa, and, to a lesser degree, by Taxus brevifolia and Pseudotsuga menziesii var. menziesii (Table II.1). Astragalus australis var. olympicus had a frequency of 30%. Community-type 5 had deep soil (75 cm), but low nutrient levels and coarse texture (Table II.3) indicated less weathering and plant-soil interaction than soils in meadow community types 3 and 4. This community occurred as tree clumps in meadows and scree. Community-type 5 was encountered at Mount Angeles only.

Pseudotsuga menziesii var. menziesii dominated community-type 6, a cluster of 5 samples with an average richness of 3.6 species (Table II.1). These trees tended to occur as small groups on steep (>33°) slopes at lower elevations (Table II.2). They were encountered alongside rock outcrops and in xeric meadows. Astragalus australis var. olympicus was absent from this community, which occurred at Mount Angeles and Hurricane Hill.

Community-type 7 represented 8 samples in Chamaecyparis nootkatensis tree clumps with an average species richness of 3.9 species per sample (Table II.1). Astragalus australis var. olympicus was present at a frequency of 12.5% (one sample). This community was physically unique in having a high average cover of bedrock (25.1%) combined with a southeasterly aspect, and an average elevation of over 1825 m (Table II.2). Although more nutrient rich, the soil in this community was texturally similar to soil from the rock outcrop community, type 2 (Table II.3). Samples from both Blue Mountain northeast buttress and Mount Angeles were placed in this cluster.

There was a significant effect of community-type on Astragalus australis var. olympicus average cover and density, but not on average plant area, height, number of stems, or number of inflorescences (Table II.4). In other words, A. australis var. olympicus abundance within a community was affected by community structure and composition, but individual size was not. Community types 3 and 4, the meadow communities, had significantly higher average cover and density of A. australis var. olympicus than communities 2, 6, and 7. A. australis var. olympicus abundance was higher in communities 3 and 4 than 1 and 5, but not significantly so (Table II.4). Although A. australis var. olympicus was a potential indicator species in the TWINSpan analysis, it was not used as such during the execution of the algorithm. Thus, comparisons between communities are legitimate.

Table II.4. Mean (n, S.E.) *Astragalus australis* var. *olympicus* cover, density, area, height, number of stems, and number of inflorescences within each community-type. Values followed by the same letter do not differ significantly at the 95% level. Data were transformed for ANOVA.

	COMMUNITY TYPE							df	F
	1	2	3	4	5	6	7		
Cover (%)	0.25ab (4,0.25)	0.09a (18,0.05)	1.02b (127,0.10)	1.00b (97,0.17)	0.28ab (10,0.18)	0.00a (5,0.00)	0.12a (8,0.12)bd	6, 262	4.70***
Density (m ⁻²)	0.06abc (4,0.04)	0.04a (18,0.02)	0.52c (127,0.06)	0.32bc (97,0.05)	0.10ab (10,0.06)	0.00a (5,0.00)	0.03a (8,0.03)	6, 259	5.90***
Area (cm ²)	288.0 (1,--)	94.5 (4,44.7)	173.7 (85,14.1)	299.4 (54,49.8)	86.3 (3,27.9)	NA	510.0 (1,--)	5, 142	1.59ns
Height (cm)	15.0 (1,--)	5.37 (4,1.55)	9.28 (85,0.35)	9.79 (54,0.59)	12.56 (3,4.22)	NA	13.0 (1,--)	5, 142	2.07ns
Stems	10.00 (1,--)	5.63 (4,3.02)	6.50 (85,0.45)	6.12 (54,0.68)	2.39 (3,0.20)	NA	17.00 (1,--)	5, 142	2.03ns
Inflorescences	38.0 (1,--)	4.5 (4,2.9)	12.8 (85,1.5)	10.7 (54,1.7)	7.1 (3,3.08)	NA	1.0 (1,--)	5, 142	1.56ns

*** P<0.0001, ns = non-significant

NA: Means absent because *Astragalus australis* var. *olympicus* missing in community 6.

-- S.E. absent because mean based on a single observation.

Tests of null hypotheses: competition--The hypotheses regarding plant abundance, competition, and the physical environment were tested on the data-set as a whole, and also separately for community types 3 and 4, the meadow communities. These communities were selected for separate analysis because they had the highest Astragalus australis var. olympicus abundances, and the largest number of samples each. Together they represented 83% of all samples. There was no significant correlation between average cover and density of A. australis var. olympicus and average total cover of associated vascular plant taxa when all samples were pooled (Fig II.3 e,f) or in community-type 3 alone (Fig. II.3 a,b). However, in community-type 4, the stable meadow, these correlations were significantly negative (Fig. II.3 c,d). Therefore, the null hypotheses that cover and density were independent of the abundance of associates were not rejected overall or in community 3, but they were rejected in community-type 4.

The null hypothesis that Astragalus australis var. olympicus moisture stress was independent of cover of associated species was rejected for the data set as a whole and for community-type 4, because there were significant negative correlations between moisture stress and cover of associates in those groups (Fig II.4 b,c). This null hypothesis was not rejected in community-type 3 (Fig. II.4a).

Correlations between the average sum of the distances to nearest neighbor in four directions and average Astragalus australis var. olympicus plant area, number of stems, and number of inflorescences

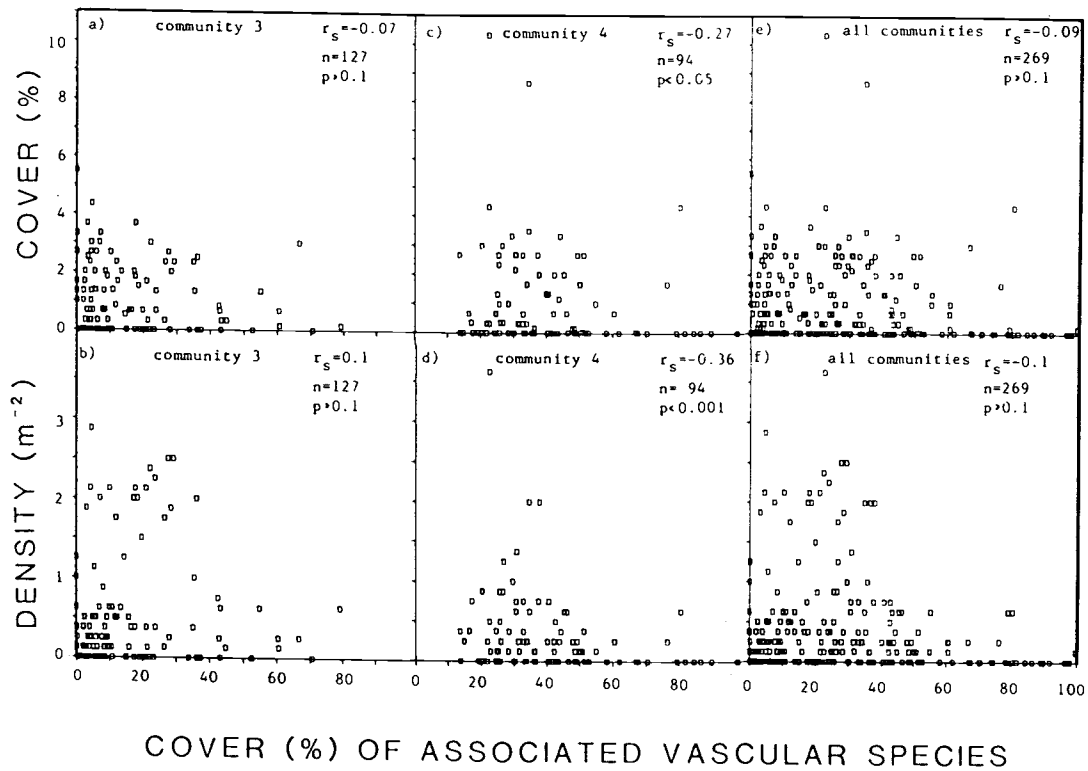


Fig. II.3. Percentage cover and density of *Astragalus australis* var. *olympicus* as a function of percentage cover of associated vascular plants in a-b) community-type 3, c-d) type 4, and e-f) all samples pooled. Significance levels (p) are experimentwise error for two comparisons per community-type or group.

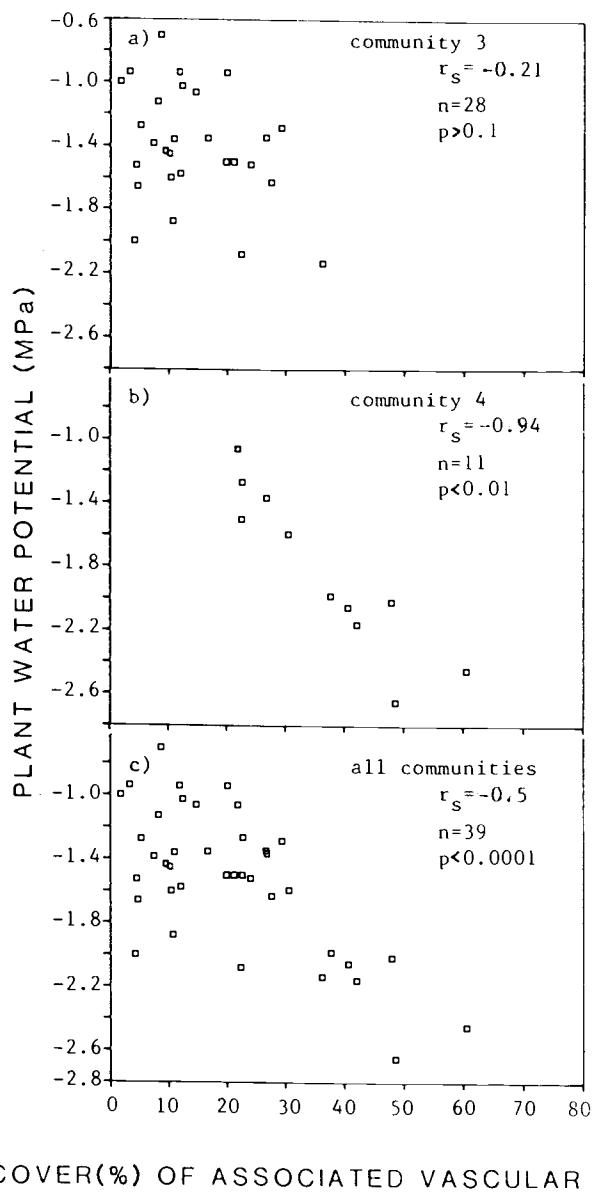


Fig. II.4. Mid-day plant water potential (MPa) of Astragalus australis var. olympicus as a function of percentage cover of associated vascular plants in a) community-type 3, b) type 4, and c) for all samples pooled.

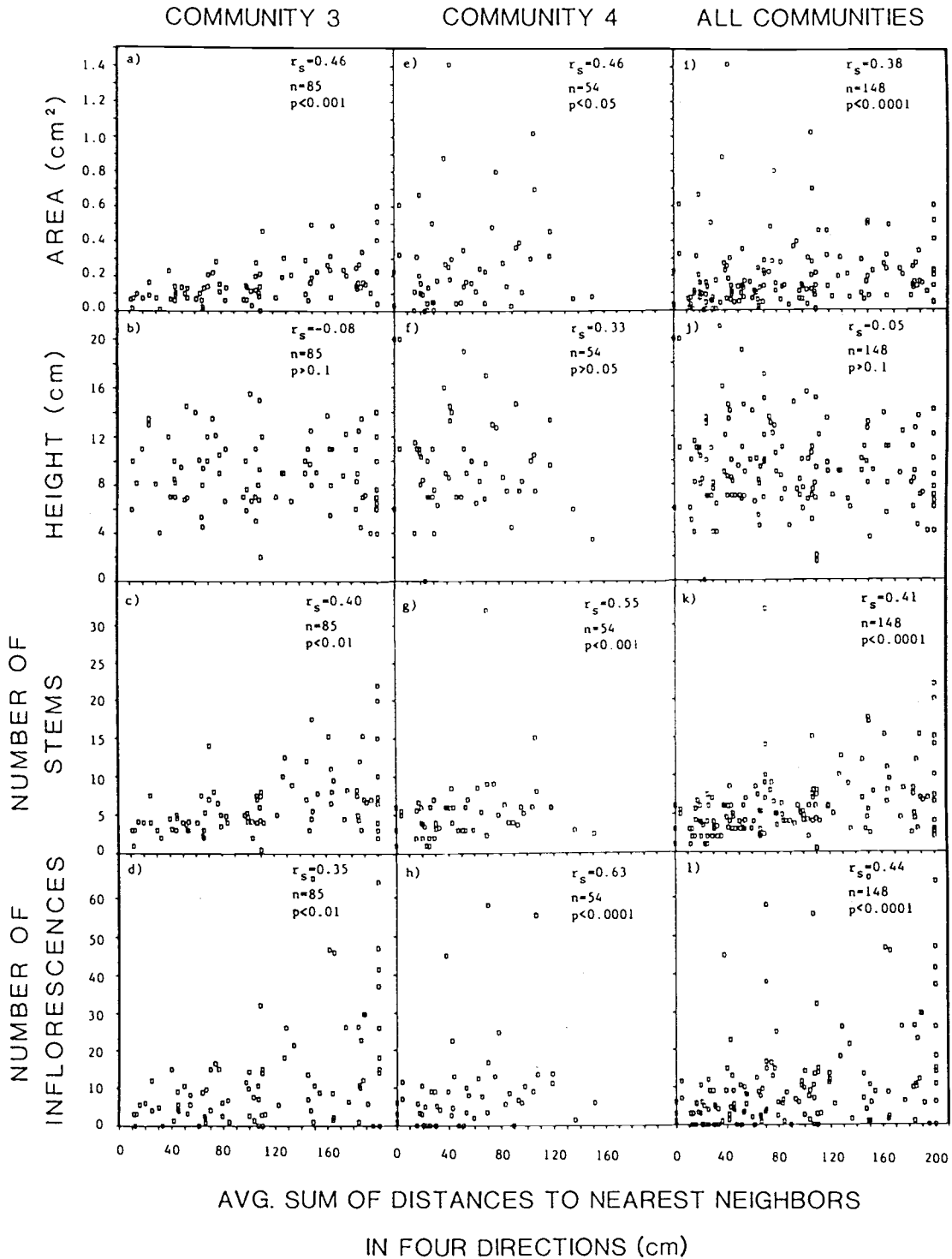


Fig. II.5. *Astragalus australis* var. *olympicus* plant size (area, height, number of stems, number of inflorescences) as a function of average sum of the distances to nearest neighbors in four directions in a-d) community-type 3, e-h) type 4, and i-l) all samples pooled. Significance levels (p) are experimentwise errors for four comparisons per community-type or group.

were significant and positive (the expected sign if competition was occurring) in community-types 3 (Fig. II.5 a,c,d) and 4 (Fig. II.5 e,g,h), and for all samples pooled (Fig II.5 i,k,l). Plant height was not significantly correlated with neighbor distance in any community or group (Fig. II.5f). Therefore, the null hypothesis that A. australis var. olympicus plant size was independent of distance to nearest neighbors was rejected for all measures of plant size, except height (Fig. II.5 b,f,j).

Tests of null hypotheses: physical environment--There was strong evidence that Astragalus australis var. olympicus distribution was related to several of the environmental variables. For all samples pooled, average cover and density were significantly negatively correlated with bedrock, and positively correlated with average cover of bare ground, and 1-5, 5-10, and 10-20 cm rock fragments. Density was significantly negatively correlated with slope and positively correlated with elevation (Table II.5). Within community-type 3 alone, cover and density were positively correlated with cover of 1-5 cm rock fragments and negatively correlated with bedrock. Again, density was negatively correlated with slope (Table II.5). In community-type 4, cover and density were significantly correlated with average cover of 1-5, 5-10, and 10-20 cm rock fragments (Table II.5).

Few soil properties were significantly correlated with Astragalus australis var. olympicus abundance. Only the percentage of soil (by weight) occupied by gravel was significantly correlated with average

Table II.5. Spearman rank correlation coefficients (r_s) between average Astragalus australis var. olympicus cover and density and soil surface and topographic variables in community-types 3 and 4, and within all samples pooled.

	community 3, n=127		community 4, n=97		all samples, n=269	
	cover (%)	density (m ⁻²)	cover (%)	density (m ⁻²)	cover (%)	density (m ⁻²)
Bare ground (%)	0.10	0.16	0.13	0.08	0.21*	0.25**
Rock fragments (%)						
1-5 cm	0.35**	0.27*	0.34*	0.44**	0.37**	0.39**
5-10	0.20	0.16	0.34*	0.35*	0.33**	0.34**
10-20	0.17	0.18	0.32*	0.35*	0.27**	0.30**
>20	0.18	0.12	0.07	0.08	0.16	0.15
Bedrock (%)	-0.29*	-0.29*	-0.09	-0.02	-0.24**	-0.22**
Litter (%)	-0.09	0.04	-0.27	-0.30	-0.11	-0.11
Slope (°)	-0.10	-0.29*	0.05	-0.02	-0.11	-0.21**
Aspect (azimuth)	-0.07	-0.12	-0.05	-0.18	-0.09	-0.16
Elevation (m)	0.11	0.26	-0.03	0.14	0.07	0.20*

* 0.05 > P > 0.01, ** P < 0.01 (experimentwise error, 20 comparisons within each community-type or group)

Table II.6. Spearman rank correlation coefficients (r_s) between average Astragalus australis var. olympicus cover and density and soil depth, chemistry, and texture variables. Significance notation as in Table II.5 (28 comparisons within each community-type or group).

	community 3, n=20		community 4, n=8		all samples, n=31	
	cover (%)	density (m ⁻²)	cover (%)	density (m ⁻²)	cover (%)	density (m ⁻²)
Depth	0.34	0.29	-0.15	-0.27	0.14	0.003
pH	-0.26	-0.39	0.32	0.24	-0.15	-0.34
Organic carbon	-0.13	-0.15	-0.95*	-0.88*	-0.39	-0.18
N	0.10	0.31	-0.83*	-0.71	0.12	0.05
P	-0.14	0.11	0.69	0.42	0.03	0.18
K	-0.17	0.14	-0.32	-0.20	-0.28	-0.13
Ca	-0.26	-0.45	-0.42	-0.42	-0.24	-0.29
Mg	0.18	0.06	-0.49	-0.51	-0.05	-0.07
Mn	0.16	0.24	-0.37	-0.34	0.05	0.05
CEC	-0.16	-0.32	-0.46	-0.39	-0.25	-0.30
>2mm fraction	0.46	0.38	0.66	0.37	0.56*	0.37
<2mm fraction						
Sand	-0.31	-0.43	0.59	0.51	-0.09	-0.23
Silt	0.16	0.12	-0.66	-0.54	-0.14	-0.05
Clay	0.38	0.61*	-0.24	-0.17	0.21	0.34

A. australis var. olympicus cover when all samples were pooled (Table II.6). There were no significant correlations with A. australis var. olympicus density overall. In community-type 3, density was significantly positively correlated only with percentage of clay (Table II.6). The correlation between cover and soil gravel was not significant in community-type 4, but there were significant negative correlations between cover and organic carbon, cover and total nitrogen, and density and organic carbon (Table II.6). The null hypotheses that A. australis var. olympicus abundance (cover and density) was independent of physical variables were consistently not rejected for hypotheses concerning cover of >20 cm rock fragments, litter, aspect, soil depth, pH, P, K, Ca, Mg, Mn, CEC, sand, and silt. They were rejected for hypotheses relating to bare ground, 1-5, 5-10, 10-20 cm rock fragments, bedrock, slope, elevation, soil organic carbon, N, soil gravel, and clay in community-types 3, 4 or in all communities pooled.

DISCUSSION

Seven plant community-types were identified through classification of the plant cover data: a nearly barren, exposed community-type (type 1), a rock outcrop community-type (type 2), an unstable scree and thin soil community-type (type 3), a stable grassy meadow community-type (type 4), and three tree-clump community-types (types 5-7). Astragalus australis var. olympicus was missing from community-type 6, a tree community dominated by Pseudotsuga menziesii var. menziesii, and was most abundant in types 3 and 4, the unstable and stable meadow communities. The four treeless communities described

here were similar to those listed by other authors working in alpine-subalpine meadows of the Olympic Mountains (e.g., Kuramoto and Bliss 1970, Belsky and del Moral 1982, del Moral 1983, Pfitsch and Bliss 1985). Five community-types listed by Kuramoto and Bliss (1970) (tall sedge, dwarf sedge, moist Saussurea, moist Valeriana, and heath shrub) were not encountered during this study, because A. australis var. olympicus was absent from the moist or late-snowmelt areas of stable soil where these communities develop. All of the communities that contained A. australis var. olympicus were at the dry end of a moisture gradient present in the alpine-subalpine ecosystem of the Olympic Mountains (Kuramoto and Bliss 1970, Belsky and del Moral 1982, del Moral 1983).

Reciprocal transplant and removal experiments involving several species associated with Astragalus australis var. olympicus show that competition increases along a productivity gradient at Blue Mountain (del Moral 1983). Assuming productivity and cover are correlated, the effects of interspecific competition on Astragalus australis var. olympicus should have been greater in areas of higher total cover. Indeed, A. australis var. olympicus water potentials decreased significantly as the cover of associated species increased, and this relationship was stronger in the high-cover, stable meadow community-type than the low-cover, unstable community-type (Fig. II.3). Also, A. australis var. olympicus cover and density were significantly negatively correlated with cover of associated species in the stable meadows, but this correlation was not significant in the unstable meadows. Apparently, interspecific competition with A. australis

var. olympicus reaches higher intensities where associated species are more abundant.

The nearest neighbor analysis corroborated this trend. When all communities were combined, the average Astragalus australis var. olympicus plant size decreased significantly as the average sum of the distances to the nearest neighbors in four directions decreased. The patterns were similar in both the stable and unstable meadows, but the correlation coefficients tended to be higher in the stable meadow community-type, suggesting that competition was more intense there. The nearest neighbor technique has been applied widely as a method of detecting intra- or interspecific competition in annuals (Mack and Harper 1977, Hickman 1979, Weiner 1982, Silander and Pacala 1985), woody shrubs (Yeaton and Cody 1976, Yeaton et al. 1977, Ehleringer 1984), and trees (Weiner 1984), but it has met with limited success in natural populations of herbaceous perennials (Waller 1981). Even so, significant effects of neighbors on A. australis var. olympicus were detected even in the unstable meadow community, where the least intense interactions could be expected because neighbors were less abundant.

One draw-back of the nearest neighbor method is that it does not reveal the mechanism(s) by (or resources for) which neighbors compete (Waller 1981). Above-ground interactions, such as shading, were unlikely in Astragalus australis var. olympicus populations because cover was not contiguous and did not form a canopy structure. However, competition for soil water was likely because there was a

negative correlation between total cover of associated species and the water potential of A. australis var. olympicus. Competition for soil nutrients was also plausible considering that competitive effects were strongest in the stable meadow community, where soils were more nutrient rich.

Just as the relative importance of competition shifted between community-types, so did the importance of environmental variables. The null hypotheses concerning Astragalus australis var. olympicus abundance and environmental variables were rejected in several cases. When all communities were pooled, cover and/or density were significantly positively correlated with the percentage cover of bare ground, 1-5, 5-10, 10-20 cm rock fragments, elevation, and percentage of the soil occupied by gravel, and negatively correlated with percentage cover of bedrock and steepness of slope. In the unstable meadows, A. australis var. olympicus abundance tended to be influenced by topography and soil texture (1-5 cm rock fragments, bedrock, slope, clay), and in the stable meadows by rock-fragments (1-5, 5-10, 10-20 cm) and soil chemistry (organic carbon and N).

One explanation for this difference is that unstable meadows covered a wider range of topographic conditions than stable meadows, including conditions with steeper slopes and greater amounts of exposed bedrock, that limited all plant growth, including Astragalus australis var. olympicus. Environmental stress probably overwhelmed most competitive effects at these sites. Fewer environmental extremes were encountered in the stable meadows, possibly allowing

competition to be more intense. A negative correlation of cover and density with organic carbon and soil nitrogen in the stable community probably did not indicate that A. australis var. olympicus was inhibited by high levels of these components, but that competition from associated species was greater where nutrients were in better supply. This interpretation is supported by the fact that the correlation coefficients between A. australis var. olympicus abundance and three soil nutrients (N, Mg, Mn) and silt and clay were consistently negative in the stable meadows and positive in the unstable meadows. In high-competition communities, A. australis var. olympicus may have been restricted to sites of weaker soil development and low nutrient availability. However, in unstable communities, where competition was reduced, A. australis var. olympicus individuals apparently were more abundant in better sites.

The coexistence of plant species is related to the presence of each species' regeneration niche (Grubb 1977). Rock fragments on the soil surface may have increased the frequency of favorable sites for germination and establishment of Astragalus australis var. olympicus plants, especially in the presence of abundant competitors. Indeed, A. australis var. olympicus abundance was more strongly related to the abundance of surface gravels in the stable meadow than the unstable meadow community. This is consistent with the observation that species diversity and, therefore, coexistence is correlated with microscale soil-surface heterogeneity in Olympic subalpine meadows dominated by Festuca idahoensis var. oregona, but not in low productivity sites (Loneragan and del Moral 1984). At least in the

stable meadows, competition may have limited A. australis var. olympicus to particular regeneration sites.

The structure of Astragalus australis var. olympicus plants suited them to areas of poorly developed, unstable soil, such as scree and thin soil over fractured bedrock. The tap root usually branched a few centimeters below the rootcrown to form spreading (>25 cm) lateral roots that penetrated deep into bedrock crevices or gravels. Fine roots were abundant only near the ends of lateral roots and over the faces of buried rocks. This structure probably allowed A. australis var. olympicus plants to remain anchored in the face of down-slope moving surface gravels and reach deep water reserves. The association of A. australis var. olympicus with vesicular-arbuscular (VA) mycorrhizae (O'dell, in prep.) may have improved its survival in nutrient-poor, calcareous soils. VA mycorrhizea in alpine areas are more common in calcareous soils, possibly because high pH and Ca levels may cause calcareous soils to be functionally phosphorus deficient (Lesica and Antibus 1985). Above ground, branches broke free of the rootcrown with surprising ease, making the plants even more resistant to being pulled from the ground by moving rocks. Branches lost in this way could be replaced because axillary buds often sprouted throughout the growing season.

Soil chemistry appeared to control the regional distribution of Astragalus australis var. olympicus. Soils within or adjacent to A. australis var. olympicus populations ranged in pH from 5.65 to 7.65 (avg.=7.06) and Ca from 12.85 to over 24.00 $\mu\text{eq}/100\text{ g}$ (avg.=18.57

$\mu\text{eq}/100\text{ g}$). These are the highest pH and Ca levels published from Olympic Mountain Range subalpine-alpine plant communities. PH ranges from 4.4 to 6.0 and Ca from 0.3 to 16.0 $\mu\text{eq}/100\text{ g}$ at sites within 1 km of the Blue Mountain summit area (Belsky and del Moral 1982, del Moral 1983). These sites are occupied in part by stable and unstable meadow communities similar to those I found in calcareous areas, but they lack A. australis var. olympicus. This supports the idea that A. australis var. olympicus was limited to high pH, calcareous sites, and suggests that soil chemistry determined the broad-scale distribution of A. australis var. olympicus, and competition and other environmental factors fine-tune its local distribution. Sites with calcareous substrates, gravelly slopes, a southern aspect, few competitors and an appropriate elevation may be infrequent in the Olympic Mountains, thus contributing to the rarity of the taxon.

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CHAPTER III

REPRODUCTIVE ECOLOGY

INTRODUCTION

Knowledge of reproduction is crucial to our understanding of the causes of rarity and for conservation of rare 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 most plants, flowers must be pollinated to form fruits, ovules must be fertilized and sustained with nutrients to form viable seeds, and seeds must be dispersed to reach substrates suitable for growth, where they must germinate in order for new individuals to become established in a population. Therefore, any weak link or break in this chain of events curtails a plant's ability to reproduce and, if permanent, may contribute to a species' rarity.

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), breeding system (Planisek 1983, Karron 1989), seed germination (Baskin and Quarterman 1969, Baskin and Baskin 1979, Halse 1988), breeding system and germination (Clampitt 1987), and seed production and predation (Menges et al. 1986). However, few studies of rare plants describe the limits to reproduction at all stages from flower production through seed germination (Massey and Whitson 1980, but see Crowder 1978). The goal of this study was to describe the reproductive ecology of Astragalus australis var.

olympicus, a local endemic of the Olympic Mountains, Washington, from pollination to seed germination to increase baseline information on the biology of the taxon, and identify any shortcomings in its capacity to reproduce.

Astragalus australis var. olympicus is a candidate for listing under the Federal Endangered Species Act of 1973 (U. S. Fish and Wildlife Service 1985), and is considered threatened by the Washington Natural Heritage Program. Only about 4000 individuals in four population centers 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 (chapter II). The high ridges and mountain tops where the plant typically grows are free of snow in early spring.

Despite the threatened status, rarity, and location of Astragalus australis var. olympicus inside a National Park, little information is available on its reproductive ecology. It is an herbaceous perennial that holds its over-wintering buds just below the soil surface. The species appears not to reproduce vegetatively (personal observation). 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 few fruits dehisce as early as late July while still on the plant, but most seed dispersal occurs in

September after fruits have fallen (Sheehan and Kaye 1986). 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 life-history of this insect is important because it may affect the population changes of predator and prey.

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, and what is its life history? Do seeds possess highly specific germination requirements?

MATERIALS AND METHODS

Study sites--Astragalus australis var. olympicus is confined to four population clusters within a 4 x 21 km east-west belt in the northeastern Olympic Mountains, Clallam County, Washington (Sheehan and Kaye 1986). Three subpopulations, each with several hundred plants, were selected to represent the known geographic spread of the taxon: Hurricane Hill (47°59'50"N, 123°32'56"W) at 1460 meters, the western-most population; Mount Angeles, First Divide (48°00'30"N,

123°27'30"W) at 1650 meters, a population near the distribution center; and the south face of Blue Mountain summit (47°57'17"N, 123°15'30"W) at 1770 meters, in the the eastern-most population center.

Pollination--A pollinator-exclusion experiment was conducted to determine if insect pollinators were necessary for fruit and seed production. Twenty reproductive plants with over ten inflorescences each were arbitrarily selected in early July of 1988 from near the center of the Blue Mountain summit population. On each plant, one inflorescence with unopened flowers was arbitrarily selected and covered with a fine-mesh nylon bag to exclude insect pollinators. A second inflorescence of as close a phenological stage as possible was subjectively selected on each plant to serve 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.

In the laboratory, percentage of fruit set and average percentage of seed set were determined for each inflorescence. To account for greater seed predation in controls, I assumed that predated seeds would have formed good 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 with untransformed data to test the null hypothesis that there was no difference between treatments.

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 "trip" the legume floral mechanism (Green and Bohart 1975, Faegri and van der Pijl 1979) were observed.

Fruit set and ovule fate--Twenty-five plants were chosen at random from near the center of each population in August of 1987 and 1988, when fruits were nearly mature. 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. 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 1987-88 before pods dehisced. 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 chosen at random from each harvested raceme by placing the pods on a numbered grid and selecting numbers at random. Pods were moistened, opened carefully so that ovules were not lost, and examined under a dissecting microscope.

Unfertilized ovules in Astragalus (Karron 1989) and other legumes (e.g., Cooper and Brink 1940, Schaal 1980), are distinguishable in mature fruits as unexpanded, membranous ovules. Ovules were counted and scored into four categories: good seed, if filled and healthy looking; predated, if any tissue was eaten; aborted seed, if the seed coat was shriveled; and unfertilized, if ovules were less than 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 under-estimated and the percentage of unfertilized ovules may have been over-estimated. In 1988, predated seeds were classified according to the volume of seed tissue removed: <5%, 5-25%, and >25%.

Before analysis, all data were transformed to meet the assumptions of analysis of variance (ANOVA) and linear regression. Data for number of flowers, fruits, and racemes per plant and number of ovules per fruit were squareroot transformed. The arcsine-squareroot transformation (Sokal and Rohlf 1981) was applied to the data for percentage of good seed, predated seed, aborted seed, and unfertilized ovules per pod, and percentage of fruit set per plant. I used one-way ANOVA to test for a site effect on flower initiation, fruit maturation, and percentage fruit set.

Nested ANOVA (SAS Institute 1985, general linear model) was used to test for site and year effects on percentage of ovules per fruit producing good seed, predated seeds, aborted seeds, and unfertilized seeds. A significant site effect on one ovule fate may have been an

artifact of variation in the other ovule fates, because all four possible ovule fates were tested simultaneously creating a problem with degrees of freedom. 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 HSD multiple range test (STSC, Inc. 1987) was applied to all one-way ANOVAs, if F was significant. I used linear regression to test for an association of percentage seed set (good + damaged seed) with number of fruits produced per raceme, and number of fruits per plant with number of flowers per plant.

Predispersal seed predators--Several Astragalus australis var. olympicus plants at each population were inspected at peak flowering to observe and catch adult insects ovipositing in buds, flowers, and newly initiated fruits. Representatives of all insects found feeding on any plant part were collected. To determine if 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 styrofoam cup, left at room temperature until October 1987, then refrigerated at 7°C until March of 1988. At this time, the pods and gravel were inspected for larvae and adults.

To determine if the seed predator found on A. australis var.

olympicus was host specific or present on other legumes, 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, and used within 9 months of collection. Seeds for experiment 2 came from the seed predation sampling at Blue Mountain and Mount Angeles in 1988.

Preliminary studies (Kaye, in prep.) indicate that most seeds require scarification to germinate, but once scarified they germinate equally well under fluorescent light or darkness (light, 100% of 60 seeds; dark, 98.3% of 60 seeds). All seeds were scarified before testing, except where otherwise noted. Seeds were placed on 5 x 5 cm cellulose germination pads ("kimpak") moistened with distilled water (except in experiment 1) in 10 cm petri plates. Germinators with 8-hr of fluorescent light were used, and petri plate positions were rotated on the shelves every second day.

In experiment 1, three constant temperatures (5 °C, 15 °C, and 25 °C) and one alternating temperature (15/25 °C) were combined with four

osmotic potentials (0, -5, -10, and -15 bars) in a 4 x 4 factorial design. 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 cc of these solutions. 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 two weeks 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 (pseudoreplicates) of 50 seeds from each predation class (<5%, 5-25%, and >25% eaten). For comparison to undamaged seeds, equal replicates of scarified and unscarified seeds were included. After two weeks, I counted the number of living seedlings with intact radicals. The fraction of seeds scored as "predated" that were actually viable was estimated by multiplying the proportion of damaged seeds in each predation class by the percentage viability of each predation class, and summing:

percentage viable =

$$[(P_{d<5\%} \times P_{v<5\%}) + (P_{d5-25\%} \times P_{v5-25\%}) + (P_{d>25\%} \times P_{v>25\%})] \times 100$$

where P_d equals the proportion damaged and P_v 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/scarification treatment effect, and means were compared with an LSD multiple range test (STSC, Inc. 1987). Multiple comparisons were performed only after a significant F value was obtained.

RESULTS

Pollination--Fruit set was significantly reduced ($t_{14,0.05}=2.74$, $P=0.016$), but seed set per fruit was not significantly affected ($t_{14,0.05}=-0.23$, $P=0.82$) when insect pollinators were excluded from inflorescences at Blue Mountain. Even though bagging lowered fruit set by over half, seed set per fruit was unchanged (Fig. III.1).

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, but one tachinid fly was also collected. At Mount Angeles,

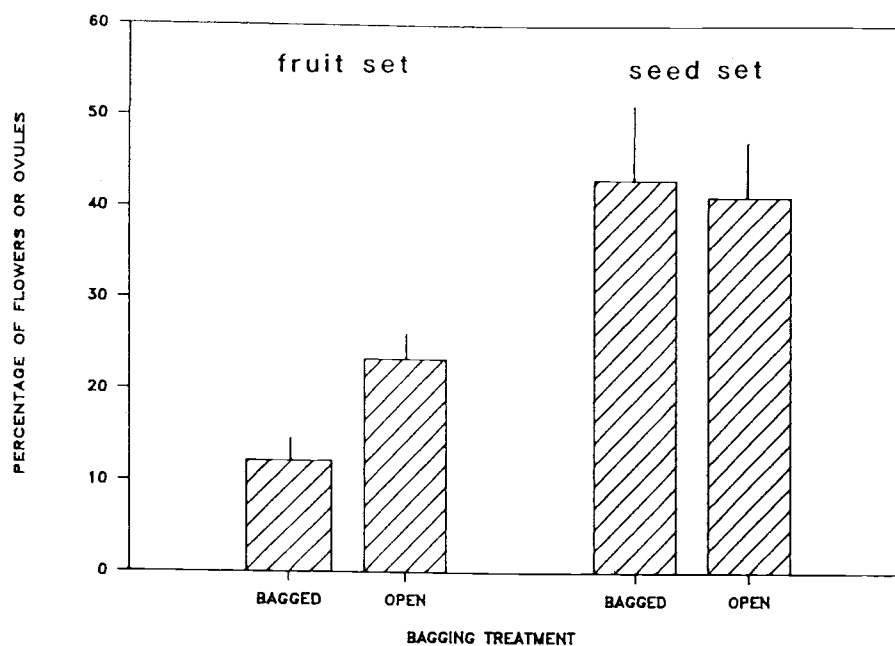


Fig. III 1. Percentage fruit set and seed set in bagged vs. open-pollinated inflorescences (\bar{X} , + 1 SE) at Blue Mountain in 1988.

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

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

Within fruits, the percentage of ovules producing good seed, predated seed, aborted seed, and unfertilized ovules also differed from site to site, but only good seed and predated seed differed between 1987 and 1988 (Table III.2). 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. III.2).

Seed predation at Blue Mountain and Mount Angeles (39.3% in 1987 and 60.9% in 1988 at Blue Mountain, 28.4% in 1987 and 49.2% in 1988 at Mount Angeles) claimed the largest percentage of ovules in both years, suggesting that seed predation is a more significant limiting

Table III.1. Mean (S.E.) inflorescence, flower, fruit, ovules, and seed production per plant and percent fruit-set per plant in 1988. Values followed by the same letter do not differ significantly at the 95% level. Data were transformed for ANOVA.

	Blue Mountain	Mount Angeles	Hurricane Hill	Average	df	F
Inflorescences	21.5(4.7)a	28.2(2.6)b	13.3(2.5)a	20.7(1.9)	2,91	8.55***
Flowers	308.9(85.5)ab	406.3(47.2)a	239.3(50.9)b	314.8(36.2)	2,91	4.98**
Fruits	32.8(8.8)a	49.5(8.5)ab	82.76(15.8)b	56.2(6.9)	2,91	3.53*
Ovules ¹	3993(1122)	4043(569)	4282(862)	4106(508)	2,72	0.53ns
Seeds	50.3(16.1)a	58.5(30.7)a	355.0(99.4)b	154.6(35.1)	2,72	17.36***
% Fruit set	15.9(3.4)a	13.9(1.7)a	45.1(4.5)b	25.8(2.0)	2,91	20.65***

¹ - Ovule means were not compared because there was no site effect in ANOVA.

*** $P < 0.0001$, ** $0.0001 < P < 0.01$, * $P < 0.05$, ns = non-significant.

Table III.2. Nested ANOVA of ovule fates at 3 sites in 1987 and 1988. See Table III.1 for explanation of significance notation.

Source of variation	d.f.	SS	F
Percentage of ovules producing good seed			
Model	3	2.10	20.30***
Site	2	1.70	24.62***
Year	1	0.40	11.67***
Error	138	4.77	---
Percentage of ovules producing predated seed ¹			
Model	2	1.49	15.69***
Site	1	0.31	6.65**
Year	1	1.17	24.73***
Error	90	4.27	---
Percentage of ovules producing aborted seed			
Model	3	2.12	27.99***
Site	2	2.06	40.78***
Year	1	0.06	2.41ns
Error	138	3.49	---
Percentage of ovules producing unfertilized ovules			
Model	3	0.87	12.53***
Site	2	0.79	17.02***
Year	1	0.08	3.55ns
Error	138	3.19	---

¹ - Hurricane Hill omitted from analysis

*** $p < 0.0001$, ** $0.0001 < p < 0.01$, ns = non-significant.

PERCENTAGE OF OVULES

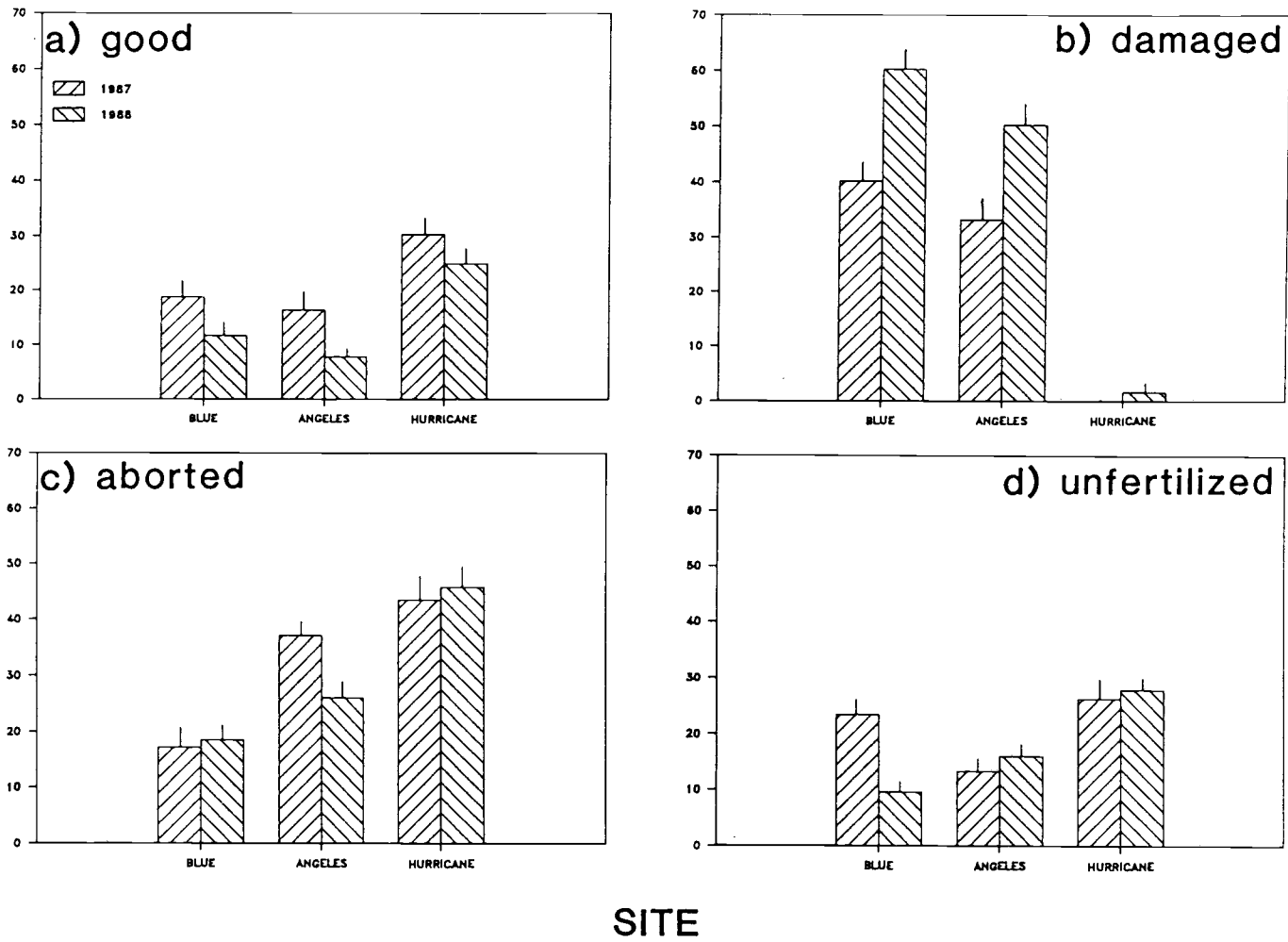


Fig. III.2. Ovule fates at Blue Mountain, Mount Angeles, and Hurricane Hill in 1987 and 1988. Percentage of ovules ($\bar{X} + 1$ SE) yielding a) good seed, b) predated seed, c) aborted seed, and d) unfertilized ovules.

factor to seed production than are seed abortion and lack of fertilization at these sites (Fig. III.2). 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 to seed abortion (Fig. III.1). 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. III.1).

The number of fruits matured per plant was strongly associated with the number of flowers per plant at Blue Mountain ($r=0.90$, $\underline{p}<0.0001$), Hurricane Hill ($r=0.95$, $\underline{p}<0.0001$), and Mount Angeles ($r=0.52$, $\underline{p}<0.01$), and when all sites were pooled ($r=0.77$, $\underline{p}<0.0001$). The regression for mean number of fruits per inflorescence with percentage seed set per fruit was significant only when all sites were pooled ($r=-0.64$, $\underline{p}<0.0001$), not within sites ($0.35>r>-0.36$, $\underline{p}>0.05$).

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. olympicus 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 and days to 50% germination, and there was a significant moisture x temperature interaction (Table III.3). At 5 °C, even a moderate decrease in osmotic potential drastically reduced germination percentage (Fig. III.3a) and rate (Fig. III.3b). At higher temperatures, however, more seeds germinated faster at low water potentials (Fig. III.3 a,b). Peak germination percentage occurred at 15/25 °C alternating temperatures and at 0.0 bars osmotic potential (distilled water). Germination was fastest at 15 °C constant temperature and 0.0 bars. 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

Table III.3. Two-way ANOVA of moisture availability and temperature effects on percentage germination and days to 50% germination of *Astragalus australis* var. *olympicus* seeds. See Table III.1 for significance levels.

Source of variation	d.f.	SS	F
Percent germination			
Main effects	6	15.13	203.65***
Osmotic potential	3	9.80	263.91***
Temperature	3	5.32	143.40***
Osmotic potential x temp	9	3.30	29.61***
Error	32	0.40	---
Days to 50% germination			
Main effect	6	19.81	112.81***
Osmotic potential	3	14.16	161.25***
Temperature	3	5.65	64.37***
Osmotic potential x temp	9	3.72	14.14***
Error	32	0.94	---

*** \underline{P} <0.0001

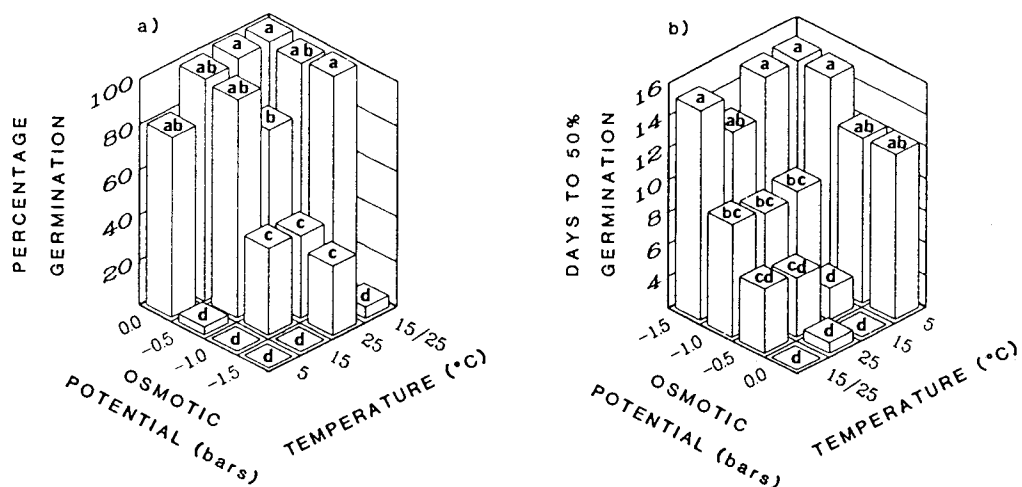


Fig. III.3. Effects of osmotic potential and temperature on a) percentage of germination and b) days to 50% of maximum germination. Higher bars in b) indicate slower germination. Axis directions are reversed in b) so that all bars can be seen. Bars with the same letter do not differ at the 95% level of probability.

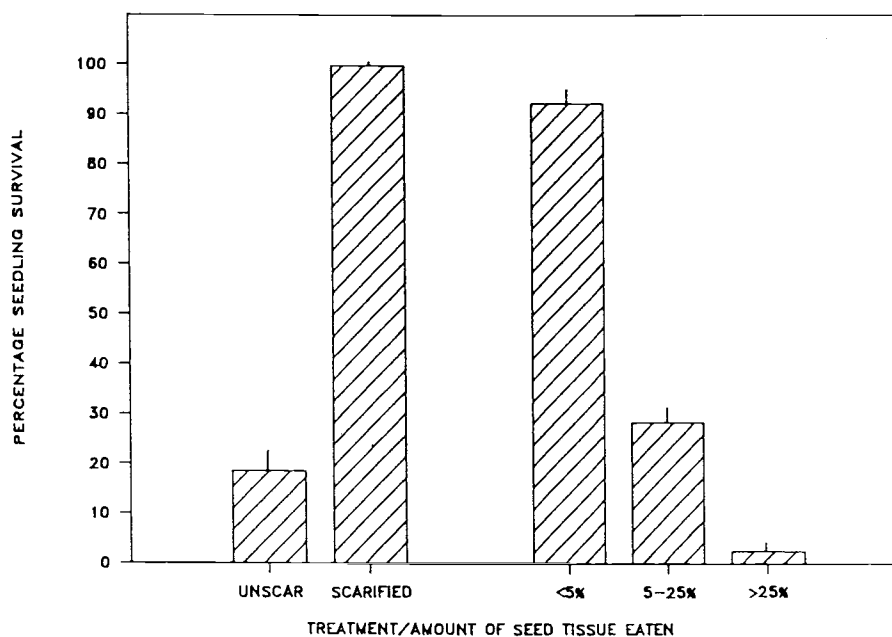


Fig. III.4. Effects of predation intensity and scarification on seedling survival after two weeks ($\bar{X} + 1$ SE). See text for explanation of predation classes. All means differed at the 95% level of probability.

seeds with larger amounts of tissue removed (5-25% and >25%) were killed (Fig. III.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 "predated" that were actually viable was estimated by multiplying the proportion of damaged seeds in each predation class by the percentage viability of each predation class, and summing. 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: $[(0.067 \times 0.922) + (0.104 \times 0.283) + (0.828 \times 0.025)] \times 100 = 11.2\%$. The distribution of 1988 predation intensities did not differ significantly between Blue Mountain and Hurricane Hill ($P < 0.05$ in t-test). Therefore, about 11% of all seeds scored as "predated" in 1988 (and probably 1987) were still viable. These seeds were also released from water-impermeable seed dormancy.

DISCUSSION

Pollination

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.

Exclusion of insect pollinators from Astragalus australis var. olympicus inflorescences reduced fruit set per inflorescence but not seed set per fruit, suggesting that this plant is typically outcrossed but genetically self-compatible. A mechanical barrier, not a genetic one, may have interfered with self-pollination. Stebbins (1957) asserts that rare plants are likely to be self-compatible. In fact, rare species of Astragalus are often self-compatible, at least in terms of seed set (Karron 1989), while common species of Astragalus may be self-incompatible (Green and Bohart 1975, Karron 1989). Inbreeding depression in seedlings from selfed seed was not tested in A. australis var. olympicus, but it limits the success of seedlings in other rare species of Astragalus (Karron 1989).

Self-compatibility may be the result of natural selection during repeated population bottlenecks (or pollinator failures) because 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). Therefore, self-compatibility in Astragalus australis var. olympicus is consistent with the view that small populations survived in the Olympic Mountains in Pleistocene glacial refugia (chapter I), and suggests that it might be able to survive future bottlenecks.

Limitation of 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 were produced in 1988. Ovules in maturing fruits were lost to predation, seed abortion, and lack of fertilization in 1987 and 1988. At the two sites where weevils were present, predation accounted for the greatest loss of ovules within fruits, followed by seed abortion, then lack of fertilization. Seed abortion still exceeded lack of fertilization where weevils were absent.

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 may 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). My data were insufficient to test these hypotheses, but some tentative conclusions can be made. For example, both pollinator and resource limitation were likely restrictions on fruit set. There was a significant 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. These hypotheses predict that the number of fruits produced should be correlated with (but less than) the number of flowers displayed per plant, because larger floral displays should mature more fruits because they attract more pollinators and represent larger energy investments in reproduction (Udovic 1981). Campbell (1987) has shown that pollinators, at least, limit fruit production in Veronica cusickii near my study sites. Both factors may interact to limit fruit production 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 in fruits of Astragalus australis var. olympicus accounted for about 1/3 of ovule losses in 1987 and 1988 at all sites combined. Studies of non-random 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 if this is generally true. In my study, a negative correlation between the number of fruits matured per raceme and percentage of seed set per fruit suggests that resources limited seed set. An insufficient amount of resources divided among an increasing number of fruits may have caused each fruit to mature fewer seeds. Water, especially, may have been limiting because of the gravelly substrate and summer drought typical of A. australis var. olympicus habitat. Selective abortion of low-quality fruits and genetically inferior seeds is common (Stephenson 1981, Weins 1984, Weins et al. 1987, Marshall and

Ellstrand 1986, Stephenson and Winsor 1986, Sutherland 1986), but it may not come into play until resources are limiting. In Cassia fasciculata, for example, low-quality fruits mature if resources are sufficient (Lee and Bazzaz 1982).

Predispersal seed predation in Astragalus australis var. olympicus was locally intense, damaging 36% and 55% of ovules in fruits 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. 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 (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 one with a sparse distribution, because larger populations of host-specific (and some generalist) seed predators can be supported (Menges et al. 1986).

Common plants may encounter predation more often and invest more energy in chemical defenses than rare plants (Menges et al. 1986). Astragalus australis var. olympicus seems to have few defenses

against the Tychius weevil, its chief seed predator. Its primitive thin-walled and glabrous fruits (Barneby 1964) offer little mechanical protection, and the nitro-toxins present in A. australis var. olympicus (Williams and Barneby 1977) do not seem to deter the Tychius larvae. 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 Oxytropis species, a genus closely related to Astragalus, but not in any other legumes, suggesting that the weevil is neither a generalist nor completely host-specific. Whether this affects recruitment in A. australis var. olympicus populations is unclear, but seed predation seems unlikely to drive A. australis var. olympicus to extinction because some sites and years partially escape predispersal seed predation. Pollinator and resource availability probably interact to limit fruit set. But once fruits are initiated, the limitations to seed production rank in this order: predispersal seed predation (if weevils are present) > resources (water?) > pollinators.

Germination

Seeds of Astragalus australis var. olympicus did not possess highly specific germination requirements. They germinated equally well in light and darkness. 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 bars were similar to those recorded for Sarcobatus vermiculatus (Romo and Edelman 1985), a halophyte! At low water potentials (-1.0 to -1.5 bars), percentage germination was greater than in one (Everitt 1983) but less than in two other (Redente 1982, Everitt 1983) common legumes. Unfortunately, comparisons with the germination responses to water stress of other alpine species are difficult to make because little is published in this area, but seeds of Oxytropis viscida (another legume) from Hurricane Hill are slightly more drought tolerant than seeds of A. australis var. olympicus (Kaye, unpub. data). 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 there is no prior evidence that any alpine seeds can germinate at temperatures below 10 °C.

Most Astragalus australis var. olympicus seeds required scarification of the seed coat to break dormancy, a trait common in Astragalus (Baskin and Quarterman 1969) and many other legumes (Rolston 1978; Grime et al. 1981, Baskin and Baskin 1988). Long-lived perennials usually do not have long-lived seed banks (Cavers 1983), but unless post-dispersal seed mortality is high, at least a portion of A. australis var. olympicus seeds produced each year are likely to lie dormant in the soil as a seed bank. Dormancy may delay germination until sufficient moisture is present (Rolston 1978), and ensure continuation of the population through periods of environmental stress, catastrophe (Harper et al. 1970), and low seed production (Baskin and Baskin 1978).

A variety of phenomena may scarify Astragalus australis var. olympicus seeds naturally, such as frost heave, solifluction, wind, ingestion by insects, rodents, birds (Amen 1966), and even 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 about 11% of all seeds eaten by larvae were released from dormancy and produced viable 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.

All reproductive processes, from pollination to seed germination seemed to function adequately to allow seedling recruitment into Astragalus australis var. olympicus populations. The weakest point in this sequence appeared to be limited dispersal of good seed due to predispersal seed predation by weevil larvae. I hypothesize that predispersal seed predation has a negative effect on population growth, but it is not responsible for the rarity of the taxon. Some A. australis var. olympicus populations occupy habitats prone to rock slides and surface disturbances by introduced mountain goats. Therefore, seed production is crucial for replacement of individuals

within populations and dispersal to new sites. Other factors not considered here, but that are important for successful reproduction, such as post-dispersal seed predation and the availability of safe sites, may limit recruitment after the pre-establishment stages.

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CHAPTER IV

DEMOGRAPHY

INTRODUCTION

Once a rare plant is protected in a natural area, its perpetuation is not necessarily assured. Weak-points in a species' life history and other biological and physical factors may threaten population viability. Effective rare plant conservation benefits from knowledge of population trends and demography (Davy and Jeffries 1981). Recent symposia on conservation of rare plants have included a number of papers about population monitoring that demonstrate how demographic studies improve management strategies (e.g., Morse and Henefin 1981, Synge 1981, Elias 1987). A single visit to a rare plant population to assess its condition is insufficient to predict its future, and generalizations from studies of other rare and common plants can only be used with caution (Fiedler 1986).

Fewer than 4000 individuals of Astragalus australis var. olympicus distributed among four population centers are known (Sheehan and Kaye 1986). This narrowly endemic taxon is listed as threatened by the Washington Natural Heritage Program and is a Category 2 candidate for listing as threatened or endangered on the Federal Register (U. S. Fish and Wildlife Service 1985). Its habitat of gravelly slopes and ridges above 1450 m in the northern Olympic Mountains is harsh but relatively stable. All populations are within the boundaries of Olympic National Park.

Although National Park Service management priorities are often based

on the most immediate problems or those most in the public view (Bratton 1981), National Park Service policy states that active management programs may be carried out "to perpetuate the natural distribution and abundance of threatened or endangered species" (Morse and Henefin 1981). The present study was unusual in that it was not initiated to ameliorate an existing crisis, but to provide baseline demographic information on a National Park resource in a way relevant to future conservation.

While information on the population's current age structure can provide some insight, a single look at a population does not reveal whether it was, is, or will be increasing or decreasing in size. Where plants cannot be aged, a stage- (or size-) based analysis of population structure coupled with long-term monitoring may be necessary to understand population trends. The transition matrix model for population growth adopted in this study was selected for its ability to estimate future trends and evaluate the impact of changes in fecundity and survival. The model is based on life history stages rather than on age (Lefkovitch 1965).

The specific objectives of this study fall into two groups. First, to describe the stage-class structure of the populations, their trends, impact by goats, and seedling mortality. Second, to use a transition matrix model to project the future direction of change. The model was also used as a tool to understand which life-stages affected population growth the most (sensitivity analysis), and show how manipulation of fecundity and seedling survival affected

projected population viability.

MATERIALS AND METHODS

Study sites--Three of the four known population areas of Astragalus australis var. olympicus were selected for study: Unicorn Peak (48°00'32"N, 123°31'15"W and 48°01'16"N, 123°30'49"W), Hurricane Hill (47°59'50"N, 123°32'56"W), and Blue Mountain. At Blue Mountain two subpopulations were sampled because the population is discontinuous: the summit area (47°57'17"N, 123°15'30"W) and the NE buttress (47°57'38"N, 123°15'10"W). These sites represent the maximum east-west range limits of the taxon.

Permanent plots--In 1985, three permanent plots were established near the population center at Unicorn Peak, two at Blue Mountain summit, and three at Blue Mountain NE buttress. Two plots were placed at Hurricane Hill in 1986. The plots were 5 x 5 m and staked with iron rebar in each corner. During sampling, each plot was marked into a grid of twenty-five 1 m square subplots with string laid across at 1 m intervals. Through 1986 the number of Astragalus australis var. olympicus plants in each subplot was counted in July. Individuals less than and greater than 10 cm in diameter were tallied separately. No effort was made to locate seedlings. In 1987 and 1988 individual plants were mapped to scale in July and September, their reproductive status was noted, and a thorough search was made for seedlings. The microsite of each seedling was classified as either coarse gravel (average particle size > 0.75 cm), fine gravel (average size < 0.75 cm), organic matter, beneath another plant, or along the margin of a

large (>5 cm) rock. In all years, damage to plants by mountain goats was noted. Grazing in 1987 and 1988 was categorized into classes of plant tissue removed: 1-5%, 5-25%, 25-50%, 50-75%, and 75-100%. A Wilcoxon signed-rank test was used to test the null-hypothesis that the number of non-seedling plants per plot and over all plots pooled remained the same from the year of plot establishment to 1988.

Transition matrices--The transition probability of each stage class--seedling (S), vegetative (V), and reproductive (R)--was calculated with data pooled from the two to three plots within each site. Fecundity was estimated based on the number of seedlings in 1988 per 1987 reproductive individual. These values were entered into a 3 x 3 transition matrix. The matrix was then post-multiplied by the 1988 stage-distribution vector and iterated ten "years"--sufficient time to achieve a stable stage distribution and equilibrium rate of increase (λ , the dominant eigenvalue of the matrix). When λ is greater than one, the population will increase. A λ value of less than one means the population will decline. Construction and mathematics of similar matrices have been described in detail elsewhere (e.g., Lefkovitch 1965, Keyfitz 1968, Bierzychudek 1982, Caswell 1982).

To compare the stable stage-class distribution of the matrix model with the observed 1988 distribution, I calculated δ , the index of dissimilarity (Keyfitz 1968). δ is the sum of the positive differences of the distribution percentages. It is a convenient estimate of the difference between the stable age distribution and

the observed distribution and may be used as a measure of the percentage of the population that is in the "wrong" stage-class (Bierzychudek 1982). In short, delta describes how well the model and the observed population fit each other.

A sensitivity analysis similar to those done by Hartshorn (1975), Enright and Ogden (1979), and Bierzychudek (1982) was performed by lowering the survival rate of each class 10% and 50% and observing the effect on lambda. Also, where populations were shown to decline in the model, I determined the fecundity and seedling survival probability required to bring lambda up to one.

RESULTS

Population structure, damage by goats, and trends--The total number of non-seedling plants decreased in nine out of ten plots since the plots were established (Fig. IV.1). In six of the nine plots, the decrease was significant at the 95% level of probability. The number of plants monitored from 1985 to 1988 decreased significantly when all plots were pooled (Fig. IV.2), excluding Hurricane Hill, because plots there were established a year late. The decrease was still significant if Hurricane Hill plots were included and the comparison was made between 1986 and 1988. The proportion of large and small plants fluctuated over the four years of sampling, but may have been related to the number of injured plants. Small plants increased in number and large plants decreased in number as injury increased (Fig.

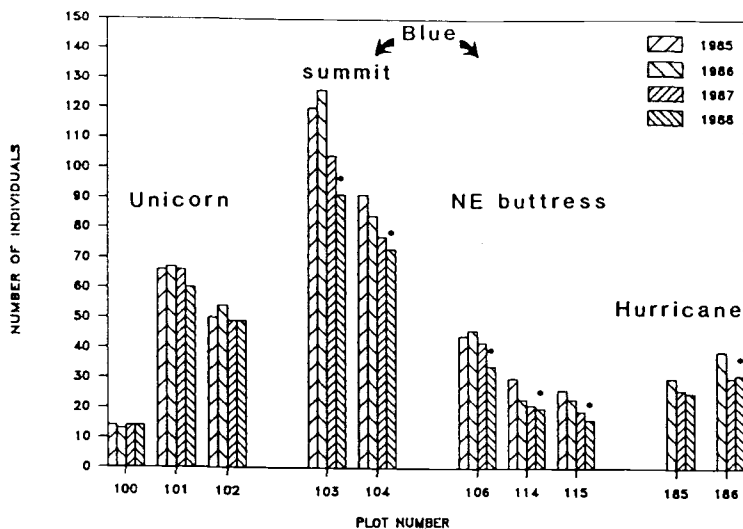


Fig. IV.1. Number of non-seedling individuals in each permanent plot (grouped by site) from 1985 through 1988. Asterisks indicate significant differences at the 0.05 level of probability between 1985 and 1988. Plots at Hurricane Hill were established in 1986.

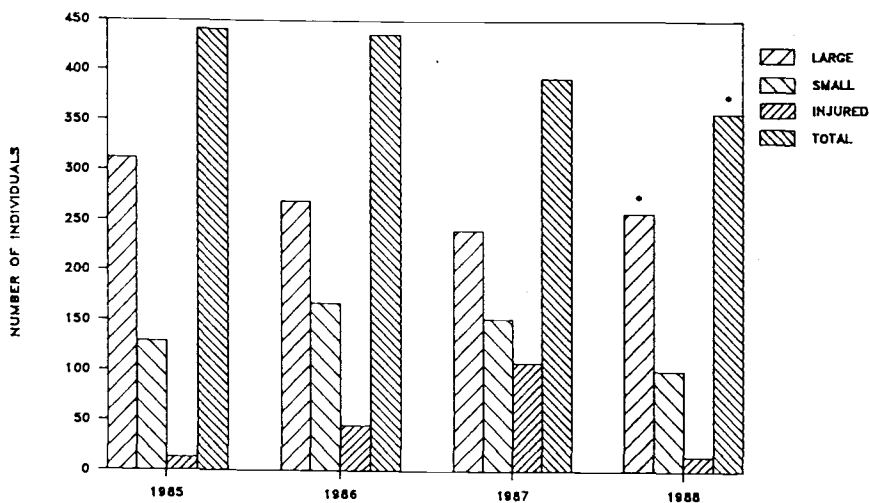


Fig. IV.2. Number of non-seedling individuals in all plots pooled from 1985 through 1988 (excluding Hurricane Hill, because plots there were not established until 1986). Asterisks indicate significant differences at the 95% level of probability.

IV.2), suggesting that injured large plants became smaller, and injured small plants stayed small.

The effect of mountain goats on plant survival depended on whether plants were grazed or trampled in goat wallows. In 1987, 78.8% of the non-seedling plants monitored in plots 101 and 102 at Unicorn Peak were grazed to some degree. This had little effect on plant survival, however. In fact, more ungrazed plants (16.7%) were dead in 1988 than grazed plants (4.5%) (Table IV.1). On the other hand, many (25.5%) reproductive plants that were grazed in 1987 resprouted as vegetative plants in 1988, but no ungrazed reproductive plants regressed in this way (Table IV.1). Goat wallows, though less common, were more likely than grazing to kill Astragalus australis var. olympicus plants. In 1986, goat wallows were found in three permanent plots. Two wallows at Blue Mountain NE buttress were responsible for two plant deaths, one in plot 6, subplot #13, and the other in plot 114, subplot #11. At Unicorn Peak, a wallow overlapping plot 102 killed two plants in subplot #10. No other wallows were observed inside permanent plots, but during a 1987 census of goat wallows in and within 50 meters of Astragalus australis var. olympicus populations, I located 129 wallows at Blue Mountain NE buttress, none at Blue Mountain summit, 39 at Unicorn Peak, and none at Hurricane Hill.

The stage-class structure of Astragalus australis var. olympicus populations was skewed toward reproductive plants at all sites in 1987 and 1988 (Fig. IV.3). Only at Blue Mountain summit and

Table IV.1. Grazing and plant survival at Unicorn Peak (plots 101 and 102), 1987. See text for description of grazing classes. Both plots combined contained 113 plants.

grazing class	%-in class 1987	%-dead in 1988	%-reproductive in 1987 returning vegetative in 1988
ungrazed	21.2	16.7	0.0
1-5%	5.3	16.7	50.0
5-25%	3.5	0.0	0.0
25-50%	10.6	8.3	33.3
50-75%	19.5	0.0	0.0
75-100%	39.8	4.4	34.5
total			
grazed	78.8	4.5	25.5

Table IV.2. Transition matrices from 1987 to 1988 for Unicorn Peak; Blue Mountain summit and NE Buttress; Hurricane Hill; and all plots pooled. Stage classes are abbreviated as S (seedling), V (vegetative), and R (reproductive). The values shown indicate the fecundity of each stage-class (top row) or proportion of each stage-class in 1987 that make the transition to each stage-class in 1988.

Stage-class in 1988	Stage-class in 1987								
	Unicorn Peak			Blue Mountain, summit			Blue Mountain, N.E. Buttress		
	S	V	R	S	V	R	S	V	R
S	0.00	0.00	0.04	0.00	0.00	0.32	0.00	0.00	0.03
V	0.11	0.58	0.25	0.00	0.52	0.03	0.17	0.67	0.15
R	0.00	0.30	0.74	0.00	0.26	0.95	0.00	0.12	0.71
	Hurricane Hill			All plots pooled					
	S	V	R	S	V	R			
S	0.00	0.00	0.40	0.00	0.00	0.21			
V	0.12	0.31	0.07	0.12	0.54	0.11			
R	0.00	0.69	0.90	0.00	0.30	0.85			

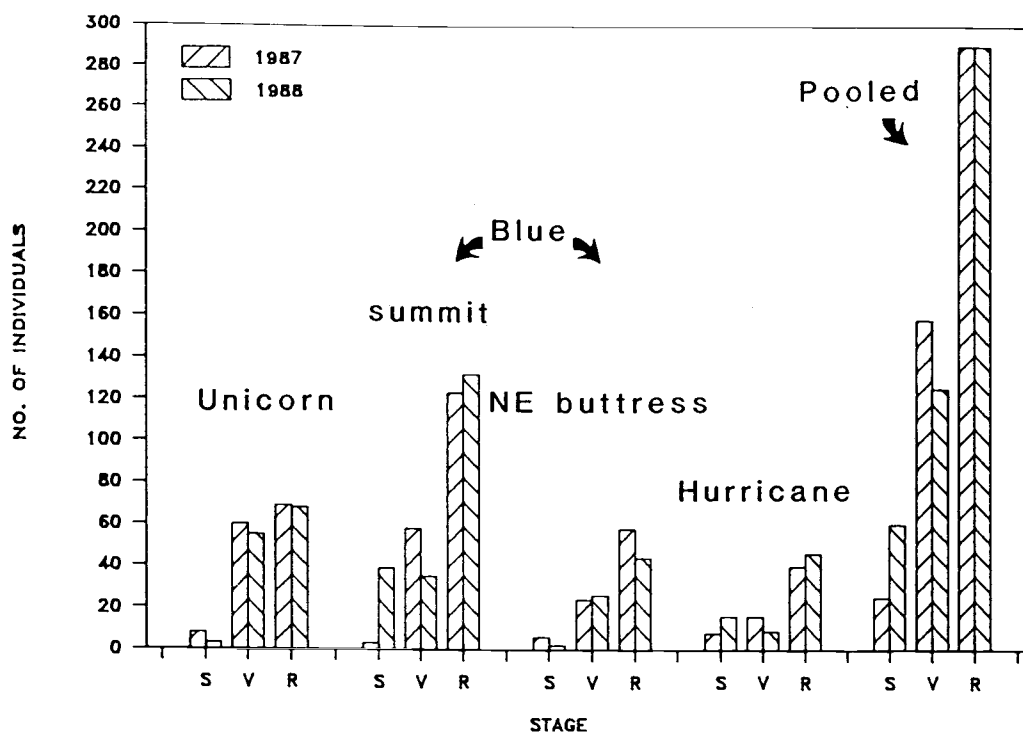


Fig. IV.3. Population stage-class structures in 1987 and 1988 at Unicorn Peak, Blue Mountain, Hurricane Hill, and all sites pooled. S=seedlings, V=vegetative plants, R=reproductive plants.

Hurricane Hill in 1988--the better seedling year--did the number of seedlings exceed the number of vegetative plants (Fig. IV.3).

Seedlings--Many seedlings of both the 1987 and 1988 cohorts died by the September 1988 sample. There were 25 seedlings in the 1987 cohort when all plots were pooled, but only three were alive in September 1988 (Fig. IV.4). The mortality rate was fairly constant for this cohort, but winter mortality was somewhat higher than summer mortality. The 1988 cohort dropped from 61 to 36 seedlings in its first summer, yielding a higher summer mortality rate than the 1987 cohort (Fig. IV.4).

The effects of microsite on seedling survival are unclear, partially because of the small and unequal sample sizes. No seedlings in the 1987 cohort that germinated in coarse gravel (six seedlings) or organic matter (two) survived through September 1988. The number of seedlings that germinated in fine gravel, the largest proportion, dropped from eleven to one over the same period. The most successful seedlings from the 1987 cohort were those that established at a rock margin: out of six, two survived through September 1988 (Fig. IV.5). Seedling microsite and survival in the 1988 cohort differed from the 1987 cohort in that the greatest proportion of seedlings were found in coarse (26 seedlings) rather than fine (11) gravel. Mortality of the 1988 cohort on the different microsites was variable over the first summer (Fig. IV.5). Only six of the sixteen seedlings growing in organic matter survived, but three out of four that germinated under another plant were still alive in September 1988. Although

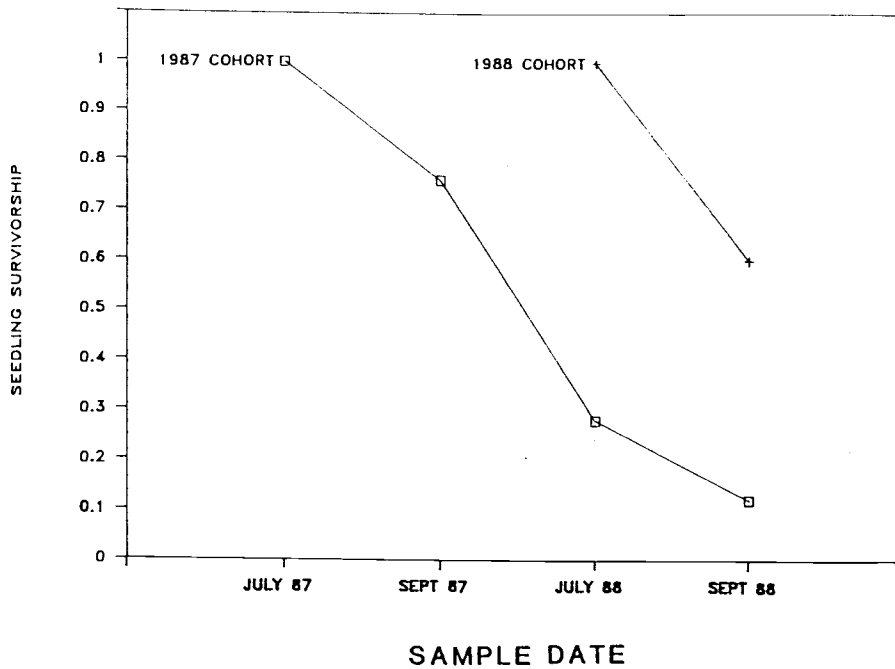


Fig. IV.4. Survivorship curves for the 1987 (squares) and 1988 (crosses) seedling cohorts. There were 25 seedlings in the 1987 cohort, and 61 in the 1988 cohort.

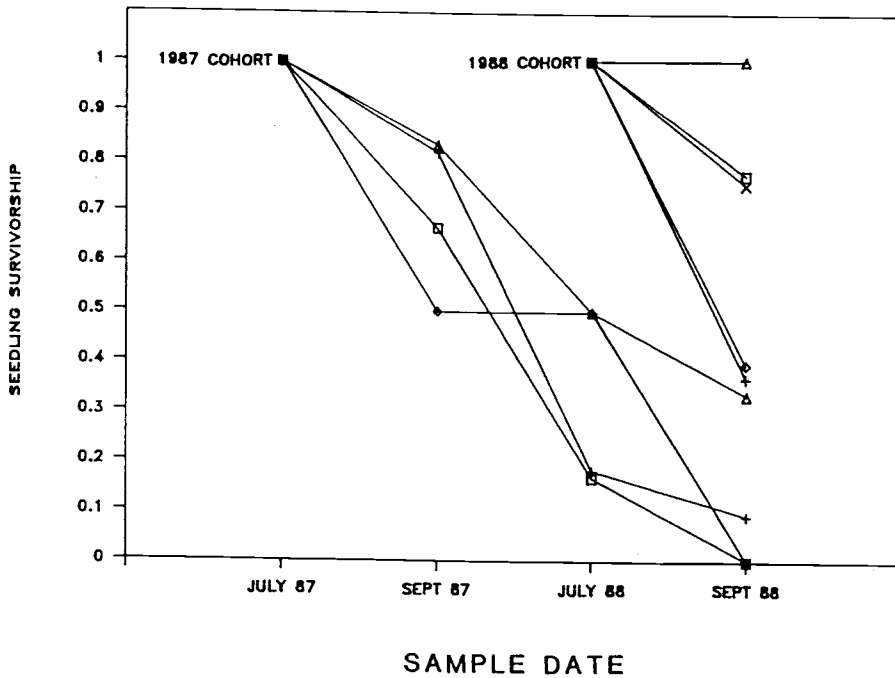


Fig. IV.5. Survivorship curves for the 1987 and 1988 seedling cohorts in each microsite. Microsite symbols are as follows: squares=coarse gravel, cross=fine gravel, diamond=organic matter, triangle=rock margin, x=beneath another plant (not encountered in 1987).

only three of the seedlings established along a rock margin, they all survived the first summer (Fig. IV.5).

Transition matrices--The transition matrices based on the 1987-1988 survival and fecundity of individual Astragalus australis var. olympicus plants (Table IV.2) indicate that populations would decline at Unicorn Peak, Blue Mountain summit, and Blue Mountain NE buttress, but the Hurricane Hill population would increase, given no change in transition probabilities. Lambda, the dominant eigenvalue of the matrix and the equilibrium growth rate ($\lambda = e^r$), was greater than one only at Hurricane Hill (Table IV.3). When lambda is greater than one, a population is projected to increase. A population would decrease if lambda is less than one. The index of dissimilarity, delta, which compares the model's projected stable stage-class distribution and the actual 1988 distribution, ranged from 3.5% to 12.5%, "averaging" 4.1% for the pooled matrix (Table IV.3). The rate of increase, lambda, was most sensitive to decreases in survival of reproductive individuals and least sensitive to decreases in seedling survival at all sites (Table IV.4).

For those populations projected to decline, the fecundity rate had to be raised about 20- to 110-fold to bring lambda up to 1.000 and "rescue" the populations (Table IV.5). Because seedling survival at Blue Mountain summit was zero from 1987 to 1988, no increase in fecundity could theoretically save this population. If seedling survival alone were increased five-fold at Blue Mountain NE buttress, lambda would reach 1.000 there (Table IV.5). At Blue Mountain

Table IV.3. Equilibrium growth rate (λ) for each population, and the index of dissimilarity (Δ) between the stable age distribution and the actual 1988 distribution. Only positive differences are summed in Δ .

Population	Stage-class	Stable distribution (%)	Actual 1988 distribution (%)	Δ (%)
Unicorn Peak $\lambda=0.947$	S	2.6	2.4	0.2
	V	39.8	43.7	--
	R	57.6	54.4	3.6
				$\Sigma=3.8$
Blue Mountain, summit $\lambda=0.970$	S	23.3	18.9	4.4
	V	5.2	17.0	--
	R	71.4	64.1	7.3
				$\Sigma=11.7$
Blue Mountain, N.E. Buttress $\lambda=0.831$	S	2.0	2.8	--
	V	48.6	36.1	12.5
	R	49.4	61.1	--
				$\Sigma=12.5$
Hurricane Hill $\lambda=1.021$	S	25.0	22.5	2.5
	V	11.2	12.7	--
	R	63.8	64.8	1.0
				$\Sigma=3.5$
All plots pooled $\lambda=0.948$	S	13.9	12.6	1.3
	V	22.2	26.3	--
	R	63.9	61.1	2.8
				$\Sigma=4.1$

Table IV.4. Equilibrium growth rate (λ) resulting from simulated decreases in survivorship of each *Astragalus australis* var. *olympicus* stage class individually. Value in parentheses is the percent decrease from the actually observed lambda.

rate of increase (lambda)					
	Unicorn $\lambda=0.947$	Blue-summit $\lambda=0.970$	Blue-NEB $\lambda=0.831$	Hurricane $\lambda=1.021$	Pooled $\lambda=0.948$

10% decrease in survival of:					
seedlings	0.946(0.1%)	0.970(0.0%)	0.830(0.1%)	1.017(0.4%)	0.947(0.1%)
vegetative	0.914(3.3%)	0.966(0.4%)	0.799(3.2%)	1.006(1.5%)	0.931(1.8%)
reprod.	0.889(5.8%)	0.877(9.3%)	0.788(4.3%)	0.942(7.9%)	0.876(7.2%)
50% decrease in survival of:					
seedlings	0.945(0.2%)	0.970(0.0%)	0.829(0.2%)	1.000(2.1%)	0.940(0.8%)
vegetative	0.812(13.5%)	0.957(1.3%)	0.733(9.8%)	0.955(6.6%)	0.880(6.8%)
reprod.	0.701(24.6%)	0.564(40.6%)	0.698(13.3%)	0.668(35.3%)	0.661(28.7%)

Table IV.5. Simulated fecundity and seedling survival rates required to raise λ to 1.000 if all other transition rates are held constant. Value in parentheses is the ratio of the simulated rate over the observed survival or fecundity rate. The Hurricane Hill population is not shown because λ was greater than 1.0 there.

	Unicorn	Blue-summit	Blue-NEB	Pooled

fecundity	0.93(21.6)	b	3.75(110.3)	1.04(5.0)
seedling survival	a	0.18(c)	0.84(5.1)	0.60(5.0)

a - a survival rate of 1.00 resulted in $\lambda > 1.000$.

b - actual seedling survival was 0.0, so no amount of increase in fecundity could raise lambda.

c - undefined

summit, where no seedlings survived from 1987 to 1988, the survival rate would need to be raised to 18% to stop population decline. At Unicorn Peak, however, even if seedling survival was 100%, lambda would still be less than one and the population would continue to follow its projected path of decline.

DISCUSSION

Population trends

The significant decrease in Astragalus australis var. olympicus numbers within permanent plots from 1985 to 1988 at all monitored populations is reason for concern. The cause of this decline is unknown. Seed production was reduced by weevil larvae at Blue Mountain and Mount Angeles (chapter II), but the impact of this seed loss on population trends was not investigated.

Grazing and wallowing by introduced mountain goats (Oreamnos americanus) may have caused some Astragalus australis var. olympicus individuals to regress from a reproductive state to a vegetative state or die. Grazing by goats on Campanula piperi and Senecio neowebsteri, other endemics of the Olympic Mountains, and Aster paucicapitatus, a species found here and also on Vancouver Island, British Columbia, reduces leaf length, flower production, and productivity (Pike 1981). Wallows and trampling caused by goats prevent establishment of typical community dominants of Olympic Mountains subalpine meadows (Reid 1983). The infrequent and sporadic nature of these goat disturbances in Astragalus australis var. olympicus populations, however, makes goat impact an unlikely

explanation for recent population declines, especially at Hurricane Hill where goat impact was consistently low. A. australis var. olympicus was probably rare in the Olympic Mountains before mountain goats were introduced.

Perhaps a better explanation for the population decline from 1985 through 1988 is low snowpack and summer drought during these years. Annual precipitation at Port Angeles, Clallam County, Washington (13 km from Unicorn Peak) has been variable over the last 30 years (1958-1988), but was below average during the period of this study (1985-1988) (Fig. IV.6). Insufficient summer soil moisture may have reduced the photosynthetic capacity, reproductive output, seed set, and seedling survival of Astragalus australis var. olympicus, lowering recruitment and killing established individuals. Reduced snowpack would have exposed soils on the windswept slopes and ridges where A. australis var. olympicus grows, making the plants susceptible to wind abrasion, desiccation, and frost heave.

Population structure

The stage-structure of Astragalus australis var. olympicus populations was dominated by reproductive plants. Seedlings were often under-represented. Reproductive individuals were often larger than vegetative plants, suggesting they may be older. Unfortunately, the plants do not record annual growth increments, so their age could not be determined. Judging from the large woody root crown and extensive root system of many plants, some may have reached considerable age--at least several decades. I suspect that

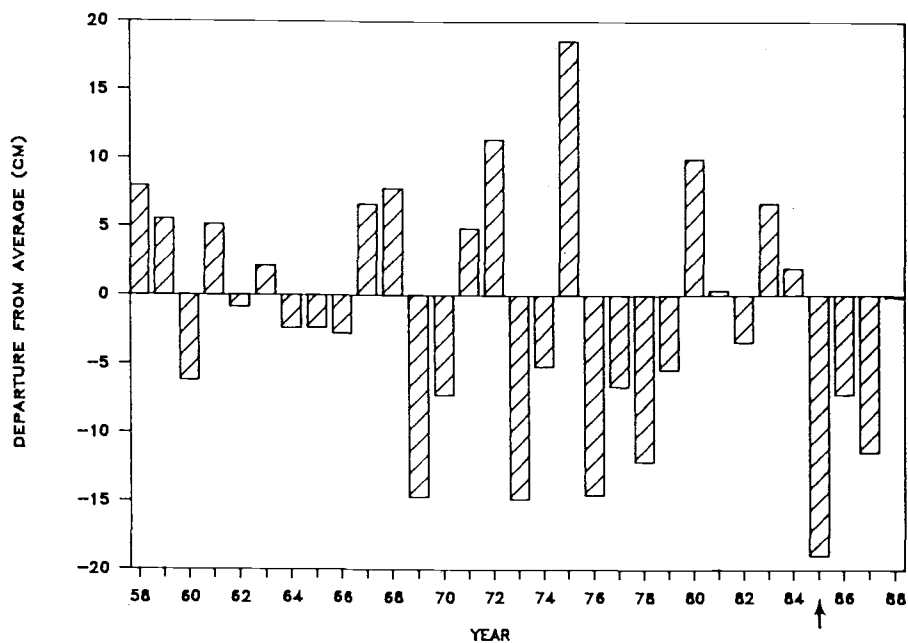


Fig. IV.6. Departure from average annual precipitation (64.47 cm) for the years 1958-1988 at Port Angeles, Clallam Co., Washington, at sea-level approximately 13 km from Unicorn Peak, the nearest study site. Data are from Climatological Data Annual Summaries (U. S. Department of Commerce, 1958-1988). Arrow denotes initiation of monitoring.

Astragalus australis var. olympicus plants do not become reproductive until they are five to fifteen years old. Dominance by large reproductive individuals suggests recruitment is low (Harper 1977), and is consistent with the observed low rate of seedling establishment.

Seedling establishment

Low seedling establishment and survival is not unique to Astragalus australis var. olympicus, but is typical of plants at high elevations (Bliss 1971). Seedling survival of A. australis var. olympicus depended on the microsite where the seed germinated. After two summers, 95% of the seedlings in the 1987 cohort in surficial organic matter and open fine or coarse gravel were dead. Thirty-three percent of those that established along the margin of a large rock survived. Summer drought and winter needle ice may be responsible for most alpine seedling mortality (Osburn 1961). Seedling establishment in the polar semidesert is restricted to moss or lichen mats and desiccation-cracks where summer moisture is more dependable (Bell and Bliss 1980). Mortality of Trifolium nanum seedlings in open gravels in an alpine area of the Colorado Rockies is attributed to low soil moisture, while death of seedlings within cushion plants is laid to competition (Bonde 1968). Needle ice and frost heave limit seedling establishment in subalpine regions of British Columbia (Brink 1964). As with Sedum lanceolatum (Jolls and Bock 1983), both summer drought and winter freezing disturbance probably restricted survival of A. australis var. olympicus seedlings to specific microsites, such as rock margins, where drought and freezing

disturbance were reduced.

Population model

The projected future trends were no more optimistic than the past decreases. The matrix models predicted that Astragalus australis var. olympicus populations would continue to decline. Equilibrium-population growth rates (λ) ranged from 0.831 to 1.021, and "averaged" 0.948 when all plots were combined into a single matrix. Only the Hurricane Hill population was projected to increase. Generalizations about the population dynamics of rare species are difficult to make. The few other rare species that have been modeled with transition matrices show that population dynamics are related more to life-history than they are to the geographic range of a taxon. Populations of rare Pedicularis furbishiae may have high equilibrium growth rates ($\lambda = 2.05$) typical of weedy, fugitive plants, reflecting a dependence on natural disturbance for establishment (Menges 1986). Rare species of Calochortus have populations with relatively low or high equilibrium growth rates (0.960-1.302), depending on the year and species (Fiedler 1987). Equilibrium growth rates of near 1.0, such as those found for Astragalus australis var. olympicus populations, may be typical of K-selected species (Enright and Ogden 1979) with low recruitment in a relatively stable environment.

Implications of sensitivity analyses

The sensitivity analyses indicated that Astragalus australis var. olympicus population growth was most sensitive to decreases in

survival of reproductive individuals. In other words, using lambda as an index, the reproductive stage-class contributed the most to the fitness of all populations, and seedlings the least. This was not surprising because the populations generally had over 60% reproductive individuals and any decrease in their survival would lower population numbers directly as well as indirectly through decreased recruitment. In contrast, other empirical sensitivity analyses working with trees (Hartshorn 1975, Enright and Ogden 1979) and herbaceous temperate forest perennials (Bierzychudek 1982) show that late pre-reproductive stages have the greatest impact on population growth rate. Another method for determining sensitivity incorporates the stable population structure and reproductive value (right and left eigenvalues of the matrix [Caswell 1978]). Studies that have used this method also have found the late pre-reproductive stages to be most important (Caswell 1978, Pinero et al. 1984). A. australis var. olympicus populations seem unusual in this respect.

Considering the importance of reproductive individuals to population fitness, damage by goats and hikers, if increased, has the potential to degrade populations quickly. Astragalus australis var. olympicus population growth rates may be most sensitive to survival of reproductive individuals, but population viability ultimately depends on seedling success. Increases in seedling recruitment would have to be substantial to arrest the projected declines. For the pooled matrix, a five-fold increase in seedling survival was necessary to stop population decline. If the observed population sizes continue to deteriorate, it may be desirable to improve seedling recruitment.

This could be accomplished by removing mountain goats from the range of A. australis var. olympicus, controlling predispersal seed predators, and sowing extra seeds and tending established plants. Goat removal is already underway, however, and the unknown taxonomic status of the primary seed predator (Tychius sp.) leaves open the possibility that it is just as rare and threatened as A. australis var. olympicus. Do we control one declining rare organism at the expense of another? The most effective approach might be to manipulate individuals directly. Seeds could be sown in favorable microsites, such as along rock margins, and seedlings and other plants could be watered during the summer. Supplemental fertilizer might also be beneficial.

Assumptions of the model

Two assumptions should be met to project the matrix in time. The transition of an individual from one year to the next must depend on its status in the first year and not on the state of that individual in any previous year (a first-order Markov process), and the transition probabilities must remain constant (Bierzychudek 1982). Conclusions drawn from transition matrix models that incorporate only one transition are only as good as that transition is typical of the future (Menges 1986). Unfortunately, as with many studies that use transition matrix models (but see Bierzychudek 1982, for an exception), I have not tested explicitly whether or not my data meet these assumptions.

Although the Astragalus australis var. olympicus transition matrices

were based on the 1987-1988 transition only, the population trends they projected were generally consistent with the observed 1985-1987 declines, suggesting that the transition probabilities used in the model are not seriously in error. In addition, the index of dissimilarity values (δ) that compared the predicted stable distributions with the actual distributions ranged from 3.4% to 12.7%, a low to modest amount of disagreement. Rarity may be the result of long term population decline punctuated by chaotic flushes of recruitment, a phenomenon difficult to detect in natural populations (Vandermeer 1982). Nevertheless, the stage-based transition matrix model seems well suited as a tool to provide short term predictions, sensitivity analyses, and estimates of seedling establishment and survival rates needed to restore declining A. australis var. olympicus populations.

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CHAPTER V

SYNTHESIS

The preceding studies of the autecology, reproductive ecology, and population dynamics of Astragalus australis var. olympicus allow an overall view of this taxon's biology to emerge. The original goal of this project was to describe several facets of the biology of A. australis var. olympicus to improve the ability of the National Park Service to manage for its perpetuation. In addition, it was hoped that these studies would shed some light on the rarity of the taxon.

This is a plant of southeast to southwest facing alpine-subalpine meadows and gravelly slopes underlaid by calcareous parent materials. Structurally, Astragalus australis var. olympicus seemed well adapted to poorly developed, thin, and unstable calcareous soils because it had a widely spreading, mycorrhizal root system that penetrated deep into gravels and bedrock crevices. Easily-detached branches lowered its chances of being pulled from the ground by sliding rocks (chapter II). It is geographically restricted in the sense that it is endemic to the Olympic Mountains of Washington, and it is rare even there, being found only in four population centers in the northeast portion of the mountain range.

Its local distribution was influenced by competition with associated vascular plants and environmental factors (chapter II). The relative importance of each shifted with plant community-type. Competition appeared to be strong in a community-type with relatively high cover of grasses and forbs and stable, nutrient rich soils. Environmental

factors such as abundance of surface gravels and soil nitrogen were correlated with Astragalus australis var. olympicus abundance in this community type. In a community-type with low cover of associates and less stable and less nutrient rich soils, competitive effects were weaker, but still detectable with nearest neighbor analysis. The significant environmental factors in this community-type shifted to topographic and soil texture variables such as slope, abundance of bedrock, and soil clay.

The effects of interspecific competition and environmental factors on Astragalus australis var. olympicus reproduction were not measured directly. However, plants with closer neighbors had fewer flower-stalks (chapter II) and plants with fewer flowers had fewer fruits (chapter III), suggesting that competition might reduce seed production. Ovules were found to meet several fates (lack of fertilization, abortion after fertilization, predispersal predation, or successful seed formation), and the proportion meeting each fate differed from site to site and year to year. Consumption by weevil larvae accounted for the greatest loss of ovules from fruits overall, abortion was second, and fertilization was third in importance (chapter III). Premature seed abortion may have been due to insufficient resources, such as water, during periods of summer drought. Water stress in A. australis var. olympicus was greater where associated species were most abundant (chapter II). Therefore, interference by associated species may have aggravated the effects of drought.

Astragalus australis var. olympicus individuals do not reproduce vegetatively. Therefore, they must produce seeds to replace themselves. Between 1985 and 1988 the total number of A. australis var. olympicus individuals in permanent plots declined (chapter IV). A transition matrix model based on individuals mapped in 1987 and 1988 predicted that this decline will continue (chapter IV). The observed mortality may have been caused by disturbance from introduced mountain goats (at least locally), other animals, hikers, a series of dry years, or a combination of these or some other factors. Regardless of the reason, the loss of plants was met with inadequate replacement by seedlings. It is doubtful that poor seed germination made seedlings uncommon. Although seeds required scarification to germinate, natural process that abrade seeds, including partial tissue removal by weevil larvae (chapter III) were probably sufficient to release most seeds from dormancy. Instead, it is hypothesized that predispersal (and post-dispersal?) seed predation and high seedling mortality (chapter IV) combine to restrict recruitment in most years. The successful establishment of new individuals may be a sporadic event typically followed by a series of years during which the population slowly declines.

The geographic rarity of Astragalus australis var. olympicus seems best explained in terms of its phytogeographic history, rather than an inability of the plants to reproduce. The taxon was probably isolated in the Olympic Mountains in the time since the Pleistocene when adjoining populations went extinct (chapter I). Populations of this "stranded" form may have experienced repeated bottlenecks in

small refugia during Pleistocene glaciations, a process that could have selected for calcicolous ecotypes (if the refugial habitat was calcareous) and self-compatibility (chapter III). Today the distribution *A. australis* var. *olympicus* in the Olympic Mountains is tied strictly to the presence of carbonates in the soil. Within a population, however, competition and characteristics of the physical environment influence its abundance (chapter II). Although some problems with seed production (chapter III) and seedling mortality (chapter IV) may restrict population growth and dispersal, a shortage of environmentally-suitable calcareous habitats may explain its rarity.

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