

SEED PRODUCTION, DISPERSAL, PREDATION, AND GERMINATION
OF SEVEN HIGH ELEVATION ROCKY MOUNTAIN LEGUME SPECIES

by

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ABSTRACT

A three year study of seed production, dispersal, predation, and germination was done on seven high elevation Southern Canadian Rocky Mountain legume species: *Astragalus alpinus*, *A. bourgovii*, *A. robbinsii*, *A. vexilliflexus* var. *nubilus*, *Hedysarum sulphurescens*, *Oxytropis podocarpa*, and *O. sericea*.

Initiation of vegetative and reproductive activity was one to two weeks earlier each year and was related to the successively warmer springs each year.

Seed production varied with species and year. The number of viable seeds produced each year was constantly high for *Oxytropis podocarpa*, whereas the number of viable seeds produced by *O. sericea*, *Hedysarum sulphurescens* and the *Astragalus* species was variable. The number of abnormal or aborted seeds was low except for *Astragalus alpinus* in 1985, *Astragalus bourgovii* in 1983 and *O. sericea* in each year. Seed production of the *Astragalus* and *Hedysarum* species was reduced by pre - dispersal seed predation by species of *Bruchophagus* (Hymenoptera : Eurytomidae). The magnitude of seed damage was related to habitat. Pre - dispersal seed predation by weevils (Coleoptera : Curculionidae) was low for the *Oxytropis* species. However, seed predation of

O. podocarpa by ptarmigan (*Lagopus lagopus*) was high in two populations each year. Foraging by elk (*Cervus elaphus*), rocky mountain bighorn sheep (*Ovis canadensis*) and the golden mantel ground squirrel (*Spermophilus lateralis*) also reduced seed production.

Seed germination varied with species, population and year. All of the viable seeds of *H. sulphurescens* germinated each year, whereas seed germination varied for the other species. The variation in seed germination is attributed to environmental factors such as day length, temperature or soil moisture which may have affected the production of impermeable 'hard' seeds.

Various physical and chemical treatments were applied to break the dormancy of these seeds, the results of which showed that with the exception of *H. sulphurescens*, all species have a seed coat imposed dormancy. Seed germination in *H. sulphurescens* was found to be temperature regulated. Seeds of all species were observed to germinate at 2°C to 5°C. Therefore, seeds of these species may germinate in the fall and overwinter as small seedlings although seedling mortality would limit recruitment.

Oxytropis sericea was considered to be the most suitable species for revegetation of high elevation disturbances, although this evaluation was based primarily on technical factors. Several of the remaining

species would be suitable, provided the technical difficulties associated with seed collection could be overcome.

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DEDICATION

This thesis is dedicated to my wife, Aileen, whose encouragement, support, and patience made this research possible.

CHAPTER I

INTRODUCTION

Research Rationale

Revegetation of alpine and subalpine disturbances presents a unique and difficult challenge for applied ecologists (Berg 1974). These areas are characterized by short growing seasons, high insolation levels, cool temperatures, and generally dry soil conditions (Billings and Mooney 1968; Billings 1974a, 1974b; Brown et al. 1976; and Ogilvie 1978). The low heat budget under which plant species must complete their life cycles in these environments does not favour commercially available species which are bred for lower altitudes and more temperate climates (Brown and Johnston 1979). Errington (1979), in his reclamation species trials in alpine areas of the Peace River Coal Block Area of British Columbia, found several commercially available grass species that performed adequately, but he did not find any commercially available legume species that performed well. Survival was poor, and growth decreased during the second growing season (Errington 1979).

It is important to include nitrogen-fixing species in the seed mixes used to revegetate mine disturbances because of the low levels of nitrogen in mine spoil (Tomm and Takyi 1981). Nitrogen is often a limiting

nutrient in undisturbed areas at these altitudes (Nishimura 1974; Luttmerding 1976; and May 1976). Therefore, long term establishment of vegetation in alpine and subalpine disturbances may be facilitated by the use of indigenous legume species that are adapted to the conditions of these environments. Unfortunately, seed of indigenous legumes is costly and not available in sufficient quantities (Berg 1974; and Hubbard and Bell 1977). Before these legumes can be more effectively used, efficient methods of propagation must be identified (Boe and Wynia 1985). Studies on sexual and vegetative reproduction characteristics of native legumes would provide critical information for mine reclamation personnel and commercial seed producers interested in propagating selected populations for potential cultivar development. A study was therefore initiated to examine the seed production, dispersal, and seed germination of several alpine and subalpine legumes in the southern Rocky Mountains of British Columbia.

Research Objectives

There were several objectives for the study: (1) to determine the phenology of reproductive development, (2) to describe seed dispersal mechanisms and dispersal patterns, (3) to describe the physical characteristics of the seeds, (4) to identify seed predators, (5) to examine seed production of various sample populations,

and (6) to determine the seed germination requirements of the selected species.

Study Area Description

Location

The study area lies within the Front Ranges of the Rocky Mountains extending northward from 49° 03' to 50° 01' North Latitude, and eastward from 115° 03' West Longitude to the Continental Divide along the British Columbia - Alberta border. The sample populations were located on the ridges and in the high elevation meadows of the Fernie Basin and surrounding mountain ranges. Most of the ridges are at elevations of 2000 to 2500m above sea level.

Geology and Geomorphology

The region contains several ranges aligned approximately in a north - south direction, parallel to sedimentary strata and the strike of westward dipping thrust faults (Holland 1976). The Fernie Basin is a complex syncline composed of sandstones, siltstones, conglomerates and coal of the Kootenay Formation, and shale of the Fernie Group (Price 1961). The high land of the Fernie Basin is represented by the Fernie, Flathead, Morrissey and Sparwood Ridges. These ridges have rounded crests and comparatively low topography, and are composed of relatively resistant sandstones and conglomerates (Holland 1976). Rock outcrops are small

and scattered except on the ridges (Ryder 1981). Gentle slopes have a mantle of morainal till, whereas steeper slopes have a veneer of morainal till, and very steep slopes have only colluvium (Ryder 1981).

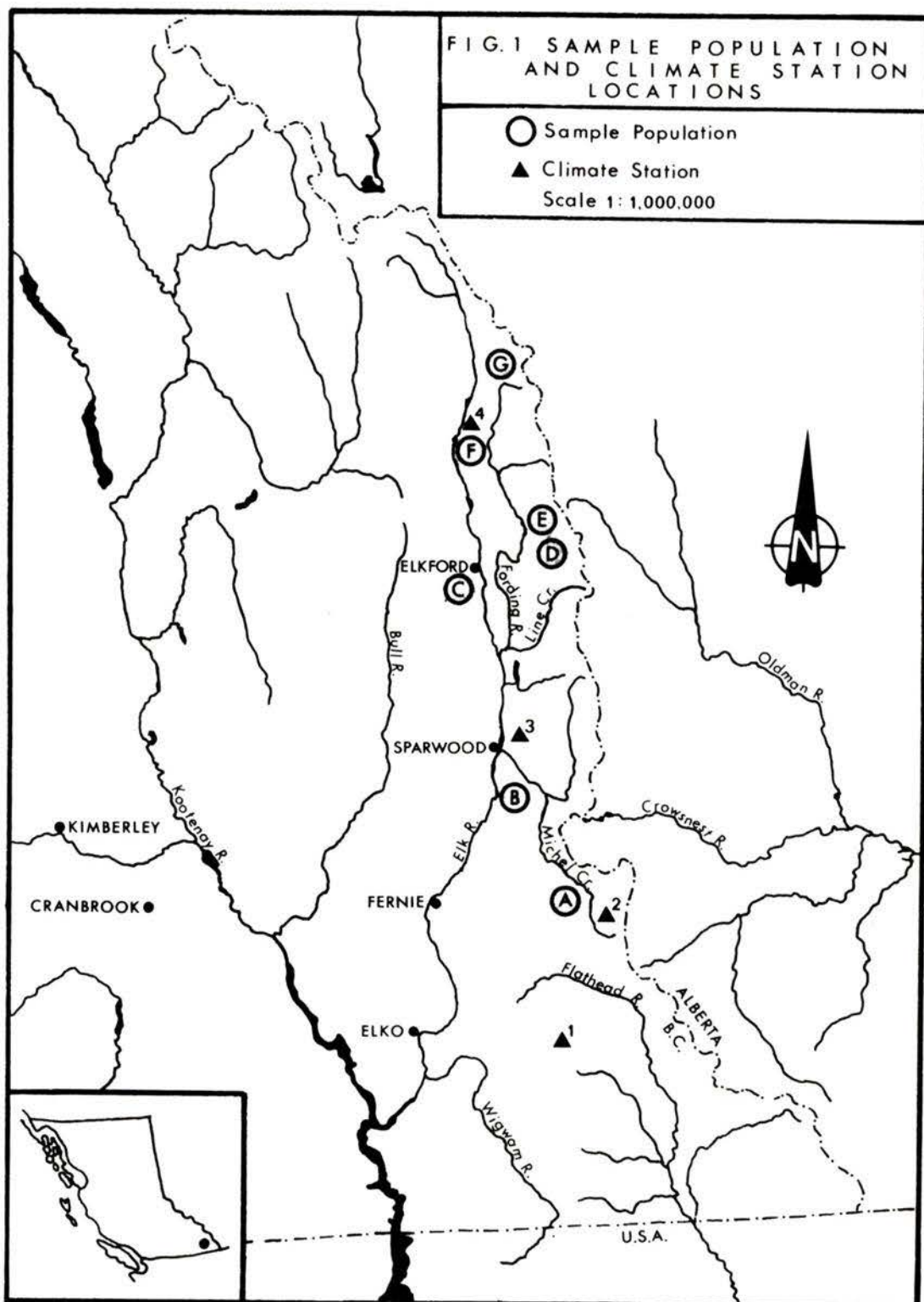
The Fernie Basin is surrounded on the east by the Flathead Range, High Rock Range and Elk Range, and on the west by the western portion of the Front Range and Lizard Range. These ranges to the east and west consist of upthrust or steeply dipped strata and are oriented in a westward or south westward direction with the steepest slopes facing eastward (Holland 1976). These ranges are underlain by resistant limestone, dolomite and quartzite of the Rundle Group (Price 1961). The Greenhills Range and Erickson Ridge are similar structurally to the surrounding ranges, but possess some sandstones and have a gentle topography with rounded crests (Ryder 1981). Surficial materials for these ranges are typically veneers of morainal till on gentle to moderately steep slopes, but colluvium dominates steep slopes and avalanche chutes at high elevations (Ryder 1981). Rock outcrops and till veneer occur on the ridge crests (Ryder 1981).

Most of the ridges within the Fernie Basin were buried beneath the relatively slow moving ice during the Pleistocene glaciation but many of the surrounding ranges were not covered by ice (Ryder 1981).

Climate

The study area is influenced by maritime air from the southwest and by continental air masses from the north and south (Hare and Thomas 1979). However, the maritime air flow from the southwest predominates (Lea 1984). The summers are short and warm, although there may be occasional nighttime frosts, and the winters are cold and long (Lea 1984). Several meteorological stations were (Air Studies Branch of the British Columbia Ministry of the Environment) or are (Canadian Atmospheric Environment Service) located within the study area (Figure 1). Analysis of the data collected at these stations from 1976 to 1980 (Figures 2 - 5) indicates that there is considerable climatic variation within the study area. Over these five years, July was the warmest month, with mean daily temperatures ranging between 11°C and 14°C. January and December are the coldest months, with mean daily temperatures ranging between -9°C and -12°C.

Precipitation is rather evenly distributed throughout the year, with slight maxima in August and December. The August peak for the 5 years ranged from 80 mm at the Dally Hill station to 125 mm at the Flathead Pass station. The December peak ranged from 78 mm at the Britt Creek station, to 124 mm at the Harmer Ridge station. June and October were the driest months for the



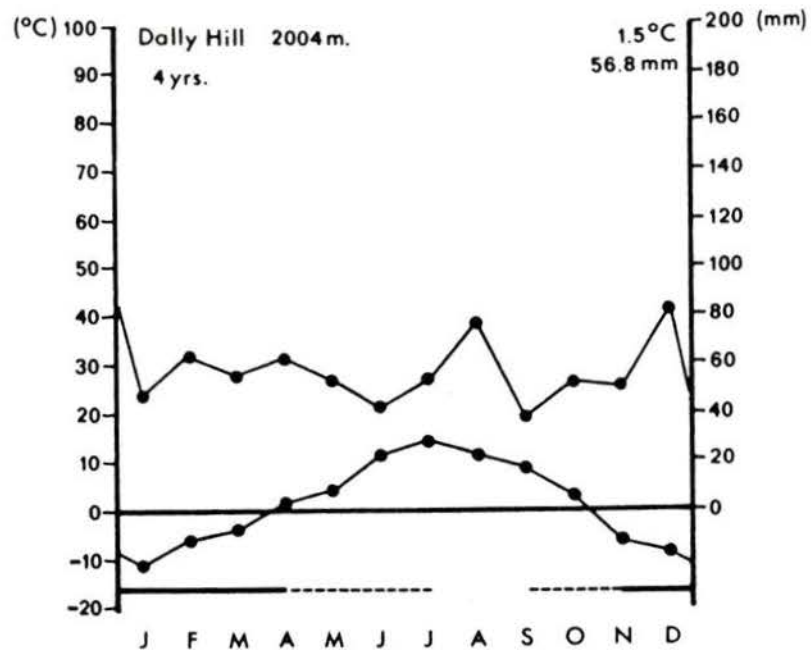


FIGURE 2 Diagram summarizing major climatic features for the Dally Hill meteorological station. Months are given on the abscissa with temperature ($^{\circ}\text{C}$) and precipitation (mm) given on the left and right ordinates respectively. The lower curve depicts average monthly temperature. The station and its elevation (m) is given in the upper left with the number of years recorded below. Average annual temperature and total precipitation are given in the upper right. The solid bar along the abscissa indicates months below 0°C , while the dashed line shows months with frost.

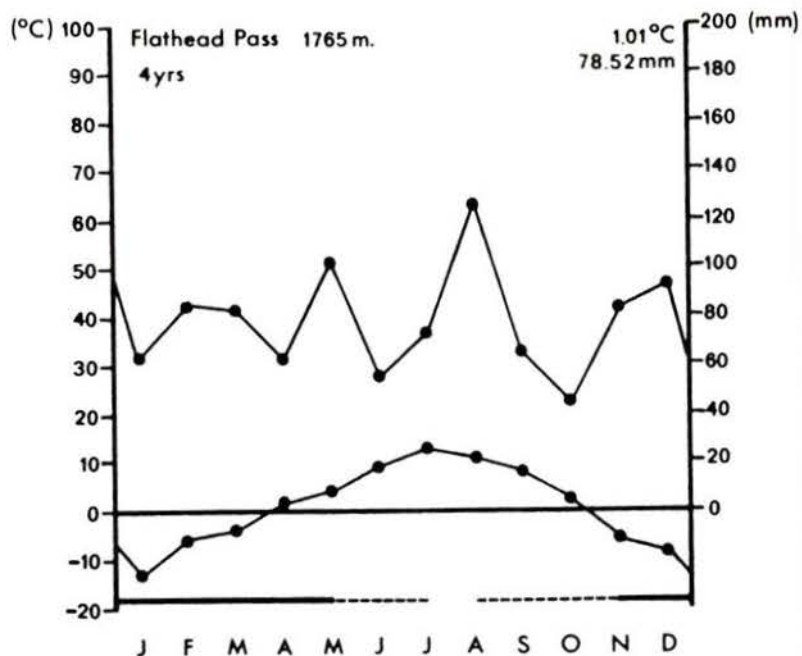


FIGURE 3 Diagram summarizing major climatic features for the Flathead Pass meteorological station. Months are given on the abscissa with temperature ($^{\circ}\text{C}$) and precipitation (mm) given on the left and right ordinates respectively. The lower curve depicts average monthly temperature. The station and its elevation (m) is given in the upper left with the number of years recorded below. Average annual temperature and total precipitation are given in the upper right. The solid bar along the abscissa indicates months below 0°C , while the dashed line shows months with frost.

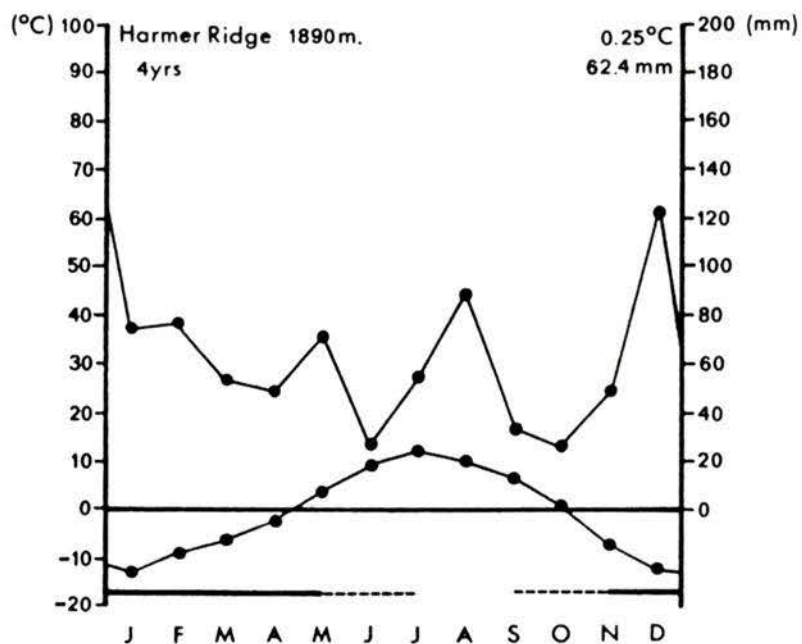


FIGURE 4 Diagram summarizing major climatic features for the Harmer Ridge meteorological station. Months are given on the abscissa with temperature ($^{\circ}\text{C}$) and precipitation (mm) given on the left and right ordinates respectively. The lower curve depicts average monthly temperature. The station and its elevation (m) is given in the upper left with the number of years recorded below. Average annual temperature and total precipitation are given in the upper right. The solid bar along the abscissa indicates months below 0°C , while the dashed line shows months with frost.

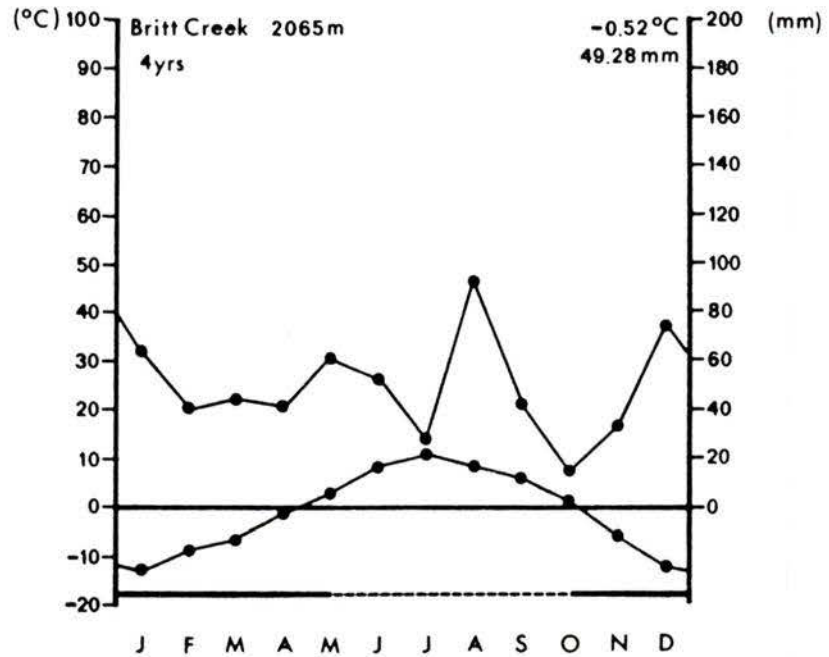


FIGURE 5 Diagram summarizing major climatic features for the Britt Creek meteorological station. Months are given on the abscissa with temperature ($^{\circ}\text{C}$) and precipitation (mm) given on the left and right ordinates respectively. The lower curve depicts average monthly temperature. The station and its elevation (m) is given in the upper left with the number of years recorded below. Average annual temperature and total precipitation are given in the upper right. The solid bar along the abscissa indicates months below 0°C , while the dashed line shows months with frost.

Flathead Pass and Harmer Ridge stations, whereas June and September were the driest months for the Dally Hill station, and July and October were the driest months for the Britt Creek station.

The available snow data are from snowcourse measurements, and thus show net accumulation of snow (cumulative snowfall minus the amount lost from melt, ablation, and compaction) (Figure 6). Measurable snow occurs from September to May, and the snowfree period is from June to August. The greatest snow depths were measured in February, March and January. Snow depth was greatest at the Dally Hill station. In general, snowfall increases northward in the study area. Certain mountainous areas may be subjected to convergence of air masses (Lea 1984), and this might explain the variation in precipitation and snowfall between stations. Moreover, it is known that local topography has a major control over snow depth and duration in the alpine, so the snow data presented here provide an approximate indication of depths for the study area.

None of the stations show a moisture deficit, as indicated by the relative positions of the temperature and precipitation curves. However, dry periods occurred in July at the Britt Creek station, and in June at the Harmer Ridge station.

Additional meteorological observations were made

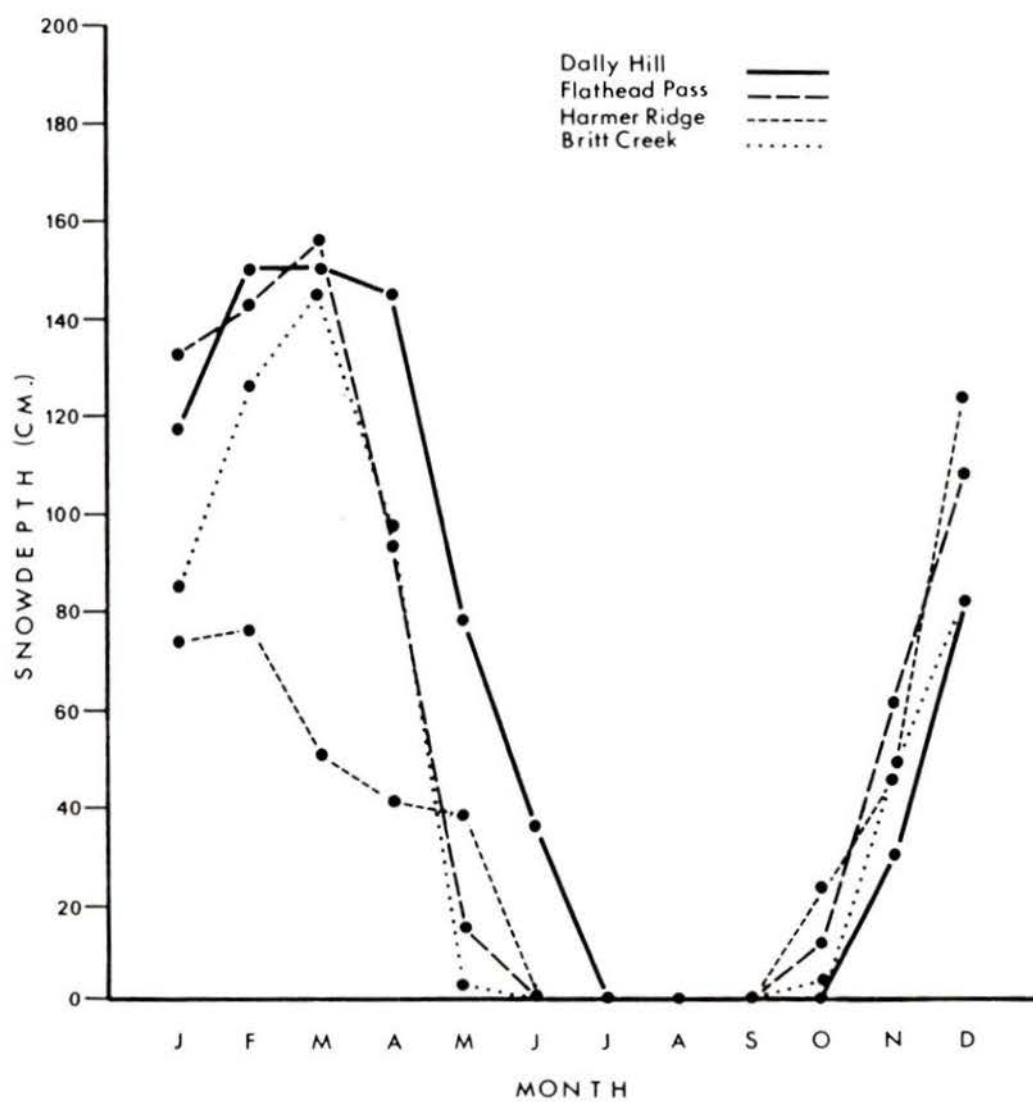


FIGURE 6 Snow Course Data for the selected Meteorological Stations.

from May through September during 1983, 1984 and 1985. The observations revealed year to year variation in weather patterns. The weather in 1983 was cool and moist from the beginning of May to the middle of July, and was followed by a warm dry period which lasted until the end of August. There were frequent late afternoon electrical storms from the middle of July to the end of the first week of August. September was cool and moist with several light snow storms. The weather in 1984 was cool and moist from the beginning of May to the end of June, and was followed by a warm dry period which lasted until the end of the third week in August. The weather in 1985 was cool and moist from the beginning of May to the middle of May and was followed by a hot dry period which lasted until the end of the first week in August. In 1984 and 1985, the weather was cool and moist following the warm period in August.

Vegetation and Soils

The vegetation of the study area has been classified by Lea (1984) according to the Biophysical Classification System of van Barneveld (1976). The classification system is based on the distribution of dominant species as determined by climatic influences. Three zones were delineated within the Fernie Basin and adjacent ranges, but sample population locations for the present study were restricted to the Lodgepole Pine -

Whitebark Pine Subzone and Krummholz Subzone of the Subalpine Engelmann Spruce - Alpine Fir Zone, and the Alpine Tundra Zone. Subzones have not been described for the Alpine Tundra Zone.

The Subalpine Engelmann Spruce - Alpine Fir Zone occurs between 1200 and 2400m. This zone is comparable to the Engelmann Spruce - Subalpine Fir Zone of Krajina's Biogeoclimatic Classification System (1965). *Picea engelmannii* Parry dominates the lower slopes while *Abies lasiocarpa* (Hook.) Nutt. dominates the upper slopes of this zone. The Lodgepole Pine - Whitebark Pine subzone is found at elevations ranging from 1650 to 2300m. This subzone is dominated by *Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm., except at elevations above 2000m where *Pinus albicaulis* Engelm. is dominant (Lea 1984). The understory is often dominated by *Vaccinium scoparium* Leiberg. Open stands of *P. albicaulis* and understory species of *Shepherdia canadensis* (L.) Nutt. and *Festuca scabrella* Torr. occur on steep or south facing slopes (Lea 1984). Rapid runoff and high insolation limit soil moisture in these sites. *Larix lyallii* Parl. often occurs as a pioneer species on exposed slopes or ridges at the upper elevations of this subzone. Stands of *A. lasiocarpa*, *P. engelmannii* and *Rhododendron albiflorum* Hook. are often found on more protected sites at high elevations. In general, the

upper elevations of this subzone are open and interspersed with meadows and tundra communities (Lea 1984).

The cool temperatures, precipitation and slightly acidic substrates affect the soils of this subzone. Most of the soils in this subzone are Orthic Humo-Ferric Podzols (Lacelle, unpublished manuscript).

The Krummholz Subzone is characterized by clumps of stunted trees surrounded by meadows, tundra vegetation, or rock (Lea 1984). This subzone is the upper elevational limit of the Subalpine Engelmann Spruce - Alpine Fir Zone and is found between 2300 and 2450m. Cold temperatures, desiccation due to insolation exposure and strong winds limit the establishment of trees. *Abies lasiocarpa* is the dominant tree species of this subzone with *P. engelmannii*, *P. albicaulis* and *L. lyallii* found in lesser amounts. *Vaccinium scoparium*, *Phyllodoce empetrifomis* (Sw.) D. Don, and various grasses and sedges are the understory species on mesic sites with deep soils where as *Dryas octopetala* L., *Antennaria lanata* (Hook.) Greene, and grasses and sedges dominate the understory on xeric to subxeric shallow soils (Lea 1984). *Valeriana sitchensis* Bong. and *Erigeron peregrinus* (Pursh) Greene are the dominant understory species on mesic to subhygric sites (Lea 1984).

Ferro Humic Podzols or Orthic Melanic Brunisols

characterize the deeper soils of this subzone. Orthic Regosols are characteristic of slumping or colluviating soils within this subzone (Lacelle, in press).

The Alpine Tundra Zone generally occurs above 2450m and is characterized by an absence of trees and the dominance of low growing plant species. Moisture availability appears to be important in determining the vegetation of this zone (Lea 1984). *Dryas octopetala*, *Poa alpina* L., *Silene acaulis* L., and lichens are characteristic of xeric shallow soil sites. *Salix arctica* Pall., *Phyllodoce empetrifomis*, and *Myosotis sylvatica* Hoffm. are common on mesic sites while *Erigeron peregrinus*, *Valeriana sitchensis*, and sedges are common on mesic to subhygric sites (Lea 1984).

Orthic Melanic Brunisols are characteristic of the deep soils of this zone. Orthic Regosols are characteristic of the colluviating and slumping soils found on the steep slopes or shallow soils of this zone (Lacelle, unpublished manuscript).

CHAPTER II

METHODS

Field Methods

Seven species of legumes were selected on the basis of their apparent affinity for disturbed steep slope habitats: *Astragalus alpinus* L., *A. bourgovii* Gray, *A. robbinsii* (Oakes) Gray, *A. vexilliflexus* var. *nubilus* Barneby, *Hedysarum sulphurescens* Rydb., *Oxytropis podocarpa* Gray, and *O. sericea* Nutt. Voucher specimens have been deposited in the University of Victoria Herbarium. Three to six populations for each species were selected as seed sources in April 1983. Selection was based on habitat variation and accessibility. Sample population boundaries and habitats were described, and between 10 and 30 rectangular 2x5 metre sample units (Westoff and Maarel 1978) were randomly located within these populations each year (Green 1979). The number of sample units was proportional to the estimated area of the population (Greig-Smith 1964). Vegetative and reproductive development, plant vigor, and wildlife utilization of each population were assessed at five-day intervals during each growing season and coded after Walmsley et al. (1980). Observations on pollinator visits were also recorded for each species.

The mechanisms of dispersal, and approximate dispersal distances for each species were observed during August

and September of each year.

Mature pods and lomenta from plants within the sample units were collected by hand every second day, placed in paper bags, and stored at 10°C until processed (Young et al. 1981). Pods and lomenta were considered to be mature when they had lost their glossy appearance and could easily be removed from the plants. Mature pods of all but *A. vexilliflexus* var. *nubilus* showed evidence of pod dehiscence. The volume of pods or lomenta collected as well as the weight of seeds was recorded for each species and population.

Laboratory Methods

The seed was processed by hand to prevent possible seed coat damage (Young et al. 1981). All seed was processed within one month of collection and stored at 10°C in plastic bags containing desiccant.

Six randomly chosen replicates of 100 seeds each were withdrawn annually from each population for germination testing. After pooling of equal portions of seed from the 1983 and 1984 populations, a further six replicates of 100 seeds per treatment and species, were withdrawn for germination enhancement experiments. Seeds were x-rayed in all cases, to determine the proportion of seeds that were filled and apparently capable of germination (Swaminathan and Kamra 1961; Kamra 1964). Seeds were placed on Kodak Type M-2 radiograph film, and

x-rayed for 2 minutes with a Faxitron 43855a X-Ray unit set at 15 KVP (Taylor pers. comm., 1983) and classified in one of five classes as in Table 1. Seeds assigned to Class 1, 2 and sometimes 4 were considered to have the capacity for germination (Figure 7).

A separate set of six replicates from each population was also withdrawn in 1983 to characterize the shape (Barneby, 1964), color (Munsell 1954), and size (length, width and depth).

Several insect damaged seeds of each species were withdrawn and the insects reared (Lees 1955) to allow identification to family or genus.

All replicates were arranged in growth chambers in completely randomized designs (Redente 1982). Plastic germination boxes (13x13.5x3.5cm) with tightly fitting lids were used to contain one layer of creped cellulose (Kimpac), one sheet of Whatman No. 1 filter paper, 100 ml. of distilled water or treatment solution, and 100 seeds of each species. Treatments applied to overcome seed dormancy are listed in Table 2. Germination responses were recorded every other day for 28 days (Scott and Jones 1982). Seeds were considered to have germinated when the radicle had emerged 1 cm (Redente 1982). Abnormal germination responses were recorded, but seeds with these responses were included in the analyses (Scott and Jones 1982).

TABLE 1 X-RAY INTERPRETATION CLASSES

Class 1	Seeds in which the fully developed embryo completely filled the embryo cavity and the seed coat appeared intact. All seeds in this class were considered to have the ability to germinate.
Class 2	Seeds in which the embryo did not appear as fully developed as in class 1 or showed slight embryo damage, and the seed coat appeared intact. All seeds in this class were considered to have the ability to germinate.
Class 3	Seeds in which the embryo was shriveled or had not developed properly. The seed coat was damaged in some cases. These seeds were not considered to have the ability to germinate.
Class 4	Seeds which showed signs of insect damage (frass or large portions missing). Some seeds of this class were considered to have the ability to germinate.
Class 5	Seeds which were empty or had negligible embryonic development. These seeds were not considered to have the ability to germinate.

Figure 7 X-ray Seed Assessment Diagrams




































	Class 1 (C1)	Class 2 (C2)	Class 3 (C3)	Class 4 (C4)	Class 5 (C5)
<i>Astragalus alpinus</i>					
<i>Astragalus bourgovii</i>					
<i>Astragalus robbinsii</i>					
<i>Astragalus vexilliflexus</i> var. <i>nubilus</i>					
<i>Hedysarum sulphurescens</i>					
<i>Oxytropis podocarpa</i>					
<i>Oxytropis sericea</i>					

Table 2 Treatments used to enhance seed germination.

Treatment	Levels tested	References
1. 2.9 mol liter H ₂ O ₂	10,20,30 minutes	Young et.al. 1981
2. Conc. H ₂ SO ₄ (18.0 mol liter)	5,10,20,30 minutes	Townsend and McGinnes 1972
3. Water Rinse	12,24,36,48, hours	Young et.al. 1981
4. Gibberellic Acid (GA)	0.3,1.4,2.9,4.3 mmol liter	Mayer and Poljakoff -Mayber 1975
5. 0.02 mol liter KNO ₂	-	Young et al. 1981
6. 1.4 GA and 0.02 mol liter KNO ₂	-	Young et al. 1981
7. Ethylene (ethephon) (2-chloroethyl) phosponic acid	-	Young et al. 1981
8. Mechanical Scarification	temperatures of 5,10,20,30°C	Kissock and Haferkamp 1983
9. Constant Temperature	no light	Redente 1982
10. Constant Temperatures	light	Redente 1982
11. Alternating Temperatures	5/10,20/10,30/20°C	-
12. Stratification (2-5°C)	1,4,8 months	-

Data Analysis

Species germination response data (each sample population or germination enhancement treatments) were pooled after germination capacity (Bewley and Black 1985) had been subjected to Bartlett's test for homogeneity of variances (Zar 1974). Seed germination behavior was characterized by survival analysis (Scott et al. 1982) with the BMDP1L software program (Benedetti et al. 1985). Cumulative survival curves were calculated using this method of analysis (Scott et al. 1982). Comparisons of survival distribution curves for seed sources or treatments of each species were made with the Breslow (1970) statistic. All seed germination calculations were based on the number of seeds capable of germination as determined by x-ray analysis.

CHAPTER III

RESULTS

Sample Population Descriptions

Populations of each species were located in a variety of sites. Habitat and vegetation descriptions for each population are presented in Tables 3 - 7. Representative photographs of the habitats are presented in Figure 8 (A and B).

Sample populations of *Astragalus alpinus* were located on south and west facing wind exposed slopes of the Alpine Zone, and on a north facing ridge in the Subalpine Engelmann Spruce - Alpine Fir Zone. The moisture regime of these habitats ranged from xeric to sub-mesic. *Astragalus alpinus* was found growing within dense swards of *Festuca scabrella* at the South Bald (SB) site, and within dense mats of *Dryas octopetala* on the wind exposed sites. The growth habit of *A. alpinus* varied from a few individuals within the grass swards to large patches on the wind exposed sites. The soils varied from Orthic Regosols on the steep slopes to Melanic Brunisols on the more gentle grass slopes.

All sample populations of *Astragalus bourgovii* were located within the Subalpine Engelmann Spruce - Alpine Fir Zone. *Pinus albicaulis* and *Vaccinium scoparium* were the dominant species, although dense almost pure stands of *A. bourgovii* were found on steep east-facing ridge

TABLE 3 SAMPLE POPULATION HABITAT DESCRIPTIONS

SAMPLE LOCATION	ELEVATION (m)	ASPECT (°)	SLOPE (%)	MESO-SLOPE POSITION	ECOLOGICAL MOISTURE REGIME	EXPOSURE
Michel Ridge (A)	2250	279	45	upper slope	sub-xeric	-
Lookout Mt. (B)	2163	100	71	crest	very xeric	-
Ewin Ridge (C)	2464	344	28	crest	sub-xeric	wind
East Ewin Ridge (C)	2461	79	60	crest	very xeric	wind insolation snow
Bald/Ewin Saddle (C)	2457	273	22	lower slope	mesic	cold air drainage
South Bald (C)	2475	198	52	mid-slope	sub-mesic	insolation wind
West Bald (C)	2490	272	46	upper slope	sub-xeric	wind frost
East Bald (C)	2495	79	53	crest	xeric	wind insolation
Mt. Banner (C)	2515	165	56	crest	xeric	wind frost
Elkford Mt. (D)	2054	85	10	mid-slope	mesic	-
Todhunter Basin (E)	2133	298	11	upper slope	sub-mesic	cold air drainage
North Greenhills (F)	2275	302	69	crest	sub-xeric	wind
Gill Peak (G)	2160	165	39	mid-slope	very xeric	insolation

NOTE: The letters associated with the sample populations represent locations on the map (Figure 1).

TABLE 4 SOUTH SECTION SAMPLE POPULATION VEGETATION DESCRIPTIONS

SAMPLE POPULATION	SPECIES	COVER (%)	SOCIABILITY	VEGETATION
Michel Ridge	<i>Astragalus bourgovii</i>	1	few individuals	<i>Pinus albicaulis</i> , <i>Polemonium pulchellum</i> and <i>Allium cernuum</i>
	<i>Astragalus robbinsii</i>	2	several individuals	"
	<i>Astragalus vexilliflexus</i> var. <i>nubilus</i>	2	several individuals	"
	<i>Hedysarum sulphurescens</i>	4	several individuals	"
	<i>Oxytropis sericea</i>	5	several individuals	"
Lookout Mt.	<i>Astragalus bourgovii</i>	6	several individuals	<i>Eriogonum umbellatum</i> , <i>Arnica rydbergii</i> and <i>Lomatium dissectum</i>

TABLE 5 SOUTH CENTRAL SECTION SAMPLE POPULATION VEGETATION DESCRIPTIONS

SAMPLE POPULATION	SPECIES	COVER (%)	SOCIABILITY	VEGETATION
Ewin Ridge	<i>Astragalus alpinus</i>	1	few individuals	<i>Dryas octopetala</i> , <i>Salix nivalis</i> and <i>Festuca ovina</i>
	<i>Oxytropis podocarpa</i>	4	several individuals	"
	<i>Oxytropis sericea</i>	4	several individuals	"
East Ewin Ridge	<i>Astragalus bourgovii</i>	20	numerous individuals	<i>Astragalus bourgovii</i> and <i>Eriogonum ovalifolium</i>
Bald Ewin Saddle	<i>Astragalus robbinsii</i>	5	several individuals	<i>Pinus albicaulis</i> , <i>Larix lyalli</i> and <i>Potentilla diversifolia</i>
South Bald	<i>Astragalus alpinus</i>	3	several individuals	<i>Festuca scabrella</i> , <i>Potentilla diversifolia</i> and <i>Myosotis sylvatica</i>
	<i>Astragalus robbinsii</i>	1	few individuals	"
	<i>Oxytropis podocarpa</i>	1	few individuals	"
	<i>Oxytropis sericea</i>	5	several individuals	"
West Bald	<i>Astragalus alpinus</i>	15	small patches	<i>Dryas octopetala</i> , <i>Salix nivalis</i> and <i>Carex nardina</i>
	<i>Oxytropis podocarpa</i>	13	numerous individuals	"
	<i>Oxytropis sericea</i>	4	several individuals	"

TABLE 6 NORTH CENTRAL SECTION SAMPLE POPULATION VEGETATION DESCRIPTIONS

SAMPLE POPULATION	SPECIES	COVER (%)	SOCIABILITY	VEGETATION
Banner Mt.	<i>Astragalus vexilliflexus</i> var. <i>nubilus</i>	10	numerous individuals	<i>Dryas octopetala</i> , <i>Potentilla nivea</i> , and <i>Carex nardina</i>
	<i>Hedysarum sulphurescens</i>	2	few individuals	"
	<i>Oxytropis podocarpa</i>	5	several individuals	"
Elkford Mt.	<i>Hedysarum sulphurescens</i>	4	large patches	<i>Pinus albicaulis</i> , <i>Arctostaphylos uva-ursi</i> and <i>Festuca scabrella</i>

TABLE 7 NORTH SECTION SAMPLE POPULATION VEGETATION DESCRIPTIONS

SAMPLE POPULATION	SPECIES	COVER (%)	SOCIABILITY	VEGETATION
Todhunter Basin	<i>Hedysarum sulphurescens</i>	2	several individuals	<i>Dryas octopetala</i> , <i>Salix vestita</i> and <i>Carex nardina</i>
	<i>Oxytropis podocarpa</i>	3	several individuals	"
North Greenhills	<i>Astragalus bourgovii</i>	8	numerous individuals	<i>Pinus albicaulis</i> , <i>Arctostaphylos uva-ursi</i> and <i>Vaccinium scoparium</i>
	<i>Astragalus robbinsii</i>	6	several individuals	"
	<i>Astragalus vexilliflexus</i> var. <i>nubilus</i>	2	few individuals	"
	<i>Hedysarum sulphurescens</i>	10	numerous individuals	"
	<i>Oxytropis sericea</i>	4	several individuals	"
Gill Peak	<i>Oxytropis sericea</i>	2	few individuals	<i>Dryas octopetala</i> , <i>Arctostaphylos uva-ursi</i> and <i>Salix nivalis</i>

FIGURE 8 Photograph of two of the study habitats:
A - Michel Ridge and B - Bald Mountain



crests where heavy snow accumulations occur. The latter habitats represent the Lookout Mountain (LM) and East Ewin Ridge (EE) populations. The moisture regime of these habitats ranged from sub-mesic to xeric. Soils varied from thin Orthic Regosols on the ridge crest sites to Eutric Brunisols on the more gentle vegetated slopes.

Sample populations of *Astragalus robbinsii* were located within both the Alpine and Subalpine Engelmann Spruce - Alpine Fir Zones. The habitats ranged from wind exposed southwest and west facing upper slopes and ridge crests to a sheltered subalpine meadow. The moisture regime for these habitats varied from sub-mesic to mesic. The vegetation ranged from *D. octopetala* and *Salix nivalis* Hook. in the wind exposed ridge crests, to *P. albicaulis* and *Arctostaphylos uva-ursi* (L.) Spreng. in the subalpine areas. The soils varied from Eutric or Melanic Brunisols on the west and southwest slopes, respectively, to a Ferro-Humic Podzol for the Bald Mountain/Ewin Ridge (BE) population.

Sample populations of *Astragalus vexilliflexus* var. *nubilus* were located on upper slopes and ridge crests in both the Alpine Tundra and Subalpine Engelmann Spruce - Alpine Fir Zone. The moisture regime for these habitats ranged from xeric to sub-xeric. *Potentilla nivea* L. and *Carex nardina* Fries were the dominant species for the

Banner Mountain (BM) population, and *P. albicaulis* and *Polemonium pulcherrimum* Hook. for the other populations. *A. vexilliflexus* was most abundant on rocky unstable slopes in the Alpine Tundra Zone. The soils were Orthic Regosols.

Sample populations of *Hedysarum sulphurescens* were located in habitats that ranged from a southwest ridge crest in the Alpine Tundra Zone to upper west facing slopes in the Subalpine Engelmann Spruce Zone. The moisture regime for these habitats ranged from xeric to mesic. *Dryas octopetala* was the dominant species for the Banner Mountain (BM) alpine population, whereas *P. albicaulis* and *A. uva-ursi* were the dominant species in the subalpine populations. The growth habit of *H. sulphurescens* varied from single individuals 1 dm high in the alpine population to large patches of individuals 1-2 m in diameter and 2-3 dm tall for the subalpine populations. The soils varied from an Orthic Regosol in the alpine population to Melanic Brunisols for the subalpine populations.

Sample populations of *Oxytropis podocarpa* were located within the Alpine Tundra Zone on wind exposed slopes and ridge crests. The moisture regime for these habitats varied from xeric to sub-mesic. *D. octopetala* and *S. nivalis* were the dominant species for all habitats except for the *F. scabrella* dominated South

Bald (SB) population. *O. podocarpa* was most abundant on steep west facing slopes. The soils ranged from Orthic Regosols on the west facing slopes to Melanic Brunisols on the more gentle south facing slopes.

Sample populations of *Oxytropis sericea* were located on ridge crests, meadows and talus slopes within the Alpine Tundra and Subalpine Engelmann Spruce Alpine Fir Zones. The moisture regime for these habitats varied from very xeric to sub-mesic. The vegetation varied from stands of *D. octopetala* and *S. nivalis* for the alpine populations to *P. albicaulis* and *A. uva-ursi* for the subalpine populations. *O. sericea* was most abundant in sparsely vegetated habitats. The soils ranged from Orthic Regosols and Eutric Brunisols on the steep slopes to Melanic Brunisols on the more gentle slopes.

Phenology

Vegetative and reproductive activity of each species varied from year to year and among the different populations. The initiation of vegetative activity was latest in 1983 and earliest in 1985. Two weeks to one month separated the initiation of vegetative and reproductive activity between 1983 and 1985. The duration of vegetative and reproductive activity was relatively constant for 1983 and 1984, but vegetative activity was two weeks to one month longer for several species in 1985. Flowers were pollinated primarily by

bumblebees (*Bombus* Latr., Apidae) and bee-flies (Bombylidae).

Vegetative activity of *Astragalus alpinus* for all populations began in the third week of June in 1983 and 1984 and the third week of May in 1985 (Figure 9). The West Bald population was the latest to initiate vegetative activity. Vegetative activity continued until the last week of August. Flowering for all populations began in the third week of July in 1983 and 1984, and the first week of July in 1985. Flowering, pod and seed development, and seed dispersal all occurred over two week periods, except for the South Bald (SB) population where flowering lasted for three weeks. Seed dispersal began in the second week of August and continued until the first week in September in each year.

Vegetative activity of *Astragalus bourgovii* began in the third or fourth week of June in 1983 and 1984, and the third or fourth week of May in 1985 (Figure 10). Initiation of vegetative activity was latest for the East Ewin (EE) population. Vegetative activity continued until the last week in August or first week in September all years. Flowering began in the third week in July during 1983 and 1984, and during first and second week in 1985. Flowering continued for two to three weeks. Pod and seed development took three weeks. Seed dispersal began during the second or third week in August in 1983

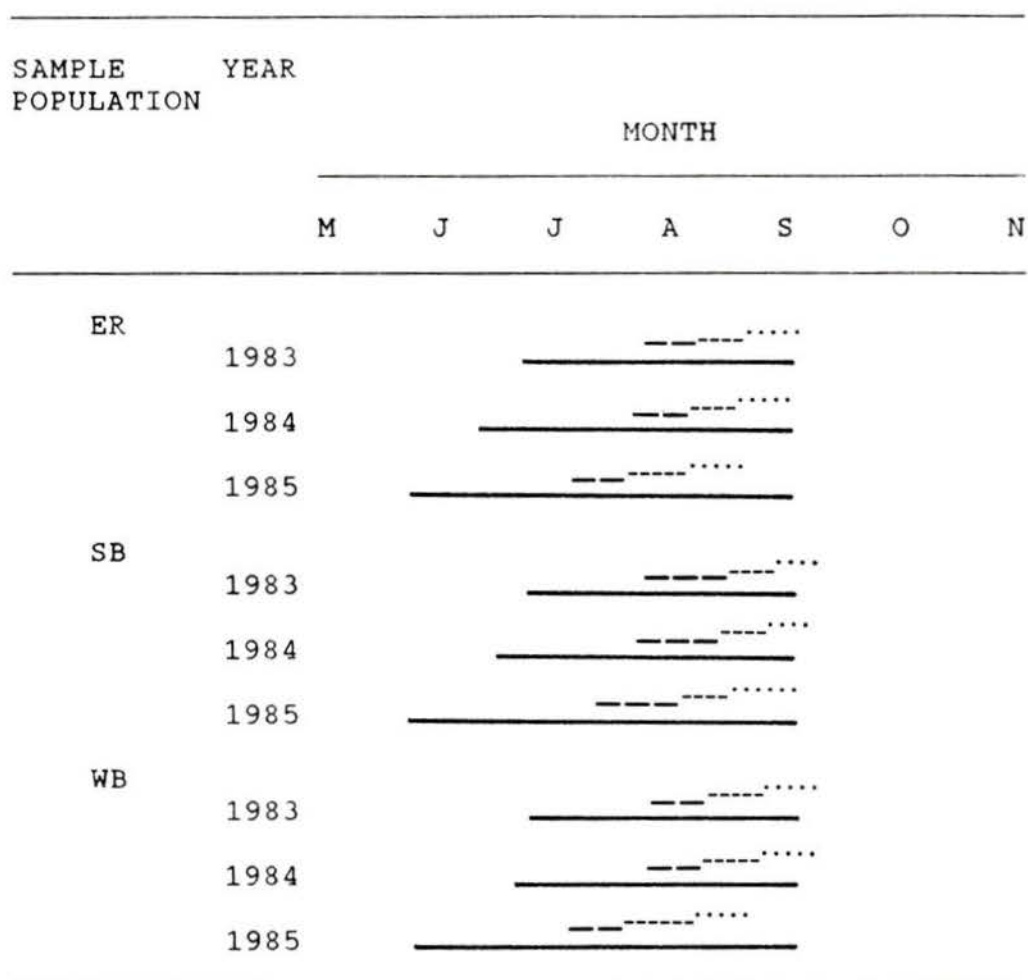


FIG. 9 *Astragalus alpinus*. A tabular calendar showing time and duration of vegetative activity———, flowering———, pod development, and seed dispersal

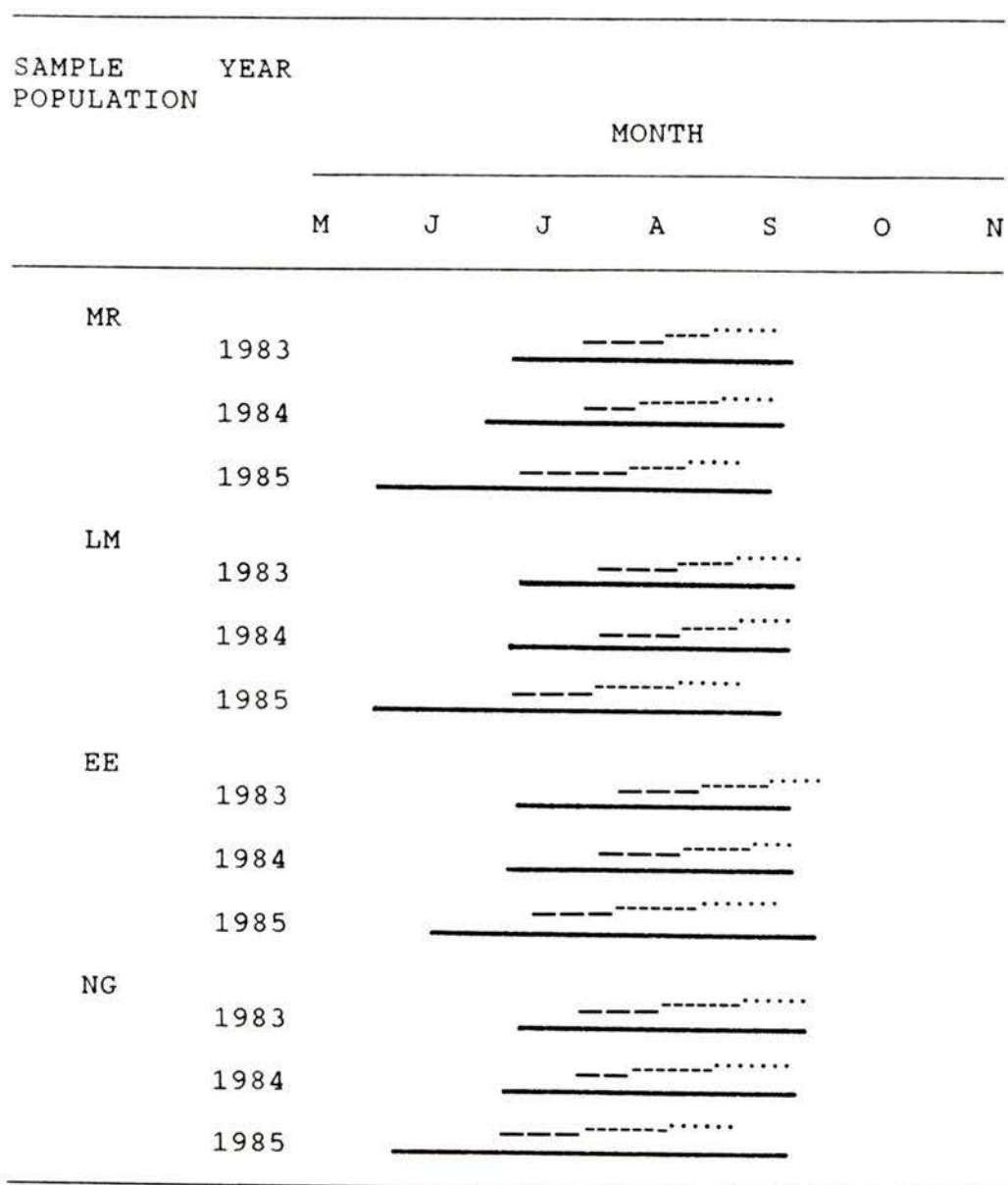


FIG.10 *Astragalus bourgovii*. A tabular calendar showing time and duration of vegetative activity———, flowering———, pod development———, and seed dispersal.....

and 1984, and the first week in August in 1985. Seed dispersal continued until the first week in September.

The initiation of vegetative activity by *Astragalus robbinsii* was variable. Vegetative activity for the Michel Ridge (MR) and Bald Mountain/Ewin Ridge (BE) populations began in the fourth week of May or first week of June in 1983 and 1984, whereas activity did not begin until the second or third week of June for the remaining populations (Figure 11). Vegetative activity for all populations was two weeks earlier in 1985. Vegetative activity continued until the last week in August or first week in September in each year. Flowering began in the second or third week in July during 1983 and 1984, and the last week in June during 1985. Pod and seed development occurred until the third week of August in 1983 and 1984, and until the first week of August in 1985. The duration of pod and seed development for the Bald/Ewin (B/E) population varied from one week in 1984 to four weeks in 1985. Seed dispersal took two weeks and was complete by the end of the second week of September in 1983 and 1984, and the last week of August in 1985.

Initiation of vegetative activity by *Astragalus vexilliflexus* var. *nubilus* varied considerably between populations and years. Vegetative activity in 1983 and 1984 began in the second week of June, for the Michel Ridge population (MR) and the third week of June for the

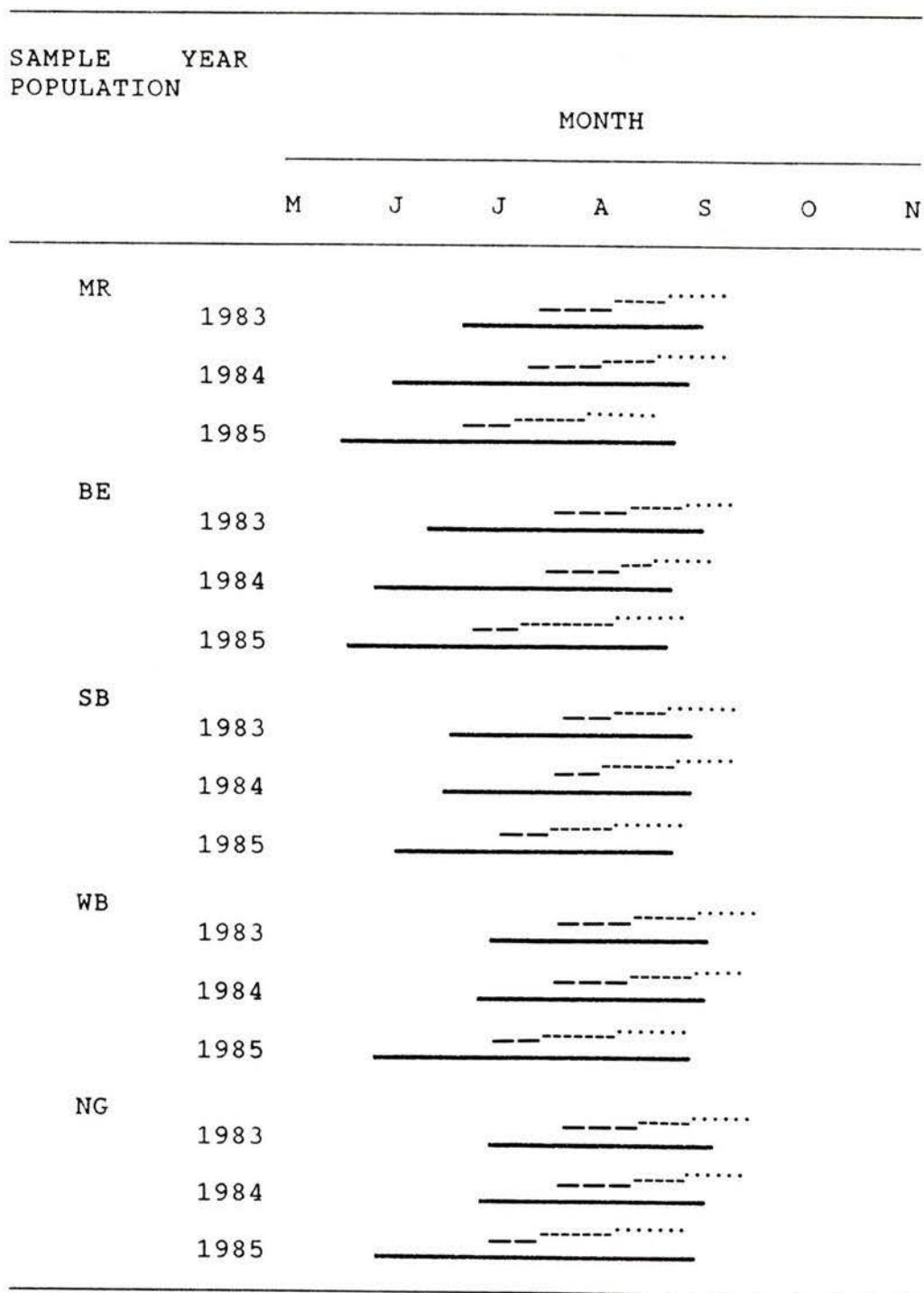


FIG. 11 *Astragalus robbinsii*. A tabular calendar showing time and duration of vegetative activity———, flowering———, pod development ———, and seed dispersal

remaining populations (Figure 12). Vegetative activity in 1985 began in the third or fourth week of May for all populations. Vegetative activity continued until the third week in September. Flowering of the Michel Ridge (MR) population began in the first week of July during 1983 and 1984, whereas flowering did not begin until the third week for the remaining populations. Flowering for all populations began in the last week of June or first week of July in 1985. Flowering continued for the duration of the growing season, but generally peaked in the first two weeks of August. The duration of pod and seed development was difficult to determine, because of indeterminate flowering, but was estimated to be similar to the other *Astragalus* species studied. Seed dispersal in each year occurred until snowfall in the second or third week in September.

Initiation of vegetative activity by *Hedysarum sulphurescens* ranged from the first week in June to the third week in June for 1983 and 1984, and the third and fourth week in May for 1985 (Figure 13). The Michel Ridge (MR) population was the earliest each year, whereas the Banner Mountain (BM) population was the latest. Vegetative activity occurred until the second week in September. Flowering for most of the populations began in the third or fourth week of July in 1983 and 1984, and one to two weeks earlier in 1985. Flowering of

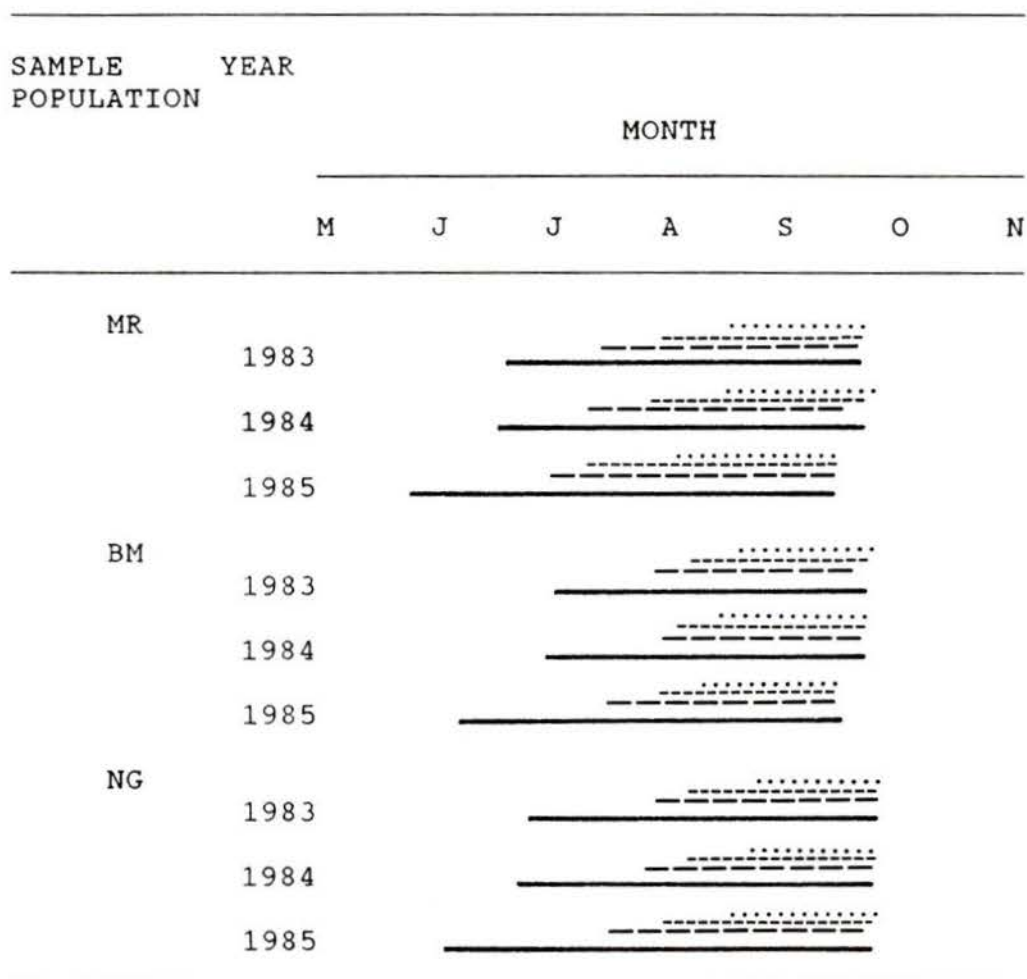


FIG.12 *Astragalus vexilliflexus* var. *nubilus*.
 A tabular calendar showing time and
 duration of vegetative activity———,
 flowering———, pod development———,
 and seed dispersal.....

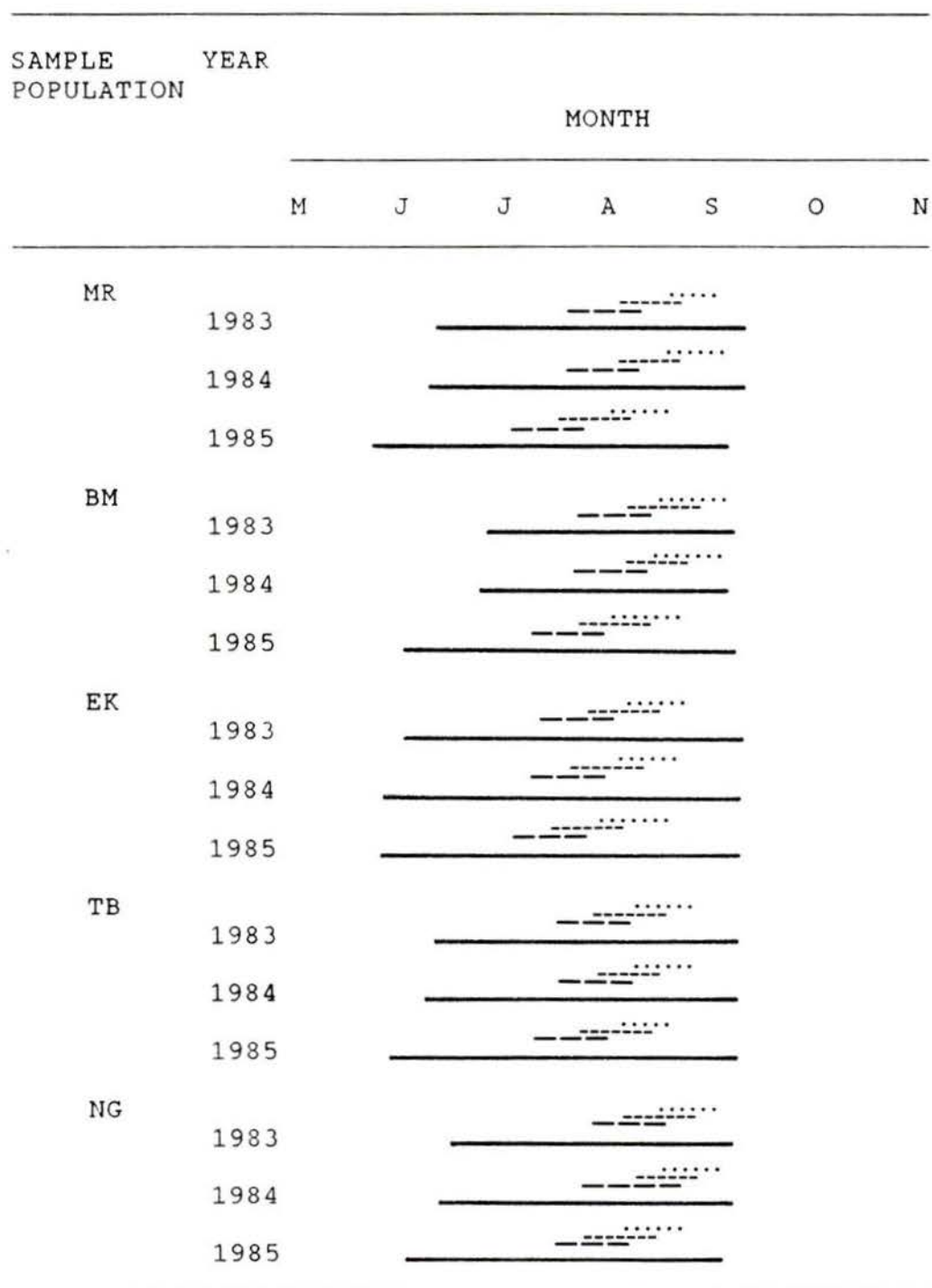


FIG.13 *Hedysarum sulphurescens*. A tabular calendar showing time and duration of vegetative activity———, flowering———, pod development, and seed dispersal

the lower elevation Elkford Mountain (EK) population was always one week earlier than the other populations. Flowering lasted for three weeks. Developing loment segments were visible on the lower portions of the racemes during the third week of flowering. Loment and seed development occurred over a two week period. Dispersal of the loment segments in 1983 and 1984 was complete by the end of August and by the third week in August of 1985.

Initiation of vegetative activity by *Oxytropis podocarpa* began in the third week of June in 1983 and was progressively earlier each subsequent year (Figure 14). Vegetative activity in each year was complete by the first week of September. Flowering in 1983 and 1984 began in the first two weeks of July except for the West Bald (WB) and Banner Mountain (BM) populations which did not begin flowering until the third or fourth week of July. Pod and seed development occurred over a three week period. Seed dispersal in 1983 and 1984 was complete by the second or third week in August with the exception of the West Bald (WB) and Banner Mountain (BM) populations. Seed dispersal in these populations was not complete until the first week in September. Seed dispersal was one to two weeks earlier in 1985.

Initiation of vegetative activity by *Oxytropis sericea* began at the beginning of June in 1983 and was progressively earlier each subsequent year (Figure 15).

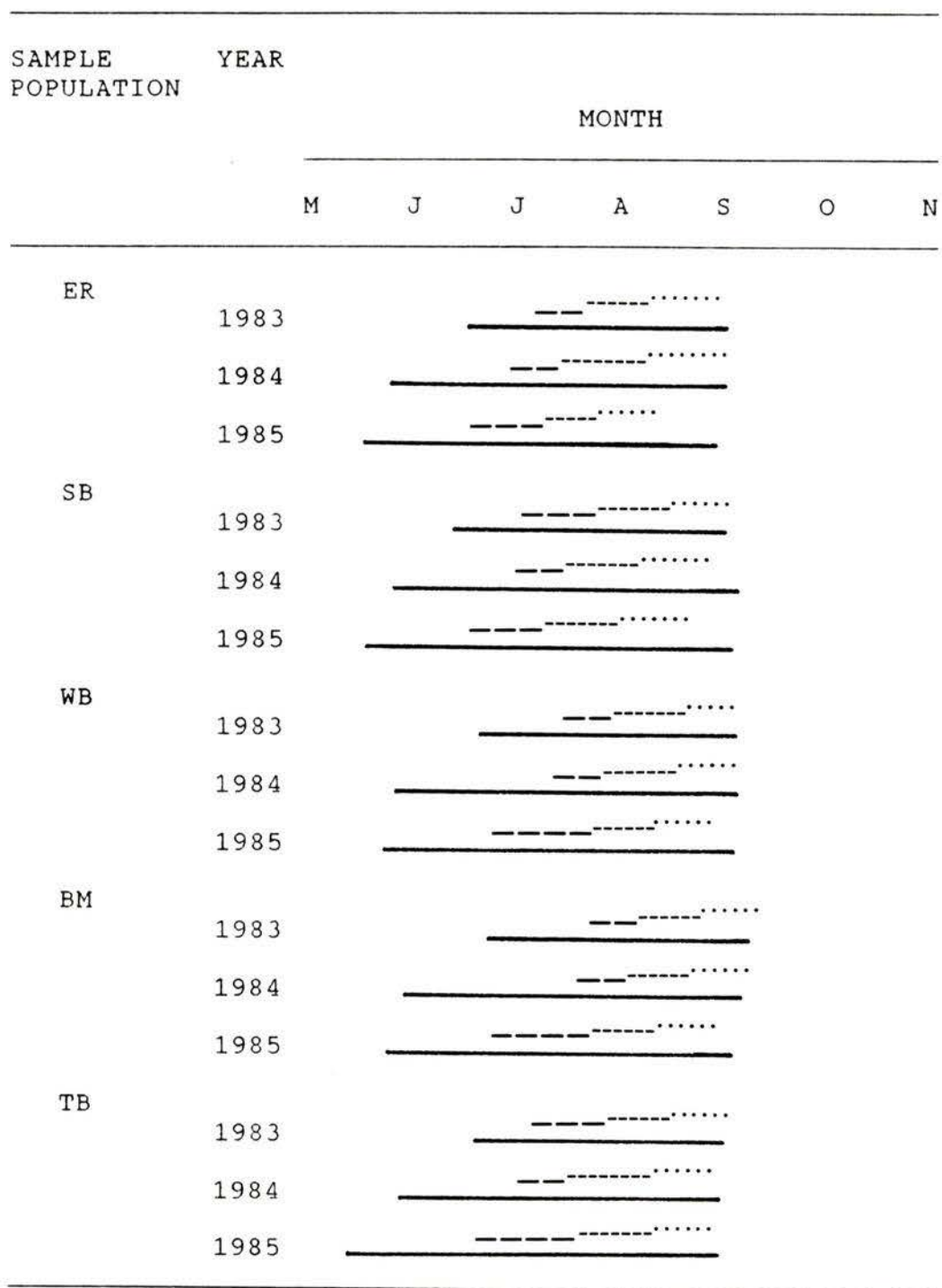


FIG.14 *Oxytropis podocarpa*. A tabular calendar showing time and duration of vegetative activity———, flowering———, pod development———, and seed dispersal.....

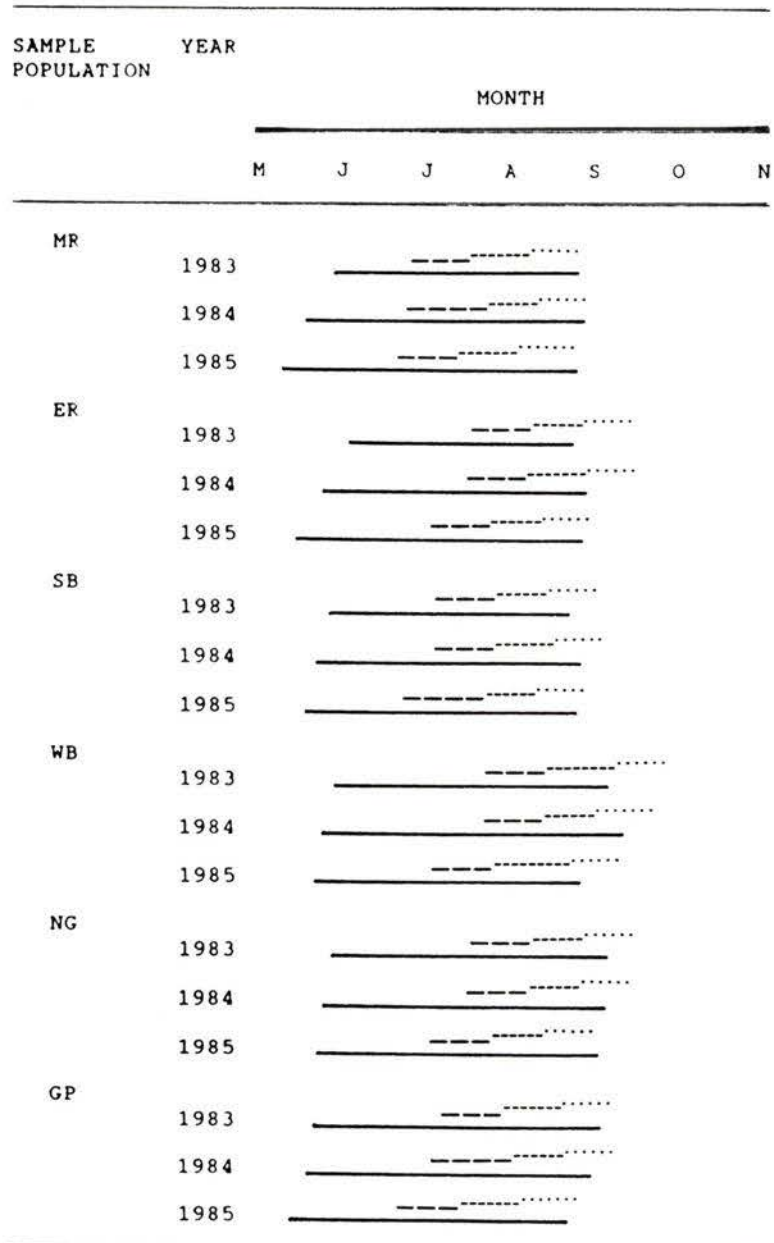


FIG. 15 *Oxytropis sericea*. A tabular calendar showing time and duration of vegetative activity——, flowering——, pod development——, and seed dispersal.....

Vegetative activity continued until the last week in August or first week in September in each year. Flowering for the Michel Ridge (MR), South Bald (SB) and Gill Peak (GP) populations in 1983 and 1984 began in the last week of June first week of July, and the third week of July for the remaining populations. Flowering continued for three weeks in each year. Pod and seed development occurred over a two to three week period. The majority of the seed was dispersed by the second week in September but some seed was retained until heavy snow covered the pods.

Seed Production

Seed production, number of viable seeds produced and seed predator damage for each species varied from year to year among populations.

Vigor, percentage of seed heads, and wildlife utilization of *A. alpinus* did not vary greatly with years or populations (Table 8). The percentage of individuals with seed heads was consistently low. Seed production was proportional to population numbers. However, the number of viable seeds varied from year to year among populations (Figure 16). The number of viable seeds (Class 1 and 2) decreased between 1983 and 1985. The number of seeds with smaller embryos (Class 2), and the number of poorly developed (Class 3) or aborted embryos (Class 4) was greatest in 1985. Insect damage

TABLE 8 SEED PRODUCTION *Astragalus alpinus*

SAMPLE		POPULATION		SEED PRODUCTION				
LOCATION	SIZE (m ²)	NUMBER*	YEAR	VIGOR	SEED "HEADS" (%)	WILDLIFE UTILIZATION	PODS (l)	SEEDS (gms)
ER	100	150	1983	good	15	none	0.35	0.97
			1984	good	18	trace	0.30	0.84
			1985	good	20	none	0.25	0.70
SB	625	300	1983	good	35	light	1.00	2.80
			1984	good	25	light	0.90	2.52
			1985	good	25	moderate	0.80	2.24
WB	300	100	1983	good	20	trace	0.45	1.27
			1984	fair	17	trace	0.40	1.23
			1985	fair	16	trace	0.40	1.14

* The numbers represent estimated abundances.

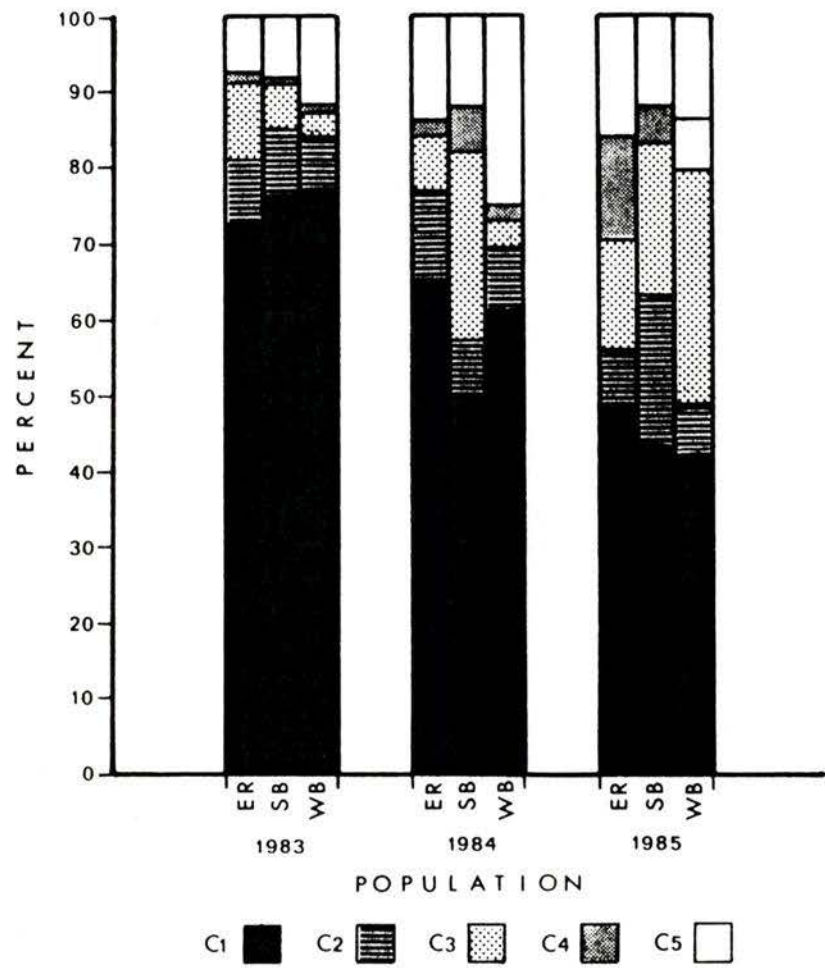


FIGURE 16 Number of Viable Seeds produced each year by *A. alpinus*

(Class 5) also increased from 1983 to 1985.

The vigor of *A. bourgovii* populations was good to excellent except for the Michel Ridge (MR) population in 1985. However, the percentage of individuals with seed heads varied with populations (Table 9). Percentage of seed heads for the Michel Ridge (MR) was very low relative to the other populations. Wildlife utilization was also low. Seed production was in general, proportional to population numbers. However, the number of viable seeds (Class 1 and 2) increased from 1983 to 1985 (Figure 17). Higher numbers of seeds with smaller embryos (Class 2) were recorded in 1983 and 1984, and there were a large number of seeds with poorly developed embryos (Class 3) in 1983. The percentage of insect damaged seeds (Class 5) was consistently low.

The vigor of *A. robbinsii* was good to excellent except for the West Bald (WB) population in 1984 and 1985 (Table 10). The percentage of seed heads was consistently high for the Michel Ridge (MR) and North Greenhills (NG) populations but was moderately low for the West Bald (WB) population. Wildlife utilization was light except for the Bald Mountain/Ewin Ridge (B/E) population. Seed production was proportional to population numbers. The number of viable seeds (Class 1 and 2) was greatest in 1985 (Figure 18). The Bald Mountain / Ewin Ridge (B/E) and South Bald (SB)

TABLE 9 SEED PRODUCTION *Astragalus bourgovii*

LOCATION	POPULATION		SEED PRODUCTION					
	SIZE (m ²)	NUMBER*	YEAR	VIGOR	SEED "HEADS" (%)	WILDLIFE UTILIZATION	PODS (l)	SEEDS (gms)
MR	125	50	1983	good	25	trace	0.75	0.94
			1984	good	20	trace	0.80	1.00
			1985	fair	5	trace	0.70	0.88
LM	90	55	1983	good	90	none	1.15	1.44
			1984	good	85	none	1.25	1.56
			1985	good	80	none	1.20	1.50
EE	850	275	1983	excellent	95	none	4.45	5.56
			1984	excellent	100	trace	4.55	5.75
			1985	good	85	none	4.50	5.63
NG	900	350	1983	excellent	100	none	6.05	7.31
			1984	excellent	100	none	6.10	7.41
			1985	excellent	100	none	5.90	7.11

* The numbers represent estimated abundances.

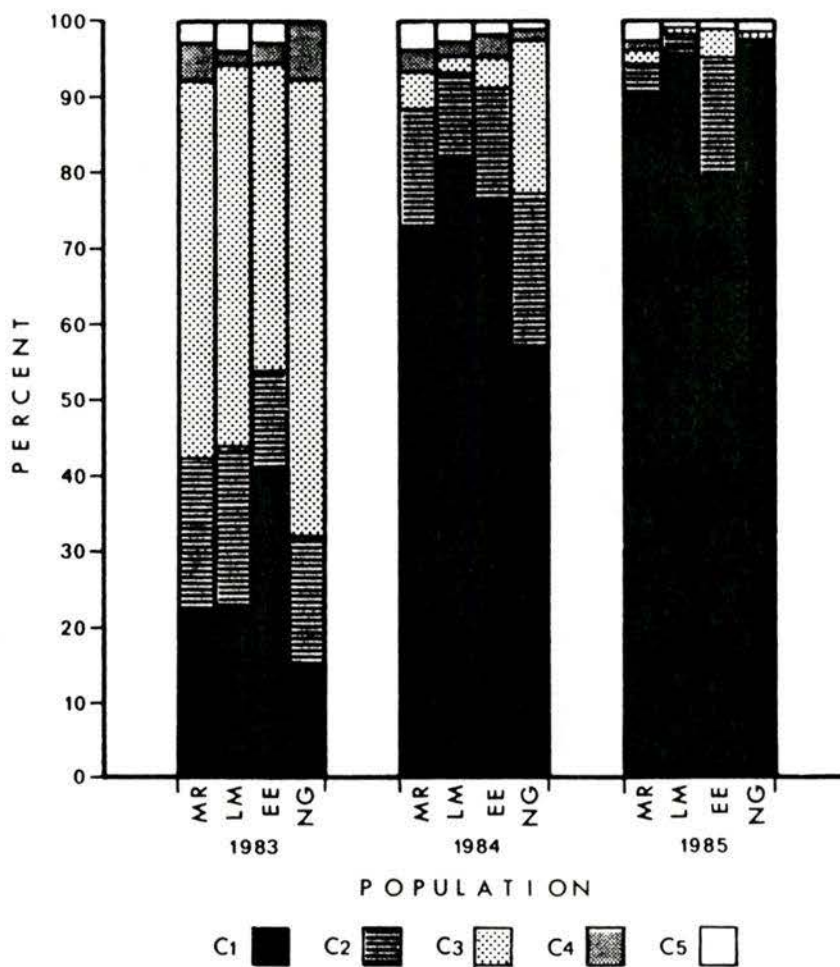


FIGURE 17 Number of Viable Seeds produced each year by *A. bourgovii*.

TABLE 10 SEED PRODUCTION *Astragalus robbinsii*

LOCATION	POPULATION		SEED PRODUCTION					
	SIZE (m ²)	NUMBER*	YEAR	VIGOR	SEED "HEADS" (%)	WILDLIFE UTILIZATION	PODS (l)	SEEDS (gms)
MR	210	150	1983	good	90	trace	0.95	3.23
			1984	good	95	light	1.50	5.10
			1985	good	90	trace	0.85	2.87
BE	435	250	1983	excellent	75	moderate	2.05	6.97
			1984	good	70	heavy	1.75	5.89
			1985	good	75	moderate	1.95	6.53
SB	600	200	1983	good	60	light	1.55	5.27
			1984	good	50	moderate	1.35	4.57
			1985	fair	45	light	1.20	4.08
WB	175	70	1983	good	65	trace	0.65	2.21
			1984	fair	35	trace	0.30	1.02
			1985	fair	55	trace	0.45	1.52
NG	700	250	1983	excellent	85	none	1.95	6.41
			1984	excellent	90	none	2.15	7.03
			1985	good	90	none	2.00	6.65

* The numbers represent estimated abundances.

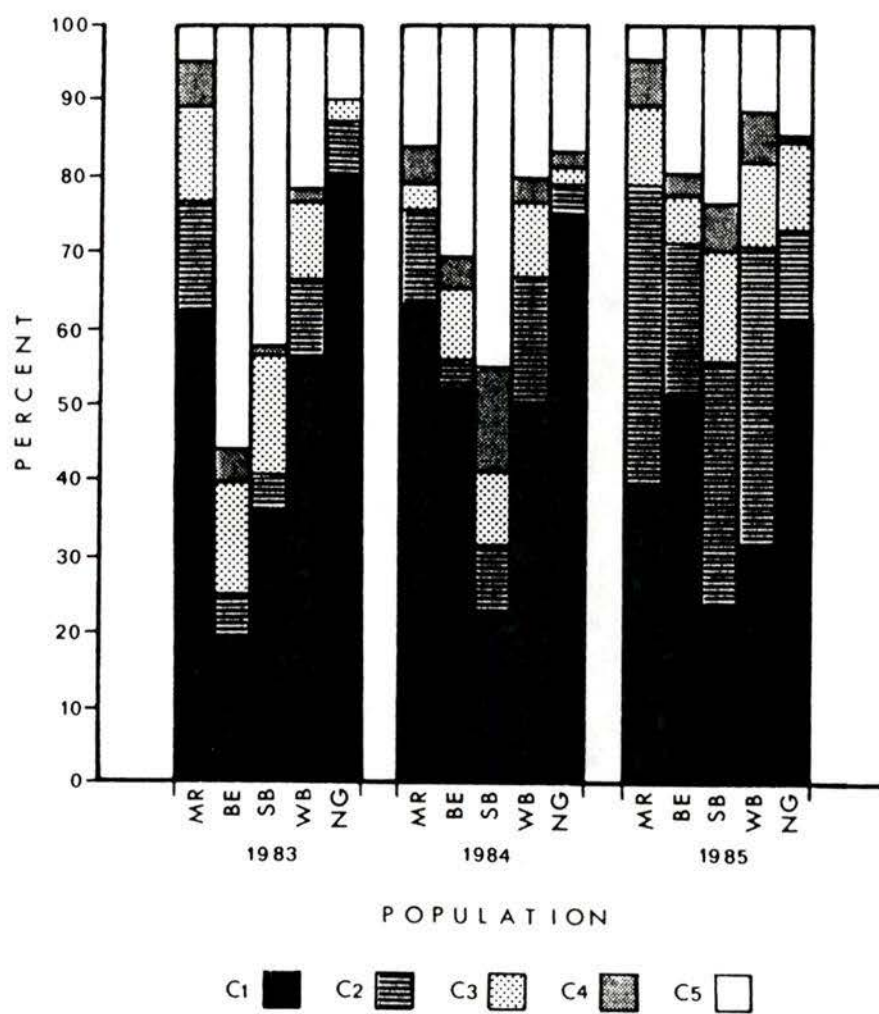


FIGURE 18 Number of Viable Seeds produced each year by *A. robbinsii*.

populations produced the lowest number of viable seeds and had the highest number of insect damaged seeds (Class 5) each year. The greatest number of seeds with smaller embryos (Class 2) was recorded in 1985. The number of poorly developed (Class 3) or aborted embryos (Class 4) was variable.

The vigor of *A. vexilliflexus* var. *nubilus* was excellent for all populations (Table 11). The percentage of individuals with seed heads was high in each year except for the Michel Ridge (MR) population. Wildlife utilization of this species was not observed. Seed production was proportional to population numbers. The number of viable seeds (Class 1 and 2) was greatest in 1984 and lowest in 1985 (Figure 19). The number of smaller embryos (Class 2) was greatest in 1985. The Michel Ridge (MR) population had the lowest number of viable seeds and the greatest number of insect damaged seeds (Class 5) each year. The greatest number of poorly developed (Class 3) and (Class 4) aborted embryos for all populations was recorded in 1985.

The vigor of *H. sulphurescens* ranged from poor to excellent (Table 12). Three of the populations had consistently good or excellent vigor, whereas the vigor of the Banner Mountain (BM) population was consistently fair. The vigor of the Todhunter Basin (TB) population improved from poor in 1983 to good in 1985. The

TABLE 11 SEED PRODUCTION *Astragalus vexilliflexus* var. *nubilus*

LOCATION	POPULATION		SEED PRODUCTION					
	SIZE (m ²)	NUMBER*	YEAR	VIGOR	SEED "HEADS" (%)	WILDLIFE UTILIZATION	PODS (l)	SEEDS (gms)
MR	150	75	1983	excellent	75	none	0.55	2.20
			1984	excellent	80	none	0.60	2.43
			1985	excellent	75	none	0.65	2.62
BM	450	250	1983	excellent	90	none	1.75	7.05
			1984	excellent	95	none	1.90	7.66
			1985	excellent	100	none	1.95	7.83
NG	125	50	1983	excellent	90	none	0.35	1.47
			1984	excellent	95	none	0.40	1.69
			1985	excellent	95	none	0.35	1.54

* The numbers represent estimated abundances.

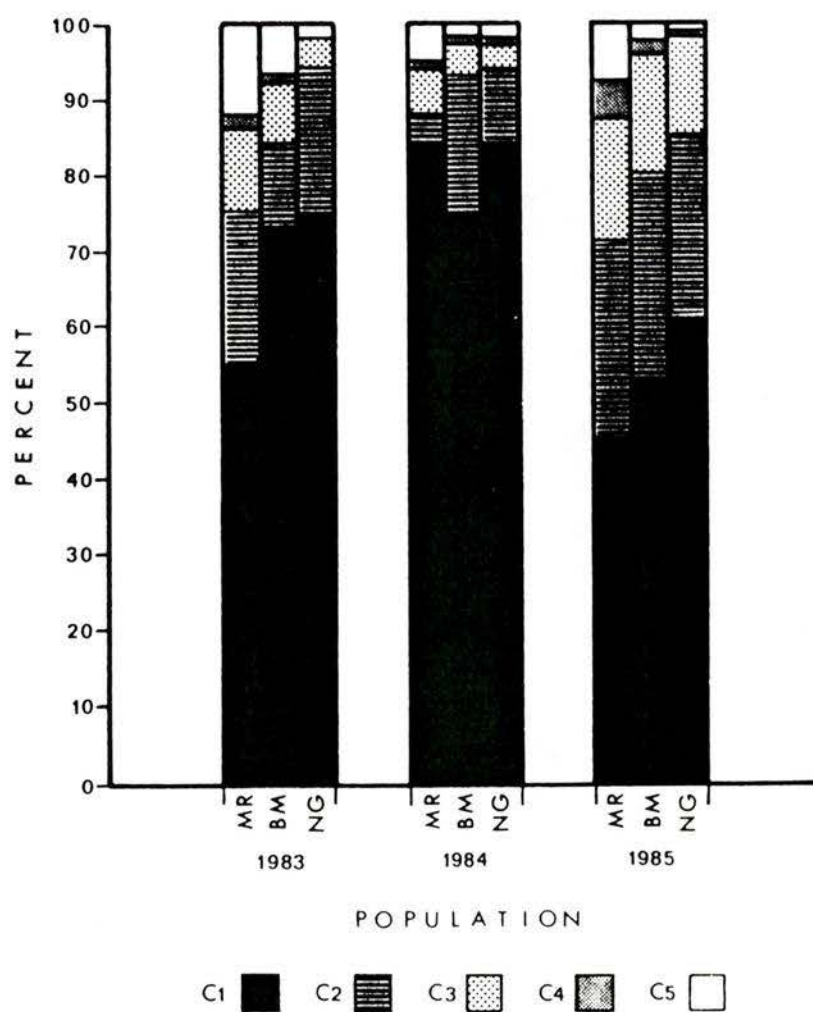


FIGURE 19 Number of Viable Seeds produced each year by *A. vexilliflexus* var *nubilus*

TABLE 12 SEED PRODUCTION *Hedysarum sulphurescens*

SAMPLE LOCATION	POPULATION		SEED PRODUCTION					
	SIZE (m ²)	NUMBER*	YEAR	VIGOR	SEED "HEADS" (%)	WILDLIFE UTILIZATION	PODS (l)	SEEDS (gms)
MR	425	200	1983	good	95	none	1.10	6.63
			1984	good	90	none	1.25	7.56
			1985	good	90	none	1.15	6.94
BM	950	550	1983	fair	35	none	0.45	2.71
			1984	fair	40	light	0.65	3.97
			1985	fair	50	light	0.55	3.33
EK	320	275	1983	good	90	none	1.55	9.34
			1984	good	90	trace	1.75	10.55
			1985	good	95	none	1.60	9.68
TB	450	275	1983	poor	60	trace	0.90	4.95
			1984	fair	65	trace	1.10	6.46
			1985	good	80	trace	1.75	10.52
NG	825	450	1983	excellent	95	light	2.35	14.13
			1984	excellent	95	heavy	2.50	14.98
			1985	excellent	100	trace	2.40	14.44

* The numbers represent estimated abundances.

percentage of seed heads was high for the three populations but moderately low for the Banner Mountain (BM) and Todhunter Basin (TB) populations. The percentage of seed heads increased each year for these two populations. Seed production was proportional to population numbers except for the Banner Mountain (BM) population. The number of viable seeds (Class 1 and 2) for most populations was greatest in 1984 (Figure 20). The Michel Ridge (MR) and Todhunter Basin (TB) populations had the lowest number of viable seeds and the greatest amount of insect damage. The percentage of poorly developed and aborted embryos was low.

The vigor of *O. podocarpa* populations was good and the percentage of seed heads was high each year (Table 13). Wildlife utilization was heavy for the South Bald (BM) and Todhunter Basin (TB) populations. Seed production was proportional to population numbers. The number of viable seeds (Class 1 and 2) was consistently high each year, although the number of seeds with smaller embryos (Class 2) was greater for the Ewin Ridge (ER) and Todhunter Basin (TB) populations in 1985 (Figure 21). The number of poorly developed (Class 3) and aborted embryos (Class 4) was low. The number of insect-damaged seeds (Class 5) was also low, possibly because seeds were consumed by predators prior to pod collection.

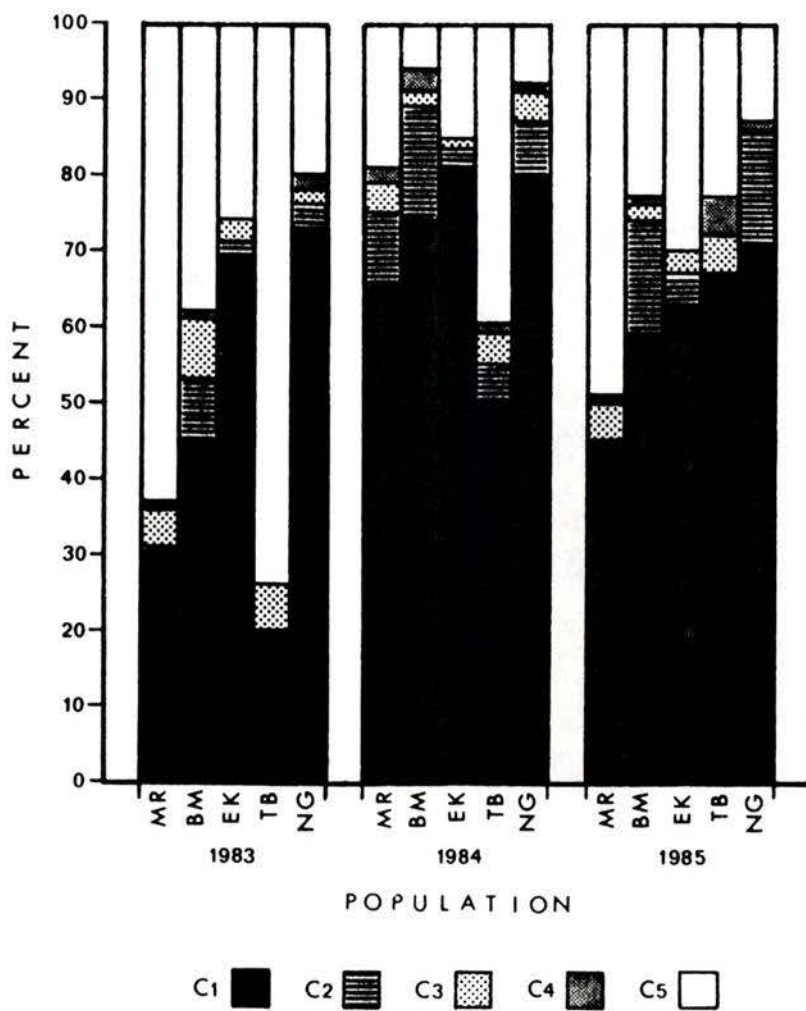


FIGURE 20 Number of Viable Seeds produced each year by *H. sulphurens*.

TABLE 13 SEED PRODUCTION *Oxytropis podocarpa*

LOCATION	POPULATION		YEAR	VIGOR	SEED PRODUCTION			
	SIZE (m ²)	NUMBER*			SEED "HEADS" (%)	WILDLIFE UTILIZATION	PODS (l)	SEEDS (gms)
ER	325	250	1983	good	80	moderate	1.25	1.65
			1984	good	90	moderate	1.30	1.73
			1985	good	85	moderate	1.25	1.63
SB	255	245	1983	good	90	heavy	1.20	1.86
			1984	good	90	heavy	1.15	1.52
			1985	good	90	heavy	1.25	1.67
WB	305	265	1983	good	75	light	1.40	1.88
			1984	good	80	light	1.45	1.91
			1985	good	80	light	1.55	2.04
BM	455	370	1983	good	80	moderate	1.95	2.57
			1984	good	80	moderate	1.90	2.55
			1985	good	80	moderate	1.90	2.52
TB	400	300	1983	good	75	heavy	1.70	2.23
			1984	good	80	heavy	1.80	2.33
			1985	good	90	heavy	1.80	2.38

* The numbers represent estimated abundances.

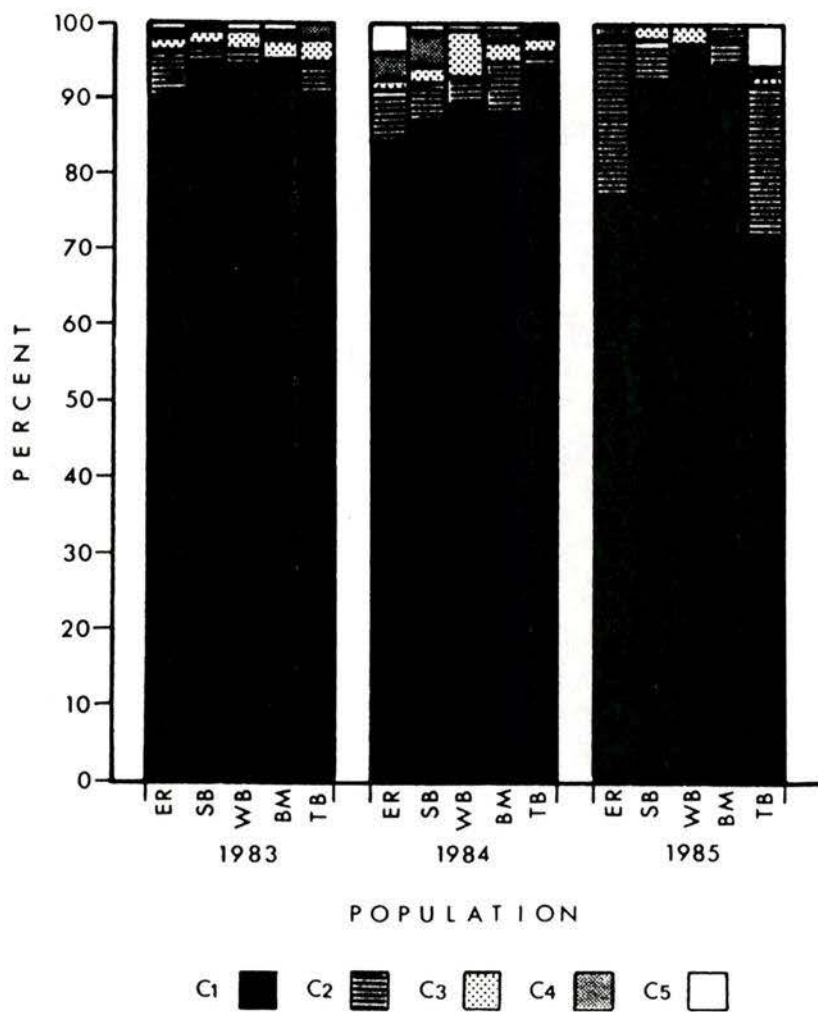


FIGURE 21 Number of Viable Seeds produced each year by *O. podocarpa*.

The vigor of *O. sericea* populations was good each year (Table 14). The percentage of seed heads was high, except for low values for the West Bald (WB) and North Greenhills (NG) populations in 1984. Wildlife utilization was low except for the Michel Ridge (MR) population in 1984. Seed production was proportional to population numbers. The number of viable seeds (Class 1 and 2) was moderately high, except for the West Bald (WB) population in 1984 and the North Greenhills (NG) population in 1985 (Figure 22). The reduced number of viable seeds in these populations was the result of higher numbers of poorly developed embryos (Class 3). The number of seeds with smaller embryos (Class 2) was high for the Ewin Ridge (ER) population in 1985. The number of seeds with aborted embryos (Class 4) and insect damaged seeds (Class 5) was low each year.

Seed Predators

All of the species were in some way affected by seed predation. Some species appeared to be more affected than others and the magnitude of predation also varied between populations of the same species. Most of the seed predators were insects, although seeds of two species were consumed by vertebrates.

Seed chalcid larvae of the genus *Bruchophagus* (Hymenoptera : Eurytomidae) were responsible for the majority of damage to the seeds of the *Astragalus* and

TABLE 14 SEED PRODUCTION *Oxytropis sericea*

LOCATION	POPULATION		SEED PRODUCTION					
	SIZE (m ²)	NUMBER*	YEAR	VIGOR	SEED "HEADS" (%)	WILDLIFE UTILIZATION	PODS (l)	SEEDS (gms)
MR	310	125	1983	good	90	trace	0.95	1.02
			1984	good	85	heavy	0.35	0.78
			1985	good	90	trace	0.90	0.99
ER	1550	500	1983	good	95	trace	2.65	2.92
			1984	good	90	light	2.80	3.28
			1985	good	95	trace	2.75	3.33
SB	2020	600	1983	good	80	trace	3.05	3.34
			1984	good	85	trace	3.00	3.31
			1985	good	80	trace	2.90	3.29
WB	410	300	1983	good	75	light	1.30	1.43
			1984	good	45	trace	0.60	0.67
			1985	good	70	none	1.15	1.28
NG	325	150	1983	good	80	none	1.10	1.21
			1984	good	40	light	0.45	0.65
			1985	good	75	none	1.00	1.23
GP	185	120	1983	good	90	none	0.75	0.84
			1984	good	95	none	0.65	0.78
			1985	good	95	none	0.65	0.83

* The numbers represent estimated abundances.

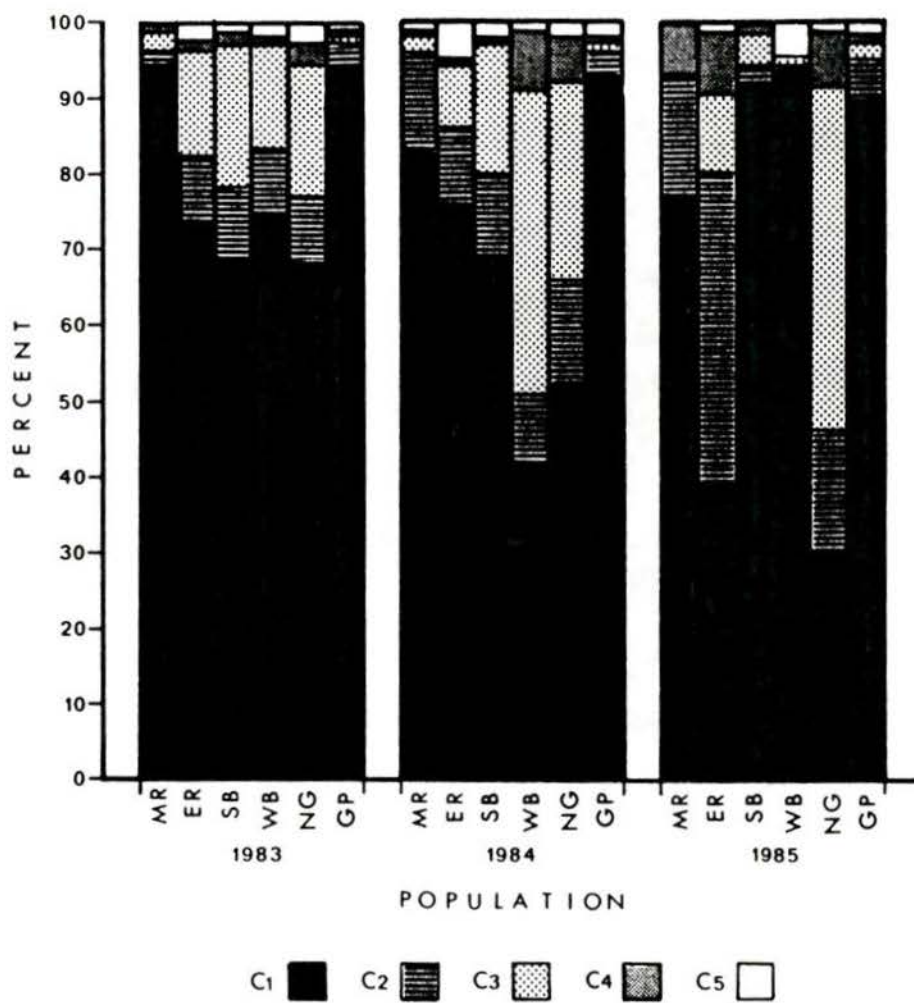


FIGURE 22 Number of Viable Seeds produced each year by *O. sericea*.

Hedysarum species studied. The larvae were within the seeds and generally consumed the entire embryo (Figure 7). The timing of oviposition is unknown. External evidence of damage consisted of 1-2 mm diameter holes in the pods or loment, and the presence of silk and frass. Adjacent damaged pods or loment were often joined together by silk and frass. Most of the seeds within the damaged pods or loment had larvae within them or had small exit holes. Damaged pods did not dehisce. The presence of larvae within the seeds was indicated by altered morphology and color. All the seeds of the *Astragalus* species with larvae present had an increase in seed depth (Table 15) and were more yellow (Table 16). Insect damaged seeds of *H. sulphurescens* also had similar color differences. However, the insect damaged seeds of this species had an increase in seed width as well as an increase in seed depth.

Seed weevils (Coleoptera : Curculionidae) were responsible for all of the damage to *O. sericea* and some of the damage to the seeds of *O. podocarpa*. External evidence for damage was the inability of the pod to dehisce and the presence of an exit hole in the pod. Considerable amounts of silk and frass were also present within the damaged pods. Seeds within the damaged pods were entirely consumed or had large portions removed (Figure 7). The seeds of *O. podocarpa*

TABLE 15 SEED SHAPES AND SIZES

SPECIES	SHAPE	SIZE (mm)					
		LENGTH		WIDTH		DEPTH	
		X	SD	X	SD	X	SD
<i>Astragalus alpinus</i>	obliquely reniform	2.133	+ 0.327	1.578	+ 0.219	0.737	+ 0.151
<i>Astragalus bourgovii</i>	obliquely reniform	2.388	+ 0.308	1.182	+ 0.168	0.924	+ 0.250
<i>Astragalus robbinsii</i>	reniform	2.000	+ 0.183	1.702	+ 0.238	0.758	+ 0.131
<i>Astragalus vexilliflexus</i> var. <i>nubilus</i>	oblong	2.490	+ 0.351	1.674	+ 0.184	0.964	+ 0.172
<i>Hedysarum sulphurescens</i>	reniform	3.284	+ 0.493	2.242	+ 0.294	0.924	+ 0.219
<i>Oxytropis podocarpa</i>	reniform	2.238	+ 0.160	2.042	+ 0.131	0.880	+ 0.069
<i>Oxytropis sericea</i>	reniform	1.864	+ 0.144	1.642	+ 0.124	0.852	+ 0.110

Note: Six replicates of 100 seeds were used for these measurements.

TABLE 16 SEED COLOR

SPECIES	HUE VALUE/ CHROMA	MUNSELL COLOR	PERCENTAGE OF SAMPLE
<i>Astragalus alpinus</i>	2.5Y 6/8	olive yellow *	3
	5Y 5/6	olive	8
	5Y 6/6	olive yellow	89
<i>Astragalus bourgovii</i>	10YR 5/8	yellowish brown	44
	10YR 3/4	dark yellowish brown	6
	2.5Y 5/6	light olive brown	39
	5Y 4/3	olive *	5
	5Y 5/4	olive	6
<i>Astragalus robbinsii</i>	2.5YR 5/4	reddish brown	40
	5YR 3/3	dark reddish brown	22
	10YR 2/1	black	1
	10YR 6/6	brownish yellow *	19
	5Y 4/2	olive gray	18
<i>Astragalus vexilliflexus</i> var. <i>nubilus</i>	7.5YR 3/2	dark brown	9
	10YR 4/4	dark yellowish brown *	1
	2.5Y 2/0	black	90
<i>Hedysarum sulphurescens</i>	5R 2/2	very dusky red	9
	7.5R 3/2	dusky red	6
	10R 5/2	weak red	5
	10YR 5/6	yellowish brown	10
	10YR 7/4	very pale brown	53
	2.5Y 6/4	light yellowish brown *	17
<i>Oxytropis podocarpa</i>	2.5YR 2/0	black	35
	2.5YR 2/4	dark reddish brown	37
	7.5YR 4/4	brown	28
<i>Oxytropis sericea</i>	10R 2/1	reddish black	19
	10R 2/2	very dusky red	24
	2.5YR 2/4	dark reddish brown	8
	5YR 3/4	dark reddish brown	33
	5YR 5/8	yellowish red	13
	7.5YR 4/4	brown	3

Note: Seed colors which indicate the presence of insect larvae have asterisks.

were also consumed by ptarmigan, *Lagopus lagopus*. The ptarmigan penetrated the pods with their beaks and removed the unripe seeds.

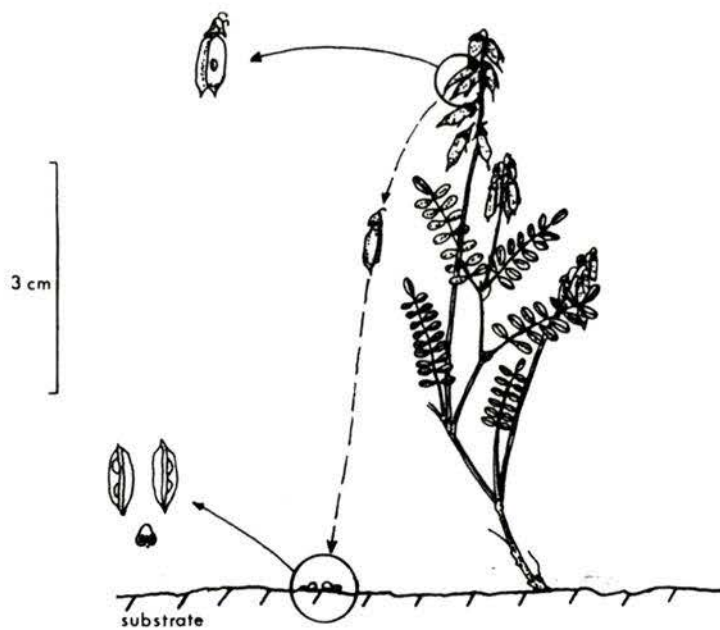
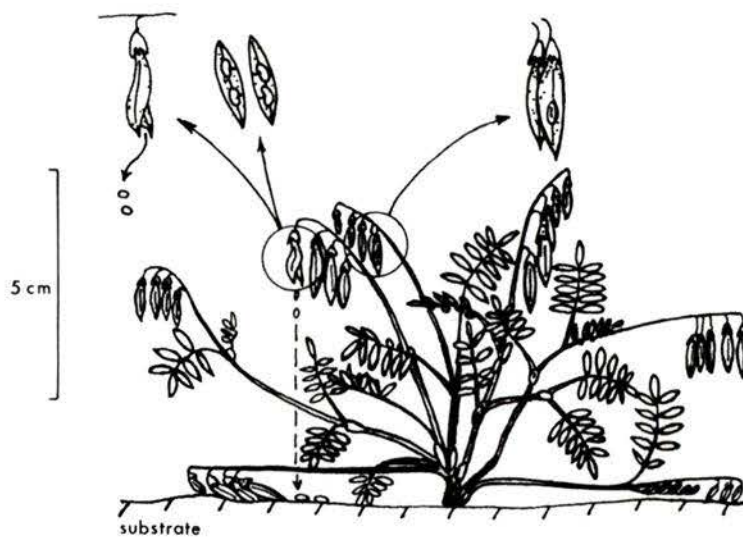
Post-dispersal seed predation is probable for all species but was only noted for *H. sulphurescens* and *O. podocarpa*. Golden mantled ground squirrels were observed removing and eating seeds from the respective loment and pods of these species.

Seed Dispersal

Seed dispersal mechanisms varied with species. The description of the seed dispersal mechanisms for *Astragalus* and *Oxytropis* followed the classification of Kaden (1965) and Voronchikhin (1982). The pods or loment of all species lost their glossy appearance at maturity and became tan colored.

Pods of *A. alpinus* dehisced along the dorsal and ventral sutures. This form of dehiscence was termed perfect dorso-ventral dehiscence by Voronchikhin (1982). The seeds were retained by the valves and dispersed up to several centimeters from the plant (Figure 23). The distance to which the seed-containing pod valves were dispersed was dependent upon the density of the surrounding vegetation, microtopography and wind exposure. Seed-containing valves were often found in soil depressions.

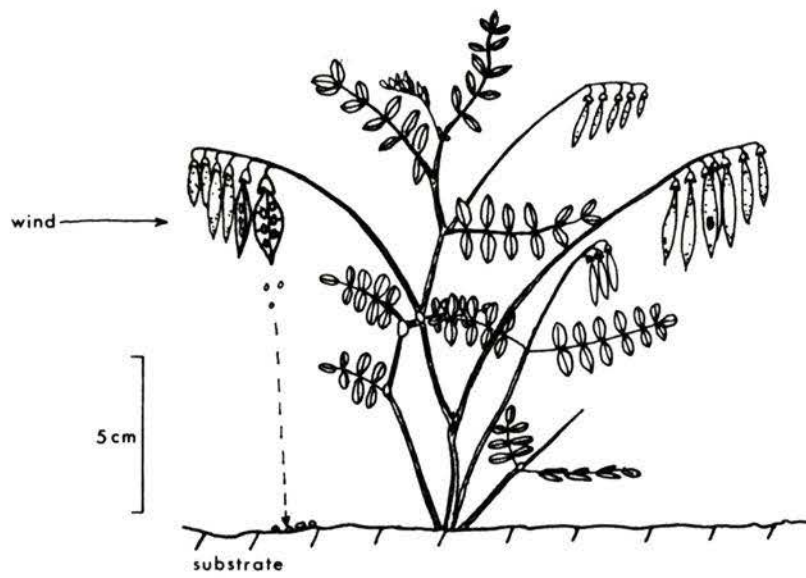
Pods of *A. bourgovii* had imperfect to perfect dorso

FIGURE 23 *Astragalus alpinus* seed dispersal.FIGURE 24 *Astragalus bourgovii* seed dispersal.

-ventral dehiscence. The distal end of the pod opened first and dehiscence progressed proximally (Figure 24). Dehiscence generally took place while the pods were attached to the raceme, but sometimes occurred after separation from the plant. Some pods twisted longitudinally when disseminating seeds, but the majority fell to the ground as separate valves. Most of the seeds were disseminated before the pods separated from the raceme, and the seeds fell directly below the racemes. Seeds and valves were in soil depressions on steep coarse textured slopes.

Pods of *A. robbinsii* had perfect dorsal dehiscence. This was the only *Astragalus* species studied in which the pods remained attached to the raceme (Figure 25). The racemes extended out from the plant and when open the wind dispersed the seeds up to 10 cm from the perimeter of the plant. The pods were hygroscopic and opened when dry and closed when moist. Slope, vegetation and microtopography were factors determining the distance over which seeds were dispersed.

Pods of *A. vexilliflexus* var. *nubilus* had perfect dorso-ventral dehiscence (Figure 26). Intact pods fell to the ground beneath the racemes and the valves separated. Most of the racemes were within the perimeter of the plant and therefore the majority of the seeds were disseminated within the foliage of the plant. The

FIGURE 25 *Astragalus robbinsii* seed dispersal.FIGURE 26 *Astragalus vexilliflexus* var. *nubilus* seed dispersal.

Pods within the plant often adhered to moist foliage and fell to the ground only when the foliage dried. This situation was common since pod release occurred during times of frequent storms. Seeds within the dispersed pods were often soft and swollen. Seeds and valves were frequently found in depressions beneath the foliage of the plants.

The loment segments of *H. sulphurescens* either separated from the plant intact or the individual loment segments separated while still attached to the plant (Figure 27). The seeds were then retained within the loment segments until animal activity, microorganism activity or soil frost action released the seeds. The loment margin did not appear to enhance wind dispersal. Most of the loment segments were dispersed within 5-10 cm of the plant and accumulated in soil depressions or among the stems of the adjacent vegetation.

Pods of *O. podocarpa* had perfect dorsal dehiscence. The suture opened distally and shortly thereafter, the pod separated from the plant (Figure 28). The pod then tumbled away from the plant, releasing the distally located seeds first. The remaining seeds were disseminated as the wind blew the pods further away from the plant. Several seeds were often retained in the pods by a fine cobwebby material that was attached to the endocarp of the pod. The distance to which pods

FIGURE 27 *Hedysarum sulphurescens* seed dispersal.

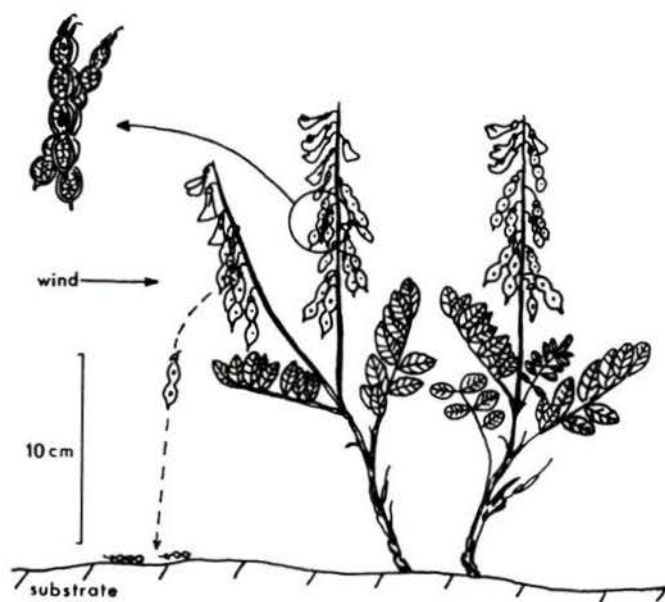
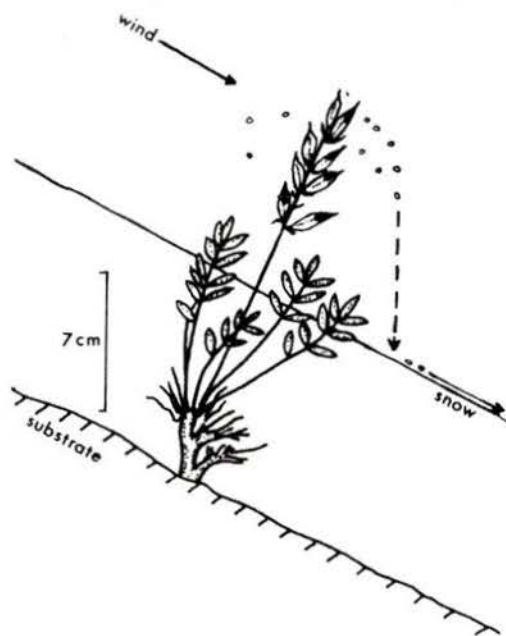


FIGURE 28 *Oxytropis podocarpa* seed dispersal.FIGURE 29 *Oxytropis sericea* seed dispersal.

disperse appears to be dependent upon wind exposure, microtopography and vegetative cover. Pods were observed to disperse 2-3 m from their point of origin.

Pods of *O. sericea* had imperfect dorsal dehiscence. However, in contrast to those of *O. podocarpa*, the pods remained attached to the plant (Figure 29). The suture opened distally and then wind or animals caused the pods to shake and disperse the seeds. This primary mechanism of seed dispersal occurred over a distance of 20 cm. A secondary form of dispersal was also observed. Seeds were observed to slide several metres on slopes when a layer of snow with an ice crust was present.

Laboratory Seed Germination

Sample Population Germination

Seed germination varied between species, and between populations and years. The proportion of seeds that germinated was low for most species. Histograms of the cumulative proportion of germinated seeds are included instead of germination survival curves. The Breslow (1970) statistic was used for the pairwise comparisons of all germination survival curves. The higher the p value the more similar the germination survival curve.

The cumulative proportion of germinated seeds of *A. alpinus* was low for all populations in 1983 and 1984, but was higher for the Ewin Ridge (ER) and West Bald (WB) populations in 1985 (Figure 30). The cumulative

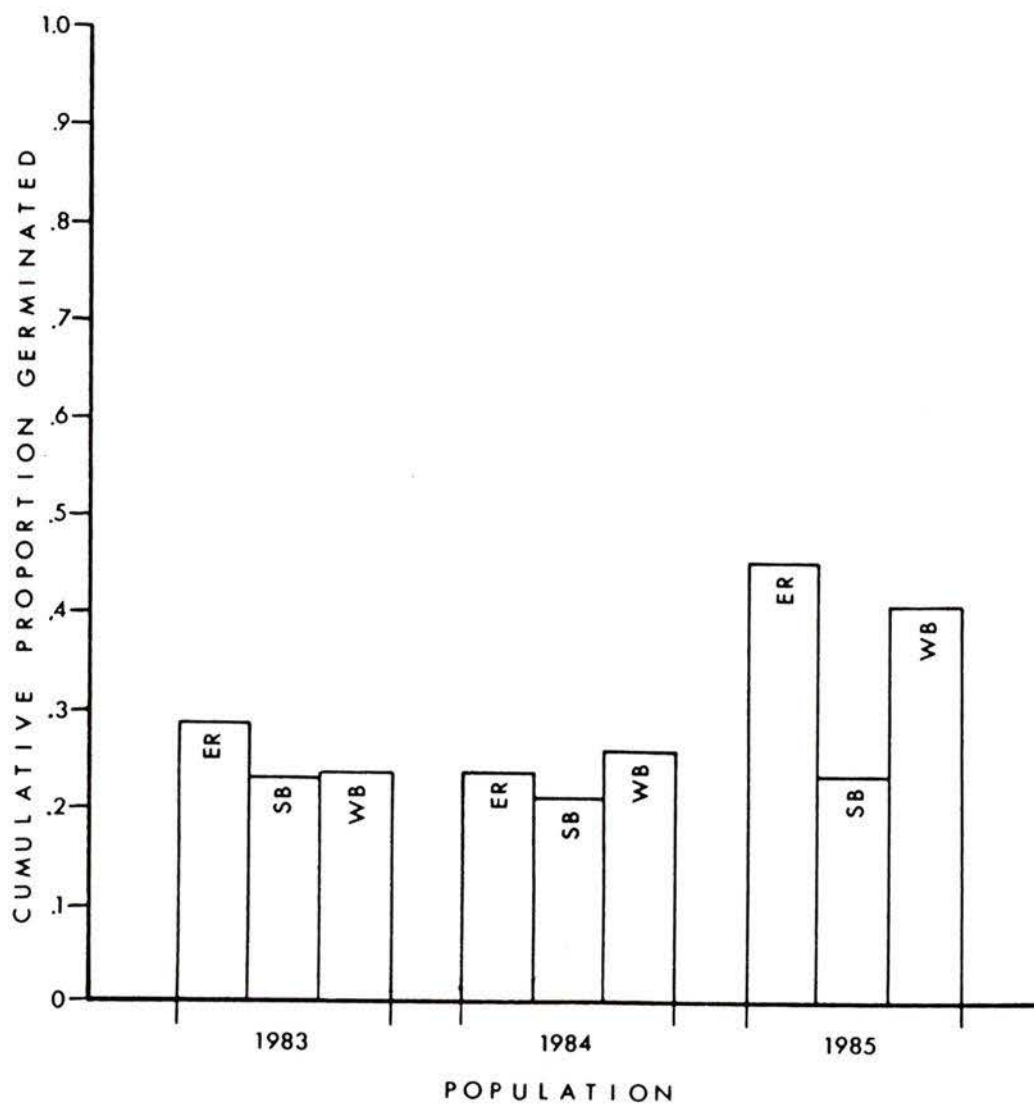


FIGURE 30 Histograms of Cumulative Proportion of Germinants for *A. alpinus*.

proportion of germinated seeds ranged from 0.22 to 0.40. Germination survival curves for all the populations in 1983 and 1984, and the South Bald population in 1985 were similar ($0.976 > p > 0.803$), whereas the Ewin Ridge and West Bald populations were similar ($p = 0.856$) in 1985. Radicle emergence for each population began on the fourth day of incubation. The percentage of abnormal germinants ranged from 0.00 in 1985 to 18.48 in 1984 (Table 17). Rotten radicles were the most common form of germinant abnormalities for all the *Astragalus* species (Figure 31).

The cumulative proportion of germinated seeds of the populations of *A. bourgovii* ranged from 0.11 to 0.27 (Figure 32). The cumulative proportion of germinated seeds for the Lookout Mountain (LM) and North Greenhills (NG) populations was highest in 1985 while the proportion of germinated seeds for the Michel Ridge (MR) and East Ewin Ridge (EE) populations was lowest in 1985. The germination survival curves were all similar ($0.764 > p > 0.134$), but the East Ewin population in 1985 was the most dissimilar. Radicle emergence began on the sixth day of incubation for each replicate. The rate of seed germination was constant, whereas the number of abnormal germinants was variable. The percentage of abnormal germinants ranged from 1.02 for the Lookout Mountain (LM) in 1985 to 30.00 for the East Ewin Ridge

TABLE 17 MEAN PERCENTAGE OF ABNORMAL SEEDLINGS

SPECIES	SAMPLE POPULATION	YEAR		
		1983	1984	1985
<i>Astragalus alpinus</i>	ER	7.52	11.24	2.22
	WB	7.69	18.48	0.00
	EB	8.62	3.37	0.00
<i>Astragalus bourgovii</i>	MR	3.70	5.88	5.13
	LM	12.86	12.50	1.02
	EE	7.50	13.73	30.00
	NG	8.48	5.88	4.79
<i>Astragalus robbinsii</i>	MR	19.85	35.78	45.88
	BE	27.47	23.68	12.66
	SB	27.46	0.00	0.00
	WB	15.00	16.39	19.64
	NG	6.86	10.23	7.06
<i>Astragalus vexilliflexus</i> var. <i>nubilus</i>	MR	11.65	7.86	10.13
	BM	2.82	7.49	35.42
	NG	6.45	3.92	7.50
<i>Hedysarum sulphurescens</i>	MR	11.67	0.77	13.81
	BM	11.99	0.91	2.84
	EK	8.05	2.86	18.30
	TB	91.38	4.38	8.25
	NG	4.55	0.63	4.51
<i>Oxytropis podocarpa</i>	ER	7.69	1.02	21.70
	SB	3.03	0.00	1.84
	WB	1.77	0.00	0.00
	BM	5.15	1.47	0.00
	TB	6.27	0.00	24.81
<i>Oxytropis sericea</i>	MR	2.92	5.32	5.95
	ER	5.92	20.13	16.28
	SB	7.17	8.87	7.69
	WB	3.86	15.28	7.18
	NG	8.68	7.28	22.55
	GP	6.45	4.88	8.57

Note: Calculations are based on six replicates of 100 seeds.

FIGURE 31 SEEDLING ABNORMALS

Normal Germinant



Rotten Germinant



Broken Radicle



Radicle Absent



Damaged Radicle Tip



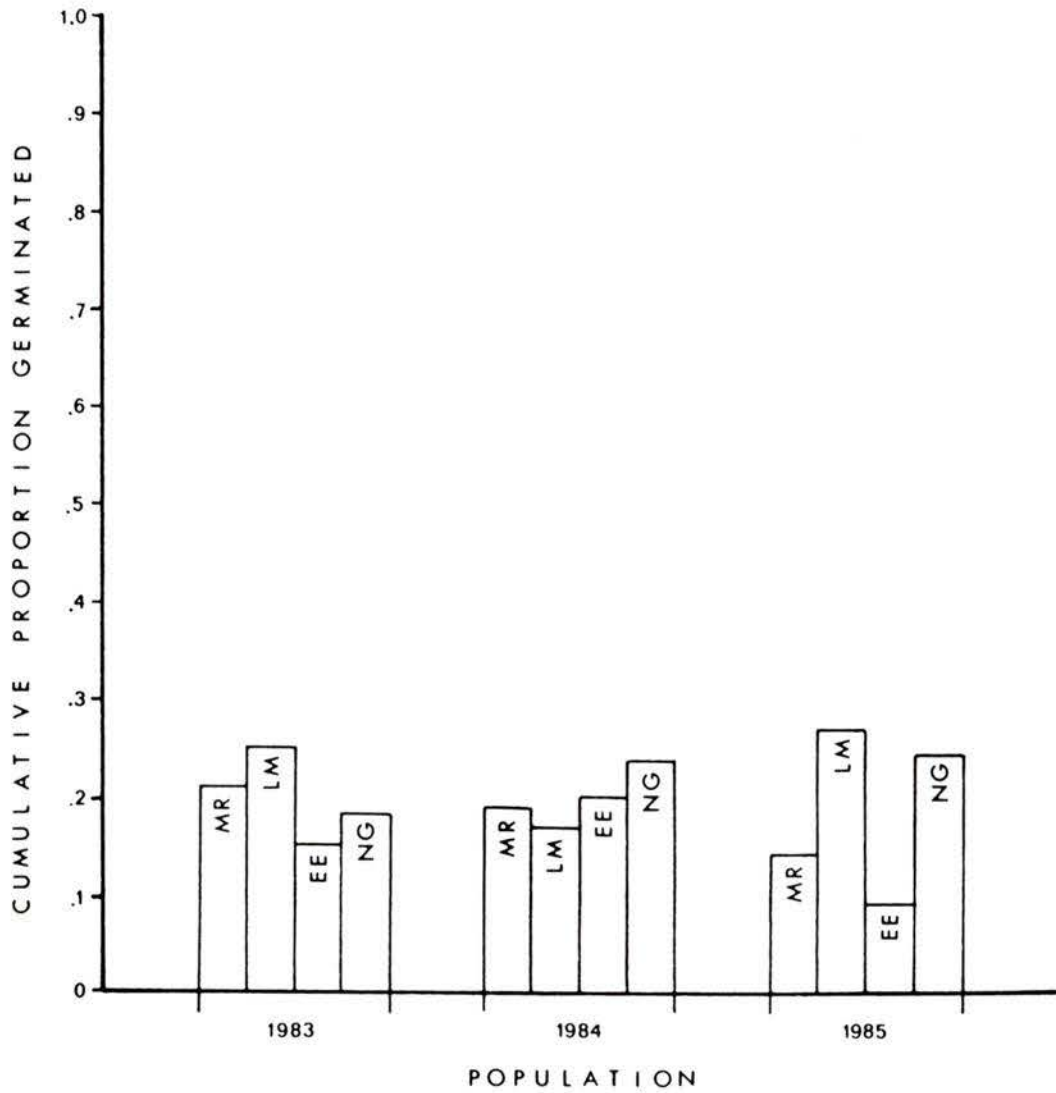


FIGURE 32 Histograms of Cumulative Proportion of Germinants for *A. bourgovii*.

(EE) in 1985 (Table 17). The percentage of abnormal germinants varied between populations and between years.

The cumulative proportion of germinated seeds of the populations of *A. robbinsii* ranged from 0.18 to 0.55 (Figure 33). The cumulative proportion of germinated seeds was highest for the South Bald (SB) and West Bald (WB) populations in 1985 and lowest for the Michel Ridge (MR), Bald Mountain/Ewin Ridge (BE), and North Greenhills (NG) populations in 1984 and 1985. The germination survival curves of each population and year were similar ($1.000 > p > 0.116$), with the exception of the South Bald and West Bald populations in 1985. The similarity of the survival curves of these two populations was ($p = 0.765$). Radicle emergence began between the fourth and sixth days of incubation. The percentage of abnormal germinants ranged from 0.00 to 45.88 (Table 17). The percentage of abnormal germinants increased each year for the Banner Mt. population, but varied for the other populations.

The cumulative proportion of germinated seeds of the populations of *A. vexilliflexus* var. *nubilus* ranged from 0.07 to 0.40 (Figure 34). The cumulative proportion of germinated seeds for the Michel Ridge (MR) population did not vary greatly, but ranged from 0.25 to 0.28, whereas the proportion for the Banner Mountain (BM) population ranged from 0.07 in 1983 to 0.40 in 1984. The

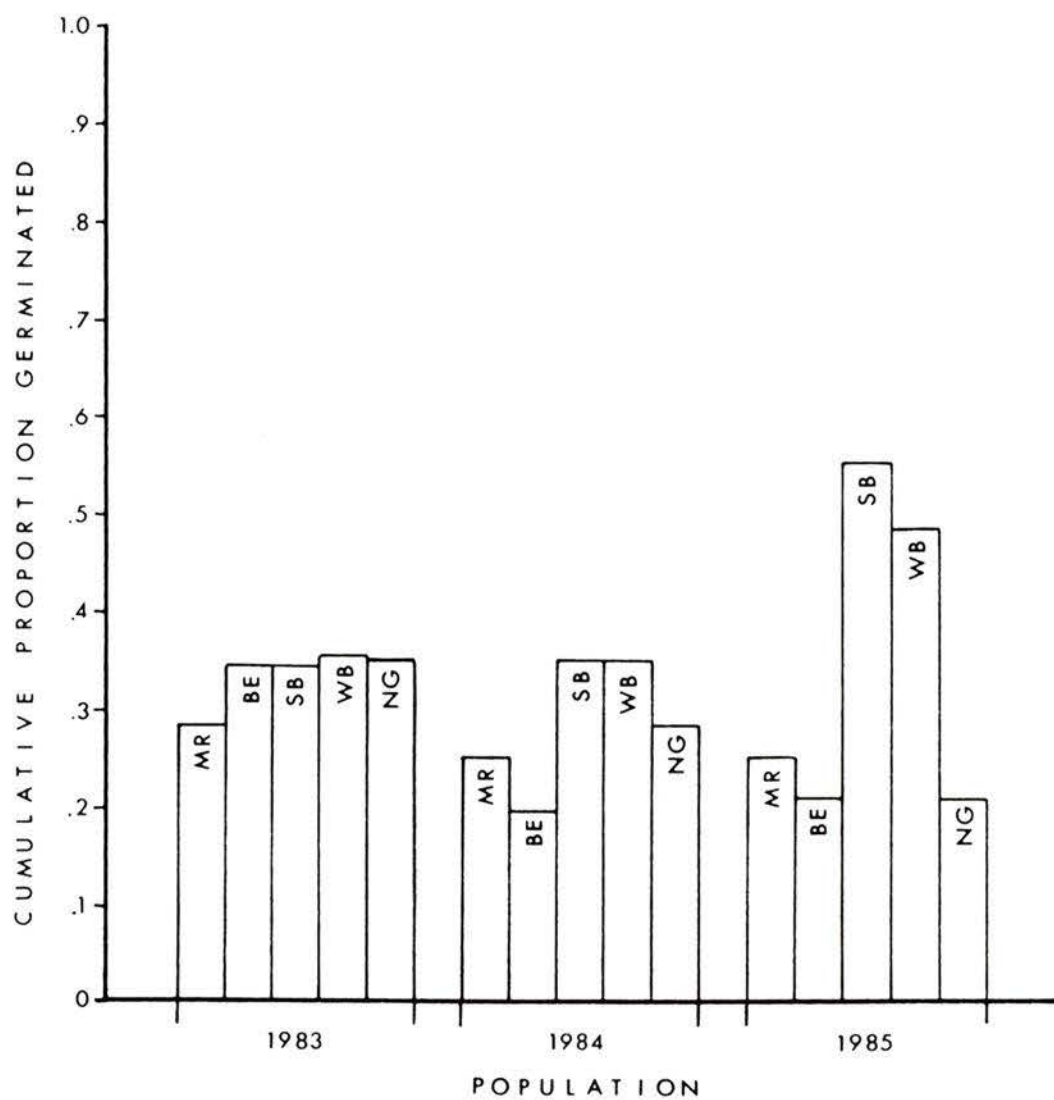


FIGURE 33 Histograms of Cumulative Proportion of Germinants for *A. robbinsii*.

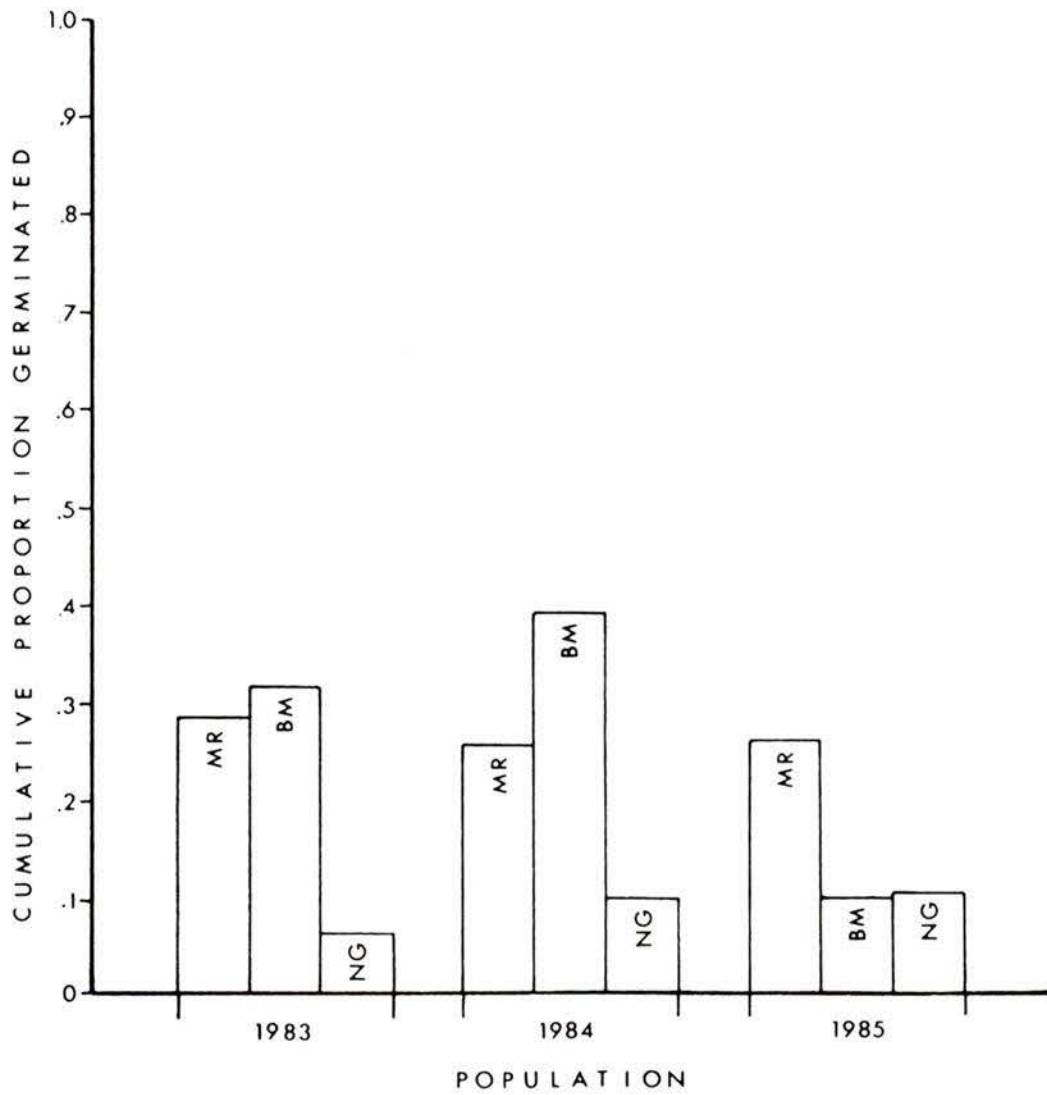


FIGURE 34 Histograms of Cumulative Proportion of Germinants for *Avexilliflexus*.

cumulative proportion of germinants for the North Greenhills (NG) was consistently low. Germination survival curves of the North Greenhills population and the Banner Mountain population in 1985 were similar ($1.000 > p > 0.801$), whereas the other sample populations were similar each year ($0.995 > p > 0.493$). Radicle emergence began within the fourth and sixth days of incubation. The percentage of abnormal germinants varied by year among populations and ranged from 2.82 to 35.42 (Table 17).

The cumulative proportion of germinated seeds for the populations of *H. sulphurescens* was high and only ranged from 0.96 to 1.00 (Figure 35). The cumulative proportion of germinated seeds was lowest in 1983. The germination survival curves were all very similar ($1.000 > p > 0.944$). Radicle emergence began within the fourth and sixth days and the rate of seed germination was rapid for the following eight days. The percentage of abnormal germinants was variable and ranged from 0.63 to 91.38 (Table 17). The percentage of abnormal germinants was consistently low for the North Greenhills (NG) population, but the lowest overall values were recorded for the 1984 population collections. Absent radicles were the most common form of germinant abnormalities (Figure 31).

Germination of seeds within lomentis was also

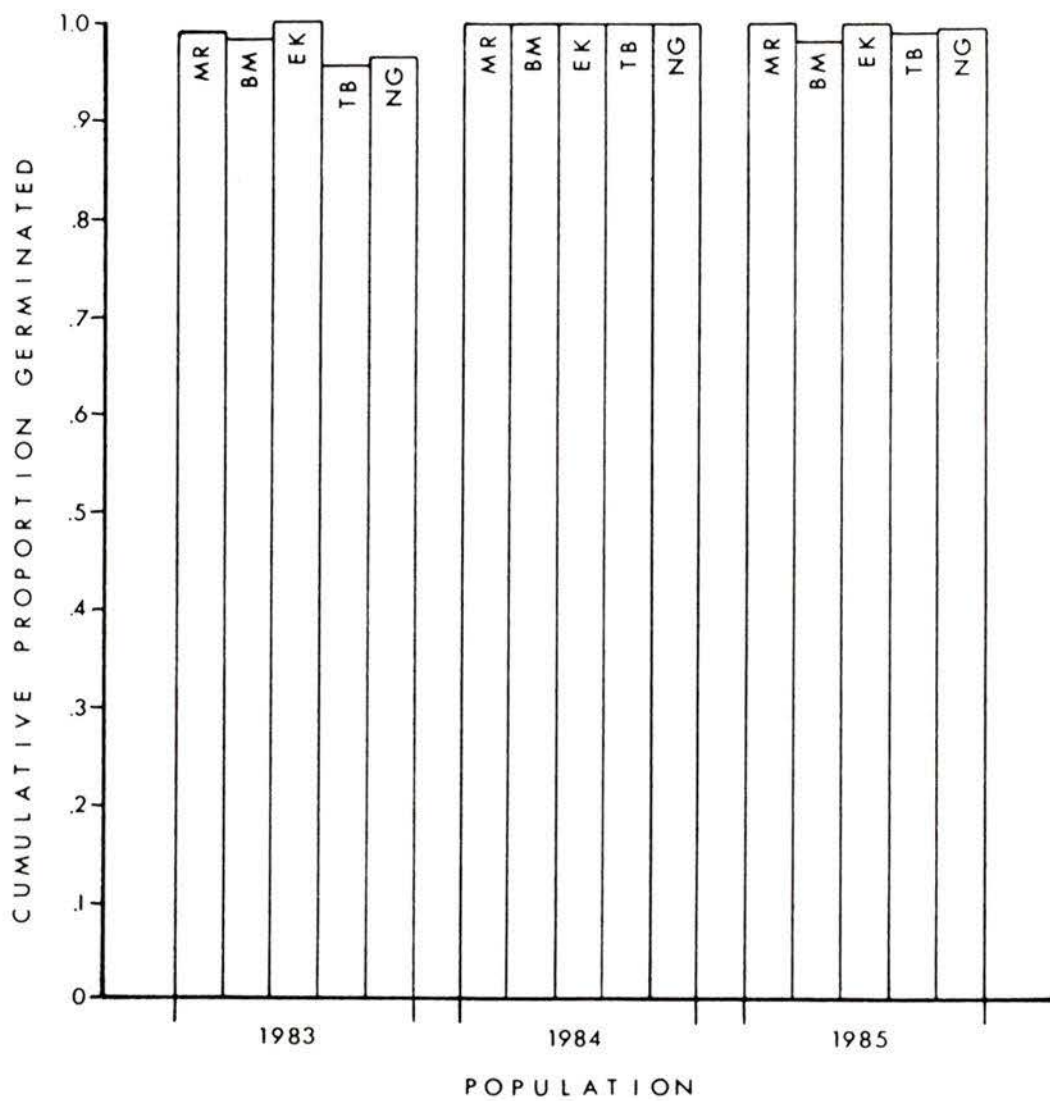


FIGURE 35 Histograms of Cumulative Proportion of Germinants for *H. sulphurens*.

compared to excised seeds. The seed germination rate was slightly slower, but the cumulative proportion that germinated was the same.

The cumulative proportion of germinated seeds for the populations of *O. podocarpa* ranged from 0.09 for the West Bald (BM) population in 1985 to 0.63 for the Banner Mountain (BM) population in 1983 (Figure 36). The cumulative proportion of germinants decreased for most populations from 1983 to 1985. The germination survival curves of the Ewin Ridge and South Bald populations in 1983, and all of the populations except the Todhunter Basin population in 1984 were similar ($1.000 > p > 0.876$). The West Bald, Banner Mountain and Todhunter Basin populations in 1983 were most similar ($0.845 > p > 0.543$), although they were somewhat similar to those of the previous group of populations ($0.342 > p > 0.115$). The Todhunter Basin population in 1984 and all of the populations in 1985 were similar ($0.956 > p > 0.323$), although there was a similarity to first group of populations ($0.345 > p > 0.103$) when the West Bald population was excluded. Radicle emergence began within between the fourth and sixth days. The rate of germination was rapid for one week and then slowed for the duration of the incubation. The percentage of abnormal germinants ranged from 0.00 to 24.81 (Table 17). The percentage of abnormal germinants was lowest in

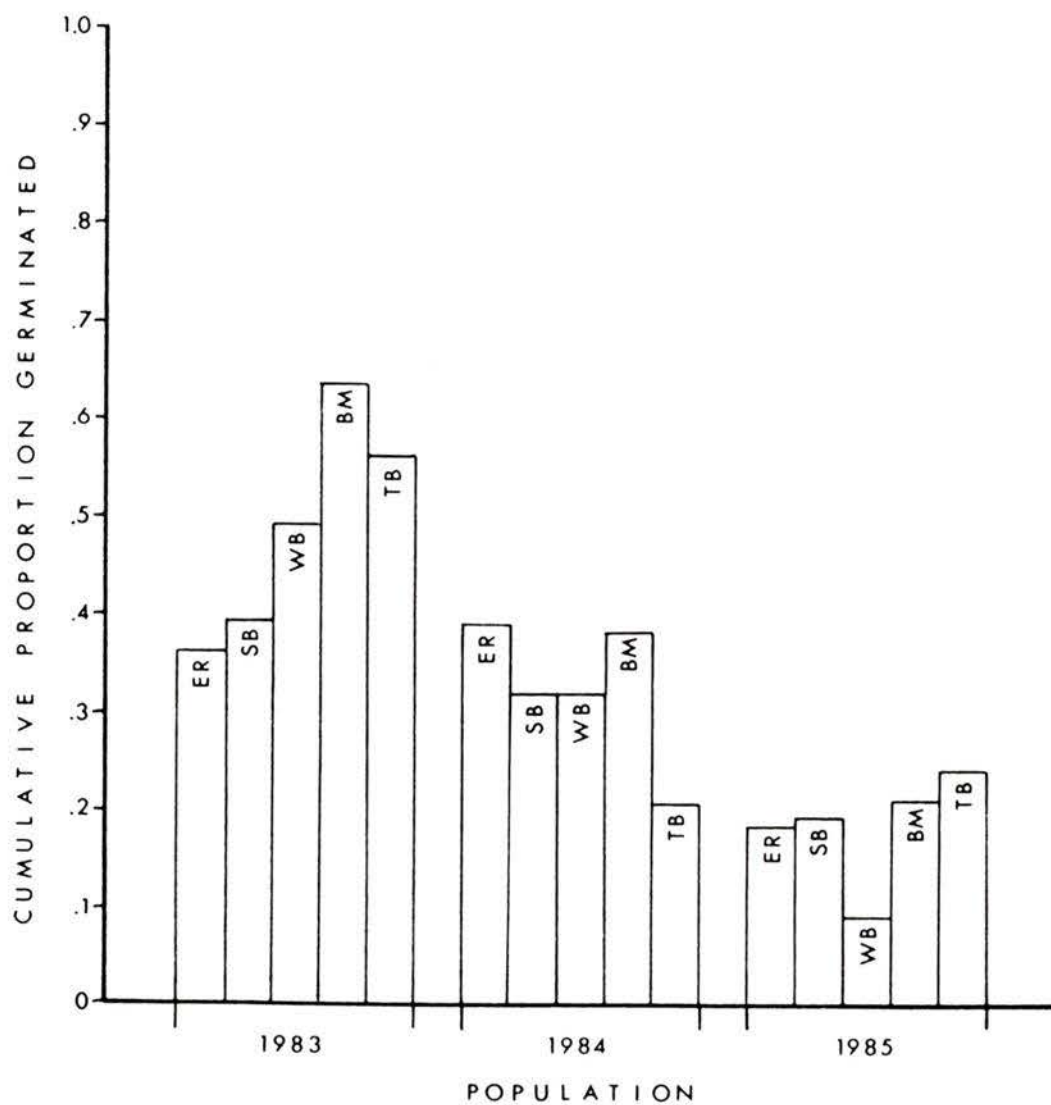


FIGURE 36 Histograms of Cumulative Proportion of Germinants for *O. podocarpa*.

1984. The West Bald (WB) had consistently the lowest number of abnormalities. Broken radicles were the most common form of abnormal germinants for the *Oxytropis* species (Figure 31).

The cumulative proportion of germinated seeds for the populations of *O. sericea* ranged from 0.06 for the Gill Peak (GP) population in 1985 to 0.75 for the West Bald (WB) population in 1983 (Figure 37). The cumulative proportion of germinants also decreased for most populations from 1983 to 1985. The cumulative proportion of germinants for the Gill Peak (GP) population was consistently very low. The survival curves of the Ewin Ridge, South Bald, and West Bald populations in 1983 were similar when compared with the North Greenhills population ($0.767 > p > 0.243$). The Michel Ridge population in 1983 and all the populations except the 1984 and 1985 North Greenhills and Gill Peak sample populations were similar ($0.907 > p > 0.452$). The germination survival curves of the Gill Peak population were very similar ($0.958 > p > 0.932$), but were also slightly similar to the 1984 and 1985 Michel Ridge and South Bald sample populations ($0.423 > p > 0.377$). Radicle emergence began on the sixth day for all populations and the rate of germination was constant. The percentage of abnormal germinants ranged from 2.92 to 22.55 (Table 17). The number of abnormal germinants

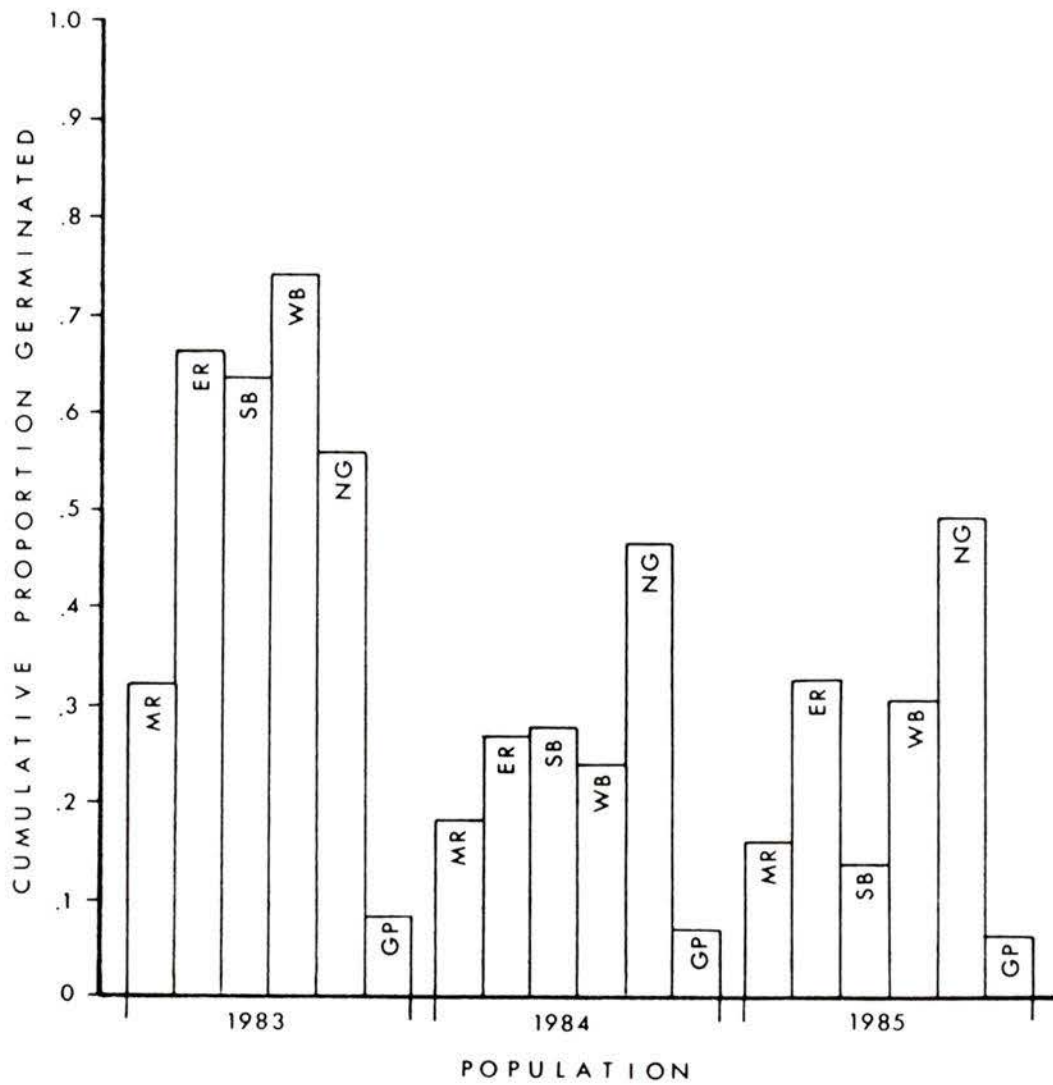


FIGURE 37 Histograms of Cumulative Proportion of Germinants for *O. sericea*.

was relatively constant in 1983 but varied in 1984 and 1985.

Germination Enhancement Treatments

Several treatments were applied to the seeds of each species to investigate the possibility of seed dormancy and to enhance seed germination. Summarized data for these treatments are listed in Tables 18 - 26. Seed germination survival curves are provided only for those treatments in which there was a significant response. The Breslow (1970) test statistic was used for pairwise comparisons of germination survival curves.

Temperature and Light

Temperature affected seed germination for all species. The cumulative proportion of germinated seeds of all species was greatest in the dark at a constant temperature of 30°C, treatment and ranged from 1.000 for *H. sulphurescens* to 0.272 for *A. alpinus* (Table 18). The increase in the cumulative proportion of germinated seeds was greatest between 5°C and 20°C for all treatments. The differences between the light and dark treatments was greatest for *A. alpinus* and smallest for the *Hedysarum* and *Oxytropis* species. Alternating temperatures yielded germination rates intermediate between the corresponding constant temperature treatments (Table 18). The majority of seed germination took place between the 14th and 22nd days of

TABLE 18 CUMULATIVE PROPORTION GERMINATED (TEMPERATURE)

TREATMENT	LEVEL	SPECIES						
		<i>Astragalus alpinus</i>	<i>Astragalus bourgovii</i>	<i>Astragalus robbinsii</i>	<i>Astragalus vexilliflexus</i>	<i>Hedysarum sulphurescens</i>	<i>Oxytropis podocarpa</i>	<i>Oxytropis sericea</i>
CONSTANT TEMPERATURE (LIGHT)	5 °C	0.026	0.086	0.055	0.067	0.042	0.035	0.073
	10 °C	0.086	0.175	0.107	0.167	0.346	0.094	0.158
	20 °C	0.183	0.232	0.137	0.262	0.948	0.224	0.225
	30 °C	0.188	0.272	0.178	0.256	1.000	0.400	0.464
CONSTANT TEMPERATURE (DARK)	5 °C	0.077	0.079	0.117	0.077	0.057	0.036	0.096
	10 °C	0.124	0.241	0.196	0.222	0.345	0.096	0.177
	20 °C	0.248	0.294	0.198	0.236	0.966	0.226	0.246
	30 °C	0.272	0.300	0.247	0.326	1.000	0.413	0.511
ALTERNATING TEMPERATURE	10/5 °C	0.043	0.138	0.101	0.114	0.083	0.065	0.158
	20/10 °C	0.168	0.205	0.112	0.230	0.867	0.141	0.183
	30/20 °C	0.183	0.285	0.188	0.315	0.988	0.381	0.429

TABLE 19 MEDIAN RESPONSE TIME (50TH PERCENTILE)
OF GERMINATION (TEMPERATURE TREATMENTS)

TREATMENT	LEVEL	SPECIES						
		<i>Astragalus alpinus</i>	<i>Astragalus bourgovii</i>	<i>Astragalus robbinsii</i>	<i>Astragalus vexilliflexus</i>	<i>Hedysarum sulphurescens</i>	<i>Oxytropis podocarpa</i>	<i>Oxytropis sericea</i>
CONSTANT TEMPERATURE (LIGHT)	5 °C	-	-	-	-	-	-	-
	10 °C	-	-	-	-	-	-	-
	20 °C	-	-	-	-	4	-	-
	30 °C	-	-	-	-	2	28	-
CONSTANT TEMPERATURE (DARK)	5 °C	-	-	-	-	-	-	-
	10 °C	-	-	-	-	-	-	-
	20 °C	-	-	-	-	4	-	-
	30 °C	-	-	-	-	2	28	-
ALTERNATING TEMPERATURE	10/5 °C	-	-	-	-	-	-	-
	20/10 °C	-	-	-	-	-	-	-
	30/20 °C	-	-	-	-	4	28	-

NOTE: The blanks represent values that exceed the 28 day incubation period.

TABLE 20 MEAN PERCENTAGE OF ABNORMAL GERMINANTS FOR TEMPERATURE TREATMENTS

TREATMENT	LEVEL	SPECIES						
		<i>Astragalus alpinus</i>	<i>Astragalus bourgovii</i>	<i>Astragalus robbinsii</i>	<i>Astragalus vexilliflexus</i>	<i>Hedysarum sulphurescens</i>	<i>Oxytropis podocarpa</i>	<i>Oxytropis sericea</i>
CONSTANT TEMPERATURE (LIGHT)	5 °C	5.26	5.19	4.17	3.33	1.84	0.44	0.00
	10 °C	7.56	5.26	9.26	4.00	4.85	5.46	3.08
	20 °C	4.60	3.00	6.67	1.74	1.34	1.60	2.20
	30 °C	0.00	0.79	3.74	1.43	1.09	0.00	0.00
CONSTANT TEMPERATURE (DARK)	5 °C	2.54	6.14	5.26	2.94	3.70	0.45	0.00
	10 °C	3.70	6.48	7.32	3.09	4.82	3.64	1.49
	20 °C	1.82	2.38	3.75	2.29	1.82	0.79	2.04
	30 °C	0.00	0.00	0.00	0.00	0.00	0.00	0.00
ALTERNATING TEMPERATURE	10/5 °C	1.39	2.27	6.38	3.55	1.51	0.47	0.00
	20/10 °C	7.00	3.64	7.50	8.66	1.55	4.00	4.23
	30/20 °C	3.57	1.65	3.88	2.86	1.10	0.00	2.42

TABLE 21 CUMULATIVE PROPORTION GERMINATED (CHEMICAL TREATMENTS)

TREATMENT	LEVEL	SPECIES						
		<i>Astragalus alpinus</i>	<i>Astragalus bourgovii</i>	<i>Astragalus robbinsii</i>	<i>Astragalus vexilliflexus</i>	<i>Hedysarum sulphurescens</i>	<i>Oxytropis podocarpa</i>	<i>Oxytropis sericea</i>
CONTROL	-	0.188	0.272	0.178	0.256	1.000	0.400	0.464
RUNNING WATER	12 hrs.	0.198	0.282	0.186	0.263	0.998	0.384	0.436
	24 hrs.	0.190	0.278	0.150	0.254	0.995	0.381	0.434
	36 hrs.	0.186	0.269	0.150	0.240	0.995	0.379	0.421
	48 hrs.	0.177	0.263	0.109	0.234	0.993	0.363	0.419
H ₂ SO ₄	5 min.	0.858	0.652	1.000	0.551	1.000	0.943	0.869
	10 min.	0.906	0.855	1.000	0.843	1.000	0.972	0.873
	20 min.	0.958	0.949	1.000	0.858	1.000	1.000	0.923
	30 min.	0.977	0.982	1.000	0.862	1.000	1.000	1.000
H ₂ O ₂	10 min.	0.200	0.227	0.165	0.324	0.997	0.278	0.180
	20 min.	0.254	0.248	0.172	0.331	0.994	0.271	0.176
	30 min.	0.255	0.255	0.176	0.351	0.994	0.270	0.175
GIBBERELIC ACID	0.3 mol.	0.202	0.312	0.124	0.259	0.995	0.220	0.187
	1.4 mol.	0.206	0.312	0.146	0.269	0.995	0.204	0.185
	2.9 mol.	0.211	0.313	0.163	0.277	0.993	0.198	0.184
	4.3 mol.	0.234	0.467	0.164	0.285	0.991	0.196	0.173
KNO ₃	-	0.189	0.296	0.197	0.279	0.993	0.328	0.367
KNO ₃ AND GIBBERELIC ACID	-	0.187	0.313	0.206	0.288	1.000	0.369	0.399
ETHYLENE	-	0.183	0.212	0.214	0.265	1.000	0.383	0.392

TABLE 22 MEDIAN RESPONSE TIME (50TH PERCENTILE) OF GERMINATION
(CHEMICAL TREATMENTS)

TREATMENT	LEVEL	SPECIES						
		<i>Astragalus alpinus</i>	<i>Astragalus bourgovii</i>	<i>Astragalus robbinsii</i>	<i>Astragalus vexilliflexus</i>	<i>Hedysarum sulphureum</i>	<i>Oxytropis podocarpa</i>	<i>Oxytropis sericea</i>
CONTROL	-	-	-	-	-	4	28	-
RUNNING WATER	12 hrs.	-	-	-	-	2	28	-
	24 hrs.	-	-	-	-	2	28	-
	36 hrs.	-	-	-	-	2	-	-
	48 hrs.	-	-	-	-	2	-	-
H ₂ SO ₄	5 min.	2	4	2	8	2	8	2
	10 min.	2	2	2	2	2	2	2
	20 min.	2	2	2	2	2	2	2
	30 min.	2	2	2	2	2	2	2
H ₂ O ₂	10 min.	-	-	-	-	2	-	-
	20 min.	-	-	-	-	2	-	-
	30 min.	-	-	-	-	2	-	-
GIBBERELLIC ACID	0.3 mol.	-	-	-	-	2	-	-
	1.4 mol.	-	-	-	-	2	-	-
	2.9 mol.	-	-	-	-	2	-	-
	4.3 mol.	-	-	-	-	2	-	-
KNO ₃	-	-	-	-	2	-	-	
KNO ₃ AND GIBBERELLIC ACID	-	-	-	-	2	-	-	
ETHYLENE	-	-	-	-	2	-	-	

NOTE: The blanks represent values that exceeded the 28 day incubation period.

TABLE 23 MEAN PERCENTAGE OF ABNORMAL GERMINANTS FOR CHEMICAL TREATMENTS

TREATMENT	LEVEL	SPECIES						
		<i>Astragalus alpinus</i>	<i>Astragalus bourgovii</i>	<i>Astragalus robbinsii</i>	<i>Astragalus vexilliflexus</i>	<i>Hedysarum sulphureum</i>	<i>Oxytropis podocarpa</i>	<i>Oxytropis sericea</i>
RUNNING WATER	12 hrs.	3.70	1.68	3.70	1.58	1.10	0.47	0.59
	24 hrs.	6.33	2.61	4.84	2.66	1.10	0.48	0.62
	36 hrs.	7.87	2.65	6.35	2.96	1.11	0.48	2.45
	48 hrs.	8.14	3.33	8.51	6.57	1.32	0.50	2.37
H ₂ SO ₄	5 min.	20.34	26.97	18.07	30.59	16.29	7.35	7.82
	10 min.	24.94	28.23	19.04	32.59	16.92	10.96	12.50
	20 min.	26.01	30.99	20.81	35.01	16.96	13.25	14.55
	30 min.	27.92	39.27	25.25	39.43	27.31	14.06	20.16
H ₂ O ₂	10 min.	1.54	7.02	15.58	2.76	2.42	0.00	4.17
	20 min.	3.67	9.65	19.51	3.57	3.07	6.37	4.29
	30 min.	7.76	26.98	27.66	6.25	3.95	7.93	5.63
GIBBERELLIC ACID	0.3 mol.	6.67	1.76	8.64	3.65	2.63	0.81	1.35
	1.4 mol.	7.37	2.50	10.94	4.00	2.63	1.75	1.39
	2.9 mol.	10.19	2.50	20.00	4.00	2.68	1.80	4.00
	4.3 mol.	15.00	2.76	32.22	4.31	4.31	1.83	5.71
KNO ₃	-	11.39	3.15	6.90	9.40	2.19	0.00	2.86
KNO ₃ AND GIBBERELLIC ACID	-	1.57	1.50	7.35	1.59	1.33	0.00	1.71
ETHYLENE	-	3.75	5.32	6.67	2.24	1.53	1.27	0.00

TABLE 25 MEDIAN RESPONSE TIME (50TH PERCENTILE) OF GERMINATION
(SCARIFICATION AND STRATIFICATION)

TREATMENT	LEVEL	SPECIES						
		<i>Astragalus alpinus</i>	<i>Astragalus bourgovii</i>	<i>Astragalus robbinsii</i>	<i>Astragalus vexilliflexus</i>	<i>Hedysarum sulphurescens</i>	<i>Oxytropis podocarpa</i>	<i>Oxytropis sericea</i>
MECHANICAL SCARIFICATION / TEMPERATURE	5 °C	22	14	18	14	12	18	9
	10 °C	10	10	16	10	8	8	6
	20 °C	2	4	10	4	4	2	2
	30 °C	2	2	2	2	2	2	2
CONTROL		-	-	-	-	2	28	-
STRATIFICATION	1 MONTH	-	-	-	-	2	28	-
	4 MONTHS	-	-	-	-	2	-	-
	8 MONTHS	-	-	-	-	2	-	-
MECHANICAL SCARIFICATION- STRATIFICATION	1 MONTH	1	1	1	1	1	1	1

NOTE: The blanks represent values that exceeded the 28 day incubation period.

TABLE 26 MEAN PERCENTAGE OF ABNORMAL GERMINANTS FOR MECHANICAL SCARIFICATION AND STRATIFICATION TREATMENTS

TREATMENT	LEVEL	SPECIES						
		<i>Astragalus alpinus</i>	<i>Astragalus bourgovii</i>	<i>Astragalus robbinsii</i>	<i>Astragalus vexilliflexus</i>	<i>Hedysarum sulphurescens</i>	<i>Oxytropis podocarpa</i>	<i>Oxytropis sericea</i>
MECHANICAL SCARIFICATION / TEMPERATURE	5 °C	14.85	1.21	1.86	1.48	1.29	1.23	2.35
	10 °C	15.04	25.50	11.08	16.27	8.11	2.72	5.47
	20 °C	15.01	23.21	8.63	15.42	6.55	1.82	2.45
	30 °C	10.21	1.46	2.72	1.38	1.55	1.34	2.43
STRATIFICATION	1 MONTH	1.82	1.27	3.94	1.86	1.66	0.91	0.10
	4 MONTHS	3.96	4.35	4.08	5.09	2.20	4.04	1.04
	8 MONTHS	41.95	39.57	57.62	60.63	19.56	58.54	52.44
MECHANICAL SCARIFICATION AND STRATIFICATION	1 MONTH	1.27	1.39	3.96	2.09	1.77	1.91	1.82

incubation for the 5°C, 10°C and 10/5°C levels, and between the 4th and 8th days for the remaining treatment levels. Germination rates peaked between the 4th and 6th days for all species, but an additional smaller peak occurred on the 16th day for the *Oxytropis* species. Median response time for germination (50th percentile) under each temperature regime exceeded the incubation period for all species except for *H. sulphurescens* and *O. podocarpa* under the 20°C, 30°C and 30/20°C temperature regimes (Table 19).

The survival distributions of *H. sulphurescens* and *Oxytropis* species were dissimilar ($p = 0.0000$) when different temperature regimes were compared, but were similar when light and dark treatments at the same level were compared ($0.0143 < p < 0.0231$). The survival distributions of the 10/5°C and 20/10°C treatment levels were similar to the 10°C constant temperature regimes ($0.0122 < p < 0.0145$). Survival distributions of the *Astragalus* species were similar ($0.0006 < p < 0.3347$) within treatments and between treatments.

The mean percentage of abnormal germinants varied with species and treatment (Table 20). *Astragalus robbinsii* had the greatest number of abnormal and *O. sericea* the lowest. The mean percentage of abnormal for each species was greatest for the 10°C constant temperature and 20/10°C alternating treatment.

Chemical Treatments

Application of selected chemical solutions did not increase seed germination greatly, with the exception of concentrated sulfuric acid. The cumulative proportion of germinated seeds of the *Astragalus* species increased slightly with the application of hydrogen peroxide, gibberellic acid, potassium nitrate, and potassium nitrate plus gibberellic acid (Table 21). Germination increased slightly with exposure to a 12 hr. water rinse, but decreased with longer soaking times (Table 21). Application of ethylene increased slightly the number of *A. robbinsii* and *A. vexilliflexus* var. *nubilus* seeds that germinated, but reduced the number of *A. alpinus* and *A. bourgovii* seeds that germinated.

Pairwise comparisons of germination survival curves for each species and treatment level were similar to the respective controls ($0.3784 > p > 0.5473$). The median response times (50th percentile) for these treatments were the same as those for the controls (Table 22). The mean percentage of abnormal germinants was highest for *A. robbinsii* and lowest for *A. vexilliflexus* var. *nubilus*. The number of abnormal germinants increased with increased treatment duration or increased solution concentration (Table 23). Most of the abnormal germinants had rotten radicles (Figure 31).

The cumulative proportion of germinated seeds of *H.*

sulphurescens and the *Oxytropis* species decreased with the application of several chemical treatments. The application of hydrogen peroxide and gibberellic acid caused the greatest reduction in germination, whereas running water, potassium nitrate, potassium nitrate plus gibberellic acid and ethylene caused only small reductions in the cumulative proportion of germinated seeds. The germination rates (Table 21) were similar to those of the controls. The median response times (50th percentile) (Table 22) were the same as those of the controls except for *O. podocarpa*. Germination survival curves of these treatments were similar to the controls ($0.0269 > p > 0.8996$) The mean percentage of abnormal germinants was greatest for *H. sulphurescens* and lowest for *O. podocarpa* (Table 23). The number of abnormal increased with increased treatment duration or increased solution concentration. Most of the abnormal germinants had mouldy radicles (Figure 31).

Application of concentrated sulfuric acid increased the germination rate and cumulative proportion of germinants of all species. The increase in germination was greatest for the *Oxytropis* species and lowest for *A. vexilliflexus* var. *nubilus* (Table 21). The germination rates were rapid (Figures 38 - 44) and the median response times (50th percentile) (Table 22) ranged from 8 days for the 5 min. exposure to 2 days for the 30 min.

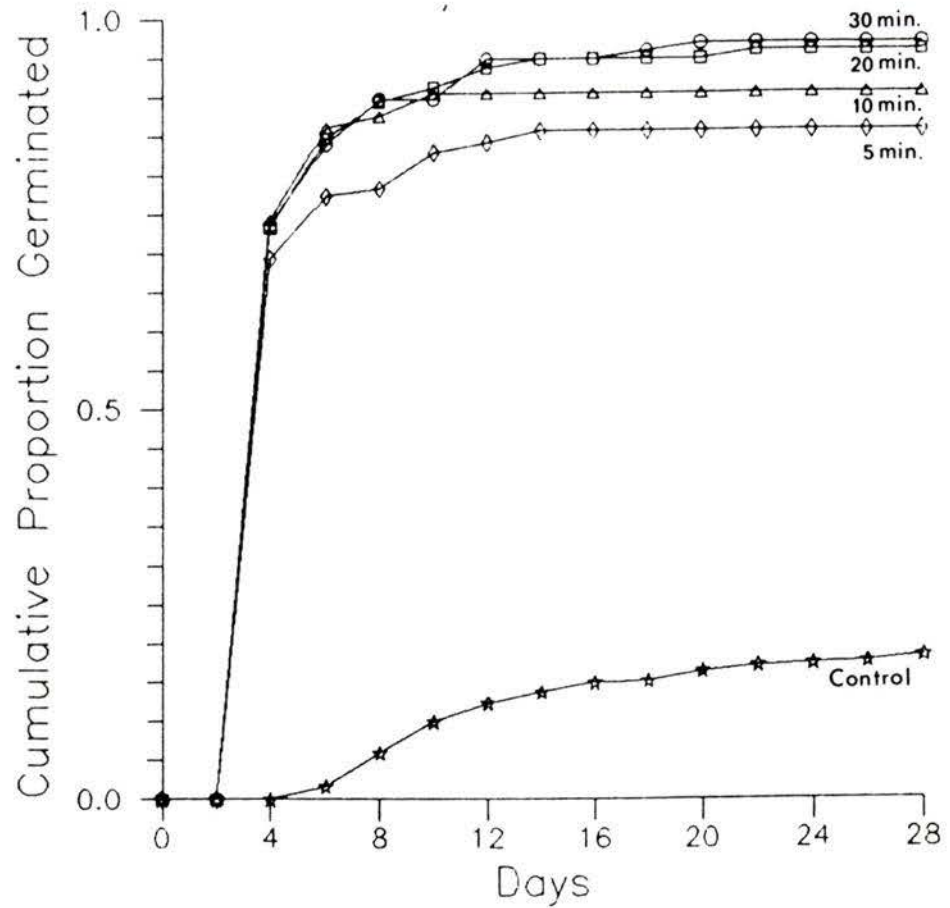


Figure 38 Survival Curves for Chemical Scarification Treatments of *Astragalus alpinus*.

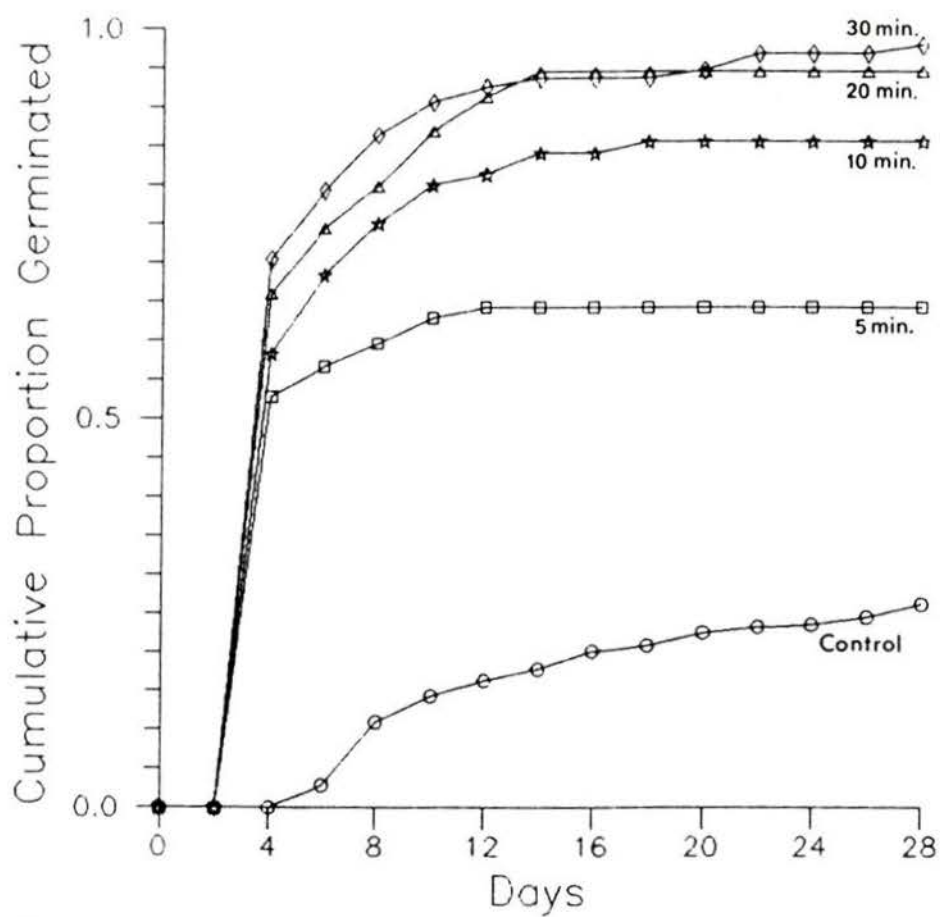


Figure 39 Survival Curves for Chemical Scarification Treatments of *Astragalus bourgovii*.

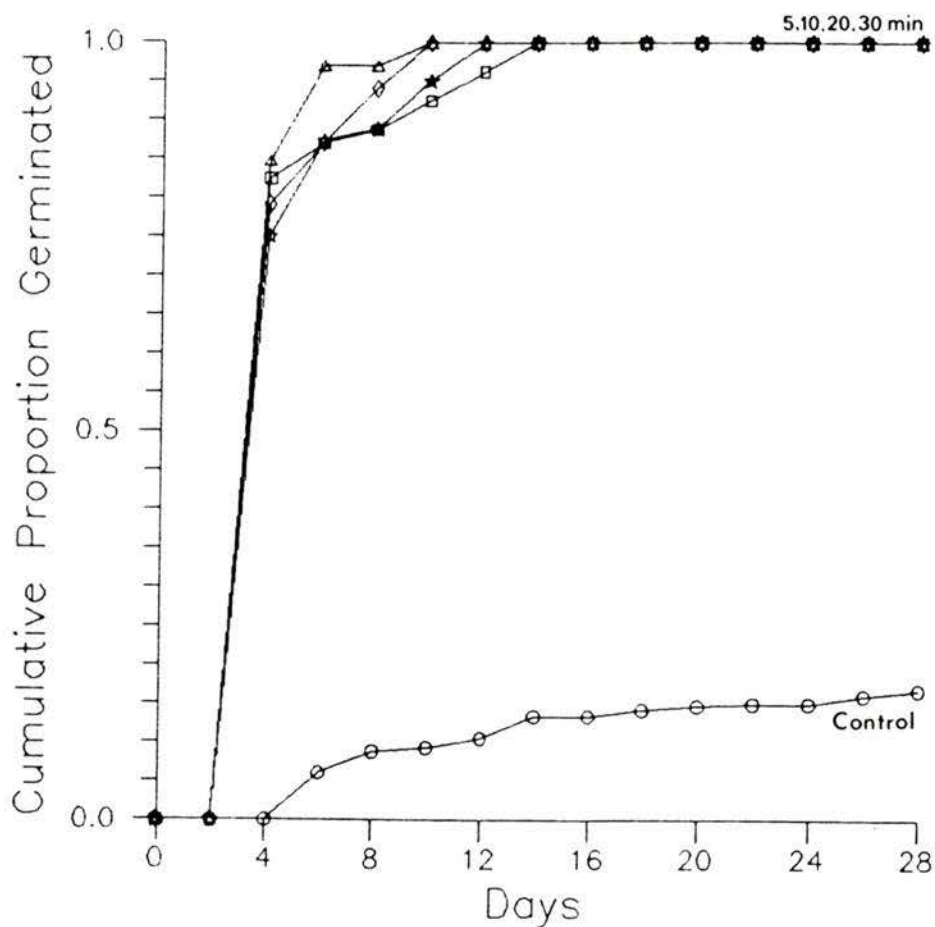


Figure 40 Survival Curves for Chemical Scarification Treatments of *Astragalus robbinsii*.

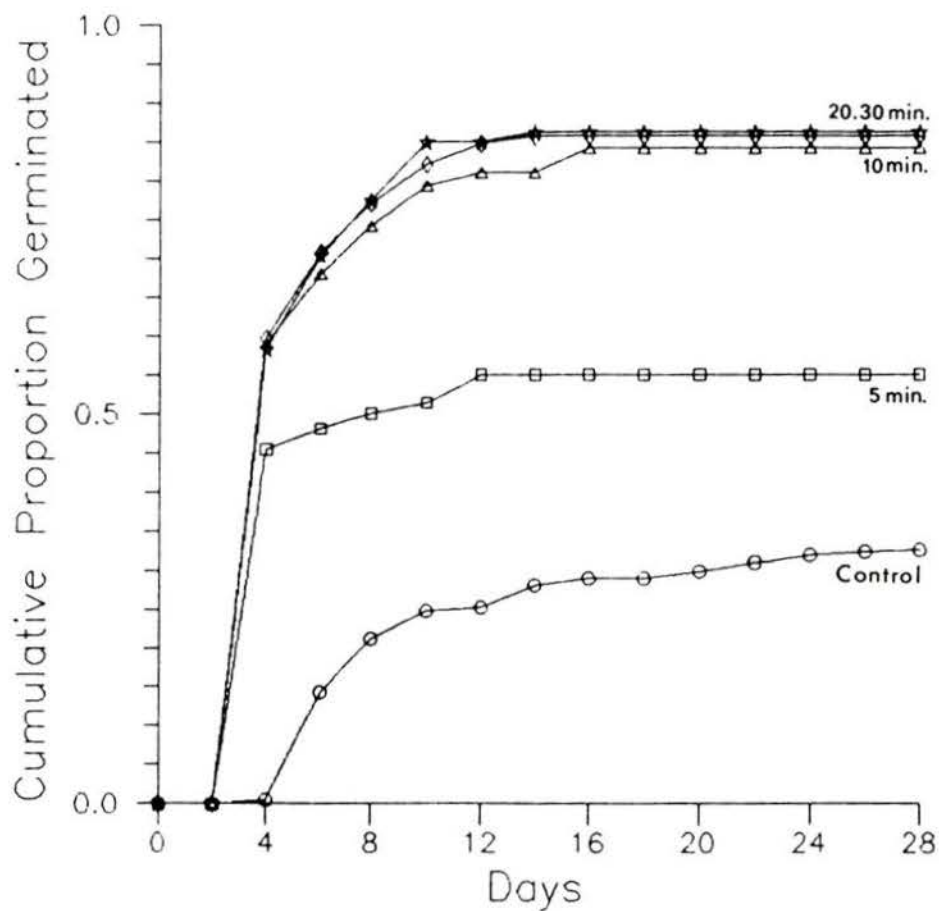


Figure 41 Survival Curves for Chemical Scarification Treatments of *Astragalus vexilliflexus* var. *nubilus*.

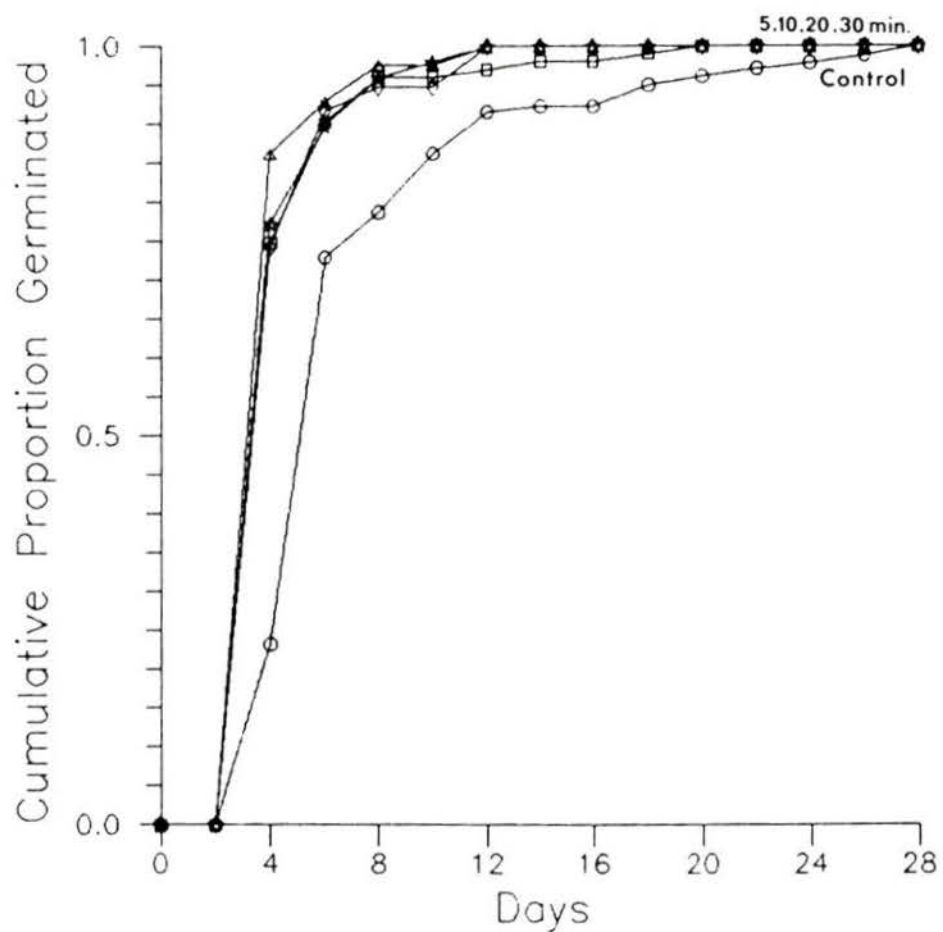


Figure 42 Survival Curves for Chemical Scarification Treatments of *Hedysarum sulphurescens*.

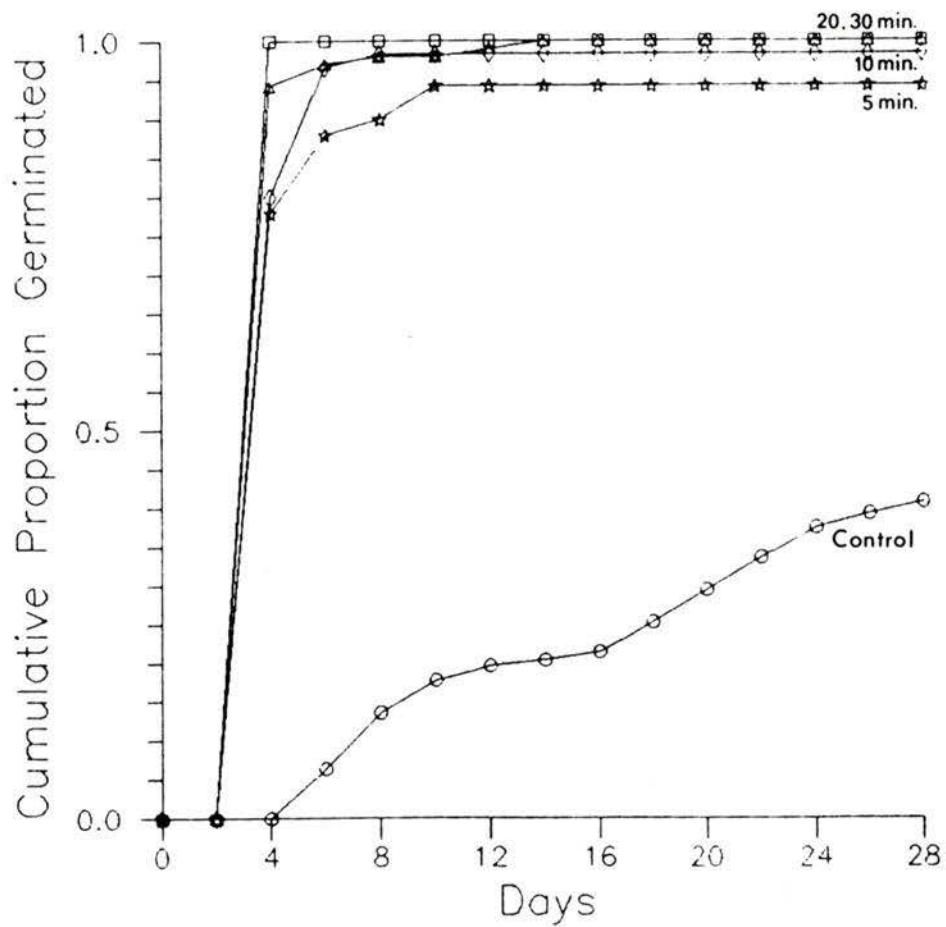


Figure 43 Survival Curves for Chemical Scarification Treatments of *Oxytropis podocarpa*.

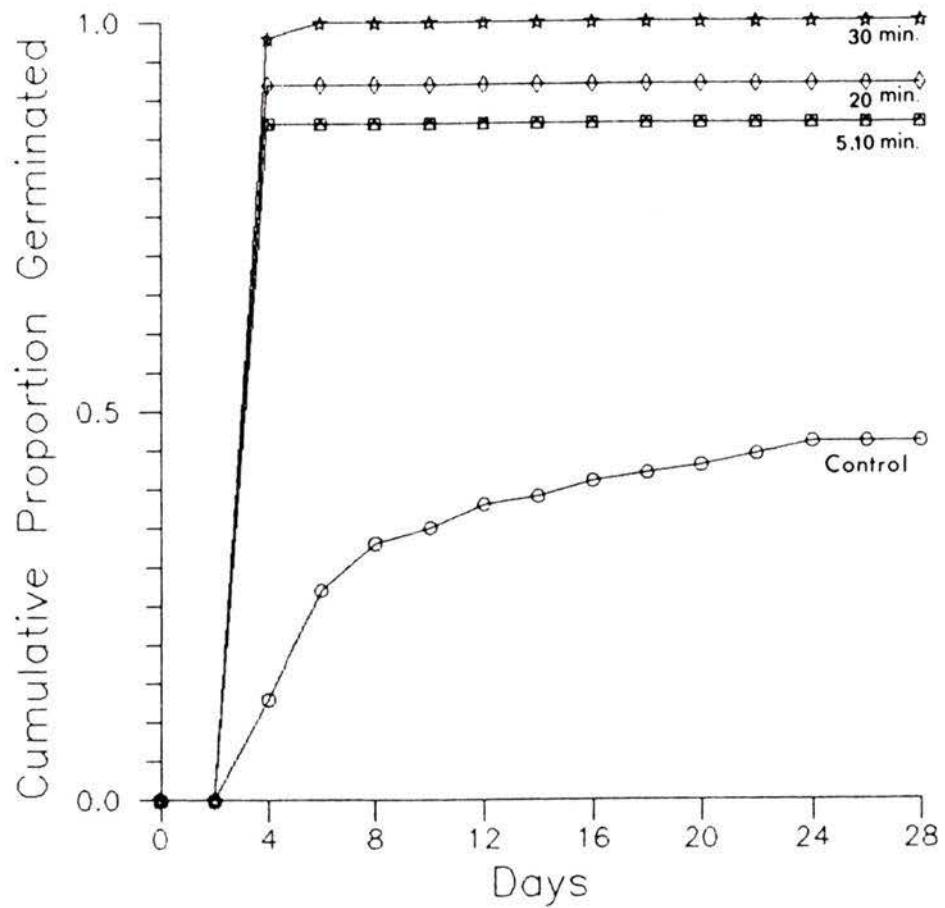


Figure 44 Survival Curves for Chemical Scarification Treatments of *Oxytropis sericea*.

exposure. Pairwise comparisons of treatments with the controls indicated that survival curves of each treatment level for all species were not equal ($p = 0.0000$). However, within treatment level comparisons for each species were similar ($0.0245 > p > 0.0366$) with the exception of the 5 minute treatment for *A. bourgovii* and *A. vexilliflexus* var. *nubilus*. The mean percentage of abnormal germinants increased with increased exposure to sulfuric acid and was greatest for *A. vexilliflexus* var. *nubilus* and lowest for *O. podocarpa* (Table 23). Most of the abnormal germinants had mouldy radicles (Figure 31).

Scarification and Stratification

The cumulative proportion of germinated seeds for each species increased with all mechanical scarification treatments (Table 24). The germination rate was high and increased with increased temperature. The median response times (50th percentile) ranged from 22 for the 5°C treatments to 2 for the 30°C treatments (Table 25). Survival curves of all treatments were not equal when compared to their respective controls ($p = 0.0000$). All treatment levels of the *Oxytropis* species, and *A. bourgovii* and *A. robbinsii* were equal ($0.8678 > p > 0.9312$), but the 5°C survival curves of *A. alpinus*, *A. vexilliflexus* var. *nubilus* and *H. sulphurescens* were different from the higher treatment levels ($p = 0.0000$). Survival curves for each species are presented in

Figures 45 - 51. The mean percentage of abnormal germinants was greatest for the *Astragalus* species and lowest for *O. podocarpa* (Table 26). The percentage of abnormal germinants was greatest for the 10°C and 20°C treatment levels (Table 26). Most of the abnormal germinants had broken or mouldy radicles (Figure 31).

Cold moist stratification caused a modest increase in seed germination for the *Astragalus* species, had little effect on *H. sulphurens*, and caused a decrease in seed germination for the *Oxytropis* species (Table 25). The majority of seed germination occurred during stratification. Cumulative seed germination decreased with increased duration of stratification (Figures 52 - 58). The lowest germination for all species was with the 8 month stratification treatment. The median response times (50th percentile) of germination for all species were the same as their respective controls (Table 25). The germination survival curves of the *Astragalus* were similar to their respective controls ($0.0124 > p > 0.7654$). The survival curves of *H. sulphurens* were similar ($p = 0.9641$), and the survival curves of the *Oxytropis* species were all dissimilar ($p = 0.0000$). The mean percentage of abnormal germinants was greatest for the 8 month stratification treatments (Table 26). Most of the abnormal germinants had mouldy radicles (Figure 31).

The application of combined scarification and

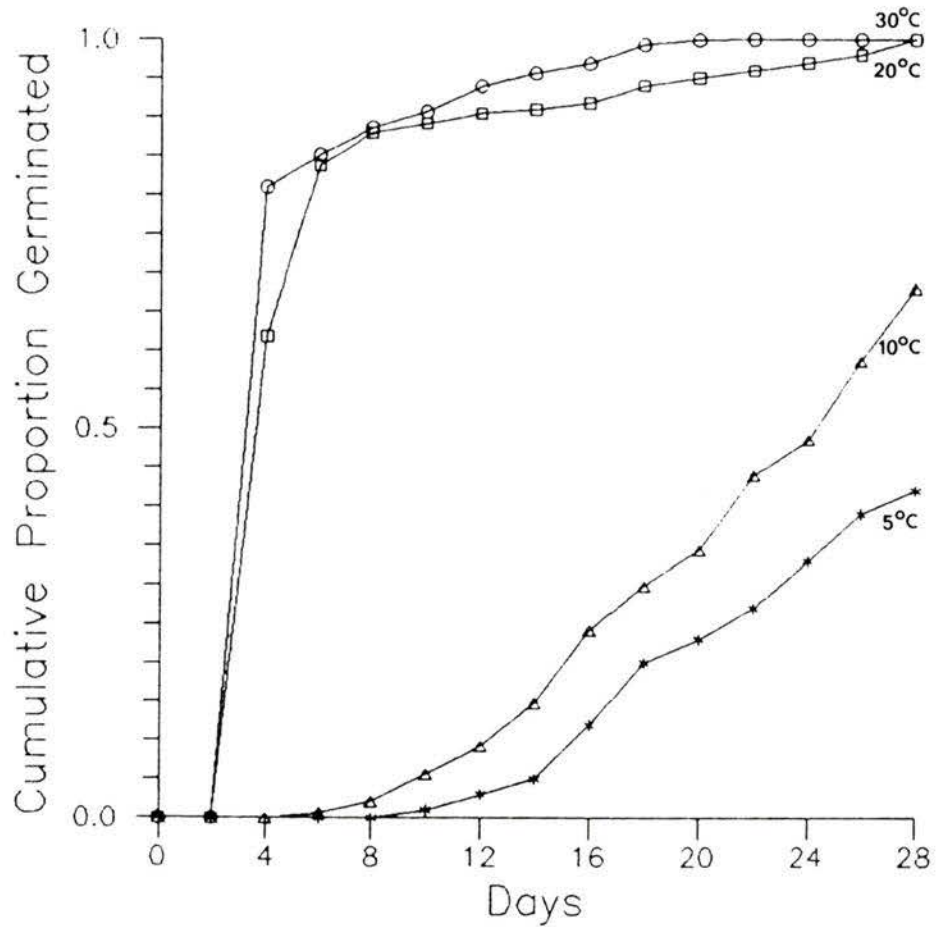


Figure 45 Survival Curves for Mechanical Scarification Treatments of *Astragalus alpinus*.

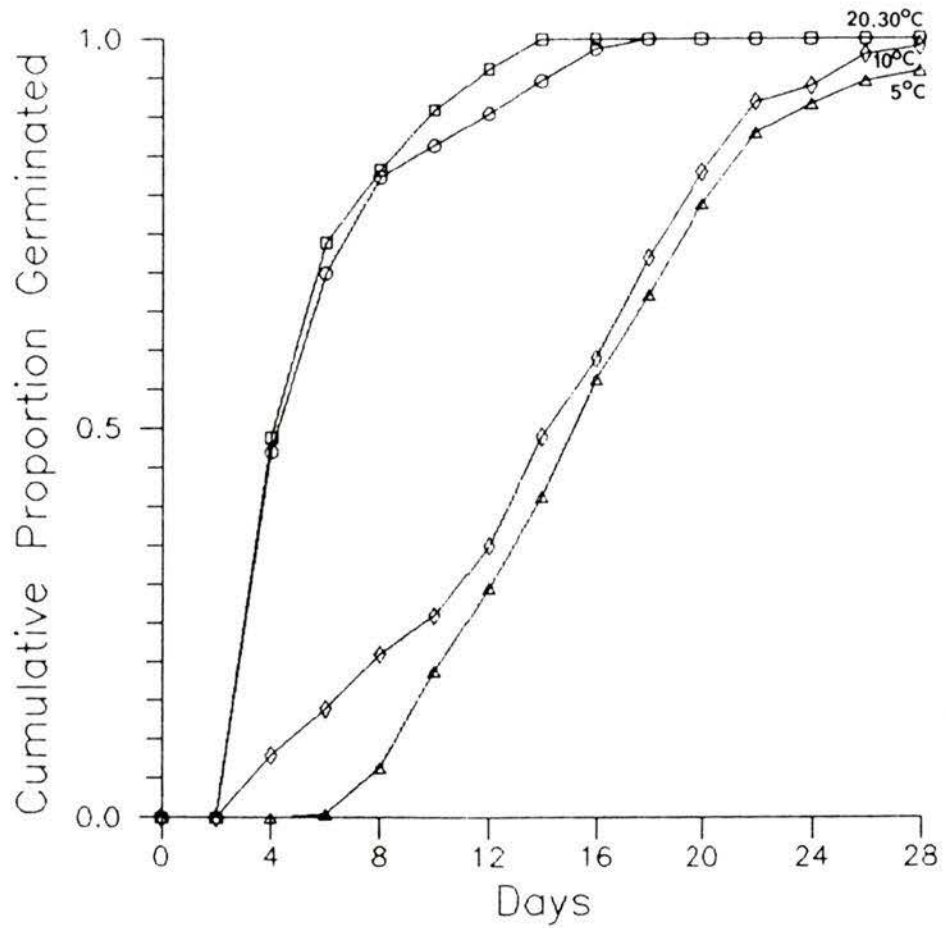


Figure 46 Survival Curves for Mechanical Scarification Treatments of *Astragalus bourgovii*.

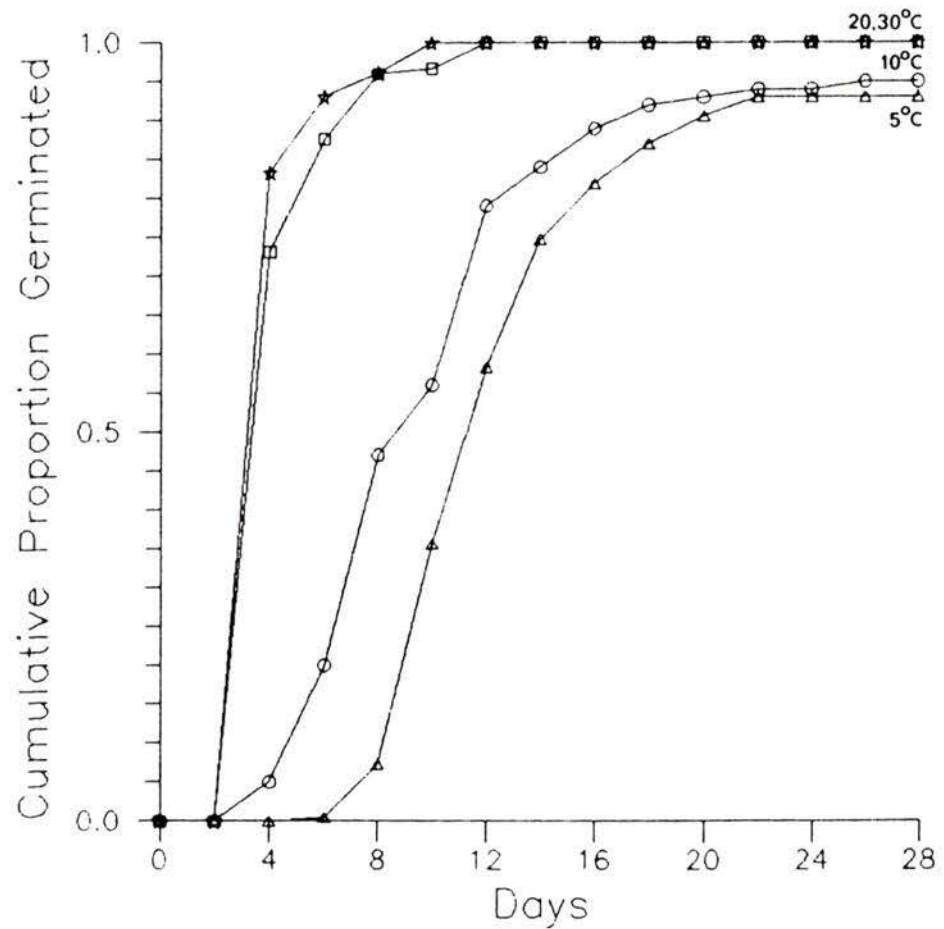


Figure 47 Survival Curves for Mechanical Scarification Treatments of *Astragalus robbinsii*.

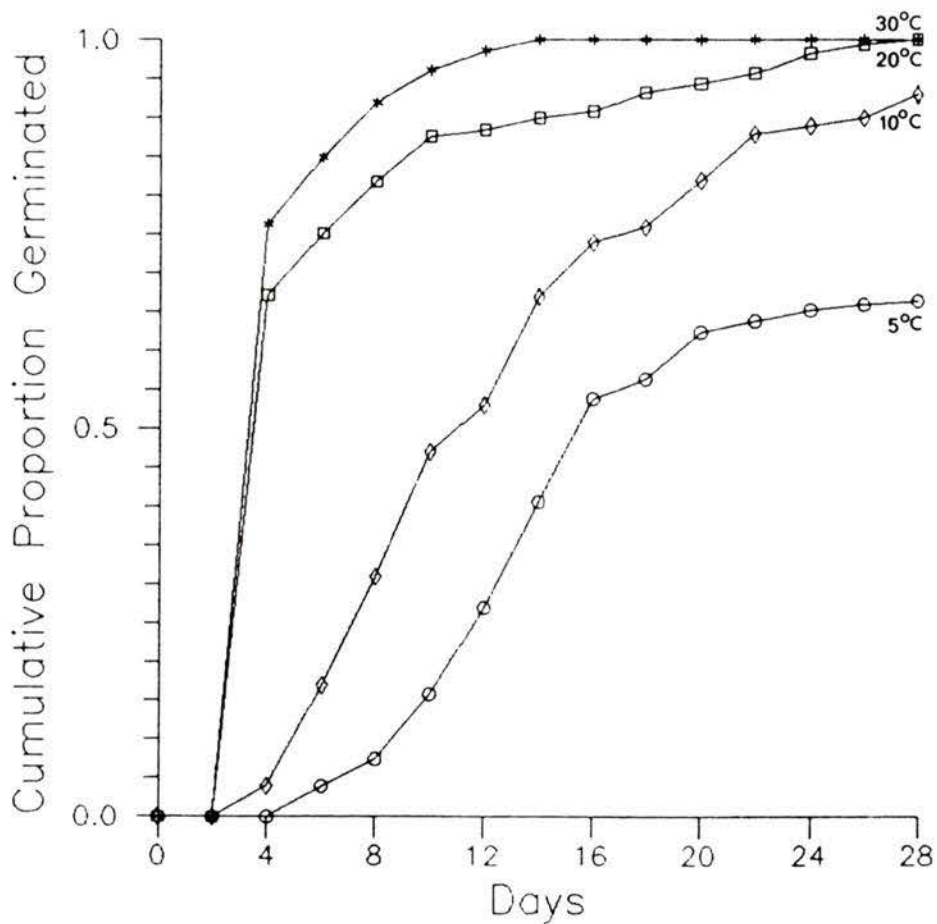


Figure 48 Survival Curves for Mechanical Scarification Treatments of *Astragalus vexilliflexus* var. *nubilus*.

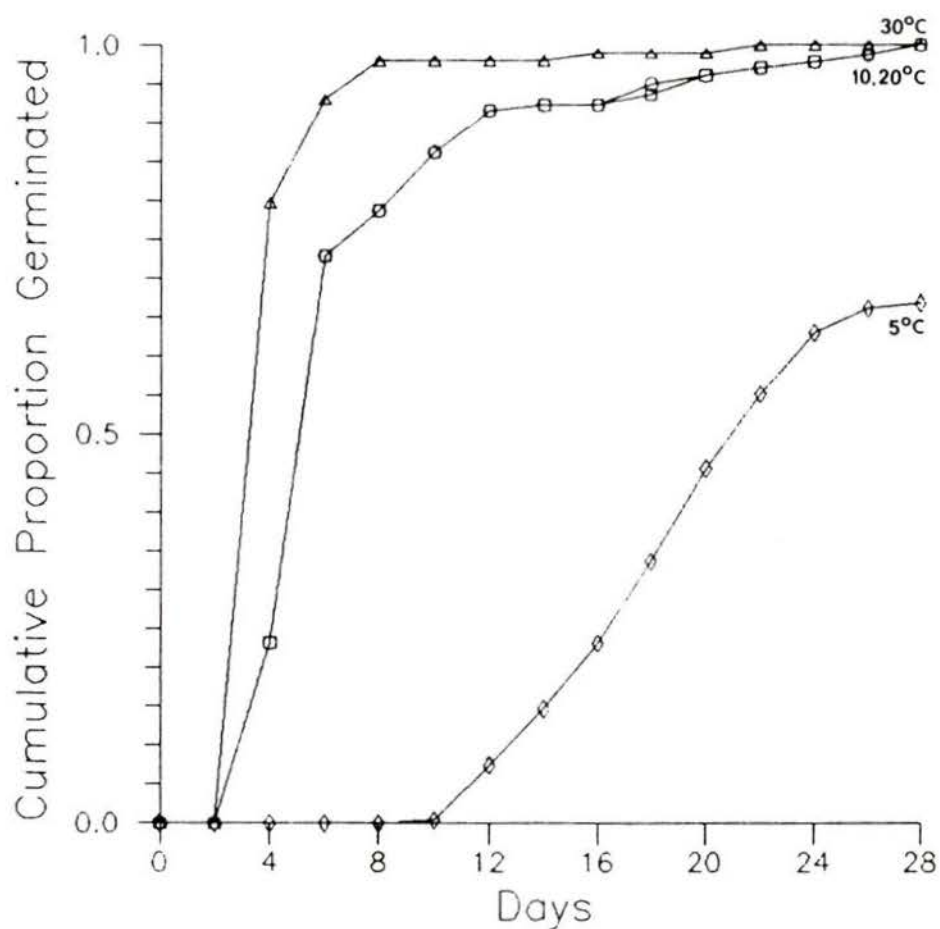


Figure 49 Survival Curves for Mechanical Scarification Treatments of *Hedysarum sulphurescens*.

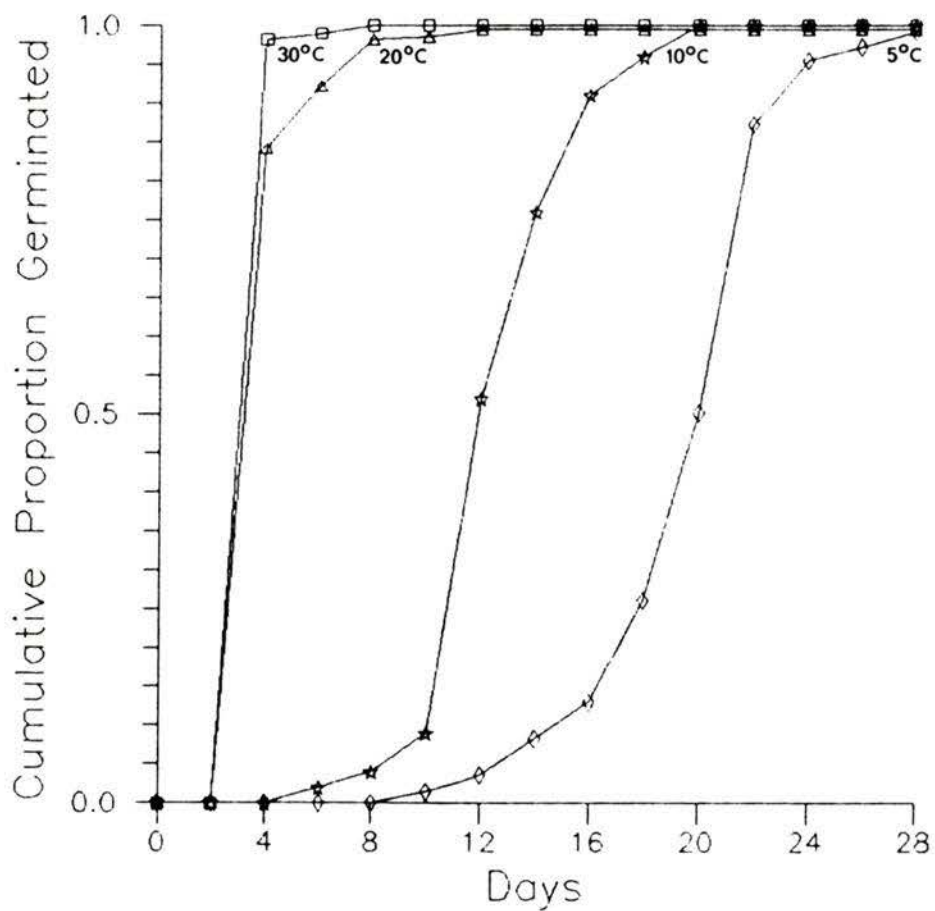


Figure 50 Survival Curves for Mechanical Scarification Treatments of *Oxytropis podocarpa*.

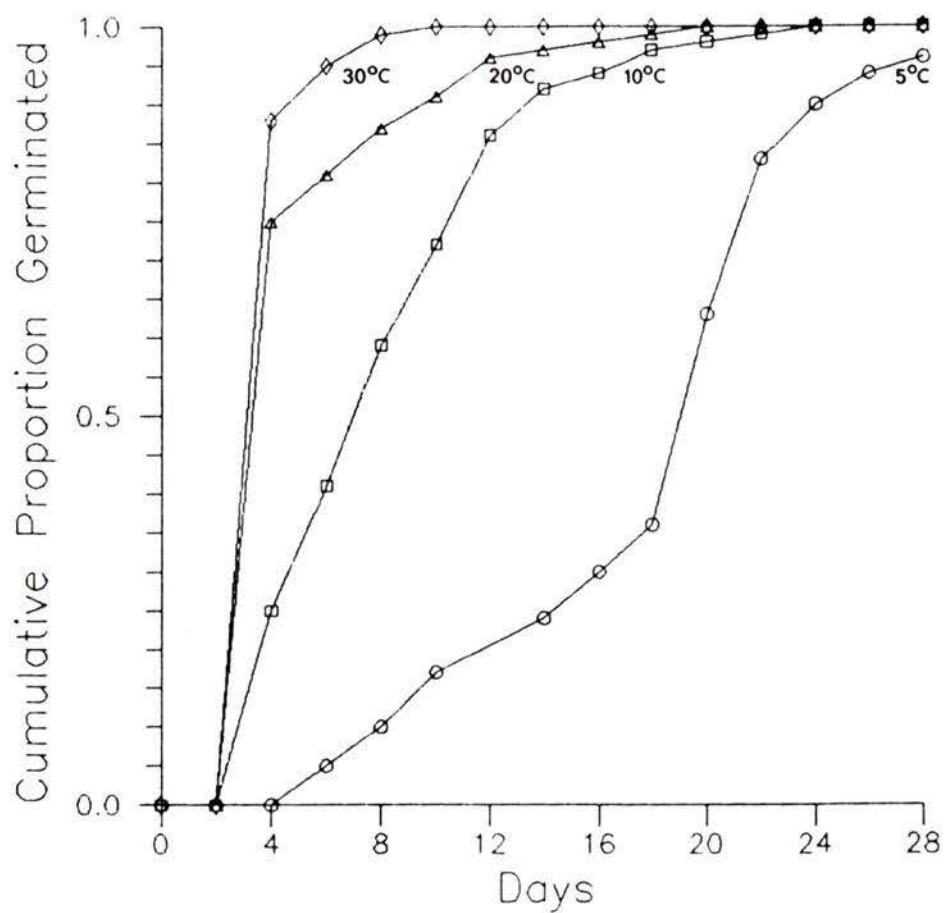


Figure 51 Survival Curves for Mechanical Scarification Treatments of *Oxytropis sericea*.

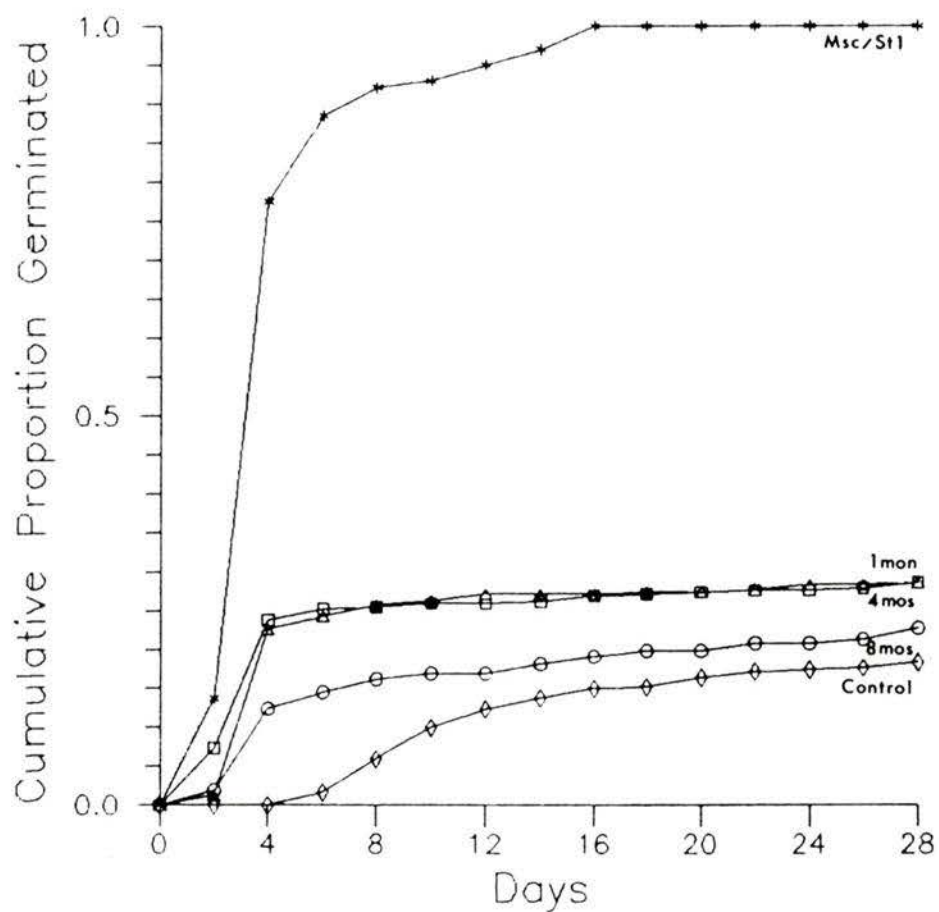


Figure 52 Survival Curves for Stratification and Scarification – Stratification of *Astragalus alpinus*.

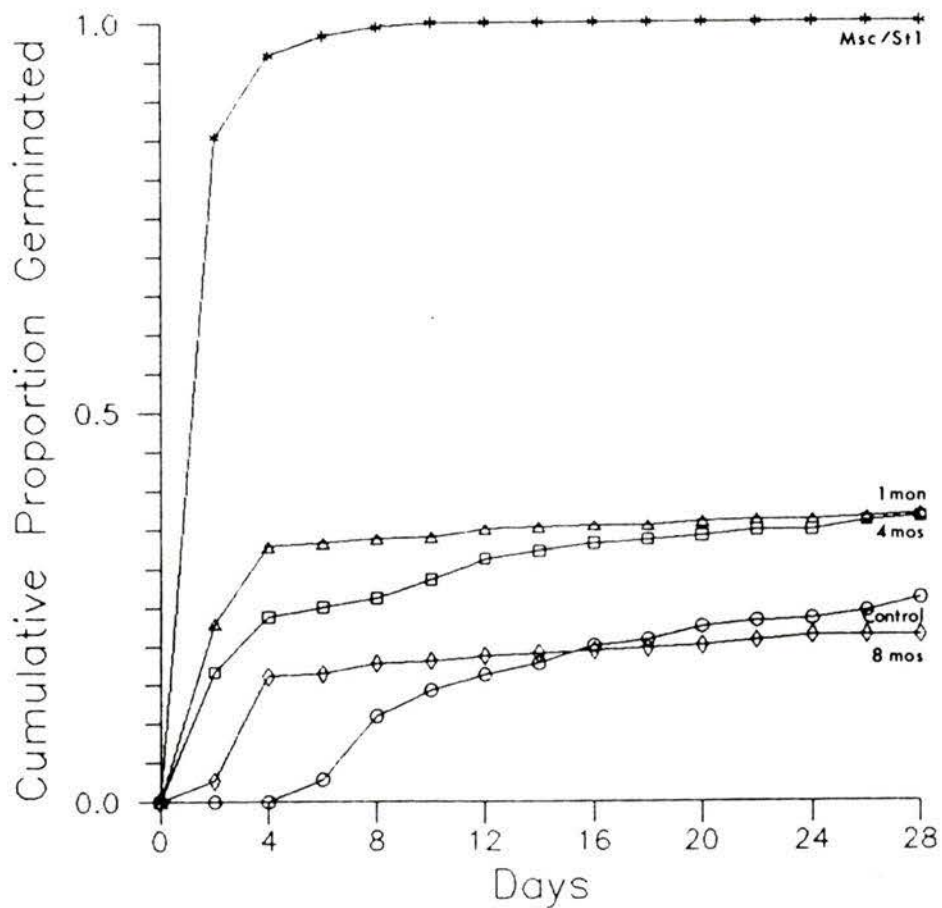


Figure 53 Survival Curves for Stratification and Scarification – Stratification of *Astragalus bourgovii*.

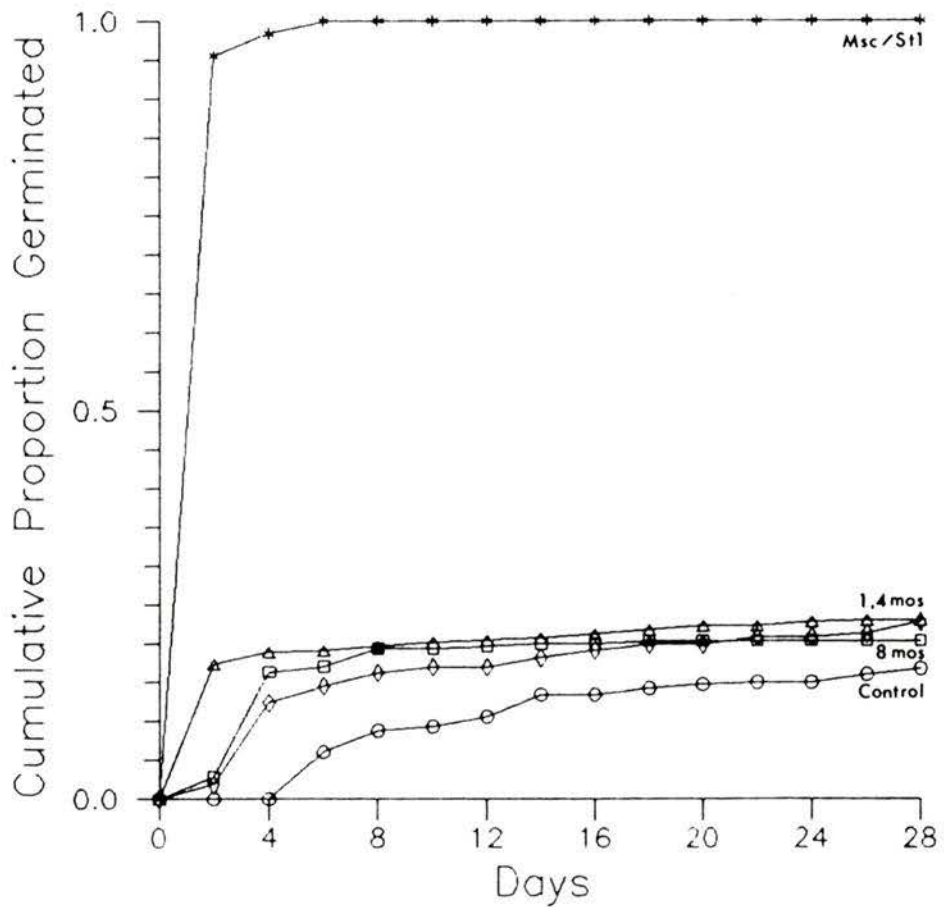


Figure 54 Survival Curves for Stratification and Scarification – Stratification of *Astragalus robbinsii*.

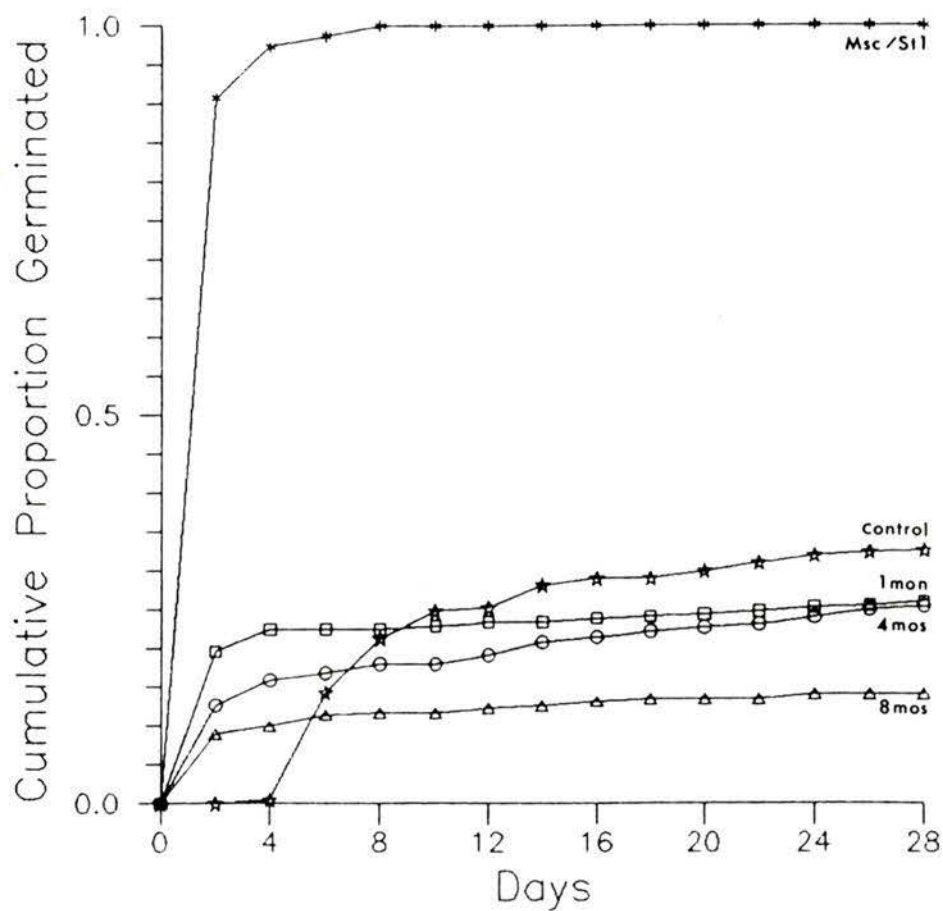


Figure 55 Survival Curves for Stratification and Scarification – Stratification of *Astragalus vexilliflexus* var. *nubilus*.

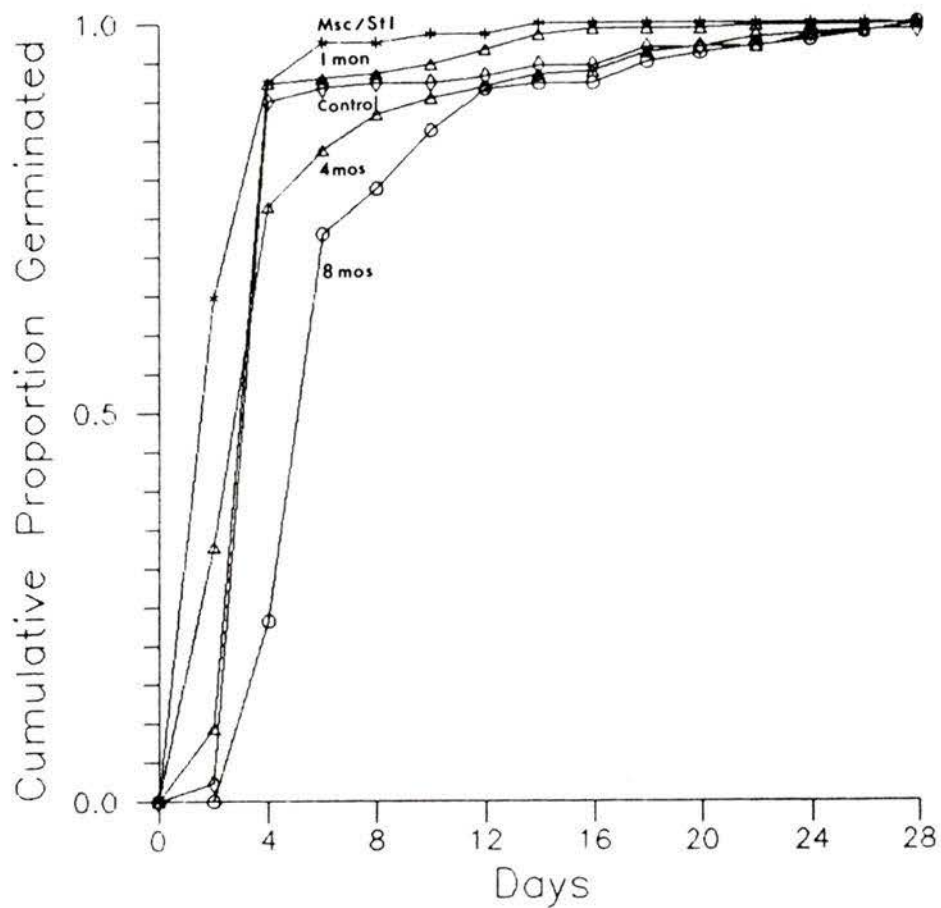


Figure 56 Survival Curves for Stratification and Scarification – Stratification of *Hedysarum sulphurescens*.

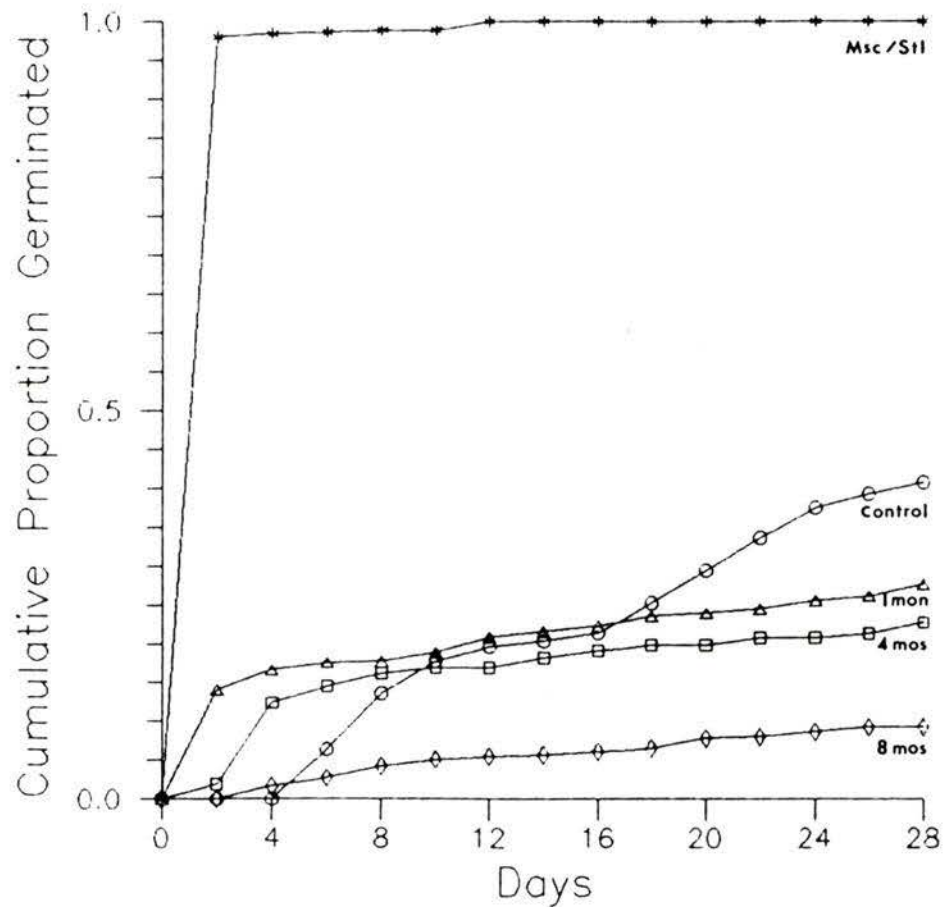


Figure 57 Survival Curves for Stratification and Scarification – Stratification of *Oxytropis podocarpa*.

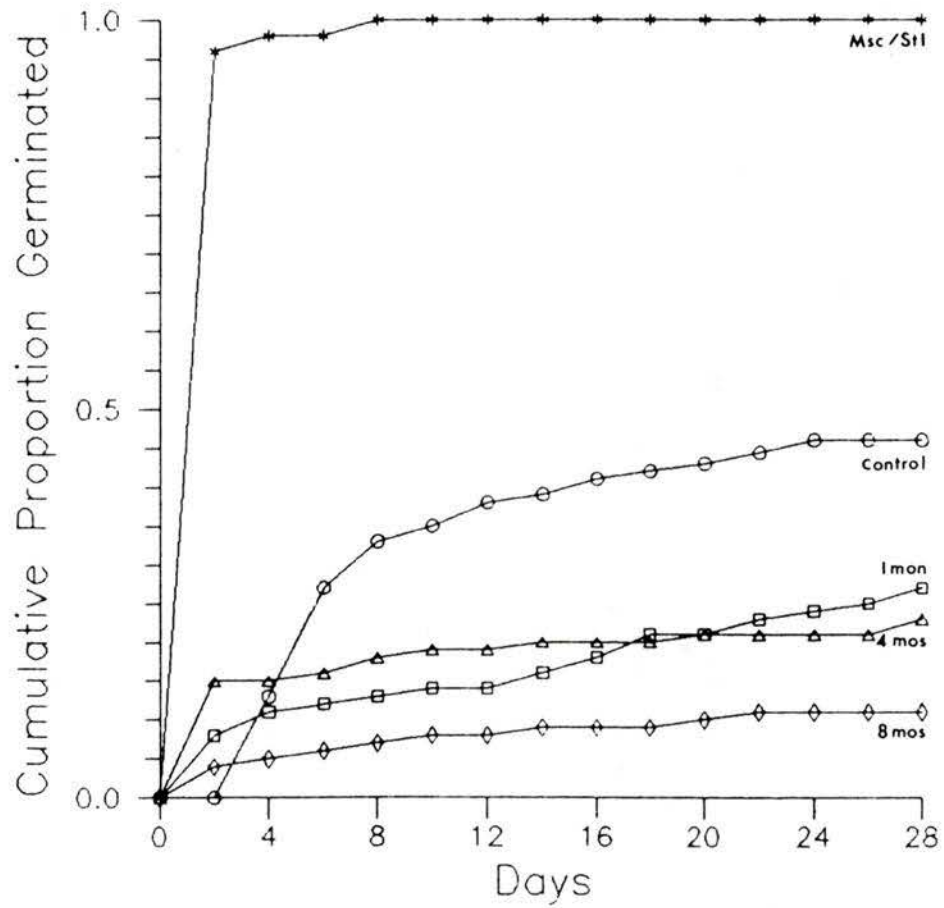


Figure 58 Survival Curves for Stratification and Scarification – Stratification of *Oxytropis sericea*.

cold moist stratification resulted in complete germination of all seeds of each species. The majority of the seeds germinated before the incubation period. The median response times (50th percentile) was 1 day for all species (Table 25). The survival curves for all species were not equal ($0.0246 > p > 0.7981$). The mean percentage of abnormal germinants was comparable to that for 1 month stratification treatment for all species (Table 26). Most of the abnormal germinants had mouldy radicles (Figure 31).

CHAPTER IV

DISCUSSION

Phenology

Vegetative activity began in May or June and continued into September each year. Vegetative and reproductive development began approximately one week earlier each year of the study and appeared to be related to the yearly variation in weather patterns. The duration of vegetative and reproductive activity for each species did not change from year to year.

The initiation of activity appeared to coincide with snowmelt and increased air temperatures. This was found in previous high elevation phenology studies as well (Holway and Ward 1965, Fareed and Caldwell 1975). The *Oxytropis* species in this study were the first to initiate vegetative development each year. This suggests that these species are physiologically active at cooler temperatures than the other legume species studied. The *Oxytropis* species and *A. vexilliflexus* var. *nubilus* were generally found in wind exposed snow-free habitats.

Astragalus vexilliflexus var. *nubilus* was usually the last species to initiate vegetative activity even though its habitats had been free of snow for two to three weeks when growth was initiated. *Astragalus bourgovii* was also slow to begin development. However, vegetative development of *A. bourgovii* was so rapid that

within a week's time, the plants were at the same developmental stage as legumes in snow-free habitats. The delay in initiation of activity by *A. bourgovii* can probably be attributed to the heavy snowfall accumulations that characterize the leeward ridge crests of the subalpine habitats of this species. The variation in seed development time among the species could be accounted for by the variation in habitat.

Yearly differences in weather conditions also account for the variation in seed development. The period during which seed development occurred varied each year. Seed development in 1983 took place during a relatively cool and moist period, whereas the conditions under which seed development occurred were drier in 1984, and even drier in 1985.

Seed Production

All of the species in this study produced viable seed each year, but the amount of seed varied according to species, population, and year. The variation in the number of viable, aborted, abnormal, and insect-damaged seeds produced by these species appeared to be the result of different biotic and abiotic factors such as weather, habitat variation, and animal interactions. The effects of these factors upon the seed production of the legumes is complex, and it is not possible to provide conclusions in many cases. More quantitative

data is needed. Seed production did not appear to be related to the vigor of the legume species. However, the reduced vigor of the the South and West Bald populations of *A. alpinus* and *A. robbinsii* in 1984 and 1985, and the Banner Mountain population of *H. sulphurescens* may have caused some reduction in seed production. The smaller amount of flowering and seed production of *A. alpinus* and *A. robbinsii* may be due to the drier conditions during these two years. Although flowering by *H. sulphurescens* increased in 1984 and 1985, the small seed production by this population may be due in part to reduced vigor as a result of the heavy infestation of the smut *Uromyces hedysari-obscuri* (DC.) Lev.. The vigor of *H. sulphurescens* usually deteriorated during the later stages of seed maturation and may have resulted in poorer quality seed.

Many arctic (Sorenson 1941) and alpine (Marks 1970) species initiate floral buds during the preceding growing season. Therefore, the flowering and seed production of each species may be affected by the growing conditions of the previous summer and the severity of the preceding winter. The variation in environmental conditions such as air temperature, soil moisture, and nutrient status (Copeland 1976) may also affect seed seed development. This would be most pronounced in the harsh habitats of the West Bald

Mountain (WB), Banner Mountain (BM), and Gill Peak populations.

Differences in seed production may have been the result of differences in the number of pollinators at the various sample population locations (Bauer 1983). The effects of pollinator visitation on seed production are inconclusive in this study, since only casual observations were made for each population.

Several mammals in the area had an impact on the seed production of several species in the study. Browsing of the flowers by elk, *Cervus elaphus*, in 1984 reduced the seed production of the Bald Ewin Saddle (BE) population of *A. robbinsii* and the Michel Ridge (MR) population of *O. sericea*. The golden mantle ground squirrel, *Spermophilus lateralis*, and the bighorn sheep, *Ovis canadensis*, were also observed browsing on the foliage and flowers of *A. robbinsii* and *H. sulphurescens*. The loss of foliage would cause a reduction in resource allocation to seed production (Willson 1983). Although damage to the sample populations of *H. sulphurescens* by grizzly bears *Ursus arctos* was not observed, two populations outside the study area were extensively damaged by these animals. This would indicate that these animals have a tremendous potential to reduce seed production of populations of *H. sulphurescens* but are erratic in their effects.

Bliss (1958, 1971) suggested that flowering intensity and seed production decreased with an increase in the severity of the microenvironmental conditions (wind exposed sites) and that seed production or seed set may occur only in some years for some species (Bliss 1971; Holway and Ward 1965; Billings 1974b). Aspects of these conclusions applied to *H. sulphurescens*. This species is primarily restricted to subalpine and krummholz areas and in these habitats it flowered and produced large numbers of viable seed each year. However, the alpine population of *H. sulphurescens* (BM) produced few flowers and seeds during the cold 1983 summer. More favorable weather conditions during 1984 and 1985 may have been the reason for the increased seed production even though the vigor of this population was poor relative to the other populations. The same pattern of decreased flowering and seed production was found with *A. robbinsii*. The cool temperatures in 1983 may have resulted in the high number of aborted or poorly developed seeds of each population of *A. bourgovii*.

A large part of the reproductive success of several species in this study depended upon the magnitude of seed predation. The results of studies on other temperate legume species support these findings (Janzen 1971, Center and Johnson 1974; Platt, Hill and Clark 1974; Fowler and Whitford 1983; and Boe and Wynia 1985).

Seed predation varied with year and population and was greatest for *A. alpinus*, *A. robbinsii* and *H. sulphurescens*. Seed predation of populations of *A. robbinsii* and *H. sulphurescens* was greatest in sheltered habitats. This may be due to the presence of a protective snow cover for the overwintering seed predators in the sheltered habitats or the inability of the small insects to land and oviposit on the wind exposed west slopes. Fowler and Whitford (1983) suggested a different reason for increased seed damage by insects. They observed that host plant densities of the *Astragalus* species affected the amount of seed damage by seed predators. This supports the findings of Fowler and Whitford (1983). Quantitative measurements are needed to confirm these observations.

Seed Predators

The interaction between the plants and their seed predators in this study appears to be very complex. Since the information presented here is observational, the results of the plant - seed predator interactions are inconclusive.

Only two pre-dispersal insect seed predators were identified, but it is probable that there are more

parasites involved, since studies of other legume species have revealed the presence of several pre-dispersal seed feeding insects on the same species (Green and Palmbald 1975). The evidence of this in the present study can be inferred from the type of insect damage. Three forms of insect damage were observed. The first form of damage was single seed predation by one or more species of *Bruchophagus*. In this case, the larva consumed the contents of the developing seed, then pupated within the seed and emerged leaving an exit hole. Unlike many species which do not show external evidence of insect damage within seeds (Fenner 1985), all of the *Astragalus* and *Hedysarum* species in this study showed external evidence of insect damage.

In the second form of insect damage, most of the seeds were consumed, which resulted in a considerable amount of silk or frass within or surrounding the pod(s) or loment(s). In this case, the *Bruchophagus* species pupated within the pod or loment segments. Humble (pers. comm. 1986) indicated that there may also be chalcidoid hyperparasites and lepidopteran larvae involved in the damage of some of these seeds.

The third form of observed insect damage was similar to the second form, but the insect that caused the damage was the seed weevil (Curculionidae). This insect was restricted to the *Oxytropis* species. The larva(e)

pupated within the pod after feeding was complete (as was the case in the second form of insect damage). The damage to the pods in the latter two forms of insect damage also prevented pod dehiscence so that undamaged seeds within the pods would not be dispersed until decomposition of the pod.

The proportion of insect-damaged seeds was greatest for *A. alpinus* and *A. robbinsii*. The pods of these species remained attached to the plant for a longer period, which provided more insect foraging time. Johnson (1981) indicated that legumes in which the pods remained attached were more susceptible to seed beetle predation (Bruchidae) than those in which the pods were released. Although members of the Bruchidae were not collected from any of the species in this study, the same situation may occur with these plants. Pre-dispersal seed predation of *H. sulphurescens* was also heavy. Janzen (1971) indicated that seed beetles (Bruchidae) preferred legume species that produced large seeds. Since *H. sulphurescens* seeds are large, this may account for the heavy insect damage of the seeds of this species.

In general, the seed predators consumed the entire embryo of each seed, though in some cases only the radicle was consumed. Incomplete seed feeding accounted for the large numbers of abnormal germinants

with absent radicles in the seed germination tests of this species.

The *Oxytropis* species along with *A. bourgovii*, and *A. vexilliflexus* var. *nubilus* had relatively little pre-dispersal insect predation. This may be due to the presence of toxic compounds, or to seed or seed coat texture (Nelson and Johnson 1982, Nelson and Johnson 1983).

Pre-dispersal seed predation by vertebrates appeared to be small except for the predation of *O. podocapa* by ptarmigan *Lagopus lagopus*. Post-dispersal seed predation by rodents such as ground squirrels was observed for *H. sulphurescens* and may be important for all species.

A great deal of taxonomic research is needed to identify the seed chalcids and seed weevils of these high elevation legume species. Research is also needed on host-predator relationships, such as host specificity (Johnson 1981), chemical defenses (Nelson and Johnson 1983), plant reproductive phenology and insect oviposition (Janzen 1971), oviposition locations (Johnson 1981), predator satiation and fruiting synchrony (Janzen 1969), and post-dispersal predation by insect and vertebrate predators (Willson 1983).

Seed Dispersal

Seed dispersal mechanisms of the legume species were variable, but certain patterns emerged. Wind was the

most important dispersing agent, and seed dispersal distances were greatest on the wind-exposed sites.

Pod dehiscence varied from perfect dorso-ventral dehiscence to imperfect dorsal dehiscence. Complete pod dehiscence resulted in rapid seed dispersal and shorter dispersal distances, whereas incomplete dehiscence resulted in slower dispersal times and greater seed dispersal distances. *Astragalus vexilliflexus* var. *nubilus* had the shortest seed dispersal distance and *O. podocarpa* had the greatest dispersal distance.

The pod structure and dehiscence of *Astragalus alpinus*, *O. podocarpa* and *O. sericea* were the most efficient in transporting seeds by wind to suitable germination locations, i.e., 'safe sites' (Harper 1977). The type of seed dispersal mechanism did not appear to be related to habitat. Wind had a greater role in seed dispersal for the efficient seed dispersers.

Humidity changes caused the pods of *A. bourgovii* and *A. robbinsii* to open and close after initial dehiscence, whereas the pod valves of the other species appeared to have thicker membranes which caused the pods to remain open after dehiscence. Seeds of *A. bourgovii* often adhered by surface tension to moist pod valves which provided a secondary form of dispersal. The seeds of *A. robbinsii* detached easily from the open pods, and therefore, were not retained very long after the initial

opening of the pod. This mechanism did not appear to be very effective in long distance dispersal.

The pods of *A. alpinus* and *O. podocarpa* served an important function in the dispersal process. Many of the seeds were dispersed in the immediate vicinity, whereas others were released as the pods were blown away by the wind. Microtopography and vegetation density were important determinants for seed dispersal distances of these species. Pods of *A. alpinus* were preferentially deposited by the wind in surface depressions in wind exposed or sparsely vegetated habitats. Voronchikhin (1982) made similar observations on other *Astragalus* species in his study conducted in Russia. Pods of *O. podocarpa* were generally deposited at the bases of grass clumps or, on the leeward sides of rocks or low shrubs.

Dispersal of the loment segments of *H. sulphurescens* was similar to pod dispersal of *A. bourgovii*. The primary dispersal mechanism was gravity, but in the more exposed sites, wind increased the dispersal distances. The loment segments, pods, and seeds of these two species were also deposited in depressions on wind exposed sites.

Dispersal by animals was not observed for any of these species, but may be a consideration where animals transport soil containing dispersed seed (Willson 1983, Fenner 1985). The ptarmigan *L. lagopus* may transport

seeds of *O. podocarpa* internally (endozoochory), but this appears to be unlikely since these animals consume the seeds of this species before the seed coat has hardened.

Oxytropis sericea had an interesting secondary stage of seed dispersal. The pods were erect and remained attached through the winter. In the fall and spring, the pods were above the snow cover and the wind caused seeds to be disseminated. The seeds were then blown along the icy surface for several metres. This appeared to be a unique development for these species.

The seed dispersal data reported here were qualitative. Quantitative studies should be undertaken to determine the pattern of seed dispersal (dispersal distribution or seed rain effects), and the role of animals in the dispersal of these seeds.

Laboratory Seed Germination

Sample Population Germination

Germination of viable seeds of all the legume species varied with population and year. The results are in agreement with the observations of Amen (1966) on seed germination and habitat variation of alpine species. Variation in seed germination of 'wild' population seed collections is often considered to be evidence for the presence of germination ecotypes (Baskin and Baskin 1973). Isolated populations, having

genotypic differences, might be expected to show germination ecotypes. Such may be the case with the isolated Gill Peak population of *Oxytropis sericea*, and the isolated North Greenhills population of *Astragalus vexilliflexus*. However, other isolated populations of *O. sericea* or *A. vexilliflexus* are inconsistent and show year to year variation in germination.

It has been suggested, through the accumulation of considerable evidence, that environmental conditions such as temperature, length of growing season, photoperiod, light quality, soil nutrients, and soil moisture under which the seeds mature on the plant may affect the dormancy and germination characteristics of seeds (Baskin and Baskin 1973). Quinlivan (1965, 1966) found that species of *Trifolium* and *Lupinus* produced more hard seeds in longer and warmer growing seasons than in short growing seasons. Gutterman (1972), Koller (1972), and Harrington (1972) found that germination rates changed with different thermoperiods and day photoperiods (preconditioning) of the parent plant. Baskin and Baskin (1973) also found that seeds grown under longer photoperiods were smaller and had thicker seed coats than those produced under shorter days. Therefore, the variation in the germination of the viable seeds of each species may have resulted from the influences of habitat variation and not by genetic and

ecotypic variation. Flowering and seed production for most of the species appeared to be synchronized within populations and would have resulted in relative homogeneity of seed size or seed coat thickness. However, *A. vexilliflexus* var. *nubilus* flowered and produced seeds until senescence and may therefore produce different proportions of 'hard' and dormant seeds depending on when seed development took place.

The year-to-year variation in the proportions of germinable and 'hard' seeds produced by each species and population would not only affect seedling recruitment, but also affect the number of seeds that would be incorporated into the soil 'seed bank' each year.

More research is needed to examine the causes of the observed differences in the production of germinable and dormant seeds of these and other high elevation species. Studies comparing the performance of seeds from 'wild' populations should be compared with the performance of seeds from plants grown in uniform conditions in order to determine if the differences in seed germination are caused by genetic or environmental differences (Baskin and Baskin 1973).

Germination Enhancement Treatments

Temperature and Light

Rapid seed germination is thought to be an adaptive mechanism for alpine species, particularly those of

exposed habitats (Oberbauer and Miller 1982). Rapid germination of seed from alpine species has been observed for temperatures between 20°C and 30°C (Bliss 1959, Amen 1966, Sayers and Ward 1966 and Bonde 1968). The cumulative proportion of germinated seeds and the germination rate for the legume species of this study were also greatest between 20°C and 30°C. Seed germination did, however, occur at temperatures between 2°C and 5°C, although the germination rate was slow. The lower temperature range is important since diurnal temperature fluctuations during the growing season often result in air and soil temperatures below freezing (Mooney and Billings 1961, Bonde 1968). Therefore, the probability of seed germination in the field would be greatest during the warm and moist periods of late June and early July. Germination would be possible during cooler or warmer periods, provided sufficient moisture was available. Rapid root establishment would be particularly important during the latter period of July. *Hedysarum sulphurescens* would be expected to have a narrower range in which seedling establishment was possible because of temperature restrictions. Temperature restrictions on germination may in part, limit the upper elevational distribution of this species.

Alternating temperatures were suggested by Sayers

and Ward (1966) as a possible thermoperiodic response requirement for germination. The seeds of these species did not, however, respond positively to this treatment. Seed germination for the alternating temperatures was always intermediate between the corresponding upper and lower constant temperature treatments.

Germination of all species was enhanced slightly in the dark, but this was not considered significant when pairwise comparisons were made. Therefore, seed germination of these species was not considered to be light sensitive. Bliss (1958) stated that species which are not light sensitive are generally from disturbed habitats which are subject to being buried. This seemed to be consistent with the ecology of most of the legumes in this study.

Chemical Treatments

The exogenous application of growth regulators such as gibberellin (Sosebee 1977) and ethylene (Bewley and Black 1982) can enhance seed germination, but had little effect on the legumes of this study. Therefore, gibberellin (GA_3) is not a limiting factor for seed germination of these species. Bewley and Black (1982) stated that gibberellin production in seeds may be promoted by cold moist stratification, but since these species did not respond to stratification, the lack of a response to gibberellin complements the results obtained

for the stratification treatments.

The concentration of nitrate ions in the soil solution in conjunction with light and temperature fluctuations is known to enhance seed germination of several low elevation disturbed soil species (Fenner 1985). However, the application of nitrogenous compounds such as potassium nitrate or the combined application of gibberellin and potassium nitrate had little effect on the seed germination of the *Astragalus* and *Hedysarum* species, and reduced the germination of the *Oxytropis* species. The lack of effect of potassium nitrate was expected, since high elevation areas generally have low levels of soil nitrogen (Nishimura 1974).

The mode of action of the growth regulators and nitrogenous compounds is not clearly understood and the function of these compounds upon permeable seeds of these species needs to be studied.

The pre-germination treatment of oxidants such as hydrogen peroxide is known to enhance seed germination of some legume species by accelerating the breakdown of storage materials (Copeland 1976). This chemical did not enhance the seed germination of any of the species. This could also be attributed to the presence of the impenetrable seed coat for the 'hard' seeds, but this treatment also did not increase the rate of germination for those seeds which did not appear to have seed coat

imposed dormancy. Therefore, it is assumed that these species are able to mobilize storage reserves rapidly when other restrictions to germination are removed.

Running water is thought to be effective in the leaching of water soluble inhibitors such as abscissic acid. Although leachate was observed from *A. bourgovii* and *A. vexilliflexus* var. *nubilus*, this treatment did not have any effect on the seed germination of these or the other species. This form of dormancy would be expected in wetter habitats.

Scarification and Stratification

All of the species in the present study except *H. sulphurescens* have seed coat-imposed dormancy. This was demonstrated with both the chemical and mechanical seed scarification treatments. These results are in agreement with the conclusions of Amen and Bonde (1964), Amen (1966), Billings and Mooney (1968), Bell and Amen (1970), Rocow (1970), and Bliss (1971) for other alpine or high elevation species. *Hedysarum sulphurescens* is the only species in the study that is primarily a lower elevation non-disturbed habitat (more stable soil) species and, therefore, the seed germination results are consistent with differences among the species.

The most positive scarification results were observed for *O. podocarpa*. The most resistant seed coat was that of *A. vexilliflexus* var. *nubilus*. *Astragalus*

vexilliflexus var. *nubilus* was the hardiest of all the species studied and was frequently found growing in alpine talus slopes or fellfields. This may also be ecologically significant.

Since many of the species in the study were found in a variety of habitats, Seed coat dormancy may be broken by a number of methods. Amen (1966), Bliss (1971), and Billings (1976) found that seed dormancy was broken through the abrasive action of soil particles in coarse-textured soils during the freeze-thaw cycles in the fall or spring. Bliss (1971) stated that seed coat dormancy seemed to be related to species of disturbed habitats. Another method for breaking seed coat dormancy is by fungal and bacterial activity (Bewley and Black 1985). It is suggested that this method would work best in meadow communities, but the process would be slow in these areas (Amen 1966). In either method, seed germination would occur over a wide number of seasons and, therefore, would have a significant role in plant community composition because seedling establishment would be determined largely by the number and size of disturbance patches in a stand.

Nelson (1924) stated that unequal restrictions imposed by the seed coat on the swelling embryos caused seedling damage. This might account for the higher number of broken radicle abnormal germinants for the

mechanical scarification treatments, whereas membrane damage to the embryo by concentrated sulfuric acid was probably the cause of the higher number of abnormal germinants for the chemical scarification treatments.

Amen (1966) found that pre-germination chilling (stratification) accounted for very little of the seed dormancy of alpine plants. The legumes of this study followed this pattern. Seed germination for all the species was either the same or was reduced by stratification. Most of the non-dormant or scarified of each species germinated in the pre-germination chilling procedure, but radicle elongation was slow. Most of the germinants in each of the stratification treatments grew normally when placed in a 30°C growth chamber. Since a period of cold treatment, such as would occur over winter, was not required for germination of these legumes, it can be concluded that they could germinate in the fall of the year when they were formed. Field germination of *Astragalus bourgovii* was observed in September 1984, but most of the germination of all of the species occurred in late June and early July. For fall germination, the seedlings could overwinter as small germinants or seedlings, although recruitment would be small due to mortality. Fall germination by seeds of *H. sulphurescens* would be very infrequent because of this species sensitivity to low temperatures.

The reduction in the cumulative proportion of germinated seeds of the *Oxytropis* species may have resulted from physiological or membrane damage by the cold, moist conditions during stratification. Since these species are most frequently found in dry snow-free habitats, it is possible that once the seeds are moist they are not able to withstand prolonged periods that are both moist and cold.

Correlation of laboratory germination tests with field trials is needed, particularly for areas of deep snow cover or areas where mechanical scarification may not be frequent. The role of microorganisms in rendering the testa permeable to water should be explored for these areas as well. The distribution of germination over the course of several seasons should also be examined to assess recruitment of seedlings under natural conditions.

Applications of Research to High Elevation Revegetation Problems

Several of these legume species are suitable for the revegetation of high elevation disturbances. Species suitability was determined by the application of the following selection criteria: (1) habitat preference of the species, (2) extent of viable seed production, (3) ease of seed collection and processing, and (4) ease of seed germination and seedling establishment. *Oxytropis*

sericea was rated highest overall, whereas the remaining species were considered to be marginal because of seed collection problems associated with their specific seed dispersal mechanisms. All the remaining species were found to be suitable in terms of habitat, seed production, and seed germination.

Small scale seed collections are possible for all species, although the more desirable method would be to establish multiplication plots where large volumes of seed could be produced on a more economical basis. The variation in seed production observed for natural populations would be reduced under managed conditions. The use of multiplication plots should be emphasized because the natural populations should not be disturbed.

Careful consideration should be given to the location of the multiplication plots, since the presence of pollinators, and insect and vertebrate predators, are important in seed production. Open, accessible tracts of land away from animal migration corridors would be the most desirable for small local programs, whereas contracts with farmers would be suitable for large scale operations.

Harvesting with conventional (farm) harvesters would be possible for *O. sericea*, but seed collection by this method would not be possible for the other species because of their dispersal mechanisms. Harvesting prior

to pod maturation is not possible because the seeds do not mature properly after separation from the plant. Therefore, the 'problem' plants would have to be grown in rows lined with plastic and the pods and seeds collected by portable vacuum once they had been disseminated. This method would be costly, but the cost could be warranted for species such as *A. vexilliflexus* var. *nubilus* which have the ability to grow in the wind exposed ridge crest habitats or, *A. bourgovii* which grows in areas of high snow accumulation. The utilization of the marginally economical species would be restricted to small localized areas where large volumes of seed are not required.

A mix of scarified and non-scarified seeds should be used in the revegetation programs. This would provide for rapid seedling establishment during the current growing season, while at the same time allowing for seedling mortality and future population recruitment. Seed should be sown in the early spring as soon as the areas to be revegetated are free of snow. Soil moisture levels required for germination would be most suitable during this period.

Mechanical scarification is the preferred method for breaking seed dormancy because chemical scarification is hazardous to the embryos. The commercially available Fosberg Line Scarifier would be

suitable for the scarification of large amounts of seed.

Although immediate application of the results is possible, more research is needed on large scale seed production, collection, and processing, before commercial seed is available. The application of current seed processing technology to the seed of these species, or the development of new technology is essential. Field seed germination studies with these species in various disturbed habitats is also required.

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APPENDIX A

APPENDIX A

List of Percent Germination for each Species
and Population by Year

SPECIES	POPULATION	YEAR	REPLICATES					
Aa	ER	1983	30.8	30.4	31.5	31.4	31.2	29.0
		1984	20.6	20.3	24.2	24.2	24.2	23.1
		1985	61.5	80.0	75.0	77.8	75.0	87.5
Aa	SB	1983	26.0	25.3	25.3	25.3	24.0	28.6
		1984	31.3	30.6	30.6	32.0	30.8	29.8
		1985	19.5	26.7	26.1	21.4	23.3	20.0
Aa	WB	1983	25.3	23.3	23.6	24.0	26.6	26.4
		1984	23.7	24.1	26.3	22.6	27.6	28.8
		1985	35.7	37.5	41.2	40.0	47.1	33.3
Ab	LM	1983	56.1	53.3	56.9	52.4	56.0	52.2
		1984	19.8	20.2	20.2	18.8	18.5	19.5
		1985	17.5	15.8	14.9	18.6	17.5	17.7
Ab	MR	1983	25.0	20.0	21.7	23.8	25.0	21.1
		1984	19.4	18.7	20.3	18.9	17.8	20.6
		1985	14.6	13.5	13.6	13.5	15.1	16.3
Ab	EE	1983	16.3	17.5	14.6	16.7	20.5	20.0
		1984	21.6	21.5	20.3	25.0	22.4	23.1
		1985	11.3	12.8	12.5	13.6	18.7	12.7
Ab	NG	1983	18.2	21.4	25.0	25.0	28.6	21.4
		1984	27.1	23.6	26.3	25.0	25.9	25.0
		1985	26.5	26.6	25.0	26.3	24.7	24.0
Ar	MR	1983	32.8	31.2	27.4	31.8	32.9	35.9
		1984	32.6	33.3	38.3	45.3	34.6	35.4
		1985	39.5	41.0	41.0	37.8	42.5	41.0
Ar	BE	1983	80.0	85.0	100.0	75.0	77.8	76.5
		1984	25.9	25.9	25.0	23.5	23.5	22.0
		1985	24.5	23.1	25.9	26.7	23.1	21.6
Ar	SB	1983	51.4	39.4	44.4	40.0	42.4	40.5
		1984	39.1	39.1	36.4	36.4	33.3	34.8
		1985	51.9	52.2	40.0	50.0	47.6	58.9
Ar	WB	1983	40.4	39.0	39.0	39.3	38.2	40.0
		1984	40.0	45.3	39.6	41.2	44.9	44.9
		1985	58.9	54.6	58.9	53.1	51.6	58.9
Ar	NG	1983	37.0	36.7	36.3	41.3	35.0	35.0
		1984	16.7	22.8	18.9	20.0	20.0	19.7

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		1985	21.7	25.0	21.9	22.2	23.4	22.2
Avn	MR	1983	29.6	31.5	31.6	31.5	30.9	32.1
		1984	28.7	29.9	25.0	26.2	28.6	26.2
		1985	27.7	29.2	26.7	28.3	29.8	28.9
Avn	BM	1983	31.1	30.1	32.5	32.9	31.5	35.7
		1984	40.5	43.6	42.1	40.3	39.4	43.6
		1985	14.8	14.8	11.5	13.2	12.7	21.8
Avn	NG	1983	8.0	5.5	7.9	6.6	5.4	7.9
		1984	11.5	9.5	10.5	10.6	8.5	8.5
		1985	11.3	9.8	12.7	11.9	10.4	10.4
Hs	MR	1983	100.0	96.9	100.0	100.0	100.0	100.0
		1984	100.0	100.0	100.0	100.0	100.0	100.0
		1985	100.0	100.0	100.0	100.0	100.0	100.0
Hs	BM	1983	100.0	100.0	100.0	100.0	100.0	100.0
		1984	100.0	100.0	100.0	100.0	100.0	100.0
		1985	100.0	100.0	100.0	100.0	100.0	100.0
Hs	EK	1983	100.0	100.0	100.0	100.0	100.0	100.0
		1984	100.0	100.0	100.0	100.0	100.0	100.0
		1985	95.4	95.9	100.0	100.0	100.0	100.0
Hs	TD	1983	100.0	100.0	100.0	100.0	100.0	100.0
		1984	100.0	100.0	100.0	100.0	100.0	100.0
		1985	100.0	100.0	100.0	98.5	98.5	98.5
Hs	NG	1983	100.0	100.0	100.0	100.0	100.0	100.0
		1984	100.0	100.0	100.0	100.0	100.0	100.0
		1985	100.0	100.0	100.0	100.0	100.0	100.0
Op	ER	1983	38.5	39.6	38.9	39.6	40.0	38.6
		1984	38.8	36.9	40.5	38.6	40.0	38.1
		1985	23.7	21.6	23.1	24.1	23.4	23.1
Op	SB	1983	43.2	42.6	42.6	42.6	42.6	43.0
		1984	39.8	41.4	43.7	43.7	41.4	47.7
		1985	19.6	19.6	19.6	19.6	19.6	20.4
Op	WB	1983	49.5	49.5	50.0	49.5	51.1	50.0
		1984	31.3	34.1	31.0	34.8	31.8	29.2
		1985	10.4	10.6	10.4	9.5	10.4	10.4
Op	BM	1983	64.9	66.3	66.7	65.6	65.3	66.0
		1984	38.6	39.5	36.4	39.3	40.0	39.1
		1985	24.0	20.7	21.3	22.1	20.7	19.6
Op	TB	1983	59.3	57.8	58.7	59.3	59.3	56.5
		1984	21.9	22.1	22.3	19.6	20.4	21.3
		1985	25.7	31.1	31.6	31.4	30.0	29.2

Os	MR	1983	42.6	43.5	43.0	43.0	44.2	41.5
		1984	19.8	20.0	18.3	18.8	18.5	19.5
		1985	15.8	19.2	18.0	18.2	19.7	20.5
Os	ER	1983	67.6	69.0	68.1	71.6	44.2	41.5
		1984	32.9	33.3	32.9	32.0	31.9	32.9
		1985	36.8	36.1	35.7	35.1	41.0	39.5
Os	SB	1983	65.2	64.2	66.7	67.7	65.7	61.2
		1984	29.0	31.3	29.0	30.4	30.0	30.0
		1985	14.1	15.6	15.6	13.2	13.2	14.1
Os	WB	1983	75.0	77.0	74.7	76.7	77.0	73.6
		1984	28.6	28.6	29.3	29.3	27.9	27.9
		1985	31.9	30.4	34.4	31.2	31.9	32.6
Os	NG	1983	58.6	59.4	56.7	55.9	62.3	60.0
		1984	50.0	55.6	49.1	50.9	49.1	50.9
		1985	56.7	56.7	56.3	58.6	55.2	56.7
Os	GP	1983	8.7	8.6	8.5	9.5	10.4	8.5
		1984	6.5	9.4	5.4	6.5	5.4	7.5
		1985	5.7	5.8	5.7	6.6	6.7	6.7

APPENDIX B

APPENDIX B

List of Percent Germination for each Treatment
for each Species

TREATMENT	SPECIES	REPLICATES					
Constant Temperature 5° C (Light)	Aa	3.9	7.1	7.5	7.1	7.1	4.3
	Ab	6.5	4.9	5.6	8.6	7.9	7.9
	Ar	8.9	6.4	6.9	8.7	7.7	8.7
	Avn	6.5	4.3	7.0	4.3	5.6	6.1
	Hs	3.7	4.9	4.8	4.1	3.6	3.7
	Op	3.6	3.7	4.8	3.5	4.1	3.9
	Os	8.3	7.2	7.5	8.1	5.9	6.9
Constant Temperature 10° C (Light)	Aa	10.2	9.9	9.5	8.6	7.4	8.5
	Ab	18.6	19.7	16.2	18.8	18.3	18.3
	Ar	13.6	9.2	10.8	11.9	13.4	9.2
	Avn	15.5	18.3	17.8	18.1	16.7	19.2
	Hs	36.4	33.8	35.5	37.7	37.4	37.3
	Op	24.5	21.7	24.5	22.6	19.8	21.1
	Os	15.1	17.9	18.2	14.3	15.9	15.6
Constant Temperature 20° C (Light)	Aa	21.4	19.7	18.6	18.6	18.3	16.2
	Ab	23.2	22.9	25.4	25.4	25.4	20.6
	Ar	15.4	16.2	15.2	12.5	14.9	15.2
	Avn	26.4	27.8	26.8	26.4	27.4	27.8
	Hs	94.7	92.2	94.8	94.7	94.7	92.0
	Op	22.8	22.0	23.1	22.8	22.0	23.4
	Os	22.7	20.0	18.8	26.9	25.4	25.4
Constant Temperature 30° C (Light)	Aa	20.0	21.4	23.9	18.8	21.1	17.4
	Ab	28.8	29.2	26.8	29.7	30.6	28.2
	Ar	22.7	23.1	21.2	20.9	25.4	23.5
	Avn	33.3	31.9	34.3	29.2	33.8	31.4
	Hs	100.0	100.0	100.0	100.0	100.0	100.0
	Op	41.3	40.6	42.4	40.2	41.5	42.2
	Os	45.2	49.4	47.6	46.8	47.6	46.0
Constant Temperature 5° C (Dark)	Aa	5.8	7.3	9.7	8.5	7.1	8.6
	Ab	8.2	7.3	7.1	8.3	7.3	8.7
	Ar	12.1	10.8	10.8	14.9	10.6	12.1
	Avn	7.0	8.3	8.5	0.6	6.9	9.7
	Hs	5.3	5.3	6.5	6.6	4.1	7.8
	Op	4.2	2.2	4.4	3.3	3.4	3.3
	Os	7.8	7.7	13.6	10.8	9.4	9.4
Constant Temperature 10° C (Dark)	Aa	12.7	11.3	12.7	14.3	13.2	12.9
	Ab	28.6	25.4	23.2	28.6	23.9	25.3
	Ar	24.2	15.4	19.2	20.9	18.5	21.2
	Avn	22.5	22.5	22.5	22.9	22.9	22.5
	Hs	36.8	36.0	35.5	35.5	33.3	39.0
	Op	10.9	9.7	9.8	10.9	9.7	8.7
	Os						

	Os	18.8	20.3	16.9	18.8	18.5	15.9
Constant Temperature 20° C (Dark)	Aa	27.1	24.3	28.6	23.5	23.4	25.0
	Ab	30.4	32.9	30.4	31.9	26.8	25.0
	Ar	23.5	22.7	20.9	27.8	22.2	20.0
	Avn	24.2	26.7	28.8	26.6	27.4	29.6
	Hs	97.4	98.7	97.4	93.4	98.6	96.0
	Op	23.9	22.8	21.5	24.5	22.0	22.0
	Os	25.8	28.1	24.2	27.7	21.9	22.7
Constant Temperature 30° C (Dark)	Aa	28.6	28.1	29.0	28.2	25.7	27.8
	Ab	31.9	31.5	29.2	29.2	32.4	28.2
	Ar	25.8	26.2	21.2	28.1	25.0	31.8
	Avn	34.3	34.3	33.8	34.3	35.8	30.6
	Hs	100.0	100.0	100.0	100.0	100.0	100.0
	Op	40.2	40.7	40.7	40.2	40.2	39.8
	Os	50.0	52.4	50.0	50.8	51.6	50.0
Alternating Temperature 10/5° C (Light)	Aa	4.3	4.3	5.6	4.4	4.4	5.7
	Ab	14.3	15.5	11.8	14.5	15.3	14.3
	Ar	10.6	10.5	11.9	7.8	10.6	9.1
	Avn	13.5	11.3	10.0	13.7	11.1	12.5
	Hs	6.8	10.3	0.1	7.3	9.2	8.0
	Op	6.5	6.5	5.6	7.5	7.5	5.6
	Os	18.5	12.9	17.2	17.2	12.9	15.6
Alternating Temperature 20/10° C (Light)	Aa	16.9	15.9	18.3	18.3	17.4	18.3
	Ab	20.3	20.3	22.6	20.0	21.4	22.9
	Ar	13.2	10.8	10.9	10.3	14.7	9.4
	Avn	24.7	25.0	23.6	23.6	24.7	20.0
	Hs	90.5	86.8	87.2	86.8	87.8	88.5
	Op	16.0	17.0	13.3	15.2	14.1	12.2
	Os	21.1	20.0	17.5	17.5	16.4	18.2
Alternating Temperature 30/20° C (Light)	Aa	18.2	19.3	17.1	18.8	18.8	20.0
	Ab	28.2	27.9	27.5	27.5	27.5	27.0
	Ar	18.0	17.7	17.9	18.1	18.7	18.1
	Avn	30.4	30.6	30.4	28.2	30.2	30.2
	Hs	97.7	97.9	98.0	100.0	100.0	100.0
	Op	39.1	38.2	38.0	38.1	38.9	40.4
	Os	42.4	41.8	42.3	41.9	41.9	41.3
Running Water 12 Hours	Aa	20.0	29.7	18.6	21.1	17.4	18.8
	Ab	28.6	29.6	27.5	26.6	30.6	28.6
	Ar	26.0	19.5	17.5	18.6	18.7	17.9
	Avn	26.2	27.1	25.6	26.8	26.2	25.5
	Hs	99.1	99.8	100.0	100.0	99.0	98.4
	Op	39.1	39.8	37.4	38.9	39.4	40.2
	Os	44.4	40.6	40.3	44.6	43.1	40.6
Running Water 24 Hours	Aa	19.0	22.2	19.3	20.1	20.6	19.2
	Ab	27.9	28.1	30.4	29.1	27.3	27.8
	Ar	15.0	15.2	16.3	15.4	14.9	15.9

	Op	24.5	21.7	24.5	22.6	29.8	21.1
	Os	18.3	17.2	17.5	18.1	15.9	16.9
Potassium Nitrate	Aa	19.7	20.0	19.7	18.6	18.8	20.3
	Ab	29.4	31.4	31.9	27.9	30.4	31.4
	Ar	19.6	18.4	19.7	20.9	22.3	18.9
	Avn	28.6	29.2	32.4	27.1	29.7	29.2
	Hs	100.0	100.0	100.0	100.0	100.0	100.0
	Op	30.0	32.8	32.6	33.9	32.8	34.7
	Os	37.4	38.8	37.8	39.2	39.0	35.4
Potassium Nitrate and Gibberellic Acid	Aa	18.3	19.9	19.3	18.0	19.3	20.9
	Ab	31.4	30.9	30.4	31.4	33.3	32.4
	Ar	22.2	18.9	21.4	22.4	19.7	20.9
	Avn	30.3	28.9	27.1	23.8	30.5	32.5
	Hs	100.0	100.0	100.0	100.0	100.0	100.0
	Op	37.2	36.4	36.4	35.3	37.2	38.7
	Os	41.3	40.8	38.3	37.8	38.6	37.9
Ethylene	Aa	18.6	19.7	17.4	20.3	19.7	19.4
	Ab	25.7	20.6	21.7	23.6	22.5	21.4
	Ar	23.4	20.6	24.6	22.1	23.1	22.4
	Avn	30.6	29.6	30.0	31.4	31.1	33.8
	Hs	100.0	100.0	100.0	100.0	100.0	100.0
	Op	28.3	28.6	28.3	29.4	27.8	29.5
	Os	38.9	38.5	37.6	40.8	39.4	39.4
Mechanical Scarification/ Temperature 5° C	Aa	43.4	43.6	41.7	42.9	43.2	40.3
	Ab	96.1	97.0	98.5	97.1	94.1	97.1
	Ar	88.1	97.0	98.5	96.9	93.9	93.8
	Avn	69.0	69.0	68.0	69.4	68.1	69.0
	Hs	71.1	68.0	68.8	68.4	67.5	65.3
	Op	100.0	98.9	97.1	98.9	98.0	98.9
	Os	100.0	98.5	98.4	96.8	100.0	98.4
Mechanical Scarification/ Temperature 10° C	Aa	69.4	68.1	67.2	69.9	71.1	72.9
	Ab	98.3	88.3	98.9	100.0	99.1	99.4
	Ar	94.0	96.0	97.3	96.2	95.2	95.3
	Avn	93.4	92.9	95.4	92.6	88.9	89.4
	Hs	100.0	98.1	99.4	98.2	99.1	98.5
	Op	100.0	100.0	100.0	100.0	100.0	100.0
	Os	98.3	100.0	100.0	98.8	99.2	100.0
Mechanical Scarification/ Temperature 20° C	Aa	100.0	100.0	98.9	99.9	99.7	99.6
	Ab	100.0	97.9	100.0	98.9	99.1	99.0
	Ar	100.0	100.0	98.9	100.0	98.9	100.0
	Avn	100.0	100.0	100.0	100.0	100.0	99.0
	Hs	100.0	98.9	97.9	100.0	98.9	99.2
	Op	100.0	100.0	99.9	100.0	98.9	100.0
	Os	100.0	100.0	97.9	100.0	100.0	98.9
Mechanical Scarification/	Aa	100.0	100.0	100.0	100.0	100.0	100.0
	Ab	100.0	100.0	100.0	99.7	98.1	100.0

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