AN ABSTRACT OF THE THESIS OF

Cheryl A. Ingersoll for the degree of Doctor of Philosophy

in Botany and Plant Pathology presented on January 7,

1991.

Title: Plant Reproductive Ecology and Community Structure

along a Subalpine Snowmelt Gradient

Signature redacted for privacy.

Abstract approved: _____

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The seasonal duration of snow cover is a primary

factor influencing the patterns of vegetation in high

subalpine and alpine environments, but little is known

concerning the responses of plant reproduction and

seedling recruitment to gradients of snow-release.

Vegetation patterns of a high subalpine site in the Oregon

High Cascades were described and related to important

environmental factors. Life history stages constraining

reproduction and recruitment of five perennial alpine

species were investigated by monitoring phenology,

reproduction, and the emergence and survival of

experimentally sown seedlings. Abundance of the

persistent buried seed bank was assessed.

Detrended Correspondence Analysis ordination revealed timing of snow-release to be the primary factor influencing vegetation patterns on the site. Degree of soil development was next in importance. Nine community types were identified, representing shifts in species dominance in response to these two gradients. Seven of these community types are widespread in alpine or high subalpine areas in the Pacific Northwest.

Reproductive phenologies of four of the five species were significantly compressed in response to late snow-release. The short growing season does not limit seed production in four of the five species; fertilization failure, fruit abortion, and seed predation did limit seed production of four species in one year. Seedling emergence and establishment were extremely low, occurring almost exclusively in protected microsites away from mature plants. For all species, the primary loss of potential offspring occurred between seed dispersal and seedling emergence, and was attributed to lethal effects of high soil surface temperatures and drought.

The abundant persistent seed bank was heavily dominated by two species with very low cover in the standing vegetation. Even bare soils contained large numbers of seeds, indicating that the establishment of vegetation on the site is not limited by availability of seeds, but of seedling safe sites.

Patterns of reproduction and recruitment explain much

of the existing vegetation patterns on this site. A more complete explanation would also require an understanding of the responses of reproduction and recruitment to long-term environmental fluctuations.

Plant Reproductive Ecology and Community Structure
along a Subalpine Snowmelt Gradient

by

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A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Doctor of Philosophy

Completed January 7, 1991

Commencement June 1991

ACKNOWLEDGEMENTS

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PLANT REPRODUCTIVE ECOLOGY AND COMMUNITY STRUCTURE ALONG A SUBALPINE SNOWMELT GRADIENT

CHAPTER I. INTRODUCTION

The dynamics of alpine plant populations and the influence of population processes on alpine vegetation patterns are very poorly understood. Because of recent human impacts on alpine areas, the vegetation patterns of relatively undisturbed alpine plant communities, the population dynamics of their component species, and the influences of population processes on the establishment and maintenance of alpine vegetation have become increasingly important to understand.

Temperate alpine regions are ecologically unique. A short growing season, low soil and air temperatures during the growing season, intense ultraviolet radiation, and strong winds combine to create a particularly severe abiotic environment, which places limits on carbon assimilation and restricts alpine floras to those few species capable of metabolizing, growing, and reproducing at low temperatures (Billings and Mooney 1968). This environment also limits plant growth forms: alpine vegetation is dominated by dwarf shrubs, cushion- or mat-forming perennial forbs, and graminoids. The short growing season places a rigorous time limit on seed production, and two or more years typically elapse between

initiation of floral buds and maturation of seeds. It has been frequently suggested that flowering and seed production are low or intermittent in alpine species (e.g., Holway and Ward 1965, Rochow 1970, Bliss 1971, Jolls 1980a) and that selection pressure for predominantly vegetative modes of regeneration is strong (e.g., Bliss 1971, Callaghan and Collins 1976). Giesel (1974), however, has argued for the advantages of enhanced genetic diversity in severe, fluctuating environments; thus, sexual reproduction may be of high selective value in alpine habitats.

In western North America, alpine and high subalpine vegetation patterns reflect local differences in topography and the depth and duration of snow cover, which interact to form steep gradients of available moisture and temperature (Billings and Bliss 1959, Billings and Mooney 1968, Billings 1974, Canaday and Fonda 1974, Andersen et al. 1979, Oberbauer and Billings 1981, Jackson and Bliss 1984, Isard 1986). Exposed windy ridge crests with little or no winter snow cover provide plants with a relatively long growing season, but also expose them to winter and summer desiccation. In contrast, late-lying snowbanks protect plants during the winter and supply ample moisture in the summer, but drastically compress the already short growing season. Between these two extremes, dramatic shifts in vegetation composition may occur within a few meters. In this harsh abiotic environment, the vegetation

itself can strongly influence microenvironments; for example, the presence of vegetation may prevent cryogenic soil disturbances such as needle ice and reduce daily fluctuations in soil and air temperatures (e.g., Billings and Mooney 1968, Fischer and Kuhn 1984).

Alpine regions are also unique from a biogeographical perspective. Most alpine habitats in western North America are quite young, due to glaciation or to recent volcanic origin. Although alpine regions as a whole support fewer species than any other terrestrial habitat (Billings and Mooney 1968), floristic diversity varies considerably among alpine regions, depending on areal extent of habitat, geographical proximity to other mountain ranges, and climatic factors. In some alpine areas, recent origin, small size, and geographical isolation have combined to result in depauperate floras that are probably still in flux (Harper et al. 1978, Price 1978).

Our lack of knowledge of alpine population and community characteristics has been attributed to logistical difficulties involved in their study (e.g., del Moral 1979b), including inaccessibility, the short and unpredictable growing season, and inclement weather. As Douglas and Bliss (1977) point out, however, alpine environments provide an excellent opportunity for the study of community patterns and processes -- patterns which are accentuated by great topographic diversity and

steep environmental gradients, a small flora, and simple
community structure. In addition, the short alpine
growing season allows examination of population and
community processes throughout the entire season. In such
species-poor communities, it may be possible to interpret
vegetation patterns through the study of the population
dynamics of a few major species which make up a large
proportion of the community.

GOALS AND OBJECTIVES

The primary goals of this dissertation research were:

1) to contribute to further understanding of alpine plant population dynamics through investigation of the patterns of reproduction and seedling recruitment in selected alpine plant populations, and

2) to determine whether patterns observed in the vegetation can be interpreted on the basis of the population dynamics of individual species.

I identified four specific objectives in support of these goals:

1) to describe the vegetation of a high subalpine/low alpine area in the Oregon High Cascades and identify environmental factors influencing vegetation patterns;

2) to identify which life history stages (flowering, fruiting, seed production, seedling emergence, and early seedling survival) constrain recruitment in selected alpine species;

3) to assess the potential contribution of the persistent buried seed bank and vegetative propagule bank to the establishment of vegetation on an alpine site; and

4) to interpret overall patterns in the vegetation based on patterns of reproduction and recruitment of the abundant species.

STUDY AREA

The study area is located on Park Ridge (44 45' N, 121 47'W) in Mt. Jefferson Wilderness Area (Willamette and Mt. Hood National Forests), Marion County, Oregon (Fig. I-1). Park Ridge lies within the High Cascades physiographic province (Franklin and Dyrness 1973) and straddles the crest of the Cascades. Mt. Jefferson lies 5 km south of the study area, Olallie Butte 10 km to the north.

Elevation in the study area ranges from approximately 1900 meters on the lower part of the ridge to 2160 m at the crest. Park Ridge is ideal for the study of high subalpine vegetation patterns and species responses to local gradients. Its combination of northern and southern exposures, steep slopes and gentle basins, and wide range of substrates provide strongly contrasting environments within a small area. The study area displays extensive topographic diversity: rock outcrops and fellfields on exposed crests are often free of snow by early June, while areas of snow accumulation in basins are not released from snow until August. Snow may fall at any time during the growing season, and typically begins to accumulate by October. Two permanent snowfields occur on the site.

Park Ridge is part of the Pliocene Minto Formation, the lavas of which form the bulk of the High Cascades (Thayer 1939). Park Butte is a volcanic plug, the eroded

remains of the approximate center of Pliocene Mount Minto.
Park Ridge consists of gabbro overlain with the basalts
and andesites of the Minto lavas. Soils in the general
area are derived primarily from Pliocene-Pleistocene
andesites and basalts, and glacial till (Baldwin 1981).
The ridge itself was probably never buried by the
Pleistocene lavas extruded from Mt. Jefferson and Olallie
Butte (Thayer 1939), although pumice deposits are
scattered throughout the study area. The broad plateau
north of Park Ridge was covered by a thick ice sheet
during the Wisconsin glaciation, and glacial striae on
rocks in the study area provide evidence that the ridge
was glaciated as well.

Definitions differentiating "alpine" from "subalpine"
habitats vary among authors (e.g., Löve 1970, Douglas
1972, Belsky and del Moral 1982). Billings and Mooney
(1968) define as "alpine" any species growing above
treeline, or with its main distribution above treeline,
and note that the alpine and subalpine vegetation zones
often interdigitate and lack absolute boundaries. Park
Ridge contains a mix of alpine and subalpine species in a
mosaic of alpine and subalpine habitats. The study area
is located well above the distribution of continuous
forest, but small islands of upright trees occur
occasionally. Trees in the upper portion of the area are
restricted to stunted erect and krummholz forms.
Vegetation in the study area includes subalpine parkland

at lower elevations, herb- and shrub-dominated tundra and
Carex meadow, and krummholz (dominated by *Abies*
lasiocarpa[1], *Pinus* *albicaulis*, and *Tsuga* *mertensiana*)
along the ridge crest. Lower in elevation, but adjacent
to the study area, closed subalpine forests are dominated
by *Tsuga* *mertensiana* and *Abies* *amabilis* and are
interspersed with *Carex* meadows and heath. While much of
the study area can be considered subalpine in character,
the north slope of the ridge, where studies of phenology
and reproduction were undertaken, is dominated by
herbaceous and shrub vegetation more characteristic of
alpine tundra than of lower elevation subalpine parkland.

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[1]Nomenclature follows Hitchcock and Cronquist (1973).

RATIONALE AND SUMMARY OF CHAPTERS

Chapter II describes the vegetation patterns of the subalpine/alpine interface of Park Ridge, and relates those patterns to environmental factors, including the annual date of snowmelt, exposure, slope, and substrate. While the alpine and subalpine vegetation of other mountain ranges in western North America, such as the Olympic Mountains (e.g., Kuramoto and Bliss 1970, Canaday and Fonda 1974, del Moral 1983a) and the North Cascades (e.g. Douglas 1972, Douglas and Bliss 1977) has been well-described, virtually nothing is known of Oregon alpine and high subalpine communities or their dominant species (Franklin and Dyrness 1973). The only available descriptions of High Cascades vegetation are Van Vechten's (1960) floristic survey of the Three Sisters area, Campbell's (1973) description of lower subalpine meadows in Mt. Jefferson Wilderness, Swedberg's (1961, 1973) and Schuller's (1978) descriptions of subalpine forest communities, and Horn's (1968) study of the Pumice Desert (Crater Lake National Park). None of these studies addresses general patterns of high subalpine or low alpine vegetation.

The Oregon High Cascades lack well-developed alpine vegetation, as most areas above treeline are either covered with rock, snow or ice, or have been recently released from snow or glaciation (Franklin and Dyrness

1973). Floristically, the alpine vegetation of the central Oregon Cascades has closer affinities with that of other volcanic peaks in southern Oregon and northern California (e.g., Mount Shasta and Mount Lassen) than with the North Cascades of Washington (Taylor 1977) or the mountain ranges of eastern Oregon (Price 1978). Because of the small areal extent, geographical isolation, and recent volcanic origin of alpine areas in the High Cascades, the vegetation of this region is likely to differ significantly from that of other, more extensive high elevation regions in western North America.

Chapter III investigates patterns of, and constraints on, reproduction and recruitment (including flowering, fruiting, seed production and seedling establishment) of five widespread alpine species abundant in the study area. This portion of the study also examines how reproductive patterns of each species change along a local environmental gradient, the annual date of snowmelt. Previous studies of the population dynamics of alpine plant species have focused on a single species (e.g., Rochow 1970, Douglas 1981, Jolls 1980b), closely related species (e.g., Reynolds 1984, Spira and Pollak 1986), or species with similar life history characteristics (Marchand and Roach 1980, Roach and Marchand 1984) within a single habitat or along an elevation gradient. The reproductive patterns of coexisting alpine species having different growth forms and life histories have rarely been

compared on a community-wide basis. In addition, virtually nothing is known concerning intraspecific variation in flower, fruit, and seed production of alpine species along local environmental gradients.

Grime (1979) and others (e.g., Reynolds 1984) propose that alpine species as a group display "stress-tolerant" life history traits characterized by low and intermittent reproduction and low recruitment rates. Despite these theoretical predictions, however, very little is actually known concerning the reproductive patterns of alpine species. Qualitative observations and limited data suggest that, for many tundra species, seed production is low (e.g., Holway and Ward 1965, Rochow 1970, Bliss 1971, Douglas 1981, Spira and Pollak 1986), and seedling mortality is high (Griggs 1956, Bonde 1968, Rochow 1970, Reynolds 1984), resulting in infrequent establishment of new individuals. Failure to produce seeds has been attributed variously to late snowmelt (Bliss 1956, Holway and Ward 1963, Reynolds 1984), drought (Bliss 1956, Oberbauer and Billings 1981, Reynolds 1984), inadequate insect pollination (Holway and Ward 1965, Bliss 1971, Douglas 1981, Spira and Pollak 1986), and fruit or seed predation (Spira and Pollak 1986).

Little is known concerning rates of, and requirements for, seedling establishment of alpine species. High seedling mortality in alpine and subalpine habitats has been attributed primarily to drought or high soil

temperatures (Brink 1964, Horn 1968, Ballard 1972) and soil disturbance by needle ice (e.g., Brink 1964, Bliss 1971, Roach and Marchand 1984, Perez 1987). While biotic interactions in alpine communities have received little attention, the results of several studies (Griggs 1956, Brink 1964, Klikoff 1965, Loneragan and del Moral 1984, del Moral et al. 1985, Perez 1987, Ratcliffe and Turkington 1987) have suggested that established vegetation may facilitate seedling establishment. However, others (e.g., Bonde 1968, Jolls and Bock 1983) have suggested that the presence of established vegetation inhibits seedling establishment.

Chapter IV examines the potential role of the persistent buried seed and vegetative propagule banks in contributing to recruitment of species in this tundra community, compares the above- and below-ground vegetation composition of the site, and compares seed bank patterns with patterns of seedling establishment. Although the extent of buried seed banks in many temperate vegetation types has become increasingly well-documented, there have been few assessments of tundra seed banks. Johnson (1975) hypothesized that buried seed banks decline with increasing latitude, and Thompson (1978) proposed a similar decrease with increasing elevation. Recent studies in arctic tundra (e.g., McGraw 1980, Freedman et al. 1982, Ebersole 1989), however, have demonstrated the existence of relatively large seed banks, comparable to

those in temperate forests. There have been too few assessments of alpine seed banks (for examples, see Fox 1983, Archibold 1984, Miller and Cummins 1987, Morin and Payette 1988) to compare them to those in other habitats. The seeds of most alpine species appear to lack dormancy (Amen 1966) and typically germinate in the season following dispersal, precluding their accumulation in the soil. On the other hand, seeds of alpine species having dormancy or narrow germination requirements may accumulate in the soil, since rates of decay and respiration are low in the cold soils of high elevation sites (McGraw and Vavrek 1989).

Finally, Chapter V provides a summary of the results of the vegetation, reproduction and recruitment, and seed bank studies, and shows how the population dynamics of the component species in the vegetation may influence observed vegetation patterns on the site. Chapter V considers whether existing vegetation patterns can be interpreted on the basis of the reproductive dynamics of individual species.

Figure I-1. The Park Ridge study area in the Oregon High Cascades (Mt. Jefferson 7.5 minute quadrangle, U.S.G.S.). Boundary of vegetation sampling area is marked by a solid line, and boundary of study area for phenology, reproduction and seed bank studies is marked by a dashed line.
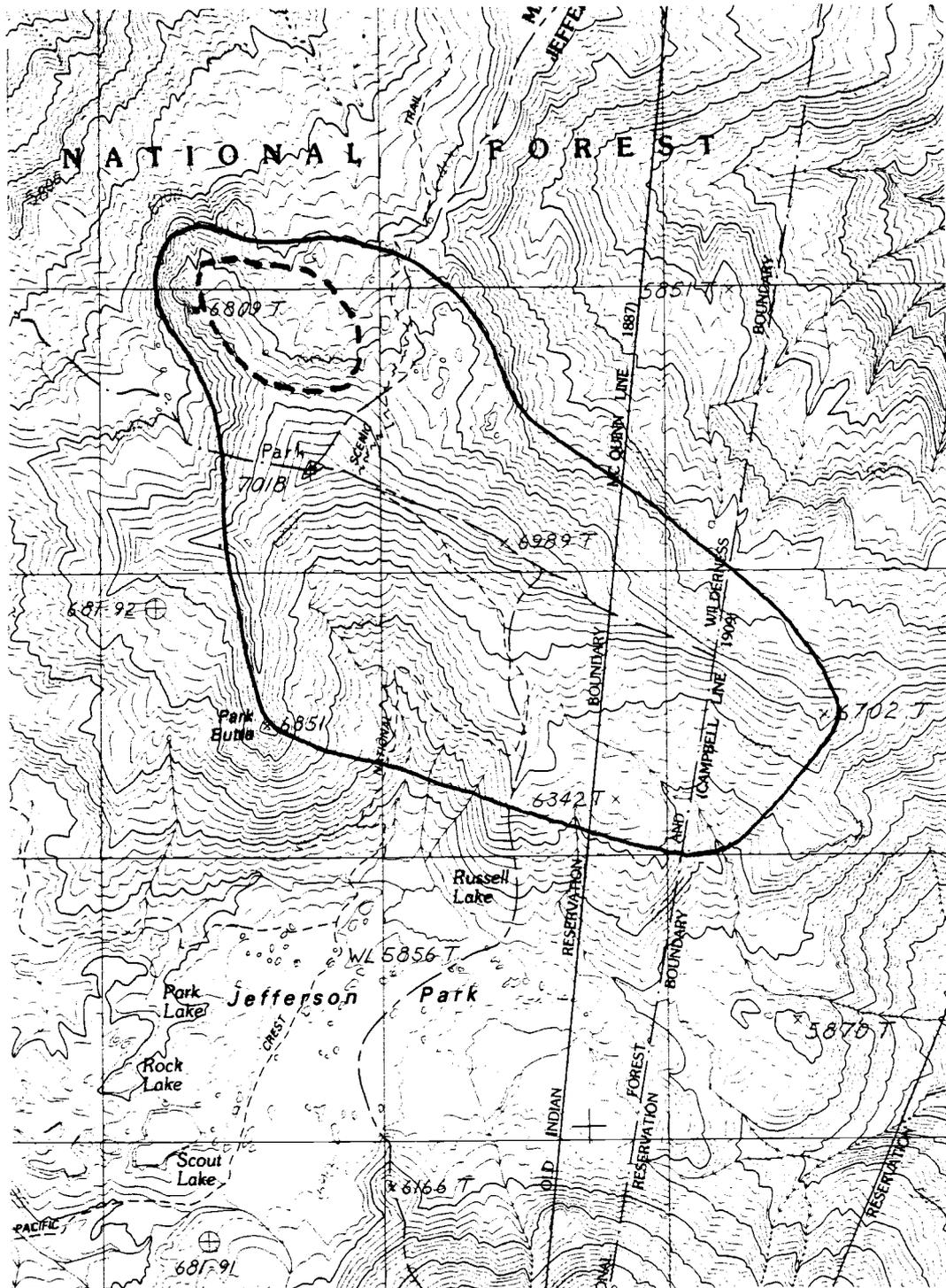
Figure I-1.

CHAPTER II. HIGH SUBALPINE VEGETATION OF

PARK RIDGE, OREGON CASCADES

INTRODUCTION

As Douglas and Bliss (1977) point out, alpine and subalpine environments provide ideal settings for the study of vegetation patterns and processes, because of steep environmental gradients, short growing seasons, small floras, and reduced community structures. Depth and duration of snow cover and availability of soil moisture have been recognized as primary factors determining patterns of species distribution in alpine and high subalpine environments (e.g., Billings and Bliss 1959, Billings 1988). These and related factors, including topography, wind exposure, and disturbance from frost activity, interract to create complex environmental gradients (e.g., Oberbauer and Billings 1981).

Patterns of alpine and subalpine vegetation and their relationships with environmental factors have been well described in some parts of western North America. Studies have documented community patterns in the North Cascade Mountains and Coast Ranges of Washington and British Columbia (e.g., Brink 1959, McLean 1970, Eady 1971, Douglas and Ballard 1971, Douglas 1972, Hamann 1972, Henderson 1973, Douglas and Bliss 1977, del Moral 1979b, Milko and Bell 1986, Ratcliffe and Turkington 1987, Evans

and Fonda 1990); and the Olympic Mountains of Washington
(e.g., Fonda and Bliss 1969, Kuramoto and Bliss 1970,
Belsky and del Moral 1982, del Moral 1983). Douglas
(1972) provides a general review of the high subalpine
plant communities of the North Cascades. Despite its
geographic extent and floristic diversity, the subalpine
and alpine vegetation of the Sierra Nevada has been
described by relatively few studies (e.g., Smiley 1915,
Hall and Grinnell 1919, Klyver 1931, Klikoff 1965, Pemble
1970, Taylor 1976, Benedict 1983). Similarly, little is
known concerning the high elevation vegetation of the
Siskiyou Mountains and southern Cascade Mountains.

Situated between the North Cascades and Olympic
Mountains to the north and the Siskiyous and Sierra Nevada
to the south, the high elevation vegetation of the Oregon
High Cascades remains virtually ignored. Exceptions
include Van Vechten's (1960) floristic survey of the Three
Sisters region; Campbell's (1973) study of subalpine
meadows in Hunt's Cove, Mt. Jefferson Wilderness; Horn's
(1968) study of the Pumice Desert in Crater Lake National
Park; and Swedberg's (1961, 1973) and Schuller's (1978)
descriptions of forest communities in the central Oregon
High Cascades.

Because of its maritime climate, the alpine and high
subalpine vegetation of the Oregon Cascades Mountains and
other ranges in the Pacific Northwest is considered to be
distinct from that of more continental mountain ranges

such as the Rocky Mountains (Franklin and Dyrness 1973).
In addition, the peaks of the High Cascades are the
products of Pliocene and Pleistocene volcanism, and the
resulting substrates are both young and unstable.
Suitable habitat for alpine and high subalpine vegetation
lies mostly on the major volcanoes, and is restricted to a
narrow elevational belt between closed subalpine forest
and rock, snow and ice. As a result, alpine habitat in
the High Cascades is fragmented and small in area compared
with the extensive areas above timberline found in the
Sierra Nevada and Rocky Mountains. In the Oregon High
Cascades, subalpine and alpine vegetation is much sparser
than that of the North Cascades, which Franklin and
Dyrness (1973) attribute to the recent origin and unstable
substrates (including extensive areas of cinder and
pumice) of the High Cascades, and to its warmer, drier
climate. Price (1978) considered the low floristic
affinity between the Three Sisters area and the eastern
Oregon mountain ranges to be the result of high cloud
cover and heavy snowfall, long-lasting snow, unstable
soils, and small geographic area in the High Cascades
compared to the other ranges.

The objectives of this study were to describe the
vegetation of a subalpine-alpine transition zone on Park
Ridge, Oregon High Cascades, and to relate patterns in the
vegetation to environmental factors.

METHODS

Study Area

The study area is located on Park Ridge (44 45' N, 121 47'W) in Mt. Jefferson Wilderness Area (Willamette and Mt. Hood National Forests), Marion County, Oregon. Park Ridge lies within the High Cascades physiographic province (Franklin and Dyrness 1973) and straddles the crest of the Cascades. Mt. Jefferson lies 5 km south of the study area, Olallie Butte 10 km to the north. Elevations in the study area range from approximately 1900 m on the lower part of the ridge to 2160 m at the crest (Fig. I-1).

No climate data are available for the immediate area; the nearest weather station, at Santiam Pass, is approximately 30 km south and 500 m lower in elevation. However, the study area lies in a region characterized by 27.0 C July mean maximum and -9.0 C January mean minimum temperatures (Franklin and Dyrness 1973). Precipitation along this part of the High Cascades crest averages about 90 cm annually, falling mostly as winter snow. In the study area, rock outcrops are often free of snow by early June, while areas of deep snow accumulation in basins are usually not released from snow until early August. Snow may fall at any time during the growing season, and typically begins to accumulate in October. Two permanent

snowfields occur on the ridge, and small snowbanks often persist year-to-year, depending on weather conditions.

Park Ridge was selected for the study of vegetation patterns because it contains extensive physiographic diversity within a small area and its heterogeneous patterns of vegetation reflect sharp topographic changes resulting from steep gradients in exposure, substrate, and timing of snow release. Plant habitats include rock walls and outcrops, unstable scree and talus slopes, gentle benches and slopes, and small ephemeral streams and ponds. Vegetation of the area consists of herb-dominated fellfields, meadows, islands of upright trees, and krummholz. Below 1900 m, the vegetation grades into subalpine forest dominated by Tsuga mertensiana and Abies amabilis. Although a heavily-used section of the Pacific Crest Trail crosses Park Ridge, human-caused disturbances are localized and most of the study area has not been affected by human activities.

Vegetation Sampling

The vegetation was sampled during July and August of 1987 and 1988, in an area approximately 2.5 km² along the crest and slopes of Park Ridge. The area sampled was cut off at either 1900 m elevation or at the upper edge of subalpine forest. A cluster sampling scheme (Steele and

Torrie 1980) was used to overcome the difficulty of traversing the area's rugged terrain. Sixty 10 x 10 m clusters were selected at random from a grid of 100-m^2 cells laid over a topographic map of the study area. These clusters were then located in the field by distance and aspect from landmarks easily recognizable both on the map and on the site. Four clusters, on very steep and unstable slopes, were eliminated from the sampling for safety reasons. Fifteen 1-m^2 plots were located at random within each cluster, except for three clusters having only 10 plots each. The small plot size was selected to detect small-scale pattern in the vegetation. A total of 825 1-m^2 quadrats in 56 clusters were sampled.

The following characteristics were recorded in each 100-m^2 cluster: topographic location (ridge crest, upper slope, lower slope, bench, and snowmelt basin), elevation, slope, aspect, and relative date of snow-release. Based on observations of snowmelt in 1987, snow-release date was scaled from 1 - 5 as follows: 1 = melt-off in mid-June or earlier, 2 = late June - early July, 3 = mid - late July, 4 = early - mid August, and 5 = late August. Aspect (in degrees) was later converted to a scale of 1 = 346.6 - 58.5° (NNE), 2 = 58.6 - 94.5°, 310.6 - 346.5°, 3 = 94.6 - 130.5°, 274.6 - 310.5°, 4 = 130.6 - 166.5°, 238.6 - 274.5°, and 5 = 166.6 - 238.5° (SSW).

In each 1-m^2 quadrat, cover of each vascular plant species, and mosses as a group, was estimated visually,

and the type of surface and degree of substrate
development were recorded. The type of surface and degree
of substrate development was scaled from 1 - 5 as follows:
1 = talus or scree, 2 = shallow, undifferentiated sand or
gravel, 3 = deeper, undifferentiated or poorly-
differentiated sand or gravel, 4 = soils showing profile
development, low in organic matter, and 5 = soils with
well-developed profile, high in organic matter.

Analysis

Detrended Correspondence Analysis (DCA) (Hill 1979,
Hill and Gauch 1980) was used to order the samples and
species along axes of changing vegetation composition.
Correlation analysis (Spearman Rank Correlation) of axis 1
and 2 ordination scores with environmental factors
(aspect, slope, snow release, and substrate type) was used
to identify factors likely to influence vegetation
patterns.

Based on the results obtained from DCA, the
vegetation samples were manually grouped into community
types. Environmental and vegetation characteristics were
summarized for each of the resulting community types.
Differences in environmental variables among community
types was analyzed by Fisher's Protected Least Significant
Difference test (FPLSD).

RESULTS AND DISCUSSION

Vegetation Characteristics

Eighty-two percent of the sample plots were
vegetated. Fifty-six vascular plant species were were
recorded overall. Most non-vegetated plots were on talus
slopes or permanent snow, and thus did not provide
suitable substrates for vegetation. The 16 most abundant
species in the study area accounted for three-fourths of
the overall cover (Table II-1). Cover is shown both as
percent of the entire study area (all plots), and as
percent of colonizable area (excluding rock and permanent
snow). Carex nigricans was the most abundant species
overall, and all species were herbaceous or woody
perennials. Tree cover (of Tsuga mertensiana, Abies
lasiocarpa, and Pinus albicaulis) constituted about 15% of
the vegetation cover, and occurred both as islands of
upright trees and as krummholz (on the ridge crest).

Environmental Gradients

The results of Detrended Correspondence Analysis
described species and sample distributions along two axes
of changing vegetation composition. Two axes were
selected because the eigenvalues of the third and higher

axes were considerably lower than those of axis 1 and axis 2, and because relationships of species and sample distributions with the environmental factors examined were not interpretable on these higher axes. Snow release date was the environmental factor most strongly correlated with axis 1 ordination scores (Table II-2). Snow on plots with high axis 1 scores melted off early in the season. Plots with low scores were located in late snow-melt flats and basins, particularly on northern exposures.

Aspect and slope also showed significant, though much weaker, correlations with axis 1 scores. These relationships are not surprising. Aspect clearly affects the timing of snow release, as south-facing slopes are generally released early in the growing season; however, some south-facing sites are not released until middle or even late summer, while rock outcrops on northern exposures may be free of snow by early June. Topography also affects patterns of snow duration: steep slopes typically accumulate less snow than do flats and basins, and are thus likely to become snow-free earlier in the season.

The degree of soil development was strongly negatively correlated (-.55) with ordination scores on axis 2. Plots with the highest axis 2 scores were located in shallow pockets of sand or gravel on bedrock outcrops, while plots in stands of trees or on mesic sedge or heath meadows, on relatively well-developed soils high in

organic matter, had the lowest axis 2 scores. Slope and aspect were significantly, but weakly, correlated with axis 2 scores. Slope and soil development were themselves related: substrates on steep slopes were generally less stable and had poorer soil development than on gentle slopes and flats, and supported lower vegetation cover.

The degree of soil development was strongly and significantly correlated with vegetation characteristics: better-developed soils supported higher total cover and more species than did poorly-developed soils (Table II-3). Aspect and date of snow-release had weak but significant effects on vegetation characteristics: plots released early (or located on southern exposures) supported higher cover than did those released late or on northern exposures. Plots on steep slopes or northern exposures had fewer species than did plots on gentle slopes and flats or southern exposures.

These results show that, on Park Ridge, the timing of snow release is the major cause of vegetation pattern. Duration of snow cover has been widely recognized as a primary factor influencing species distributions in subalpine and alpine habitats (Billings and Bliss 1959, Johnson and Billings 1962, Holway and Ward 1965, Canaday and Fonda 1974, Douglas 1977, del Moral 1979b, Oberbauer and Billings 1981, Isard 1986, Billings 1988, Evans and Fonda 1990). Timing of snow release may affect soil moisture availability, particularly in summer-dry

climates, so that vegetation in locations released early in the growing season may be limited by moisture availability by mid-summer (e.g., Ehleringer and Miller, 1975, Oberbauer and Billings 1981). Late-release locations may be supplied with ample moisture, but their dramatically compressed growing seasons influence vegetation composition. In the Cascades, however, subsurface soils generally remain moist throughout the summer. Soil moisture availability may not affect the growth of established plants, but may influence vegetation patterns through effects on seedling establishment (Horn 1968, Chapin and Bliss 1988). Duration of snow cover also affects soil temperature, with cold soils potentially inhibiting plant growth on late snowmelt sites (Holway and Ward 1963, Day et al. 1989, Evans and Fonda 1990), and high surface temperatures inhibiting seedling establishment on sites released early in the season (e.g., Brink 1964). Differential physiological and phenological responses to soil moisture availability, soil temperatures, and length of the growing season (e.g., Ehleringer and Miller 1975, Andersen et al. 1979, Peterson and Billings 1982, Jackson and Bliss 1984) are translated into shifting patterns of vegetation along the snow release gradient on Park Ridge, as has been recognized in other subalpine areas (e.g., Kuramoto and Bliss 1970, Douglas 1972, Canaday and Fonda 1974, Douglas and Bliss 1977, Belsky and del Moral 1982).

The relationship between soil development and vegetation patterns forms a complex interaction, because not only do soil characteristics influence vegetation pattern, but vegetation characteristics also influence soil development. The soil - vegetation complex of high elevation environments is determined by interrelated factors of moisture availability, depth of snow, and length of the growing season (French 1986). Soil characteristics have been examined in several studies of subalpine and alpine vegetation (e.g., Klikoff 1965, Kuramoto and Bliss 1970, Belsky and del Moral 1982, Ratcliffe and Turkington 1987), but, in general, soil development has not been interpreted as an environmental gradient influencing vegetation patterns. On Vancouver Island, however, Milko and Bell (1986) found patterns of subalpine meadow vegetation to be influenced by the degree of soil development (ranging from talus to well-developed humic soils) and interpreted this as a successional gradient as well. In addition, Douglas (1972) differentiated communities on "rawmark" (chronically disturbed and having little or no soil development) from those on "residual" (well-developed) soils. He concluded that soil development was strongly correlated with the duration of snow cover, with late snowmelt sites having poorly developed soils in comparison with sites released early in the season. This relationship does not appear to hold on Park Ridge, since the degree of soil development

was not correlated with the date of snow release
(correlation coefficient = +.07, Spearman Rank Correlation
test). On this site, some early snowmelt plots had very
poorly-developed substrates, and some plots released in
mid-season were located on well-developed soils.

Better-developed soils on Park Ridge also supported
higher vegetation cover and greater species richness than
did poorly-developed soils (Table II-3). Although the
relationship between soil development and vegetation cover
is a two-way interaction (as vegetation aids in the
development of soil), the degree of soil development
probably strongly influences species richness on this
site. Bare, poorly-developed substrates on Park Ridge
have higher surface temperatures, lower surface moisture
availability, and higher rates of needle ice disturbance
than do better-developed, vegetated soils. These factors
are likely to inhibit seedling establishment of many
species that are able to establish in better-developed
soils, and result in lower species richness.

Communities

The distribution of plots (Fig. II-1) and species
(Fig. II-2) along the first and second DCA axes and
patterns of differential species dominance were used to
identify 9 community types (Fig. II-3). These types

actually represent phases of vegetation changing gradually
along environmental gradients. The classification into
community types is used simply to facilitate comparison of
the results of this study with other descriptions of
subalpine vegetation in the Pacific Northwest. The types
were named for dominant or co-dominant species, except in
the case of the HERB community type, in which several
herbaceous species dominated different plots. Table II-4
summarizes species cover, composition, and diversity of
each community type. Environmental factors characterizing
each type are summarized in Table II-5.

The _Penstemon davidsonii_ (PEDA) community type was
widely separated from all others in ordination space,
occurring on poorly-developed soils in the middle range of
snow release dates (Fig. II-3). It was found on bedrock
outcrops on the crest and upper slopes of Park Ridge, on
sites which were released from snow in mid-June to early
July (Table II-5). Plants were rooted in shallow pockets
of sand and gravel on these outcrops. The vegetation was
characterized solely by _P_. _davidsonii_, and only small
amounts of a few other species, primarily _Carex_
spectabilis, were occasionally present. Vegetation cover
(18%) and diversity (1.6) were the lowest of any community
(Table II-4).

The herb (HERB) community type, located at the early
end of the snow release gradient, spanned a wide range of
soil development (Fig. II-3). This type occurred on

gentle to moderate slopes in the lower part of the study area, almost exclusively on southern exposures released from snow during June. Overall, _Lupinus latifolius_ and _Polygonum newberryi_ were the dominant species, but some plots were dominated by _Spraguea umbellata_, _Lomatium martindalei_, or _Arenaria capillaris_. Better-developed soils on shallow slopes were typically dominated by _L. latifolius_. This community type was low in total cover (24%) and species diversity (1.9).

The _Juniperus communis_ - _Pinus albicaulis_ (JUCO - PIAL) community type, released slightly later than the herb community, also spanned a wide range of soil development (Fig. II-3). This type was found on steep upper slopes and along the crest of Park Ridge, mostly on southern and western exposures. Snow release ranged from mid-June to early July. Deeper, better-developed soils were generally dominated by _P. albicaulis_, with _J. communis_ dominating coarser, shallower soils. Small shrubs and herbs included _Penstemon davidsonii_, _Lupinus latifolius_, _Lomatium martindalei_, and _Arenaria capillaris_, all characteristic of open sites, and _Vaccinium scouleri_ and _Vaccinium deliciosum_, generally found under partial tree canopy and at forest edges. Total cover (56%) and diversity (2.1) were higher than in the very open and depauperate PEDA and HERB community types.

The _Abies lasiocarpa_ - _Tsuga mertensiana_ (ABLA - TSME) community type occupied a narrow middle range on the

snow release gradient and spanned a moderate range of soil
development (Fig. II-3). This community was released from
snow between mid-June and early July, but slightly later
than the JUCO-PIAL type. This community type occurred
both along the ridge crest and occasionally as islands of
upright trees on both north and south slopes. On the
ridgecrest, both Abies lasiocarpa and Tsuga mertensiana
occurred either as krummholz or as upright but stunted
forms. Vaccinium deliciosum, characteristic of the edges
of subalpine forest, and Luetkea pectinata were the most
abundant understory species. Overall cover was high
(85%), due to the partial tree canopy and well-developed
understory. Because of the presence of both subalpine
understory species (including Luzula hitchcockii,
Pedicularis racemosa, Sorbus sitchensis, and Arnica
latifolia) and open site species (such as Lomatium
martindalei, Nothocalais alpestris, Penstemon davidsonii,
Polygonum newberryi, Spraguea umbellata, and Antennaria
alpina), the TSME - ABLA community type was one of the
most diverse in the study area.

The group of plots located on the late end of the
snow release gradient and covering a middle range of soil
development was separated into five types, each
representing a center of dominance by a different species
(Fig. II-3). The Saxifraga tolmiei (SATO) community type
occurred at the latest end of the snow release gradient,
on relatively poorly-developed soils. This type was found

on sites released from snow in late July to mid-August,
almost exclusively on north-facing aspects (Table II-5).
Many of these plots were in steep gullies with coarse,
erodable soils, which generally remained moist throughout
the growing season. Saxifraga tolmiei was the only
abundant species. Small amounts of Carex spectabilis,
Carex nigricans, Cardamine bellidifolia, Juncus
drummondii, and mosses occasionally occurred. Because of
the extremely short growing season and poor soil, the SATO
community was very low in total cover (22%) and species
diversity (1.9) (Table II-4).

The Carex spectabilis (CASP) community type was
located adjacent to the SATO community in the ordination,
with slightly earlier release from snow (Fig. II-3),
ranging from mid-June to late July (Table II-5). Like the
SATO type, it was found primarily on coarse, poorly-
developed soils on northern (but occasionally on southern)
exposures. Besides C. spectabilis, small amounts of
several other species occurred frequently, including
Antennaria alpina, Cardamine bellidifolia, Carex
nigricans, Juncus drummondii, Luetkea pectinata,
Phyllodoce empetriformis, and Saxifraga tolmiei. Overall
cover (29%) and diversity (2.1) were slightly higher than
in the SATO community (Table II-4).

The Carex nigricans (CANI) community type was located
adjacent to the SATO type in the ordination, with slightly
earlier snow release and better developed soils (Fig. II-

3). This community occurred on both northern and southern exposures, on gentle slopes and in basins where snowmelt water often ponded in early summer. Soils were very well-developed, but poorly drained. The vegetation was heavily dominated by C. nigricans, and mosses were abundant. While Carex spectabilis dropped to a minor component, many associates of the CASP community type occurred here, with the addition of Aster alpigenus and Cassiope mertensiana. Dodecatheon jeffreyi, Tofieldia glutinosa, Mimulus tilingii, Caltha biflora, and Gentiana calycosa were common along a small stream on the south side of the ridge. Vegetation cover (62%) of the CANI type was much higher than that of the CASP or SATO communities.

The Phyllodoce empetriformis (PHEM) community type, located adjacent to the CANI community in the ordination, was typically found on hummocks adjacent to CANI meadows, on sites released from snow slightly earlier. Soils were well-developed, but better-drained than those of the CANI community. Phyllodoce empetriformis had the highest cover, but Cassiope mertensiana and Luetkea pectinata were also important species, and mosses were abundant (Table II-4). Other species characteristic of this community type were Aster alpigenus, Carex nigricans, and Vaccinium deliciosum, and a number of other species occurred in small amounts. Vegetation cover was high (62%), and along with the ABLA - TSME community, the PHEM type was the most diverse in the study area.

The <u>Luetkea</u> <u>pectinata</u> (LUPE) community type was located in close proximity to the PHEM community, both in ordination space (Fig. II-3) and in the study area. The two types were released from snow at about the same time (early to mid-July), but the LUPE community occurred on slightly coarser, better-drained and less-developed soils. Species composition of the two types was similar, except that, in the LUPE community, ericaceous shrubs, mosses, and <u>Carex</u> <u>nigricans</u> were reduced to minor components, and the cover of <u>Carex</u> <u>spectabilis</u> increased. Both overall plant cover (27%) and species diversity were much lower as well.

Comparison With Other Subalpine Vegetation
in the Pacific Northwest

Several communities identified on Park Ridge show strong similarities with others described in high subalpine and low alpine areas in the Pacific Northwest. The SATO, PHEM, LUPE, CANI, and CASP communities on the northern exposure of Park Ridge are arrayed along the gradient of snow release in a manner highly similar to vegetation patterns in the western North Cascades (Evans and Fonda 1990).

The high subalpine and low alpine <u>Phyllodoce</u> <u>empetriformis</u> - <u>Cassiope</u> <u>mertensiana</u> community type,

occurring on well-developed, well-drained soils on mid- to late-snowmelt sites, is widespread throughout the Pacific Northwest. It has been described in the Coast Range of British Columbia (e.g., Brink 1959, Brooke et al. 1970), in the western (e.g., Douglas and Bliss 1977, Evans and Fonda 1990), as well as the drier east-central North Cascades (del Moral 1979b), and in central Oregon (Campbell 1973). In all descriptions, Luetkea pectinata and Vaccinium deliciosum are the major associates of the dominant heath species. Campbell's (1973) lower elevation Phyllodoce empetriformis - Cassiope mertensiana community in the same area is much poorer in species, particularly forbs, than the type on Park Ridge. A Vaccinium deliciosum community lying between this heath community and Tsuga - Abies forest, has been recognized in several studies (Brooke et al. 1970, Douglas 1972, Campbell 1973). On Park Ridge, Vaccinium deliciosum was an important component of the Tsuga mertensiana - Abies lasiocarpa community, but of minor importance in the Phyllodoce community (Table II-4), and the separation of a Vaccinium type from these others did not seem justified.

A second widespread high subalpine or low alpine community type in the Pacific Northwest is the Carex nigricans meadow, variations of which are found as far north as southeast Alaska (Douglas 1972). It has been described by Douglas (1972), Henderson (1974), Douglas and Bliss (1977), and Evans and Fonda (1990) in the North

Cascades and by Brink (1959) in British Columbia.
Campbell (1973) recognized two variants of the C.
nigricans community at lower elevations in Hunt's Cove: C.
nigricans - Aster alpigenus and C. nigricans -
Polytrichum, on very late snowmelt sites. Throughout the
Pacific Northwest, most Carex nigricans communities are
distinguished by high cover of the sole dominant, with
Luetkea pectinata typically of secondary importance.
Elsewhere, as on Park Ridge, these "short-sedge" meadows
occur in poorly-drained depressions, such as old pond
basins, where alluvium accumulates. Snowmelt in the sedge
meadow is slightly later than in the heath community,
which generally occurs on the higher margins of C.
nigricans meadows.

Saxifraga tolmiei-dominated communities similar to
the one recognized on Park Ridge have been described in
the North Cascades by Douglas (1972), Henderson (1974),
Douglas and Bliss (1977), and Evans and Fonda (1990).
They are always found on north-facing slopes at high
elevation, with very late snowmelt and very poorly-
developed, chronically disturbed soils. This community
has not been recognized in the Olympic Mountains or in the
dry east-central North Cascades. In Oregon, it appears to
be restricted to high subalpine and alpine sites (e.g.,
Van Vechten 1960), probably because of the earlier
snowmelt and longer growing season at lower elevations.

The <u>Carex</u> <u>spectabilis</u> community described in this study is not widely recognized and appears to be far more variable in habitat and species composition than the types previously discussed. According to Franklin (1988), <u>C</u>. <u>spectabilis</u> is a dominant species in a lush herbaceous community type widespread throughout the Pacific Northwest, and a <u>C</u>. <u>spectabilis</u> community has been described in lower subalpine sites with early snowmelt (Douglas 1972, Evans and Fonda 1990). Douglas and Bliss (1977) described a <u>Carex</u> <u>spectabilis</u> community, similar to those of Douglas (1972) and Evans and Fonda (1990), at high elevations. Neither type corresponds in habitat or species composition to the <u>Carex</u> <u>spectabilis</u> community type on Park Ridge. On the basis of habitat and species composition, the CASP community type on Park Ridge most closely resembles del Moral's (1979a,b) sparsely vegetated <u>Carex</u> <u>spectabilis</u> - dominated communities on late snowmelt sites at high elevations in the North Cascades.

<u>Luetkea</u> <u>pectinata</u> is a common and widespread component of many subalpine plant associations, but it has rarely been recognized as a community dominant. A <u>Luetkea</u> <u>pectinata</u> community comparable to that on Park Ridge occurs in the Olympic Mountains (Evans and Fonda 1990). In the North Cascades, Douglas (1972) also described a <u>L</u>. <u>pectinata</u> community similar to that on Park Ridge, occurring on poorly-developed, well-drained soils on moderate-steep north-facing slopes. Such sites have a

slightly longer growing season than those dominated by _Saxifraga tolmiei_ and the vegetation contains elements of both the _Saxifraga tolmiei_ and _Phyllodoce empetriformis_ communities.

The _Abies lasiocarpa_ - _Tsuga mertensiana_ community on Park Ridge corresponds closely with Schuller's (1978) _T. mertensiana_ / _Luzula hitchcockii_ community type in the highest portion of the mountain hemlock zone on the east slope of the High Cascades. In the North Cascades, Douglas and Ballard (1971) described alpine krummholz vegetation dominated by _A. lasiocarpa_ and _T. mertensiana_, with an understory (e.g., _Phyllodoce empetriformis_, _Vaccinium deliciosum_, _Luetkea pectinata_, _Arnica latifolia_, and _Pedicularis racemosa_) quite similar to that of the Park Ridge community type. The ABLA - TSME community type also resembles Douglas' (1972) _T. mertensiana_ - _Abies amabilis_ (immature) community, which both invades and is closely associated with heath and _Vaccinium_ meadows. _Abies amabilis_ is a major species of the subalpine _Tsuga mertensiana_ zone in Washington, but decreases in importance in Oregon (Franklin and Dyrness 1973), and is replaced by _A. lasiocarpa_ on cold, dry sites at high elevation. These two community types have a number of understory species in common, including _Vaccinium deliciosum_, _Luetkea pectinata_, _Cassiope mertensiana_, _Phyllodoce empetriformis_, and _Sorbus sitchensis_.

Pinus albicaulis - dominated communities occur elsewhere in the High Cascades, generally along dry, windswept ridges. On Bachelor Butte, as on Park Ridge, P. albicaulis grows in a wide range of soils, from thin, very rocky soil to well-developed loam in older groves (Lueck 1980). The Juniperus communis - Pinus albicaulis community type on Park Ridge resembles the P. albicaulis - Juniperus communis - Penstemon davidsonii community, which occurs on ridges and knolls in the eastern North Cascades (del Moral 1979b). As this community type occurs on dry, exposed sites, it may not be a major component of the vegetation in the cooler, moister western North Cascades. A Penstemon davidsonii community type has not been recognized elsewhere, and P. davidsonii is characterized as a major component of the J. communis - P. albicaulis community described by del Moral (1979) in the eastern North Cascades. On Park Ridge, P. davidsonii is frequently associated with the understory of, or rocky areas adjacent to, the JUCO - PIAL community.

The HERB community type on Park Ridge lacks a close analog in the North Cascades, although Lupinus latifolius communities have been described there (Henderson 1974, Douglas and Bliss 1977), and the community on Park Ridge bears some resemblance to Kuramoto and Bliss' (1970) "mesic grass type" on early snow-melt sites in the Olympic Mountains. On Park Ridge, however, Festuca idahoensis is lacking as a major associate, and Polygonum newberryi,

important on Park Ridge, is absent from the sites in the Olympics. The herbaceous communities of the North Cascades have higher vegetation cover and species richness than does the HERB type on Park Ridge. Several major components of the Park Ridge HERB community type -- e.g., Polygonum newberryi, Lomatium martindalei, and Arenaria capillaris -- are widespread components of dry subalpine communities on volcanic soils elsewhere in the Northwest (del Moral 1979a, 1979b; Belsky and del Moral 1982, Douglas and Bliss 1977).

These comparisons with other studies show that the vegetation of Park Ridge in the Oregon High Cascades has some distinct similarities with that of the North Cascades and Olympic Mountains. The lack of subalpine vegetation studies in the Siskiyou Mountains and northern California Cascades and Sierra Nevada precludes evaluation of the relative affinities among the vegetations of these areas. While many of the dominant species in the communities described on Park Ridge are also found in the Sierra Nevada (e.g., Carex nigricans, Carex spectabilis, Saxifraga tolmiei, Tsuga mertensiana, Juniperus communis, and Pinus albicaulis) (Munz 1968), there is a lack of detailed information on high elevation vegetation in this large and diverse mountain range, and no close analogs of the community types discussed here appear to have been described in the Sierra Nevada. Carex meadows in the Sierra Nevada are primarily dominated by species other

than _Carex_ _nigricans_, although Pemble (1970) recognized a _Carex_ _nigricans_ - _Vaccinium_ meadow type, and _Pinus_ _albicaulis_ and _Tsuga_ _mertensiana_ are important components of mixed subalpine conifer forest in the northern portion of the range (Barbour 1988).

The mesic late-snowmelt communities on Park Ridge -- _Carex_ _nigricans_, _Phyllodoce_ _empetriformis_, _Saxifraga_ _tolmiei_, and _Luetkea_ _pectinata_ -- are examples of widespread, apparently rather consistent high subalpine-low alpine community types in the Pacific Northwest. The _Juniperus_ _communis_ - _Pinus_ _albicaulis_, _Penstemon_ _davidsonii_, and _Abies_ _lasiocarpa_-_Tsuga_ _mertensiana_ communities are also probably closely related to communities in drier portions of the North Cascades. The other communities on Park Ridge (CASP and HERB types) are less widespread and show greater site-to-site variation in habitat and species composition. The lush herbaceous communities described in most studies of subalpine vegetation in the North Cascades (e.g., Henderson 1974) are lacking on Park Ridge. In the vicinity of the study area, these lush herb communities are restricted to lower elevations, occurring primarily in gaps in the subalpine forest.

Del Moral (1979b) suggests that it is difficult to extrapolate vegetation patterns and community types much beyond a specific area, because species behave individually in response to environmental gradients, and

species associations will therefore change with differing environmental conditions among sites. However, despite the individuality of species behavior, and despite the fact that the floristic affinities of the Oregon High Cascades appear to be closer to the Siskiyou Mountains and northern California Cascade peaks than to the North Cascade and Olympic Mountains (Taylor 1977), several of the community types on Park Ridge show strong similarities to those described elsewhere in the Pacific Northwest. That these community types form a rather predictable sequence of vegetation change is not surprising, given the large pool of species common to both the North Cascades and Oregon High Cascades subalpine vegetation, individualistic species responses to environmental gradients, and the overwhelming influence of a major environmental gradient, duration of snow cover, throughout the Pacific Northwest.

Table II-1. Cover of the 16 most abundant species in the study area. "Overall" value is for entire study area (825 1-m^2 plots); "Vegetated plots" includes all those plots not completely covered by talus or permanent snow (676 1-m^2 plots). Species with less than 0.1% total cover were grouped as "all other species".

	Cover (%)	
Species	Overall	Vegetated Plots
Carex nigricans	5.1	6.2
Luetkea pectinata	4.1	5.0
Mosses	3.4	4.2
Phyllodoce empetriformis	3.3	4.0
Vaccinium deliciosum	3.3	4.0
Cassiope mertensiana	3.2	3.9
Carex spectabilis	2.5	3.0
Tsuga mertensiana	2.5	3.0
Abies lasiocarpa	1.9	2.3
Juniperus communis	1.6	2.0
Pinus albicaulis	1.6	2.0
Saxifraga tolmiei	1.1	1.3
Vaccinium scoparium	0.8	1.0
Polygonum newberryi	0.7	0.8
Juncus drummondii	0.7	0.8
Aster alpigenus	0.7	0.8
All other species (40)	12.1	14.8
Total Cover	48.6	59.1

Table II-2. Relationship between DCA sample scores on axes 1 and 2 and environmental factors. Values shown are Spearman rank correlation coefficients and P-values (in parentheses). Aspect, snow release date, and soil development were scaled factors. Aspect ranged from 1 = NNE to 5 = SSW. Snow release date ranged from 1 = mid-June to 5 = late August. Soil development ranged from 1 = talus and scree to 5 = well-developed soil profile, high in organic matter.

Factor	Axis 1 Score	Axis 2 Score
Elevation (m)	+ .05 (.172)	+ .04 (.297)
Aspect	+ .20 (.000)	− .12 (.001)
Slope (degrees)	+ .09 (.019)	− .08 (.045)
Snow Release Date	− .46 (.000)	+ .07 (.069)
Soil Development	− .03 (.451)	− .55 (.000)

Table II-3. Relationships between vegetation characteristics and the environmental factors that were significantly correlated with ordination scores. Values shown are Spearman rank correlation coefficients and P-values (in parentheses). Aspect, snow release date, and soil development were scaled factors. Aspect ranged from 1 = NNE to 5 = SSW. Snow release date ranged from 1 = mid-June to 5 = late August. Soil development ranged from 1 = talus and scree to 5 = well-developed soil profile, high in organic matter.

	Vegetation Cover		Species Richness	
Snow Release Date	− .15	(.000)	− .05	(.219)
Soil Development	+ .63	(.000)	+ .56	(.000)
Aspect	+ .19	(.000)	+ .12	(.002)
Slope (degrees)	− .04	(.311)	− .12	(.002)

Table II-4. Mean percent cover of species found in 9 community types on Park Ridge. A " + " indicates species mean cover was less than 0.5 %. Community types are as follows: PEDA = _Penstemon davidsonii_, HERB = herbaceous, JUCO - PIAL = _Juniperus communis_ - _Pinus albicaulis_, ABLA - TSME = _Abies lasiocarpa_ - _Tsuga mertensiana_, SATO = _Saxifraga tolmiei_, CASP = _Carex spectabilis_, CANI = _Carex nigricans_, PHEM = _Phyllodoce empetriformis_, LUPE = _Luetkea pectinata_. Diversity measure is Simpson's Index (defined as the inverse of the sum of the squares of the proportional cover values).

Species	PEDA	HERB	JUCO PIAL	ABLA TSME	SATO	CASP	CANI	PHEM	LUPE
					Community Type				
Abies lasiocarpa			+	15					
Agrostis variabilis							+	+	
Antennaria alpina				+	+	1		+	+
Arenaria capillaris	2	2		+				+	+
Arnica latifolia				+					
Aster alpigenus			+	1	+	+	2	2	+
Caltha biflora							+		
Cardamine bellidifolia		+	+	+	1	1	1	+	1
Carex nigricans				+	4	2	34	4	
Carex phaeocephala						+		+	
Carex spectabilis	3			+	2	15	1	1	7
Carex sp.			2						
Cassiope mertensiana				5		+	1	12	1
Castilleja parviflora				1		+	+	+	1
Cryptogramma acrostichoides									+
Deschampsia atropurpurea					+				
Dodecatheon jeffreyi						+	1	+	+
Epilobium alpinum						+	+		+
Erigeron peregrinus							+		
Gaultheria humifusa							+		
Gentiana calycosa					+		1	+	+

Table II-4 continued.

Species	PEDA	HERB	JUCO PIAL	ABLA TSME	SATO	CASP	CANI	PHEM	LUPE
Hieraceum gracile				+		+		+	+
Hieraceum scouleri			+						
Juncus drummondii				+	2	2	1	1	2
Juncus mertensianus					+	+	+		+
Juniperus communis		1	21	+			+		
Kalmia microphylla					+	+	+	+	
Ligusticum grayii				1		+	+	+	+
Lomatium martindalei	1	2	1	1					
Luetkea pectinata	+	+	+	9		1	2	12	9
Lupinus latifolius		7	2					+	
Luzula hitchcockii			+	3		+		1	+
Lycopodium sitchense							+		
Mimulus tilingii							+		+
Nothocalais alpestris		+		+			+		
Penstemon davidsonii	13	+	2	+		+			+
Pedicularis racemosa				+					
Phyllodoce empetriformis				1	+	1	1	15	1
Phyllodoce glanduliflora	+					+		+	
Pinus albicaulis			18	3			+	+	
Poa cusickii		1							
Polygonum newberryi		7	1	+		+		+	
Saxifraga ferruginea								+	
Saxifraga tolmiei	+				11	1	1	+	
Selaginella densa						+			
Senecio fremontii						+			
Sitanion hystrix		1	+						
Sorbus sitchensis				2					
Spraguea umbellata		3	1	+				+	

Table II-4 continued.

Species		PEDA	HERB	JUCO PIAL	ABLA TSME	SATO	CASP	CANI	PHEM	LUPE
	Community Type									
<u>Tofieldia</u> <u>glutinosa</u>								+		
<u>Tsuga</u> <u>mertensiana</u>		+	+	+	16		+		2	2
<u>Vaccinium</u> <u>deliciosum</u>				3	21		+	+	3	1
<u>Vaccinium</u> <u>scoparium</u>			6	3		+				
Mosses			+		1	1	3	14	7	1
Total Cover		18	24	56	85	22	29	62	62	27
Diversity		1.6	1.9	2.1	2.8	1.9	2.1	2.1	2.8	2.2

Table II-5. Environmental characteristics of community types on Park Ridge. Different letters indicate factors differing among types at the 95% level (Fisher's Protected LSD). Aspect, snow release date, and soil development were scaled factors. Aspect ranged from 1 = NNE to 5 = SSW. Snow release date ranged from 1 = mid-June to 5 = late August. Soil development ranged from 1 = talus and scree to 5 = well-developed soil profile, high in organic matter. Community types are as follows: PEDA = _Penstemon davidsonii_, HERB = herbaceous, JUCO - PIAL = _Juniperus communis_ - _Pinus albicaulis_, ABLA - TSME = _Abies lasiocarpa_ - _Tsuga mertensiana_, SATO = _Saxifraga tolmiei_, CASP = _Carex spectabilis_, CANI = _Carex nigricans_, PHEM = _Phyllodoce empetriformis_, LUPE = _Luetkea pectinata_.

					Community Type				
Factor	PEDA	HERB	JUCO PIAL	ABLA TSME	SATO	CASP	CANI	PHEM	LUPE
Elevation (m)	2043ab	1983e	2068a	2043ab	2042ab	2022c	1999d	2016c	2014cd
Slope (degrees)	8e	12de	20a	15bc	16bc	11de	10de	11de	13cd
Snow Release Date	1.4d	1.0d	1.4d	1.6d	3.5a	2.5c	3.0b	2.4c	2.4c
Aspect	3.0cd	3.7ab	3.9a	3.1cd	1.8f	2.8d	3.4ab	3.0cd	2.7d
Soil Development	2.2d	3.6b	3.7b	4.5a	3.1c	3.5b	4.5a	4.5a	3.6b

Figure II-1. Detrended Correspondence Analysis (DCA) of high subalpine vegetation on Park Ridge showing the 676 vegetated sample plots in ordination space. A high axis 1 score indicates early date of snow-release (June); a low score indicates late snow-release (August). A high axis 2 score indicates poorly-developed substrates (talus and scree); a low score indicates well-developed soil.
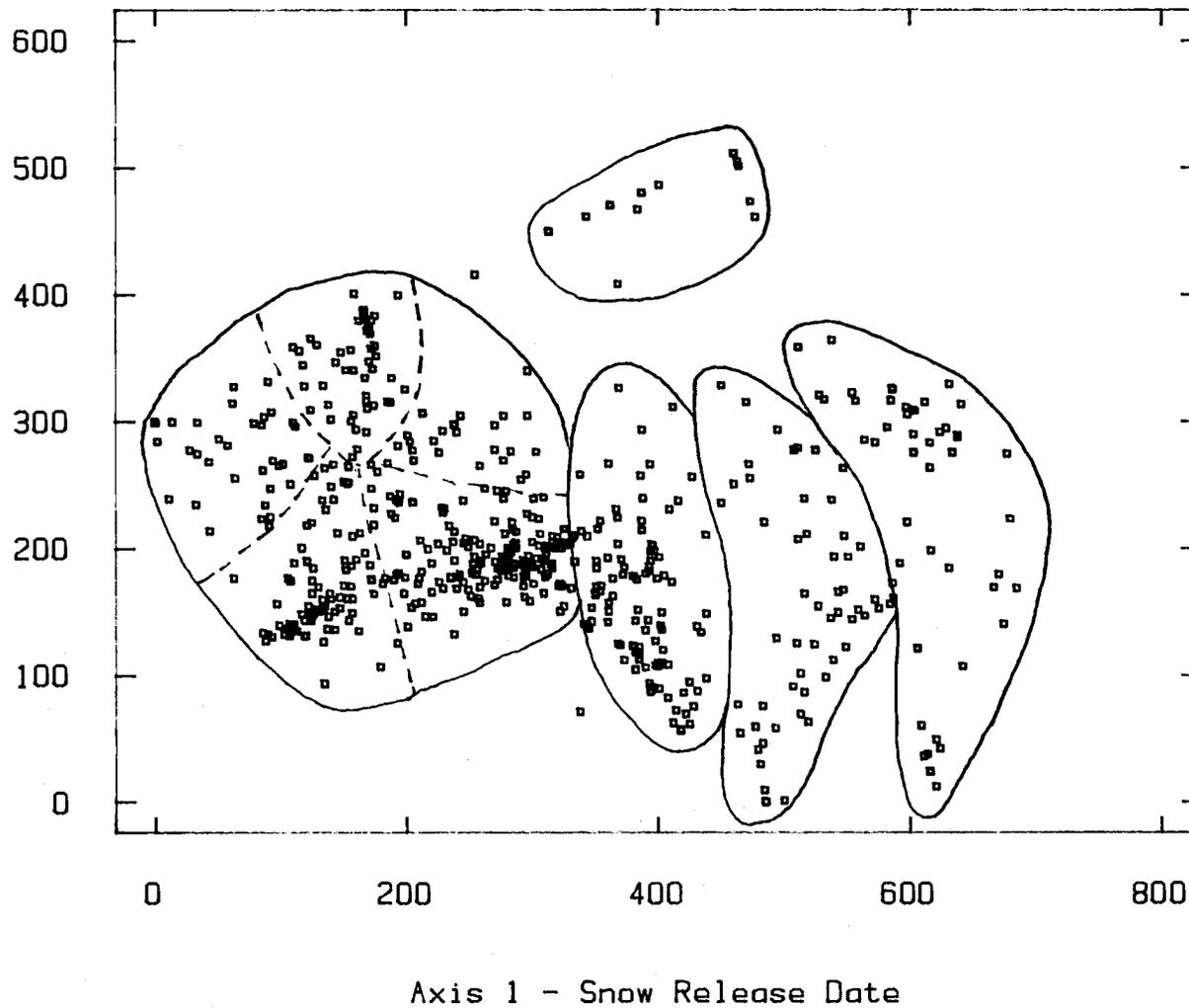
Figure II-1.

Figure II-2. Detrended Correspondence Analysis (DCA) of high subalpine vegetation on Park Ridge showing the major species in ordination space. A high axis 1 score indicates early date of snow-release (June); a low score indicates late snow-release (August). A high axis 2 score indicates poorly-developed substrates (talus and scree); a low score indicates well-developed soil. Species codes are as follows: ABLA = <u>Abies</u> <u>lasiocarpa</u>, ARCA = <u>Arenaria</u> <u>capillaris</u>, ASAL = <u>Aster</u> <u>alpigenus</u>, CABE = <u>Cardamine</u> <u>bellidifolia</u>, CANI = <u>Carex</u> <u>nigricans</u>, CASP = <u>Carex</u> <u>spectabilis</u>, CAME = <u>Cassiope</u> <u>mertensiana</u>, JUDR = <u>Juncus</u> <u>drummondii</u>, JUCO = <u>Juniperus</u> <u>communis</u>, LOMA = <u>Lomatium</u> <u>martindalei</u>, LUPE = <u>Luetkea</u> <u>pectinata</u>, LULA = <u>Lupinus</u> <u>latifolius</u>, MOSS = mosses, PEDA = <u>Penstemon</u> <u>davidsonii</u>, PHEM = <u>Phyllodoce</u> <u>empetriformis</u>, PIAL = <u>Pinus</u> <u>albicaulis</u>, PONE = <u>Polygonum</u> <u>newberryi</u>, SATO = <u>Saxifraga</u> <u>tolmiei</u>, SPUM = <u>Spraguea</u> <u>umbellata</u>, TSME = <u>Tsuga</u> <u>mertensiana</u>, VADE = <u>Vaccinium</u> <u>deliciosum</u>, VASC = <u>Vaccinium</u> <u>scoparium</u>.
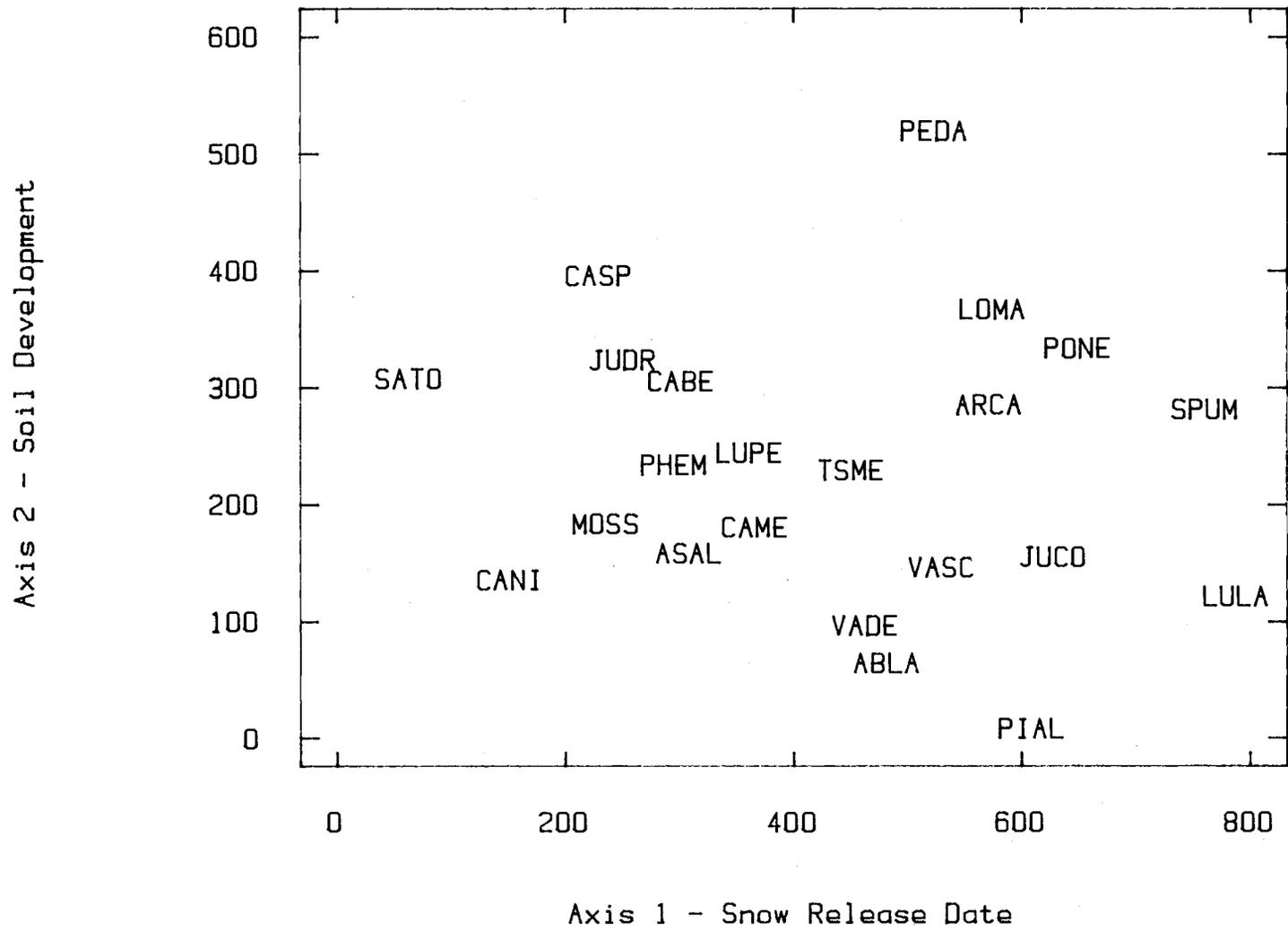
Figure II-2.

Figure II-3. Detrended Correspondence Analysis (DCA) of high subalpine vegetation on Park Ridge showing division into 9 community types based on differential dominance and shifts in species composition. A high axis 1 score indicates early date of snow-release (June); a low score indicates late snow-release (August). A high axis 2 score indicates poorly-developed substrates (talus and scree); a low score indicates well-developed soil. Community types are named after dominant species, as follows: PEDA = <u>Penstemon davidsonii</u>, HERB = <u>Lupinus latifolius</u>, <u>Polygonum newberryii</u> or other herbaceous species; JUCO-PIAL = <u>Juniperus communis</u> - <u>Pinus albicaulis</u>, ABLA-TSME = <u>Abies lasiocarpa</u> - <u>Tsuga mertensiana</u>, SATO = <u>Saxifraga tolmiei</u>, CASP = <u>Carex spectabilis</u>, CANI = <u>Carex nigricans</u>, PHEM = <u>Phyllodoce empetriformis</u>, and LUPE = <u>Luetkea pectinata</u>.
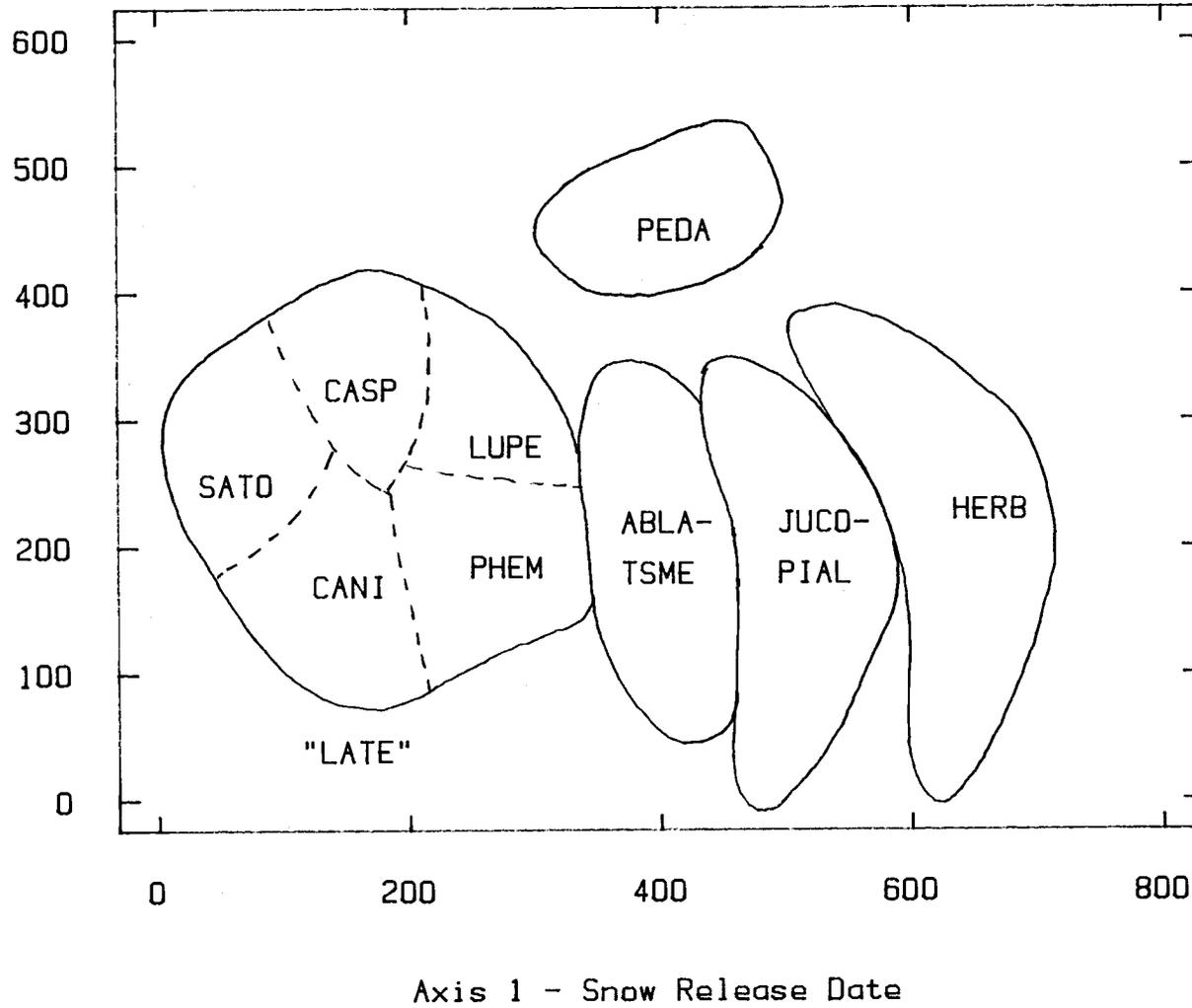
Figure II-3.

CHAPTER III. ALPINE PLANT PHENOLOGY, REPRODUCTION, AND
RECRUITMENT ALONG A LOCAL SNOWMELT GRADIENT

INTRODUCTION

The short growing season of alpine and high subalpine
habitats is widely believed to severely restrict plant
reproduction (e.g., Callaghan and Collins 1976, Jolls and
Bock 1983), and perennial species typically require the
entire growing season to mature fruits and seeds (Jackson
and Bliss 1984). It has been widely assumed that, because
of the low probability of seedling establishment in tundra
environments, vegetative regeneration is the primary means
of recruitment in most populations (e.g., Callaghan and
Collins 1976). The very low rate of seedling recruitment
generally observed in alpine plant communities (e.g.,
Rochow 1970, Douglas 1981) has been attributed to various
factors, including low and/or intermittent flower
production (Rochow 1970, Jackson 1982, Jackson and Bliss
1984) due to late snowmelt (e.g., Holway and Ward 1963) or
soil drought (Bliss 1956, Oberbauer and Billings 1981),
failure of initiated floral buds to expand (Holway and
Ward 1965), scarcity of pollinators or poor weather
conditions for pollination (Holway and Ward 1965, Pojar
1974, Moldenke 1979, Douglas 1981, Galen 1985, Spira and
Pollak 1986), low seed set (Rochow 1970, Bliss 1971,
Oberbauer and Billings 1981, Spira and Pollak 1986), and

high seedling mortality (Griggs 1956, Brink 1964, Bonde 1968, Rochow 1970, Reynolds 1984, Roach and Marchand 1984), or a combination of low reproductive allocation and low rates of germination and seedling establishment (Jolls and Bock 1983). These studies show that the magnitude of flower, fruit, and seed production in tundra habitats is quite variable and can be influenced by a variety of biotic and abiotic factors.

Alpine and high subalpine habitats are characterized by steep environmental gradients, particularly in seasonal duration of snow cover, which controls the length of the growing season and is a primary determinant of vegetation patterns (Chapter II, Billings and Bliss 1959, Canaday and Fonda 1974). While a number of studies have addressed interspecific variations in parameters of reproduction among diverse habitats or along broad-scale environmental gradients such as elevation (e.g., Johnson and Cook 1968, Douglas 1980, Jolls 1980, Kawano and Masuda 1980, Jolls and Bock 1983), very little is known concerning within-population variation in reproduction along local gradients, or whether differential reproductive success influences observed shifts in vegetation patterns along such gradients.

The goal of this study was to investigate patterns of, and constraints on, alpine plant reproduction and recruitment. The approach was to examine reproductive phenology; magnitude of flower, fruit, and seed

production; and seedling emergence and establishment among five coexisting species along a local environmental gradient, the annual date of snow release.

The specific questions addressed in this study were:

1) Do phenological changes along a gradient of duration of snow cover affect flower, fruit, or seed production? Phenologies of alpine and high subalpine species are strongly influenced by the date of snow release (e.g., Canaday and Fonda 1974). Phenology has been shown to affect reproductive success in many habitats, and for a variety of reasons (e.g., Gross and Werner 1983, review in Rathcke and Lacey 1985). Seed set of alpine plants may be limited by local environmental factors (e.g., timing of snow-release) or internal developmental constraints that result in delayed flowering (Bliss 1956, Holway and Ward 1963, 1965; Bell and Bliss 1979, Spira and Pollak 1986). Thus, plants released from snow late in the summer, or having slow reproductive phenology, may be unable to mature fruits and seeds before the end of the growing season. On the other hand, observations of some species suggest that the lengths of phenological stages are compressed where a long duration of snow cover shortens the growing season (Billings and Bliss 1959, Canaday and Fonda 1974, Bell and Bliss 1979). If phenologies are compressed, a second question is, does this compression lead to the production of fewer flowers, fruits, or seeds?

2) Does current reproduction reduce future reproduction? That is, is a year of abundant flower production by an individual followed by a year of low flower, fruit, or seed production? A basic tenet of life history theory is that the high cost of sexual reproduction leads to decreased survival, growth, or reproduction in following years (e.g., Snow and Whigham 1989, Stearns 1989). Data supporting this tenet, however, are few and often inconclusive (Smith and Young 1982, Horvitz and Schemske 1988). An inverse relationship between the components of reproduction (flowering, fruiting, or seed production) in consecutive years may be expected to be a widespread phenomenon among alpine species. Alpine habitats are chronically low in resources (Rochow 1970, Jackson and Bliss 1984) and the magnitude of flowering has been observed to vary considerably from year-to-year (Bliss 1971).

3) Does the presence of surrounding vegetation facilitate seedling establishment? Seedling establishment in alpine habitats has generally been considered a rare event (Osburn 1961, Bonde 1968, Rochow 1970, Bliss 1971), but occasionally seedlings have been observed in abundance (Bliss 1956, 1971; Osburn 1961; Jolls 1980). High seedling mortality in alpine and arctic tundra has been attributed to harsh abiotic conditions, such as soil disturbance from needle ice (Johnson and Billings 1962, Roach and Marchand 1984, Perez 1987) and drought and high

soil surface temperatures (Brink 1964, Ballard 1972). The presence of established vegetation can ameliorate these conditions (Griggs 1956, Brink 1964, Ballard 1972, Loneragan and del Moral 1984, del Moral et al. 1985, Ratcliffe and Turkington 1987). On the other hand, competitive effects of established vegetation may inhibit seedling establishment (Griggs 1956, Bonde 1968, Jolls and Bock 1983, Loneragan and del Moral 1984). Del Moral et al. (1985) found that safe sites for seedling establishment on a dry fellfield were located in association with surrounding vegetation, but safe sites in mesic, more productive areas were located away from established vegetation.

METHODS

Study Site

The study site is located at treeline on Park Ridge
(2100 m elevation; 44 45' N, 121 47'W; Fig. I-1), about 5
km north of Mt. Jefferson, in Mt. Hood National Forest,
Oregon, USA. The area lies within the High Cascades
physiographic province (Franklin and Dyrness 1973) and
straddles the crest of the Cascade Mountains. Park Ridge
is a volcanic plug of Pliocene origin, consisting of
gabbro overlain with basalt and andesite (Thayer 1939).

Park Ridge is diverse in both topography and
vegetation (Chapter II). The site selected for this study
encompasses about 100 ha on the treeless, north-facing
slope of the ridge. Vegetation cover is patchy, and
vegetated areas are interspersed with extensive talus
slopes. Meadows dominated by Carex nigricans or Carex
spectabilis occur on deep, poorly-drained soils released
in mid-late summer. These Carex meadows occur primarily
in snowmelt basins on shallow slopes and support high
vegetation cover. Fellfields occur on sites released
early to mid-season, on shallow to steep slopes, with
coarse, unstable, and poorly-developed soils. Vegetation
cover is very low, and is dominated by rosette- or mat-
forming herbaceous and woody species, including Polygonum

newberryi, Spraguea umbellata, Penstemon davidsonii, and
Luetkea pectinata.

The site is typically covered with snow from mid-
October through June, and snow can fall at any time during
the summer. Outcrops are often snow-free by mid-June,
while other areas remain snow-covered until early- or mid-
August. In order to encompass the full range of length of
growing season, reproduction was studied in microsites
ranging from the outcrops to an area lying at the base of
a permanent snowbank, under snow until August.

Study Species

The following five species were selected for study
because of their high relative cover and/or abundance on
the site (Chapter II), and to represent a variety of
growth forms. Cardamine bellidifolia L. var. pachyphylla
Cov. & Leib. (alpine bittercress)[2] is a small tap-rooted
wintergreen perennial. Carex spectabilis Dewey (showy
sedge) is a tall sedge with short rhizomes and dense,
fibrous roots. Luetkea pectinata (Pursh) Kuntze
(partridge-foot) and Saxifraga tolmiei T.& G. var. tolmiei
(alpine saxifrage) are mat-forming evergreen sub-shrubs.
Phyllodoce empetriformis (Sw.) D. Don (red mountain-

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[2] Study species are hereafter referred to by genus name
only.

heather) is a prostrate evergreen shrub. All five species have widespread distributions from the mountains of Alaska to northern California; _Saxifraga_ and _Carex_ occur in the Sierra Nevada as well. Although the five species have differing abundances along the snow release gradient, all can be found coexisting along most of its length. _Cardamine_, a small rosette, is never dominant, but occurs frequently across the site. _Luetkea_ and _Phyllodoce_ are most abundant on sites released early to mid-summer. _Carex_ dominates the vegetation on well-drained soils on mid-late snowmelt sites, while _Saxifraga_ is frequently the only species found on poorly-developed soils on moist, late snowmelt sites (Chapter II). Together the five study species constitute about 75% of the total vegetation cover on the site.

Little information is available concerning the breeding systems and pollinators of these species. Many high-elevation species are at least partially self-compatible, and are often "cornucopian" in the sense that they attract a variety of pollinators (e.g., Pojar 1974, Moldenke 1979). _Carex_ _spectabilis_ has been reported to be self-compatible (Pojar 1974), and most ericaceous species with urceolate flowers (such as _Phyllodoce_) are considered to be self-compatible (Fryxell 1957). Members of _Saxifraga_ and _Cardamine_ display a wide range of breeding systems, from self-incompatibiliy to autogamy. On the study site, _Cardamine_ _bellidifolia_ and _Saxifraga_ _tolmiei_

appear to be self-compatible, since in both species, fruits were observed to develop and mature on flowers that had only partially opened. Carex spectabilis is anemophilous; the other four species are entomophilous. On the study site, Phyllodoce flowers were observed to be most often visited by hymenopterans, while flies were most commonly observed on Cardamine, Luetkea, and Saxifraga flowers.

Field Methods

During the summer of 1986, six reproductive-sized individuals of each species were selected at random along transects running from the earliest to latest snowfree areas. Each individual was assigned a number and marked with a surveyor's flag for relocation. In 1987, more individuals were added, for a total of 15 individuals of each species. Flags were lost from some individuals during the course of the study, so that sample sizes vary among species and among years. Observations of reproductive phenology were made from 1986 through 1988; and observations of flowering, fruiting and seed production were made in 1988 and 1989.

Phenology

During the summers of 1987 and 1988, weekly
observations were made to determine the date of snow
release for each individual, and its dominant reproductive
phenological stage. A plant was classed as "vegetative"
if no reproductive structures were visible; "floral bud"
if inflorescences had elongated and floral buds were
fully-formed but closed; "flowering" if most flowers were
in anthesis; "fruiting" if most flowers were post-anthesis
and ovaries visibly enlarged; and "dispersed" if most
fruits had shed seeds. An individual was placed in two
classes if no single stage was clearly dominant. In 1987,
the areal cover of each plant was measured. Since
vegetative growth rates were extremely low, the size of
plants was assumed not to change over the duration of the
study.

Reproduction

Estimates of the number of flowers, fruits, seeds,
inflorescences and infructescences were made for each
plant in 1987 and 1988. On each sample date, flowers and
fruits were counted on each individual. To estimate the
total number of flowers and/or fruits on very large
individuals, inflorescences (or infructescences) were
counted, and random subsets of 15 flowers (fruits) per

inflorescence (infructescence) were sampled. For species with multiple-seeded fruits (all species except Carex), a random sample of ten ripe fruits was collected from each plant, returned to the lab, and seeds were counted. On Carex, a random sample of ten female spikes was collected, and the number of achenes on each was counted.

Seedling Establishment

On Park Ridge, fellfield vegetation is located on a moderate slope with coarse, unstable soil, and supports very low plant cover. The Carex meadow, in contrast, occurs in a basin below a permanent snowbank. Soils are relatively deep and stable and vegetation cover is nearly continuous. Preliminary studies were done to compare soil temperatures and occurrence of needle ice in the Carex meadow and the fellfield. Bare soils in the fellfield underwent significantly greater diurnal temperature fluctuations in the top 5 cm than did bare soils in the meadow. In both habitats, high midday temperatures at the soil surface were significantly reduced by the presence of vegetation (Fisher's Protected Least Significant Difference Test, $P < .001$). By noon on clear days, nonvegetated soils reached surface temperatures as high as 43 C, compared with 23 C on vegetated surfaces.

Needle ice is a widespread phenomenon at high elevations, and its formation is facilitated by low

vegetation cover and high soil moisture availability (Lawler 1988), conditions pertaining to the fellfield site in early autumn. The occurrence of soil disturbance by needle ice was assessed by planting toothpicks 1.5 cm deep in the soil in three types of microsites: open soil, bare soil at the edges of overhanging rocks, and vegetation. During late summer 1988 minor needle ice disruption occurred in open microsites in the fellfield. By the end of September, 72% of the toothpicks in open soil, and 31% of the toothpicks around rocks, were overturned in the fellfield. No toothpicks were overturned in vegetated microsites in the fellfield or in any microsite in the meadow, and these microsites showed no other evidence of soil disturbance.

Based on these preliminary results, the following hypotheses were proposed concerning seedling establishment:

1) In the fellfield, seedling establishment will be higher in the presence of surrounding vegetation than in nonvegetated microsites, because soil surface temperatures remain moderate and needle ice disturbance is low.

2) In the Carex meadow, where high temperature and needle ice stresses are reduced or absent, the net effect of surrounding vegetation will be inhibitory, and seedling establishment will be higher in gaps in vegetation.

3) The growth form of the surrounding vegetation will affect seedling establishment: seedling establishment will

be lower within the dense growth form and copious litter
of <u>Carex</u> than within the open prostrate growth form of
<u>Luetkea</u>.

4) Due to the effects of dry soil surfaces on early
snow-release sites, and the short growing season on late-
release sites, seedling establishment will be higher in
the middle of the snow-release gradient than on either of
the extremes.

To test these hypotheses, seeds of each of the five
species were sown in 15 x 15 cm randomly located plots in
each of the following microsites: "open" (bare soil),
"protected" (bare soil at overhanging edges of rocks),
"<u>Luetkea</u>" (mature <u>Luetkea</u> <u>pectinata</u> mats), and "<u>Carex</u>"
(mature <u>Carex</u> <u>spectabilis</u> clumps). Ripe seeds of each of
the five study species were collected in August and
September, 1987, and the seeds were sown in October, in
order to allow them to overwinter in the soil. One-
hundred seeds of a single species (in the case of
<u>Cardamine</u>, 50 seeds) were sown in four replicate plots in
each of the four microsites, for a total of 20 plots per
microsite. This experimental design was repeated in both
the fellfield and meadow at three points (early, mid, and
late) along the snow-release gradient, for a total of 48
plots per species in both the fellfield and the meadow.
Emergence and survival of seedlings in each plot were
monitored throughout the summer of 1988. Contamination of
the experimentally-sown plots by locally dispersed seeds

of the study species was monitored in unsown control plots adjacent to each sown plot. Emergence in the control plots was extremely low; these emergence values were subtracted from emergence values in the adjacent sown plot.

As a check on the experimental results, during late summer of 1988, naturally-occurring first-year seedlings were sampled in 135 15 x 15 cm plots located at random along transects.

Analysis

Phenology

Mean phenostage lengths (snow release to floral bud, bud to flower, flower to fruit initiation, fruit initiation to seed dispersal, and snow release to fruit maturation) were calculated for each of the five species. Differences among species in the length of phenological stages were analyzed by single-factor Analysis of Variance. Fisher's Protected Least Significant Difference test (FPLSD, 95% level) was used to identify those species differing significantly in phenology.

Between-year (1987 and 1988) comparisons of phenostage lengths were made using a t-test for paired comparisons. Correlation analysis was used to examine

within-species changes in phenostage length along the snow release gradient.

Reproduction

The magnitude of each component of reproduction (numbers of inflorescences, infructescences, flowers, fruits, seeds, flowers per inflorescence, fruits per infructescence, and seeds per fruit) was determined for each individual. Measures of proportional maturation (the number of infructescences produced per inflorescence developed, the number of fruits produced per flower developed, and the number of seeds produced per flower developed) were calculated for the components of reproduction.

For each species, the Wilcoxon Signed Rank test was used to compare between-year variations in the components of reproduction. The effects of snow release date and plant size on the components of reproduction and proportional maturation were analyzed using linear regression. Rank correlation analysis was used to assess the effects of flower and fruit production on parameters of reproduction the following year. Total site-wide seed production for each species in 1988 and 1989 was calculated on the basis of seed production of individual plants and total vegetation cover of each species.

Seedling Establishment

A square-root transformation (Conover 1980) was applied to all data on seedling emergence and establishment, and the effects of species differences, microhabitat differences, and gradient position on emergence and establishment were analyzed by three-factor Analysis of Variance (ANOVA). Fisher's Protected Least Significant Difference test (FPLSD, 95% level) was used to identify those factors having significant effects on emergence and establishment.

Potential Number of Offspring

For each species, an estimate of the potential number of offspring produced per parent plant at each reproductive stage (flowering, fruiting, fruit maturation, seedling emergence, and seedling establishment) was calculated, using data from the reproduction study and from the seedling emergence and establishment study. The number of potential offspring per plant at flowering (PO_{fl}), fruit initiation (PO_{fr}), fruit maturation (PO_{mat}), seedling emergence (PO_{em}), and seedling establishment (PO_{est}) were calculated as follows:

$$PO_{fl} = \frac{1}{n} \sum \frac{\text{flowers developed}}{\text{plant area}} \times \frac{\text{seeds}}{\text{fruit}}$$

$$PO_{fr} = \frac{1}{n} \sum \frac{\text{fruits initiated}}{\text{plant area}} \times \frac{\text{seeds}}{\text{fruit}}$$

$$PO_{mat} = \frac{1}{n} \sum \frac{\text{seeds}}{\text{plant area}}$$

$$PO_{em} = PO_{mat} \times \frac{\text{total emergence}}{\text{total seeds sown}}$$

$$PO_{est} = PO_{em} \times \frac{\text{total survival}}{\text{total emergence}}$$

Because only mature seeds, not unfertilized ovules, were counted, PO_{fl} underestimates the number of potential offspring and the post-fertilization values (PO_{fr}, PO_{mat}, PO_{em}, and PO_{est}) overestimate the number of potential offspring.

RESULTS

Phenology

Species Comparisons

Date of snow release along the gradient averaged 25 days later in 1988 than in 1987 (means of July 13 and June 18, respectively). The range in release dates was May 22 - August 1 in 1987 and June 16 - August 18 in 1988). There was no significant difference among species in mean dates of snow release, except <u>Saxifraga</u>, which was released an average of 12 days later than any other species (FPLSD, P < 0.05).

The five species showed significant variation in timing of reproduction and in mean lengths of phenological stages (Table III-1). In general, phenological stages were compressed in 1988 relative to 1987. In <u>Cardamine</u>, <u>Luetkea</u>, and <u>Phyllodoce</u> this compression was statistically significant for one or more reproductive stages (Table III-1). Despite between-year variation, <u>Luetkea</u> was consistently the slowest, and <u>Cardamine</u> and <u>Saxifraga</u> consistently the most rapid, in overall reproductive phenology, while <u>Carex</u> and <u>Phyllodoce</u> showed intermediate phenologies. In 1988, <u>Cardamine</u> and <u>Saxifraga</u> each took about 50 days from snow release to seed maturation and dispersal. <u>Phyllodoce</u> and <u>Carex</u> each required about 68

days, while Luetkea required 75 days to produce mature
seeds.   Luetkea was always the slowest to form floral
buds, requiring nearly 4 weeks from snow release for buds
to become fully formed and inflorescences elongated; at
the other extreme, Cardamine and Saxifraga averaged
slightly over 1 week to develop floral buds. In general,
the time required for the maturation of fruit was quite
long in comparison with other reproductive stages, except
in Luetkea, which underwent a long vegetative stage prior
to budding. Despite differences in phenology, all
individuals of each species matured most or all of their
surviving fruit in all three years of study.

Changes in Duration of Phenostages Along Gradient

Correlation analyses of the effect of within-season
snow release date on the length of reproductive stages in
1987 and 1988 are summarized in Table III-2 and Fig. III-
1. In both years, there was a general tendency toward
compression of reproductive phenology in individuals at
later points on the snow-release gradient. In both years,
Carex and Saxifraga displayed significant compression of
the overall time from snow release to fruit initiation
(1987) or fruit maturity (1988) with later dates of snow
release (Table III-2). For Carex, this compression
resulted primarily from accelerated development of floral
buds; for Saxifraga, other stages were more rapid as well.

In 1988, the overall times required for fruit maturation in _Phyllodoce_ and _Cardamine_ were also significantly reduced at later snow release dates. While _Luetkea_ showed a tendency toward phenostage compression along the gradient, its response was not statistically significant. In 1988, _Saxifraga_ showed a significantly longer bud to flower stage with later snow release, and in _Phyllodoce_, the flowering stage was longer with later snow release (significantly so in 1988).

Reproduction

Comparisons among Species and between Years

The proportion of plants flowering each year over the study period (1987-1989) varied among species. All individuals of _Saxifraga_ and _Carex_ flowered every year. All _Phyllodoce_ and _Cardamine_ individuals flowered in one or more of those years, while nearly one-third of _Luetkea_ plants remained vegetative throughout the study period.

The components of reproduction for these species include both the absolute magnitude of reproduction (i.e., the numbers of flowers, fruits, and seeds produced), the size of reproductive structures (e.g., the number of flowers produced per inflorescence and number of seeds per fruit) and the proportion of inflorescences and flowers

actually maturing into infructescences, fruits (i.e.,
fruitset), and seeds. For some species, the components of
reproduction varied considerably between years (Table
III-3).

While flower production did not vary significantly
between years, the proportion of inflorescences and
flowers that developed into infructescences and fruits
varied considerably among species and from year-to-year
(Table III-3). In Luetkea, infructescence to
inflorescence and fruit to flower ratios were
significantly lower in 1989 than 1988, owing to heavy
grazing of young infructescences by marmots (Marmota
flaviventris). Some additional loss of individual fruits
resulted from lack of fertilization of flowers. These
losses resulted in lower overall fruit and seed production
in Luetkea in 1989. In Saxifraga, all components of
reproduction except the number of flowers and
inflorescences were significantly lower in 1989 than in
1988. While a few infructescences on Saxifraga plants
were removed by marmots, the low infructescence to
inflorescence and fruit to flower ratios in 1989 were
mostly due to abortion of young fruits. On Saxifraga
inflorescences, only the terminal (earliest opening)
flower matured as a fruit and the remainder of developing
fruits were aborted. On some inflorescences, no fruits
completed development. Surviving Saxifraga fruits were
also smaller (contained significantly fewer seeds) than in

1988. These post-anthesis losses resulted in significantly lower total fruit and seed production in 1989. Several components of Carex reproduction were also reduced in 1989 relative to 1988. In both years, the ovaries of Carex were occasionally invaded by a smut (Cintractia sp.), resulting in a minor loss of seeds. In 1989, many Carex spikes withered prior to, or during, anthesis, resulting in low fruit to flower ratios, and the production of fewer seeds overall. Cardamine was the only species to show a significant increase in any component of reproduction in 1989 over 1988. In 1989, fruit to flower ratios were reduced because many developing fruits were aborted. However, those fruits that did mature contained significantly more seeds than in 1988, so that overall seed production did not differ between years. Phyllodoce showed no significant between-year variation in any component of reproduction.

Effects of Reproduction on Subsequent Reproduction

Of the 50 comparisons made between the densities of flower and fruit production in 1988 and selected components of reproduction in 1989, 40 showed positive correlations (Table III-4). Of the eight significant correlations, six were positive. The two significant negative correlations (in Luetkea) were between flower and fruit density in 1988 and fruit set (flower-to-fruit

ratio) the following year. In <u>Saxifraga</u>, between-year relationships were strongly positive: individuals that produced abundant flowers and fruits in 1988 produced abundant flowers, fruits, and seeds the following year.

Effects of Snow Release Date

There were few significant decreases in the components of reproduction with later dates of snow release, despite about a 70-day difference between date of first release and date of last release in 1988 (Table III-5). Although <u>Phyllodoce</u>, at later snow-release dates, produced fewer seeds per fruit, total seed production was not affected. For <u>Luetkea</u>, the components of reproduction were all negatively related to the date of snow release in both years. These negative relationships were statistically significant for the number of flowers and fruits in 1988 and the number of seeds and seed-to-flower ratios in both years. In 1988, <u>Cardamine</u> showed mostly weak to moderate positive responses to later dates of snow release; in 1989, however, its fruit-to-flower ratio was significantly reduced at later dates.

Effects of Plant Size on Reproduction

Larger individuals of all species should have greater magnitude of reproduction than smaller plants, because

they have higher carbohydrate reserves, and should be better able to exploit external resources. In general, this expectation was met, but species differed somewhat in the manner that this greater reproduction was manifested (Table III-6). Within a species, larger individuals produced more inflorescences and flowers than did smaller ones, and this was generally reflected in higher infructescence, fruit, and seed production. Larger individuals of Luetkea (which has indeterminate inflorescences) not only produced more inflorescences and infructescences, but inflorescences and infructescences were larger (contained more flowers and fruits) as well. The weak correlation between the size of Saxifraga individuals and fruit and seed production in 1989 is likely due to the abortion of developing fruits. In Luetkea the weak 1989 correlations are probably due to the effects of marmot predation. While densities of inflorescences, flowers, fruits, and seeds tend to be positively related to plant size, fruit to flower and seed to flower ratios (except in Luetkea) were only weakly related. In fact, in 1989, the relationship between plant size and fruit to flower ratio was significantly negative for Luetkea.

Seed Production

Overall seed production of each of the five species varied considerably among species and between years (Table III-7). The seed production of <u>Cardamine</u>, <u>Carex</u>, <u>Luetkea</u>, and <u>Saxifraga</u> declined dramatically between 1988 and 1989. The most dramatic decline was in <u>Saxifraga</u>, which produced nearly 200,000 seeds/m^2 of plant cover in 1988, but only about ten percent of that in 1989. <u>Phyllodoce</u> was the only species for which 1989 seed production was greater than in the previous year: the number of seeds produced was nearly double that in 1988.

Because both total vegetation cover and cover of the five study species on the study site is quite low, seed production on a site-wide basis is much lower than on the basis of plant cover (Table III-7). However, the average total annual seed input to the site of nearly 6000 to 8000 seeds/m^2 is still much larger than the density of naturally-occurring seedlings (Table III-7).

Seedling Establishment

At both the fellfield and meadow sites, seedling emergence from sown seeds was extremely low (Table III-8). Of 21,600 seeds sown, a total of 60 seedlings of the study species emerged in the <u>Carex</u> meadow, and only two survived

the first growing season. Of the 83 emergents in the
fellfield, 42 survived the first growing season. Species
and microsite differences had significant effects on
emergence in both the meadow and fellfield (Table III-9).
In the fellfield, emergence and survival of Cardamine was
significantly greater than that of any other species (Fig.
III-2). Saxifraga did not emerge under any microsite
conditions in the meadow. In the fellfield, overall
seedling emergence was significantly higher in the
abiotically-protected (edges of overhanging rocks)
microsite than in any other. Survival through the first
growing season was higher in the abiotically-protected and
Luetkea mat microsites than in others but the difference
was not statistically significant (Table III-9). In the
meadow, emergence was significantly higher in open
microsites than in other types. Position on the snow-
release gradient significantly influenced emergence in the
meadow (Table III-9, Fig. III-2). Emergence in the mesic
meadow declined with later dates of snow release. The
significant two-way interactions between microsite and
snow-release date on emergence and establishment in the
fellfield resulted from the fact that, in the late-release
plots, emergence and establishment were higher in the
abiotically-protected microsite than in any other. In the
meadow, a significant microsite by species interaction
resulted from high emergence of Luetkea, Carex, and
Cardamine in open microsites.

Potential Number of Offspring

In <u>Cardamine</u>, <u>Carex</u>, <u>Luetkea</u>, and <u>Saxifraga</u>, the greatest proportional rate of loss in potential offspring as indicated by the slopes of the curves in Fig. III-3, occurs between fruit maturation (and dispersal) and seedling emergence. In <u>Phyllodoce</u>, the greatest rate of loss occurs between seedling emergence and establishment. Reproductive losses prior to seed dispersal, although they sometimes significantly reduced seed production, were minor in magnitude when compared to these post-dispersal seed losses.

DISCUSSION

Phenology

Significant between-year variation in the length of one or more phenological stages in Cardamine and Phyllodoce (Table III-1) suggests that the phenologies of these species respond strongly to external environmental cues. In contrast, while Luetkea reached anthesis significantly faster in 1988 than 1987, its consistently long period of vegetative growth prior to formation of floral buds and elongation of inflorescences suggests that genetically controlled developmental constraints during pre-reproductive phases influence its phenology. According to Mooney and Billings (1960), early-flowering tundra species rely on previously-assimilated carbohydrates to initiate growth while still under snow, but later-flowering ones may rely more on current-year carbohydrate assimilation for the development of flowers. Cardamine and Saxifraga consistently flowered rapidly, with anthesis slightly over a week following snowmelt; Carex inflorescences developed concurrently with vegetative growth (Table III-1), indicating that these three species utilize stored reserves to develop flowers. Although Luetkea utilizes energy reserves from the previous year to initiate floral primordia, its long period of vegetative growth prior to flowering suggests

that this species depends on current year assimilates to complete bud and flower development. Reliance on current photosynthate may be a reason for the intermittent flowering observed in Luetkea. Species utilizing stored reserves to flower may be more buffered from short-term fluctuations in environmental conditions affecting productivity.

The position of an individual plant along the gradient of snow-release influenced its reproductive phenology and, in some cases, reproductive output. The reproductive phenologies of all five species were strongly compressed with later dates of snow-release; for all species except Luetkea, this relationship was highly significant (Table III-2, Fig. III-1). What factors might be responsible for this observed compression in phenology? Intra-population differences in flowering times have been demonstrated elsewhere (e.g., Gross and Werner 1983, Brown et al. 1985) and phenological variation among individuals with respect to the timing of snow release has previously been observed (e.g., Billings and Bliss 1959, Holway and Ward 1965). Floral bud initiation and flowering of a number of alpine species is influenced by photoperiod (e.g., Billings and Mooney 1968). On Park Ridge, photoperiod control cannot explain the faster bud and flower development observed on late snowmelt sites, as these rapid-flowering plants experienced shorter daylengths when released from snow in August than did

plants released in June. Heat sum effects (interaction between photoperiod and temperature) also cannot explain this phenological compression, as not only were days shorter in August than in June, but mean temperatures were lower as well. In addition, the fact that plants released from snow later in the season matured their fruits significantly later than early-released plants argues against tight photoperiodic control of overall reproductive phenology.

Other possible sources of these intra-population phenological differences include variation in environmental conditions among microsites (e.g., Jackson 1966) and genetic determinants (e.g., McMillan and Pagel 1958, Rathcke and Lacey 1985). For environmental induction of phenological compression to occur, microsite conditions must vary along the gradients and species must respond to these conditions. Environmental factors such as soil moisture and temperature typically change along alpine snow-release gradients, and low soil moisture availability may exert stress on plant growth and reproduction on early snowmelt sites in the Rocky Mountains (Billings and Bliss 1959, Scott and Billings 1964, Ehleringer and Miller 1975, Oberbauer and Billings 1981). In the coarse volcanic soils of the Cascade Mountains, however, moisture stress gradients are likely to be less severe. While shallow-rooted plants may experience moisture stress, soil water potentials at

depths greater than 20 cm remain high throughout the season, due to deep water penetration, low evaporation rates, and reduced transpiration losses due to low plant cover (Chapin and Bliss 1988). Soil temperatures on late snowmelt sites probably remain lower during the growing season than on early release sites (e.g., Holway and Ward 1965), because of chilling from cold snow-melt water.

Such changes in environmental conditions may exert a strong influence on phenology. Species clearly display individualistic phenological responses to position along snow release gradients. For example, Billings and Bliss (1959) and Holway and Ward (1965) noted that the phenologies of some species were compressed with later dates of snowmelt. Holway and Ward (1965) reported that a few species (e.g., Geum turbinatum) budded faster in microsites with late release, but most species underwent more rapid expansion of floral buds in microsites released from snow early in the summer. Phenology of Caltha leptosepala is more rapid in mid-snow release microsites than in early or late ones, which Rochow (1969) attributed to accelerated growth in the presence of plentiful soil moisture, adequate temperature, and a moderately long growing season. While the phenology of Carex spectabilis has elsewhere been reported to be unaffected by timing of snow release (contrary to the results of this study), that of Carex nigricans, a dominant species on late snow-release sites, is compressed (Canaday and Fonda 1974).

Response of flowering phenology to timing of snow release may be influenced by differential species abilities to absorb water at low soil temperatures (Holway and Ward 1965). This ability may be enhanced by high concentrations of soluble carbohydrates in roots (Billings and Mooney 1968) or by an abundance of roots in the warmer upper portion of the soil (Holway and Ward 1965). On Park Ridge, _Saxifraga tolmiei_ is often found on wet microsites released very late in the summer, and is less abundant on drier, early snow-release sites (Chapter II). Because of its shallow root system, it probably depends on the availability of near-surface soil moisture and hence its reproductive phenology may be slowed by low soil moisture on early snow-release microsites.

Flower initiation and development in the alpine herb _Geum turbinatum_ is inhibited by root-zone temperatures greater than 15 C (Spomer and Salisbury 1968). On the other hand, the reproductive phenology of other species is delayed by irrigation with snow-melt water, which reduces soil temperatures (Holway and Ward 1963). Flowering in high altitude populations of _Poa alpina_ is significantly reduced at higher experimental temperatures (Hermesh and Acharya 1987), and Billings and Mooney (1961) suggested that, for _Oxyria digyna_ and other tundra species, high summer air temperatures may determine their lower altitudinal limits.

If the hypothesis is valid that differential species responses to microsite conditions control their phenological patterns along the snow-release gradient, it still cannot fully explain the patterns observed among these five species. If, as Rochow (1969) suggested, acceleration of phenology is positively correlated with microsite favorability, then these species (except possibly, Luetkea) would be expected to be more abundant on later snow-release sites. Luetkea and Phyllodoce are abundant (indeed dominate the vegetation) on microsites released early in the summer (Chapter II) and decline considerably in importance on sites released late in the season, suggesting that both species find their ecological optima on early snow-release sites. In addition, despite their phenological compression (moderate in Luetkea), Luetkea produced significantly fewer flowers, fruits and seeds on late snowmelt microsites (Table III-5), and Phyllodoce produced fruits with fewer seeds (although overall seed production was not significantly reduced). Thus, late snow-release sites do not appear to be relatively favorable for Luetkea and Phyllodoce. Of the other species with compressed phenologies, both Carex and Cardamine are abundant along nearly the entire length of the snow-release gradient. Saxifraga is the only species that might be considered to find very late snow-release microsites the most favorable for growth.

High intra-population genetic differentiation, in response to strong selection pressure exerted by shifts in environmental conditions along the snow-release gradient, is also possible (e.g., Holway and Ward 1965). Plants at high elevations typically show more rapid initiation of vegetative growth, bud expansion and flowering than conspecific populations at lower elevations (Billings and Mooney 1968, Rochow 1970, Chabot and Billings 1970, Kawano and Masuda 1980, but see Hermesh and Acharya [1987]) Alpine snowbank species often initiate growth at air and soil temperatures little above 0 C, sometimes even while still covered with snow (Billings and Bliss 1959, Bliss 1971). This accelerated onset of growth and reproduction has been attributed to selection for rapid reproduction in response to a short growing season (Bliss 1971, Kimball et al. 1973). In Alaska, distinct ecotypes of <u>Dryas</u> <u>octopetala</u>, differing in their degree of phenotypic plasticity, occurred only a few meters apart along a local snowmelt gradient (McGraw and Antonovics 1983). Delayed flowering of plants in a snowbed habitat relative to those in a fellfield reduced pollen flow between the two populations, and was suggested to be a primary factor maintaining ecotypic differentiation in <u>Dryas</u>. Similarly, on Park Ridge, the complete lack of overlap between periods of anthesis of individuals at opposite ends of the gradient effectively eliminates the possibility of cross-pollination among them. This suggests that there is

opportunity for genetic differentiation in phenology in response to microsite conditions, since the timing of flowering can respond rapidly to selection (e.g., Paterniani 1969).

Reproductive Trade-offs

The concept of reproductive trade-offs has played a major role in life history theory (Stearns 1989). It has been widely assumed that flower and fruit production entail significant demographic costs. Studies attempting to assess these presumed demographic costs, however, have yielded variable results. Flower and fruit production can result in decreased subsequent growth (e.g., Eis et al. 1965, Law 1979, Sohn and Policansky 1977, Snow and Whigham 1989), survival (Smith and Young 1982), and reproduction (e.g., Montalvo and Ackerman 1987). However, such effects are not universal (Horvitz and Schemske 1988). In the current study, vegetative growth was not assessed, but reproduction clearly had no effect on the short-term survival of individuals. There was no mortality of monitored adults during the 3-year period, and overall adult mortality on the study site was observed to be extremely low.

The magnitude of reproduction varied greatly between years for most species (Table III-3), but for four of the

five species, the correlations between 1988 and 1989
parameters of reproduction were mostly moderately to
strongly positive (Table III-4). These results indicate
that either differences in microhabitat quality or genetic
variability among individuals had more important effects
on reproduction than did the costs of previous
reproduction.

In _Luetkea_, flowering was intermittent year-to-year,
and individuals that produced abundant flowers and fruits
in 1988 showed significantly reduced fruit set (fruits per
flower) in 1989 (Table III-4). However, factors other
than demographic costs of reproduction, including
variation in abiotic or biotic factors affecting
reproduction, may have contributed to this negative
correlation. In _Luetkea_, the number of flowers produced
in 1988 and the number produced in 1989 showed a moderate
positive correlation, suggesting that plants in more
favorable microsites produced more reproductive structures
year-to-year. However, there was a significant negative
correlation between flower and fruit production in 1988
and fruit set (fruits-to-flower ratios) in 1989. Fruit
predation by marmots is often selective (Holway and Ward
1965) and can vary considerably in intensity from year-to-
year (Spira and Pollak 1986). On Park Ridge, both year-
to-year variability in grazing intensity and selectivity
in grazing were apparent. In 1988, marmot predation of
Luetkea inflorescences was negligible. In 1989, however,

some individuals of <u>Luetkea</u> lost most or all of their infructescences to marmots, while neighboring plants were not grazed. Marmots appeared to prefer individuals with conspicuous flower and fruit displays (personal observation); thus, predation intensity in 1989 may have increased with increasing inflorescence densities. If plants with high densities of flowers and fruits were more vulnerable to severe predation by marmots, negative correlations between years in flowering, fruiting and fruit to flower ratios could result from a combination of density-dependent predation and variability in predation between years. This is supported by the significant negative correlation between plant size and fruit-to-flower ratios in <u>Luetkea</u> in 1988 (Table III-6).

As Horvitz and Schemske (1988) point out, negative year-to-year correlations among the components of reproduction do not demonstrate that reproduction in a given year results in reduced reproduction the following year. Nor do positive correlations indicate the absence of such reproductive costs. Correlative analysis demonstrates only the combined (net) effects of a variety of biotic and abiotic factors that influence the components of reproduction. For all the study species except <u>Luetkea</u>, however, the evidence indicates that the net effect of other factors, such as microsite favorability, outweighs the possible costs of reproduction

in determining the patterns of reproduction observed among individuals.

Fruit-to-Flower Ratios

Angiosperms regularly initiate far more flowers than they produce mature fruits (Stephenson 1981, Sutherland 1986, Stephenson and Winsor 1986, Wiens et al. 1987). Low fruit set in many species has been attributed variously to maternal adjustment of reproduction (e.g., due to risks from pollination failure, herbivory, predation, or limited resources (Lloyd 1980, Stephenson 1981, Montalvo and Ackerman 1987, Stock et al. 1989), to uncoupling of the functions of flowers and seeds (e.g., pollinator attraction vs. propagule dispersal [Stephenson 1979, 1981; Sutherland 1986]), and to genetic factors (including genetic load or developmental selection [Stephenson and Winsor 1986, Wiens et al. 1987]). There has been considerable discussion of the factors actually limiting fruit set in a wide variety of species (e.g., Stephenson 1980, 1981; Wiens et al. 1987, Charlesworth 1989, Ayre and Whelan 1989). Stearns (1976) proposes that low fruit to flower ratios can result from a "bet-hedging strategy", an hypothesis resting on the assumption that resource availability fluctuates through time and that the production of "surplus" flowers allows individuals to

capitalize on years when conditions are favorable for maturation of fruits and seeds.

Low fruit-to-flower ratios might be expected to be a widespread phenomenon in plants at high elevations for two reasons. First, abundance of insect pollinators may be low in comparison with other habitats, or weather conditions may restrict pollinator activity (e.g., Moldenke 1979). Dense floral displays may be selected for in order to attract scarce insect pollinators (e.g., Waser 1983), with little chance that all flowers will be pollinated and mature as fruits. Second, because alpine plants generally initiate floral primordia at least one year prior to fruit maturation, resource availability during these two stages is likely to differ. The relative roles of stored versus current year assimilates in fruit maturation are poorly understood (Rathcke and Lacey 1985). Clearly, alpine species with preformed flower buds or very rapid development of flowers (e.g., Cardamine and Saxifraga) must rely on stored assimilates to complete these stages. However, these species may still rely on current-year assimilate to actually mature their fruits, and the long time interval between floral initiation and fruit maturation is expected to increase the unpredictability of fruit set (Sutherland 1986), because of year-to-year variation in the availability of resources. For example, Catalpa speciosa initiates fruits before it has the resources available to mature them,

resulting in variable fruit set (Stephenson 1980).
Indeed, high flowering but low seed set has often been
observed in alpine species, such as Thlaspi alpestre
(Rochow 1970). For the species in this study, flower
production did not vary significantly between 1988 and
1989 (Table III-3). Fruit-to-flower ratios in 1988 were
at the high end of ranges provided by Sutherland (1986)
[.65 for herbaceous perennials, .29 for woody plants], but
for all species except Phyllodoce, fruit to flower ratios
were significantly lower in 1989 (Table III-3). This
year-to-year variability suggests that, while flowering
may remain relatively constant year-to-year, fruit
maturation can be resource-limited for these species. The
variability in fruit set among years also indicates the
importance of more than one year of study in assessing
fruit to flower ratios and the potential factors
controlling fruit set.

Seedling Establishment

The hypotheses concerning seedling establishment
were, for the most part, rejected. The first hypothesis
was that surrounding vegetation would facilitate seedling
establishment in the fellfield. Seedling emergence was
significantly higher in abiotically-protected microsites
than in any other microsite, including vegetation (Fig.

III-2). Survival through the first summer was also highest in this microsite (P = 0.054, Table III-9). In abiotically-protected microsites, seedlings were partially shaded, somewhat protected from drought, and needle ice was minimal. Although seedling establishment was slightly higher in Luetkea mats than in open soil microsites, there was no clear evidence for biotic facilitation. The second hypothesis, that surrounding vegetation would inhibit seedling establishment in the meadow, was partially supported. Seedling emergence was significantly higher in bare microsites than in any other. However, very few seedlings survived the first growing season, so that the overall effects of vegetation on seedling establishment could not be assessed.

Hypothesis 3, that Carex vegetation would inhibit establishment more than would the open growth form of Luetkea, was not supported. While emergence and establishment of seedlings in the fellfield was higher in Luetkea than in Carex, the differences were not significant. Previous studies have shown varied responses of seedling establishment to the presence of vegetation. In British Columbia, seedling survival was higher in moss cushions than on bare soil, because of reduced soil disruption from needle ice (Brink 1964). However, Bonde (1968) found low rates of seedling survival in established cushion plants; he attributed high seedling mortality to competition for light, water, and nutrients. Del Moral et

al. (1985) found that adults of graminoid species
(especially _Carex_ _spectabilis_) inhibited establishment of
most other species. On Park Ridge, although seedling
emergence was highest in open sites away from meadow
vegetation, seedling survival through the first growing
season did not differ between vegetated and open
microsites.

Microsite conditions are highly variable in alpine
environments, and small-scale differences in the abiotic
environment may be extremely important to seedling
establishment (e.g., Osburn 1961, Bliss 1971, Jolls 1980,
del Moral 1985). Because rocks can reduce soil heaving
from needle ice, and may provide shade and more favorable
moisture conditions, seedlings may establish better in
such microsites. In Andean alpine vegetation, Perez
(1987) observed that, while seedlings established around
large stones and in cushion plants, stones provided the
most favorable microsites. On Park Ridge, abiotically-
protected microsites provide similar advantages to
germinating seedlings as do mat-forming vegetation:
partial shade, reduced soil surface temperatures, and
minimal soil disruption from needle ice formation.
However, vegetation can also exert inhibitory effects on
seedlings. For example, meadows dominated by _Carex_
spectabilis are competitive environments providing
few refuges for the establishment of seedlings (del Moral
1985). Transpiration from established alpine vegetation

can severely deplete soil moisture and result in highly
negative soil water potentials at mid-day (Oberbauer and
Billings 1981, Douglas and Bliss 1977). Thus, the
inhibitory effects of established vegetation on seedlings
may counterbalance or outweigh any amelioration of the
harsh abiotic environment, limiting seedling emergence and
establishment to microsites protected from abiotic
stresses, but lacking in competition.

Hypothesis 4, that emergence and establishment would
be higher at mid-points along the snow-release gradient,
was rejected. In the meadow, emergence was highest at the
early end of the gradient, and declined with later release
dates. In the fellfield, emergence and establishment
increased with later snow-release dates (but not
significantly so). This response may result from the fact
that, on the dry fellfield, the late snow-release plots
tended to be located on slight slope concavities, where
soil moisture may have been greater. The meadow was
released from snow later than the fellfield, and was
located in a topographically uniform basin beneath a
snowfield. However, the reduced length of the growing
season cannot explain the trend of decreasing seedling
emergence in the meadow at later positions along the
gradient (Fig. III-2).

The combined effects of differences among species in
rooting depth and drought tolerance may explain patterns
of seedling establishment among species. Root growth

rates vary considerably among alpine species (Roach and Marchand 1984). In some species, such as _Oxyria digyna_, shoots grow very slowly during the first year, but root growth is extremely rapid (Billings and Mooney 1968). Seedlings with rapid root growth are relatively insulated from short-term fluctuations in soil surface temperatures and moisture during the first growing season and are the only species capable of colonizing open, frost-disturbed soils (Roach and Marchand 1984). Soil disruption from needle ice can be a primary cause of seedling mortality in some alpine habitats (e.g., Brink 1964, Soons 1967), and Brink (1964) suggested that seedlings can establish only in microsites with continuous soil moisture supply and lack of cryopedogenic disturbance. On the Park Ridge fellfield, however, most seedlings died before the first occurrence of needle ice in the autumn. Surface temperatures over 80 C have been recorded in alpine soils (Tranquillini 1964) and high surface temperatures can be an important factor reducing seedling establishment (Brink 1964, Ballard 1972). On subalpine sites in British Columbia, bare soil surfaces repeatedly reached temperatures lethal to tree seedlings, while temperature amplitudes were considerably less on vegetated surfaces (Ballard 1972). Despite high moisture availability in deeper soils in the Cascade Mountains, the upper layers of these volcanic soils can attain very low water potentials (Horn 1968, Chapin and Bliss 1988) and high temperatures.

Horn (1968) attributed the very low rate of revegetation on a pumice soil to dry soil surfaces and high diurnal temperature flux. On Park Ridge, while drought stress may have little effect on growth or reproduction of adult plants, it may have a significant impact on patterns of seedling establishment, among both species and microsites. For example, Cardamine, a tap-rooted perennial, germinates rapidly, has relatively large cotyledons, and has roots that grow rapidly during the first growing season. This rapid growth probably aids in tapping subsurface moisture and helps to stabilize seedlings when soil is disrupted by the formation of needle ice. Cardamine not only had the highest rate of seedling emergence and establishment and the highest establishment to emergence ratio in the experimental study, it was the most abundant seedling to occur under natural conditions as well (Tables III-7 and III-8). Despite these seedling growth characteristics improving its chances of establishment, even Cardamine established best in abiotically-protected microsites.

Loss of Potential Offspring

Because of the magnitude of post-dispersal, pre-emergence losses (Fig. III-3) and the lack of safe sites for emergence and establishment (Table III-8), pre-dispersal losses of potential offspring from abortion and

predation may be negligible in overall importance to the
population dynamics of these species. The impact of seed
losses (through lack of fertilization, abortion, or seed
predation) on overall population dynamics may depend on
the density of safe sites for seedling establishment. If
very few safe sites are available, such losses may have
little or no impact on recruitment (Andersen 1989).
Recruitment in populations of long-lived perennial plants,
in particular, may often be limited more by the
availability of safe sites than of seeds (e.g., Miles
1972, Peart 1989, Andersen 1989). On the other hand, if
the probability of a dispersed seed landing in a safe site
is very small (e.g, if safe sites are widely scattered
through space or time and dispersal is not directed [sensu
Howe and Smallwood 1982) the more seeds that an individual
produces, the greater the chance that a few seeds will
land in safe sites. Thus, it is difficult to assess the
impact of pre-germination seed losses to the overall
population dynamics of long-lived perennial species such
as were studied here. Searches for seedlings of these
species over a four-year period suggest that, at least for
Luetkea and Phyllodoce, seedling establishment occurs very
infrequently; first-year seedlings of both species always
failed to survive the first summer, and second-year plants
were never found. In addition, there are very few small
(i.e., several-year-old) individuals of these species on
the study site. Still, summers of greater cloud cover or

higher than normal precipitation may occasionally provide conditions suitable for abundant seedling establishment on Park Ridge.

Overall seed production of these species (except for Cardamine) was much higher than their occurrence as seedlings on the site (Table III-7). What are the fates of these seeds? Seeds could be lost by high overwintering seed mortality, remain dormant in the soil, or die immediately after germination. Amen (1966) attributed infrequent seedling establishment of alpine species to high mortality of overwintering seeds. Roach and Marchand (1984) found two peaks of seedling mortality during the first year: immediately after germination and following the first autumn frost, which uprooted seedlings. Since Park Ridge is covered with deep snow throughout the winter, high overwintering mortality seems unlikely; temperatures under snow remain fairly constantly around freezing, and rates of respiration and microbial decay are probably very low (McGraw and Vavrek 1989). The seeds of relatively few alpine species appear to have innate dormancy mechanisms (Amen 1966, Bliss 1971, Chabot and Billings 1971, Marchand and Roach 1980). According to Billings (1974), the seeds of alpine species do not germinate readily at low temperatures or low soil moisture, and dormancy may be environmentally-enforced. The seeds of all five of the Park Ridge study species germinated readily at 20 C in the laboratory without

pretreatment. In the field, the seeds of these species may not experience the necessary combinations of adequate soil moisture and temperature to germinate, because, in most microsites, soil surfaces dry out quickly following snowmelt. Thus, many seeds may remain in an environmentally-enforced dormant state.

For seeds that do germinate, high rates of seedling mortality soon after germination may account for much of the seed losses in these species. The period immediately after germination is typically a critical time for seedling survival (Harper 1965, 1977), and seedlings on Park Ridge face extremely harsh abiotic conditions in the microenvironment of the soil surface. While subsurface soils can remain moist through most of the summer, surfaces dry rapidly after snowmelt, and soil drought (and perhaps, lethal soil surface temperatures) probably causes most seedling mortality for these species. The fact that Cardamine, with its rapid root growth, has the highest rate of seedling establishment among the five species, supports the idea that most seedlings of the other species succumb to drought soon after germination.

Table III-1. Length of reproductive phenological stages in 1987 and 1988. Values shown are mean stage lengths (days). Letters differing across rows indicate that stage length differed significantly among species (FPLSD, 95% level; log-transformed data). Asterisks indicate that the mean length of that phenostage differed significantly between years (t-test for paired comparisons).

1987

Stage	Cardamine	Carex	Luetkea	Phyllodoce	Saxifraga
Release-bud	9a	17ab	26b	**17ab	10a
Bud-flower	**11a	11a	**19a	11a	9a
Flower-fruit	*13a	18a	16a	13a	12a
Release-fruit	35a	46ab	61b	**41ab	31a

1988

Stage	Cardamine	Carex	Luetkea	Phyllodoce	Saxifraga
Release-bud	9a	11a	27b	8a	8a
Bud-flower	6a	8a	9ab	13b	7a
Flower-fruit	5a	23d	15c	9ab	10ab
Fruit-maturity	31ab	25a	22a	39b	25a
Release-fruit	20a	41b	52b	31a	26a
Release-maturity	51a	66b	75b	70b	51a

*: 0.01 < P < 0.05; **: 0.001 < P < 0.01

Table III-2. Correlation between phenostage length (in days) and dates of snow release in 1987 and 1988. Values shown are Pearson correlation coefficients. A negative coefficient denotes that the length of that stage decreased with later dates of snow release; a positive coefficient denotes that the length of the stage increased. Absence of coefficient indicates that sufficient data were not recorded for that stage. n = the number of reproductive individuals monitored of each species.

1987

Stage	Cardamine n = 5	Carex n = 11	Luetkea n = 4	Phyllodoce n = 12	Saxifraga n = 12
Release-bud		-.83 **	-.73	-.75 **	-.74 **
Bud-flower		.27	.81	.24	-.36
Flower-fruit	-.16	-.51		.59	-.72 **
Release-fruit	-.24	-.76 **		-.61	-.89 **

1988

Stage	Cardamine n = 10	Carex n = 14	Luetkea n = 7	Phyllodoce n = 12	Saxifraga n = 14
Release-bud	-.64 *	-.80 **	-.82 *	-.45	-.65 *
Bud-flower	.29	.01	.13	-.47	.76 **
Flower-fruit	.75	-.20	.05	.79 **	.32
Fruit-maturity	-.66	-.11	-.59	-.58	-.71 **
Release -maturity	-.87 **	-.93 ***	-.75	-.92 ***	-.93 ***

*: $0.01 < P < 0.05$, **: $0.001 < P < 0.01$, ***: $P < 0.001$

Table III-3. Comparison of components of reproduction (mean densities per 100 cm2) and ratios of densities between 1987 and 1988. Asterisks indicate that densities differed significantly between years (Wilcoxon Signed Rank Test).

	Species				
	Cardamine	Carex	Luetkea	Phyllodoce	Saxifraga
Number of inflorescences					
1988	25.8	6.2	1.1	5.5	15.6
1989	14.6	5.4	2.6	8.2	10.2
Number of infructescences					
1988	21.5	5.5	1.1	5.3	14.4 **
1989	13.8	4.3	0.9	8.1	5.6
Number of flowers					
1988	112.7	718.3	13.3	32.6	39.2
1989	56.5		20.8	51.6	30.3
Number of fruits					
1988	75.0	627.3 **	8.0 *	31.0	27.5 **
1989	30.4	156.3	2.1	49.0	5.7
Number of seeds					
1988	568.5	627.3 **	116.4 *	2592.9	1932.2 **
1989	353.5	156.3	27.2	4836.8	230.1
Infructescences per inflorescence					
1988	.91	.91	.99	.94	.91
1989	.93	.75	.42 ***	.95	.45 ***
Fruits per flower					
1988	.66	.90	.57	.94	.75
1989	.38 *	.20 ***	.26 **	.86	.18 ***
Seeds per fruit					
1988	7.4	---	13.0	91.3	70.1
1989	11.4 **	---	12.6	68.4	41.5 ***
Seeds per flower initiated					
1988	4.9	0.9	7.4	85.0	55.0
1989	5.1	0.2 ***	2.2 ***	60.0	32.1 ***

*: 0.01 < P < 0.05; **:0.001 < P < 0.01

Table III-4. Correlations between 1988 flower and fruit density (number/cm^2) and 1989 components of reproduction. Values shown are Spearman Rank Correlation Coefficients. A positive coefficient indicates that the value of that component in 1989 increased with a higher density of flowers or fruits in 1988; a negative coefficient indicates that the value of that component decreased.

	Species				
	Cardamine	Carex	Luetkea	Phyllodoce	Saxifraga
FLOWER DENSITY 1988					
Flower density 1989	.39	.60 *	.45	.42	.63 **
Fruit density 1989	.44	.31	.42	.43	.57 *
Fruits per flower 1989	.20	.19	-.57 *	-.20	.09
Seed density 1989	.43	.41	.37	.37	.58 *
Seeds per flower 1989	.12	.04	.24	.16	.17
FRUIT DENSITY 1988					
Flower density 1989	-.01	.24	.15	.47	.46
Fruit density 1989	-.12	.32	.19	.46	.56 *
Fruits per flower 1989	-.12	-.00	-.56 *	-.05	-.16
Seed density 1989	-.11	.32	.18	.25	.62 *
Seeds per flower 1989	.01	.33	.17	.04	.11

*: 0.01 < P < 0.05, **:0.001 < P < 0.01

Table III-5. Summary of correlation analysis of effects of 1988 and 1989 snow release dates on the density (number/100 cm^2) of components of reproduction in the same year. Values shown are Pearson correlation coefficients. A negative coefficient indicates that density of the component decreased with later dates of snow release; a positive coefficient indicates that density increased.

	Cardamine	Carex	Luetkea	Phyllodoce	Saxifraga
Number of inflorescences					
1988	.01	.08	-.51	-.02	.07
1989	-.07	-.03	-.33	.07	.14
Number of infructescences					
1988	.05	.26	-.51	.01	.14
1989	-.12	.06	-.20	.06	.09
Number of flowers					
1988	.16	-.13	-.58 *	-.07	.16
1989	-.18	-.05	-.03	.00	-.04
Number of fruits					
1988	.23	.10	-.68 *	-.02	.04
1989	-.32	.30	-.27	.00	.08
Number of seeds					
1988	.29	.10	-.68 *	-.22	-.05
1989	-.36	.30	-.57 *	.30	.18
Flowers per inflorescence					
1988	.49	.09	-.42	-.05	-.49
1989	---	-.52	-.24	-.19	-.14
Fruits per inflorescence					
1988	.58 *	.17	-.53	-.05	-.49
1989	---	-.36	-.19	-.29	-.14
Fruits per flower					
1988	-.06	.20	-.06	.21	-.26
1989	-.54 *	.21	-.10	-.12	-.06
Seeds per fruit					
1988	.31	---	-.45	-.59 *	-.39
1989	-.14	---	-.10	-.12	-.06
Seeds per flower					
1988	.43	.46	-.68 *	-.55 *	-.34
1989	-.26	.21	-.56 *	-.12	-.27

*: P < 0.05

Table III-6. Effect of plant size (area, cm^2) on components of 1988 and 1989 reproduction. Values shown are Pearson correlation coefficients. A positive coefficient indicates that values increased with increasing plant size; a negative coefficient indicates that the value of that component decreased.

	Cardamine	Carex	Luetkea	Phyllodoce	Saxifraga
		Number of inflorescences			
1988	.46	.91 ***	.62 *	.96 ***	.95 ***
1989	.73 **	.70 **	.95 ***	.91 ***	.87 ***
		Flowers per inflorescence			
1988	---	.44	.85 ***	.50	-.18
1989	---	.14	.60 *	.21	.50
		Number of flowers			
1988	.40	.76 **	.74 **	.98 ***	.83 ***
1989	.79 ***	---	.91 ***	.91 ***	.83 ***
		Number of infructescences			
1988	.51 *	.91 ***	.62 *	.95 ***	.95 ***
1989	.73 **	.60 *	.71 **	.82 ***	.91 ***
		Fruits per infructescence			
1988	---	-.05	.85 ***	.50	-.11
1989	---	.13	.36	.24	.15
		Number of fruits			
1988	.40	.82 ***	.74 **	.95 ***	.90 ***
1989	.57 *	---	.40	.90 ***	.29
		Seeds per fruit			
1988	-.12	---	.31	.11	-.12
1989	---	-.07	.21	.16	.31
		Number of seeds			
1988	.44	.80 ***	.71 **	.88 ***	.82 ***
1989	.47	-.04	.35	.89 ***	.37
		Fruits per flower			
1988	-.15	.20	-.27	-.01	.26
1989	-.01	-.23	-.59 *	.13	-.26
		Seeds per flower			
1988	.46	.20	.43	.11	.07
1989	.06	-.23	-.10	.17	-.09

*: $0.01 < P < 0.05$, **: $0.001 < P < 0.01$, ***: $P < 0.001$

Table III-7. Site-wide seed production of the five study species in 1988 and 1989, and density of naturally-occurring first-year seedling sampled along the transect.

	Species					
	Cardamine	Carex	Luetkea	Phyllodoce	Saxifraga	Total
Total plant cover (%)	0.1	1.8	1.0	1.0	2.2	6.1
No. seeds per m^2 of plant area, 1988	51,751	73,833	21,600	314,100	149,727	611,011
No. seeds per m^2 of site, 1988	36	1,329	216	3,141	3,294	8,016
No. seeds per m^2 of plant area, 1989	27,143	10,333	3,600	519,000	16,636	576,712
No. seeds per m^2 of site, 1989	19	186	36	5,190	366	5,797
No.naturally-occurring seedlings per m^2, 1988	22	1	0	0	4	27

Table III-8. Emergence and survival by microsite of seedlings from experimentally sown seeds through the first growing season (1987). In each microsite, 1200 seeds of each species were sown. Values shown are total number of emergents and total number of survivors (in parentheses). "Mat" = established Luetkea mat, "Gram" = established Carex clump, "Open" = bare soil, "Protected" = bare soil at edges of rock overhangs.

	Species					
	Cardamine	Carex	Luetkea	Phyllodoce	Saxifraga	Total
FELLFIELD						
Mat	11 (6)	3 (1)	1 (0)	0	1 (0)	16 (7)
Gram	1 (1)	0	1 (0)	1 (0)	1 (0)	4 (1)
Open	11 (4)	1 (0)	0	0	1 (0)	13 (4)
Protected	27 (23)	3 (1)	13 (4)	3 (0)	4 (2)	50 (30)
Total	50 (34)	7 (2)	15 (4)	4 (0)	7 (2)	83 (42)
MEADOW						
Mat	0	0	0	0	0	0
Gram	0	1 (0)	0	0	0	1 (0)
Open	16 (2)	3 (0)	15 (0)	12 (0)	0	46 (2)
Protected	3 (0)	5 (0)	2 (0)	3 (0)	0	13 (0)
Total	19 (2)	9 (0)	17 (0)	15 (0)	0	60 (2)
GRAND TOTAL	69 (36)	16 (2)	32 (5)	19 (0)	7 (2)	143 (44)

Table III-9. Summary of 3-factor ANOVA of effects of microhabitat, gradient position, and species on seedling emergence and establishment in the fellfield, and seedling emergence in the Carex meadow. Data were square-root transformed prior to analysis.

	d.f.	F-ratio	Sig. Level
FELLFIELD - EMERGENCE			
MAIN EFFECTS	9	4.1	.000
microsite	3	5.5	.001
snow release date	2	1.3	.280
species	4	4.4	.002
INTERACTIONS	26	1.9	.008
microsite x release	6	5.8	.000
microsite x species	12	0.9	.572
release x species	8	0.5	.838
FELLFIELD - ESTABLISHMENT			
MAIN EFFECTS	9	3.4	.001
microsite	3	2.6	.054
snow release date	2	2.4	.096
species	4	4.6	.001
INTERACTIONS	26	1.6	.046
microsite x release	6	3.9	.001
microsite x species	12	0.8	.613
release x species	8	0.9	.532
CAREX MEADOW - EMERGENCE			
MAIN EFFECTS	9	6.0	.000
microsite	3	12.3	.000
snow release date	2	3.2	.043
species	4	2.7	.030
INTERACTIONS	26	1.7	.025
microsite x release	6	1.9	.075
microsite x species	12	2.2	.012
release x species	8	0.7	.706

Figure III-1. Relationship between overall phenology (days from snow-release to seed maturation and dispersal) and date of snow-release in 1988. Lines show least-squared regressions. *: 0.01 < P < 0.05; **: 0.001 < P < 0.01; *** P < 0.001. Snow release date ranges from June 10 (160) to August 18 (230).
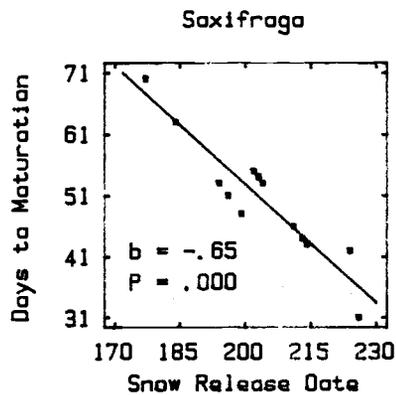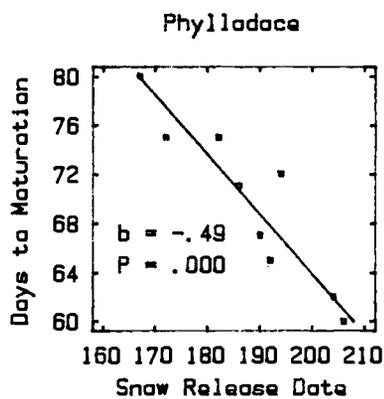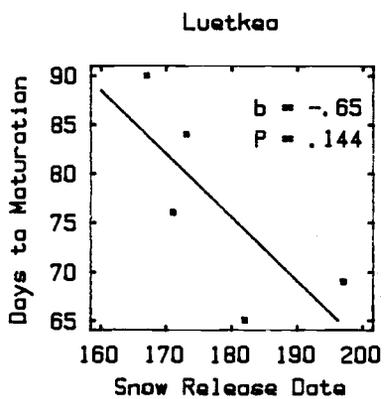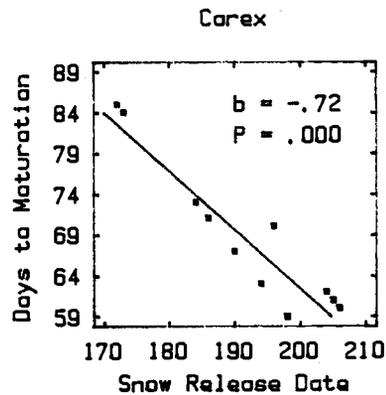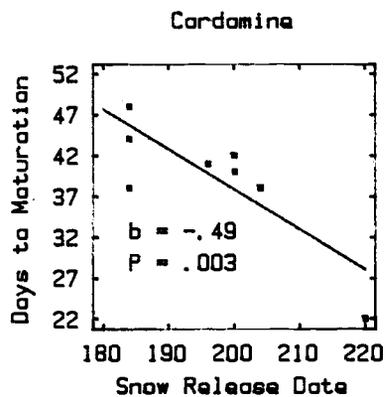
Figure III-1.

Figure III-2. Average (and 95% LSD intervals) for
seedling emergence and establishment in the fellfield and
for seedling emergence in the _Carex_ meadow. A square-
root transformation was applied to data prior to analysis.
Species are: LU = _Luetkea_, PH = _Phyllodoce_, CS = _Carex_, SA
= _Saxifraga_, and CB = _Cardamine_. Microsites are: MA =
established _Luetkea_ mat, GR = established _Carex_ clump, OP
= open nonvegetated, and PR = bare soil under rock
overhangs. Snow release dates are: early = June, mid =
July, and late = August. Graphs of fellfield emergence by
snow release date, fellfield establishment by microsite,
and fellfield establishment by snow release date are not
shown because F-tests failed to reveal heterogeneity
across the main effects.
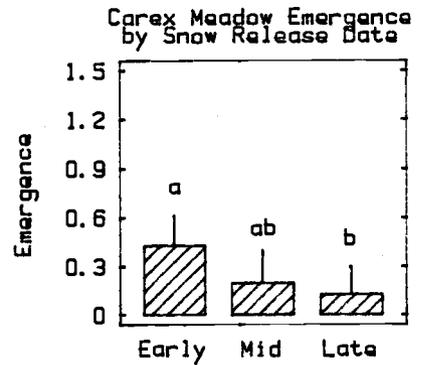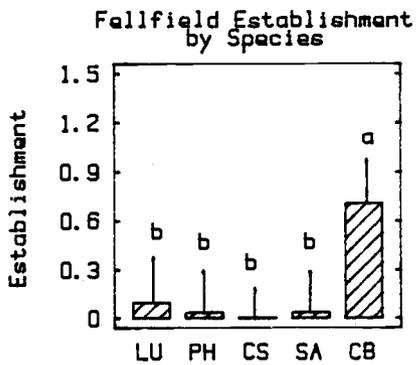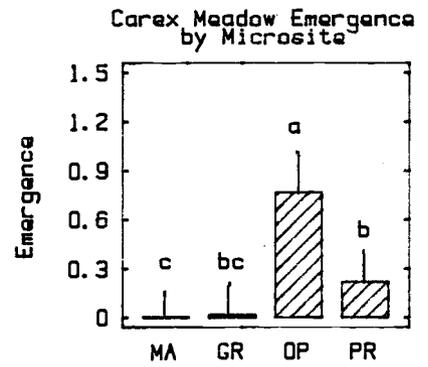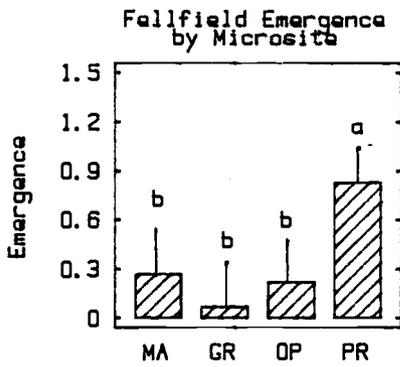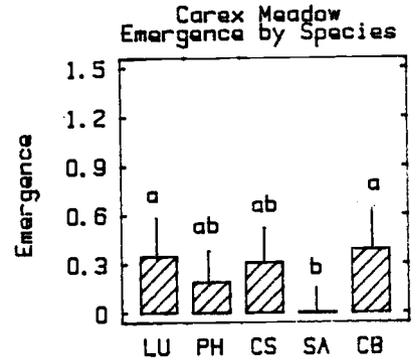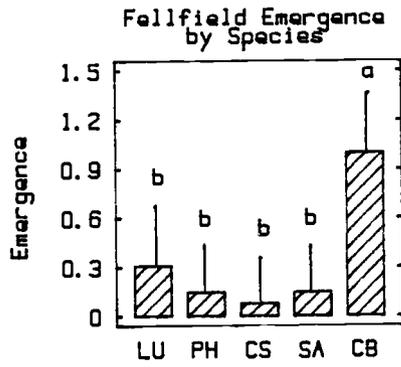
Figure III-2.

**Figure III-3.** Stages of loss of potential offspring in 1988 and 1989. Stages of reproduction are: 1 = flowering, 2 = fruit initiation, 3 = fruit maturation (dispersal), 4 = seedling emergence, and 5 = seedling establishment (end of first growing season).
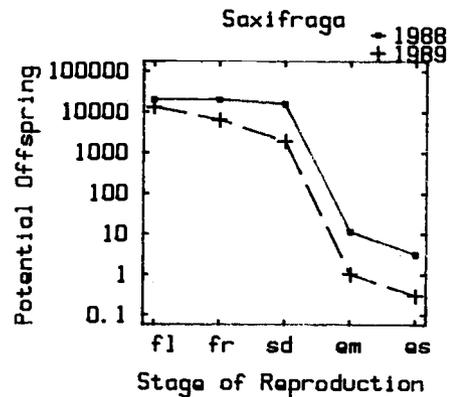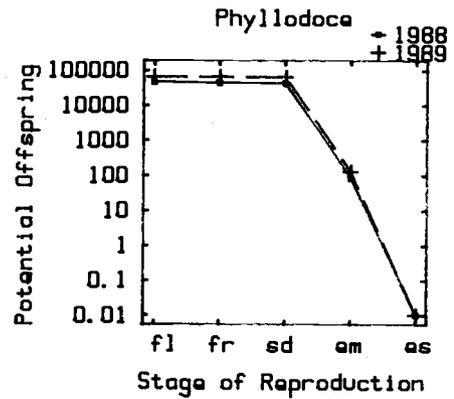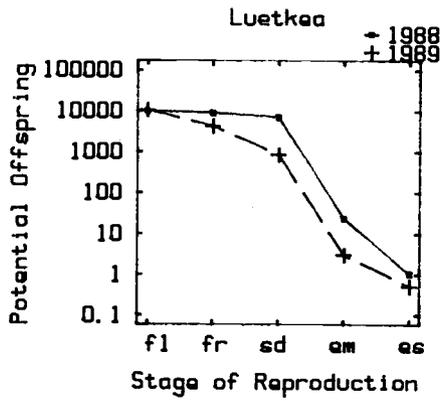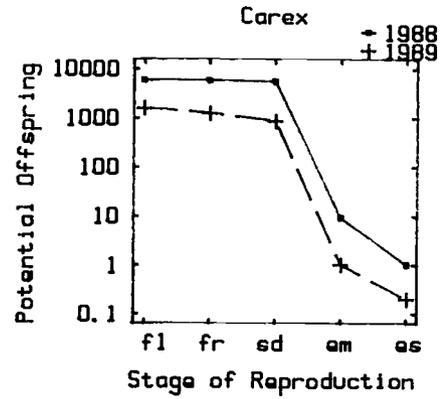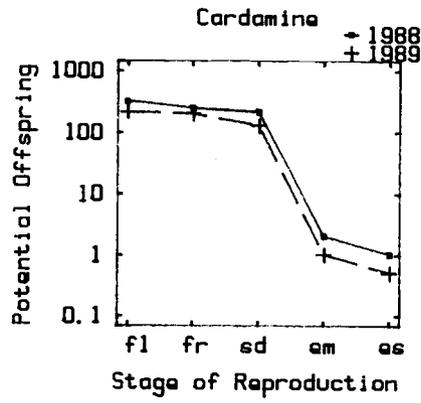
Figure III-3.

CHAPTER IV. BURIED PROPAGULES OF A
SUBALPINE TUNDRA COMMUNITY

INTRODUCTION

The search for geographical patterns in the size of
buried seed banks has led to the hypothesis that seed
banks in tundra are quite small in comparison with those
in other types of vegetation. Johnson (1975) proposed
that buried seed populations decline with increasing
latitude, and Thompson (1978) suggested a similar
reduction in seed bank size at high altitudes. A paucity
of buried seeds in tundra vegetation has been attributed
to low primary productivity (Billings and Mooney 1968),
low energy allocation to sexual reproduction (e.g.,
Callaghan and Collins 1976, Jolls 1980, Douglas 1981), and
selection for rapid germination in response to the short
growing season (Bliss 1971, Kimball et al. 1973).
However, several recent studies of seed banks in arctic
tundra have shown populations of buried seeds to be larger
than previously thought, comparable in many cases to those
of temperate forests and grasslands (e.g., McGraw 1980,
Roach 1983, Ebersole 1989). There has also been growing
recognition of the major role of seed banks in the
reestablishment of vegetation following disturbances in
tundra (e.g., McGraw 1980, Gartner et al. 1983, Ebersole
1989).

Few studies have assessed alpine and high subalpine seed banks (for the few examples, see Fox 1983, Weidman 1983, Archibold 1984, Miller and Cummins 1987, Morin and Payette 1988), making comparisons to seed banks in other habitats difficult. Persistent seed banks might be expected to be small if, as Amen (1966) suggests, most alpine species lack innate seed dormancy, and germinate as soon as environmental conditions are suitable. On the other hand, McGraw and Vavrek (1989) suggest that, due to the high frequency of small-scale soil disturbance in tundra and the greater success of seedling establishment in such disturbances (Freedman et al. 1982, McGraw and Shaver 1982, Gartner et al. 1983, 1986), seed dormancy may be selected for in tundra species. Tundra seeds are likely to be long-lived due to slow rates of respiration and decay in soils remaining cold most of the year, and dormant seeds may accumulate in the soil over long periods of time (Miller and Cummins 1987, McGraw and Vavrek 1989).

A common view is that tundra species rely more heavily on vegetative than sexual regeneration (Billings and Mooney 1968, Bliss 1971, Billings 1974, Callaghan and Collins 1976, Roach 1983). Thus, tundra communities might be expected to have relatively large vegetative propagule banks. However, the relative contributions of seeds and vegetative propagules in tundra has rarely been assessed (see Roach 1983, Archibold 1984). Better understanding of the propagule banks of alpine tundra is important for two

reasons. First, many alpine habitats have low vegetation
cover and large areas may be completely lacking
vegetation, so that dispersed or buried seeds are
necessary for colonization and establishment of
vegetation. Second, human impacts in alpine tundra are
increasing, and vegetation recovery after disturbance will
depend on the availability of seeds and buried vegetative
regenerative structures (e.g., Miller and Cummins 1987).

Total annual seed rain among five species common on
Park Ridge, in the Oregon High Cascades, ranged from
6000 - 8000 seeds/m^2 over a two-year period (Chapter III).
Seedling emergence of these species, however, from both
experimentally-sown and naturally-dispersed seeds, was
extremely low. The discrepancies between the magnitude of
seed production and seedling emergence could result from
mortality of overwintering seeds, innate seed dormancy,
environmentally-induced seed dormancy, or mortality of
seedlings immediately following germination. The first
two possibilities were deemed unlikely causes of this
discrepancy; the first (overwintering seed mortality)
because predation and rates of respiration and microbial
decay are probably extremely low for seeds buried under
winter snow (McGraw and Vavrek 1989); the second (innate
dormancy) because the seeds of all five species germinated
readily under laboratory conditions. This study was
undertaken to assess the potential contribution of the
buried seed and propagule bank to the establishment of

vegetation on a high subalpine site, and to investigate whether accumulation of seeds in a buried seed bank could explain the discrepancy between seed production and seedling emergence of the five study species.

The objectives of this study were: 1) to assess the persistent buried propagule bank of this high subalpine tundra community, 2) to compare seed populations in vegetated and bare soils, 3) to compare the composition of the buried propagule bank to that of the vegetation, and 4) to investigate whether low availability of buried seeds limits establishment of vegetation on this site.

METHODS

Study Site

The study site is located approximately at treeline
on Park Ridge (2100 m elevation; 44 45' N, 121 47'W; Fig.
I-1), about 5 km north of Mt. Jefferson, in Mt. Hood
National Forest, Oregon, USA. The area lies within the
High Cascades physiographic province (Franklin and Dyrness
1973). Park Ridge is a volcanic plug of Pliocene origin,
consisting of gabbro overlain with basalt and andesite
(Thayer 1939). The site covers approximately 100 ha on
the north-facing slope of the ridge. The Pacific Crest
Trail passes immediately to the east, but the site itself
is little used and apparently free from human-caused
disturbances. Vegetation on the site consists of a mosaic
of Carex meadows (dominated by C. nigricans and C.
spectabilis), Phyllodoce empetriformis - Cassiope
mertensiana heath, late snowmelt areas vegetated almost
solely by Saxifraga tolmiei, and open fellfields dominated
by cushion and mat-forming plants such as Luetkea
pectinata. Vegetation cover is patchy and interspersed
with extensive talus slopes and areas of bare mineral
soil. Below the site, the vegetation grades into Tsuga
mertensiana - Abies lasiocarpa parkland, while above,
along the ridgecrest, lie patches of Pinus albicaulis -
Abies lasiocarpa krummholz. The entire site is typically

covered by snow from mid-September or October through June. Outcrops are often snow-free by mid-June, while other areas lie in late snowmelt basins below permanent snowbanks.

Vegetation Characteristics

In August 1988, cover and species composition of the vegetation were sampled in 75 1-m^2 plots placed at random along six randomly located 50-m transects. Species composition and density of first- and second-year seedlings was sampled in 115 225-cm^2 plots, located at random along 15 50-m transects located at random across the site.

In 1988 and 1989, annual seed production was estimated for five of the most abundant species on the site (Cardamine bellidifolia var. pachyphylla, Carex spectabilis, Luetkea pectinata, Phyllodoce empetriformis, and Saxifraga tolmiei var. tolmiei). Individual cover was estimated on each of 15 randomly-selected plants of each species, and the number of fruits was counted on each individual. A sample of 10 mature fruits per plant was collected, returned to the lab, and the number of seeds in each was counted. For Carex, which produces single-seeded fruits, the number of achenes per spike was counted. These methods are described in more detail in Chapter II.

Collection of Soil Cores

In order to assess the persistent buried seed bank, soil samples were taken during late July and early August, 1988, after germination but before any seed dispersal was observed. A 6.8-cm diameter metal cylinder, 5 cm deep, was used to collect the samples. One-hundred-sixty-one soil samples (for a total area of 0.58 m^2) were taken at random points across the site. The microsite of each sample (moss-dominated vegetation, vascular plant vegetation, bare soil within 0.5 m of vegetation, and bare soil with vegetation more than 0.5 m away) was recorded. The samples were individually bagged and returned to Oregon State University, where each was moistened and placed in cold storage over the winter (September through February), to simulate the winter stratification experienced on the site. In March, 1989, each sample was spread in a thin layer (about 1 cm deep) over a 2:1 mixture of sterile soil and sand in a 12 x 16 cm flat. The flats were kept in the greenhouses at Oregon State University, and emergence was monitored semi-weekly from March through October. Flats were misted as needed to keep soils moist. On each monitoring date, each emergent was marked with a toothpick, classified as a seedling or vegetative emergent, and identified to species. Forty-five control flats of sterile soil and sand were interspersed among the sample flats to assess

contamination by dispersal of local seeds. The only species emerging in the control flats were local or greenhouse weeds that did not grow on the study site; these species were omitted from the analysis. When the study was terminated, certain flats were retained to allow identification of unknown individuals and to double-check identification of <u>Juncus</u> and <u>Carex</u> emergents, since two or more species of these genera occurred in the standing vegetation of the site.

Analysis

The effects of microsite on total emergence, emergence of the ten most abundant species, and species richness were analyzed by Analysis of Variance (ANOVA). Fisher's Protected LSD test (FPLSD, 95% level) was used to identify microsites that differed significantly in emergence. Prior to analysis, a square-root transformation (Conover 1980) was applied to the data on emergence of individual species.

To assess the correspondence between the propagule bank and vegetation characteristics, Percent Similarity (Brower and Zar 1977) between the composition of the standing vegetation and that of the propagule bank, between the standing vegetation and naturally-occurring first-year seedlings, and between naturally-occurring

seedlings and the buried propagule bank were calculated. For the five species for which reproduction was assessed, relative vegetation cover, seed production, number of buried seeds, and number of naturally-occurring seedlings were compared.

RESULTS

Twenty-two species occurred in the vegetation sample plots (Table IV-1). Cover was very low (< 10%) and five species (Saxifraga tolmiei, Carex spectabilis, C. nigricans, Luetkea pectinata, and Phyllodoce empetriformis) constituted 70% of the total. Most species had less than 1% cover on the site. The total density of naturally-occurring first-year seedlings was also quite low, only 38 seedlings/m^2 (Table IV-1). Except for Saxifraga tolmiei, the seedlings found on the site belonged to species with very low (< 0.1%) aboveground cover. Nearly 60% of the seedlings were Cardamine bellidifolia, a small perennial with low cover but frequent occurrence on the site. No second-year seedlings were found.

A total of 1805 individuals in 21 taxa emerged in the greenhouse flats, corresponding to a propagule bank density of 3141 propagules/m^2 (Table IV-2). Emergence was overwhelmingly dominated by seedlings; only 16 individuals (29/m^2) originated from vegetative structures. Juncus drummondii and J. mertensianus, emerging almost entirely from buried seeds, were by far the most abundant species, together constituting 75% of the total propagule bank. Saxifraga tolmiei and Carex nigricans each contributed about 10% of all individuals, and 18 other taxa were represented in small amounts. Eleven of the 16 vegetative

emergents were _Carex_ _nigricans_ individuals; 5 other species were represented by a single emergent.

Soil samples dominated by mosses constituted 19% of the samples collected and vascular plant-dominated vegetation constituted 5%. Thirty-three percent of the samples were from bare soils less than 0.5 m from vegetation, and 43% were from bare soils more than 0.5 m from vegetation. Characteristics of the buried propagule bank varied among these microsites (Table IV-2). Moss-dominated vegetation averaged 7518 emergents/m^2, vascular plant vegetation 5654/m^2, bare soil < 0.5 m from vegetation 2876/m^2, and bare soil > 0.5 m from vegetation 1189 emergents/m^2. Bare soil > 0.5 m from vegetation produced significantly fewer total emergents (and no vegetative emergents) than any other microsite. Emergence from vegetative structures was significantly higher in vegetation (83-137/m^2) than in bare soil (0-20/m^2). Species richness of the propagule bank was significantly greater in the two vegetated microsites than in bare soil.

Emergence of the individual species also varied significantly among microsites. _Juncus_ _drummondii_ was significantly more abundant in vegetation (4000 seedlings/m^2) than in bare soil. In contrast, _Juncus_ _mertensianus_ was significantly more abundant in moss (3630/m^2) than in other microsites, and was absent in vascular plant vegetation. Emergence of _Saxifraga_ _tolmiei_ was highest (431/m^2) in areas > 0.5 m from vegetation.

Carex nigricans was most abundant in vascular plant vegetation (828 seedlings/m^2, 103 sprouts/m^2) and was more abundant in both types of vegetation than in bare soils. Emergence of Carex spectabilis was significantly higher in vascular vegetation (69/m^2) than in any other microsite. Emergence of the other abundant species, Agrostis variabilis, Cardamine bellidifolia, Epilobium alpinum, Phyllodoce empetriformis, and Luetkea pectinata, did not differ among microsites (Table IV-2). With the overwhelming effects of the two Juncus species removed, seedling emergence of all other species was highest in the vascular plant microsites, and significantly higher in both vegetated microsites than in either of the bare soils.

Cardamine bellidifolia, despite having the lowest vegetation cover and seed production among the five species studied intensively (Table IV-3), was by far the most abundant naturally-occurring seedling on the site. In contrast, Phyllodoce empetriformis had the highest seed production among the five species but was poorly represented in the persistent seed bank, and none of its seedlings were found on the site. Saxifraga tolmiei, which had the highest vegetation cover and produced abundant seeds, was the most abundant of the five species in the seed bank, and occurred as seedlings on the site. Luetkea pectinata, which had low relative seed production,

was rare in the seed bank, and was not found as seedlings on the site.

Percent Similarity between the composition of the standing vegetation and the seed bank was only 18%. While 22 species occurred in the vegetation, only 12 of these were represented in the seed bank. However, 92% of the species present in the seed bank occurred on the study site, and <u>Gaultheria humifusa</u>, which grows in subalpine meadows immediately below the site, was the only off-site species represented in the persistent seed bank. Very few species present as adults on the site occurred as first-year seedlings (Percent Similarity = 24%), and very few species in the buried seed bank were found as seedlings (Percent Similarity = 20%). Only five of the 13 taxa identified in the greenhouse study were found as seedlings on the site (Tables IV-1 and IV-2), and the magnitude of the seed bank was far greater than populations of first-year seedlings on the site (3112 vs. 38 seedlings/m^2).

DISCUSSION

Density of the Propagule Bank

The overall seed bank density estimated for this site (3112 seeds/m^2), approximates the highest values reported for other tundra communities (Leck 1980, McGraw 1980, Freedman et al. 1982, Gartner et al. 1983, Roach 1983, Ebersole 1989), and is considerably higher than previous estimates for subalpine and alpine tundra, which range from 13-1800 emergents/m^2 (Fox 1983, Weidman 1983, Archibold 1984, Morin and Payette 1988). The seed bank on this site is remarkably large given 1) the very low cover of standing vegetation (< 10%), 2) the fact that these values represent only the persistent, not the total, seed bank, and 3) the possibility that seeds of some species might have failed to germinate after stratification and exposure to greenhouse conditions. In the studies cited above, only Roach (1983) and Freedman et al. (1982) provide values for aboveground vegetation cover, ranging from 40-70%, and their seed banks (with one exception) were much smaller. In addition, in some studies it is not clear whether the total (persistent plus transient) or only the persistent banks were sampled; Fox (1983) and Archibold (1984) indicate that their values represent the total germinable seed bank. Morin and Payette (1988) found larger total seed banks in subalpine and alpine

communities in Quebec, but by far the bulk of these seed banks consisted of species with seeds that lost viability soon after dispersal; that is, the persistent seed bank was quite small. The magnitude of seed rain among five of the most abundant species on Park Ridge, 6905 seeds/m^2 (Table IV-3), suggests that the total seed bank on this site is actually much higher than the estimate of the persistent bank (3112/m^2).

The very minor contribution of vegetative structures to the propagule bank on this site was not simply a consequence of the low cover of standing vegetation, because even vegetated microsites contained few vegetative emergents (83-107/m^2). In contrast to this sparse vegetative propagule bank, the alpine tundra propagule bank examined by Archibold (1984) was heavily dominated by vegetative emergents and contained as many as 20,000 vegetative emergents per m^2 (mostly graminoids such as _Carex_ spp.). Although a number of rhizomatous species occur on Park Ridge, many may be unable to sprout vegetatively from independent fragments, and vegetative regeneration may depend on the maintenance of connections between a vigorous plant and its shoots. The exception is _Carex nigricans_, which sprouted readily from small rhizome fragments.

Patterns Among Species

The contrasting patterns in seed bank abundance among microsites probably result primarily from differences in species occurrence in the standing vegetation, but patterns of seed dispersal and the seed-trapping abilities of microsites may also be important. The buried seeds of _Juncus drummondii_ and _Carex nigricans_ are most dense in moss mats and vascular vegetation, and adults of these species are typically associated with these microsites. Adults of _Juncus mertensianus_ are primarily found growing with mosses in moist microsites, and rarely occur with other vascular plants; the seeds of this species are most abundant in moss microsites and are absent from vascular vegetation. In contrast, _Carex spectabilis_ rarely grows with moss, but is commonly associated with other vascular species; its seeds are most abundant in microsites dominated by vascular plants.

The low species richness of the seed bank in bare soils probably reflects both the occurrence of adults and patterns of seed dispersal. For example, _Saxifraga tolmiei_ often grows with other vascular plants or with mosses, but also occurs alone in extremely moist, late snowmelt microsites (e.g., Chapter II). Large areas of bare ground are found in late snowmelt gullies and flats, where _S. tolmiei_ is generally the sole vascular plant. In these areas, the small seeds of _S. tolmiei_ may be

dispersed considerable distances in runoff from snowmelt, and deposited in microsites reached by few other seeds.

Correspondence Between Components
of the Vegetation

Most studies of seed banks in natural ecosystems have reported low correspondences between the composition of buried seed banks and that of the standing vegetation [e.g., Kellman 1970, 1974; Strickler and Edgerton 1976; Roberts 1981: Thompson 1986). Analysis of nine other seed bank studies in tundra and subalpine/boreal forest, in which above-ground vegetation characteristics (presence/absence or percent cover) were provided, show tremendous variability in the degree of correspondence between the standing vegetation and the seed bank (Table IV-4). In the bulk of these studies, while Percent Similarity ranges from low to moderately high, there is wide variation in the proportion of species occurring in the seed bank that are present in the standing vegetation. In tundra vegetation, most species in the seed bank (even seed banks dominated by ruderal species) are consistently present either on, or adjacent to, the site (Table IV-4, Ebersole 1989).

A number of factors influence the degree of correspondence between seed banks and the above-ground vegetation. Many species found in the seed banks of mature and old-growth coniferous forests are species characteristic of early successional stages (e.g., Oosting and Humphreys 1940, Livingston and Allessio 1968, Ingersoll and Wilson 1990). Ruderal species may accumulate large seed banks that persist over long periods of time despite shifts in the standing vegetation. Thus, the composition of the buried seed bank can differ greatly from the composition of the standing vegetation. In contrast, species composition of seed banks dominated by non-persistent seeds may track shifts in the above-ground vegetation more closely (e.g., Morin and Payette 1988). For example, Hendersen et al. (1988) attributed relatively high correspondence between the seed bank and standing vegetation of desert grassland to frequent disturbance, which limited the vegetation to early successional species relying on a seed bank to colonize disturbed sites. On Park Ridge, the most abundant species in the seed bank are rare in the vegetation, but, these abundant species are restricted to moist sites in the vegetation, and do not appear to be able to colonize disturbed soils.

Seed banks might differ in composition from the standing vegetation because of differential accumulation of species in the seed bank. Due to low or intermittent reproduction, many species abundant above-ground do not

contribute substantially to the seed rain of a site (e.g., Rabinowitz 1981). Some species produce seeds with short viability (e.g., Morin and Payette 1988), or that germinate rapidly. Other species that are not present aboveground could be present in the persistent seed bank because of dispersal from other communities. In this study, there was virtually no off-site representation in the persistent seed bank: all species occurred in the standing vegetation on, or adjacent to, the site.

The high correspondences between the above- and below-ground components of vegetation observed in tundra studies can probably be attributed primarily to the long persistence of these communities over time (e.g., Morin and Payette 1988), in contrast to the distinct successional shifts observed in forests. This correspondence between above- and below-ground components probably results from the maintenance of a wide range of vegetation within a small area through small-scale disturbances (McGraw 1980, Gartner et al. 1983). On Park Ridge, however, the seed bank was overwhelmingly dominated by two species (Juncus drummondii and Juncus mertensianus) that are strongly associated with very moist microsites and do not appear (at least on this site) to establish in open, disturbed microsites. Despite the abundance of these species in the seed bank, only one Juncus seedling was found in the field, indicating that either mortality of emergent seedlings is extremely high, or these species

undergo periodic flushes of germination and establishment from the persistent bank in response to suitable environmental conditions.

The seed bank samples were collected after natural emergence had occurred on the site. Why did these seeds germinate in the greenhouse samples but not on the site? It is likely that field conditions were not suitable for germination. Temperature optima for germination of alpine species are typically high, around 20 C (Mooney and Billings 1961, Chabot and Billings 1972, Amen 1966, Sayers and Ward 1966, Billings and Mooney 1968). On Park Ridge, soil surfaces reach high daytime temperatures soon after snowmelt (Chapter III) and the upper 1 cm of soil dries out rapidly. Most buried seeds probably do not have adequate soil moisture at the same time that soil temperatures are optimum for germination (e.g., Billings 1974). In the greenhouse, however, soils were maintained at moderate temperatures and provided with ample moisture. In addition, some deeper-buried seeds in the field may have had adequate moisture but inadequate temperatures or light to germinate.

The discrepancy between the magnitude of viable seed production, presence in the seed bank, and seedling establishment of four of the five species studied intensively at Park Ridge, strongly suggests that pre- or early post-germination mortality is very high under field conditions. Experimental data showing extremely low rates

of seedling emergence and establishment in these species
(Chapter III) support this conclusion.

The Seed Bank and
Establishment of Vegetation

Archibold (1984) concluded that, because of extremely
low reserves of buried seeds, recovery of alpine tundra
following disturbances would occur primarily through
vegetative regeneration. In contrast, Sohlberg and Bliss
(1984) suggested that there existed enough viable seeds in
arctic tundra communities to develop continuous vegetation
cover if environmental conditions were appropriate for the
establishment of seedlings. In British Columbia, Brink
(1964) noted that large areas of bare ground occurred
adjacent to well-established vegetation, and attributed
the lack of vegetation to failure of seedling
establishment through cryogenic activity, soil drought,
and high soil surface temperatures. In arctic tundra,
frequent small-scale disturbances (e.g., freeze-thaw and
rodent activity) create local vegetation mosaics and
buried seeds are an important source of colonizers in
these disturbances (e.g., McGraw 1980, Gartner et al.
1983). Drought and soil temperatures may be less severe
in arctic tundra than on alpine sites. On Park Ridge,
bare soil microsites (except where altered by microrelief)

are subjected to chronic disturbances, such as freeze-thaw
activity and gullying from runoff, as well as high soil
surface temperatures, which can prevent establishment of
seedlings. These harsh conditions are minimized in
vegetated microsites (Chapter III). The results of this
study suggest that the low vegetation cover of this site
cannot be attributed to a lack of viable seeds in the
soil, because even bare areas away from established
vegetation support a large persistent seed bank.
Colonization of bare soils on Park Ridge is limited more
by high pre- and/or early post-emergence mortality than by
low seed rain or the availability of viable seeds in the
soil. It appears doubtful whether, under current
environmental conditions, the large persistent seed bank
will contribute substantially to establishment of
vegetation on bare soils.

Table IV-1. Species composition, percent cover, and seedling density on the study site. Vegetation was sampled in 75 1-m^2 plots; seedlings were sampled in 115 225-cm^2 plots.

SPECIES	Vegetation Cover (%)	Number of Seedlings	Seedling Density (per m^2)
Saxifraga tolmiei	2.2	10	3.9
Carex spectabilis	1.8		
Carex nigricans	1.0		
Luetkea pectinata	1.0		
Phyllodoce empetriformis	1.0		
Juncus drummondii	0.5		
Penstemon davidsonii	0.5		
Cassiope mertensiana	0.4		
Cardamine bellidifolia	0.07	57	22.0
Hieraceum gracile	0.02	5	1.9
Agrostis variabilis	0.02		
Antennaria alpina	0.01		
Carex phaeocephala	0.01		
Castilleja parviflora	0.02		
Cryptogramma acrostichoides	0.01		
Epilobium alpinum	0.01	17	6.6
Juncus mertensianus	0.03		
Luzula hitchcockii	0.04		
Phyllodoce glanduliflora	0.01		
Vaccinium deliciosum	0.01		
Spraguea umbellata	<0.01		
Polygonum newberryi	<0.01		
Carex sp.		4	1.5
Unknown dicots		3	1.2
Juncus sp.		3	1.2
TOTAL	8.7 %	99	38

Table IV-2. Total, seedling, and vegetative sprout emergence in greenhouse flats. Emergence of vegetative sprouts and of individual species were square-root transformed prior to analysis. Differing letters denote significant differences in emergence among microhabitats (FPLSD, 95% level). Microsites are: "Moss" = moss-dominated sites, "Veg." = sites dominated by vascular plants, ">0.5 m" = bare soils greater than 0.5 m from vascular vegetation, and "<0.5 m" = bare soils less than 0.5 m from vascular vegetation.

SPECIES	MICROSITE DENSITY (No./m^2)				TOTAL DENSITY (No./m^2)	POOLED S^2	F
	Moss n=30	Veg. n=8	>0.5m n=70	<0.5m n=53	n=161		
Seedlings							
Juncus drummondii	2667a	4000a	387c	1268b	1279	2.2	15.9 ***
Juncus mertensianus	3630a	0d	81cd	1090b	1069	2.1	24.8 ***
Saxifraga tolmiei	231ab	207ab	431a	115b	276	0.6	8.5 ***
Carex nigricans	528a	828a	60b	194b	229	0.5	15.9 ***
Agrostis variabilis	148	0	40	37	62	0.2	0.2
Epilobium alpinum	83	310	85	63	88	0.3	1.7
Cardamine bellidifolia	19	0	32	16	22	0.1	0.9
Phyllodoce empetriformis	46	0	0	21	15	0.1	1.0
Carex spectabilis	19b	69a	0b	0b	7	0.1	3.9 *
Luetkea pectinata	0	0	4	16	7	0.0	0.8
Cassiope mertensiana	0	0	0	5	2		
Gaultheria humifusa	0	0	0	5	2		
Hieraceum gracile	0	0	0	5	2		
unknown (8 species)	46	103	73	26	52	0.2	1.3
Total Seedling Density	7435a	5517ab	1189c	2856b	3112	232.6	16.3 ***
Total w/o Juncus	1120ab	1517a	725bc	503c	764	11.8	4.6 **

Table IV-2 continued.

SPECIES	MICROSITE DENSITY (No./m²)				TOTAL DENSITY (No./m²) n=161	POOLED S²	F
	Moss n=30	Veg. n=8	>0.5m n=70	<0.5m n=53			
Vegetative Emergents							
<u>Juncus</u> <u>drummondii</u>	9	0	0	0	2		
<u>Saxifraga</u> <u>tolmiei</u>	0	0	0	5	2		
<u>Carex</u> <u>nigricans</u>	56	103	0	10	19	0.1	5.9 ***
<u>Cardamine</u> <u>bellidifolia</u>	0	34	0	0	2		
<u>Carex</u> <u>spectabilis</u>	9	0	0	0	2		
<u>Luetkea</u> <u>pectinata</u>	9	0	0	0	2		
Total Sprout Density	83a	137a	0b	20b	29	0.1	8.6 ***
GRAND TOTAL	7518a	5654ab	1189c	2876b	3141	232.9	16.8 ***
SPECIES RICHNESS	2.8a	3.0a	1.5b	1.8b		1.4	11.3 ***

*: $0.01 < P < 0.05$; **: $0.001 < P < 0.01$; *** $P < 0.001$

Table IV-3. Relative vegetation cover, absolute and relative seed production, relative seed bank abundance, and relative seedling abundance among the five intensively-studied species.

Species	Relative vegetation cover (%)	Seed production /m^2	Relative seed production (%)	Relative seedbank abundance (%)	Relative seedling abundance (%)
Cardamine bellidifolia	1.1	27	0.4	6.7	80.3
Carex spectabilis	29.7	757	11.0	2.1	5.6
Luetkea pectinata	16.5	126	1.8	2.1	0
Phyllodoce empetriformis	16.5	4165	60.3	4.6	0
Saxifraga tolmiei	36.2	1830	26.5	84.4	14.1
Total	100.0	6905	100.0	100.0	100.0

Table IV-4. Correspondence between the species composition of seed banks and standing vegetation in arctic and alpine tundra and subalpine/boreal forest vegetation.

Vegetation (Source)	Percent Similarity	Percent of Seed Bank Species Present in Standing Vegetation
	TUNDRA	
Subalpine tundra (this study)	18	92
Subalpine meadows (Weidman 1983)	15-53	86-92
Alpine tussock-tundra (Fox 1983)	9	100
Subalpine-alpine (Morin and Payette 1988)		
Subalpine meadow	30	92
Alpine krummholz	59-61	78-86
Alpine shrub	66	78
Alpine tundra	43-76	83-87
Arctic tussock tundra (Roach 1983)	51	77
Arctic tussock tundra (Freedman et al. 1982)	---	100
	FOREST	
Subalpine forest (Whipple 1978)	2-7	0-75
Subalpine Forest (Morin and Payette (1988)	38	86

Table IV-4 continued.

Vegetation (Source)	Percent Similarity	Percent of Seed Bank Species Present in Standing Vegetation
Boreal forest (Granstrom 1982)		
16 yr.	57	80
29 yr.	6	14
50 yr.	38	60
120 yr.	35	71
169 yr.	27	80
Boreal forest (Fyles 1989)	---	43-57
Boreal forest (Johnson 1975)	*	*

*: No seeds germinated from soil cores.

CHAPTER V. CONCLUSIONS

The first objective of this study was to describe the vegetation of a high subalpine/low alpine site in the Oregon High Cascades and to identify environmental factors influencing vegetation patterns. On Park Ridge, patterns of vegetation respond primarily to the timing of snow release, as influenced by exposure, slope, and depth of snow cover (Chapter II). Duration of snow cover is the most widespread environmental factor determining vegetation patterns in high subalpine and alpine habitats (e.g., Billings and Bliss 1959, Johnson and Billings 1962, Holway and Ward 1965, Canaday and Fonda 1974, Douglas 1977, Isard 1986, Evans and Fonda 1990), because of its effects on length of the growing season, soil moisture availability, and soil and air temperatures. On Park Ridge, and elsewhere in the Cascade Mountains, the effect of timing of snow release on soil moisture availability may influence plant distributions primarily through control of seedling establishment (Chapter III).

Arrays of similar communities along snow-release gradients are found in the cooler, moister North Cascades, particularly on leeward slopes where deep snow accumulates and melts late in the growing season (Evans and Fonda 1990). The lush herbaceous communities (e.g., _Veratrum viride_ and _Valeriana sitchensis_ meadows) occurring on early-release windward slopes in the North Cascades and at

lower elevations in the Oregon Cascades (Campbell 1973) are absent from the vegetation on Park Ridge, and many other species characteristic of lower subalpine vegetation are absent as well. Overall vegetation cover in the _Saxifraga tolmiei_, _Carex nigricans_, _Phyllodoce empetriformis_ and _Luetkea pectinata_ communities on Park Ridge are much lower than in comparable communities of the western North Cascades (Chapter II, Evans and Fonda 1990). Sparse vegetation cover in the Oregon High Cascades compared with that of the North Cascades appears to be a general phenomenon, attributable to the recent origin of its volcanic soils and to its warmer, drier climate, which makes plant establishment more difficult (Franklin and Dyrness 1973).

The second objective (covered in Chapter III) was to identify which life history stages (flowering, fruiting, seed production, seedling emergence, and early seedling survival) constrain recruitment in selected alpine species. Of the five species studied intensively, all occur along the entire length of the snow-release gradient examined on the northern exposure of Park Ridge. Despite a 60-70 day separation between the earliest and latest-released plants, all species produced at least some viable seeds each year at all locations along the gradient. _Luetkea_ was the only species to show a significant reduction of seed production with later dates of snow-release. All species except _Luetkea_ displayed significant

compression of reproductive phenology at later dates of snow-release; such compression is either a phenotypically plastic response to microhabitat conditions or is the result of genetic micro-differentiation in response to the very short growing season.

Constraints on recruitment in these species can occur during several of the life history stages examined in this study (Fig. IV-1, Fig. V-1). Despite differences among these species in phenology and in the magnitude of pre-dispersal losses of offspring to fertilization failure, abortion, and fruit predation, the loss of offspring between seed dispersal and seedling emergence dwarfs the magnitude of all others. In addition, the survival of emerging seedlings through the first growing season was quite low (averaging 12%), except in Cardamine (52%). Cardamine has the most rapid seedling root growth of these species, which probably allows it to tap deeper soil moisture and resist uprooting by needle ice. Total seedling establishment did not respond significantly to the timing of snow release. Although viable seeds of these species are produced along the entire snow-release gradient, seedling establishment is uniformly very rare at all points along the gradient (Chapter III).

The extremely low overall vegetation cover of the study site and the many viable seeds found in bare soil suggest that seedling establishment is controlled largely by the abiotic environment. Plant-plant interactions,

however, may be locally important for seedling establishment. For the five intensively-studied species, abiotically-protected microsites (e.g., around stones) appear to be a requirement for the early survival of emerged seedlings. Such sites protect seedlings from drought, high soil temperatures, and soil disruption from autumn needle ice, and lack the inhibitory qualities of established vegetation. Unusual years of high summer precipitation may provide opportunity for greater seedling establishment. The five species studied intensively are nearly absent from the vegetation on the southern exposure of Park Ridge (Chapter III; although Phyllodoce and Luetkea do occur in late snow-melt sites on the south slope). These species may approach their limits of temperature and/or moisture tolerance on Park Ridge, since they appear to respond favorably to the ample moisture and cooler temperatures, and to tolerate the short growing season, on the northern exposure of the study area.

The third objective of this research was to assess the potential contribution of the persistent buried seed and vegetative propagule bank to the establishment of vegetation on this site. The magnitude of the persistent buried seed bank on Park Ridge was much higher than expected, while the vegetative propagule bank was negligible (Chapter IV). The seed bank dominants, Juncus mertensianus and Juncus drummondii, had very low cover in the standing vegetation. With the exception of Saxifraga,

the seeds of the five study species (all abundant in the standing vegetation) were rare or absent in the persistent seed bank.

Three hypotheses may explain the discrepancies between abundance in the standing vegetation, seed production, seedling emergence, and abundance in the buried seed bank. First, accumulation in a persistent buried seed bank may provide a temporal refuge for some species, allowing rapid reestablishment after long periods of conditions unfavorable for seedling establishment (Billings and Mooney 1968). For example, the seeds of _Juncus mertensianus_, _Juncus drummondii_, and _Saxifraga tolmiei_ may accumulate as a result of innate or environmentally-enforced seed dormancy and germinate during occasional cool, rainy summers suitable for their establishment. Because the adults of these species (particularly _J_. _mertensianus_ and _S_. _tolmiei_) grow primarily in moist microsites, most seedlings emerging in drier microsites probably die before reaching maturity. Several species (_Carex spectabilis_, _Luetkea_, and _Phyllodoce_) produce viable seeds lacking innate dormancy, but their experimentally-sown seedlings failed to establish and naturally-occurring seedlings were rarely or never found. These species were also rare in the persistent seed bank, suggesting that their seeds have short life spans. A second hypothesis is that abundant seed production each year may allow these species to take

advantage of occasional years of suitable conditions for seedling establishment or increase the chances that, in many years, at least a few seeds will be dispersed to safe sites for establishment.

A third hypothesis, applying both to species abundant in the standing vegetation but not establishing, and to the Juncus species rare above-ground but abundant in the seed bank, is that these species cannot establish readily under the current environmental conditions on Park Ridge. The climate of the Pacific Northwest has been undergoing a warming trend since about 1900, in comparison with cooler temperatures for about 300 years previous (Graumlich and Brubaker 1986). Klikoff (1965) suggested that a drying trend in the Sierra Nevada since 1915 may be responsible for the degradation of dense Carex exerta-dominated communities to sparsely vegetated communities dominated by more drought-resistant species. Changes in climate may act on different population processes, such as seed production or seedling establishment. In the Front Range of Colorado, the graminoid Kobresia bellardii currently displays a skewed age structure and is not reproducing by seeds. Bell and Bliss (1979) attributed this current lack of viable seed production to higher temperatures, which trigger premature dispersal of seeds with partially-developed embryos. Reproduction in other alpine species is inhibited by high soil or air temperatures (e.g., Spomer and Salisbury 1968, Hermesh and Acharya 1987,

Billings and Mooney 1961). Climatic changes may also have significant effects on establishment of seedlings. Seedlings are highly sensitive to microsite conditions, and on Park Ridge establish almost exclusively in microsites that are partially shaded, have reduced surface temperatures, and greater moisture availability. The warming trend during this century has probably reduced the availability of such protected microsites. Reduction of safe sites may be a crucial factor influencing the establishment of species with slowly growing seedlings. On the other hand, warmer conditions may allow the establishment of more drought-tolerant species (e.g., Polygonum newberryi and Spraguea umbellata), that are currently rare or absent on the north exposure of Park Ridge, but abundant on open pumice soils throughout the High Cascades.

The fourth objective of this research was to intepret the overall patterns in the vegetation based on patterns of reproduction and recruitment of selected abundant species. The patterns of viable seed production, seed bank abundance, and seedling establishment in the species studied here do not fully explain the current vegetation patterns observed on Park Ridge. In long-lived species, it is difficult to assess, even over a several-year period, the effects of failures in reproduction and recruitment on overall population and community dynamics, because consistently low rates of establishment or rare

episodes of abundant establishment may balance mortality in these populations. In addition, populations of long-lived perennials may show long time lags in response to climatic changes (Davis 1986), because adult mortality is generally less sensitive than is recruitment to environmental changes.

The current species composition of the northern exposure of the study area may reflect both the cooler past environment and recent release from permanent snow. Henderson (1974) hypothesized a successional sequence on newly released substrates on Mt. Rainier from <u>Saxifraga tolmiei</u> to <u>Carex</u> meadow, to <u>Phyllodoce</u> - <u>Cassiope</u> heath, to subalpine forest, suggesting an upward migration of forest species to sites now dominated by herbs and shrubs. On Park Ridge, succession on newly released substrates is restricted by very late snowmelt, lack of propagules of tolerant species, sparsity of colonizable substrates, unstable soils, high surface temperatures, disturbance by needle ice formation, and inhibition of seedling establishment by mature plants. Eventual invasion by trees is likely to be quite slow and intermittent, as has been observed elsewhere in the Pacific Northwest (Brink 1959, Franklin et al. 1971, Henderson 1974), requiring a combination of abundant seed production, early snowmelt, and availability of suitable microsites for seedling survival. On Park Ridge, recent tree establishment has been limited to heath communities on the lower portion of

the study area. A combination of late snowmelt, high water table, and frost formation may inhibit tree invasion into Carex meadows (Schuller 1978).

The study of reproductive dynamics in undisturbed communities such as Park Ridge has implications for the response of alpine and subalpine vegetation to human-caused disturbances. Vegetation cover of alpine sedge and herb communities is rapidly lost through human disturbances such as trampling (e.g., Bell and Bliss 1973). Willard and Marr (1971) suggested that up to 1000 years may be required for the recovery of disturbed Kobresia meadows following 25 years of trampling by visitors. The slow recovery of such communities is attributable to the short growing season, low primary productivity, lack of seed availability, and low rates of seedling establishment.

On Park Ridge, seedling establishment is very low both in the presence of vegetation and in bare soil. Thus, although buried seeds are abundant even in bare soils, colonization of extensive barren areas with poorly-developed soils will be extremely slow. If vegetation cover is removed by human activities, soil surfaces will undergo greater diurnal temperature fluctuations and disturbances such as needle ice formation will increase, resulting in other forms of erosion (Soons 1967). On this subalpine site, human disturbances would be expected to have particularly inhibitory effects on the already slow

development of vegetation through direct destruction of aboveground cover and reduction of seedling establishment.

Figure V-1. Generalized life cycle showing factors constraining reproduction and recruitment of the five study species at various life history stages. Solid lines indicate stages examined in this study; dashed lines indicate stages not examined.
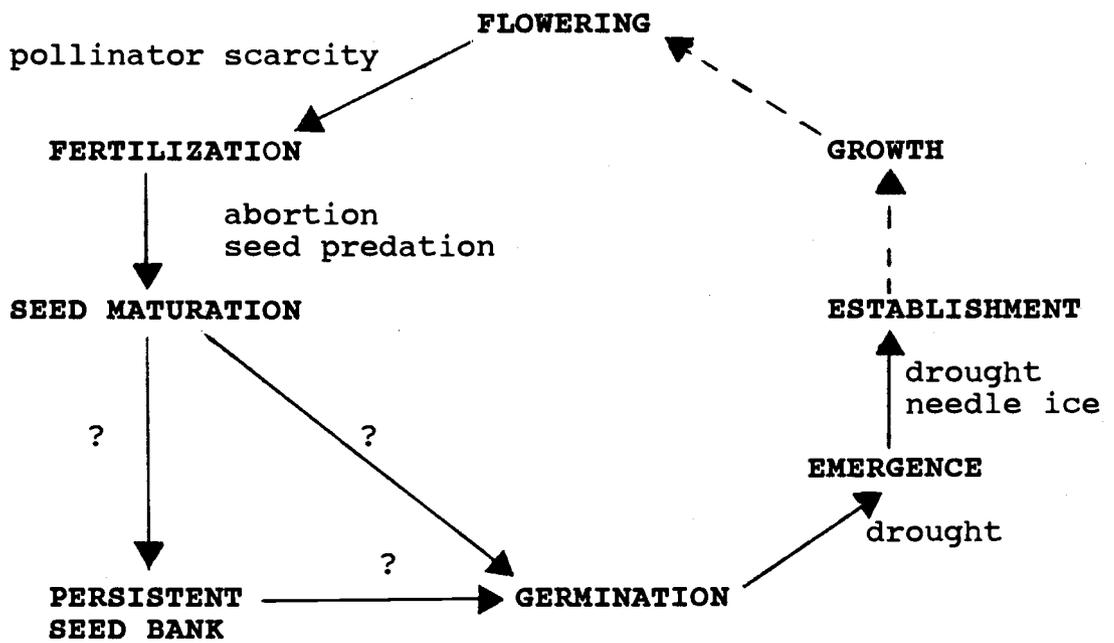
Figure V-1.

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