Ecological Monographs (1977) **47**: pp. 113–150

ALPINE AND HIGH SUBALPINE PLANT COMMUNITIES OF THE NORTH CASCADES RANGE, WASHINGTON AND BRITISH COLUMBIA[1]

GEORGE W. DOUGLAS[2]

AND

L. C. BLISS

Department of Botany, University of Alberta, Edmonton, Alberta, Canada

Abstract. Community types were described from 209 stands in the alpine zone of the North Cascades Range. The maritime to continental climatic change from west to east has a profound effect on regional vegetation patterns. Most of the community types in the eastern North Cascades are closely related to those in the Rocky Mountains, southern Alaska and the southern Yukon whereas communities in the western North Cascades are more similar to communities in other west coast ranges.

Soils in the region include Entisols, Inceptisols, and Spodosols. Physical properties are quite similar in most soils. Organic matter, total cation exchange capacity, and pH generally decrease from west to east while exchangeable cations and nutrient levels are low throughout the region.

A fellfield-dry graminoid-mesic environmental gradient was examined on Grouse Ridge, Mt. Baker. High soil temperature and low soil moisture regimes were typical of the ridgetop fellfield. During drought periods, on the vegetated portion of the slope, soil temperatures decreased and soil moisture stress increased with distance downslope; a reflection of increased plant cover and greater evapotranspiration towards the base of the slope. Species at the base of the slope had reduced vigor and much lower leaf water potential than those upslope. Phenological patterns were closely related to date of snowmelt and early-season temperature regimes along the gradient.

Key words: Alpine; British Columbia; high subalpine; microenvironment; North Cascades Range; phenology; plant communities; soils; species diversity; Washington; water relations.

INTRODUCTION

Alpine environments have interested some ecologists for many years. These extreme environments provide an excellent opportunity for the study of species and community patterns. The patterns are usually accentuated in alpine regions because of topographic diversity and often change abruptly due to rapid shifts in environmental gradients. Several other advantages of alpine vegetation studies are the relatively small flora, the dwarfed stature of the plants, and the reduced community structure (Bliss 1969).

High mountain vegetation in the Northwest Pacific Coast region has received attention only recently. The rugged physiography of the region, its inaccessibility, and a frequently unfavorable summer climate have all contributed to this lack of ecological study. Studies have been completed in the Olympic Mountains of Washington (Bliss 1969; Fonda and Bliss 1969; Kuramoto and Bliss 1970), the western North Cascades of Washington (Douglas 1972), the southern Coast Range of British Columbia (Archer 1963; Brooke et al. 1970), and in the eastern North Cascades of British Columbia (McLean 1970). Localized or more general accounts of the vegetation or flora have been provided for the Olympic Mountains (Peterson 1971), the western North Cascades of Washington (Franklin and Dyrness 1973; Kruckeberg 1969; Douglas 1971; Douglas and Ballard 1971; Lowery 1972), the eastern North Cascades of Washington (Arno and Habeck 1972), the southern Coast Range of British Columbia (Brink 1959), and the interior plateau region of south-central British Columbia (Eady 1971). A general phytogeographic survey of northwestern North America has been presented by Schofield (1969).

This study examines the plant communities of the alpine zone in the North Cascades of Washington and British Columbia. Because of its greater accessibility and general representativeness of the western North Cascades, a more detailed study of microenvironment and plant response was conducted on Grouse Ridge, Mt. Baker. The objectives of the study were to: (1) obtain quantitative and qualitative data on the composition, structure, and pattern of the plant communities of the region; (2) obtain information on the soils associated with the major plant communities;

[1] Manuscript received 30 October 1975; accepted 23 August 1976.

[2] Present address: Douglas Ecological Consultants Ltd., 406—912 Selkirk Ave., Victoria, British Columbia, Canada.

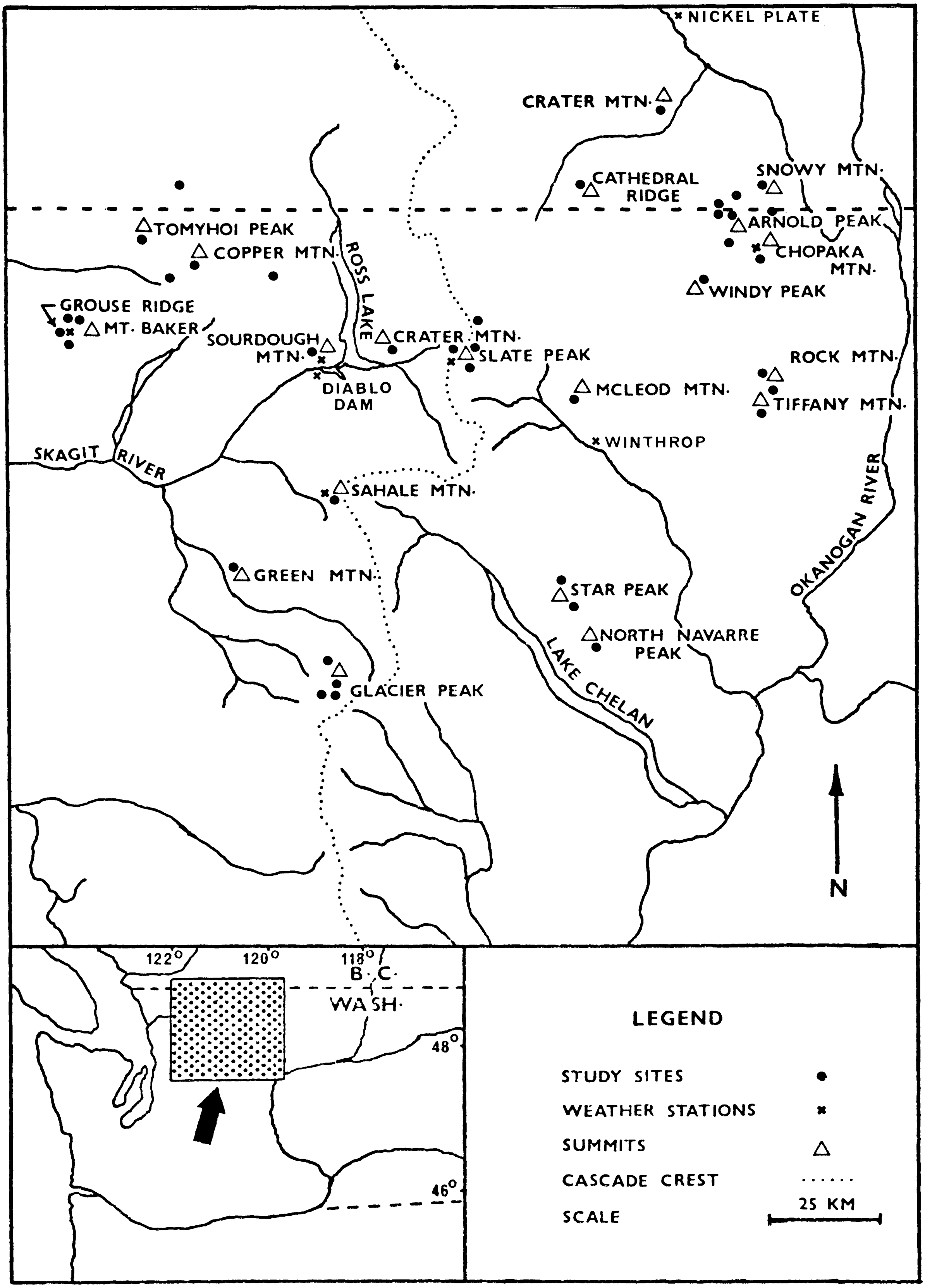


FIG. 1. Map of the study sites in the North Cascades Range of Washington and British Columbia.

(3) acquire mesoclimate data from several localities in the region; (4) determine the interrelationships between soils, climate, and plant communities and develop a comprehensive classification or ordination system for the alpine vegetation of the region; (5) examine in detail several communities along an environmental gradient in a localized area and compare them with regard to their composition, structure, pattern, pedology, microclimate, phenology, physiology (water relations), and snowmelt pattern; and (6) relate the distribution of the North Cascadian alpine and high subalpine communities to other areas in western North America.

Study Area

Location

The Cascade Range, extending from southern Oregon to just north of the Washington-British Columbia border, can be subdivided into a number of ecological provinces on the basis of geology, soils, topography, climate, and vegetation. The northernmost of these provinces, the western and eastern North Cascade provinces (Douglas 1972), were selected as the site of this study (Fig. 1). The area extends for about 130 km in a north-south direction, encompassing about 18,000 km^2.

The alpine zone is defined as that area above the occurrence of upright trees including krummholz and some subalpine communities. This zonation system has been used in the Cascade Range of northern Washington and British Columbia and the St. Elias-Kluane Ranges of southwestern Yukon by Douglas (1971, 1972, 1974) and differs only slightly from that proposed by Dansereau (1957) and Meusel et al. (1965) and recommended by Löve (1970).

Dansereau (1957), Meusel et al. (1965), and Löve (1970), however, include the krummholz belt within the subalpine zone. In contrast, a number of workers have included krummholz within the alpine zone (e.g., Clausen 1965; Bliss 1969; Krajina 1969; Kawano 1971; Franklin and Dyrness 1973). Vegetational and floristic data acquired during the present study substantiate the inclusion of krummholz within the alpine zone, at least in the North Cascade Range.

The lower limit of the alpine zone ranges from 1,950 m on the west side of the range to 2,100 m on the east side. The highest continuous cover of alpine vegetation found on the western side was at 2,176 m. Above this, and often at lower elevations, sheer rocky slopes, snowfields, and glaciers restrict the establishment of continuous vegetation. The upper limit of continuous alpine vegetation increases eastward, with the highest communities at $\approx$ 2,600 m on the eastern side of the North Cascades.

Geology and geomorphology

The complex geologic history of the North Cascades has been studied in some detail by Misch (1952, 1966). The oldest rocks are crystalline basement rocks (mainly gneisses). They predate the strata of sedimentary and volcanic rocks, including Middle Devonian fossiliferous limestones. During the Late Paleozoic Era, depositions of clastic sediments took place on the floor of a vast shallow sea. These thick deposits were associated with a geosyncline that extended from Alaska to California. The clastic sediments include graywacke, shale, and sandstone. At this time, volcanic eruptions also contributed basaltic and andesitic rocks to the deposition. These ancient geosynclinal rocks were then metamorphosed during a period of compression and folding which occurred simultaneously with the withdrawal of the sea during the Jurassic. Resulting metamorphic rocks include slate, phyllite, schist, and greenschist. During Middle to early Late Cretaceous time, major orogeny occurred in the North Cascades.

In the Tertiary, further deposition, erosion, volcanism, and orogeny took place. Granites, diorites, quartz diorites, and granodiorites in the central and eastern parts of the range were formed. Final uplifting of the North Cascades took place in the Pliocene and subsequent weathering, mass wasting, and erosion contributed to the deeply dissected landscape of today. Schist, gneiss, and granite outcrops predominate throughout most of the range.

During late Pliocene and early Pleistocene times, the volcanic cones of Mt. Baker and Glacier Peak (3,712 and 3,181 m, respectively) were superimposed on the existing range and other volcanic cones were formed (Coombs 1939).

Although the period of major volcanic activity appears to have been at the beginning of the Pleistocene epoch, there were later eruptions and flows. In the North Cascades, ash layers originating from Glacier Peak, Mt. Mazama, Mt. St. Helens have been recognized. The oldest of these ashfalls is that from Glacier Peak 12,000 years before present (YBP) (Powers and Wilcox 1964). Additional eruptions occurred more recently (ca. 6,600 YBP—Mt. Mazama; 3,000 and 500 YBP—Mt. St. Helens; and 2,300 and 2,000 YBP—Mt. Rainier) (Wilcox 1965; Westgate et al. 1969; Crandell et al. 1969). These deposits influence soil horizonation in some areas.

The continental ice sheet and alpine glaciers advanced and receded 2× in the North Cascades during the Salmon Springs Glaciation of the late Pleistocene (early to middle Wisconsinan) (Crandell 1965). The broad, U-shaped valleys of the region were filled with ice during these advances. Evidence of this past glaciation can be seen throughout the range in the

TABLE 1. Climatic data for weather stations in the Cascade Range[a]

Weather station	Elevation (m)	Total precipitation (cm)		Mean temperature (°C)	
		Annual	June to August	Annual	June to August
Diablo Dam	272	189	14	9	17
Winthrop	535	37	6	7	19
Stevens Pass	1,245	192	15	4	12
Mt. Baker	1,265	280	28	5	12
Allison Pass	1,341	175	12	3	13
Mt. Rainier[b]	1,691	253	13	4	11
Nickel Plate	1,768	60	15	2	10

[a] Data from British Columbia Department of Agriculture (1963) and U.S. Weather Bureau (no dates).
[b] The Mount Rainier (Paradise) station is located 120 km south of the study area.

form of cirques, jagged ridges, steep-walled valleys, and the rounded tops of the lower mountains. Numerous, relatively small remnants of the once extensive alpine glaciers still remain in the region.

More recently alpine glaciers (Fraser Glaciation—ca. 25,000 YBP and Neoglaciation—ca. 2,000 YBP), continental ice advance (ca. 15,000–13,000 YBP), and the Hypsithermal Interval (ca. 10,000–5,000 YBP) have further modified the landscape.

Climate

The climate of the North Cascades varies considerably from maritime on the western slopes to more continental on the eastern slopes. Due to the prevailing westerlies from the Pacific Ocean crossing the mountain massif, annual and summer (June to August) precipitation is considerably lower on the eastern than on the western slopes (Table 1). The subalpine Mt. Baker station is probably representative of conditions on the western slopes with a mean annual precipitation of 280 cm and a mean summer precipitation of 28 cm. The subalpine Nickel Plate station, on the eastern flanks of the Cascades, is probably representative of conditions in that region (mean annual precipitation of 60 cm and a mean summer precipitation of 15 cm).

METHODS

Vegetation

A general reconnaissance of the alpine zone of the North Cascades was made in early summer 1970, and during a previous study (Douglas 1972). From this survey, tentative plant community types, recognized by their dominant species and plant structure, were delimited. Relatively homogeneous stands (with respect to floristics and plant structure) representing these types were then selected for sampling. The term "stand" refers to a particular example of vegetation that was sampled and "community" or "community type" to a grouping of similar stands. A total of 209 stands, varying in size from 150 to 1,500 m², were sampled on 39 mountains in the study area (Fig. 1). The community types were sampled by 4 to 10 stands. Rock outcrops and streamsides were not sampled.

For the regional survey, in examining all but the krummholz stands, twenty 20 × 50 cm quadrats were set out perpendicular to the slope contours by a restricted random technique (Bliss 1963) in a 5 × 10 m area. Numerous alpine studies in North America have shown this to provide a sample of adequate size, including nearly all species in a stand. Crown cover, using the methods and cover classes of Daubenmire (1959, 1968), was estimated by strata for all plant species (except cryptogams on rocks and trees) in each quadrat. Additional species, which occurred outside the quadrats but within the stands, were also tallied. Frequency and average cover for each species were calculated and converted to prominence values (PV) by multiplying the average percentage cover by the square root of the species frequency in each stand. This modified index of Beals (1960) provides a method by which cover and frequency may be combined into a single value for use in equations and more easily interpreted tables.

Sampling replications were repeated three times in each of three stands, all differing in composition and structure. The replications indicated that, for all of the most prominent species, sampling was within ±14% of the mean prominence value for communities with continuous plant cover and ±26% for species in communities with discontinuous (boulderfield and fellfield) cover. The average coefficient of similarity was also computed for the replicates using the formula $c = 2w/(a + b) \times 100$ (Gleason 1920), where w is the sum of the lowest prominence values of species common to both stands, and a and b are the total prominence values of all species in stands a and b. Replicated samples from the same stand had average similarity coefficients of 0.78 to 0.81 when plant cover was continuous, whereas the average fellfield similarity coefficient was only 0.47. Sampling adequacy also met the "minimal area" criteria (Cain 1938). Sampling was terminated, in almost all cases, well after the plateau in the species-area curve was reached. Minimum stand size was ≈ 150 m². Krummholz stands were examined by a "releve" method, since their size and floristic composition were extremely variable. Each stand was divided into four equal quarters and the crown cover for all species was estimated by visual observation in each quarter. Forty-two stands, varying in size from 25 to 100 m^2, were treated in this manner.

A third sampling procedure was used for analysis of species distribution along a 65 × 7 m belt transect on Grouse Ridge, Mt. Baker. At 2-m intervals down the slope, five 20 × 50 cm quadrats (from a possible 10), were randomly selected and set out at 5-dm intervals along and perpendicular to the slope contours.

Similarity coefficients ($C = 2w/(a + b) \times 100$) between stands were computed. Species were not adjusted in relation to their maximum values of frequency and cover as in Bray and Curtis (1957). Dissimilarity values ($1 - C$) were then computed and used for the construction of two-dimensional ordinations (Bray and Curtis 1957; Beals 1960). The ordinations allowed the grouping of stands into community types that correlated with several environmental gradients. Several agglomerative hierarchical clustering techniques (Pritchard and Anderson 1971), were also used for syntheses of herbfield, boulderfield, fellfield, and vegetation stripe communities. Community types are named after the one or two major dominants.

Nomenclature, authorities, and taxonomy follows Hitchcock and Cronquist (1973) for the vascular plants, Lawton (1971) for mosses, Schofield (1968) for hepatics, and Hale and Culberson (1970) for lichens, with the following exceptions. The lichens *Cladonia gracilis* (L.) Willd. and *Peltigera canina* (L.) Willd. were not treated at the varietal level since the variants were often indistinguishable. *Thamnolia vermicularis* (Sw.) Ach. *ex* Schaer, has been included with *Thamnolia subuliformis* (Ehrh.) W. Culb. Chemical tests revealed that 25% of all material collected was *Thamnolia vermicularis.* In the text only the binomial is used for any plant having just one variant in the North Cascades. A full set of voucher specimens has been placed in the University of Alberta herbarium (ALTA). Partial sets are in the Department of Agriculture (Ottawa) (DAO), New York Botanical Garden (N.Y.), U.S. Forest Service (Fort Collins, Colorado), University of Washington (WTU), and Western Washington State College herbaria.

Soils

Soil pits were dug in 16 representative communities across the North Cascades and composite samples collected from each described horizon. Seven additional pits were dug along the environmental gradient on Grouse Ridge. Samples were collected from two additional soil pits opened by Bockheim (1972). Laboratory analyses of the fine (<2 mm) fraction included: texture by the hydrometer method (Bouyoucos 1951); pH using a saturated paste (Doughty 1941); and organic matter by the Walkley-Black wet oxidation method (Walkley and Black 1934). Exchangeable cations were extracted with neutral *N* ammonium acetate and determined by atomic absorption spectrophotometry. Levels of nitrogen, phosphorus, and potassium were determined at the Alberta Soil and Feed Testing Laboratory: nitrogen was determined by the phenoldisulfonic method; phosphorus by the combined nitric acid-vanadate-molybdate colorimetric method; and potassium was extracted with *N* ammonium acetate at pH 7.0 and determined by flame photometry. Soil color was described for moist soil using the Munsell Color Charts in natural light.

Microenvironment

Because of the large climate gradient across the mountains, summer mesoenvironment (i.e., temperature, atmospheric moisture, solar radiation, precipitation, and wind) in the North Cascades was monitored at five different locations (Fig. 1) during the summers of 1970 through 1972 at approximately weekly intervals. Temperature and atmospheric moisture were monitored with Belfort and Lambrecht hygrothermographs placed in white-painted, louvered shelters with sensors between 5 and 25 cm above the ground. Solar radiation was measured with Rabitsch actinographs set with sensors 10 cm above and parallel to the soil surface. Precipitation was measured with Trucheck® rain gauges set at 60 cm above and parallel to the soil surface. Wind was monitored with Belfort three-cup totalizing anemometers with cups placed 60 cm above the ground. These sensor positions were used to enable comparisons with data from previous studies and because of the physical limitations of the instruments used.

Microenvironment was monitored during the study period along the environmental gradient on Grouse Ridge. Four stations were established at 15- to 25-m intervals for a distance of 61 m down the slope. Soil and air temperatures were measured with laboratory-calibrated RCA™ 1N2326 diodes, set in #3M Scotchcast™ No. 10 electrical resin. Soil temperature diodes were placed in 13 mm (outside diameter) aluminium pipe probes, sealed off, and buried horizontally at depths of 2, 10, 20, and 30 cm. Air temperature diodes were placed in double-shielded, open aluminum tubes, painted white outside and silver inside. These diodes were located at heights of either 5 and 15 cm or 10 and 20 cm; the latter heights being used for the taller vegetation at the base of the slope. Resistances were measured with a bridge meter powered by a mercury battery cell. Field measurements were precise within ±0.5°C. Coleman soil moisture blocks (Coleman and Hendrix 1949) were positioned in the same pits with the diodes at depths of 10 and 20 cm or 10 and 30 cm, the lower depth was determined by depth of the root system. Soil moisture was also determined periodically (approximately monthly) with gravimetric samples taken at the same depths and within 2 m of the Coleman blocks. Available soil moisture (0.3 and 15 bars) was determined from desorption curves run on the <2 mm soil fraction. Temperatures and soil moisture data, except during July 1972, were collected at approximately weekly intervals.

Phenology

Phenological stations were established at 10-m intervals along the 70-m belt transect on Grouse Ridge. Phenological notes were taken on 32 species at weekly intervals during 1971 and bi- to tri-weekly intervals during 1972. Observations, within a 2 × 2 m plot at each station, included the following phases: vegetative, flowering, fruiting, seed dispersal, and dormancy.

Plant water relations

Leaf water potential (ψ) was determined in the field during 1971 for 10 species on Grouse Ridge with a portable pressure chamber (Scholander et al. 1964).

Leafy stems or leaves cut at the petiole were put directly into plastic bags from which all possible air was expressed. The bags were sealed, kept at ambient temperature out of direct sunlight, then measured within 0.5 h of cutting. This procedure had little, if any, effect on leaf ψ (Hickman 1970). Measurements were made between 1300 and 1500 h and at 2400 h, times of near minimum and maximum leaf ψ, respectively (Hickman 1970; Kuramoto and Bliss 1970).

Results

Regional vegetation

Two-dimensional ordinations were constructed, using prominence values, to provide an understanding of alpine community relationships and patterns (Fig. 2). Since high beta diversity, or a high degree of compositional change between communities along gradients (Whittaker 1960), reduces ordination performance (Gauch and Whittaker 1972) the North Cascadian communities were treated as three separate regions (west, central, and east). Although the ordinations are based only upon floristic dissimilarities between sample stands, the stand groupings or community types do indicate some general environmental relationships. Time of snowmelt is the most obvious environmental factor illustrated by the ordinations (Fig. 2).

Snowbed community types.—Six community types in the North Cascades are consistently associated with snowbed habitats. Several others, are not restricted exclusively to snowbeds, but occur in them in at least part of their range. They are discussed within the shrub community types.

a) *Saxifraga tolmiei-Luzula piperi* community. This community occurs on gentle to moderately steep, mainly southerly slopes in the western North Cascades (Fig. 3). Snow remains until late July or early August. Soils are poorly developed, poor to fairly well drained, and show indications of surficial movement. A similar habitat and plant community occurs in the subalpine zone of the western North Cascades (Douglas 1972).

The *Saxifraga-Luzula* community is characterized by a low average total plant cover and few species per stand (Tables 2 and 3). *Saxifraga tolmiei* and *Luzula piperi* are the only constant species. Other less prominent plants are *Carex pyrenaica, Juncus drummondii*, and the bryophytes, *Polytrichum sexangulare* and *Marsupella brevissima.*

b) *Eriogonum pyrolaefolium-Luzula piperi* community. In the central North Cascades (Fig. 3), this community type is most commonly found on slight to moderately steep, northern slopes. This habitat is similar to that of the *Saxifraga-Luzula* type found farther west. Snowmelt is late (early to late July) and soil surfaces are unstable. These sites, in contrast to the *Saxifraga-Luzula* habitat, are well drained and have a lower soil moisture content in late summer.

This community type, with low average total plant cover and relatively few species, is the most sparsely vegetated of all the alpine communities examined. *Eriogonum pyrolaefolium* and *Luzula piperi* are the only constant species.

c) *Carex nigricans* community. Concave to level, poorly drained sites are typical of this community throughout its western to central range in the North Cascades (Fig. 3). This type has the greatest snow accumulation and shortest snow-free period of all habitats in the region, with snow persisting until late July or early August, or in years of high snowfall, early September. Soils are poorly drained and remain moist for most of the summer. This type is also common in the subalpine zone of the western North Cascades.

Carex nigricans forms a low, dominant mat with a high average cover and frequency. Other prominent species are *Luetkea pectinata* and *Deschampsia atropurpurea* (Table 2). *Polytrichadelphus lyallii, Kiaeria blyttii, Lescuraea radicosa*, and the lichen *Lepraria neglecta* are important cryptograms.

d) *Antennaria lanata* community. This type is found from the central to eastern North Cascades

(Fig. 3) in snowbed habitats similar to those of the *Carex nigricans* type. In the central North Cascades, where the ranges overlap, the two communities may be found adjacent to each other. The *Antennaria* type, however, becomes snow-free 2 to 4 wk earlier (late June to late July) and since the soils have better drainage, the sites become drier during late summer.

Plant cover of the *Antennaria* community is similar to that of the *Carex nigricans* community but a greater contribution is made by mosses and lichens in the former. The *Antennaria* community is also floristically richer. *Antennaria lanata* has a high frequency and a moderate mean cover. *Carex nigricans* and *Leutkea pectinata* are important components in the central North Cascades with *Salix cascadensis* and *Carex scirpoidea* var. *pseudoscirpoidea* becoming prominent farther east. *Polytrichum piliferum* and *Lepraria neglecta* are common cryptograms throughout the range whereas *Cetraria islandica* is important in the eastern North Cascades.

e) *Carex breweri* community. This snowbed type occurs mainly in concave sites in the eastern North Cascades although several stands were encountered on slight slopes just south of Glacier Peak (Fig. 3). These well-drained sites are snow-free by the latter part of July, and become dry during late summer. A large number of xerophytic species (e.g., *Carex scirpoidea* var. *pseudoscirpoidea*, *Carex nardina*, etc.) occur here.

Carex breweri has a moderate average cover and a high frequency in this floristically rich community. *Erigeron aureus*, *Lupinus lepidus* var. *lobbii*, and *Danthonia intermedia* occur with moderate frequency and relatively low cover. Prominent cryptogams are *Polytrichum piliferum*, *Kiaeria blyttii*, *Lepraria neglecta*, and *Cetraria islandica* (Table 2).

f) *Carex capitata* community. This is a common type at higher elevations (2,300 m to 2,450 m) in

→

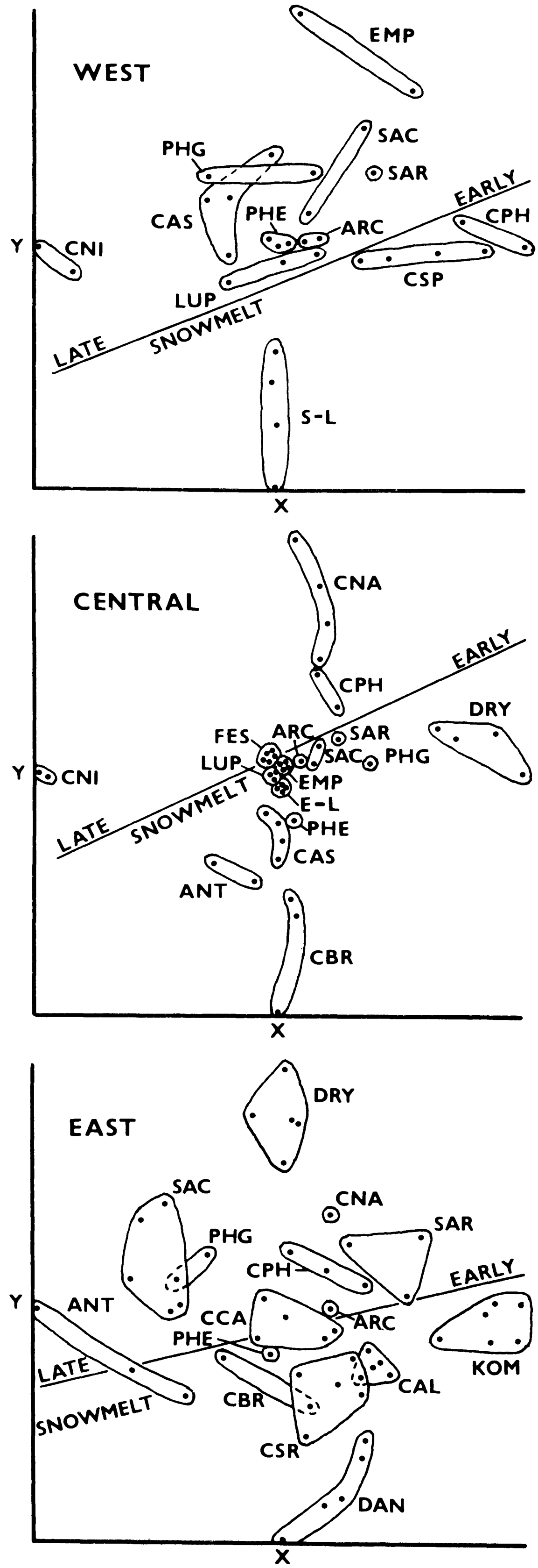


FIG. 2. Ordination of 128 stands in the alpine zone of the North Cascades. The stands are included in three ordinations according to region (west, central, and east). Lines delimit community types whose names are derived from the dominant species. Abbreviations: S-L—*Saxifraga tolmiei-Luzula piperi*; E-L—*Eriogonum pyrolaefolium-Luzula piperi*; CNI—*Carex nigricans*; ANT—*Antennaria lanata*; CBR—*Carex breweri*; CCA—*Carex capitata*; LUP—*Lupinus latifolius*; FES—*Festuca viridula*; CAS—*Cassiope mertensiana*; PHE—*Phyllodoce empetriformis*; PHG—*Phyllodoce glanduliforia*; ARC—*Arctostaphylos uva-ursi*; EMP—*Empetrum nigrum*; SAR—*Salix nivalis*; SAC—*Salix cascadensis*; DRY—*Dryas octopetala*; DAN—*Danthonia intermedia*; CAL—*Calamagrostis purpurascens*; CSP—*Carex spectabilis*; CPH—*Carex phaeocephala*; CSR—*Carex scirpoidea* var. *pseudoscirpoidea*; CNA—*Carex nardina*; KOM—*Kobresia myosuroides*.

TABLE 2. Composition of plant community types in the alpine zone of the North Cascades Range. Data are for prominence value indices

Species	Community types[a,b,c]																						
	S-L (4)	E-L (4)	CNI (4)	ANT (5)	CBR (5)	CCA (5)	LUP (6)	FES (4)	CAS (8)	PHE (5)	PHG (5)	ARC (4)	EMP (7)	SAR (5)	SAC (9)	DRY (10)	DAN (5)	CAL (5)	CSP (4)	CPH (7)	CSR (5)	CNA (5)	KOM (6)
VASCULAR SPECIES																							
Saxifraga tolmiei	135																						
Luzula piperi	46	18	14	2			13		12	1	1		T		2								
Carex pyrenacia	26	4		1	9																		
Juncus drummondii	12		21	8					1														
Carex nigricans	5		733	26			1		7	14			T										
Phyllodoce empetriformis	1						4		38	307													
Carex spectabilis	1		2	13			180		10		19	136	4		3				547	1		T	
Luetkea pectinata	1		261	28			23		102	16	33												
Hieracium gracile	T		8	T			13	T	2	1	6		1										
Vaccinium deliciosum	T						91		64	68	58		2										
Eriogonum pyrolaefolium		46																					
Erigeron aureus		4		1	60	5				T	10	T	3	14	17	5	1	2		1	6	22	7
Poa sandbergii		2		P	T	6						10		2	T	1	8	4		14	19		
Antennaria lanata		1	31	346	22	14	18	63	43	42	4		9		2		12			2			
Sibbaldia procumbens		1		7	7	8	T		1	5	22		8		T	T	1		38	3	2	1	1
Haplopappus lyallii		T			6			P			T	T		1	2	T	T	12		3	7	4	18
Agoseris glauca var. *dasycephala*		T					3	59				4	2				2	3		15	12	P	T
Sedum lanceolatum var. *lanceolatum*		T		3	5	1		T		T	3	1		4	8	10	9	1	2	21	7	10	2
Festuca ovina var. *brevifolia*		T		8	20	52			3	8	4	22	9	31	43	13	13	40	20	40	52	31	39
Antennaria alpina		P			21	15			T	T			T	8	4	3			30	11	2	18	
Deschampsia atropurpurea			75	T			15		2	T	T												
Erigeron peregrinus var. *scaposus*			35				49	4	3	9							3		2				
Veronica cusickii			2	4		1	28	8	2				T						1				
Phyllodoce glanduliflora			1	2			13		83	7	352		27		P	P	T						
Potentilla flabellifolia			1				25	58	T		1												
Salix cascadensis				108		62					19		15	2	246	P							
Carex scirpoidea var. *pseudoscirpoidea*				75	25	51					T	14		13	5	T	232	210		80	346	2	120
Arenaria capillaris				18	11		14	60	T	8	12	1	1	7	3	T	104	T		22	31	P	T
Arenaria obtusiloba				21	10	11					1	9		16	12	16	71	100		56	48	30	74
Carex breweri				20	317										3				67	5			
Luzula spicata				11	2	7		1		T	T	2	3		2	T	3	10	4	25	30	7	8
Carex phaeocephala				13	20	28		1		P	2			1	16	2	2	3	19	261	91	15	1
Cassiope mertensiana				3			4		408	75	2		T										
Trisetum spicatum				2	6	11	4	3	T	2	1	3		11	9	T	3	10	1	6	14	2	29
Stellaria longipes				1	T	11					T	8		3	T		6	5		7	17	T	12
Poa alpina				1	T	8				T	1	T	T	2	1			2		1	13		5
Selaginella densa				1		9					4	2		23	4	4	31	45	4	21	24	15	39
Potentilla diversifolia var. *diversifolia*				2	39	136	15	3		1	T	14		14	5	2	221	85	5	73	105	2	73

TABLE 2. Continued

Species	Community types[a,b,c]																						
	S-L (4)	E-L (4)	CNI (4)	ANT (5)	CBR (5)	CCA (5)	LUP (6)	FES (4)	CAS (8)	PHE (5)	PHG (5)	ARC (4)	EMP (7)	SAR (5)	SAC (9)	DRY (10)	DAN (5)	CAL (5)	CSP (4)	CPH (7)	CSR (5)	CNA (5)	KOM (6)
Lupinus lepidus var. *lobbii*				T	55				T			T	26	23		19			5	17	T	58	
Dryas octopetala				T	T						13			1	14	214		T			T		7
Carex pachystachya				P	T	40					1										1		
Danthonia intermedia					41	1	41					8					559		55	T	27		T
Solidago multiradiata					20	76	20				4	6	7	8	1	1	33	14	155	21	14		53
Silene acaulis					10	1								1	T	T	1	5	P	2	6	1	7
Phlox hendersonii					9																	57	
Agrostis variabilis					6	12					11	4	T				1	1		1	1		15
Polygonum viviparum					4	33					T	T		1	11		1						2
Achillea millefolium					3	T	2	4			P	8					19		40	8	13		1
var. *alpicola*																							
Carex capitata					2	569						10		4	1		8			6	P		
Vaccinium caespitosum					2	2	1				4	2	11										
Carex nardina					1						T			10		3	18			T		179	T
Erigeron compositus					1							4		3		2	2	2		11		9	
var. *glabratus*																							
Smelowskia ovalis					1									16	T	1		4		T		29	1
Salix nivalis					T	6							16	299	1			T		2			78
Empetrum nigrum					T		6		4		3	503		T								P	
Kobresia Myosuroides					T									4			T	P					423
Cerastium arvense					T									1				T	47	2	4		T
Oxytropis campestris						14						16		36	P	2	46	105	P	30	11		78
var. *gracilis*																							
Antennaria umbrinella						12						1	6				17	13	1			10	18
Penstemon procerus						2	3	T	T	1		T	6		2	T	7	T	9	22	3	1	
Calamagrostis purpurascens						T								T		3	2	379		3	P	2	P
Sedum roseum						T								T	T			P			10		
Lupinus latifolius							622	59	6	1		1	5						3				
var. *subalpinus*																							
Polygonum bistortoides							163	24	1		3	18	4						38				
Festuca viridula							81	474					3										
Valeriana sitchensis							46																
Phlox diffusa							26	4	2	9		2	5	2	T				216	33			
Anemone occidentalis							17	T					2										
Aster foliaceus							12												T				
var. *foliaceus*																							
Juncus parryi							9	56	5	5													
Vaccinium scoparium							5	1	1	38	P												
Erythronium grandiflorum							2	26															
Pedicularis contorta							2	4					T						14				
Artemisia norvegica								55															
Arnica rydbergii								33															
Pedicularis racemosa											14												
var. *racemosa*																							
Arctostaphylos uva-ursi										1		615	3		T	T							

TABLE 2. Continued

Species	S-L (4)	E-L (4)	CNI (4)	ANT (5)	CBR (5)	CCA (5)	LUP (6)	FES (4)	CAS (8)	PHE (5)	PHG (5)	ARC (4)	EMP (7)	SAR (5)	SAC (9)	DRY (10)	DAN (5)	CAL (5)	CSP (4)	CPH (7)	CSR (5)	CNA (5)	KOM (6)
	Community types[a,b,c]																						
Lycopodium alpinum											15												
Carex albonigra												13		T		3	5	1		T	4		1
Campanula rotundifolia												P	6	T					37	1			
Cassiope stelleriana													19										
Agrostis scabra													1						T	11		1	
Silene douglasii																	14			3	1		
BRYOPHYTES																							
Polytrichum sexangulare	10			11										T									
Marsupella brevissima	10																						
Pohlia nutans	1		T	18					1	T				T	1								
Polytrichum piliferum		8	4	161	128	4	1	8	19	50	44	T	12	9	68	10	20	T	123	53	19	7	2
Rhacomitrium canescens		2			T	1			5	1			11	T	2				1	1			
var. *ericoides*																							
Polytrichum juniperinum		1		50	6	85			T		6	12	1	19	4	T	39	28	2	20	4	18	35
Polytrichadelphus lyallii			74	2		22			2	T						T							
Kiaeria blyttii			36		70				2		5												
Lescuraea radicosa			24						1														
Dicranum spadiceum			14																				
Bryum cf. *angustirete*				11	3						4				3		T			1	4	2	
Desmatodon latifolius					3	T								18				T	1	T	10	4	T
var. *latifolius*																							
Tortula ruralis					1	21						2		10		1	37	5	18	22	65	25	96
Aulacomnium palustre					1	12																	
Dicranum muehlenbeckii						87															4		
Drepanocladus uncinatus						29					T				T								
Bryum cf. *pallens*						15									1								
Ceratodon purpureus						4		5			8			1	T				14	1			
Bryum caespiticum								1						T			1	5	T	3	2		15
Dicranum fuscescens								T	37														
Dicranum scoparium											33									2	1		12
Dicranum tauricum												T							10	T			
Heterocladium dimorphum														1					12	T			
Bryum weigelii																					43		
LICHENS																							
Lepraria neglecta	T	4	69	171	87	T			87	18	48			26	34	9			2	4	T	10	
Cladonia gracilis		T	T	3	4	2			3	T	11	1	1		T	T			139	41			
Cladonia pyxidata		T		33	24	39				T	4	1	9	2	13	3	23	36	14	43	29	12	59
Cladonia sp.		T		11	1			7	1	1	6			25	2	2				4	10		
Cetraria islandica		P	T	56	35	13			25	1	86	1	41	28	34	10	31	31		12	37	T	36
Peltigera canina		P		10	8	21	1	T	3	3	10	T	9	6	11	5	5		19	5	29	3	9
Solorina crocea		P		4	16				T	P			T	T	2	T							
Cladonia ecmocyna			T	8		1	20		5	T	4		4	T	1		T	T			T		T
Stereocaulon alpinum				16		2					3			9	7	16	1		6	20	T		T
Lecidea granulosa				15					2		T					T				5	34		

TABLE 2. Continued

Species	S-L (4)	E-L (4)	CNI (4)	ANT (5)	CBR (5)	CCA (5)	LUP (6)	FES (4)	CAS (8)	PHE (5)	PHG (5)	ARC (4)	EMP (7)	SAR (5)	SAC (9)	DRY (10)	DAN (5)	CAL (5)	CSP (4)	CPH (7)	CSR (5)	CNA (5)	KOM (6)
	Community types[a,b,c]																						
Cetraria nivalis				1	12	8					3	T		16	4	8	5	25	T	3	16	1	24
Thamnolia subuliformis				T	16	10				T	8	T	8	22	9	11	11	22	12	40	11	33	24
Cornicularia aculeata					17	T					3	T		21	9	12	6	44	T	15	8	46	16
Candelariella sp.					3									4	1	T				4	3	20	1
Lecidea rufonigra					1											T	T	2			3	1	11
Cladina mitis					1	6	1		7	T	24	T	5	4	4	T			81	38			
Ochrolechia upsaliensis					T	T							T	2	T	T	3	16		T	1	17	4
Buellia epigaea					T	2								1	1		T	2				22	1
Cetraria ericetorum						40	T					13	19		1	T	12	32	54	38	14	1	30
Cetraria cucullata						1										T	T	26		2	5		55
Cladonia bellidiflora						T				6	11									T			
Cladonia subsquamosa										17	T												
Cladonia coccifera											21												
AVERAGE COVER (%)																							
Vascular species	29	14	126	82	82	127	192	120	89	76	73	114	81	63	44	40	194	146	149	99	113	57	148
Bryophytes	4	2	18	26	23	35	2	3	4	11	11	2	3	8	10	2	12	6	22	13	19	6	23
Lichens		1	8	29	26	17	3	11	17	8	30	3	14	20	19	9	13	28	39	31	24	20	24
Bareground	21	58	2	4	11	4	9	26	12	12	16	13	19	12	25	19	5	6	16	9	7	26	3
Rocks	56	27		1	5	1			6	7	6	6	1	21	9	41	6	15		10	6	15	8
All plants ($\bar{x} \pm$ SD)	33 ±11	17 ±2	152 ±47	137 ±39	131 ±43	189 ±38	197 ±36	124 ±28	110 ±25	95 ±4	114 ±45	119 ±31	98 ±30	91 ±48	73 ±17	51 ±15	219 ±13	180 ±13	210 ±35	143 ±45	156 ±35	83 ±17	178 ±25
TOTAL NUMBER OF SPECIES																							
Vascular species	10	21	15	37	46	36	48	39	35	35	51	44	42	51	46	48	42	44	35	61	43	44	42
Bryophytes	6	3	6	6	10	14	2	6	9	6	7	5	6	15	11	4	7	6	13	18	13	8	7
Lichens	2	8	7	14	18	20	6	2	12	15	24	10	13	16	22	25	16	14	13	22	23	18	17
All plants	18	32	28	57	74	70	56	47	56	56	82	59	61	82	79	77	65	64	61	101	79	70	66
AVERAGE NUMBER OF SPECIES																							
Vascular species	5	12	9	15	16	20	17	24	13	14	17	18	12	22	16	17	25	25	18	21	22	20	27
Bryophytes	2	2	2	3	4	6	0	2	3	3	3	2	2	4	3	2	3	4	5	4	4	2	6
Lichens	1	2	2	7	7	9	1	1	4	6	10	3	4	12	10	10	8	12	7	9	9	10	12
All plants ($\bar{x} \pm$ SD)	8 ±2	15 ±8	14 ±5	25 ±5	27 ±14	35 ±6	18 ±3	27 ±6	20 ±3	22 ±4	30 ±6	23 ±12	18 ±6	38 ±8	28 ±6	28 ±6	36 ±8	41 ±7	30 ±4	34 ±7	35 ±7	32 ±3	44 ±6

[a] Abbreviations: S-L—*Saxifraga tolmiei-Luzula piperi*, E-L—*Eriogonum pyrolaefolium-Luzula piperi*, CNI—*Carex nigricans*, ANT—*Antennaria lanata*, CBR—*Carex breweri*, CCA—*Carex capitata*, LUP—*Lupinus latifolius*, FES—*Festuca visidula*, CAS—*Cassiope mertensiana*, PHE—*Phyllodoce empetriformis*, PHG—*Phyllodoce glanduliflora*, ARC—*Arctostaphylos uva-ursi*, EMP—*Empetrum nigrum*, SAR—*Salix nivalis*, SAC—*Salix cascadensis*, DRY—*Dryas octopetala*, DAN—*Dantonia intermedia*, CAL—*Calamagrostis purpurascens*, CSP—*Carex spectabilis*, CPH—*Carex phaeocephala*, CSR—*Carex scirpoidea* var. *pseudoscirpoidea*, CNA—*Carex nardina*, KOM—*Kobresia myosuroides*; T (trace) indicates a mean prominence value of less than 0.5, P (present) indicates that a species was present but not tallied in the community type.

[b] Number of stands sampled are enclosed in parentheses.

[c] Only those species with a prominence value of 10, or more, in at least one community type are included in this table.

TABLE 3. Summary of community characteristics for alpine and high subalpine communities, Northern Cascades Range

Community type	Region[a] W	C	E	Elevation range (m)	Aspect	Snowmelt date	Total no. species	Mean no. species	Mean cover (dominants) (%)	Mean frequency (dominants) (%)	Mean total plant cover (%)
Saxifraga tolmiei-Luzula piperi	×			1,750–2,100	South	Late Jul-early Aug	18	8± 2	15± 8 7± 6	78±17 35±24	33±11
Eriogonum pyrolafolium-Luzula piperi		×		2,000–2,200	North	Early-late Jul	32	15± 8	6± 1 3± 0	68±17 29±15	17± 2
Carex nigricans	×	×		1,750–2,100	All	Late Jul-early Aug	28	14± 5	75±18	95±10	152±47
Antennaria lanata		×	×	2,000–2,200	All	Late Jun-late Jul	57	25± 5	35±15	100± 0	137±39
Carex breweri		×	×	2,100–2,300	All	Late Jun-late Jul	74	27±14	32±11	92±15	131±43
Carex capitata			×	2,300–2,450	All	Early-late Jun	70	35± 6	57±15	100± 0	189±38
Lupinus latifolius	×	×		1,750–2,150	South	Late May-early Jun	56	18± 3	62±15	100± 0	197±36
Festuca viridula		×		1,850–2,150	South	Late May-early Jun	47	27± 6	48±12	96± 9	124±28
Cassiope mertensiana	×	×		1,750–2,150	South	Early Jun-early Jul	56	20± 3	42±11	94± 7	110±25
Pyllodoce empetriformis	×	×	×	1,750–2,150	South	Early Jun-early Jul	56	22± 4	34± 8	82±10	95± 4
Phyllodoce glanduliflora	×	×	×	1,800–2,400	All	Early Jun-late Jul	82	30± 6	36±22	89±14	114±45
Arctostaphylos uva-ursi	×	×	×	1,750–2,250	South	Late May-mid Jun	59	23±12	63±22	92±15	119±31
Empetrum nigrum	×	×		1,750–2,100	South-West	Late May-mid-Jun	61	18± 6[b]	52±18	94±10	98±30
Salix nivalis	×	×	×	1,900–2,400	South	Mid-May-early Jun	82	38± 8	31±16	92±12	91±48
Salix cascadensis	×	×	×	1,900–2,450	All	Mid-May-early Jun	79	28± 8	27±10	83±14	73±17
Dryas octopetala		×	×	2,100–2,450	All	Early-late May	77	28± 6	23± 7	80±11	51±15
Danthonia intermedia			×	2,100–2,350	All	Mid-May-early Jun	65	36± 8	56±10	99± 2	219±13
Calamagrostis purpurascens			×	2,250–2,600	South-West	April-early May	64	41± 7	38± 6	97± 4	180±13
Carex spectabilis	×			1,750–2,175	South	Mid-May-early Jun	61	30± 4	55±16	100± 0	210±35
Carex phaeocephala	×	×	×	1,850–2,400	All	Early-late May	101	34± 7	27±10	94± 7	143±45
Carex scirpoidea			×	2,200–2,600	All	Mid-Apr-early May	79	35± 7	36±14	94±11	156±35
Carex nardina			×	2,200–2,600	All	Late-Apr-early May	70	32± 3	19± 5	94± 7	83±17
Kobresia myosuroides			×	2,250–2,600	All	Essentially snowfree	66	44± 6	43±15	98± 4	178±25

[a] W = west, C = central, E = east.
[b] Average ± standard deviation.

the eastern North Cascades (Fig. 3) where it occurs in level to slightly concave sites, often with hummocky topography (Fig. 4). Of all the snowbed types in the region, the *Carex capitata* community generally has the least snow accumulation and is the first to become snow-free (June). Soils, due to drainage from upslope, remain moist well into the summer.

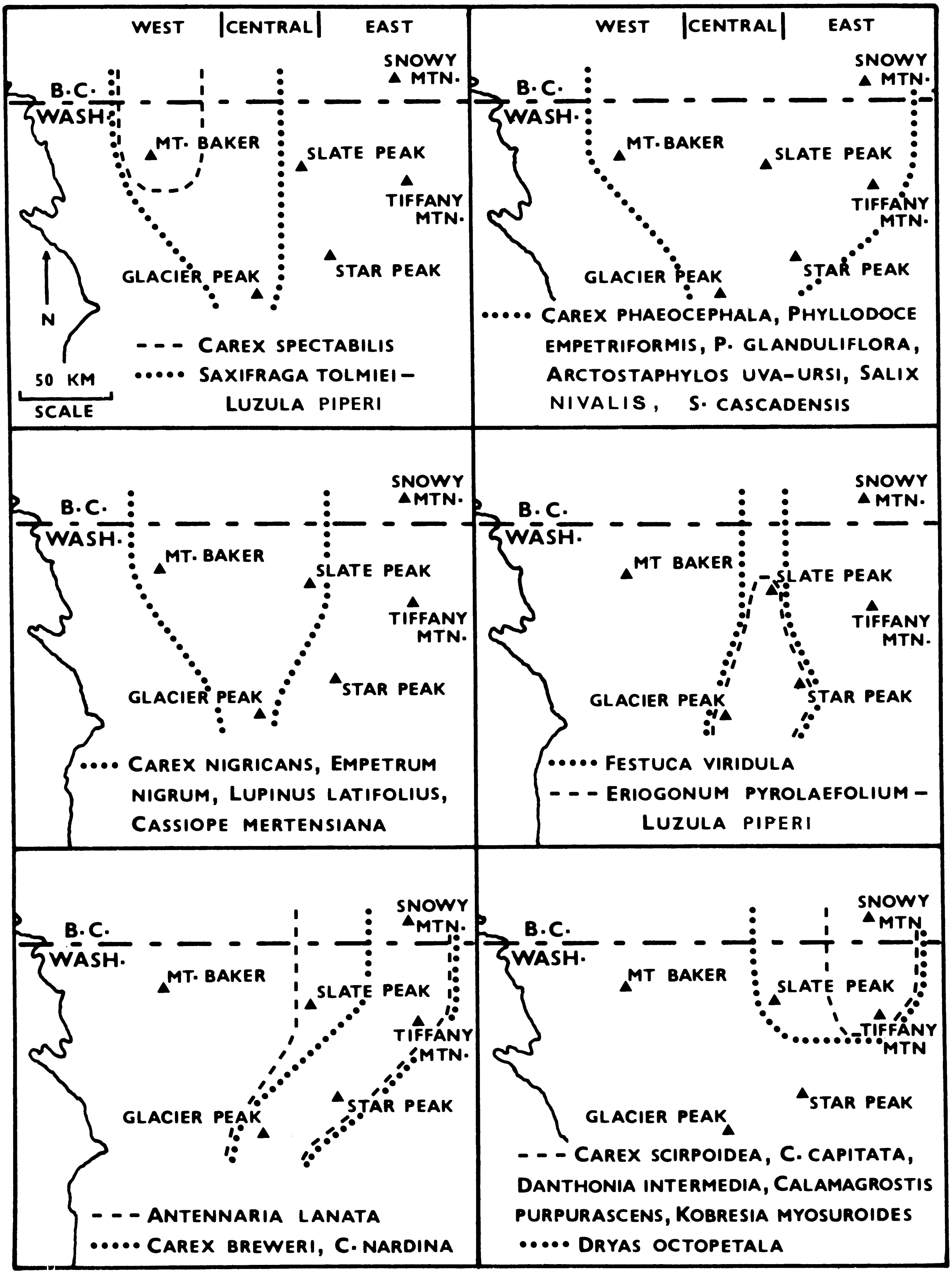


FIG. 3. Distribution of major community types in the alpine zone of the North Cascades Range.

FIG. 4. A *Carex capitata* community at 2,380 m on Arnold Peak, Washington. The *Carex scirpoidea* var. *pseudoscirpoidea* community covers the extensive slopes in the background.

Communities of this type have a high average total plant cover, including the highest average bryophyte cover of any snowbed community in the region (Table 2). *Carex capitata* has a high mean cover and frequency. Important vascular plants in this floristically rich community are *Potentilla diversifolia* var. *diversifolia*, *Solidago multiradiata*, *Salix cascadensis*, *Festuca ovina* var. *brevifolia* and *Carex scirpoidea* var. *pseudoscirpoidea* (Table 2). Prominent mosses and lichens are *Dicranum muehlenbeckii*, *Polytrichum junipernum*, *Cetraria ericetorum*, and *Cladonia pyxidata.*

Mesic herb community types.—Two of the North Cascadian alpine communities are included within the mesic herb types. These communities are characterized by a dense cover of herbs and usually lack a cryptogamic stratum.

a) *Lupinus latifolius* community. The *Lupinus* type, found at lower elevations (1,750 m to 2,150 m) in the western to central North Cascades (Fig. 3), is a subalpine community that extends into the lower alpine zone adjacent to stands of krummholz. It occurs most frequently on moderate to steep southern, well-drained slopes (Fig. 5). Snowmelt occurs in late May to early June. Although no data are available for this community in the subalpine zone of the central North Cascades, alpine stands appear to be floristically similar to subalpine stands.

The *Lupinus* community is characterized by relatively few species and a dense cover of mesophytic herbs and sedges. *Lupinus latifolius* var. *subalpinus* has a high frequency and mean cover. *Carex spectabilis*, *Polygonum bistortoides*, *Vaccinium deliciosum*, *Festuca viridula*, *Erigeron peregrinus* var. *scaposus*, and *Valeriana sitchensis* are major associates (Table 2).

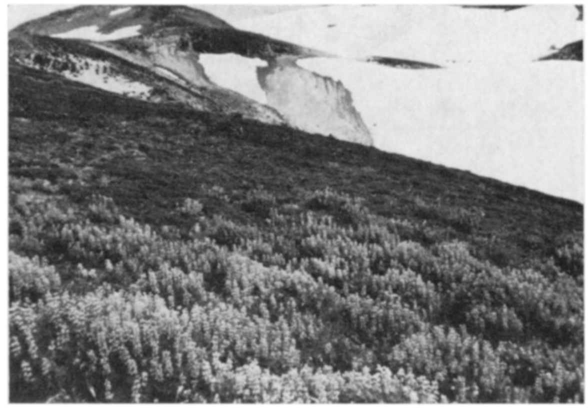


FIG. 5. A *Lupinus latifolius* community at 1980 m on Glacier Peak, Washington. The *Empetrum nigrum* occurs on the adjacent upper slopes.

b) *Festuca viridula* community. This community type is apparently restricted to lower elevations (1,850 m to 2,150 m) on southern, well-drained slopes in the central North Cascades (Fig. 3). These slopes become free of snow about the same time as in the *Lupinus* habitats but soils become drier during late summer. This community is floristically similar to those in the subalpine. Because of its occurrence only in the lower alpine zone, it may best be considered a high subalpine community.

This community is closely related to the *Lupinus* type with a large number of species common to both (Table 2). Total vascular plant cover is much lower, however, and the average number of species per stand is greater in the *Festuca viridula* type. *Festuca* has a relatively high average cover and frequency. Other important plants are *Antennaria lanata*, *Arenaria capillaris*, *Agoseris glauca* var. *dasycephala*, *Lupinus latifolius* var. *subalpinus*, *Potentilla flabellifolia*, *Juncus parryi*, and *Arnica rydbergii*.

Dwarf shrub community types.—In the North Cascades eight dwarf shrub community types occur in a variety of habitats. This group contains five of the six community types which range across the entire North Cascadian region.

a) *Cassiope mertensiana* community. This is one of the most common communities in the western North Cascades, ranging east to the Slate Peak and Glacier Peak areas in the central part of the range (Fig. 3). Mesic, well-drained, moderately steep to steep, southern slopes are typical sites. This community is closely related to the *Phyllodoce empetriformis* and *Phyllodoce glanduliflora* types (Fig. 2). In the subalpine zone of the western North Cascades, *Cassiope mertensiana* and *Phyllodoce empetriformis* commonly occur together as codominants (Douglas 1972). Comparison of the heath communities of the

North Cascades (Table 4) indicates that distinct alpine and subalpine phases may be recognized.

The *Cassiope* community has a high average total plant cover. *Cassiope mertensiana* occurs with a high frequency and average cover. *Luetkea pectinata*, *Phyllodoce glanduliflora*, *Antennaria lanata*, and *Vaccinium deliciosum* are important associates; the latter is restricted mainly to the western North Cascades. In the central part of the region, *Phyllodoce empetriformis* becomes prominent. *Lepraria neglecta* is the major cryptogam with *Cetraria islandica* and *Polytrichum piliferum* occurring frequently, but with low cover.

b) *Phyllodoce empetriformis* community. This type is found on sites that appear quite similar to those of the *Cassiope* type, at least in the western and central Cascades where both are extremely common. At the eastern extent of its range (Fig. 3), it is restricted to slight snowbed depressions in the lower alpine zone. In this drier region of the Cascades, snow melts at approximately the same time (early June to early July) as in the more exposed central and western habitats.

Phyllodoce empetriformis has a mean high cover and frequency. Other prominent species are *Antennaria lanata* (occurring across the entire range), *Vaccinium deliciosum* and *Cassiope mertensiana* (both restricted to the western and central Cascades) and *Vaccinium scoparium* (found from the central to eastern Cascades). *Polytrichum piliferum* and *Lepraria neglecta* are conspicuous crytogams in most stands while *Dicranum fuscescens* is important in the western North Cascades.

c) *Phyllodoce glanduliflora* community. The more exposed, upper slopes are typical sites of this community type in the western North Cascades. Farther east the type occurs in more protected habitats although time of snowmelt is similar (early to late June). This type occurs on all aspects and soils ranging from well drained, on smooth slopes, to more poorly drained on hummocky terrain.

Floristically, the *Phyllodoce glanduliflora* community is the richest of the heath types and has a high average plant cover. *Vaccinium deliciosum* and *Luetkea pectinata* are important associates in the western North Cascades whereas *Antennaria lanata* and *Salix cascadensis* are prominent components in the eastern stands. Moss and lichen cover is the highest of all heath types. Important cryptogams throughout the range are *Cetraria islandica*, *Lepraria neglecta*, and *Polytrichum piliferum*. In the eastern North Cascades the moss, *Dicranum scoparium* is conspicuous.

d) *Arctostaphylos uva-ursi* community. The *Arctostaphylos* community is found mainly on southern sites where soils are generally poorly developed, but

TABLE 4. Prominence values of alpine and subalpine phases of the *Cassiope mertensiana* and *Phyllodoce empetriformis* communities

Species	*Cassiope mertensiana* Alpine (8)	*Phyllodoce empetriformis* Alpine (5)	*Cassiope mertensiana-Phyllodoce empetriformis* Subalpine[a] (7)
Vascular Plants			
Cassiope mertensiana	408	75	441
Luetkea pectinata	102	16	73
Phyllodoce glanduliflora	83	7	----
Vaccinium deliciosum	64	68	92
Antennaria lanata	43	42	----
Phyllodoce empetriformis	38	307	386
Luzula piperi	12	1	----
Carex spectabilis	10	----	1
Carex nigricans	7	14	2
Lupinus latifolius	6	1	4
Juncus parryi	5	5	----
Empetrum nigrum	4	----	----
Erigeron peregrinus	3	9	T
Phlox diffusa	2	9	----
Festuca ovina	3	8	----
Vaccinium scoparium	1	38	----
Sibbaldia procumbens	1	5	----
Carex phaeocephala	1	----	----
Arenaria capillaris	T	8	----
Lupinus lepidus	T	----	----
Castilleja rupicola	T	----	----
Antennaria alpina	T	T	----
Pedicularis racemosa	----	14	----
Erigeron aureus	----	T	----
Poa alpina	----	T	----
Bryophytes and Lichens			
Lepraria neglecta	87	18	----
Dicranum fuscescens	37	----	41
Cetraria islandica	25	1	2
Polytrichum piliferum	19	50	----
Cladonia subsquamosa	----	17	----
Rhacomitrium sp.	----	----	41
Cladonia sp.	----	----	----
Total number of species			
Vascular plants	35	35	27
Bryophytes	9	6	8
Lichens	12	15	11
All plants	56	56	46

[a] Subalpine data after Douglas (1972). T (trace) indicates a prominence value <0.5. Number of stands sampled appears in parentheses.

well drained. It occurs infrequently throughout the North Cascades (Fig. 3) in sites where snowmelt occurs from late May to mid-June. This type is found sporadically in the subalpine zone.

Arctostaphylos uva-ursi is the sole dominant, except in the western North Cascades where *Carex spectabilis* is an important associate. The high cover and dominance of *Arctostaphylos* limits other species, especially cryptogams, to a low prominence in the type. In the eastern North Cascades, species richness is markedly higher than in the western North Cascades.

e) *Empetrum nigrum* community. This community type occurs on moderately steep, well drained, south to west slopes at lower elevations (1,750 m to 2,100 m) in the western to central North Cascades (Figs. 3 and 5). Snowmelt (late May to mid-June) is similar to that in the heath types.

Empetrum nigrum has a high average cover and frequency. *Phyllodoce glanduliflora*, although a common associate, occurs with low cover and frequency. In the Glacier Peak area, *Lupinus lepidus* var. *lobbii* becomes prominent; *Cetraria islandica* is the only prominent and constant cryptogam.

f) *Salix nivalis* community. Communities of this type occur throughout the region (Fig. 3) on level to moderately steep, exposed, southern slopes. The soils are extremely rocky and often show indications of frost action (i.e., unsorted nets, frost-boils). Snowmelt is relatively early, generally occurring between mid-May and early June.

This community is the only one that shows a significant structural change from west to east. In the western and central North Cascades, vascular plant cover (29 to 43%, respectively) is much lower than in the eastern North Cascades (60 to 121%). Species richness is also slightly higher in the eastern North Cascades.

The *Salix nivalis* community has a moderate average plant cover and is relatively rich, floristically. *Festuca ovina* var. *brevifolia* and *Selaginella densa* are constant associates in all stands (Table 2), whereas *Oxytropis campestris* var. *gracilis* is important in the eastern part of the region. The lichens, *Thamnolia subuliformis*, *Cornicularia aculeata*, *Cetraria islandica*, and *Lepraris neglecta* are frequent throughout the range. *Polytrichum juniperinum* and *Desmatodon latifolius* are important mosses in the eastern North Cascades.

g) *Salix cascadensis* community. In the western North Cascades this community is found on sites similar to those of the *Salix nivalis* community. In the eastern part of its range, however, the *Salix cascadensis* type occurs on gentle slopes or level sites of all aspects and often occupies snowbed habitats. Although the latter habitats become snow-free later (early June) than those on exposed sites, drainage is good and they become quite dry.

Salix cascadensis occurs with relatively high average cover and frequency. Throughout the range, *Festuca ovina* var. *brevifolia* and *Carex phaeocephala* are characteristic components. *Erigeron aureus* and *Arenaria obtusiloba* are important in the central and eastern North Cascades whereas in the Glacier Peak area, *Lupinus lepidus* var. *lobbii* is a conspicuous associate. The prominent cryptogams in most stands are *Polytrichum piliferum*, *Cetraria islandica*, and *Lepraria neglecta*.

h) *Dryas octopetala* community. The *Dryas* type occurs on slight to moderate slopes of all aspects from the central to eastern North Cascades (Fig. 3). These sites usually have well-drained, poorly developed soils. Snowmelt is relatively early (early to late May).

This community has one of the lowest total plant covers of all types in the region (Table 2). *Dryas octopetala* var. *hookeriana* has a moderate mean cover and a high frequency. Typical associates, with low prominence, are *Lupinus lepidus* var. *lobbii*, *Arenaria obtusiloba* and *Festuca ovina* var. *brevifolia*. Many cryptogams occur frequently but all are of low importance.

Dry graminoid community types.—Two grass and five sedge communities are included in the dry graminoid community types. These communities are all characterized by a high total plant cover and are floristically rich.

a) *Danthonia intermedia* community. Communities of this type cover large expanses in the lower alpine and subalpine zones of the eastern North Cascades (Fig. 3). The moderate to steep slopes are well drained and receive moisture from upslope for much of the summer. Snowmelt takes place from mid-May to early June.

Total average plant cover in this type is the highest in the alpine zone. *Danthonia intermedia* has a high frequency and average cover, and dominates all stands. Many associates, such as *Carex scirpoidea* var. *pseudoscirpoidea*, *Potentilla diversifolia* var. *diversifolia*, *Arenaria capillaris* and *Arenaria obtusiloba* also have high prominence values (Table 2). Common cryptogams are *Polytrichum juniperinum*, *Polytrichum piliferum*, *Tortula ruralis*, *Cetraria islandica* and *Cladonia pyxidata*.

b) *Calamagrostis purpurascens* community. Small stands of this community type are frequent at higher elevations (>2,250 m) in the eastern North Cascades (Fig. 3). Slopes are moderate to steep, well drained, and often rocky. Snow accumulation is slight with snowmelt occurring relatively early (April to early May).

Calamagrostis purpurascens has a high mean cover and frequency and is common only to this type. *Carex scirpoidea* var. *pseudoscirpoidea*, *Arenaria obtusiloba*, *Oxytropis campestris* var. *gracilis*, and *Potentilla diversifolia* var. *diversifolia* are prominent species (Table 2) in this floristically rich type. *Cornicularia aculeata*, *Cladonia pyxidata*, *Cetraria ericetorum*, and *Cetraria islandica* are the most conspicuous of the large number of lichens present. *Polytrichum juniperinum* is the only constant moss of importance.

c) *Carex spectabilis* community. This community type is restricted to drier, moderately steep to steep, upper slopes in the western North Cascades (Fig. 3). These southern, well drained habitats are free of snow relatively early (mid-May to early June). This community type also occurs in the subalpine zone (Douglas 1972) but comparison of plant composition (Table 5) indicates that both an alpine and subalpine phase should be recognized.

Total average plant cover is one of the highest of all the alpine types in the region. *Carex spectabilis* has a high average cover and frequency. Other prominent species are *Solidago multiradiata*, *Valeriana sitchensis* and *Carex breweri* (Table 2). Cryptogamic cover is high with *Cladonia gracilis*, *Cladina mitis*, *Cetraria ericetorum* and *Polytrichum piliferum* being major components.

d) *Carex phaeocephala* community. This type is common on moderately steep to steep, well drained, upper slopes in the western North Cascades. Farther east it becomes less frequent and often grades into the closely related *Carex scirpoidea* var. *pseudoscirpoidea* community. The *Carex phaeocephala* community occurs mainly on southerly aspects although several stands in the eastern North Cascades were found on northwest or northeast aspects. In the western North Cascades this major plant community is the first to become snow free, whereas in the eastern part of the region, although snowmelt is about the same (May), several other types precede it in the snowmelt sequence.

Carex phaeocephala, with a moderately high mean cover and frequency, is the most prominent species in the community. Floristically, this is the richest and most variable type in the region. In the western stands *Phlox diffusa* is a major associate. *Lupinus lepidus* var. *lobbii* is important only in the central North Cascades whereas *Arenaria obtusiloba* is common here as well as farther east. *Carex scirpoidea* var. *pseudoscirpoidea* is the most conspicuous associate in the eastern part of the region. Prominent lichens, occurring only in the western North Cascades, are *Cladonia gracilis* and *Cladina mitis*. The moss *Polytrichum piliferum* and the lichens *Cetraria ericetorum*, *Cladonia pyxidata*, and *Thamnolia subuliformis* are important throughout the range (Table 2).

e) *Carex scirpoidea* var. *pseudoscirpoidea* community. In the eastern North Cascades (Fig. 3) this type is frequently found on dry, well-drained slopes at all elevations and aspects. These sites become snow free between mid-April and early May.

Carex scirpoidea var. *pseudoscirpoidea* has a high mean cover and frequency. This species is also one of the most common and abundant plants in a number of other alpine communities in the eastern North Cascades. *Potentilla diversifolia* var. *diversifolia*, *Carex phaeocephala*, *Festuca ovina* var. *brevifolia*, and *Arenaria obtusiloba* occur with moderate frequency and cover in the type. Prominent crypto-

TABLE 5. Prominence values of alpine and subalpine phases of the *Carex spectabilis* community[a]

Species	Alpine phase (4)	Subalpine phase (5)
Vascular plants		
Carex spectabilis	547	782
Phlox diffusa	216	----
Solidago multiradiata	155	----
Carex breweri	67	----
Danthonia intermedia	55	----
Cerastium arvense	47	----
Achillea millefolium	40	----
Polygonum bistortoides	38	30
Sibbaldia procumbens	38	----
Campanula rotundifolia	37	----
Antennaria alpina	30	----
Festuca ovina	20	----
Carex phaeocephala	19	----
Lupinus lepidus	5	----
Selaginella densa	4	----
Luzula spicata	4	----
Lupinus latifolius	3	42
Sedum lanceolatum		----
Carex nigricans	----	16
Valeriana sitchensis	----	15
Epilobium angustifolium	----	8
Viola glabella	----	7
Aster foliaceous	T	7
Bryophytes and lichens		
Cladonia gracilis	139	----
Polytrichum piliferum	123	----
Cladina mitis	81	----
Cetraria ericetorum	54	----
Peltigera canina	19	----
Tortula ruralis	18	----
Ceratodon purpureus	14	----
Cladonia pyxidata	14	----
Heterocladium dimorphum	12	----
Thamnolia subuliformis	12	----
Dicranum tauricum	10	----
Total number of species		
Vascular plants	35	30
Bryophytes	13	0
Lichens	13	0
All plants	61	30

[a] Subalpine data after Douglas (1972). T (tract) indicates a prominence value of <0.5. Number of stands sampled appears in parentheses.

FIG. 6. A *Kobresia myosuroides* community at 2,400 m on Arnold Peak, Washington. *Salix nivalis, Oxytropis compestris,* and *Arenaria obtusiloba* are the most prominent plants occurring between the *Kobresia* clumps.

gams are *Tortula ruralis, Bryum weigelii, Cetraria islandica,* and *Lecidea granulosa* (Table 2).

f) *Carex nardina* community. This community extends along the eastern flanks of the North Cascades (Fig. 3). It is restricted to dry upper slopes of the higher peaks and shows no aspect preference. Winter snow cover is thin, thus snowmelt is relatively early (late April to early May).

Carex nardina has a high frequency and a moderately high cover. Common associates, although with low prominence throughout the community type, are *Festuca ovina* var. *brevifolia, Arenaria obtusiloba,* and *Smelowskia ovalis* (Table 2). In the southeastern part of the area (Star Peak) *Phlox hendersonii* is an abundant species. Important cryptogams are *Tortula ruralis, Thamnolia subuliformis,* and *Cornicularia aculeata.*

g) *Kobresia myosuroides* community. The *Kobresia myosuroides* type occurs on high (>2,250 m elevation), well-drained, moderately steep to steep, dry upper slopes (Fig. 6) in the eastern part of the region (Fig. 3). These exposed habitats remain essentially snow free most of the winter. Shallow snow accumulation is found only between the tufts of *Kobresia myosuroides* or among low earth hummocks in the type.

Kobresia myosuroides has a high average cover and frequency. Prominent associates are *Carex scirpoidea* var. *pseudoscirpoidea, Salix nivalis, Oxytropis campestris, Arenaria obtusiloba, Potentilla diversifolia* var. *diversifolia,* and *Solidago multiradiata.* The total cryptogam cover is the highest in the North Cascadian alpine. The most important of the many taxa are *Tortula ruralis, Polytrichum juniperinum, Cladonia pyxidata, Cetraria islandica, Cetraria ericetorum,* and *Cetraria cucullata.*

Herbfield, fellfield, boulderfield, and vegetation stripe community types.—The level or gently sloping summits of almost every mountain in the North Cascades have accumulations of coarse rock detritus. Since most of these sites remain essentially snow free all winter, frost has caused extensive breaking of the bedrock. Other frost-associated phenomena, such as nonvegetated sorted and unsorted circles and nets on level surfaces and nonvegetated unsorted stripes (Washburn 1956) or vegetation stripes on slopes, are also common to these summits.

Four general communities (herbfields, vegetation stripes, boulderfields, and fellfields) based on amount or arrangement of plant cover or size of rock detritus may be recognized. If total plant cover is >50%, the term herbfield is used. Vegetation stripes, where the vegetation is arranged in long parallel strips, 1 to 2 m apart, are a second group. These patterns result from downslope soil and rock creep. If rock or boulder cover comprises at least 50% of the ground cover, the term boulderfield is appropriate. If none of the above criteria is met the site is then classified as fellfield.

Thirty-nine stands, containing a total of 94 vascular plant and 38 cryptogam species, were sampled and analyzed. *Beta* diversity (Whittaker 1960) was so great in these stands that most of them plotted in a single, undecipherable group in the center of ordinations. Separation of the stands into the above four classes (i.e., fellfields, herbfields, etc.) or into major geographic regions did not improve ordination performance. Use of several cluster techniques (Pritchard and Anderson 1971) illustrated stand relationships more clearly, or at least verified that *beta* diversity is extremely high. The cluster techniques indicated that no fewer than 24 sets could be recognized within the 39 sampled stands. These sets had little or no correlation with amount of plant or rock cover and revealed no regional pattern.

These communities throughout the North Cascades have many major species in common (Table 6). This large number of common species and their relatively low constancy and varying abundance results in a continuous floristic change within which no divisions can be satisfactorily made, at least within the community concept used in this study. It is quite likely that, with more intensive sampling, reduced plot size, and the inclusion of all cryptogams, a "community" pattern would emerge, at least from the fellfields and boulderfields. These stands would probably be recognizeable at a microcommunity level and would correspond to microhabitats (microtopography) within the fellfields or boulderfields.

In general, the most notable floristic differences are due to those species having restricted geographic distributions in the North Cascades. A number of species (e.g., *Solidago multiradiata, Oxytropis cam-*

TABLE 6. Mean prominence values of the major plant species in the herbfield (H), fellfield (F), boulderfield (B), and vegetation stripe communities of four regions in the North Cascades[a]

	Northwest				North-central				Southeast		Northeast		
Species	H (3)	F (6)	B (3)	V (3)	H (2)	F (1)	B (3)	V (3)	H (9)	F (1)	H (1)	B (3)	V (1)
Phlox diffusa	250	31	1	37	68		25	3	5				
Potentilla diversifolia	232	1		8	20		5	10	12		6	25	3
Oxytropis campestris	147	8	T	37									
Solidago multiradiata	141	16	1	10									
Carex albonigra	97			8		T		13				1	
Achillea millifolium	74	T	1	9									
Poa alpina	62		T	7								T	
Cerastium arvense	52	T	T	25									
Carex phaeocephala	49	3		5	46		3	9	25		72	10	T
Selaginella densa	48	10		7	70		13	1			51	3	3
Festuca ovina	40	2	2	17	23	T	1	5	19	21	8	30	25
Antennaria rosea	17												
Trisetum spicatum	16	T	1	3	1	T	T	T	10		20	5	1
Sedum lanceolatum	13	T		2	12		3	2	18		23	3	4
Silene acaulis	9	T	15	29				1			120	29	8
Draba praealta	8			T									
Haplopappus lyallii	2	3	26		2		9	1	3		13	3	11
Luzula spicata	4	T		4	13		T	2	9		6	22	9
Phacelia sericea	1	T		7		4		T					
Draba incerta	1			2					8			1	T
Silene parryi	T				16		T						
Lupinus lepidus var. *lobbii*		4	5	2		1		5	53	310		68	124
Saxifraga bronchialis		4			11							T	
Antennaria alpina		1	1	9	11		T	2	12		5	28	
Smelowskia ovalis		1	1						8		24	1	T
Arenaria obtusiloba		T	2		6	4	1	28	60		62	48	61
Agropyron caninum var. *latiglume*				10									
Erigeron compositus var. *glabratus*				4	1			9	9		20	13	2
Stellaria lonipes				T	T	5		3					
Arenaria capillaris					56		52		53				
Arctostaphylos uva-ursi					32		T	T					
Erigeron aureus					16		5		14		T	5	1
Penstemon procerus					2				9		T		
Vaccinium scoparium					1		5						
Draba paysonii					T	43		7	2			T	T
Eriogonum ovalifolium						18							
Carex nardina							2		15		67	5	
Salix nivalis								13					
Phlox hendersonii									70				
Carex cf. *scopulorum*									19				
Carex breweri									8				
Carex straminiformis									7				
Eritrichum nanum									6				
Anemone drummondii									6				
Douglasia nivalis									6				
Arabis lyallii									6				
Collomia debilis var. *larsenii*										36			
Carex scirpoidea var. *pseudoscirpoidea*										18			
Poa sandbergii													5

[a] Only species with a prominence value of 5, or more, in at least one stand are included in this table. Number c stands sampled are enclosed in parentheses. T (trace) indicates a prominence value of <0.5.

pestris var. *gracilis*, *Achillea millefolium* var. *alpicola*, and *Cerastium arvense*) are often important in the four community groupings in the northwestern Cascades, but are absent in these communities elsewhere in the range.

Several species reach their geographical distribution limits in the North Cascades. *Phlox hendersonii* extends north only to the extreme southern part of the study area (Star Peak), where it is an important herbfield component. Less important species occurring with the latter and having a similar northen range limit, are *Eritrichum nanum* and *Douglasia nivalis*. Farther west, in the Glacier Peak area, *Collomia debilis* var. *larsenii* reaches its northern limits and is often abundant in fellfields. Rocky Mountain or arctic elements, extending into only the northcentral or northeastern part of the North Cascades are *Carex scirpoidea* var. *pseudoscirpoidea*, *Potentilla nivea*, and *Potentilla uniflora*.

Krummholz stands.—The overstory composition of krummholz stands changes markedly from west to east in the North Cascades. On the western side of the range, *Abies lasiocarpa* is the dominant overstory species. *Tsuga mertensiana* and *Chamaecyparis nootkatensis* occur infrequently and rare occurrences of *Abies amabilis* were noted. In the central North Cascades, *Abies lasiocarpa*, *Picea engelmannii*, and *Larix lyallii* are common. The latter is occasionally found in a prostrate form, but more often is erect, with flagged tops. *Pinus albicaulis* also occurs in the central North Cascades but is less frequent than the previous species. On the eastern side of the range, *Abies lasiocarpa* and *Larix lyallii* decrease in abundance while *Picea engelmannii* and *Pinus albicaulis* are common.

The understory of the 42 krummholz stands sampled during the study showed low cover and considerable variation in composition (Table 7). The use of ordination and cluster techniques failed to correlate understory composition with either overstory composition or geographical region. The sparse understory flora appeared to be selected from nearby communities irrespective of the community type. Regional separation is not consistent since speices such as *Phyllodoce glanduliflora* and *Festuca ovina* var. *brevistyla* may be important across the entire range (Table 7). *Carex concinnoides* and *Ledum groenlandicum* are the only species essentially restricted to krummholz stands in the alpine zone of the North Cascades. *Vaccinium scoparium* is the only species that reaches its maximum prominence beneath krummholz stands.

Soils

Morphology.—Alpine soils are relatively poorly developed and fall within the Spodosol, Inceptisol, and Entisol Orders. All but the latter have developed in parent materials that contain a high pyroclastic component. These pyroclastic deposits originated from a number of recent volcanic eruptions within, and to the south of, the study area (van Ryswyk 1969; Bockheim 1972).

The Spodosols of the region occur mainly beneath krummholz and heath vegetation. The best development occurs beneath krummholz, especially in the western North Cascades. These profiles have moderately thick (up to 7 cm) organic layers, moderately well-developed eluvial horizons, and illuvial horizons characterized by high organic matter content. The following profile (#10) is typical of krummholz stands in the western North Cascades:

Horizon	Description
01	7 to 1 cm; fresh coniferous (krummholz) litter;
02	1 to 0 cm; partially humified forest litter;
A2	0 to 7 cm; dark reddish gray (10 R 3/1) sandy loam; weak, medium subangular blocky structure; breaking down to moderate fine crumb; very friable; abundant fine to medium roots; extremely acidic (pH 4.0); abrupt, wavy boundary;
B21	7 to 19 cm; dark reddish brown (2.5 YR 2/4) loam; weak, medium subangular blocky structure, breaking down to moderate, fine crumb; friable; abundant fine to medium roots; extremely acidic (pH 4.3); abrupt, smooth boundary;
B22	19 to 44 cm; dark brown (7.5 YR 3/2) very gravelly loam; weak, very fine crumb structure; friable; few fine roots; very strongly acidic (pH 4.6); abrupt, irregular boundary;
R	44 to 55 cm or more; weathered shale.

Spodzols associated with heath vegetation are characterized by thin organic horizons (1 cm), absent or imperceptible albic horizons, and abundant organic matter in the illuvial horizons. Profile #9 is typical of heath communities in the western North Cascades. Detailed analyses of this profile by Bockheim (1972) showed that in the *B*2 horizon, the ratio of percent pyrophosphate-extractable Fe + Al to percent dithionite-extractable Fe + Al exceeds 0.5, thus placing it within the Spodosol Order:

Horizon	Description
01	Trace, fresh plant litter (mainly heath species);
02	1 to 0 cm; partially humified herbaceous plant litter;
A1	0 to 8 cm; dark reddish brown (5 YR 3/3) fine sandy loam; moderate, fine crumb structure; very friable; abundant very fine to medium roots; extremely acidic (pH 4.3); clear, smooth boundary;
B21	8 to 16 cm; dark yellowish brown (10 YR 3/4) fine sandy loam; moderate, fine crumb structure; friable; abundant fine to medium roots; very strongly acidic (pH 5.0); gradual, smooth boundary;
B22	16 to 37 cm; dark yellowish brown (10 YR 4/4) gravelly sandy loam, weak to moderate, fine crumb structure; friable; plentiful very fine to fine roots; very strongly acidic (pH 4.9); abrupt, smooth boundary;

TABLE 7. Mean prominence values of plant species in four krummholz types in three regions (west, central, and east) of the North Cascades Range[a]

	Krummholz dominants							
	Abies lasiocarpa		*Larix lyallii*		*Picea engelmannii*		*Pinus albicaulis*	
Species	West (6)	Central (3)	Central (5)	East (2)	Central (4)	East (5)	Central (3)	East (11)
CONIFERS								
Abies lasiocarpa	950	885	----	----	----	----	----	3
Pinus albicaulis	----	10	----	----	----	1	869	834
Picea engelmannii	----	7	----	----	850	963	1	T
Laris lyallii	----	----	740	975	----	----	----	----
VASCULAR PLANTS								
Phyllodoce glanduliflora	68	----	----	----	----	18	----	90
Carex spectabilis	61	----	----	----	----	----	----	----
Vaccinium deliciosum	53	----	----	----	----	----	----	----
Phyllodoce empetriformis	42	----	6	----	----	----	----	----
Leutkea pectinata	40	3	45	----	----	----	----	----
Cassiope mertensiana	12	103	340	----	----	----	----	----
Pedicularis racemosa	----	10	----	----	----	----	----	----
Poa sandbergii	----	6	5	----	4	----	----	----
Erigeron aureus	----	6	----	----	8	7	1	7
Arenaria capillaris	----	6	9	----	3	2	----	1
Haplopappus lyallii	----	5	12	4	1	4	7	6
Phlox hendersonii	----	3	----	----	4	----	7	----
Anenome drummondii var. *drummondii*	----	3	1	----	10	----	7	----
Penstemon procerus	----	----	58	----	----	----	----	T
Poa nervosa	----	----	19	----	4	2	----	1
Phlox diffusa	----	----	11	----	2	----	----	----
Agoseris glauca	----	----	5	----	----	----	----	T
Empetrum nigrum	8	----	----	----	----	----	----	----
Arnica latifolia var. *gracilis*	5	----	----	----	----	----	----	----
Festuca ovina var. *brevistyla*	5	----	----	9	1	6	1	9
Hieracium gracile	2	9	8	----	1	----	----	----
Luzula wahlenbergii	1	----	101	----	----	----	----	----
Veronica wormsjoldii	1	4	6	----	----	----	----	----
Vaccinium scoparium	----	158	24	----	100	2	----	26
Penstemon davidsonii var. *davidsonii*	----	11	----	24	1	4	4	35
Arenaria obtusiloba	----	----	----	33	1	3	----	1
Dryas octapetala	----	----	----	4	----	24	----	14
Juniperus communis	----	----	----	2	----	2	199	42
Carex phaeocephala	----	----	----	2	1	5	1	2
Ledum groenlandicum	----	----	----	----	12	----	----	----
Carex rossii	----	----	----	----	8	----	----	----
Carex concinnoides	----	----	----	----	----	1	----	10

[a] Only those species with a prominence value of 5, or more, in at least one type are included in this table.

C 37 to 66 cm or more; yellowish brown (10 YR 5/4) very gravelly sandy loam; massive; friable; few to plentiful fine roots; very strongly acidic (pH 4.8).

Most of the communities in the North Cascades have soils typical of the Inceptisol Order. The Inceptisols are rather weakly developed, lacking significant illuviation, eluviation, or extreme weathering. These soils have moderately thick (4 to 10 cm) turfy *A* horizons and relatively high accumulations of organic matter in the illuvial horizons. Communities associated with the Inceptisols range from the poorly drained snowbed types to the well-drained dry grass and dry sedge types.

Inceptisols in poorly drained depressions often have one or more ash layers present. Buried *A* horizons may also occur below these ash layers. Profile #28 illustrates the characteristics of these soils in a *Carex nigricans* community in the central North Cascades:

Horizon	Description
01	Trace; fresh sedge (*Carex nigricans*) litter;
02	2 to 0 cm; partially humified sedge litter;
A1	0 to 5 cm; very dark grayish brown (10 YR 3/2) loam; weak, fine crumb structure; friable; abundant very fine roots; very strongly acidic (pH 4.7); abrupt, wavy boundary;

*B*21 5 to 11 cm; dark brown (10 YR 3/3) sandy loam; weak, fine crumb structure; friable; plentiful very fine roots; strongly acidic (pH 5.2); gradual, smooth boundary;

*B*22 11 to 21 cm; dark brown (10 YR 3/3) sandy loam; weak, fine crumb structure; friable; plentiful very fine roots; strongly acidic (pH 5.5); abrupt, wavy boundary;

*C*1 21 to 24 cm; grayish brown (10 YR 5/2); sandy loam; weak, fine crumb structure; few very fine roots; strongly acidic (pH 5.5); abrupt, wavy boundary;

*C*2 24 to 28 cm; dark yellowish brown (10 YR 4/4) sandy clay loam; weak, fine crumb structure; few very fine roots; strongly acidic (pH 5.5); abrupt, wavy boundary;

*C*3 28 to 31 cm; brown (10 YR 4/3) sandy loam, weak, fine crumb structure; few very fine roots; strongly acidic (pH 5.5); abrupt, wavy boundary;

*C*4 31 to 34 cm; dark brown (10 YR 3/3) sandy loam; weak, fine crumb structure; few very fine roots; strongly acidic (pH 5.4); abrupt, wavy boundary;

*C*5 34 to 60 cm or more; dark yellowish brown (10 YR 3/4) sandy loam; weak, fine crumb structure; few very fine roots; strongly acidic (pH 5.2).

Well-drained sites have *A-B-C* profiles typical of the Inceptisols. The following profile (#27) occurred beneath a *Kobresia myosuroides* community in the eastern North Cascades:

Horizon	Description
*0*1	3 to 2 cm; fresh sedge litter;
*0*2	2 to 0 cm; partially humified sedge litter;
*A*1	0 to 9 cm; black (10 YR 2/1) sandy loam; weak, fine crumb structure; friable; abundant, very fine to fine roots; strongly acidic (pH 5.3); gradual, wavy boundary;
*B*21	9 to 19 cm; very dark brown (10 YR 2/2) sandy loam; weak, fine crumb structure; friable; plentiful, very fine roots; medium acidic (pH 5.7); abrupt, wavy boundary.
*B*22	19 to 24 cm; dark yellowish brown (10 YR 3/4) sandy loam; weak, very fine crumb structure; friable; few very fine roots; medium acidic (pH 5.7); abrupt, irregular boundary;
C	24 to 60 cm or more; brown (10 YR 4/3) gravelly sandy loam; weak, fine crumb structure; friable; few very fine roots; medium acidic (pH 5.8).

The most poorly developed soils in the region are the Entisols. These soils are associated with either unstable snowbed sites or the high windswept ridges and plateaus. The latter areas usually support boulderfield and fellfield communities although several of the shrub community types may also occur on these sites. The Entisols generally have only thin surficial *A* horizons beneath the sparse plant cover. Profile #7 is typical of the Entisols occurring in the boulderfields and fellfields of the western North Cascades.

Horizon	Description
*C*1	0 to 2 cm; very dark gray (5 Y 3/1) gravelly loam; structureless; friable; no roots; very strongly acidic (pH 4.7); gradual, smooth boundary;
*C*2	2 to 18 cm; very dark grayish brown (2.5 Y 3/2) gravelly sandy loam; structureless; friable; no roots; very strongly acidic (pH 4.6); abrupt, wavy boundary;
R	18 cm or more; weathered shale.

Physical and chemical properties.—Physical and chemical properties of soil profiles were determined in a number of the major plant communities across the North Cascades Range. Soil pH varies markedly both within and between soil profiles, but generally decreases with depth. The most acidic soils (pH 3.8 to 5.0) are those associated with krummholz and heath vegetation in the western North Cascades. Inceptisols are also highly acidic (pH 3.9 to 5.1) in the western part of the region. Less acidic (pH 4.7 to 5.9) soils occur in snowbed and fellfield habitats throughout the range. The least acidic (pH 5.2 to 6.0) soils are those associated with *Dryas octopetala* and dry graminoid communities in the eastern mountains.

All soils become coarser textured with depth. Total sand generally increases with depth. Maximum clay concentrations usually occur in the upper *B* horizon. Sand plus silt to clay ratios are relatively high in all soils, possibly a reflection of the large amounts of pyroclastic materials present.

Organic matter is highest in the surface mineral horizons (except *A*2 horizons) and decreases with depth in the western North Cascades. Farther east, organic matter levels are lower and maximum organic matter concentration often occurs in the upper *B*2 horizons.

Total exchange capacity levels are positively correlated with the organic matter trends. Exchangeable cations in soil profiles of the region generally decrease with depth. Sodium occurs only in small quantities, except in the *A*2 horizons of krummholz stands and *A*1 horizons of *Kobresia myosuroides* communities. Calcium, magnesium, and potassium levels are low, but are comparable to those determined on similar parent materials in other alpine areas (Klikoff 1965; Nimlos and McConnell 1965; Bliss 1966; Johnson 1970; Knapik et al. 1973). In the eastern North Cascades (British Columbia), van Ryswyk (1969) found much higher sodium and slightly higher calcium levels in alpine soils.

Available phosphorus generally decreases with depth in contrast to some alpine soils in which phosphorus increases with depth (Nimlos and McConnell 1965). Kuramoto and Bliss (1970) also found that phosphorus decreased with depth in the Olympic Mountains of Washington. Potassium levels also decrease with depth and have their highest levels (162.5 to 217.5 meq/100 g) in *Carex nigricans* and *Antennaria lanata* snowbed communities. Available nitrogen levels are low throughout the region. Nimlos et al. (1965) also reported low nitrate nitrogen levels in alpine soils in Montana, although "total" nitrogen was high. In the eastern North Cascades, van Ryswyk (1969) reported low nitrogen values whereas in the western North Cascades, Bockheim (1972) reported higher nitrogen values.

Microclimate

Solar radiation.—Summer solar radiation fluctuated markedly from year to year due to varying amounts of cloud cover. In general, average radiation increased from west to east (Table 8) due to the increased cloudiness in the western North Cascades. The highest recorded value 34.22 MJ/($m^2 \cdot$ day) [= 818 ly/day] occurred several times during 1972 on Chopaka Mountain. In the central North Cascades (Slate Peak) maximum values of 31.59 to 31.88 MJ/($m^2 \cdot$ day) [= 755 to 762 ly] occurred on several occasions. At Grouse Ridge maxima were typically between 27.62 and 28.45 MJ/($m^2 \cdot$ day) [= 660 to 680 ly/day] although 33.05 MJ/($m^2 \cdot$ day) [= 790 ly/day] was recorded once.

Temperature.—The long-term summer mean, minimum, and maximum temperature patterns show higher temperatures in the eastern Cascades and lower temperatures in the western Cascades (U.S. Weather Bureau, no dates). During 1970, when storm frequency was high, temperature varied greatly. Periods of continuous, relatively high temperatures were common during 1971 and 1972. Mean daily maxima of 15.8 to 17.5°C, mean daily minima of 4.8 to 6.2°C, and mean daily temperatures of 10.2 to 11.8°C occurred on Grouse Ridge (Table 8). The Slate Peak station had even higher temperatures (19.8 to 25.2°C, 6.4 to 11.5°C, 12.6 to 17.9°C respectively) during this period. On less than 5% of the nights (June–August) temperatures <0°C occurred, although lows of 5° to 10°C were most common.

Precipitation.—Long-range climatic data for the few permanent weather stations show a decreasing summer rainfall pattern from west to east (U.S. Weather Bureau, no dates). This pattern may be broken during individual summers, such as in 1972 when precipitation (17 cm) on east Chopaka Mountain exceeded that (8 cm) on west Grouse Ridge (Table 8). Length of the intervals between rainfall fluctuated greatly. The summer of 1970 was characterized by frequent storms while lengthy periods without precipitation occurred during the summers of 1971 and 1972. Winter precipitation and snow depth data are not available.

Atmospheric moisture.—Average vapor-pressure deficits (VPD) are relatively low across the entire North Cascades Range (Table 8). Mean daily VPD at Grouse Ridge during each of the three summers was 0.11 cm Hg while farther east at Slate Peak and Chopaka Mountain mean daily VPD was 0.14 (1971) and 0.13 cm Hg (1972), respectively. Maximum VPD at Grouse Ridge during the study period was 0.58 cm Hg, 0.90 and 0.88 cm Hg at Slate Peak, and 1.15 cm Hg at Chopaka Mountain. In general, the data indicate that evaporation is highest in the eastern Cascades and lowest in the western Cascades.

Wind.—Wind speeds are lower in the western North Cascades and slightly higher in the central and eastern North Cascades (Table 8). Maximum average velocity (2.4 m/s) at Grouse Ridge occurred during a 24-h stormy period in early August 1971. Wind speeds were highest (5.3 m/s over 7 days) at Sahale Mountain. This is likely due to its ridgetop location at the headwaters of two large drainage systems. The average maximum weekly velocities at Slate Peak and Chopaka Mountain were 3.0 and 4.5 m/s respectively, during 1972.

Environmental gradient

Vegetation.—An alpine slope at 1,790-m elevation on Grouse Ridge, Mt. Baker, was selected for an intensive plant distribution-environmental gradient study. This slope was chosen because of its relative ease of access (3-km hike) and the general representativeness of its plant cover. The changes in species composition and structure along this continuum are, for the most part, gradual (Figs. 7 and 8), as is the angle of the slope.

At the ridge top, where the slope angle is slight (<11%) and exposed to stronger winds, the vegetation occurs in patches (total cover 2 to 60%, $\bar{x}$ = 18%) among the frost-shattered rocks. *Phlox diffusa*, *Solidago multiradiata*, *Silene parryi* and the lichen *Cladina mitis* are the most prominent plants in this fellfield habitat.

TABLE 8. Environmental data for five weather stations in the North Cascades Range

Date	Station[a] and elevation (m)	Solar radiation (langley/day)[j] 15 cm	Temperature (°C) 15 cm			Wind (m/s) 60 cm	VPD (cm Hg) 15 cm	Precipitation (cm) 60-cm
			$\bar{x}$ daily min	$\bar{x}$ daily	$\bar{x}$ daily max			
1970								
6/13–7/5[b]	Grouse 1785	515	6.8	12.2	16.9	1.9	.09	2.57
7/6–8/2		484	6.1	11.0	15.9	1.4	.12	8.39
8/3–8/29[c]		475	6.7	11.2	15.8	1.4	.12	1.65
1971								
6/30–8/1	Grouse 1785	567	4.8	10.3	15.8	1.7	.12	2.67
8/2–8/30[d]		528	6.2	11.3	17.1	2.0	.10	2.20
1972								
6/30–7/30[e]	Grouse 1785	----	5.8	11.8	17.5	2.0	.11	8.07
8/7–8/22		----	5.5	10.2	16.4	----	.11	----
1971								
7/21–7/29	Slate 2135	----	11.5	17.9	25.2	2.8	.17	0.00
7/30–9/3[f]		641	7.2	13.1	19.8	2.9	.14	3.31
1972								
7/23–8/15[g]	Slate 2135	734	6.4	12.6	20.6	2.3	----	3.07
1970								
8/6–8/30	Sourdough 1970	----	2.8	9.4	18.0	----	.10	0.54
8/31–9/13		----	----	----	----	----	----	5.25
1970								
7/4–7/30	Sahale 2045	----	----	----	----	4.5	----	8.76
7/31–8/30		----	----	----	----	4.2	----	2.27
1972								
6/6–6/25[h]	Chopaka 2400	773	0.1	2.7	6.3	----	.03	11.05
6/26–7/16		----	1.0	5.7	11.1	3.7	.08	1.06
7/17–8/16[i]		573	6.5	14.0	23.5	3.2	.24	5.27

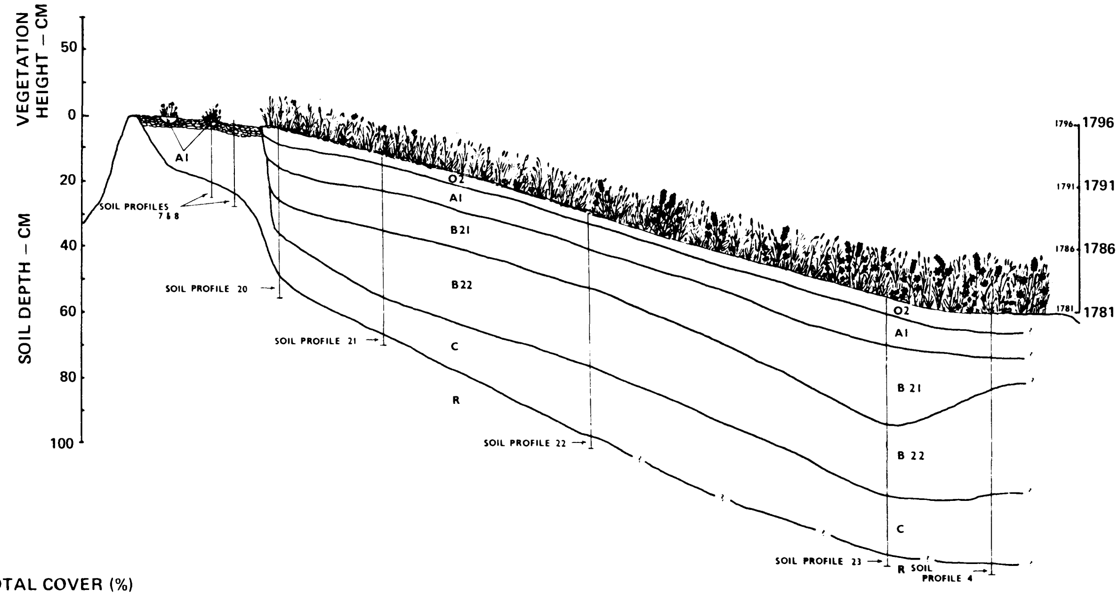
[a] Weather station locations appear on Fig. 1.
[b] Temperature, average vapor pressure deficit, and solar radiation based on 18, 18, and 13 days data, respectively.
[c] Temperature and VPD based on 19 days data.
[d] Temperature, VPD, and solar radiation based on 24, 21, and 20 days data, respectively.
[e] Temperature and VPD based on 22 days data.
[f] Solar radiation based on 18 days data.
[g] VPD and solar radiation based on 13 and 9 days data, respectively.
[h] Solar radiation based on 7 days data.
[i] VPD and solar radiation based on 20 and 10 days data, respectively.
[j] To convert langleys to joules per square meter, multiply by 4.184×10^4.

Farther downslope (11 to 13 m), the slope angle increases to 27% and the vegetation is essentially continuous. Total cover is higher (85 to 112%, $\bar{x}$ = 95%) with *Phlox diffusa*, *Solidago multiradiata*, *Carex phaeocephala*, *Carex spectabilis*, and *Polygonum bistortoides* dominating. *Cladina mitis*, *Cetraria ericetorum*, *Cladonia gracilis*, and *Polytrichum piliferum* are important cryptogams in the understory.

Total cover continues to increase downslope reaching a maximum of 156 to 217%, $\bar{x}$ = 172%, at the base of the slope (nearly level). From ≈ 41 m downslope, *Carex spectabilis*, *Polygonum bistortoides*, *Lupinus latifolius* var. *subalpinus*, and *Potentilla flabellifolia* become the major dominants, while other vascular plants and cryptogams are of low prominence. *Claytonia lanceolata*, although dormant at the time of the vegetation survey, had a mean cover of 29% and a frequency of 100% at the base of the slope during early July.

Soils.—Soils of the environmental gradient vary markedly from the poorly developed Entisols in the fellfield to the relatively better developed Inceptisols found on the remainder of the slope (Fig. 7). Fellfield soils show no profile development except for thin, surficial *A* horizons beneath the scattered clumps of vegetation.

The major portion of the gradient is characterized by Inceptisols beneath continuous vegetation. The horizons, except for increased thickness downslope, show only slight morphological variation.



TOTAL COVER (%)

VASCULAR SPECIES	16.8	62.0	109.4	89.5	158.5	166.5	171.5
BRYOPHYTES	.1	3.5	14.0	2.0	–	–	–
LICHENS	1.5	19.5	63.0	62.5	4.0	–	–
ALL PLANTS	18.4	85.0	186.4	154.0	162.5	166.5	171.5

TOTAL NUMBER OF SPECIES

VASCULAR SPECIES	9	15	16	13	9	5	4
BRYOPHYTES	2	5	5	1	1	–	–
LICHENS	3	9	6	3	3	–	–
ALL PLANTS	14	29	27	17	13	5	4

0 10 20 30 40 50 60 70

DISTANCE – M

FIG. 7. Vegetation-soil relationships along an environmental gradient on Grouse Ridge, Mt. Baker, Washington.

Physical and chemical properties were determined for seven proflies along the environmental gradient. All properties were comparable to those found in similar communities in the western North Cascades. Organic matter, total exchange capacity, exchangeable cations, available phosphorus and potassium were highest, but pH was lowest, at the base of the slope. Sand plus silt to clay ratios are relatively high throughout the gradient (Douglas 1973).

Microenvironment.—The general environmental data for Grouse Ridge were presented in a previous section (Table 8). A more detailed account of the microenvironment appears in Fig. 9. Patterns of temperature, VPD, solar radiation, and precipitation fluctuate markedly, both during and between summers, in this maritime type alpine region.

Air temperatures (+5 and +15 cm at 4, 19, and 36 m downslope and +10 and +20 cm at 61 m downslope), soil profile temperatures (–2 and –10 cm on both vegetated and nonvegetated sites at 4 m downslope and –10, –20, and –30 cm at 19, 36, and 61 m downslope), and soil moisutre regimes (–5 cm on both vegetated and nonvegetated sites at 4 m downslope, –10 and –20 cm at 19 and 36 m downslope, and –10 and –30 cm at 61 m downslope) were monitored along this gradient.

Seasonal temperature profiles along the transect vary considerably from the top of the ridge to the base of the slope although all stations have the same increasing seasonal pattern (Fig. 10). Fellfield air (+5 and +15 cm) temperatures at the top of the transect, in contrast to those on the remainder of the slope, were usually lower than temperatures at subsurface depths. Highs of near 35°C were reached several times during 1971 and 1972 at –2 cm. These high subsurface temperatures are due mainly to a higher rock content, lower plant cover, and the low heat capacity of the moisture-poor substratum. Temperatures beneath vegetation were generally 2 to 3°C lower than for adjacent nonvegetated sites. Average temperatures at –10 cm in the fellfield were ≈ 7° to 8°C lower than that at –2 cm.

Subsurface temperatures along the remainder of the transect showed sharp vertical gradients over relatively short distances. The steepest gradients were between the surface and –10 cm level. These profile temperature gradients remained relatively constant throughout the summer except during periods of rapidly decreasing air temperatures. Temperatures at –10 to –30 cm decreased slightly (2° to 4°C) with distance downslope, reflecting the insulation afforded by increased plant cover.

Soil moisture along the environmental gradient closely paralleled the summer precipitation pattern. This was especially evident in 1970 when frequency of summer rainfall was high (Fig. 9), and soil moisture regimes fluctuated accordingly. Soil moisture declined steadily throughout the summers of 1971 and 1972 due to low precipitation. The use of the –15-bar soil water potential to estimate permanent wilting percentage is somewhat questionable (Slatyer 1967). However, it gives an indication of increasing water stress. Soil moisture usually remained well above –15 bars until mid-August, except in the fellfield where levels often fell below –15 bars by mid-July. Soil moisture stress increased slightly, with distance, down the continuously vegetated portion of the transect during drought periods, probably due to the greater transpiration losses associated with increased plant cover.

Plant water relations.—Leaf water potentials (ψ) of eight plant species along the environmental gradient, and two other nearby species, were measured during and after a drought period in 1971 (Table 9). The readings for each species at each site were relatively consistent with standard deviations varying between 0.3 and 1.5 bars. The first measurements were taken on July 20 after a 1-wk period without precipitation. The lowest leaf ψ (–14 to –15 bars) were obtained 20 m downslope in an area that had been snow-free for 4 to 5 wk. Readings in the fellfield and at 40 to 43 m downslope were also relatively low (–12 to –14 bars). Higher leaf ψ of –5 bars was recorded at the base of the slope, an area that had been snow-free for only 3 wk.

Measurements taken 24 days later showed only slightly lower leaf ψ although soil ψ had markedly decreased to –14 to –17 bars. The lowest leaf ψ for most species was recorded at this time. *Lupinus latifolius* (at 21 m downslope) and *Phyllodoce empetriformis* (adjacent to the transect at ≈ 25 m downslope) reached lows of –27 and –22 bars, respectively. The *Lupinus* plants were wilted at this time and died back several days later. The *Phyllodoce empetriformis* plants appeared normal. Other species reached lows of –12 to –18 bars. At this time soil ψ was ≈ –14 bars at 19 m downslope and –14 to –17 bars at 36 m downslope. Similar low leaf ψ have been reported from the Olympic Mountains (Kuramoto and Bliss 1970; Peterson 1971) and the Colorado Rockies (Ehleringer and Miller 1975).

A third set of readings was obtained on August 30, 7 days after a heavy rain (2.2 cm). Most plants were dispersing seeds at this time. Leaf ψ, except for *Vaccinium caespitosum*, were slightly higher for species near the top of the slope. The lowest leaf ψ for species at the base of the slope were reached at this time. These leaf ψ were still much higher than those attained by the same species upslope. Readings showed high diurnal amplitudes with species increasing by as much as 11 bars at 2400 h from their afternoon lows. Therefore, the plants may spend part of the day at a lower leaf ψ and still be photosynthetically active in the morning. Kuramoto and Bliss (1970), working in the Olympic Mountains, Washington, found that at a soil ψ of –15 bars, *Festuca idahoensis*, *Lupinus latifolius* var. *subalpinus* and *Eriophyllum lanatum* still maintain a photosynthetic rate ≈ 40% that at –0.3 bars in plants from a subalpine meadow.

Phenology.—Plant phenology can often be helpful in describing microenvironmental differences between various habitats (Bliss 1962) as well as along environmental gradients. During the summers of 1971 and 1972, 32 species were observed at 10-m intervals along the transect.

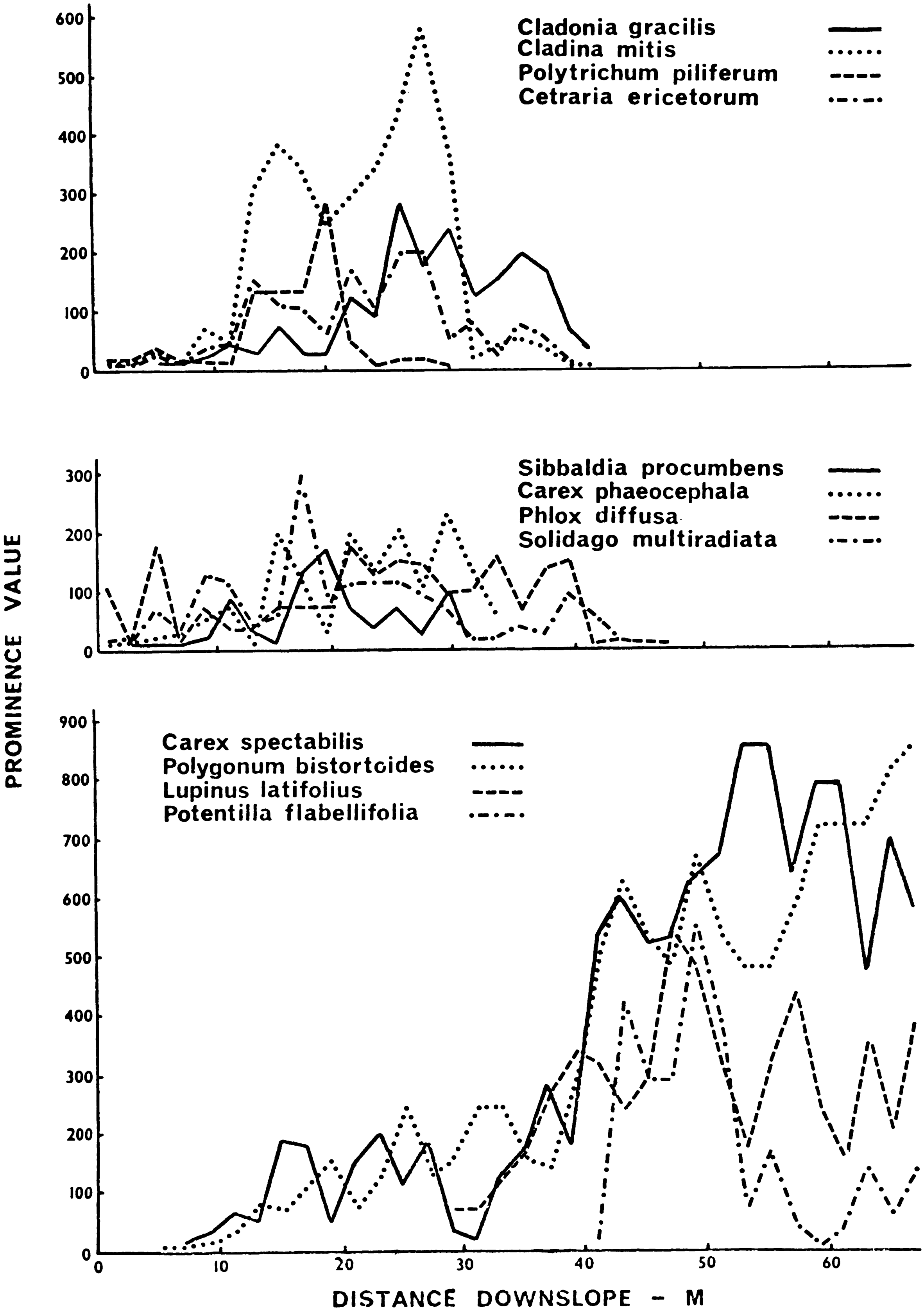
Phenological phases varied considerably among species along the gradient (Fig. 11). Length of a given phenological phase was relatively consistent within species, regardless of the year or position on the slope.

Snowmelt took place at about the same time in both 1971 and 1972. The upper part of the slope was free of snow by 18 June and at the base by 28 June. The much higher temperatures in late June and early July during 1972, however, resulted in more vigorous vegetative growth and an earlier flowering for most species. This was especially notable in the upper part of the gradient. *Silene parryi*, in the fellfield, and *Potentilla flabellifolia*, at the base of the transect, were exceptions to this pattern.

At any given point on the environmental gradient, most of the species have similar flowering phases, an indication that local microenvironments govern phenological development (Bliss 1956). The most notable exceptions to this were the late development of *Aster foliaceus* and the early development of *Claytonia lanceolata*. In general, most species flowered 14 to 24 days after initation of growth. They re-

→

FIG. 8. Distribution and abundance of major plant species along an environmental gradient on Grouse Ridge, Mt. Baker, Washington.



Cladonia gracilis
Cladina mitis
Polytrichum piliferum
Cetraria ericetorum
Sibbaldia procumbens
Carex phaeocephala
Phlox diffusa
Solidago multiradiata
Carex spectabilis
Polygonum bistortoides
Lupinus latifolius
Potentilla flabellifolia
PROMINENCE VALUE
0
100
200
300
400
500
600
700
800
900
10
20
30
40
50
60
DISTANCE DOWNSLOPE - M

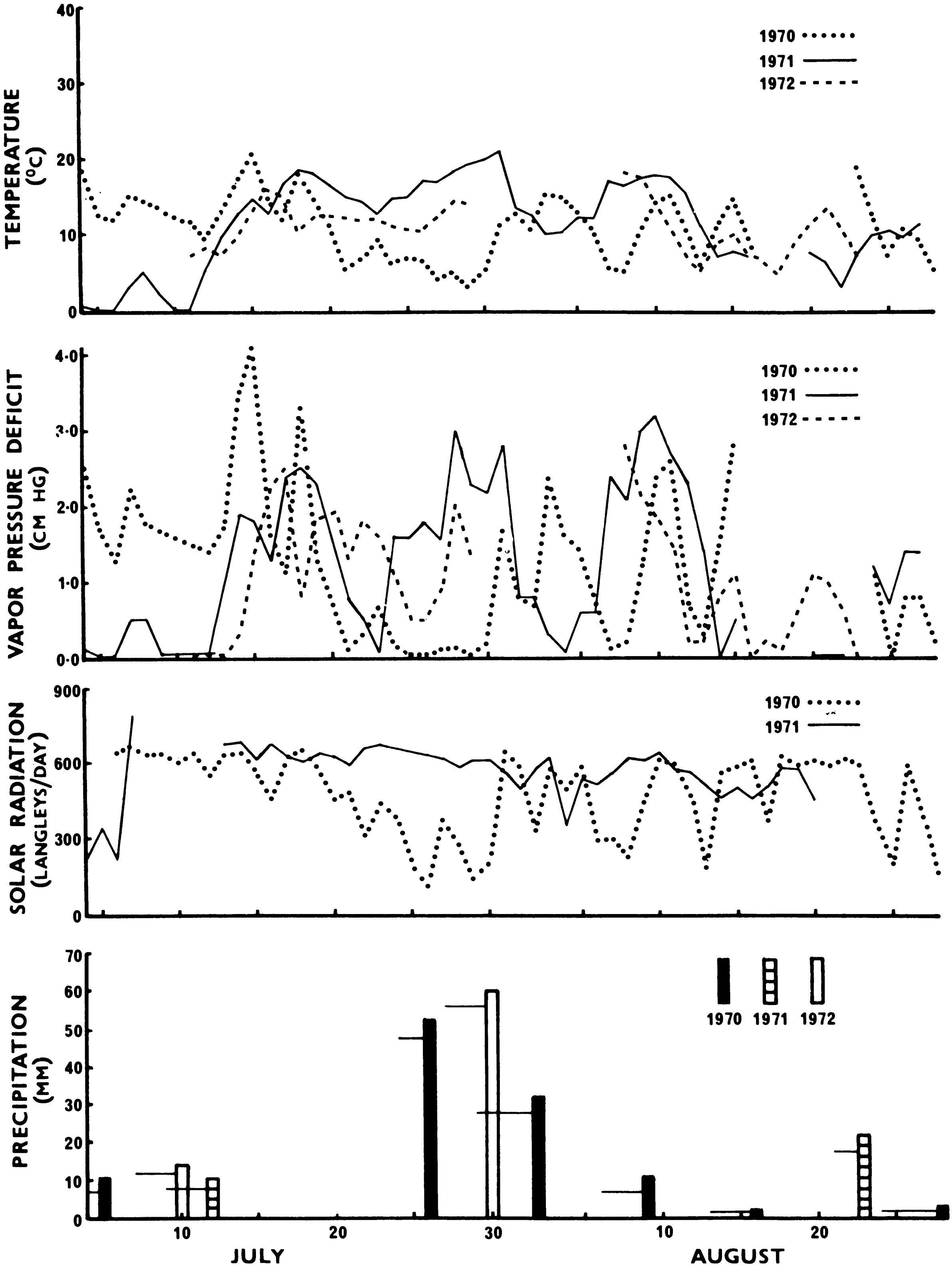


FIG. 9. Seasonal variation in temperature, average vapor-pressure deficits (VPD), solar radiation, precipitation at the Grouse Ridge weather station during 1970, 1971, and 1972. Horizontal lines adjacent to the precipitation bars represent the period over which the precipitation reading was accumulated. To convert langleys to joules/m², multiply by 4.184×10^4.

mained in flower for 8 to 20 days before entering a 10- to 24-day fruiting stage prior to seed dispersal.

Discussion

Community pattern

Distribution of alpine plant communities in the North Cascades is in response to complex environmental factors and environmental gradients. When environmental gradients are steep, abrupt changes in species composition occur, creating a mosiac of plant communities on the landscape. If these gradients are gentle, more gradual changes create a continuum. In the North Cascades, the mosiac pattern is more common, especially in the western and central portions of the range. This is due to the complex topography and greater snowfall which results in variable snow depths and snowmelt times and a broad range of summer soil moisture regimes. These environmental factors are also of prime importance in the eastern North Cascades, but to a lesser extent. In the eastern mountains the more gentle topography, lower snowfall, and more rapid snowmelt result in a gradual shift in community pattern.

The importance of the time of snowmelt is demonstrated by the two-dimensional ordinations (Fig. 2) of the major community types. The date of snowmelt also determines the summer soil moisture regime, at least for the earlier, and probably the most important part of the growing season.

In the western mountains, a distinct mosaic appears repeatedly on the landscape. Snow depth and snowmelt time varies considerably. In snowbank sites, communities are dominated by *Carex nigricans* unless the soils are unstable, in which case the *Saxifraga tolmiei-Luzula piperi* community occurs.

On better drained habitats where snowmelt is earlier, the heath communities, dominated by either *Cassiope mertensiana*, *Phyllodoce empetriformis*, *Phyllodoce glanduliflora*, *Arctostaphylos uva-ursi*, or *Empetrum nigrum*, are common. The latter is most frequently found on exposed or northerly aspects. Exposed sites with slightly earlier snowmelt times are dominated by *Salix cascadensis* or *Salix nivalis*.

Communities on warm, moist, lower southerly slopes are dominated by the *Lupinus latifolius* type. The closely related *Carex spectabilis* community occurs on similar, but slightly drier and often higher slopes. Where the earliest snowmelt occurs (Fig. 3), the sites become relatively dry by mid-summer and are dominated by *Carex phaeocephala*.

On ridgetops, which have little snow cover during most of the winter, herbfields, fellfields, boulderfields, and vegetation stripes are typical. These sites may be occupied by a variety of species, either in clumps, where the surface is stable, or in vegetation stripes where slow downslope creep takes place. Prominent plants in these habitats are *Phlox diffusa, Potentilla diversifolia* var. *diversifolia*, *Solidago multiradiata*, *Oxytropis campestris* var. *gracilis*, and *Carex albonigra*.

Changes in macroclimate in an easterly direction result in gradual changes in the plant community pattern. Lower snow accumulation, slightly earlier snowmelt, and somewhat drier and warmer summers in the central North Cascades result in the absence of some communities and the appearance of others. Late-melting snowbanks are still occupied by *Carex nigricans* but snow accumulation sites that become snow-free earlier are dominated by *Antennaria lanata* or *Carex breweri* (Fig. 2). *Antennaria lanata* communities often occur in close proximity to the *Carex nigricans* type, but the former are better drained sites and become drier in late summer. The segregation of communities within an alpine snowbank site was also noted in the Presidential Range of New Hampshire (Bliss 1963), the Rocky Mountains (Billings and Bliss 1959; Johnson and Billings 1962) and the Olympic Mountains of Washington (Bliss 1969). In steep, unstable snow-accumulation areas in the central North Cascades, the *Eriogonum pyrolaefolium-Luzula piperi* community replaces the *Saxifraga tolmiei-Luzula piperi* community.

The same heath communities found to the west occupy similar habitats in the central region. Communities dominated by *Salix cascadensis* or *Salix nivalis* also occupy drier exposed slopes. The driest of these exposed slopes, and some of the ridgetops, are characterized by extensive mats of *Dryas octopetala*.

Warm, moist, southern lower slopes are occupied by the *Lupinus latifolius* community but the closely related *Carex spectabilis* community is apparently replaced on drier central region sites by *Festuca viridula*. *Carex phaeocephala* again dominates sites that are snow-free earlier, but on the most exposed upper slopes *Carex nardina* becomes the most prominent species.

The herbfields, fellfields, boulderfields, and vegetation stripes in this region are also extremely variable in plant and rock cover and species composition. Important plants are *Selaginella densa*, *Phlox diffusa*, *Carex phaeocephala*, and *Arenaria capillaris*, and farther south, *Phlox hendersonii* and *Lupinus lepidus* var. *lobbii*.

The dry, warm summers and lower winter snowfall in the eastern North Cascades provide community patterns that are in marked contrast to those to the west. Although mosiac patterns are still common, many extensive slopes show gradual changes in species composition in response to more gradual environmental gradients. Communities which span

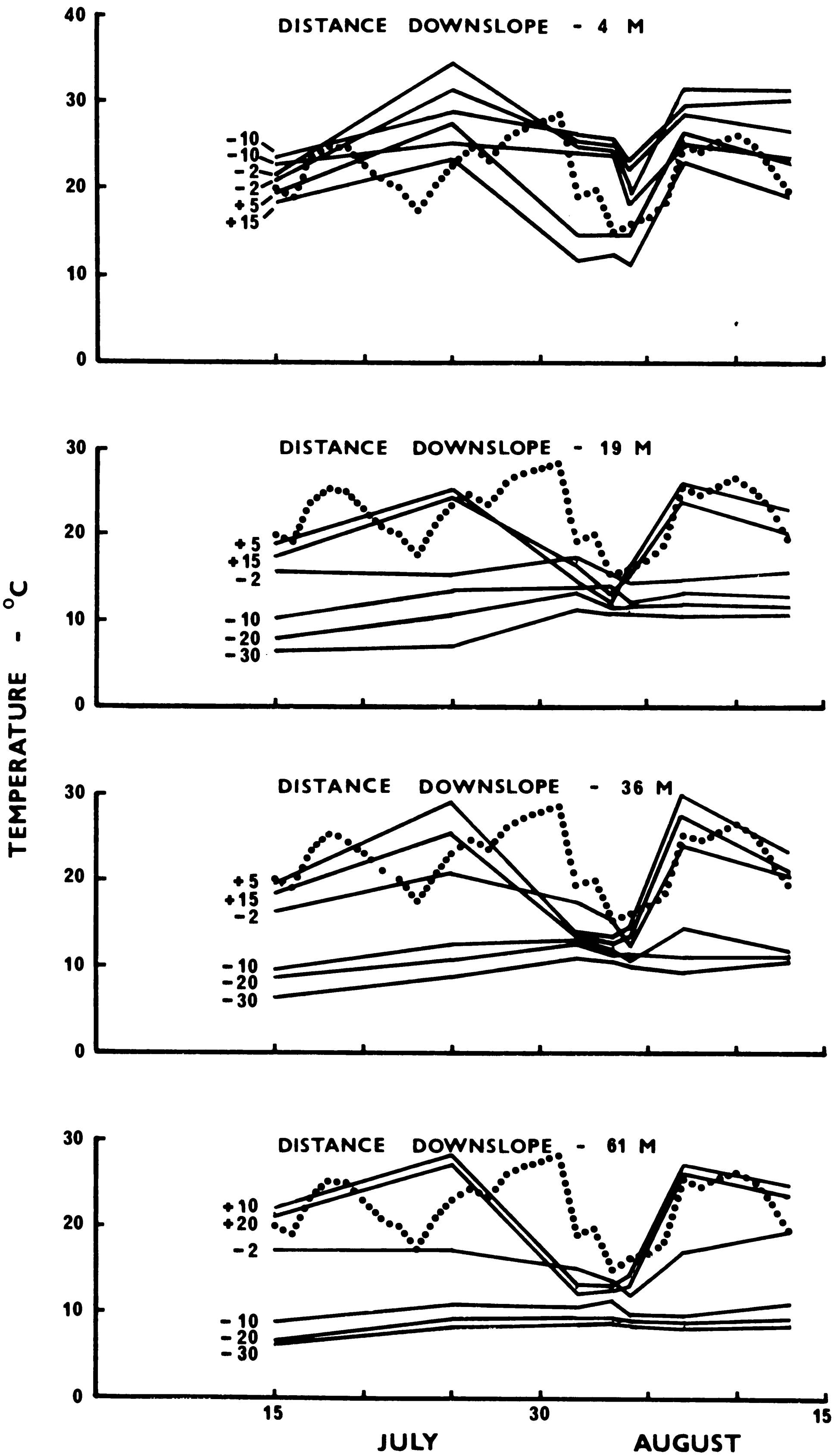

DISTANCE DOWNSLOPE - 4 M
-10
-10
-2
-2
+5
+15
DISTANCE DOWNSLOPE - 19 M
+5
+15
-2
-10
-20
-30
TEMPERATURE - °C
DISTANCE DOWNSLOPE - 36 M
+5
+15
-2
-10
-20
-30
DISTANCE DOWNSLOPE - 61 M
+10
+20
-2
-10
-20
-30
40
30
20
10
0
15
30
15
JULY
AUGUST

TABLE 9. Seasonal leaf water potential (bars) of 10 plant species along an environmental gradient on Grouse Ridge, Mt. Baker, Washington during 1971. Data are means of at least three readings taken between 1300 and 1500 h; except those in parentheses which were taken at 2400 h

Species	Downslope distance (m)	Date		
		July 20	August 13	August 30
Lupinus lepidus	1		−13.8	
Solidago multiradiata	5		−15.2	
Solidago multiradiata	7	−11.9	−13.1	
Polygonum bistortoides	7		−17.9	
Polygonum bistortoides	9	−13.8	−15.5	
Solidago multiradiata	19	−15.0	−15.9	−15.1
Polygonum bistortoides	19	−15.0	−17.9	−15.2 (−4.5)
Lupinus latifolius	19		−27.4	
Vaccinium caespitosum	21	−13.8	−14.1	−17.0 (−7.9)
Erigeron peregrinus	21		−17.2	
Polygonum bistortoides	36	−11.8	−12.4	
Lupinus latifolius	36	−12.0	−12.9	
Aster foliaceus	43			−11.0 (−5.5)
Polygonum bistortoides	61	−5.1	−5.2	−5.8 (−2.1)
Lupinus latifolius	61	−5.0	−5.5	
Lupinus latifolius	63		−7.6	−9.2 (−3.4)
Castilleja miniata	Not on transect		−16.2	
Vaccinium deliciosum	Not on transect	−10.2	−12.4	−8.3 (−6.5)
Phyllodoce empetriformis	Not on transect	−15.6	−22.1	−21.9

the entire range may change with respect to composition and habitat (e.g., *Phyllodoce empetriformis*, *P. glanduliflora*, and *Salix cascadensis*) or structure (e.g., *Salix nivalis*).

Numerous snowbank communities occur in this region. *Carex nigricans* is essentially restricted to the subalpine zone with *Antennaria lanata* or *Carex breweri* dominating the alpine sites where snow accumulation is greatest (Fig. 2). Snowbed sites that open slightly earlier are occupied by *Phyllodoce empetriformis*, *Phyllodoce glanduliflora*, or *Salix cascadensis*. At higher elevations, level areas or depressions which receive moisture for much of the summer from upslope, are dominated by *Carex capitata*.

On well-drained habitats where snowmelt is earlier, communities may be dominated by *Carex phaeocephala*, *Arctostaphylos uva-ursi*, *Salix cascadensis*, *Salix nivalis*, or *Dryas octopetala*, with the latter two occupying the driest sites. At lower elevations in the alpine and subalpine zones of the eastern region, where soil moisture levels are greater, broad expanses are dominated by *Danthonia intermedia*. Upslope, this community often grades into the *Carex scirpoidea* var. *pseudoscirpoidea* type, another extensive community.

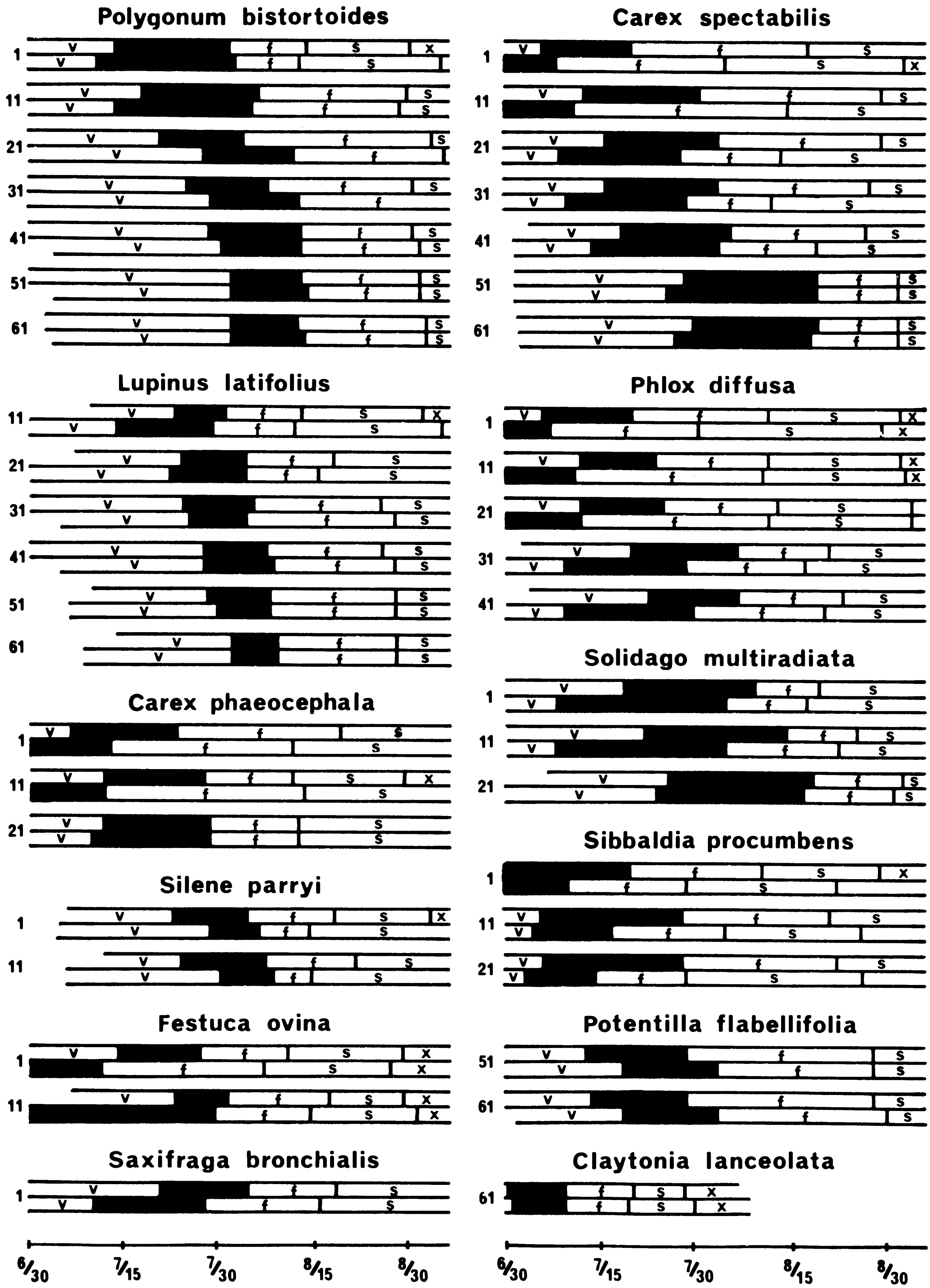
The driest of the major alpine communities occurs on the higher slopes and summits. These are dominated by *Carex nardina*, *Calamagrostis purpurascens*, or *Kobresia myosuroides*. The topographical position of the *Kobresia myosuroides* community suggests that these sites are essentially free of snow with ephemeral microdrifts occurring during the winter, such as Bell (1973) reported for this type in the Rocky Mountains of Colorado. The *Calamagrostis purpurascens* stands often occur in rocky sites within larger *Kobresia* communities. These rocky sites may provide slightly better protection during the winter.

The herbfields, boulderfields, and vegetation stripes which occupy the driest, snow-free ridgetops, vary considerably in composition. *Lupinus lepidus* var. *lobbii*, *Arenaria obtusiloba*, and *Festuca ovina* var. *brevifolia* are prominent species.

The overstory composition of krummholz stands changes markedly across the North Cascades. In the western part of the range, *Abies lasiocarpa* predominates. *Abies lasiocarpa*, along with *Picea engelmannii* and *Larix lyallii*, is common in the central North Cascades. Farther east *Picea engelmannii* and *Pinus albicaulis* dominate the krummholz stands. Regional separation on the basis of understory composition is inconsistent due to considerable variation in com-

←

FIG. 10. Seasonal variations in soil and air temperature profiles at various heights (cm) and depths (cm) along an environmental gradient on Grouse Ridge, Mt. Baker, Washington during 1971. The dotted line represents the daily maximum air temperature at an adjacent weather station. Temperature profile data are for readings taken between 1300 and 1500 h. Soil temperatures in the fellfield (4 m downslope) were monitored on both nonvegetated (NV) and vegetated (V) sites.


Polygonum bistortoides
Carex spectabilis
Lupinus latifolius
Phlox diffusa
Solidago multiradiata
Carex phaeocephala
Sibbaldia procumbens
Silene parryi
Festuca ovina
Potentilla flabellifolia
Saxifraga bronchialis
Claytonia lanceolata
6/30
7/15
7/30
8/15
8/30

position and the distribution of several important species across the entire range (Table 7). Some of the herb and shrub species associated with the krummholz stands are subalpine species that reach their upper limits in these snow protected sites.

Community-soil relationships

Jenny (1941) stated that any soil property is a function of the regional climate, parent materials, topography, biota, and time. The vegetation of a region is also a function of these factors (Major 1951). In the North Cascades, all of these factors, with the exception of the parent materials, vary considerably. This relatively uniform parent material is due, in large part, to the extensive pyroclastic deposits present in the region. These deposits, mixed with the residuum of the various geologic strata, modify the residuum to such an extent that they have no detectable influence on the regional vegetation and soil patterns. This is in contrast to many regions where ultramafic (Kruckeberg 1954, 1969; Whittaker 1954), sandstone-dolomite (Mooney et al. 1962), or calcareous (Bamberg and Major 1968) parent materials have marked effects on vegetation and soil patterns.

The pattern of alpine soil types in the North Cascades generally corresponds to the vegetation pattern. Beneath krummholz and heath vegetation, cheluviation is a common process. This process is most intense in the western North Cascades where leached *A*2 horizons and iron-rich *B* horizons are typical.

Inceptisols are typical of many of the community types in the North Cascades, especially in the eastern part of the range. The most notable differences within the Inceptisols are the chemical characteristics, which vary markedly from west to east. The western soils usually have higher organic matter, cation exchange capacity, and nutrient levels, and are more acidic.

Sites that are unstable and sparsely vegetated are characterized by Entisols. These soils usually have only shallow *A-C* profiles beneath vegetation and have low organic matter, cation exchange capacity, and nutrient levels.

Response of species to an environmental gradient

The environmental gradient on Grouse Ridge provided an opportunity to examine the response of various species to gradual changes in microenvironment along an alpine slope. Plant community data collected along the transect also indicate a gradual, but notable, change in structure and composition (Fig. 8). The fellfield is characterized by sparse clumps of vegetation (total average cover of 21%) and moderate species richness (*S*, average of 20 species). In the ecotonal area between discontinuous and continuous vegetation, species richness reaches a maximum ($S = 29$). Total plant cover increases to 217% while species richness decreases ($S = 4$) at the base of the slope.

Soil temperature and soil moisture measurements monitored for two summers indicated that high soil temperature and low soil moisture regimes are typical of the ridgetop fellfield while lower temperatures and higher moisture levels occur downslope. Soil temperature decreases slightly, while soil moisture stress increases, with distance down the vegetated portion of the slope during drought periods. The pattern of these environmental parameters is likely due to the increased vegetative cover and greater evapotranspiration rates at the base of the slope.

Measurements of leaf ψ also indicate varying responses to slope environmental gradients. Leaf ψ generally increased with distance downslope. Measurements obtained on the upper slope (at 21 m) were generally between ≈ -14 and -18 bars, except in the case of *Lupinus latifolius* with a low of -27 bars. The plants, from which the latter values were obtained, died back within several days, indicating that *Lupinus latifolius* probably cannot tolerate leaf ψ much lower than that attained in *Polygonum bistortoides* (-15 to -18 bars). The highest leaf ψ (-5.2 to -9.2 bars) were measured at the base of the slope. These higher values indicate that the bulk of the water requirements of the plants are being sufficiently met from near the -30 cm level where soil moisture stress is seldom, if ever, critical.

The leaf ψ values may explain the distribution pattern and relative abundance of *Lupinus latifolius*, *Polygonum bistortoides*, and *Carex spectabilis* along the gradient. At the base of the slope, where leaf ψ was never low (Table 9), *Lupinus latifolius*, *Polygonum bistortoides*, and *Carex spectabilis* reach their lushest and most vigorous growth, excluding almost all other plants. Farther upslope, (at 36 m) where leaf ψ is lower, these three plants are still able to grow, but with reduced vigor. Habitat heterogeneity thus increases resulting in increasing species richness.

←

FIG. 11. Phenological patterns of 12 plant species on Grouse Ridge, Mt. Baker, Washington during 1971 (upper bar) and 1972 (lower bar). Distance (m) downslope appears on the ordinate axis; month and day are on the abscissa. Symbols are: v—vegetative growth; solid bar—in flower; f—in fruit; s—seed dispersal; x—signs of dormancy.

The plants occurring in the fellfield are adapted to an entirely different set of environmental factors than those downslope. *Polygonum bistortoides* and *Carex spectabilis* occur only near the edge of the fellfield in large (1 to 2 m^2) clumps. Since these clumps are probably not snow-free during the winter, these plants do not have to endure the high winds, low temperatures, and frequent frost cycles common to the rest of the fellfield. The fellfield species are also adapted to adverse summer conditions. Soil temperatures and soil moisture stress are high and possibly might exclude other plants even though they may be able to endure winter conditions.

Observations showed that phenological phases are closely related to time of snowmelt and early-season temperature regimes. The ability of *Claytonia lanceolata* to flower within several days after snowmelt and complete its life cycle just before the vegetative canopy closes, at the base of the slope, is due in large part to its ability to initiate growth beneath the snow during fall or winter. Douglas and Taylor (1972), also working on Grouse Ridge, found *Claytonia lanceolata* relatively well developed and in bud under 2 m of snow. Kimball et al. (1973) found new apical growth in early fall in Rocky Mountain populations of *Claytonia lanceolata.* Other workers have also noted the ability of this and other alpine species to initiate growth at near-freezing temperatures beneath snow (Billings and Bliss 1959; Mooney and Billings 1961; Halleck and Wiens 1966; Spomer and Salisbury 1968; Bell 1973). The fellfield species also show early phenological development, enabling them to complete much of their seasonal growth before conditions become unfavorable.

Distribution of alpine and subalpine community types in western North America

The numerous floristic works dealing with various regions of North America document the geographic range of most alpine vascular plant taxa adequately. The North Cascadian flora is an exception. Recent collections have resulted in significant new range extensions for 20 alpine species in western North America (Douglas and Taylor 1970; Douglas et al. 1973; Taylor et al. 1973).

The alpine flora of the North Cascades has floristic affinities with many regions. The strongest affinities are with the arctic and cordilleran regions to the north and east. A smaller segment of the flora is restricted to the Pacific Coast, ranging from British Columbia to northern California. The Cascadian endemic element that ranges into the North Cascades consists of only a few species.

In contrast to our knowledge of plant ranges, information on the abundance of a taxon in a particular region is conspicuously poor. A number of papers, although describing the general vegetation of various regions, usually fail to document the relative abundance of the taxa, thus making it difficult to recognize vegetation types for comparative purposes. The following discussion is based on the few studies that do allow comparisons with the North Cascadian communities. Future work will surely increase the geographic ranges of the communities presented here.

The range of alpine plant communities is not necessarily restricted to the alpine zone. A number of them have subalpine-alpine distributions, both in the North Cascades and elsewhere. Tables 10 and 11 lend support for the inclusion of krummholz within the alpine zone, at least in the North Cascades, because more of the communities and a larger segment of the flora associated with krummholz occur in the alpine tundra above than in the tree-clump meadows or subalpine zone below.

A number of community types may be restricted to the North Cascades. These include the *Calamagrostis purpurascens*, *Eriogonum pyrolaefolium-Luzula piperi*, *Danthonia intermedia*, *Carex breweri*, and *Carex capitata* types.

Of the snowbed communities, the *Carex nigricans* type appears to be the most widespread. It occurs in both the subalpine and alpine zones in the Cascades of Oregon (Van Vechten 1960) and central Washington (Meredith 1972), the Olympic Mountains of Washington (Bliss 1969; Kuramoto and Bliss 1970), southern British Columbia (Archer 1963; Brooke et al. 1970; Eady 1971), north to southern Alaska (Cooper 1942), and east to the Canadian Rockies (Beder 1967; Hrapko 1970; Knapik et al. 1973). The *Antennaria lanata* community, which also occurs in the subalpine zone of the eastern Cascades, is found in the alpine zone of the Olympics (Bliss 1969) and the Canadian Rockies (Beder 1967; Hrapko 1970; Knapik et al. 1973). The *Eriogonum pyrolaefolium-Luzula piperi* community may be restricted to the North Cascades although similar, but drier, communities dominated by *Eriogonum pyrolaefolium* (but lacking *Luzula*) have been reported from Oregon (Van Vechten 1960). The *Saxifraga tolmiei-Luzula piperi* type occurs only in the subalpine and alpine zones of the North Cascades and the nearby Coast Range of British Columbia (McAvoy 1931, Brooke et al. 1970).

Lush herb communities dominated by *Festuca viridula* and *Lupinus latifolius* are found in the subalpine and alpine zones in, and south of, the North Cascades. *Festuca viridula-Lupinus latifolius* (Franklin and Dyrness 1973; Franklin et al. 1971) and *Lupinus latifolius* types (Meredith 1972) have been reported on Mount Rainier, Washington. These types

TABLE 10. Elevational distribution of alpine zone plant communities in three regions (west, central, and east) of the North Cascades Range

Elevational distribution[a]	Region			Total
	West	Central	East	
Alpine tundra		*Carex breweri* *Carex nardina*	*Carex breweri* *Carex nardina* *Carex capitata* *Salix nivalis* *Calamagrostis purpurascens* *Kobresia myosuroides*	6
Alpine tundra + krummholz	*Phyllodoce glanduliflora* *Empetrum nigrum* *Salix nivalis* *Salix cascadensis* *Carex phaeocephala*	*Phyllodoce glanduliflora* *Empetrum nigrum* *Salix nivalis* *Salix cascadensis* *Carex phaeocephala* *Eriogonum-Luzula* *Dryas octopetala*	*Phyllodoce glanduliflora* *Salix cascadensis* *Carex phaeocephala* *Dryas octopetala* *Carex scirpoidea*	8
Alpine tundra + krummholz + tree clump/meadow	*Saxifraga-Luzula* *Carex nigricans* *Cassiope mertensiana* *Phyllodoce empetriformis* *Carex spectabilis* *Arctostaphylos uva-ursi*	*Carex nigricans* *Cassiope mertensiana* *Phyllodoce empetriformis* *Arctostaphylos uva-ursi* *Antennaria lanata*	*Phyllodoce empetriformis* *Arctostaphylos uva-ursi* *Antennaria lanata* *Danthonia intermedia*	9
Krummholz + tree clump/meadow	*Lupinus latifolius*	*Lupinus latifolius* *Festuca viridula*		2

[a] Definitions: The tree clump/meadow zone or subalpine zone is defined as that area above the continuous forest and below the upper limit of conifers as an upright tree form (Douglas 1971, 1972). The krummholz zone is a narrow band of dwarfed or prostrate conifer clumps interspersed with meadows and has been referred to in this paper as the lower alpine zone. Above the krummholz is the alpine tundra or upper alpine zone.

have also been documented in the Three Sisters (Van Vechten 1960) and Mt. Jefferson (Swedberg 1961) areas in Oregon. Farther east, in the Wallow Mountains, Strickler (1961) has studied communities dominated by *Festuca viridula.* A similar *Festuca* (*Festuca idahoensis*) type occurs in the subalpine zone of the Olympic Mountains (Kuramoto and Bliss 1970).

TABLE 11. Elevational distribution of alpine zone vascular plant species in three regions (west, central, and east) of the North Cascades Range

Elevational distribution	NUMBER OF SPECIES Region			
	West	Central	East	All regions
Alpine tundra[1]	7	13	17	26
Alpine tundra + krummholz	56	57	49	70
Alpine tundra + krummholz + tree clump/meadows	72	90	80	104
Krummholz + tree clump/meadows	34	32	19	50
Total species	169	191	165	250

[1] Definitions: see Table 11.

Several of the North Cascadian shrub types have wide geographic ranges. *Dryas octopetala*, a circumpolar species, occurs as a major dominant north to Alaska and the Yukon (Hanson 1951; Price 1971), east to the Rocky Mountains of Alberta (Beder 1967; Bryant and Scheinberg 1970; Hrapko 1970; Knapik et al. 1973) and south in the Rockies to Colorado (Johnson and Billings 1962; Holway and Ward 1965; Marr 1967; Bamberg and Major 1968). The several heath types are also widely distributed in both the subalpine and alpine zones. They occur in the Olympics (Kuramoto and Bliss 1970) the Cascades of Oregon (Van Vechten 1960) and central Washington (Franklin et al. 1971; Meredith 1972), north to northern British Columbia (McAvoy 1931; Archer 1963; Brooke et al. 1970; Eady 1971; Welsh and Rigby 1971) and the southwestern Yukon (G. W. Douglas, *personal observation*), and in the Rocky Mountains of Alberta (Heusser 1956; Beder 1967; Hrapko 1970;

Knapik et al. 1973) and Montana (Bamberg and Major 1968). *Cassiope tetragona*, found mainly in small clumps and on north aspects in the eastern North Cascades, becomes a recognizable type farther north (northwestern British Columbia and the southwestern Yukon) and east (Rocky Mountains of Alberta) (Hrapko 1970; Welsh and Rigby 1971; Knapik et al. 1973; G. W. Douglas, *personal observation*). *Empetrum nigrum*, a circumpolar species, occurs as a community type in Alberta, the southwestern Yukon, and northern Alaska (Bliss 1956; Hrapko 1970; G. W. Douglas, *personal observation*). The *Salix nivalis* community has been reported elsewhere as a major dominant from western Montana (Bamberg and Major 1968), and southwestern Alberta (Knapik et al. 1973). The *Salix cascadensis* community is also rare in the literature, being documented only from Wyoming (Billings and Bliss 1959). The *Arctostaphylos uva-ursi* type has been reported from western Montana by Bamberg and Major (1968).

Kobresia myosuroides, a wide-ranging circumpolar species, has been reported as a dominant in many regions. This type has been described from Colorado to Alberta in the Rocky Mountains (Cox 1933; Marr 1967; Bamberg and Major 1968; Hrapko 1970; Bell 1973; Knapik et al. 1973) and north to the Kluane Ranges of the southwestern Yukon (G. W. Douglas, *personal observation*) and Mt. McKinley in Alaska (Hanson 1951). It also occurs in the Sierra Nevada Mountains of California where it is a disjunct species (Major and Bamberg 1963). Reports of other North Cascadian sedge types are sparse. *Carex scirpoidea* var. *pseudoscirpoidea* stands have been recorded in the Snowy Mountains of central Montana (Bamberg and Major 1968) and the Sierra Nevada Mountains in California (Major and Bamberg 1963). *Carex nardina* is reported as a dominant in the alpine of southwestern Alberta (Bryant and Scheinberg 1970). The *Carex spectabilis* community appears to be mainly restricted to the subalpine and alpine zones of northwestern Washington and southern British Columbia (Kuramoto and Bliss 1970; Eady 1971; Douglas 1972) although it also occurs as an alpine snowbed community in the Sierra Nevada Mountains (J. Major, *personal communication*).

In general, the communities restricted to the western or central North Cascades have closer affinities to coastal areas both to the north and south. Those communities restricted to the eastern North Cascades show closer affinities to Rocky Mountain and far northern areas.

Acknowledgments

Thanks are extended to the many people who assisted in the course of this study. Drs. J. G. Bockheim, S. Pawluk, and W. W. Pettapiece provided suggestions and aid with regard to soils. Dr. T. M. Ballard supplied the specifications for construction of the bridge-meter. The following taxonomists kindly identified or verified difficult taxa: C. D. Bird, A. Cronquist, G. G. Douglas, C. Feddema, F. J. Hermann, C. L. Hitchcock, N. H. Holmgren, G. A. Mulligan, M. Ostafichuk, W. L. Peterson, R. J. Taylor, and D. H. Vitt.

The cooperation and logistical support provided by the staff of North Cascades National Park is also appreciated. This study was supported by National Research Council Grant NRC A-4879 to Bliss.

Special thanks are due to Gloria G. Douglas. Her cheerful aid during the long hours of field and laboratory work proved invaluable.

Literature Cited

Archer, A. C. 1963. Some synecological problems in the alpine zone in Garabaldi Park. M.S. thesis. Univ. British Columbia, Vancouver, B.C. 129 p.

Arno, F., and J. R. Habeck. 1972. Ecology of alpine larch (*Larix lyallii* Parl.) in the Pacific Northwest. Ecol. Monogr. **42**:417–450.

Bamberg, S. A., and J. Major. 1968. Ecology of the vegetation and soils associated with calcareous parent materials in three alpine regions of Montana. Ecol. Monogr. **38**:127–167.

Beals, E. 1960. Forest bird communities in the Apostle Islands of Wisconsin. Wilson Bull. **72**:156–181.

Beder, K. 1967. Ecology of the alpine vegetation of Snow Creek Valley, Banff National Park, Alberta. M.S. thesis. Univ. of Calgary, Calgary, Alberta. 243 p.

Bell, K. L. 1973. Autecology of *Kobresia myosuroides*: why winter snow accumulation patterns affect local distribution. Ph.D. thesis. Univ. of Alberta, Edmonton, Alberta. 173 p.

Billings, W. D., and L. C. Bliss. 1959. An alpine snowbank environment and its effects on vegetation, plant development, and productivity. Ecology **40**:388–397.

Bliss, L. C. 1956. A comparison of plant development in microenvironments of arctic and alpine tundras. Ecol. Monogr. **26**:303–337.

———. 1962. Adaptations of arctic and alpine plants to environmental conditions. Arctic **15**:117–144.

———. 1963. Alpine plant communities of the Presidential Range, New Hampshire. Ecology **44**:678–697.

———. 1966. Plant productivity in alpine microenvironments on Mount Washington, New Hampshire. Ecol. Monogr. **36**:125–155.

———. 1969. Alpine community patterns in relation to environmental parameters, p. 167–184. *In* K. N. H. Greenridge [ed.] Essays in Plant Geography and Ecology. Nova Scotia Museum, Halifax, Nova Scotia.

Bockheim, J. G. 1972. Effects of alpine and subalpine vegetation on soil development, Mount Baker, Washington. Ph.D. thesis. Univ. of Washington, Seattle, Wash. 171 p.

Bouyoucos, G. J. 1951. A recalibration of the hydrometer method for making mechanical analysis of soil. Agron. J. **43**:434–438.

Bray, J. R., and J. T. Curtis. 1957. An ordination of upland forest communities of southern Wisconsin. Ecol. Monogr. **27**:325–349.

Brink, V. C. 1959. A directional change in the subalpine forest-heath ecotone in Garabaldi Park, British Columbia. Ecology **40**:10–16.

British Columbia Department of Agriculture. 1963. Climate of British Columbia. Queens Printer, Victoria. 53 p.

Brooke, R. C., E. B. Peterson, and V. J. Krajina. 1970.

The subalpine mountain hemlock zone, p. 147–349. *In* V. J. Krajina and R. C. Brooke [eds.] Ecology of western North America, Vol. 2. Dept. of Botany, Univ. of British Columbia, Vancouver, B.C.

Bryant, J. R., and E. Scheinberg. 1970. Vegetation and frost activity in an alpine fellfield on the summit of Plateau Mountain, Alberta. Canadian J. Bot. **48**: 751–772.

Cain, S. A. 1938. The species-area curve. Am. Midl. Nat. **17**:725–740.

Clausen, J. 1965. Population studies of alpine and subalpine races of conifers and willows in the California High Sierra Nevada. Evolution **19**:56–68.

Coleman, E. A., and T. M. Hendrix. 1949. The fibreglass electrical soil-moisture instrument. Soil Sci. **67**: 425–438.

Coombs, H. A. 1939. Mt. Baker, a Cascade volcano. Geol. Soc. Am. Bull. **50**:1493–1510.

Cooper, W. S. 1942. Vegetation of the Prince William Sound region, Alaska; with a brief excursion into post-Pleistocene climatic history. Ecol. Monogr. **12**:1–22.

Cox, C. F. 1933. Alpine plant succession on James Peak, Colorado. Ecol. Monogr. **3**:299–372.

Crandell, D. R. 1965. The glacial history of western Washington and Oregon, p. 341–353. *In* H. E. Wright, Jr. and D. G. Frey [eds.] The Quaternary of the United States. Princeton Univ. Press, Princeton, New Jersey.

Crandell, D. R., D. R. Mullineaux, R. D. Miller, and M. Rubin. 1969. Pyroclastic deposits of recent age at Mount Rainier, Washington. U.S. Geol. Surv. Prof. Pap. 450-D. 64 p.

Dansereau, P. 1957. Biogeography. Ronald Press, New York. 394 p.

Daubenmire, R. F. 1959. A canopy-coverage method of vegetational analysis. Northwest Sci. **33**:43–66.

Daubenmire, R. 1968. Plant communities. Harper and Row, New York. 300 p.

Douglas, G. W. 1971. The alpine-subalpine flora of the North Cascade Range, Washington. Wasmann J. Biol. **29**:129–168.

———. 1972. Subalpine plant communities of the western North Cascades, Washington. Arct. Alp. Res. **4**:147–166.

———. 1973. Alpine plant communities of the North Cascades Range, Washington and British Columbia. Ph.D. thesis. Dept. Bot., Univ. Alberta. 145 pp.

———. 1974. Montane zone vegetation of the Alsek River region, southwestern Yukon. Canadian J. Bot. **52**:2505–2532.

Douglas, G. W., and T. M. Ballard. 1971. Effects of fire on alpine plant communities in the North Cascades, Washington. Ecology **52**:1058–1064.

Douglas, G. W., D. B. Naas, and R. W. Naas. 1973. New Plant records and ranges for Washington. Northwest Sci. **47**:105–108.

Douglas, G. W., and R. J. Taylor. 1970. Contributions to the flora of Washington. Rhodora **72**:496–501.

Douglas, G. W., and R. J. Taylor. 1972. The biosystematics, chemotaxonomy, and ecology of *Claytonia lanceolata* Pursh in western Washington. Canadian J. Bot. **50**:2177–2187.

Doughty, J. L. 1941. The advantages of a soil paste for routine pH determinations. Soil Sci. **22**:135–138.

Eady, K. 1971. Ecology of the alpine and timberline vegetation of Big White Mountains, British Columbia. Ph.D. thesis. Univ. British Columbia, Vancouver, B.C. 239 p.

Ehleringer, J. R., and P. C. Miller. 1975. Water relations of selected plant species in the alpine tundra, Colorado. Ecology **56**:370–380.

Fonda, R. W., and L. C. Bliss. 1969. Forest vegetation of the montane and subalpine zones, Olympic Mountains, Washington. Ecol. Monogr. **39**:271–301.

Franklin, J. F., and C. T. Dyrness. 1973. Natural vegetation of Oregon and Washington. U.S. For. Serv. Gen. Tech. Rep. PNW-8. 417 p.

Franklin, J. F., W. H. Moir, G. W. Douglas, and C. Wiburg. 1971. Invasion of subalpine meadows by trees in the Cascade Range, Washington and Oregon. Arct. Alp. Res. **3**:215–224.

Gauch, H. G., Jr., and R. H. Whittaker. 1972. Comparison of ordination techniques. Ecology **53**:868–875.

Gleason, H. 1920. Some applications of the quadrat method. Bull. Torrey Bot. Club **46**:21–33.

Hale, M. E., Jr., and W. L. Culberson. 1970. A fourth checklist of the lichens of the continental United States and Canada. Bryologist **73**:499–543.

Halleck, D. K., and D. Wiens. 1966. Taxonomic status of *Claytonia rosea* and *C. lanceolata* (*Portulaceae*). Ann. Missouri Bot. Gard. **53**:205–212.

Hanson, H. C. 1951. Characteristics of some grassland, marsh, and other plant communities in western Alaska. Ecol. Monogr. **21**:317–378.

Heusser, C. J. 1956. Postglacial environments in the Canadian Rocky Mountains. Ecol. Monogr. **26**:263–302.

Hickman, J. C. 1970. Seasonal course of xylem sap tension. Ecology **51**:1052–1056.

Hitchcock, C. L., and A. Cronquist. 1973. Flora of the Pacific Northwest. Univ. Washington Press, Seattle, Wash. 730 p.

Holway, J. G., and R. T. Ward. 1965. Phenology of alpine plants in northern Colorado. Ecology **46**:73–83.

Hrapko, J. O. 1970. An ecological study of the alpine plant communities on Signal Mountain, Jasper National Park. M.S. thesis. Univ. Alberta, Edmonton, Alta. 283 p.

Jenny, H. 1941. Factors of soil formation. McGraw-Hill, New York. 281 p.

Johnson, K. L. 1970. Alpine vegetation and soils of Mesa Seco Plateau, San Juan Mountains, Colorado. Ph.D. thesis. Univ. Illinois, Urbana, Ill. 217 p.

Johnson, P. L., and W. D. Billings. 1962. The alpine vegetation of the Beartooth Plateau in relation to cryopedogenic processes and patterns. Ecol. Monogr. **32**:105–135.

Kawano, S. 1971. Studies on the alpine flora of Hokkaido, Japan. 1. Phytogeography. J. Coll. Lib. Arts **4**:13–96.

Kimball, S. L., B. D. Bennett, and F. B. Salisbury. 1973. The growth and development of montane species at near-freezing temperatures. Ecology **54**:168–173.

Klikoff, L. G. 1965. Microenvironmental influence on vegetational pattern near timberline in the central Sierra Nevada. Ecol. Monogr. **35**:187–211.

Knapik, L. J., G. W. Scotter, and W. W. Pettapiece. 1973. Alpine soil and plant community relationships of the Sunshine Area, Banff National Park. Arct. Alp. Res. **5**:A161–A170.

Krajina, V. J. 1969. Ecology of forest trees in British Columbia. Ecology of western North America. **2**:1–146.

Kruckeberg, A. R. 1954. The ecology of serpentine soils. III. Plant species in relation to serpentine soils. Ecology **35**:267–274.

———. 1969. Plant life on serpentinite and other ferromagnesian rocks in northwestern North America. Syesis **2**:15–114.

Kuramoto, R. T., and L. C. Bliss. 1970. Ecology of subalpine meadows in the Olympic Mountains, Washington. Ecol. Monogr. **40**:317–347.

Lawton, E. 1971. Moss flora of the Pacific Northwest. Hattori Botanical Laboratory, Nichinan, Miyazaki, Japan. 362 p.

Löve, D. 1970. Subarctic and subalpine: where and what? Arct. Alp. Res. **2**:63–73.

Lowery, R. F. 1972. Ecology of subalpine zone tree clumps in the North Cascade Mountains of Washington. Ph.D. thesis. Univ. Washington, Seattle, Wash. 137 p.

Major, J. 1951. A functional, factorial approach to plant ecology. Ecology **32**:392–412.

Major, J., and S. A. Bamberg. 1963. Some Cordilleran plant species new for the Sierra Nevada of California. Madrono **17**:93–109.

Marr, J. W. 1967. Ecosystems of the east slope of the Front Range in Colorado. Univ. Colorado Stud. Ser. Biol. No. 8. 134 p.

McAvoy, B. 1931. Ecological survey of the Bella Coola region. Bot. Gaz. **92**:141–171.

McLean, A. 1970. Plant communities of the Similkameen Valley, British Columbia, and their relationships to soils. Ecol. Monogr. **40**:403–424.

Meredith, D. H. 1972. Subalpine cover associations of *Eutamias amoenus* and *Eutamias townsendii* in the Washington Cascades. Am. Midl. Nat. **88**:348–357.

Meusel, H., E. Jager, and E. Weinert. 1965. Vergleichende chorologie der zentraleuropaischen flora. I. Gustav. Fischer, Jena.

Misch, P. 1952. Geology of the northern Cascades of Washington. Mountaineer **45**:4–22.

———. 1966. Tectonic evolution of the northern Cascades of Washington State. Canadian Inst. Mining and Metallurgy Spec. Vol. **8**:101–148.

Mooney, H. A., G. S. Andre, and R. D. Wright. 1962. Alpine and subalpine vegetative patterns in the White Mountains of California. Am. Midl. Nat. **68**:257–273.

Mooney, H. A., and W. D. Billings. 1961. Comparative physiological ecology of arctic and alpine populations of *Oxyria dygnia*. Ecol. Monogr. **31**:1–29.

Nimlos, T. J., and R. C. McConnell. 1965. Alpine soils in Montana. Soil Sci. **99**:310–321.

Nimlos, T. J., R. C. McConnell, and D. L. Pattie. 1965. Soil temperature and moisture regimes in Montana alpine soils. Northwest Sci. **39**:129–138.

Peterson, S. M. 1971. Microenvironment and water relations of two alpine species, Olympic National Park. M.S. thesis. Univ. Alberta, Edmonton, Alberta. 63 p.

Powers, H. A., and R. E. Wilcox. 1964. Volcanic ash from Mount Mazama (Crater Lake) and from Glacier Peak. Science **144**:1334–1336.

Price, L. W. 1971. Vegetation, microtopography, and depth of active layer on different exposures in subarctic alpine tundra. Ecology **52**:638–647.

Pritchard, N. M., and A. J. B. Anderson. 1971. Observations on the use of cluster analysis in botany with an ecological example. J. Ecol. **59**:727–747.

Schofield, W. B. 1968. A checklist of Hepaticae and Anthocerotae of British Columbia. Syesis **1**:157–162.

———. 1969. Phytogeography of northwestern North America: bryophytes and vascular plants. Madrono **20**:155–207.

Scholander, P. F., H. T. Hammel, E. A. Hemmingsen, and E. D. Bardstreet. 1964. Hydrostatic pressure and osmotic potential in leaves of mangroves and some other plants. Proc. Natl. Acad. Sci. **52**:119–125.

Slatyer, R. O. 1967. Plant-water relationships. Academic Press, New York. 266 p.

Soil Survey Staff. 1970. Selected chapters from the unedited text of the soil taxonomy of the National Cooperative Survey. U.S. Dep. Agric., Soil Conserv. Serv., Soil Surv., Washington, D.C., December, 1970.

Spomer, G. G., and F. B. Salisbury. 1968. Eco-physiology of *Geum turbinatum* and implications concerning alpine environments. Bot. Gaz. **129**:33–49.

Strickler, G. S. 1961. Vegetation and soil condition changes on a subalpine grassland in eastern Oregon. U.S. For. Serv. Pacific Northwest For. Range Exp. Stn. Res. Pap. 40. 46 p.

Swedburg, K. C. 1961. The coniferous ecotone of the east slopes of the northern Oregon Cascades. Ph.D. thesis. Oregon State Univ., Corvallis, Oregon. 118 p.

Taylor, R. J., G. W. Douglas, and L. M. Sundquist. 1973. Contributions to the flora of Washington. II. Northwest Sci. **47**:169–179.

U.S. Weather Bureau. (no dates). Station climatic records for Mt. Baker, Winthrop, Mt. Rainier, Stevens Pass and Diablo Dam, Washington.

van Ryswyk, A. L. 1969. Forest and alpine soils of south-central British Columbia. Ph.D. thesis. Washington State Univ., Pullman, Washington. 178 p.

Van Vechten, G. 1960. The ecology of the timberline and alpine vegetation of the Three Sisters, Oregon. Ph.D. thesis. Oregon State Univ., Corvallis, Oregon. 111 p.

Walkley, A., and T. A. Black. 1934. An examination of the Dectjareff method for determining soil organic matter and a proposed modification of the chronic acid titration method. Soil Sci. **37**:29–38.

Washburn, A. L. 1956. Classification of patterned ground and review of suggested origins. Bull. Geol. Soc. Am. **67**:823–865.

Welsh, S. L., and J. K. Rigby. 1971. Botanical and physiographic reconnaissance of northern British Columbia. Brigham Young Univ. Sci. Bull. Biol. Ser. 15. 49 p.

Westgate, J. A., D. G. W. Smith, and H. Nichols. 1969. Late Quaternary pyroclastic layers in the Edmonton Area, Alberta, p. 179–186. *In* S. Pawluk [ed.] Pedology and Quaternary research. Univ. Alberta, Edmonton, Alta. 218 p.

Whittaker, R. H. 1954. The ecology of serpentine soils. IV. The vegetational response to serpentine soils. Ecology **35**:275–288.

———. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. Ecol. Monogr. **30**:279–388.

Wilcox, R. E. 1965. Volcanic-ash chronology, p. 807–816. *In* H. E. Wright, Jr. and D. G. Frey [eds.] The Quaternary of the United States. Princeton Univ. Press, Princeton, New Jersey. 922 p.