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By HANSFORD T. SHACKLETTE

CONTRIBUTIONS TO GEOCHEMICAL PROSPECTING FOR MINERALS

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The origin, composition, and biogeochemical significance of a plant community that grows on soil derived from mafic rocks in a subarctic nonglaciated refugium

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PHYTOECOLOGY OF A GREENSTONE HABITAT AT EAGLE ALASKA

By Hansford T. Shacklette

ABSTRACT

A plant community is described that owes its existence at this site to both the chemical nature of the substrate and the absence of glaciation. A study of the geochemical cycle here enables an evaluation of the amounts and movements of the chemical elements, and an examination of the floristic composition and phytosociology of the plant community confirms the glacial history of the region that has been deduced from geologic evidence. The distinctive species have survived at this site because of freedom from glaciation and because the chemical and physical nature of the soil has prevented or reduced competition with species that are more "aggressive" but less tolerant of toxic elements.

Chemical analyses show that, because of the high content of most phytotoxic elements and the small amount of the macronutrient element phosphorus, the soils of the study area at Eagle are chemically less favorable for plant growth than the typical soils of the Temperate Zone. The plants sampled at Eagle contained much greater amounts of barium, nickel, and zinc and notably lesser amounts of cobalt, iron, lead, lanthanum, manganese, molybdenum, yttrium, and zirconium than the average amounts found in Temperate Zone plants.

The enrichment of certain elements in soils as set forth by the Goldschmidt enrichment principle as well as by other processes of soils formation has concentrated in the soil both plant nutrient and phytotoxic elements to levels greater than those found in the basaltic greenstone, the parent material of the soil. The chemical characteristics and origin of this soil resemble, in most respects, the "serpentine soils" described in botanical literature except that the Eagle soil is high in calcium content. The abundant calcium appears to have reduced the deleterious effects of the phytotoxic elements that are present—the plants growing here show no toxicity symptoms. The pH of the soil horizons ranges from 5.8 to 8.2, and calcification is evident in the lower horizons. The hypothesis is suggested that this soil has not had sufficient time, owing to reduced biological and chemical activity in this cold climate, to allow concentrations of phytotoxic elements that are as great as those characteristic of Temperate Zone "serpentine soils." Plants at this site appear to be continually enriching the soil in the phytotoxic elements barium, chromium, cobalt, nickel, and strontium; and given enough

time, the concentrations of these elements in the soil may further restrict the species of plants that can occupy this site.

Analyses of soil samples alone, without the analyses of associated vegetation, cannot be used to reliably estimate the concentration of all elements in the underlying bedrock. Soils do not merely present a pattern of diffusion halos representing dilutions of the elements in the bedrock—they also reflect the ability of the bedrock elements to remain in resistates during rock weathering or to be "selectively" absorbed by plants and then added to the soil as concentrates in plant residue.

The plant community is discontinuous as a ground cover, yet it appears to be in a state of dynamic equilibrium: the rate of establishment of new plants equaling the disappearance of others. All plants except one winter-annual are perennial species, and many are of great age for the species. The hemicryptophytic life form predominates, followed in diminishing order by phanerophytic, chamaephytic, and cryptophytic life forms.

The abstract phytosociological features of this type of community indicate that two species of plants are most characteristic; therefore, the plant community that grows on steep slopes of mafic and ultramafic-rock outcrops in the Yukon-Tanana uplands of Alaska is named the ***Bupleurum americanum-Zygadenus elegans*** association. However, in Alaska it is usually impossible to determine the location of mafic and ultramafic-rock outcrops by means of distant or aerial observation of the vegetation because the characteristic scarcity or absence of trees of this plant association ordinarily is caused by factors other than the chemical nature of the substrate.

The plants of this community are classified by their phytogeographical affinities, and the percentage composition of the total species at this site are reported as follows: North American radiants, 30 percent; Cordilleran endemics, 22 percent; widespread taxa of Europe, Asia, and North America, 20 percent; amphi-Pacific species, 17 percent; and Alaska-Yukon Territory endemics, 11 percent. The presence of Cordilleran and Alaska-Yukon Territory endemic species indicates the absence of Pleistocene and Recent glaciation at this site. ***Cryptantha sobolifera, Eriogonum flavum, Erysimum angustatum,*** and ***Phacelia sericea*** belong to these two groups of endemic species, and this paper reports these species from Alaska for the first time.

INTRODUCTION

While conducting biogeochemical field studies in Alaska for the U.S. Geological Survey in June 1960, I found a community of vascular plants of unusual interest on Eagle Bluff which overlooks the town of Eagle. My attention was called to the site by the impressive display of brightly colored flowers that grew in abundance on the southwest-facing talus slope of the bluff. The brilliant flowers of the species that, in Alaska, are restricted to or characteristic of the area adjacent to Yukon Territory—*Pentstemon gormani*, *Campanula aurita*, and *Phacelia mollis*—dominated the color pattern of this portion of the slope. However, closer examination revealed other species of special interest and novelty in the Alaskan flora. Four species of plants previously unknown to occur in Alaska, and other species that are but seldom found in the State grew in a plant community of approximately 500 square yards. The site was observed in late June when the plants were at the height of their flowering season. The plant community was studied in detail because of the significant ecological and phytogeographical principles that it exhibited. The biogeochemical processes in operation at the site and their relationship to the vegetation of this bluff are described in this report.

I extend my appreciation to Mr. Robert M. Chapman, geologist, U.S. Geological Survey, College, Alaska, for his assistance in the field work; to Dr. Eric Hultén, Naturhistoriska Riksmuseet, Stockholm, Sweden, for his critical examination of the vascular species reported in this paper; and to the chemists of the U.S. Geological Survey laboratories, Denver, Colo., for their generous cooperation in the analysis of my samples. Specimens of the plants reported here are in the Herbarium, University of Michigan Museums, Ann Arbor, Mich., the Herbarium of the U.S. National Museum, Washington, D.C., and the Herbarium of the Naturhistoriska Riksmuseet, Stockholm, Sweden.

GEOGRAPHY

The site of the plant community described in this report is approximately one-half mile north of the town of Eagle, Alaska. The town is on the west bank of the Yukon River about 6 miles west of the Alaska-Yukon Territory boundary (fig. 1), and in 1960 it had about 30 inhabitants. The site of Fort Egbert, one of the early U.S. Army forts established in Alaska, is nearby. The mule barn and two other buildings of the fort are still standing (R. M. Chapman, written commun., August 1965). Around the barn and in the town grew many species of weedy plants which probably had been introduced to the area by the imported mule feed or by commercial activities of the river port town. The weeds were found only in the alluvial fill of the Yukon River and of Mission Creek which debouches here—none were found in the plant community of the bluff slope. This fact supports my belief that the bluff community is a natural one, and that occupancy by its component species antedates settlement of the area. Moreover, the species of special interest on the bluff (the endemic species, and those of disjunct distribution) are not species that are likely to be introduced in animal feed or by commerce, for they are neither found in meadows or croplands, nor are they ruderal.

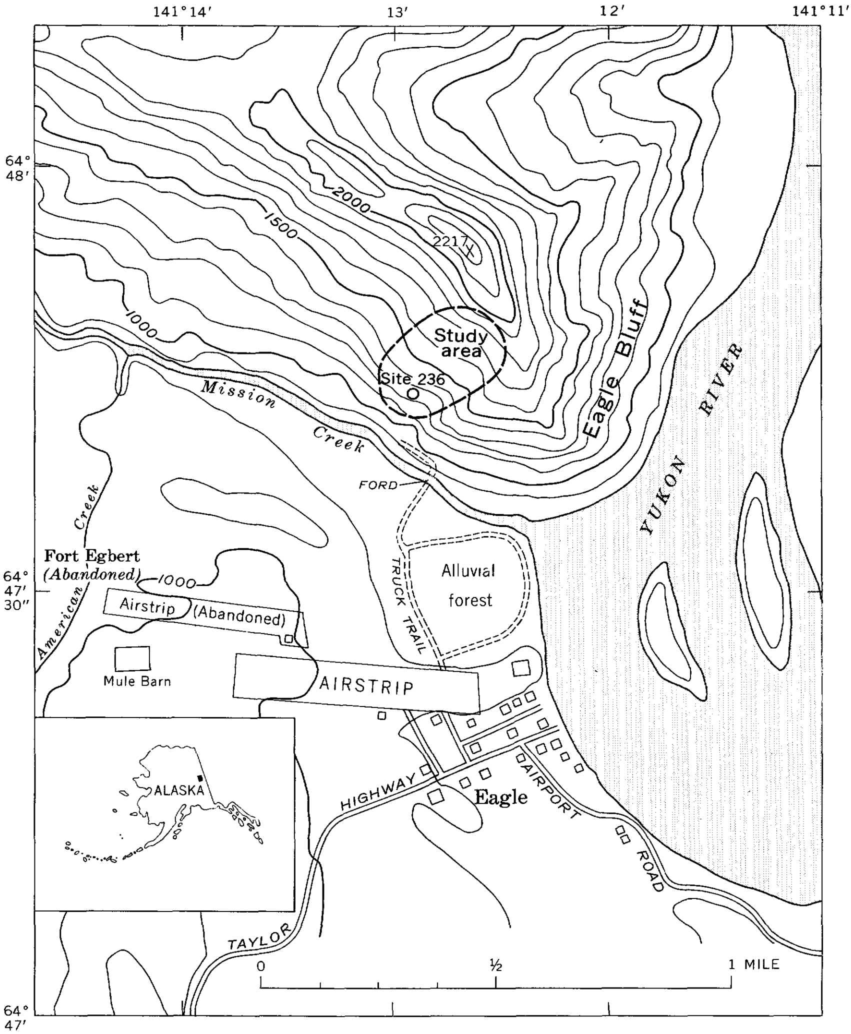


FIGURE 1.—Map of Eagle, Alaska, and vicinity, showing the location of the Eagle Bluff plant community study area. Topographic base enlarged and redrafted from U.S. Geological Survey Eagle (D–1) quadrangle, Alaska; scale 1 : 63,360. Contour interval 100 feet.

CLIMATE

The climate of the region is continental in character, with long and extremely cold winters and short warm summers of long days. The mean annual temperature at Eagle is 24.4° F, with a minimum of −75° F having been recorded. The mean temperature in July is 59.1° F, with a recorded maximum of 95° F. Precipitation is light, averaging 10.73 inches per year, of which about 6.5 inches occurs in June through September. The average snow cover is 52.7 inches (U.S. Weather Bureau, 1943).

GEOLOGY

The rocks at the study site were stated by Mertie (1930, p. 148–149) to be of Paleozoic age, and he has described them as follows: "The greenstone that forms the bold bluff at Eagle and continues northwestward up the north side of Mission Creek is essentially a basaltic greenstone, with which are interbedded flow breccia and tuff, also of greenstone habit, as well as more or less quartzite and crystalline limestone. This body of greenstone is mainly of effusive origin, though it may contain some intrusive rock." Wedow (1954, p. 3) said of the rocks of this outcrop, "They supposedly lie along a fault zone trending westward up Mission Creek." This site shows no evidence of having been glaciated. This observation agrees with Mertie's (1930, p. 16) statement, "In the Yukon-Tanana region, however, practically no glaciation has occurred."

There have been reports of a mineralized zone on this bluff, but Chapman and I could not find one. This site has been examined for radioactivity by Wedow (1954, p. 4) who wrote, "Several samples of sulfide ore encrusted with cobalt bloom, purportedly collected from a gold- and nickel-bearing vein on Eagle Bluff by a prospector in 1948, showed no radioactivity when scanned with a portable survey meter. A traverse along the face of the bluff also revealed no radioactivity. The equivalent uranium content of several samples of highly altered, black shaly rock from the south side of Eagle Bluff is only 0.002 percent or less."

SOIL

The soil at the study site is largely autochthonous—that is, it originated from decomposition of the bedrock of the bluff—but there has been large-scale downslope displacement of both the soil and talus owing to gravity and frost action. The soil on the 35° to 42° parts of the slope (fig. 3) is greatly mixed with talus, and the soil horizons have been obscured or obliterated by the displacement. This soil is a lithosol.

On the slight benches of less steep slope (fig. 2) rather distinct horizons were found, and some calcification had occurred in the B horizon. A description of this soil profile is given in table 1.

TABLE 1.—*Description of the soil profile at site 236, Eagle Bluff near Eagle, Alaska*

[Ambient noon temperature, 75.5°F. Discontinuous cover of forbs, grasses, and a few mosses. Fragments of rock throughout the profile. Site overdrained, with southern exposure. Frozen ground not found. Site examined June 26, 1960]

Horizon	Description	pH	Temperature, °F
A_{00}	Very small amount of tree leaf and herbaceous litter	------	73.5
A_0	1 in. thick; light to medium brown; coarse crumb structure; few roots present	5.8	67.0
A_1	1½ in. thick; medium brown; very loose texture; crumb structure; many roots	6.8	65.5
A_2	15 in. thick; tan to reddish; silt loam; very fine crumb structure; many roots present	7.2	51.8
B	12 in. thick; olive, tan, and gray; grain structure, clayey; slight calcification; few roots present	8.2	44.5
C	Thickness not determined—merges into bedrock; fine to coarse talus of greenstone, with some sedimentary rock fragments; intermixed finer portion clayey and grayish, dark brown, or nearly black; very few roots present	8.2	43.0

This soil probably is best classified as Subarctic Brown Forest soil, according to the system of Kellogg and Nygard (1951); however, it has several features that are not typical of this soil group. The small amount of humus present appeared not to be base forming, as indicated by the low pH of the A_0 horizon and the higher pH of the B and C horizons. A moderate degree of calcification occurred in the C horizon, but the calcified strata and lenses were not as distinct here as in the B horizon. Calcification was not reported to occur in Alaska by Kellogg and Nygard (1951); it was, however, observed by Lutz (1956, p. 72) in the upper Matanuska Valley, Alaska. Podzolization ordinarily takes place in Alaska at a site having the exposure and drainage of the Eagle Bluff study area; but here the alkalinity of the C horizon, the upward movement of water resulting from surface evaporation, the lack of permafrost in the soil horizons, and the small amount of acid-forming humus have prevented the development of a podzol at this site.

The physical nature of the soil, which may be characterized as loose and granular in the principal root zones, is favorable to the growth of vegetation. On the other hand, the unstable nature of the soil caused by frost action and downslope gravitational displacement and the dryness of the surface during the growing season deter the establishment of new plants on this site. The southern exposure of the slope permits a relatively long growing season in a region where the number of frost-free days may be a critical factor in the growth of certain plants, but the steepness of the slope may reduce the depth of snow cover below the amount required for the protection of some herbs.

THE PLANT COMMUNITY

DESCRIPTION

The vascular plants at the study site formed a discontinuous ground cover, and the soil between these plants was virtually bare; mosses and lichens have been largely prevented from occupying the interstices by the unstable nature of the soil (fig. 2, 3), Two species of mosses, *Rhytidium rugosum* (Hedw.) Lindb. and *Tortula ruralis* (Hedw.) Schwaegr., grew here, both species being common on mineral soil of dry, exposed sites. The colonization rate of vascular plants appeared to have come into equilibrium with the rate of plant disappearance; thus a dynamically stable community was formed that theoretically is open to invasion by many additional plants, but the physical and chemical properties of the soil greatly reduced the rate of the invasion. A discontinuous plant community of this type in boreal and arctic regions of Alaska ordinarily is composed largely of perennial plants. Data on life form, derived from table 2, show the Eagle Bluff community to consist of 1 winter annual (3 percent) and 35 perennial species (97 percent).

The one winter annual at this site, *Androsace septentrionalis*, a species of widespread northern distribution, produces many seeds per plant and is otherwise also well adapted to colonize bare soil. The perennial plants do not require a high rate of seedling survival to maintain their proportional composition of the community because they may live many years after their initial establishment. I saw very few seedlings of perennial species on Eagle Bluff. If the annual species did not have a much higher rate of seedling survival than the perennial species, the annual would be very rare in this community; however, its survival rate in this environment was low, as is shown by its abundance-cover value in table 2. Some of the perennial plants were of great age, as shown by their dense stools, very large crowns or caudices, or stout woody roots.

Hemicryptophytes, as classified by Raunkiaer life form, predominated at this site, as is shown by table 2. The life-form spectrum (expressed in percent) of vascular plants of Eagle Bluff is compared with that of St. Lawrence Island, Alaska (Oosting, 1956, p. 70), and

FIGURE 2.—Plant community on the lower slopes of Eagle Bluff, near Eagle, Alaska, that is rich in Cordilleran and Alaska-Yukon Territory endemic species. This part of the community is between altitudes of 1,200 and 1,300 feet in the study site (fig. 1). Photographed June 25, 1960.

FIGURE 3.—Plant community on the upper slopes of Eagle Bluff, near Eagle, Alaska. Two characteristic species (*Bupleurum americanum*, a, and *Zygadenus elegans*, b) are prominent, and a few common species of interior Alaska also grow here, but much of the talus is unoccupied by plants. The small trees in the background are *Populus tacamahacca*, c, and *P. tremuloides*, d. This part of the community is between altitudes of 1,900 and 2,000 feet in the study site (fig. 1). Photographed June 25, 1960.

TABLE 2.—*List of the vascular plant species growing at Eagle Bluff near Eagle, Alaska and the phytosociological, morphological, and phytogeographical characteristics of these species*

[*Androsace septentrionalis* L. is a winter annual; all other plants are perennial]

Abundance-cover and sociability scales (Braun-Blanquet, 1932):
Abundance-cover values:
2=With any number of individuals covering 1/20 to 1/4 of the sampled area, or with very numerous individuals but covering less than 1/20 of the area.
1=Numerous, but covering less than 1/20 of the sampled area, or fairly sparse but with greater cover value.
+=Sparse and covering only little of the sample area.
r=Very rare and covering only very little of the sampled area (usually only one example).
Sociability values:
3=In small patches or polsters; distinct groups.
2=In small groups or clusters.
1=Growing singly.
Raunkiaer life forms (Oosting, 1956):
P=Phanerophytes (trees and shrubs; perennating buds least protected).
Ch=Chamaephytes (perennating buds at ground level).
H=Hemicryptophytes (perennating buds buried in or partly protruding from the surface soil).
Cr=Cryptophytes (perennating buds deeply buried and food-storing).
Phytogeographical affinities: Derived from our field studies and from the records of species distribution given by the following authors: Anderson, 1959; Fernald, 1950; Hultén, 1941–50; Polunin, 1940; Porsild, 1943, 1951, 1955, 1957; Rydberg, 1917; Scoggan, 1957; Ulke, 1934; and Wiggins and Thomas, 1962.

Species	Abundance-cover values (left) and sociability values (right)	Raunkiaer life form	Phytogeographical affinities
Androsace septentrionalis L.	+. 1	H	Europe, Asia, North America.
Arabis lyrata ssp. *kamchatica* (Fisch.) Hult. (Kamchatka rockcress).	1. 1	H	Amphi-Pacific.
Arctostaphylos uva-ursi (L.) Spreng. (bearberry).	+. 3	Ch	Europe, Asia, North America.
Artemisia frigida Willd. (arctic wormwood).	1. 3	Ch	Do.
Betula resinifera Britton (white birch).	+. 1	P	North American radiant.
Bupleurum americanum Coult. and Rose (American thoroughwort).	2. 1	H	Cordilleran endemic.
Calamagrostis purpurascens R. Br. (purple reedgrass).	1. 3	H	Amphi-Pacific.
Campanula aurita Greene (harebell)	+. 2	H	Alaska-Yukon endemic.
Cornus stolonifera Michx. (red osier dogwood).	r. 1	P	North American radiant.
Cryptantha sobolifera Payson	+. 2	Ch	Cordilleran endemic.
Erigeron compositus var. *discoideus* Gray (fleabane).	r. 3	Ch	North American radiant.
Eriogonum flavum Nutt. (wild buckwheat).	r. 1	Ch	Cordilleran endemic.
Erysimum angustatum Rydb. (narrow-leaved wallflower).	1. 1	H	Alaska-Yukon endemic.
inconspicuum (S. Wats.) Macmillan.	1. 1	H	North American radiant.
Festuca altaica Trin. (rough fescue)	1. 3	H	Amphi-Pacific.
Galium boreale L. (northern bedstraw)	2. 2	H	Europe, Asia, North America.
Hedysarum mackenzii Richards. (wild sweetpea).	1. 1	H	Amphi-Pacific.
Juniperus communis var. *montana* Ait. (low juniper).	+. 2	P	Europe, Asia, North America.

TABLE 2.—*List of the vascular plant species growing at Eagle Bluff near Eagle, Alaska and the phytosociological, morphological, and phytogeographical characteristics of these species*—Continued

Species	Abundance-cover values (left) and sociability values (right)	Raunkiaer life form	Phytogeographical affinities
Linum perenne ssp. *lewisii* (Pursh) Hult. (Lewis wild flax).	1. 1	H	Cordilleran endemic.
Minuartia laricifolia (L.) Schinz and Thell. (larch-leaved sandwort).	1. 3	Ch	Amphi-Pacific (disjunct).
Oxytropis viscida f. *albida* L. H. Jordal (viscid oxytrope).	1. 1	H	Cordilleran endemic.
Pentstemon gormani Greene (Gorman beardtongue).	1. 2	H	Alaska-Yukon endemic.
Phacelia mollis Macbr. (soft phacelia)	+. 1	H	Do.
sericea (Grah.) A. Gray (silky phacelia).	r. 1	H	Cordilleran endemic.
Picea glauca (Moench) Voss (white spruce).	r. 1	P	North American radiant.
Populus tacamahacca Mill. (balsam poplar).	r. 1	P	Do.
tremuloides Michx. (aspen)	r. 1	P	Do.
Potentilla pensylvanica var. *strigosa* Pursh (Pennsylvania cinquefoil).	+. 1	H	Do.
Rosa acicularis Lindl. (prickly rose)	+. 1	P	Europe, Asia, North America.
Saxifraga reflexa Hook. (Yukon saxifrage).	r. 1	Ch	Cordilleran endemic.
Senecio conterminus Greenm. (groundsel).	1. 1	H	Do.
Shepherdia canadensis (L.) Nutt. (soapberry).	r. 1	P	North American radiant.
Silene repens ssp. *purpurata* (Greene) Maguire (campion).	+. 1	H	Amphi-Pacific species.
Solidago multiradiata Ait. (northern goldenrod).	1. 2	H	North American radiant.
Vaccinium vitis-idaea ssp. *minus* (Lodd.) Hult. (lingenberry).	+. 2	P	Europe, Asia, North America.
Zygadenus elegans Pursh (glaucous zygadenus).	2. 2	Cr	North American radiant.

with the normal life-form spectrum (Braun-Blanquet, 1932, p. 298) as follows:

	Eagle Bluff spectrum	*St. Lawrence Island spectrum*	*Normal spectrum*
Phanerophytes	25	0	46
Chamaephytes	19	23	9
Hemicryptophytes	53	61	26
Cryptophytes	3	15	6
Therophytes	0	1	13

The Eagle Bluff spectrum and the St. Lawrence Island spectrum differ chiefly in the absence of phanerophytes (trees and tall shrubs) on the arctic island. The same difference is noted if the Eagle Bluff spectrum is compared with spectra of the high Alps of Switzerland

and the arctic island of Spitzbergen (Braun-Blanquet, 1932, p. 298). From the physiognomic standpoint, the relatively high percentage of phanerophytes at Eagle Bluff (a characteristic of most north-boreal plant communities) is the outstanding difference between the Eagle Bluff community and arctic or arctic alpine communities. Phanerophytes have the least amount of protection for the overwintering buds of any life form, yet survive in regions that have minimum temperatures as low or lower than those of the arctic regions where phanerophytes are very rare or absent. Thus the factor limiting the survival of trees and tall shrubs in arctic regions is not the extremes of low temperature but is, as was suggested by Hopkins (1959, p. 216), the number of degree-days above a certain temperature. The abundance of hemicryptophytes at the Eagle Bluff site demonstrates that this life form is well adapted for survival on unstable soil, in addition to its well-known adaptation for survival in regions of low temperature.

AUTECOLOGICAL RELATIONSHIPS

THE EFFECTS OF THE SOIL ON THE VEGETATION

The supply of the major and minor nutrient elements in the soil at Eagle Bluff probably is adequate for the growth of any plant species in the region. Nitrogen content of the soil was not determined; however, the appearance of the plants growing there indicated that the supply of this element was not a limiting factor. The soil content of nickel and chromium is shown in table 3 to be higher than that of Temperate Zone soils derived from rocks other than serpentine. The high content of these elements at the study site most likely is derived from basaltic greenstone, which in nearby outcrops (on American Creek and Mount Sorensen) was noted by Mertie (1930) to be altered to serpentine. Soils derived from this greenstone and from serpentine probably do not differ greatly in their content of elements, and this Eagle Bluff soil has, in general, the chemical nature of "serpentine soil" as the term is used in ecological literature.

Walker (1954, p. 266), in discussing the effects of serpentine soils on plant growth, wrote, "They differ from other soils in these principal characteristics: low contents of total and adsorbed calcium, high magnesium content, and high contents of chromium and nickel." The soil at Eagle Bluff has the high magnesium, chromium, and nickel content that is typical of serpentine soils, but it also has a high calcium content, which is not characteristic of these soils. The normal growth of plants on Eagle Bluff supports Walker's (1954) assertion that it is the low calcium content, rather than the high nickel and chromium content, that inhibits plant growth on serpentine soils.

TABLE 3.—*Analyses of soil, rock, and plant samples from site 236, Eagle Bluff, Alaska, and comparable analyses of Temperate Zone soils and plants*

[Analysts: Maurice Devalliere and J. B. McHugh. Analyses in parts per million]

Element	Samples from Eagle Bluff, Alaska								Samples from Wisconsin and adjacent States, Missouri, and Kentucky			
	Soils (ppm of dry weight)			Rock (ppm of dry weight)	Vascular plants (ppm in ash)				Vascular plants		Soils	
	A horizon (lab. No. 60–3159)	B horizon (lab. No. 60–3160)	C horizon (lab. No. 60–3161)	C–D horizon, basaltic greenstone (lab. No. 60–3243)	Aspen stems, ash yield 4.5 percent of dry weight (lab. No. 60–162)	White birch stems, ash yield 4.5 percent of dry weight (lab. No. 60–163)	White spruce stems and leaves, ash yield 4.8 percent of dry weight (lab. No. 60–164)	Low juniper stems and leaves, ash yield 4.3 percent of dry weight (lab. No. 60–165)	Number of samples in a total of 1,501 samples that contained the element in measurable amounts	Average amount of the element in samples in which found (ppm in ash)	Number of samples in 395 that contained the element in measurable amounts	Average amount of the element in samples in which found (ppm of dry weight)
Ag	<1	<1	<1	<1	2	3	<2	<2	23	5		
B	30	50	50		200	300	200	200	1,501	311	395	37
Ba	1,000	2,000	1,000	200	2,000	10,000	7,000	1,000	1,501	2,524	395	539
Be	1.5	1.0	1.0	<1	<5	<5	<5	<5	48	9	160	2.7
Bi	<10	<10	<10	<10	<20	<20	<20	<20	41	30	0	
Ca	13,000	43,000	8,800	30,000	320,000	280,000	200,000	24,000	[1] 586	236,000	395	12,200
Cd	<20	<20	<20	<20	<50	<50	<50	<50	2	30	0	
Co	10	10	7	30	<10	10	<10	<10	126	123	319	10
Cr	70	100	70	150	<10	<10	<10	50	1,421	10	395	60
Cu	40	30	40	150	100	150	30	50	1,490	112	395	12
Fe	20,000	20,000	20,000	150,000	1,000	1,000	1,500	1,000	1,501	2,900	395	14,500
Ga	5	7	5	30	<10	<10	<10	<10	3	11	395	7
K	17,000	16,000	22,000	1,700	110,000	94,000	170,000	110,000	[1] 580	127,000	395	17,000
La	<50	<50	<50	<50	<100	<100	<100	<100	87	170	150	62
Mg	3,000	150,000	1,500	50,000	20,000	30,000	50,000	20,000	1,501	54,700	395	4,500
Mn	500	500	150	1,000	1,000	3,000	700	150	1,501	5,144	395	615
Mo	<2	<2	2	<2	<5	<5	<5	<5	176	25	60	2
Ni	75	50	50	100	10	50	10	150	1,234	38	391	14
P	60	80	80	80	18,000	24,000	24,000	12,000	1,501	19,300	395	419
Pb	10	15	20	<10	<10	<10	<10	<10	1,321	111	395	39
Sc	15	10	15	30	<10	<10	<10	<10	0		190	10
Sn	<10	<10	<10	<10	<20	<20	<20	<20	29	68	2	13
Sr	150	500	100	100	1,000	1,000	1,500	1,000	1,501	1,439	395	111
Ti	3,000	3,000	3,000	7,000	50	100	150	1,000	1,501	200	395	3,158
V	100	100	100	300	15	15	15	30	224	23	395	47
Y	20	15	15	20	<10	<10	<10	<10	148	72	395	16
Zn	50	50	25	50	1,200	6,000	1,000	200	1,500	1,010	394	104
Zr	150	150	70	100	<50	<50	<50	<50	247	35	395	308

[1] Calcium and potassium were found by spectrographic analysis to be in all samples; however, only the indicated number of samples were analyzed by the colorimetric chemical method which permitted the upper range of values to be determined.

The plant species at Eagle Bluff do not have pronounced xerophytic adaptations, although they receive but little rainfall during the growing season, and the soil is overdrained. Insolation on this south-facing slope causes a high rate of water loss by evaporation from the soil and transpiration of the plants, and the unimpeded air movements increase the loss. The soil temperature is higher than the average of the region; this has prevented or eliminated permafrost in the root zones at the site, although frozen ground is common elsewhere in the region during the growing season. The plant roots on this slope are enabled, therefore, to extend into the C horizon of the soil. This great root depth not only enhances the plants' water supply, but their nutrient-element supply as well. Roots in the soil reach to a depth of 30 inches (table 1).

The xeric nature of the site may control species composition of the community by means of its effect on the establishment of new plants from seed, and thus the discontinuous character of the vegetation cover may be preserved. In the seedling stage of a plant's life cycle not only is the water supply often critical, but the susceptibility of the plant to damage or death from frost heaving and other soil movements is also greatest. The rapidity with which roots penetrate the soil to the lower horizons may be an inherent feature controlling the establishment of species on this site. Many, but not all, species in this community have tap roots when they are fully grown; however, the rooting characteristics of seedlings were not studied.

The distribution of roots, shown in table 1 and figure 4, in soil horizons having greatly different pH values makes the generally used terms "calciphilic," "circumneutral," and "acidophilic" meaningless in classifying this plant community. Root growth in these horizons may be controlled by water supply, aeration, response to soil chemical qualities, or by other factors, including the unknown ones inherent in the species, rather than by pH itself. A plant that is becoming established at this site may "select" its pH "preference" by a proliferation of roots in soil horizons that range from pH 5.8 to 8.2, if its inherent capabilities of root growth permit. It is unwarranted to designate a plant community on soil of this type as acidophilic merely because the surface soil is acid; the roots may be most numerous in an alkaline horizon. Conversely, the community should not be classified as calciphilic because the growth of seedlings is largely dependent on the acid horizons near the soil surface. It is an oversimplification of these complex relationships to designate the community as circumneutral. Individual species, however, could be classified by pH requirements or limitations if their rooting habits as influenced by soil pH were observed, or if the areal distribution of the species related to the occurrence of parent acid- or base-forming soil material. These aspects of the problem were not included in this study.

THE EFFECTS OF THE VEGETATION ON THE SOIL

The concentration of elements in plants depends on the ability of the species to absorb elements, and on the abundance of elements in an available form in the soil. The occupancy of a site by a particular species is governed by the presence of an adequate supply of the nutritive elements and a tolerable concentration of the toxic elements in the soil in relation to the capabilities of the species to react to these elements. Little is known of these reactions of most native plant species, and only tendencies in biotic adjustments within a certain chemical environment can be suggested.

At the Eagle Bluff study site certain elements, both toxic and nutritive, have become enriched in the soil horizons, at least partly by means of the Goldschmidt enrichment principle (Rankama and Sahama, 1950, p. 333–334). Thus the nutritive elements (Sutcliffe, 1962, p. 6) calcium, magnesium, molybdenum, and potassium; the toxic elements (McMurtrey and Robinson, 1938, p. 814–826) barium, beryllium, lead, and strontium; and the ballast element (Rankama and Sahama, 1950, p. 331) zirconium are more concentrated in some horizons of the soil than in the basaltic greenstone. The effectiveness of plants in causing this accumulation of calcium, potassium, magnesium, barium, and strontium is suggested by the high concentrations of these readily mobile elements in the plant ash (table 3).

Beryllium in the vegetation, if present, was below detection limits, yet the soil contained more of this element than did the bedrock. Zalashkova and others (1958, p. 12) stated "herbs and the leaves of woody plants play a particularly important role because each year they are the principal factors of beryllium concentration in the process of soil formation." It is possible that at the Eagle Bluff site beryllium has become concentrated in the soil from the very small amounts absorbed by plants, but beryllium also may have come from the weathered bedrock. Its mobility is stated by Hawkes and Webb (1962, p. 361) to be "probably low, limited by insolubility of beryl in weathering."

Rock weathering alone, exclusive of plant action in transporting elements, can result in soil enrichment of elements that are sufficiently immobile to remain in the residuum. The amounts of lead, molybdenum, and zirconium in vegetation at Eagle Bluff are below detection limits, and their concentration in the soil may be, for the most part, directly from rock weathering. Lead was said by Hawkes and Webb (1962, p. 368–370) to be generally low in mobility, and the mobility of molybdenum was stated by the same authors to be limited by the rate of solution of primary MoS_2, sorption on limonite, and precipitation in carbonate-rich environments. Rankama and Sahama (1950, p. 566) stated, "most zirconium in igneous rocks is contained in zircon, a mineral which is very stable against mechanical and chemical weathering. Therefore, zircon remains largely in the resistates, which usually contain considerably more zirconium than do the hydrolyzates."

A comparison of the element concentration in such different media as living plants, soils, and rocks is never completely satisfactory; for these media cannot be reduced to a similar state for analysis and still represent their role in the geochemical cycle. Concentrations of elements are expressed as proportions of the total weight of the material that is analyzed. Living plants contain water and organic compounds in addition to inorganic compounds. Most soils are largely inorganic, but upper horizons typically contain some organic material, and rocks are mostly inorganic. In this study the plant samples were burned to ash and the element content of the ash was determined. The soils and rocks were oven dried before analysis. Therefore the samples were comparable in that they were largely inorganic and free of water when analyzed. The small percentage by weight of organic material in the soil at this location was ignored—the soils were not burned before analysis. However, even with these procedures the comparisons of element content in the different media are artificial to a certain extent; for in the biogeochemical cycle the plant detritis is incorporated into the soil as organic material—not as just the inorganic materials of plant ash—and the cyclic process is continual in the incorporation and release of the elements as components of organic and inorganic compounds.

Trees and shrubs at Eagle Bluff were chosen for chemical analysis because they were known to have roots that extend to bedrock and because the element content of many samples of these plants was known from studies in other regions of Alaska. Although herbs compose the greater part of the vegetation at the site, I believe that they are less effective in transporting elements of the bedrock to the soil horizons than are trees and shrubs.

Processes of soil formation, including both rock weathering and plant transport of elements, have concentrated in the soil all plant nutritive elements except copper and iron and all phytotoxic elements except cobalt and chromium to levels greater than those found in the bedrock, as is shown diagrammatically in figure 4. Zinc and copper are micronutrients in low concentrations and phytotoxins in high concentrations. Copper was as abundant in plant ash as in the bedrock,

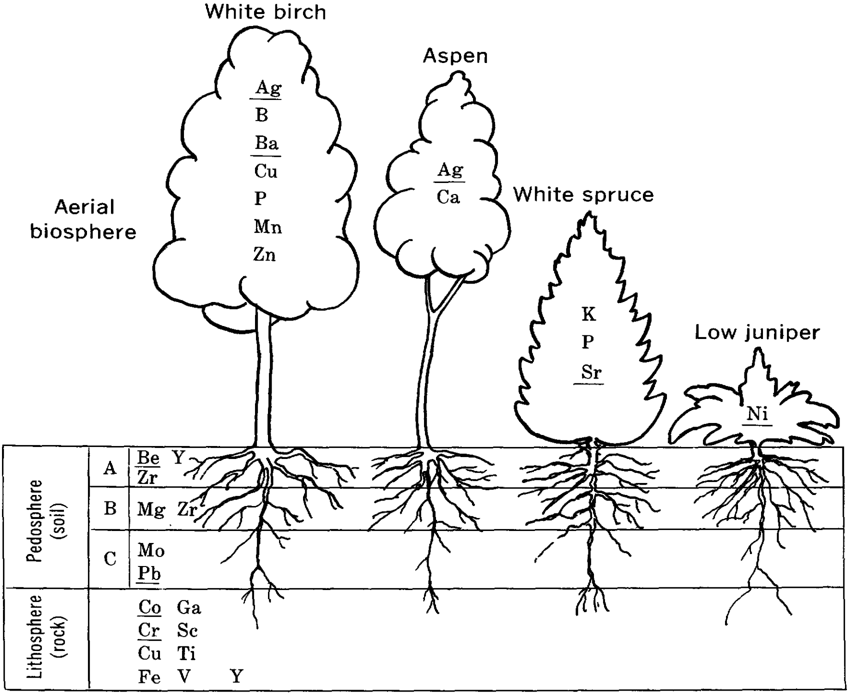


FIGURE 4.—Location in the environment of the highest concentrations of certain elements at site 236, Eagle, Alaska. Toxic elements are underscored; the nontoxic ballast elements are gallium, scandium, titanium, vanadium, yttrium, and zirconium, and the remaining elements are nutritive. The micronutrients boron, copper, manganese, and molybdenum may be toxic if greatly concentrated.

and very great concentrations of zinc occurred in three plant species, but these elements had not become greatly enriched in the soil. The lack of soil enrichment in copper and zinc probably was because of the great mobility of these elements which, although continually added to the surface soil by decomposition of plants, were leached from the soil and returned to the bedrock horizon or removed by drainage water. Therefore it is likely that these two elements will never reach toxic concentrations in the soil by means of plant decomposition.

Small amounts of silver may be found in plant ash, but for some unknown reason silver was not found in the soil; the very small amounts that may be present and the low toxicity of this element do not suggest that it will ever become a detriment to plant growth at this site. Barium and strontium are two phytotoxins that appeared to have been concentrated in the soil by plant action, and the amounts of these elements may continue to increase. They occurred in the B horizon in at least twice the amounts that were found in the other soil horizons and in bedrock. Nickel is another toxic element that was being concentrated by at least one species of plant, and the occurrence in the A horizon of a larger amount of this element than was found in other soil horizons suggests that concentration of nickel in the soil will continue. This soil already contained about four times the amount of nickel found in Temperate Zone soils derived from rocks other than serpentine, as is shown in table 3. The amount of chromium in the Eagle Bluff soil was somewhat greater than in typical soils, and this soil enrichment may be at least partly attributed to the transportation of this element from the bedrock to the soil by low juniper; however, the soil content did not equal the bedrock content. Cobalt appeared to be largely immobilized in the bedrock, although white birch absorbed small amounts and the upper soil horizons had a slight cobalt enrichment.

The biogeochemical cycles of the phytotoxic elements may be summarized by stating that plants at this site are continually enriching the soil in barium, chromium, cobalt, nickel, and strontium although the concentrations in the soil of some of these elements have not yet reached the levels that were found in the bedrock.

The nutrient elements calcium, magnesium, and potassium occurred in large amounts in the plants and were more concentrated in the soil than in the bedrock. This soil enrichment most likely has resulted from plant decomposition. Phosphorus occurred in large amounts as a nutrient in plants, but the soil contained no more of this element than was in the bedrock. Rankama and Sahama (1950, p. 589) stated, "During weathering, phosphorus is largely liberated from minerals. The weathering solutions contain alkali phosphates and dissolved or colloidal calcium phosphate. A part of the phosphorus is soon re-precipitated as calcium phosphate, but the bulk is carried to the sea. Calcium phosphate is soluble in carbon dioxide-bearing water and probably also in waters rich in organic matter." The Eagle Bluff soils have had no concentration of phosphorus as a result of rock weathering, and the phosphorus held and recycled by organisms was probably the most significant amount in the phosphorus cycle at this site.

A study of the analyses of soils and bedrock given in table 3 should emphasize the caution that is necessary in using analyses of soils to predict the element content of underlying bedrock without considering the elements in the plants that are being incorporated into the soil. Soils do not merely present a pattern of diffusion halos representing dilutions of the various elements that are in the bedrock—they also reflect the ability of the bedrock elements to remain in resistates during rock weathering or to be "selectively" absorbed by plants and then added to the soil as concentrates in plant residue. Thus, for example, the barium content of the B horizon of the Eagle Bluff soil (table 3) of 2,000 ppm (parts per million) does not indicate a barium anomaly in the bedrock at this site. If the barium content of white birch ash (10,000 ppm) is considered, a possible source of barium enrichment in this soil is apparent. The same general relationships exist in the calcium, magnesium, and potassium content of soils, plants, and bedrock. Therefore, analyses of soil samples alone, without the analyses of associated vegetation, cannot be used with reliability in estimating the content of all elements in the underlying bedrock.

The Eagle Bluff soils are generally less favorable for plant growth than are the typical soils of the Temperate Zone; for the Eagle Bluff soils are as high or higher in most phytotoxic elements than the typical soils and contain a much smaller amount of phosphorus—an important nutrient element that commonly is a limiting factor in plant growth. (See table 3, which compares the element content of the Eagle Bluff soils and plants to the average content of Temperate-Zone soils and plants from Wisconsin and adjacent States, Missouri, and Kentucky.) No mafic- and ultramafic-rock sites were studied in these States, although the parent materials of the soil samples were highly varied, including limestone, dolomite, sandstone, and granite rocks and loessal, fluvial, and lacustrine deposits. The Eagle Bluff plants as a group contained conspicuously greater amounts of barium, nickel, and zinc, and notably lesser amounts of cobalt, iron, lead, lanthanum, manganese, molybdenum, yttrium, and zirconium than the average amounts found in the Temperate Zone plants. The Eagle Bluff soils had more barium, chromium, copper, iron, magnesium, nickel, strontium, and vanadium, and less lanthanum, lead, phosphorus, zinc, and zirconium than the average of these elements in the Temperate Zone soils that were studied.

Element concentration during soil formation at the Eagle Bluff site may be summarized as follows: Certain elements, both nutritive and toxic, accumulate in the soil in concentrations exceeding those of the parent soil material (bedrock) at the site. If concentration of toxic elements in the topsoil continues indefinitely, the soil will eventually contain enough of these elements to restrict or prohibit plant growth. I (Shacklette, 1962a) have shown that, in Alaska, the vigor of the plants which form the vegetation cover of serpentine soils does not differ significantly with that of the vegetation on nearby nonserpentine soils. This observation does not agree with many similar ones made in Temperate Zone environments, for, in general, the distinctiveness of "serpentine floras" is well known. I propose the hypothesis that soils on mafic and ultramafic rocks in Alaska have not had sufficient time to reach their potentially maximum concentration of phytotoxic elements because of the reduced chemical and biological activity in this cold climate.

Outcrops having large amounts of phytotoxic elements generally are neither common nor of great extent. Wandering herbivorous animals may retard the buildup of toxic elements in soils on these outcrops by eating the vegetation growing thereon and carrying away the elements that are concentrated in plants. These toxic elements are then deposited elsewhere by the animals in their excretions or their dead bodies. Data have been presented (Shacklette, 1962b) that suggest herbivorous mammals may ingest large amounts of certain metals per year in some regions of Alaska. Thus animals grazing in a region having such outcrops tend to equalize the distribution of the elements in soils throughout the region. This dispersal of elements may benefit plants growing on sites rich in phytotoxic elements by reducing the amounts of these elements to below the toxic level in the soil and at the same time supply plants growing elsewhere with essential micronutrient elements that may be deficient in their soils.

SYNECOLOGICAL RELATIONSHIPS

The low abundance-cover and sociability values of most species shown in table 2 indicate that this community was composed of scattered individual plants or small groups of plants and that the vegetation cover was discontinuous, as shown in figures 2 and 3. Table 2 also shows that most of the community was composed of forbs (broad-leaved herbs) with grasses numerous as individuals but having a low cover value. Trees and shrubs were stunted and mostly restricted to small drainage features where the water supply was greater than elsewhere. There was very little competition among species for space in the community, as is shown in figures 2 and 3 by the amount of unoccupied soil surface.

Two features of the "abstract plant community," constancy (the degree to which a species consistently occurs in this type of community) and fidelity (the degree of exclusive occurrence in this type of community), must be determined by considering the total occurrences of each species in different communities of the region. These two features cannot be evaluated for all species listed in table 2. The known occurrence of some species in Alaska is only at Eagle Bluff, and others are very rare in this State. However, many species at Eagle Bluff may be assigned constancy and fidelity values because they have a wide distribution in the region, and these values are given in table 4.

TABLE 4.—*Evaluation of constancy and fidelity of certain vascular plants in communities associated with mafic and ultramafic-rock outcrops in the Yukon-Tanana uplands of Alaska*

Constancy (Oosting, 1956, p. 74):
1=Rare (in 1-20 percent of the stands).
2=Seldom present (in 21-40 percent of the stands).
3=Often present (in 41-60 percent of the stands).
4=Mostly present (in 61-80 percent of the stands).
5=Constantly present (in 81-100 percent of the stands).
Fidelity (Oosting, 1956, p. 74):
1=Strangers appearing accidentally.
2=Indifferents without pronounced affinity for any community.
3=Preferents present in several communities but predominant in one.
4=Selectives found especially in one community but found occasionally in others.
5=Exclusives found only, or almost so, in only one community.

Species	*Constancy*	*Fidelity*
Androsace septentrionalis	3	2
Arabis lyrata ssp. *kamchatica*	2	2
Arctostaphylos uva-ursi	4	2
Artemisia frigida	3	2
Betula resinifera	4	2
Bupleurum americanum	5	4
Calamagrostis purpurascens	5	3
Cornus stolonifera	1	1
Festuca altaica	4	3
Galium boreale	5	2
Hedysarum mackenzii	4	2
Juniperus communis var. *montana*	5	3
Linum perenne ssp. *lewisii*	3	3
Minuartia laricifolia	5	4
Picea glauca	4	2
Populus tacamahacca	2	1
tremuloides	4	2
Rosa acicularis	3	2
Solidago multiradiata	3	2
Zygadenus elegans	5	4

Five species of table 4—*Bupleurum americanum*, *Calamagrostis purpurascens*, *Juniperus communis* var. *montana*, *Minuartia laricifolia*, and *Zygadenus elegans*—have the highest combined constancy-fidelity values on Alaskan mafic- and ultramafic-rock outcrops. From this standpoint they may be considered characteristic species of the communities on these outcrops. Of these species, *Bupleurum americanum* and *Zygadenus elegans* are shown in table 2 to have the highest abundance-cover and sociability values. From the phytosociological viewpoint, therefore, these two are the most important and characteristic species. The abstract plant community that grows on steep slopes of mafic- and ultramafic-rock outcrops in the Yukon-Tanana uplands of Alaska is hereby named the *Bupleurum americanum-Zygadenus elegans* association.

This designation does not imply that these two species are community dominants in the sense that they "control" the frequency, sociability, or vitality of other species in the community. In fact, from this standpoint, no dominant species occur here—the control of the community is largely the physical, not the biotic, environment. Also, this usage of the term "association" follows the so-called Zurich-Montpelier school of phytosociology as presented by Braun-Blanquet

(1932). "Association" is the lowest category of this plant community classification system, and it is named for the characteristic species, as defined above. In contrast, the "association" of the so-called Clementsian school of phytosociology is next to the top of the classification hierarchy (Weaver and Clements, 1938, p. 93, 99), and its use implies the concept of dominance. This concept is shown to be inapplicable to the plant community described in this report.

The chemical requirements and tolerances of white birch, aspen, and white spruce are of such amplitude that these trees may grow on soil derived from any kind of rock in this region if the physical factors at the site are tolerable. That is, the water supply and water loss, the depth of the soil to permafrost, and the degree of exposure of the site to wind and sun ordinarily are more important in determining the distribution of these species than are the chemical features of the sites. Therefore, it is only on slopes that are too dry and too exposed to sun and wind for these trees to thrive that the *Bupleurum americanum-Zygadenus elegans* association attains the status of a physiographic climax. At more mesic and less exposed sites on mafic and ultramafic rocks, this association appears to be only a successional stage in afforestation—at least I observed this relationship at a pyric disclimax site near Livengood, Alaska. Thus, it is usually impossible to determine the location of outcrops of mafic and ultramafic rocks by means of aerial or distant observation of the vegetation cover because the absence of trees at a site ordinarily is caused by factors other than the chemical nature of the substrate. The cutting and burning of forests is widespread in this region of Alaska, and this fact further limits terrain evaluation by means of aerial or other distant views.

My field studies indicate that the development of the plant association named in this report is controlled by both physical and chemical characteristics of the site and that it is dependent on soils derived from parent mafic and ultramafic material. Very different plant associations develop at other sites in the region that have similar physical features but that overlie schist, slate, or limestone. The combination of plant species found at Eagle Bluff appears to relate to the tolerance of the species to toxic elements ultimately derived from bedrock. Amounts of the nutritive elements most probably are sufficient to support any plant in this region, but some species have more resistance to damage from toxic elements than others. If the amounts of toxic elements in the soil continue to increase by means of physical and biological processes, as suggested earlier in this report, this site will become even more restrictive in the species that it can support. However, the time required for significant changes in the composition of the community probably would be measured in centuries, if we may judge from present chemical characteristics of the site and the unknown, but certainly very long, period of time that plants have been growing there.

PHYTOGEOGRAPHICAL AFFINITIES

FLORISTIC COMPOSITION

The unique flora at the study site was due to two factors—freedom from glaciation and edaphic characteristics which permitted the survival of the distinctive species. Undoubtedly, the Alaska-Yukon Territory and Cordilleran endemics are pre-Pleistocene relict species that have occupied this site for a long time. These species are not "aggressive" weedy plants; they have not extended their range beyond this site to other sites that appear to be favorable, although eventually some dissemination probably will occur. In company with these rare species were arctic and north boreal plants that are common throughout northern North America and that form the greater part of the Eagle Bluff community. These common species may also have persisted at this site for a long time, but it seems more likely that at least most of them have been entering the community more or less continually to the present time. The list of all vascular plant taxa that were found at Eagle Bluff is given in table 2.

ADDITIONS TO THE KNOWN FLORA OF ALASKA

The most interesting of the four additions to the flora of Alaska is *Eriogonum flavum*. This species was said by Rydberg (1917, p. 217) to occur on "dry hills, mountains and canyons, Manitoba, Nebraska, Colorado, to Alberta." Scoggan (1957, p. 248) gave its range as "Temperate western America: southern British Columbia to southern Manitoba, south to Colorado and Nebraska." Through the kindness of Dr. A. E. Schuyler of the Philadelphia Academy of Sciences I was allowed to examine this species in the herbarium of this institution. One specimen bears the label, "Calgary, N.W. Terr., July, 1900. Dr. Charles Schäffer, Collector." Insofar as I know, this was the most northern collection of this species before my Eagle Bluff collection was made, yet Calgary is about 1,300 miles southeast of Eagle. This species, if it occurs elsewhere in the Yukon-Tanana uplands of Alaska, must be rare, for it is a very distinctive and conspicuous plant not likely to have been overlooked by the many botanists who have collected in this region.

Phacelia sericea has not been previously reported to occur in either Alaska or Yukon Territory. *Phacelia mollis* is closely related to this species but has a longer pubescence and more seeds in the capsule, according to Hultén (1948, p. 1328). Rydberg (1917, p. 706) wrote that

P. sericea is found in "high mountains of Colorado, Nevada, Washington, and British Columbia." Ulke (1934, p. 78) reported this species from a single locality in Yoho Park, British Columbia as follows: "On Mt. Stephens at 2300 m. Occasional." I do not find this species listed in any other Canadian flora. Anderson (1959, p. 402) mentioned having collected an unidentified species of *Phacelia* at Chicken in the Fortymile district of Alaska; this plant most likely is *P. sericea*, judging from his description of it and the locality where it was found.

Cryptantha sobolifera is also apparently a new addition to the list of Alaskan-Yukon Territory plants, and this Eagle specimen was far north of any natural occurrences of the genus that have been reported. Another species of this genus, *C. torreyana* (A. Gray) Green, was reported as an introduced plant at Skagway, Alaska by Hultén (1949, p. 1352) and Anderson (1959, p. 407). Although Rydberg (1917) lists six species of this genus as native to Canada, none of these are reported in the Canadian floras that I have examined, and Scoggan (1957, p. 462) excludes three species from the flora of Manitoba that previously had been reported to occur in that province. The specimen from Eagle probably represents the most northern extent of this genus in North America.

Erysimum angustatum previously was known only from the Klondike region of Yukon Territory. This region is but a short distance (about 75 miles) up the Yukon River from Eagle, Alaska; therefore the discovery of this plant in Alaska was not unexpected. This endemic species has a very limited known range, and its taxonomic status is not entirely clear. Hultén (1945, p. 883) said of this species, "The western American *Erysimum* species are very closely related and probably this type, isolated in unglaciated Yukon, may be regarded as a subspecies of one of these, but the material in my hands is too small for a proper judgment to be formed on this point."

OTHER EAGLE BLUFF PLANTS OF RESTRICTED DISTRIBUTION IN ALASKA

There are seven plant taxa that generally are rare in Alaska and whose distribution is mostly or entirely restricted to the upper part of the Yukon River drainage system in Alaska and Yukon Territory (figs 6–8). These plants are: *Campanula aurita*, *Erysimum inconspicuum*, *Oxytropis viscida* forma *albida*, *Pentstemon gormani*, *Phacelia mollis*, *Potentilla pensylvanica* var. *strigosa*, and *Silene repens* subsp. *purpurata*. With the exception of *Erysimum* and *Potentilla*, these plants are endemic to Alaska and Yukon Territory. It is noteworthy that so many rare Alaska plants were found in the small study area on Eagle Bluff.

GEOGRAPHICAL DISTRIBUTION OF TAXA

The numerous location records of the common species of plants in Alaska show that botanical collecting has been widespread in this State; therefore, species having but few locations shown may in fact, be rare species. The distribution in northwestern North America of the Eagle Bluff plants is given in figures 6–8. The symbols on the distribution maps of these figures indicate the approximate location where the specimens, now preserved in herbaria, originally grew.

The present distribution of plant species in northwestern North America was determined by the reduction of the range of species by glaciation, the persistence of species in unglaciated refugia, and the dispersal of species into new land areas following recession of the glaciers. In describing the effects of glaciation on vegetation during the Pleistocene Epoch Hultén (1958, p. 4) wrote, "The result of these mighty changes was that the large circumpolar belts of vegetation were torn up into fragments. Many species were exterminated altogether, others had their range split up into smaller isolated areas in which different conditions of life prevailed. Their original populations changed under the pressure of these varying conditions, their content of biotypes diminished, all this resulting in slightly different races being formed. * * * When the climate ameliorated during the interglacial periods the plants spread and reoccupied areas lost during the glacial ages."

Halliday and Brown (1943, p. 357, 359) wrote that the Yukon River valley was a refugium for plants during Illinoian and Wisconsin Glaciations. According to Hultén (1958, p. 5), "There can hardly be any doubt that the unglaciated area in Alaska-Yukon and the northern part of the present Bering Sea area together with the unglaciated valleys of the rivers in north-eastern Siberia offered shelter to a large part of the northern flora during the glacial period, even if other areas may have played a similar role, though on a smaller scale."

The phytogeographical significance of the Wisconsin Glaciation was emphasized by Halliday and Brown (1943, p. 357) as follows: "While it is conceded that the Illinoian and the Kansan glaciations were the most severe in their effects, it is the extent of the last, or Wisconsin, which principally determines the present distribution pattern of the constituted tree species of the [Canadian] forest * * *." Figure 5 shows the extent of glaciation during the Wisconsin in northwestern North America. The nonglaciated land areas were potential biotic refugia during this time. In addition to the ice-free areas indicated in this figure, minor refugia existed in the area of the Cordilleran ice sheet (Halliday and Brown, 1943, p. 361, 363) where endemic and other species could have been preserved.

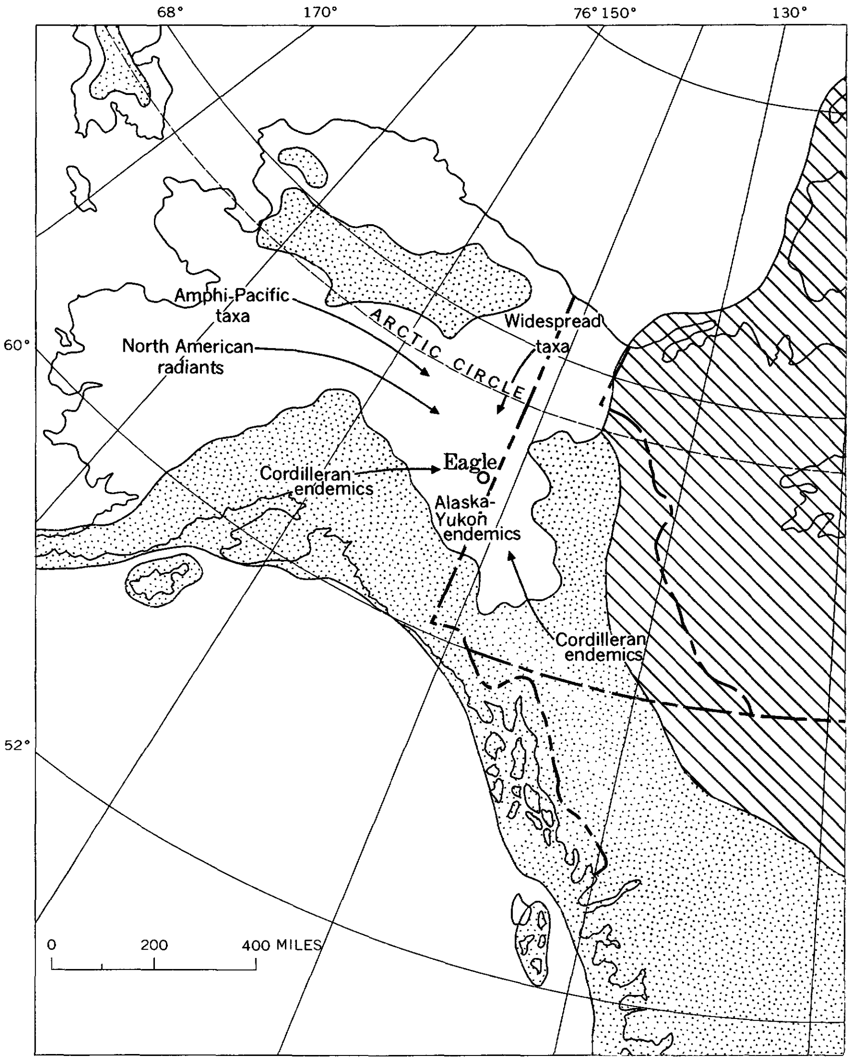


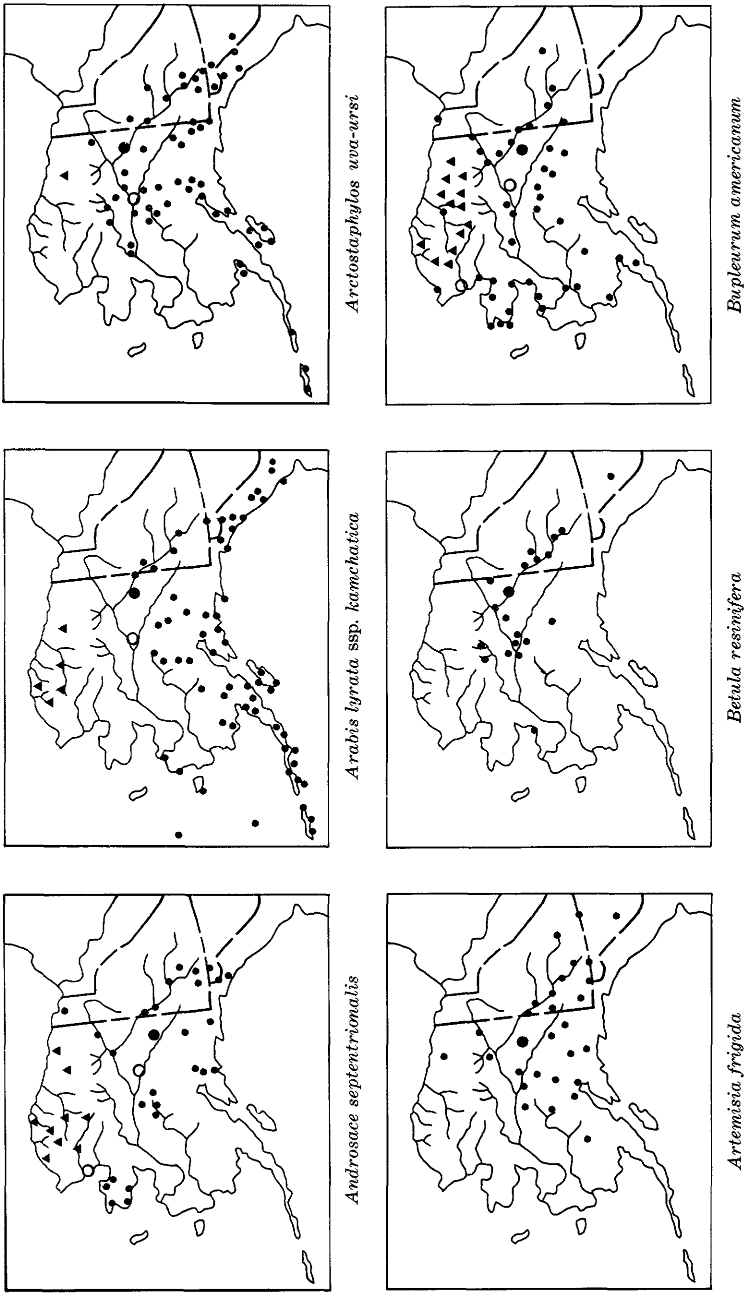
FIGURE 5.—Glaciation of Wisconsin age in northwestern North America (adapted from Halliday and Brown, 1943) and postulated sources of the present flora at Eagle Bluff, Alaska. Cordilleran ice sheets indicated by stipple pattern; Keewatin ice sheet indicated by diagonal lines.

The dispersion of plants from refugia during interglaciations was discussed by Halliday and Brown (1943, p. 357) as follows: "The capacity of species left in refugia to repopulate the land-mass was modified by the vicissitudes they had undergone. Those species which were depauperated as to biotypes, and thus as to potential variability, are considered as 'rigid' species, and are likely to be found in their original refugia at the present time; while others, more fortunate in retaining their biotypes, are termed 'plastic' species, and are those that have been able to recolonize large areas in postglacial times." Löve (1962, p. 35) published a map of the dispersal of plant species which showed that 47 species were preserved in the Yukon River valley refugium and that some of these species have spread from there in postglacial times as far as eastern Canada and Greenland.

The plants at Eagle Bluff may be arranged in five groups that express their phytogeographical affinities (table 1 and fig. 5). The naming of these groups and the assignment of species to the groups is based largely on Hultén's publications (1937, 1941–50). The sources of the species at Eagle Bluff are suggested in figure 5; however, the migration routes indicated by arrows should not be construed to represent the only paths of dispersion of the phytogeographic groups. Neither should the suggested migrations be assumed to have occurred only during Wisconsin time—in fact, the Cordilleran endemic species could scarcely have migrated during the period of maximum glacial extent. These Cordilleran species, and others, may have already occupied the Yukon River valley refugium before the onset of the Wisconsin Glaciation.

By applying the principles given by Halliday and Brown (1943, p. 357) as stated above, we can interpret the distribution patterns of species that are shown in figures 6–8. Some species (the Alaska–Yukon Territory endemics and a few others) are presently restricted to this refugium; they may therefore be designated "rigid" species. The distribution of other species indicates that they have been able to migrate more freely, being able to adjust to more diverse environmental conditions than the former; thus they may be designated "plastic" species.

The Cordilleran endemic species of disjunct distribution that now grow at Eagle Bluff are relict stands of a distribution pattern that once connected with regions far to the south where these species now occur in greater abundance. These disjunct endemic species in the Yukon River valley have not been able to reestablish their continuity of distribution since the last glaciation; they may be "rigid" biotypes of the species, having reduced dissemination and competition potential, that have persisted at Eagle Bluff because of their adaptation to



Androsace septentrionalis
Arabis lyrata ssp. *kamchatica*
Arctostaphylos uva-ursi
Artemisia frigida
Betula resinifera
Bupleurum americanum

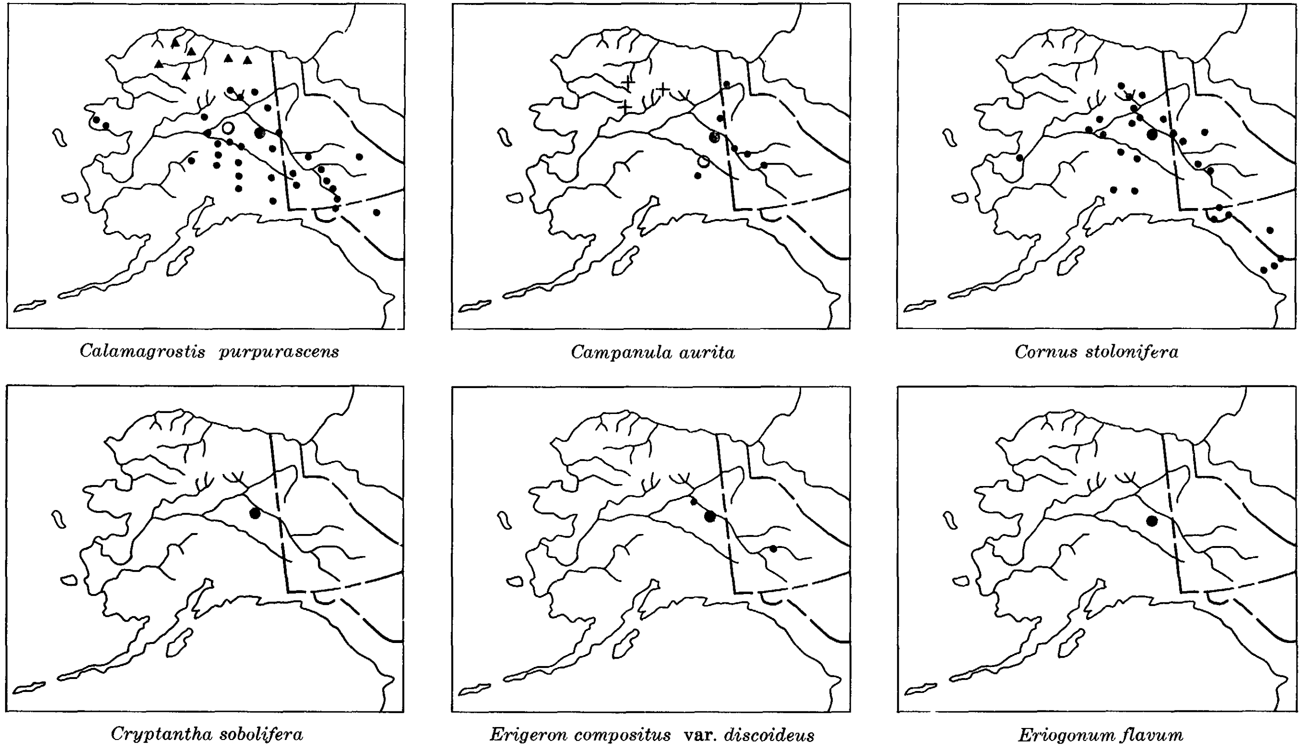
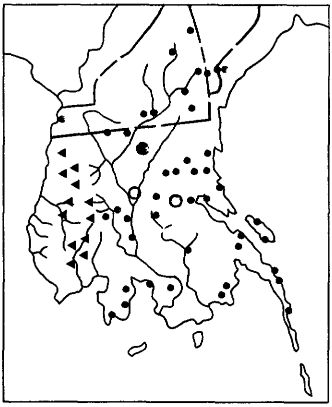
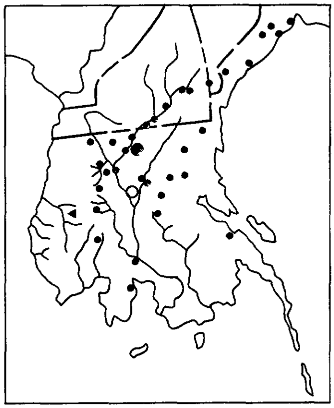


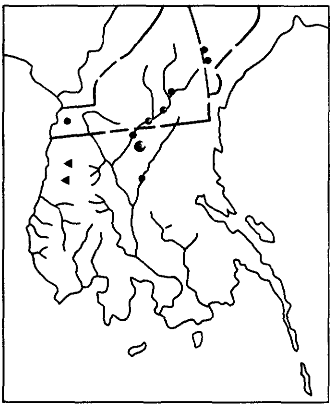
FIGURE 6.—Distribution of selected vascular plants in northwestern North America: ⬤, Eagle Bluff, near Eagle, Central Yukon River district, Alaska; ○, Shacklette's other Alaskan collections; ●, adapted from distribution maps of Hultén (1941–50); ▲, adapted from Wiggins and Thomas (1962); +, S. G. Shetler (written commun., 1965).



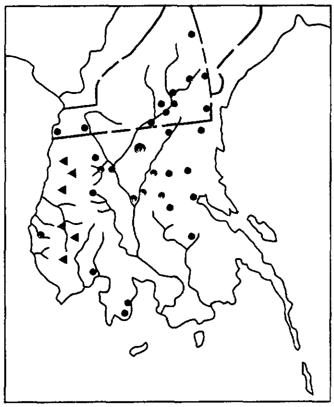
Festuca altaica



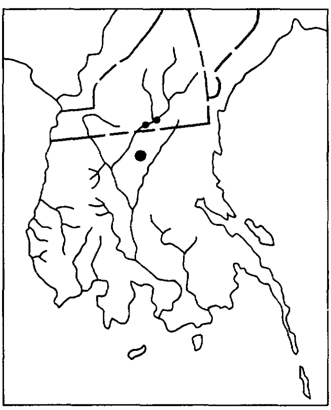
Juniperus communis var. *montana*



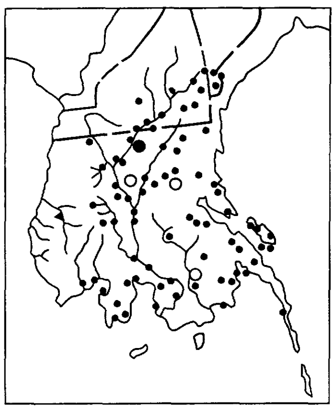
Erysimum inconspicuum



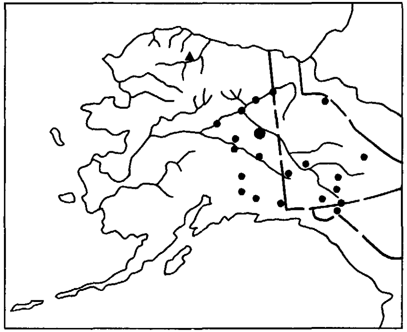
Hedysarum mackenzii



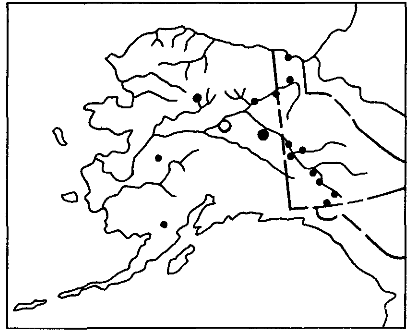
Erysimum angustatum



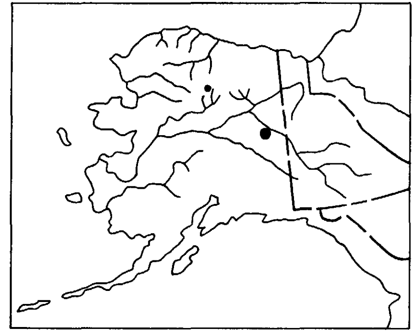
Galium boreale



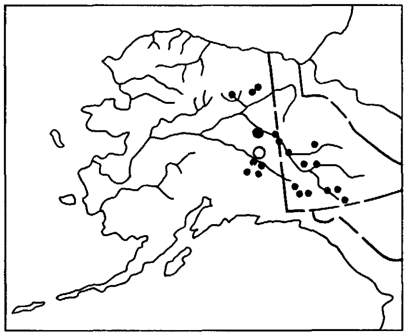
Linum perenne ssp. *lewisii*



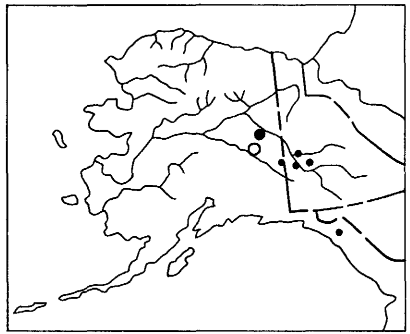
Minuartia laricifolia



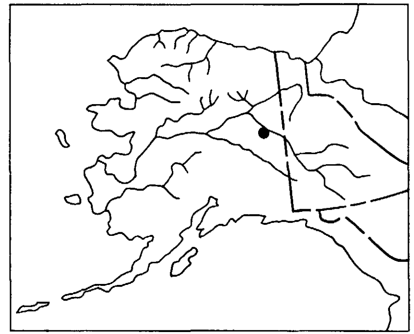
Oxytropis viscida forma *albida*



Pentstemon gormani

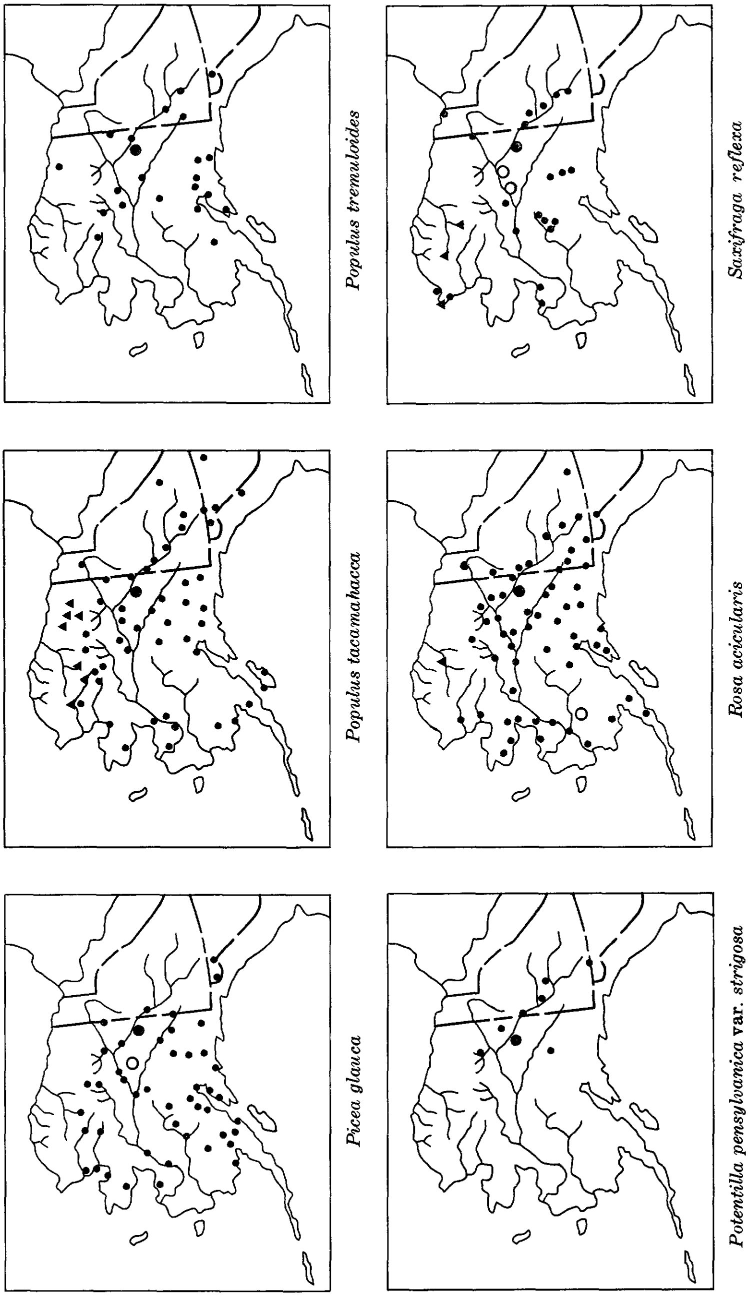


Phacelia mollis



Phacelia sericea

Figure 7.—Distribution of selected vascular plants in northwestern North America: ⬤, Eagle Bluff, near Eagle, Central Yukon River district, Alaska; ○, Shacklette's other Alaskan collections; ●, adapted from distribution maps of Hultén (1941–50); ▲, adapted from Wiggins and Thomas (1962); +, S. G. Shetler (written commun., 1965).


Populus tremuloides
Saxifraga reflexa
Populus tacamahacca
Rosa acicularis
Picea glauca
Potentilla pensylvanica var. strigosa

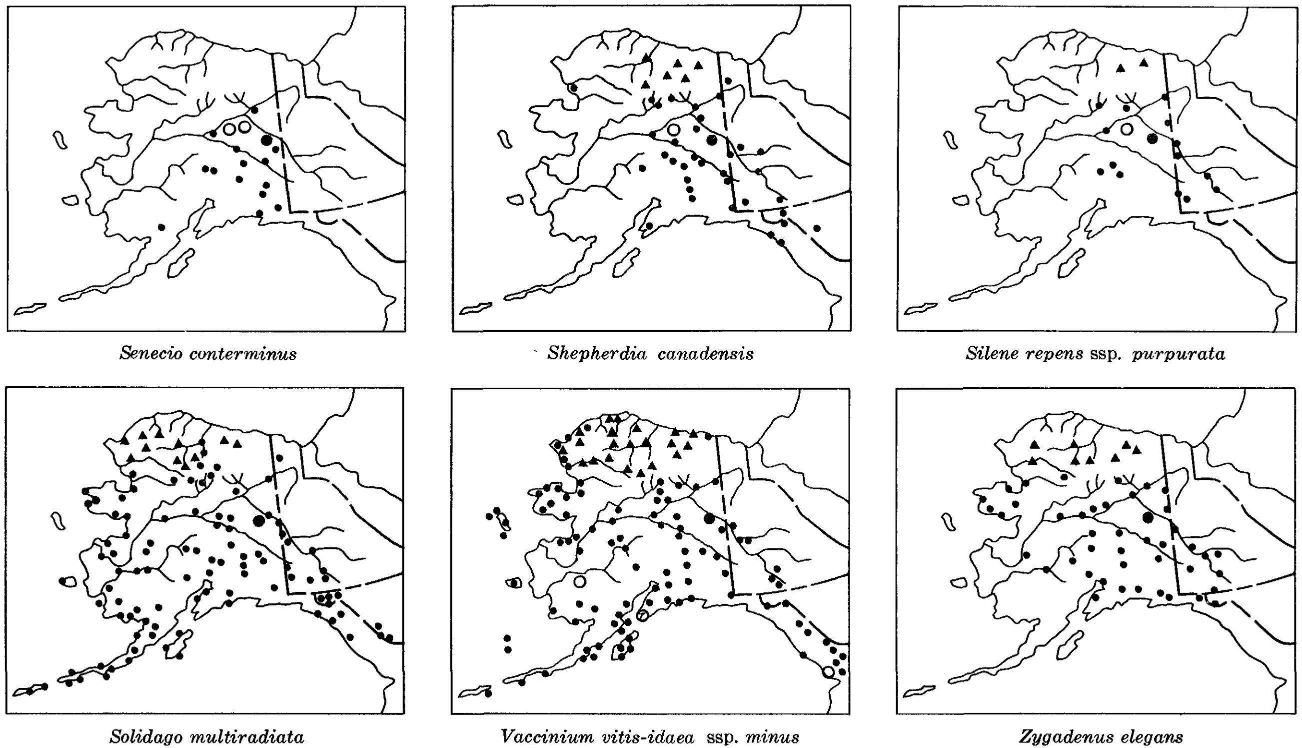


FIGURE 8.—Distribution of selected vascular plants in northwestern North America: ●, Eagle Bluff, near Eagle, Central Yukon River district, Alaska; ○, Shacklette's other Alaskan collections; ●, adapted from distribution maps of Hultén (1941–50); ▲, adapted from Wiggins and Thomas (1962); +, S. G. Shetler (written commun., 1965).

edaphic conditions that reduced competition with the more "aggressive" species of the region.

The phytogeographical groups to which the Eagle Bluff plants are assigned, and their percentage of the total flora at this study site, are listed as follows:

North American radiants (30 percent):
- *Betula resinifera*
- *Cornus stolonifera*
- *Erigeron compositus* var. *discoideus* (the variety a preglacial relict in Alaska–Yukon Territory)
- *Erysimum inconspicuum*
- *Picea glauca*
- *Populus tacamahacca*
- *P. tremuloides*
- *Potentilla pensylvanica* var. *strigosa* (the variety a preglacial relict in Alaska)
- *Shepherdia canadensis*
- *Solidago multiradiata*
- *Zygadenus elegans*

Cordilleran endemics (22 percent):
- *Bupleurum americanum* (preglacial relict in northwest North America)
- *Cryptantha sobolifera* (disjunct preglacial relict at Eagle, Alaska)
- *Eriogonum flavum* (disjunct preglacial relict at Eagle, Alaska)
- *Linum perenne* ssp. *lewisii* (ssp. *typicum* is in Europe and Asia)
- *Oxytropis viscida* (the forma *albida* is endemic to Alaska)
- *Phacelia sericea* (disjunct preglacial relict in the Yukon River valley)
- *Saxifraga reflexa* (chiefly in unglaciated Alaska–Yukon Territory; its status as a Cordilleran endemic is questionable)
- *Senecio conterminus*

Widespread taxa of Europe, Asia, and North America (20 percent):
- *Androsace septentrionalis*
- *Arctostaphylos uva-ursi*
- *Artemisia frigida*
- *Galium boreale*
- *Juniperus communis* var. *montana* (the variety in Europe and Asia limited to arctic regions)
- *Rosa acicularis*
- *Vaccinium vitis-idaea* ssp. *minus*

Amphi-Pacific species (17 percent):
- *Arabis lyrata* ssp. *kamchatica*
- *Calamagrostis purpurascens*
- *Festuca altaica*
- *Hedysarum mackenzii*
- *Minuartia laricifolia* (disjunct distribution)
- *Silene repens* ssp. *purpurata* (the subspecies endemic to unglaciated Alaska–Yukon Territory)

Alaska–Yukon Territory endemic species (11 percent):
- *Campanula aurita*
- *Erysimum angustatum*
- *Pentstemon gormani*
- *Phacelia mollis*

LITERATURE CITED

Anderson, J. P., 1959, Flora of Alaska and adjacent parts of Canada: Ames, Iowa State Univ. Press, 543 p.

Braun-Blanquet, J., 1932, Plant sociology: New York, McGraw-Hill Book Co., 439 p.

Fernald, M. L., 1950, Gray's manual of botany, [8th ed.]: New York, American Book Co., 1632 p.

Halliday, W. E. D., and Brown, A. W. A., 1943, The distribution of some important forest trees in Canada: Ecology, v. 24, no. 3, p. 353–373.

Hawkes, H. E., and Webb, J. S., 1962, Geochemistry in mineral exploration: New York and Evanston, Ill., Harper & Row, 415 p.

Hopkins, D. M., 1959, Some characteristics of the climate in forest and tundra regions in Alaska: Arctic, v. 12, no. 4, p. 215–220.

Hultén, Eric, 1937, Outline of the history of arctic and boreal biota during the quaternary period: Bokförlags Aktiebolaget Thule, Stockholm, 168 p.

——— 1941–50, Flora of Alaska and Yukon: Lunds Universitets Årsskrift, new ser., sec. 2 in 10 pts.—1941, v. 37, no. 1, p. 1—128; 1942, v. 38, no. 1, p. 129–412; 1943, v. 39, no. 1, p. 413–568; 1944, v. 40, no. 1, p. 569–796; 1945, v. 41, no. 1, p. 797–978; 1946, v. 42, no. 1, p. 979–1066; 1947, v. 43, no. 1, p. 1067–1200; 1948, v. 44, no. 1, p. 1201–1342; 1949, v. 45, no. 1, p. 1343–1482; 1950, v. 46, no. 1, p. 1483–1902.

——— 1958, The amphi-Atlantic plants and their phytogeographical connections: Kungl. Svenska Vetenskapsakademiens Handlingar, Fjärde Serien, v. 7, no. 1 [Stockholm, Almqvist and Wiksell], 340 p.

Kellogg, C. E., and Nygard, I. J., 1951, Exploratory study of the principal soil groups of Alaska: U.S. Dept. Agriculture, Agriculture Mon. 7, 138 p.

Löve, Doris, 1962, Plants and Pleistocene, *in* Seminar on problems of the Pleistocene and arctic: McGill Univ. Mus. Pub. 2, v. 2, p. 17–39.

Lutz, H. J., 1956, Ecological effects of forest fires in the interior of Alaska: U.S. Dept. Agriculture Tech. Bull. 1133, 121 p.

McMurtrey, J. E., Jr., and Robinson, W. O., 1938, Neglected soil constitutents that affect plant and animal development, *in* Soils and Men: U.S. Dept. Agriculture Yearbook of Agriculture, 1938, p. 807–829.

Mertie, J. B., Jr., 1930, Geology of the Eagle-Circle district, Alaska: U.S. Geol. Survey Bull. 816, 168 p.

Oosting, H. J., 1956, The study of plant communities: San Francisco, W. H. Freeman & Co., 440 p.

Polunin, Nicholas, 1940, Botany of the Canadian Eastern Arctic, Part I, Pteridophyta and Spermatophyta: Natl. Mus. Canada Bull. 92, biol. ser. 24, 408 p.

Porsild, A. E., 1943, Materials for a flora of the continental Northwest Territories of Canada: Sargentia, no. 4, p. 1–78.

——— 1951, Botany of southeastern Yukon adjacent to the Canol Road: Natl. Mus. Canada Bull. 121, biol. ser. 41, 400 p.

——— 1955, The vascular plants of the Western Canadian Arctic Archipelago: Natl. Mus. Canada Bull. 135, biol. ser. 45, 226 p.

——— 1957, Illustrated flora of the Canadian Arctic Archipelago: Natl. Mus. Canada Bull. 146, biol. ser. 50, 209 p.

Rankama, Kalervo, and Sahama, Th. G., 1950, Geochemistry: Chicago, Univ. Chicago Press, 912 p.

Rydberg, P. A., 1917, Flora of the Rocky Mountains and adjacent plains: New York, published by the author, 1110 p.

Scoggan, H. J., 1957, Flora of Manitoba: Natl. Mus. Canada Bull. 140, biol. ser. 47, 619 p.

Shacklette, H. T., 1962a, Influences of the soil on boreal and arctic plant communities: Univ. Mich. doctoral dissertation available on film from University Microfilms, Inc. [349 p.], Ann Arbor, Mich.

——— 1962b, Biotic implications of Alaskan biogeochemical distribution patterns: Ecology, v. 43, no. 1, p. 138–139.

Sutcliffe, J. F., 1962, Mineral salts absorption in plants: New York, Pergamon Press, 194 p.

Ulke, Titus, 1934, A flora of Yoho Park, British Columbia: Contr. Biol. Lab. Catholic Univ. of America, no. 14, 89 p.

U.S. Weather Bureau, 1943, Climatic atlas for Alaska: Rept. 444, 72 p.

Walker, R. B., 1954, The ecology of serpentine soils, [pt.] 2 of Factors affecting plant growth on serpetine soils: Ecology, v. 35, p. 259–266.

Weaver, J. E., and Clements, F. E., 1938, Plant ecology: New York, McGraw-Hill Book Co., 601 p.

Wedow, Helmuth, Jr., 1954, Reconnaissance for radioactive deposits in the Eagle-Nation area, east-central Alaska: U.S. Geol. Survey Circ. 316, 9 p.

Wiggins, I. L., and Thomas, J. H., 1962, A flora of the Alaskan arctic slope: Toronto, Univ. Toronto Press, Arctic Inst. North America Spec. Pub. 4, 425 p.

Zalashkova, N. E., Lizunov, N. V., and Sitnin, A. A., 1958, Essai de leve métallometrique du béryllium dans une zone de pegmatites à béryl recouvertes d'alluvions, *in* Prospection et Protection du Sous-sol: Service d'Information Geol. B.R.G.G.M. Annales, no. 39, p. 8–13. [Translated from Russian, Razvedka i okhrana nedr, Moscow, August 1958]

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