AN ABSTRACT OF THE THESIS OF

DENNIS RANDALL JAQUES for the MASTER OF SCIENCE
(Name) (Degree)

in BOTANY presented on April 2, 1973
(Major) (Date)

Title: RECONNAISSANCE BOTANY OF ALPINE ECOSYSTEMS ON PRINCE OF WALES ISLAND, SOUTHEAST ALASKA

Abstract approved: Signature redacted for privacy.
Kenton L. Chambers

A study of the Prince of Wales Island alpine areas was undertaken to determine what species occur in the region and to describe plant communities making up the alpine vegetation.

For one month in 1972, specimens were collected and 78 microplots were analyzed for cover, frequency and constancy data. Three basic habitat types were discovered, with different associations being recognized on calcareous and noncalcareous substrates.

Alpine vegetation patterns are formed in a physiographically unstable area. However, where conditions remain favorable for a long enough period of time, a climatic climax of Empetrum-heath vegetation develops. Elsewhere topographic climax vegetation exists.

The region is thought to have maintained a flora of significant proportions at least since early post-Pleistocene time. The presence of many disjunct species indicates that floral elements may have

survived Pleistocene ice advances in various refugial sites. The west coast of Prince of Wales Island appears to have served as a small migration center following Pleistocene ice recession.

Reconnaissance Botany of Alpine Ecosystems on Prince of Wales Island, Southeast Alaska

by

Dennis Randall Jaques

A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Master of Science

June 1973

APPROVED:

Signature redacted for privacy.

Professor of Botany
in charge of major

Signature redacted for privacy.

Head of Department of Botany

Signature redacted for privacy.

Dean of Graduate School

Date thesis is presented April 2, 1973

Typed by Virginia Jaques for Dennis Randall Jaques

ACKNOWLEDGEMENTS

I would like to extend special thanks to Kenton Chambers, especially for his assistance in obtaining funds which made the 1972 field study possible. His editing advice in the completion of the thesis is also greatly appreciated. Robert Dennis made many valuable suggestions for which I am grateful.

Stanley Welsh was of great help in checking all of my determinations of taxa and his correspondence provided valuable information on the flora of Alaska. Arland Harris and Douglas Swanston of the U. S. Forest Service aided the research in many practical ways.

Special thanks go to John and Ruth Cassell of Hollis, Alaska for providing a cabin for me during the field studies, for allowing me the use of their mail service and for providing me with many hot meals after cold, exhausting climbs to and from my study sites.

Finally, thanks go to my wife, Ginny, for her editing assistance and for typing the manuscript.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

RECONNAISSANCE BOTANY OF ALPINE ECOSYSTEMS ON PRINCE OF WALES ISLAND, SOUTHEAST ALASKA

INTRODUCTION

Previous reconnaissance studies of Southeast Alaskan vegetation have been concentrated in areas surrounding the ports of the Archipelago (Figure 1). Very little study has been conducted on areas above 500 feet in elevation. During the summer of 1971, plants were collected from 14 peaks in Southeast Alaska and evaluated to determine if a detailed reconnaissance study would be of value. A significant number of range extensions for North American taxa were discovered. Consequently, from July 3 to August 4, 1972, the author conducted a reconnaissance study on the alpine areas of the Prince of Wales Island mountain system. Harris Peak (3392 feet in elevation), Granite Mountain (3445 feet in elevation) and the Klawock Mountains (3996 feet in elevation) were chosen for study since these are in the only insular area in Southeast Alaska whose soils have been mapped (Gass, et al., 1967) and whose geological history and composition have been studied (Sainsbury, 1961; Swanston, 1967, 1969). Three days were also spent on a study of the vegetation of Virginia Mountain, a limestone peak 2700 feet in elevation on the northern tip of Prince of Wales Island. The locations of these four sites are indicated by arrows in Figure 2.

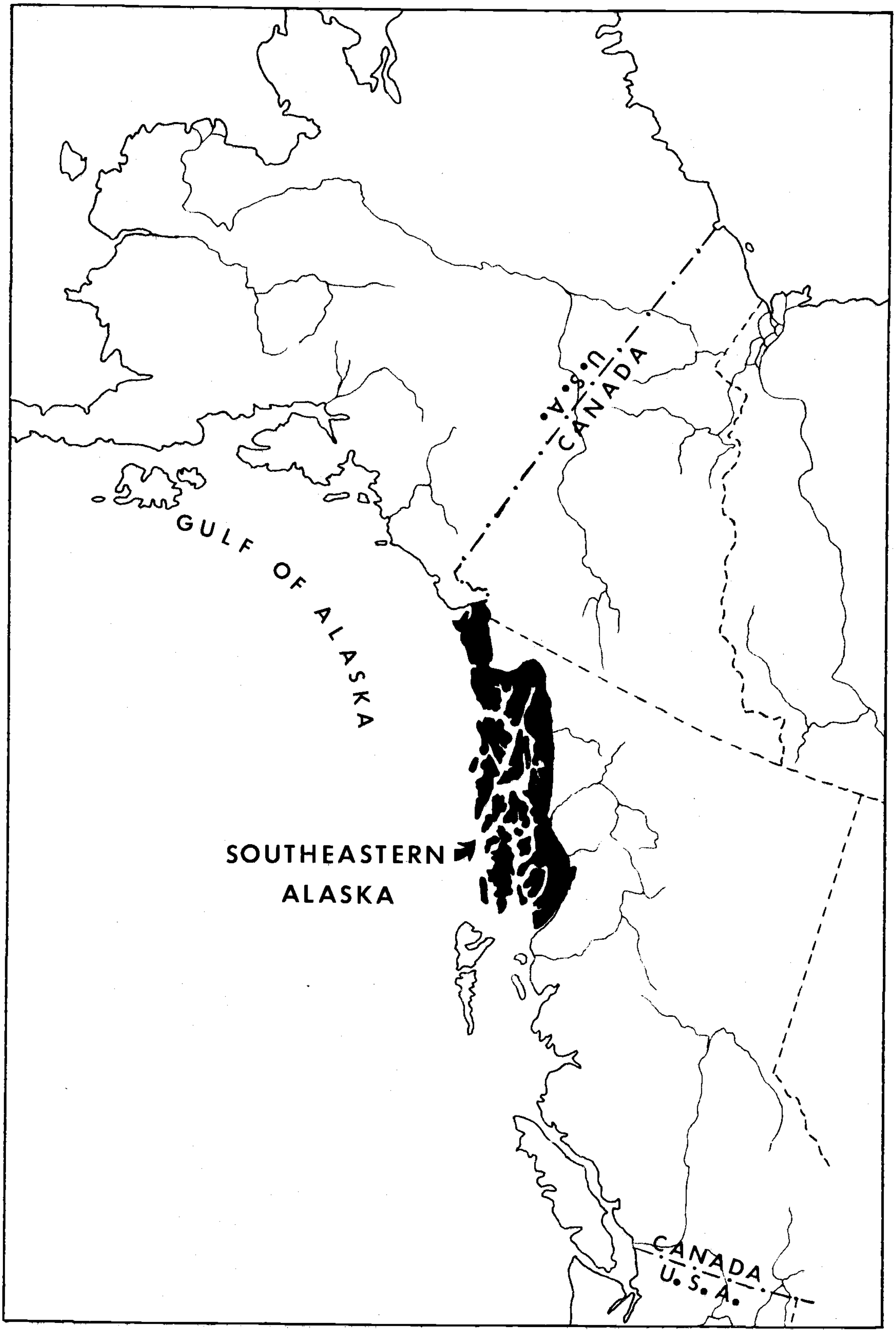


Figure 1. Southeastern Alaska.

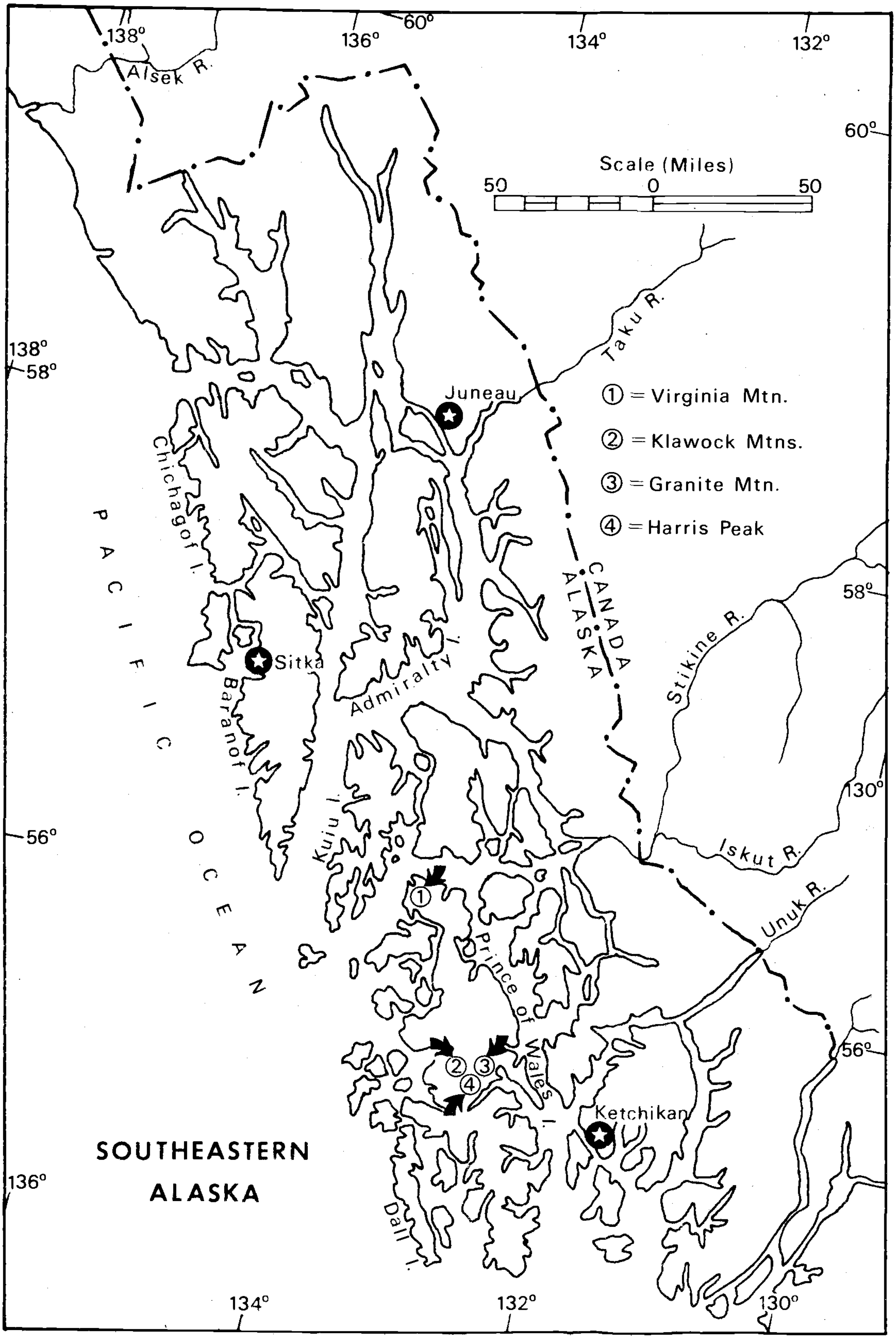


Figure 2. Collection sites in Southeast Alaska.

Objectives of the research are: 1) to make a detailed reconnaissance study of a few alpine ecosystems in this poorly collected region, 2) to describe vegetation types and plant communities occurring in the alpine, and 3) to gain insight into the origin of the coastal alpine flora of northwest North America.

DESCRIPTION OF THE AREA

Location

Southeast Alaska, also known as the Alexander Archipelago or "The Panhandle," is a glacier-carved region of rugged mountains and fiords. The region extends from latitude 54°40' North to about 60°00' North and from 130° West to 138° West longitude.

Southeast Alaska is bounded on the west by the open Pacific Ocean. Its eastern boundary is the rugged Coast Range mountains which are broken infrequently by rivers flowing from British Columbia. South of the Archipelago are Portland Canal and Dixon Entrance. On the north lie the St. Elias Mountains and the great piedmont glaciers, including Malaspina Glacier with its massive front extending 50 miles along the coast. Glacial activity, past and present, is a prominent force in shaping the landscape.

The major physiographic features undoubtedly existed before Pleistocene ice advanced (Figure 3). Regional control of the major physiographic features is exerted by the general northwest trend of faults, bedrock strike and lineaments. These features were deepened and accentuated by glacial action. The Coast Range is composed of rugged peaks of quartz diorite and granodiorite (Buddington and Chapin, 1929). The intrusives are Cretaceous in age, and subsequent Tertiary uplift formed the mountain system (Miller, 1958b). Adjacent

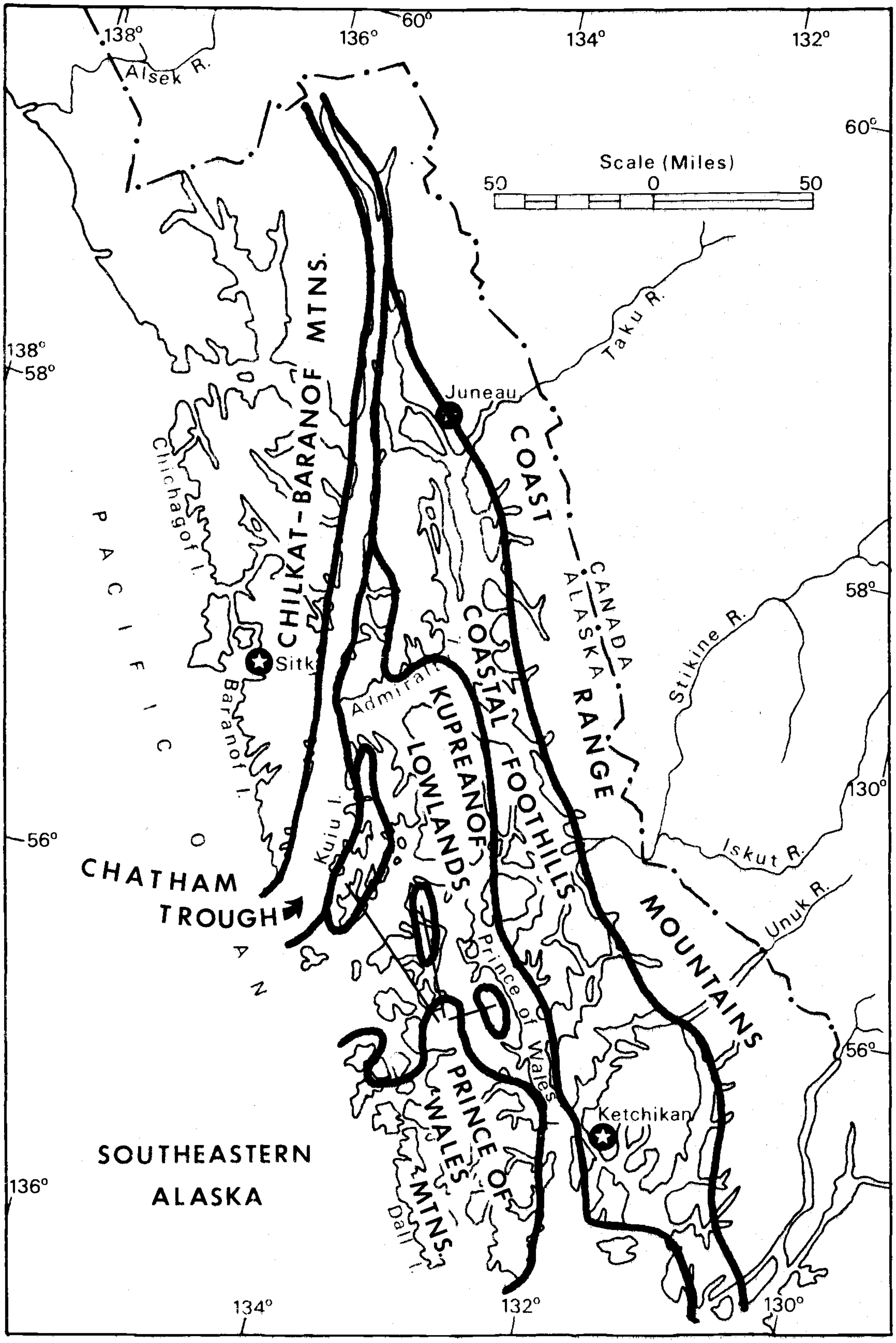


Figure 3. Physiographic divisions of Southeast Alaska.

to the west side of this Coast Range granitic batholith is a metamorphic contact zone varying from two to thirty-five miles in width. This zone of Wrangell-Revillagigedo metamorphic rocks forms the foothills of the Coast Range. West of these foothills is the Kupreanof Lowland which includes southwest Admiralty, Kupreanof, Kuiu, northern Prince of Wales, and Kosciusko Islands. This is an area of more subdued relief with broad, relatively level expanses. West of this area are the Chilkat-Baranof Mountains of the Chilkat Peninsula-Glacier Bay area and Chichagof-Baranof Islands. Also west of the Kupreanof Lowlands are the Prince of Wales Mountains, including those on the southern two-thirds of Prince of Wales Island, Dall Island, and isolated mountains northward on Prince of Wales and Kuiu Islands.

History of Exploration and Research

Southeast Alaska was first seen by a white man in 1741 when Captain Chirikoff, on the ship St. Paul (part of Captain Vitus Bering's famous expedition to Alaska), sited what were probably the Klawock Mountains on Prince of Wales Island and the mountains on Baranof Island. No collections are reported by Louis Croyère, the naturalist on board the St. Paul.

The next naturalists to visit the Panhandle were Thaddeus Haenke and Luis Nees. They travelled with Captain Malaspina. On

June 27 through July 5, 1791, they visited Port Mulgrave and Haenke Island in Yakutat Bay. Presl (1825-1835) published their findings.

Archibald Menzies accompanied Captain Vancouver on his voyages and in 1793 and 1794 made numerous landings in Southeast Alaska. Georg Langsdorff and Wilhelm Tilesius travelled with Krusenstern on his voyage around the world in 1805 to 1806. They spent 13 days in June, 1806, in Sitka. In 1827, Carl Mertens collected extensively at Sitka while stopped there with Lütke's expedition. Bongard's (1833) subsequent publication of these collections are the first published accounts of the flora of Southeast Alaska.

During the period from 1865 to 1895 William Dall collected numerous specimens from Sitka north to the Arctic Coast. His specimens are preserved at the National Herbarium and the Gray Herbarium. In 1882 Arthur and Aurel Krause collected at the head of Lynn Canal. Their collections are in the Botanical Museum, Berlin-Dahlem. In 1883 Thomas Meehan collected in Southeast Alaska. In 1891 Grace Cooley made a large collection from the region. Frederick Funston collected a large number of plants in Yakutat Bay, and these were published three years later by F. V. Coville (1895). Coville himself made a significant Southeast Alaska collection as a member of the Harriman Alaska Expedition of 1899. His collections are housed in the United States National Herbarium. In 1902 Charles Newcomb collected on Prince of Wales Island. His specimens, collected at Kazan, Kazan Mountain, Karta Lake, Nichols Bay and Copper Mountain, are located in the Field Museum of Natural History, in Chicago. Charles Piper collected at Sitka in 1904.

Jacob Peter Anderson collected extensively during his stay in the Panhandle from 1914 to 1941. He published many reports culminating in his Flora of Alaska and Adjacent Parts of Canada (1959). In 1916, 1924 and 1935 William Cooper made many collections in Glacier Bay and on the Stikine River, and numerous publications resulted from his work.

Eric Hultén collected at a few localities in Southeast Alaska in 1932. Then, beginning in 1941, he compiled the monumental Flora of Alaska and Yukon, completed in 1950. This work contains excellent discussions of each taxon, distribution maps and lists of specimens used to construct the maps. In 1968, after numerous corrections and additions to his earlier work, Hultén published the Flora of Alaska and Neighboring Territories.

In 1929 Robert Taylor of the United States Forest Service put together a manual of Alaska trees (Pocket Guide to Alaska Trees) which contains much information on plant distribution. Leslie Viereck and Elbert Little, Jr., also with the United States Forest Service, enlarged upon the earlier project and published a useful and artistic guide to Alaska Trees and Shrubs (1972).

The Juneau Icefield Research Project has contributed knowledge of the plants of these glacier-enveloped nunataks. Heusser (1954) made a checklist of all plants located at the many nunatak sites studied.

Several significant studies have been done on the territories adjacent to Southeast Alaska. These add much to an understanding of the distribution patterns and ecology of the flora of the Panhandle. The most significant of these works is the Flora of the Queen Charlotte Islands by James Calder and Roy Taylor (1968). Other areas of British Columbia have been studied by Raup (1934) and Welsh and Rigby (1971b). The region just north of Southeast Alaska has been extensively studied. The southern Yukon Territories were collected by Raup (1947), Porsild (1951, 1966) and Löve and Freedman (1956). Welsh and Rigby (1971a) have contributed a fine work on the flora of northern Yukon Territory. Murray (1968, 1971) has added to an understanding of the flora in the St. Elias Mountains. These studies, along with herbarium material from Oregon State University, Corvallis and the University of British Columbia, Vancouver, have been useful in constructing distribution maps (Appendix).

Geology and Glacial History

The geology of Prince of Wales Island has been studied extensively by Buddington and Chapin (1929), W. Condon (1961), C. Sainsbury (1961) and D. Swanston (1967, 1969). A two-fold system of bedded rocks occurs in the Maybeso-Harris River valleys. These bedded rocks are middle Ordovician to lower Silurian black shaley to slatey argillites overlain by predominantly grey-green greywacke (Swanston, 1967, p. 24). Middle Cretaceous age intrusives also form a large part of the geology in this area. These igneous rocks are generally quartz diorite and are thought to be satellite bodies of the Coast Range batholith which was intruded over an extensive period in the Cretaceous. One sample from Tolstoi Point was determined to be 100 million years old, or roughly middle Cretaceous in age (Sainsbury, 1961, p. 339). Numerous and highly variable Paleozoic and Mesozoic dikes occur throughout the region. No ultrabasic rocks have been described from the Maybeso-Harris River valleys.

Granite Mountain is mainly composed of a large satellite pluton consisting of very uniform quartz diorite. On its north side, near Twelvemile Arm, the pluton comes in contact with greywackes. The southern contact is predominantly with black slatey argillite beds that are highly folded. A very steep east-west divide, intricately faulted and forming numerous cliffs, is also associated with this southern contact. Sainsbury (1961, p. 337) suggests this may be related to the forceful intrusion of the pluton.

Harris Peak and Ridge are somewhat more complex lithologically than Granite Mountain. The horn-arête system in which Harris Peak is found extends about four miles on an east-west axis, and the peaks in this system are composed of small quartz diorite plutons. Surrounding the peaks on all sides from one-fourth to one mile in width are beds of predominantly grey-green greywacke. The easternmost extension of the ridge is made up of black shaley to slatey argillites. Within both of these bedded rock-types are occasional limestone beds and locally abundant minute calcite lenses and crystals.

The Klawock Mountains supposedly consist of the same rock-types, but contacts and aerial extent of each type are unknown.

Virginia Mountain has never been mapped geologically. However, Buddington and Chapin (1929) mapped the coastal rocks at this locality and found them to be Silurian limestones with local beds of conglomerate. For purposes of this study, Virginia Mountain is assumed to be composed of these same rocks.

Throughout the entire Southern Coast of Alaska are deposits of alluvium and glacial till of various ages. Southeast Alaska was and is presently being carved by glacial activity. No glaciers are found on Prince of Wales Island, but perennial snowfields exist.

Swanston (1969) presented evidence supporting the occurrence of two late-Pleistocene glacial advances in the Maybeso Valley of Prince of Wales Island. Sainsbury (1961) described the possibility of similar episodes in the northeast portion of the Craig Quadrangle, Prince of Wales Island.

The older advance is evidenced by deeply weathered brown till which underlies a younger, compact, bluish-grey till. This layering sequence has been observed in one spot in the Maybeso Valley. However, the older till is well represented by erratics and is believed to be exposed in patches on the ridges bordering the valley (Swanston, 1967, p. 45). The older till may be correlative to numerous rounded ridge tops and striations and grooves which are abundant at higher elevations in the area. This higher level glaciation apparently reached about 3000 feet in the Maybeso-Harris valleys; all but the tallest peaks were covered by ice. Swanston (1969, p. 33) believes that the lack of any appreciable weathering rind on pebbles and boulders in this till indicates that it is no older than intermediate Wisconsin.

The younger till is very abundant and extends up to 1500 feet on the mountain slopes. A series of four recessional moraines associated with this last major ice advance have been located in the Maybeso Valley and are described by Swanston (1967). From the oldest to the most recent they are called the Maybeso moraine (one-half mile up the valley from Hollis anchorage), Crackerjack moraine (two miles up valley), Haystack Butte moraine (three miles up valley) and Snowdrift moraine (five miles up valley). These represent the dying pulsations of the last major main valley ice advance before the close of the classical Wisconsin glaciation of North America. A marine beach on Indian Creek near Maybeso Valley gives a date of 9,510±280 years B. P. for the latest valley bottom deposit of the younger till (Swanston, 1967, p. 96). Subsequently, these glaciers receded to their highland sources and no longer exist.

Earlier Pleistocene ice advances undoubtedly occurred but any evidence of these advances has been obliterated by the more recent intense glaciations. Post-Pleistocene advances and retreats have also probably affected the area. Sainsbury (1961, p. 331) has described a high level moraine on Granite Creek which is at least 30 feet thick. No definite ages can be assigned these deposits but the last glaciers probably receded from the area several hundred years ago.

Both Swanston (1967) and Sainsbury (1961) support the hypothesis that even during maximum Pleistocene advances the Klawock Mountains served as the source area for the glaciers that carved the Maybeso and Harris valleys. Mineral content and lithologies of the glacial deposits and the fact that till fabric and glacial striations have an eastward orientation indicate that the source area was west of the Maybeso Valley (e. g. the Klawock Mountains).

The Mt. Calder-Virginia Mountain area undoubtedly supported minor glaciers during the Pleistocene. Striations observed on the rounded ridge extending west from Virginia Mountain indicate that ice passed over this ridge moving in a southwesterly direction. The

Coast Range mountains to the east were possibly the source area for this ice. The upper limits of Pleistocene ice are unknown but the sharp relief of both Mt. Calder and Virginia Mountain indicates that at least the last major ice advance did not completely cover these peaks.

Abandoned glacial cirques on Prince of Wales Island show a distinct five-fold pattern (Swanston, 1967, p. 81). Approximately 30 cirques at 700 to 900 feet elevation have been equated by Swanston to the glaciation represented by the older till. About 58 cirques that occur from 1100 to 1300 feet are considered correlative to the glaciation represented by the younger till.

In post-Pleistocene time isostatic readjustment of the land and rising sea level have contributed to changes in beach positions. At the mouth of Indian Creek in the Harris Valley, at an elevation of 30 feet above sea level, Swanston (1967) located a marine beach overlying the younger till. This indicates that after recession of the late Pleistocene glaciers the land has rebounded at least 30 feet. Twenhofel (1952) has plotted apparent changes in altitude of land relative to present day sea level all along the southern Alaska coast. Values range from as much as +500 feet at Portland Canal and Juneau to -40 feet at the mouth of the Copper River.

Soils

Soils found in the Harris Peak-Klawock Mountains locality have been studied and mapped by the United States Forest Service, and 20 soil series have been described. The physical, chemical and historical processes operating to form these soils are many and varied. However, certain dominant forces can be seen which affect past and present structure of soils in the alpine. At lower elevations the high rainfall, together with the mixing effects of glaciations, tend to mask the effects of parent material on vegetation. Heavy leaching in these well drained soils lowers the amounts of available nutrients. In alpine sites, on the other hand, parent material adds much to the diversity of vegetation composition and community development.

Alpine soils are classed into four series by Gass et al. (1967). These are the Hydaburg Series, Sunnyhay Series, St. Nicholas and Lithic Cryaquepts Series, and alpine rock land. Other series important to subalpine vegetation and the subalpine-alpine ecotone are the Kina and Kogish Series.

Hydaburg soils are very poorly drained peat soils occurring on concave surfaces or low sloping surfaces in the alpine. Depths of the upper highly organic layers vary from a few inches to over one foot. Beneath these plant remains are several inches of dark brown to black muck which grades into a lighter gravelly loam overlying the bedrock.

Bedrock almost always lies less than two feet below the surface of these soils.

The Sunnyhay Series occurs on the convex slopes of the alpine where better drainage allows for the growth of more diversified vegetation. The upper layer is matted roots and prostrate stems of living vegetation in a dark reddish-brown mucky peat. This soil series also supports scattered copses of mountain hemlock (Tsuga mertensiana), Sitka spruce (Picea sitchensis) and subalpine fir (Abies lasiocarpa). Soil depth to bedrock is six inches to as much as one and one-half feet.

The St. Nicholas Series is a very gravelly loam soil found on steep slopes. A thin surface layer of black gravelly silt loam covers six to eighteen inches of dark reddish-brown gravelly silt loam which rests on the bedrock. On very steep snowslide areas, St. Nicholas and Lithic Cryaquepts soils consist of thin ($<$15 inches) layers of dark brown silty loam over compact till or bedrock.

Kina and Kogish soils occur on moderate slopes and develop in areas called "muskegs." Ponds form in these muskegs, thus indicating the poor drainage character of these soils. Kina soils are composed of three to four feet of reddish-brown sedge peat over compact glacial till; whereas Kogish soils are composed of moss peat overlying woody peat.

Rock outcrops, cliffs and ledges are common features of alpine and subalpine areas. Rock outcrops occur on all steep terrain but are rare at lower elevations where vegetation cover is much more complete. Many bare alpine areas are primitive surfaces which were exposed by the scouring action of glaciers and subsequently have developed little or no soil.

Soil temperatures, recorded at the bedrock-soil interface, have been charted for the Sunnyhay, Hydaburg and St. Nicholas Series (Gass et al., 1967). Average annual temperatures were 38^{o}F (St. Nicholas), 39^{o}F (Hydaburg) and 40^{o}F (Sunnyhay). Average summer temperatures were 44^{o}F (St. Nicholas), 49^{o}F (Hydaburg) and 50^{o}F (Sunnyhay), with highs of 46^{o}F, 54^{o}F and 55.5^{o}F respectively.

In the Klawock Mountains-Harris Peak-Granite Mountain locality alpine areas occupy 65,985 acres out of a total area of 484,000 acres (Gass et al., 1967, p. 39). The total extent of subalpine areas has not been determined. The 65,985 acres of alpine areas represent 13.1 percent of the total land area in this region, a figure which can be assumed to be representative of the entire Prince of Wales Mountain system. In comparison, tidal marshes, which are very significant for waterfowl and other marine life, occupy 0.2 percent of the total land area.

Of the 65,985 acres in alpine vegetation, 14,644 acres (22.2 percent) are rocklands, 30,301 acres (45.9 percent) are Sunnyhay and Hydaburg soils, and 21, 040 acres (31. 9 percent) are St. Nicholas and Lithic Cryaquepts soils.

Climate

Southeast Alaska is located in a Humid Maritime climate zone which is generally characterized by cool and moist conditions the year round. Summer drought is not a common occurrence. However, certain local conditions and occasional dry summers do cause periods of water stress.

Several factors have an overriding influence upon the climate of Southeast Alaska. Generally, the "Aleutian Low" brings moisture-laden air masses into the region from September through March. From April through August slightly drier conditions prevail, especially in the southern section of the Panhandle--southern Prince of Wales, Dall and Revillagigedo Islands. The "North Pacific High" exerts some moderating influence at this time. For example, Ketchikan receives an average of 14. 92 inches of precipitation per month during the September through March period while the April through August period averages 8. 66 inches per month.

Climate in the section of Southeast Alaska north of Icy Strait and the mainland coastal region is greatly influenced by an area of high pressure overlying the Yukon Territories and northern British Columbia. Moderate winter temperatures and ample summer rainfall characterize the outer islands, where climate is greatly influenced by the presence of the Pacific Ocean. Northern and mainland sections receive cold north winds in the winter, and high and low maximum temperatures reach greater extremes in these areas. Lesser amounts of rain fall inland and in the rain-shadow of the tall Coast Range mountains. In short, this area has a more continental climate than the outer islands.

The highly dissected and mountainous terrain of the region causes wide variations in local climatic conditions. May through September air temperature isotherms show the effects of the presence of large land masses on heat radiation. The larger islands reradiate enough summer heat to cause local increases in temperatures. Anderson (1955) constructed simple east-west isotherms for average May through September summer temperatures and attempted to correlate the ranges of forest tree species with these isotherms. Bishop (personal communication) has reinterpreted these data (Figure 4). He shows higher average summer temperatures on Chichagof, Baranof, Admiralty, Kuiu, Kupreanof, Prince of Wales and Revillagigedo Islands than on the surrounding ocean areas. The climate of Southeast Alaska is much more complex than was at first supposed. Because our knowledge of the distributions of many plant species is extremely fragmentary in Southeast Alaska, no close

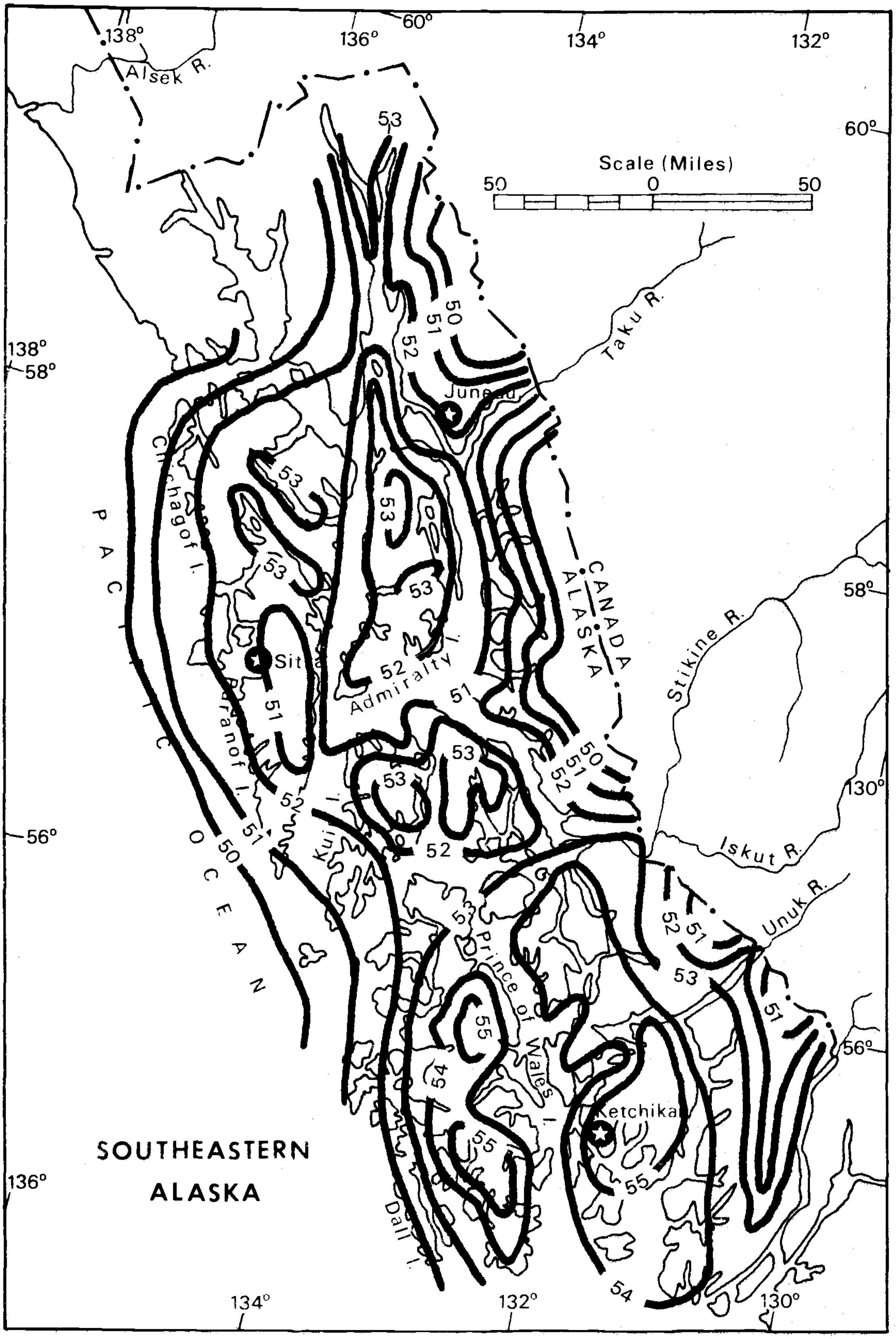


Figure 4. Average May through September temperatures.

correlations can be made between distributions and climatic data at this time.

No climatic data have been gathered in any alpine sites. However, regarding temperature difference, a figure of $3^{\circ}F$ drop per 300 feet rise in elevation is considered accurate in still air. Aspect, slope and air drainage patterns cause local variations. Climatic data for 21 sites are listed in Table 1.

All coastal stations are located at sea level. The table essentially compares water availability (Precipitation) with water need or Potential Evapotranspiration (PET). The Indices of Humidity and Aridity are percentages expressed by:

$$\text{Index of Humidity} = \frac{100\ (\text{Precipitation})}{\text{PET}}$$

$$\text{Index of Aridity} = \frac{100\ (\text{PET-AET})}{\text{PET}}$$

The Moisture Index (MI) relates the Humidity Index (IH) to the Aridity Index (IA) and is expressed by Thornthwaite (1948) in the following equation: MI = IH - 0.6 (IA). The 60 percent weight for aridity is used by Thornthwaite in recognition of the fact that during the growing season moisture used by perennial plants is not restricted to that which they receive from current rainfall, but they may also utilize soil moisture stored from previous seasons.

The number of frost-free days is an important influence on the length of the growing season. Therefore, these data have been added

Table 1. Climatic data, Southeastern Alaska.

	Elevation (ft.)	Latitude (N.)	Longitude (W.)	Mean Annual Temperature (°F)	Mean Annual Precipitation (in.)	Potential Evapotranspiration	Actual Evapotranspiration	Surplus	Index of Humidity	Index of Aridity	Moisture Index	Summer Need (%)	Frost-free Days
Angoon	35	57°30'	134°35'	40.7	39.10	21.10	20.51	18.00	85.3	2.8	+84	72	155
Annette	18	55°04'	131°39'	45.6	96.54	23.70	23.70	72.89	307.6	0	+308	66	197
Calder	20	56°10'	132°27'	43.1	112.26	22.20	22.17	90.06	405.7	0.1	+405	68	---
Cape Decision	39	56°00'	134°08'	43.7	76.49	21.73	21.73	54.76	252.0	0	+252	69	221
Craig	13	55°29'	133°09'	44.9	106.26	23.46	23.46	82.80	352.9	0	+353	67	---
Haines	100	59°14'	135°26'	40.3	60.64	20.79	18.53	39.85	191.7	10.6	+185	70	---
Haines Junction	1960	60°46'	137°35'	26.5	10.94	16.57	10.94	---	---	34.0	-20.4	77	---
Hollis	15	55°28'	132°40'	44.2	103.58	22.83	22.71	80.75	353.7	0.5	+353	68	---
Hyder	9	55°55'	130°01'	40.9	89.58	21.30	21.06	68.28	320.6	1.12	+320	70	---
Juneau	72	58°18'	134°24'	42.5	90.25	21.89	21.89	68.36	312.2	0	+312	69	177
Kake	8	56°59'	133°55'	42.7	54.51	21.89	21.38	32.62	149.0	2.4	+148	69	---
Ketchikan	15	55°21'	131°39'	46.1	151.19	23.74	23.74	127.45	536.0	0	+537	66	170
Little Port Walter	14	56°23'	134°39'	43.2	222.47	22.32	22.32	200.15	896.7	0	+897	68	184
Petersburg	50	56°49'	132°57'	42.3	105.01	21.69	21.69	83.32	383.7	0	+384	69	138
Sitka	67	57°03'	135°20'	43.3	96.33	22.64	22.64	73.69	323.5	0	+326	67	155
Skagway	18	59°27'	135°19'	41.1	29.86	20.87	16.57	8.99	43.1	20.6	+31	70	109
Taku Pass	175	58°33'	133°41'	39.0	60.3	20.83	20.28	39.47	189.5	2.6	+188	70	---
Telegraph Creek	550	57°54'	131°09'	25.9	12.59	14.33	9.49	---	---	33.8	-20.3	81	---
Unuk River	5	56°04'	131°06'	40.5	118.82	18.94	18.70	99.88	527.3	1.3	+526	73	---
Wrangell	37	56°28'	132°23'	43.7	82.90	22.60	22.56	60.30	266.8	0.2	+267	68	165
Yakutat	28	59°31'	139°40'	39.3	134.15	19.80	19.80	114.35	577.5	0	+578	72	---

(After Patrick and Black, 1968, p. 6-21) as available. Although the number of frost-free days is not an exact measure of the length of the growing season, this information provides tentative comparisons between different localities as to growth periods. Figure 5 is a precipitation map which shows that the high precipitation values on southern Baranof Island gradually diminish inland as far as the Coast Range where a rise is again noted. Local orographic effects have not been measured but are undoubtedly significant in a region as mountainous as Southeast Alaska. Walker's (1961) study of precipitation in the western Cordillera showed that maximum precipitation occurred at cloud base. Although this study was conducted at continental sites, Walker's general conclusion is probably valid for coastal sites as well. The time period from July 3 to August 1, 1972 at Hollis on Prince of Wales Island included eight sunny days with no cloud cover, nine days of rainfall at sea level and thirteen days with a cloud base of about 1400 feet with rainfall at this elevation and above. If this pattern is normal, studies should indicate that progressively higher elevations receive proportionatly greater amounts of precipitation. Berry, Bollay and Beers (1945) suggest that orographic effects may be measured by the formula $r_h = r_o + 0.072h$. "r_h" is the precipitation at elevation "h" (in feet) above the base of the mountain and "r_o" is the precipitation at the base of the mountain. Using this formula, the average annual precipitation at the towns of Hollis, Craig and Calder allows us to estimate

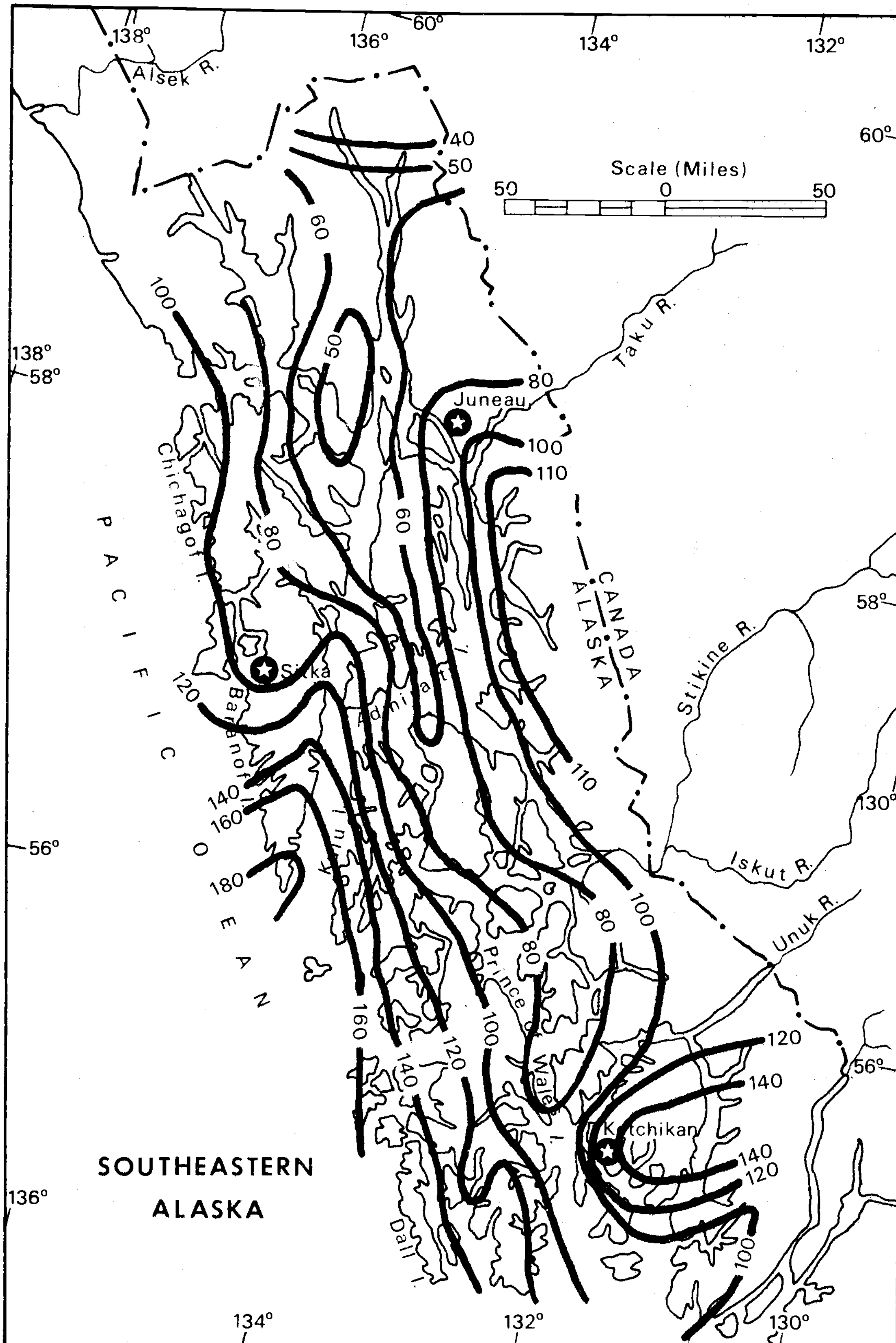


Figure 5. Average annual precipitation.

the precipitation on Harris Peak, the Klawock Mountains and Virginia Mountain respectively. Between 2000 and 3000 feet elevation on Harris Peak precipitation varies from 247.58 to 319.58 inches; the 2000 to 3000 foot level on Virginia Mountain receives 256.26 to 328.26 inches; and the 3000 to 4000 foot level on the Klawock Mountains provides estimate values of 322.26 to 394.26 inches. Wind patterns and rain-shadow effects will cause local variations in rainfall as well as orographic effects.

No snow accumulation data are available for sites above sea level in Southeast Alaska. Figure 6 shows mean dates of first snowfall, and last snow cover dates are plotted on Figure 7. The first permanent snow course was established during the summer of 1972 at Harriet Hunt Lake near Ketchikan.

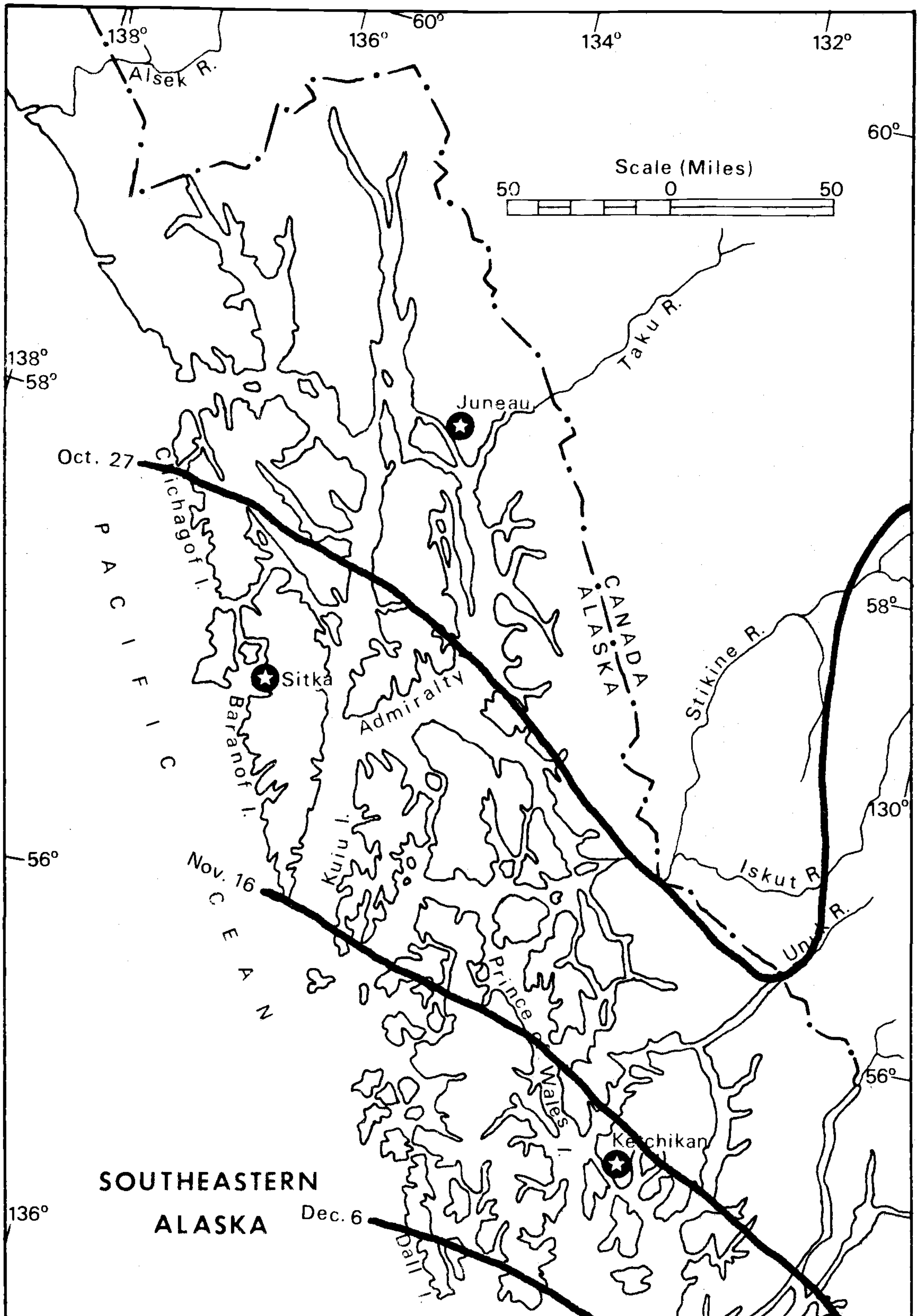


Figure 6. Mean date of first snow cover (≥1 in.).

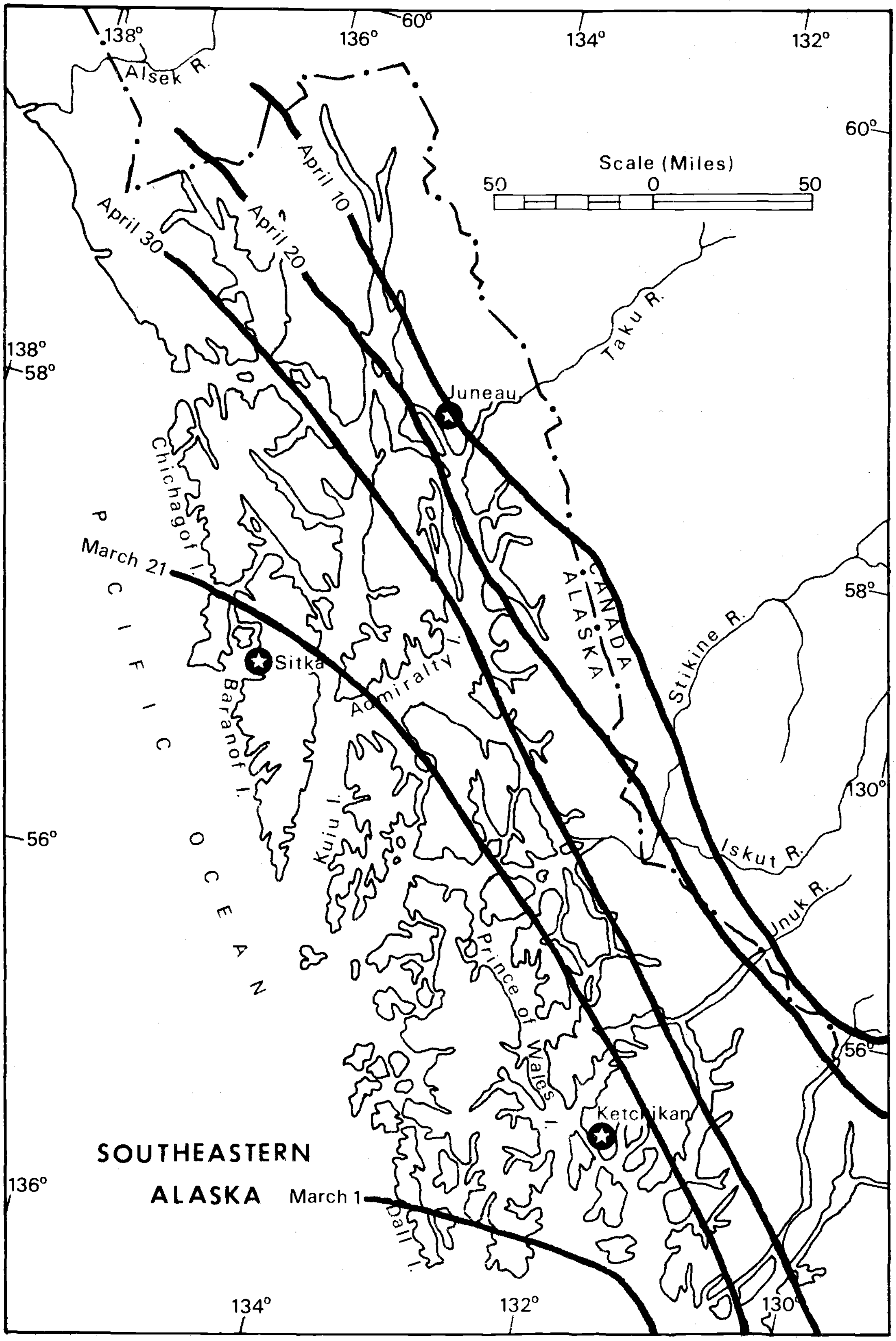


Figure 7. Mean date of last snow cover (≥ 1 in.).

DESCRIPTION OF THE VEGETATION

No systematic study of the vegetation of subalpine or alpine sites in Southeast Alaska has previously been made. General descriptions of alpine heath vegetation found in the Panhandle have been made by Anderson (1916) and Heusser (1954). More recent studies by Calder and Taylor (1968), Archer (1964), Krajina (1965), Peterson (1965), Brooke (1965) and Brooke, Peterson and Krajina (1970) describe alpine and subalpine vegetation patterns in British Columbia. Douglas (1971a) has described subalpine plant communities located in the North Cascade Mountains of Washington. Krajina, Peterson, Brooke and Archer concentrated on the vegetation of southwestern British Columbia in the Garibaldi Park area. Their sites are located inland and are 550 miles south of Prince of Wales Island in Southeast Alaska. Significant vegetation differences do occur between the Prince of Wales Island vegetation and these other subalpine areas. Much of Calder and Taylor's (1968) description of montane (alpine) communities may be directly applied to vegetation found on Prince of Wales Island. Again, significant differences in species composition are noted, although the Queen Charlotte Islands are separated from Prince of Wales Island by only 67 miles of open ocean.

The subalpine and alpine ecosystems on Prince of Wales Island are included in Krajina's (1965) Pacific Coast Subalpine Forest

Region and Alpine Tundra Region respectively. These correspond to formations (sensu Clements, 1928 and Weaver and Clements, 1929) in that regional climate exerts the broadest controls on vegetation types and species composition. The Mountain Hemlock Zone of the Pacific Coast Subalpine Forest Region is characterized by two fairly distinct subzones: the subalpine forest subzone and the subalpine parkland subzone. The Alpine Zone has been subdivided according to varied zonal concepts.

A detailed look at vegetation units prompted adoption of the concept of a functional and factorial approach to the study of vegetation patterns and dynamics as described by Major (1951). According to this concept, one attempts to isolate independent factors (i. e. climate, parent material, relief, organisms and time) from highly complex and variable factors (i. e. soil) which result from interactions between the various independent factors.

In this paper no formal phytosociological units are constructed. Plant communities in the alpine-subalpine zones of Southeast Alaska are difficult to define because many species occur from mountain summits to sea level areas.

Subalpine Vegetation

On Prince of Wales Island, the lower limits of the subalpine zone occur at approximately 1800 feet elevation on south-facing, moderate slopes. The zone's upper limits extend to about 2700 to 2800 feet; however, zone boundaries vary due to frequency of snow-slides, slope gradient, and exposure. On all north slopes and steep south slopes the lower limits of the zone may descend to 1600 or 1400 feet and the upper boundary may reach as high as 2000 feet. Zone limits are perhaps more accurately defined according to specific characteristics of the zonal vegetation. Accordingly, the lower limit of the subalpine zone may be defined as being the point at which mountain hemlock (Tsuga mertensiana) becomes the dominant tree species. The upper limit may be established as the elevation at which tree species occur with a single main trunk and are at least six feet tall. The true alpine zone is the area located above this boundary.

Where the subalpine and alpine zones meet, the floras of the two zones intermingle. This area is called the subalpine parkland subzone, or alpine-subalpine ecotone. In places, the area of overlap between the two zones is very wide; therefore, it seems best to treat the area as a subzone of the subalpine zone rather than an ecotone.

Deep snow accumulations and resultant late snow-melts are major environmental characteristics of the subalpine mountain hemlock zone. In 1972 snow had completely melted by July 10 up to 1400 feet elevation on Harris Peak and Granite Mountain, while the entire subalpine zone remained snow-covered. By July 15 the lower subzone was snow-free except for concave areas and north slopes. The upper subzone was still snowbound but snow was rapidly melting around tree groups. The insulating effect of tree groups is important and has been described by many workers. By July 21 open areas in the upper subzone remained covered by one to two feet of snow. These habitats are the last areas to become snow-free; by July 26 they were completely free of snow.

The vegetation of the entire subalpine zone is characterized by the following species:

Tsuga mertensiana
Cladothamnus pyrolaeflorus
Rubus pedatus
Abies lasiocarpa

Differentiating species for the two subzones are listed below. Many of these species are seen at lower and higher elevations, but when they are growing together with the character species listed above they typify the subalpine zone.

Differentiating Species

Lower Subzone	Upper Subzone
Tsuga heterophylla	*Cassiope mertensiana*
Menziesia ferruginea	*Cassiope stelleriana*
Vaccinium alaskense	*Phyllodoce glanduliflora*
Listera cordata	*Luetkea pectinata*
Streptopus roseus ssp. *curvipes*	*Vaccinium caespitosum*

No communities were sampled in the subalpine zone. However, Peterson (1965) recognizes some 14 associations (phytocoenoses) in southwestern British Columbia.

Altitudinal effects on species composition are quite evident. In the lower subzone, mountain hemlock may be associated with western hemlock and Sitka spruce. Here the shrub and herb layers are predominantly Menziesia ferruginea, Vaccinium ovalifolium, Vaccinium alaskense, Rubus pedatus, Streptopus roseus ssp. curvipes, Listera cordata, Tiarella trifoliata and Cornus unalaschensis. At 1900 to 2000 feet elevation the forest takes on a slightly more open appearance. Cassiope mertensiana, Cassiope stelleriana, Coptis aspleniifolia, Vaccinium caespitosum and Carex nigricans are found in small openings surrounded by Caltha biflora, Fauria crista-galli and Erigeron peregrinus. Adjacent to these small openings are typical forest and understory vegetation. With increasing elevation, the shrubby ericaceous species (Vaccinium caespitosum, Cassiope stelleriana and Cassiope mertensiana) and Fauria crista-galli become the dominant ground cover in the open parks. These parks also increase in area. With increasing elevation, Vaccinium ovalifolium, Vaccinium alaskense and Menziesia ferruginea become restricted to the area under mountain hemlock. Rubus pedatus, Coptis aspleniifolia and Streptopus roseus ssp. curvipes are rare (occurring in 15 percent of the microplots sampled); Listera cordata and Tiarella trifoliata are very rare (occurring in <10 percent of the microplots sampled). Ponds are common features on flat ridgetops and benches above 2000 feet. Luetkea pectinata is very abundant around the edges of these ponds and on moist slopes.

The area above 2400 feet is called the upper parkland subzone. This subzone is composed of open heaths of Phyllodoce glanduliflora, Cassiope mertensiana, Cassiope stelleriana, Vaccinium caespitosum, Luetkea pectinata and Cornus unalaschensis; bogs and drainage channels bearing Fauria crista-galli, Caltha biflora and Carex nigricans; cliffs with Saxifraga ferruginea, Hieracium triste and Erigeron peregrinus; and copses of mountain hemlock with a scattered understory of Cassiope mertensiana, Rubus pedatus, Streptopus roseus ssp. curvipes, Coptis aspleniifolia and Cassiope stelleriana.

Timberline

No continuous line marks the upper limit of forest tree growth in northwest North America. Upper subalpine tree cover is patchy where snow duration prohibits seedling establishment. These open areas become larger with increasing elevation and finally coalesce, leaving individual trees in isolated spots where growing conditions are favorable. Northwestern North American forests are also characterized by this general lack of a true krummholz growth; deep snow is more of a limiting factor than low temperatures or high winds (Faegri, 1966). Snow cover most greatly influences seedling establishment and early growth. Once established seedlings attain certain heights, their growth is not prevented by extended snow cover. As a result, subalpine heath vegetation is often surrounded by normal, well-developed trees.

Soils undoubtedly have a great effect upon the position of timberline. Raup (1951, p. 106) states:

> ...it is possible to interpret the timber line as a zone of transition from relatively stable to relatively unstable soils, and to look upon climate as having an indirect effect through its influence upon congeliturbation.

On Prince of Wales Island, low and middle alpine belts are not greatly affected by frost action, while in upper alpine areas frost action is severe. Seedlings and small prostrate individuals of Sitka spruce, mountain hemlock and subalpine fir were frequently encountered in low and middle alpine heath vegetation, but no individuals were observed in the upper alpine areas. This indicates that severe frost action may be a limiting factor for seedling establishment and growth in the upper alpine belt.

Bamburg and Major (1968) plotted the elevation limits of timberline in western North America. In general, with increasing latitude there is a gradual lowering in the elevation at which timberline occurs. On Prince of Wales Island timberline, marking the lower boundary of the alpine zone, is generally at 2800 feet on gentle, south-facing slopes.

Alpine Vegetation

Terrain in the alpine zone is characteristically less steep than in the subalpine zone. Ice action rounded ridgetops below 3000 feet and slopes are gentler. However, the number of rock outcrops is significantly greater in the alpine zone.

Dahl (1956) divided the alpine zone into three "belts." The low alpine belt is composed predominantly of lichen heaths associated with ericaceous plants and a few shrubs. Bogs are also present. In the mid-alpine belt heaths cover large areas but bogs are entirely absent. Above this region is the high alpine belt where stonefields and soils greatly affected by solifluction dominate vegetation patterns.

On Prince of Wales Island the low alpine belt is characterized by Trientalis europaea, Carex nigricans and Fauria crista-galli. The middle alpine belt is identified by the absence of these character species and bog habitats. High alpine vegetation characteristically affected by cryopedogenic processes are observed only on the highest peaks of the Klawock Mountains. This scheme of subdivision in the alpine zone reflects environmental and physical factors which tend to override competition and community development in the alpine zone (Savile, 1960).

No two locations within the alpine areas of Prince of Wales Island have exactly the same species composition. Many species common at lower elevations are also found in alpine sites and, conversely, many alpine species also occur at lower elevations. These phenomena have been observed and described by Dahl (1951), Hultén (1937b), Raup (1934, 1947) and Calder and Taylor (1968). Dahl (1951) supports the theory that the distributions of many alpine plant species are controlled to a large degree by maximum summer temperatures. In plotting the distributions of many species occurring in Scandinavia, Dahl found a very close correlation between ranges and various isotherms of average maximum summer temperatures. He suggested that by plotting average maximum summer temperatures for any region one should be able to locate areas where alpine species will grow at or near sea level. As several species which he studied are also found in Southeast Alaska, their possible limiting temperatures are given in Table 2 (from Dahl, 1951, p. 33, 34, 36).

Mild coastal areas provide cool summers in many localities, and would therefore be places where some species could have wide altitudinal distributions. This temperature factor appears to be a dominant one in the growth of vegetation in the Alexander Archipelago. Bogs occur in step-like fashion from sea level to subalpine areas and provide suitable habitats for several alpine species at low elevations. Species on Prince of Wales Island which inhabit low elevation bogs are: Vaccinium caespitosum, Cornus unalaschensis, Vaccinium uliginosum, Empetrum nigrum, Coptis aspleniifolia, Dodecatheon jeffreyi and

Table 2. Limiting summer maximum temperatures for selected circumpolar species.

Species	°C	°F
Cryptogramma crispa	27	80.6
Woodsia glabella	27	80.6
Polystichum lonchitis	27	80.6
Phleum commutatum	29	84.2
Vahlodea atropurpurea	26	78.8
Trisetum spicatum	24-25	75.2-77.0
Poa arctica	23	73.4
Luzula arcuata	25	77.0
Luzula parviflora	26-27	78.8-80.6
Salix reticulata	26	78.8
Oxyria digyna	26	78.8
Arenaria rubella	22	71.6
Silene acaulis	25	77.0
Thalictrum alpinum	27	80.6
Draba lactea	22	71.6
Cardamine bellidifolia	26	78.8
Sedum rosea	25	77.0
Saxifraga nivalis	27	80.6
Saxifraga oppositifolia	26	78.8
Saxifraga rivularis	25	77.0
Viola biflora	28	82.4
Loiseleuria procumbens	27	80.6
Pedicularis oederi	24	75.2
Erigeron humilis	23	73.4
Artemisia arctica	22	71.6

Trientalis europaea. Stream channels and snowslide paths also provide lower elevation habitats for alpine species. It appears that disseminules, carried down these channels and paths by meltwater, snow and/or wind, eventually germinate and grow in suitable localities. Species utilizing this mode of dispersal to descend slopes on Prince of Wales Island include: Romanzoffia sitchensis, Saxifraga mertensiana, Ribes bracteosum, Ranunculus occidentalis ssp. occidentalis, Heuchera glabra, Aquilegia formosa, Claytonia sibirica, Tiarella trifoliata, Saxifraga punctatus ssp. charlottae, Parnassia fimbriata, Rubus spectabilis, Cardamine umbellata, Leptarrhena pyrolaefolia, Geranium erianthum, Oxyria digyna, Aconitum delphinifolium, Luzula parviflora, Angelica lucida, Lupinus nootkatensis, Caltha biflora, Agrostis borealis, Veratrum viride ssp. eschscholtzii and Fritillaria camschatcensis. In a few cases the reverse situation seems to have occurred. Species which are very abundant at lower elevations have been discovered growing atop alpine peaks. These cases indicate fortuitous distribution by various other means (i. e. wind and birds). For example, Eriophorum angustifolium was observed in one alpine bog at 3100 feet on Baird Peak north of Granite Mountain. Its plumed ackenes are usually dispersed by wind. On the top of Harris Peak (3392 feet) several flowering individuals of Rubus chamaemorus were found. Rubus chamaemorus is a very common bog plant of lower elevations. Many species of birds utilize its fruits as food, and it seems likely that they served as the dispersal mechanism for this small colony of individuals. Approximately eight individuals were observed, and all were staminate. These cases indicate that the assumed downslope dissemination of alpine plants to subalpine areas is not necessarily correct for every species. Several of these alpine species are extremely abundant in various habitats at lower elevations as well as in alpine sites. These species are: *Vaccinium caespitosum*, *Cornus unalaschensis*, *Claytonia sibirica*, *Tiarella trifoliata*, *Vaccinium uliginosum*, *Empetrum nigrum*, *Rubus spectabilis*, *Coptis aspleniifolia*, *Dodecatheon jeffreyi*, *Trientalis europaea*, *Caltha biflora* and *Fritillaria camschatcensis*.

Calcareous and Noncalcareous Substrates

In Southeast Alaska plant diversity can be related to types of bedrock available for soil development. As Major (1951, p. 343) states, "... only the parent material of the soil is independent of the other landscape or ecosystem properties which determine both vegetation and soils." In this study on Prince of Wales Island, differentiation is made between calcareous and noncalcareous parent materials.

Noncalcareous parent materials include the various greywackes, argillites, and dioritic intrusives discussed earlier. Closer analysis of the noncalcareous parent materials will undoubtedly bring to light minor vegetation differences not noted here. For example, Heusser

(1954), at the Taku River, noted that plants growing on diorite intrusives were not the same as those growing in granodioritic materials. He discussed several reasons for the difference. Calcareous parent materials include limestone, highly calcified greywacke and local areas where calcite is present in sufficient quantities to support calcareous vegetation.

In a study of the low elevation forest-bog complex in Southeast Alaska Neiland (1971, p. 6) states:

> A surface feature possibly related to important vegetational variations is the presence of extensive areas of limestone near study areas on Coronation Island, near Craig and on Admiralty Island, as compared with an almost complete lack of even small amounts of surface limestone near the other areas included in the study.

The section of Prince of Wales Island north of Whale Pass contains many limestone areas including caverns, sink holes, and marble deposits (at Calder). Virginia Mountain and Mt. Calder are composed of massive Silurian limestone. In the Klawock Mountains and on Harris Ridge, local spots contain calcareous lenses and highly calcified greywacke.

No quantitative measurements of calcium carbonate content at these sites were made. However, a relative test using 1N HCl was conducted on various samples. The results are presented in Table 3. Tables 4 through 6 are lists of species collected at the sites from which soil samples were taken and tested. Species found on all

Table 3. Bedrock analysis of calcium carbonate content.

Sample #	Site	Parent Material	Reaction
11	Virginia Mountain, 2700'el. on top of peak	Limestone	Very strong, immediate
6	Ridge just west of Harris Peak	Greywacke/ Calcareous lenses	No reaction / Strong
17	Ridgetop one mile east of Harris Peak	Greywacke/ Calcareous lenses	No reaction/ Strong
31	Klawock Mountains, south ridge	Highly calcified greywacke	Very strong, immediate
23	Ledge just east of Harris Peak	Calcified greywacke	Strong, slight delay
47	Knob one half mile west of Harris Peak	Calcified greywacke	Strong, slight delay
1261	Top of Granite Mountain	Diorite	No reaction
1231	Top of Harris Peak	Diorite	No reaction
24	Ridgetop, south ridge of Klawock Mountains	Diorite	No reaction

Table 4. Species collected at bedrock sample site 11.

Abies lasiocarpa	Dryas drummondii	Rubus pedatus
Achillea millefolium	Empetrum nigrum	Rubus spectabilis
Aconitum delphinifolium	Erigeron humilis	Salix arctica
Actaea rubra	Erigeron peregrinus	Salix reticulata
Adiantum pedatum	Festuca brachyphylla	Salix stolonifera
Androsace chamaejasme	Fritillaria camschatcensis	Saxifraga caespitosa
Anemone narcissiflora	Geum calthifolium	Saxifraga lyattii
Anemone parviflora	Habenaria dilatata	Saxifraga oppositifolia
Angelica lucida	Heracleum lanatum	Saxifraga punctata ssp. pacifica
Aquilegia formosa	Heuchera glabra	Sedum rosea
Arabis lyrata	Leptarrhena pyrolaefolia	Senecio lugens
Arctostaphylos alpina	Listera cordata	Senecio triangularis
Arenaria rubella	Lloydia serotina	Silene acaulis
Arnica latifolia	Luetkea pectinata	Solidago multiradiata
Artemisia arctica	Lupinus nootkatensis	Streptopus roseus
Aruncus sylvester	Lycopodium selago ssp. miyoshianum	Thalictrum alpinum
Asplenium viride	Lycopodium selago ssp. selago	Tiarella trifoliata
Caltha biflora	Mitella pentandra	Tofieldia coccinea
Cardamine umbellata	Oxyria digyna	Trisetum spicatum
Carex scirpoidea	Oxytropis campestris	Tsuga heterophylla
Cassiope mertensiana	Parnassia fimbriata	Tsuga mertensiana
Cassiope stelleriana	Pedicularis oederi	Vaccinium alaskense
Castilleja parviflora	Petasites nivalis	Vaccinium caespitosum
Cerastium beeringianum	Phyllodoce glanduliflora	Vaccinium ovalifolium
Chamaecyparis nootkatensis	Picea sitchensis	Vaccinium uliginosum
Cladothamnus pyrolaeflorus	Pinguicula vulgaris	Valeriana sitchensis
Coptis aspleniifolia	Poa alpina	Veratrum eschscholtzii
Cornus unalaschensis	Polygonum viviparum	Viola biflora
Dodecatheon jeffreyi	Polysticum lonchitis	Viola glabella
Dodecatheon pulchellum	Potentilla villosa	Viola langsdorffii
Draba lactea	Ranunculus eschscholtzii	Woodsia glabella
Draba lonchocarpa	Ranunculus occidentalis	

Table 5. Species collected at bedrock sample sites 6, 17, 23 and 47.

Abies lasiocarpa
Cystopteris fragilis
Draba lonchocarpa
Epilobium alpinum
Erigeron humilis
Festuca brachyphylla
Lloydia serotina
Poa alpina
Poa macrocalyx
Polygonum viviparum
Polystichum lonchitis
Potentilla villosa
Salix arctica
Salix stolonifera
Saxifraga adscendens
Saxifraga nivalis
Sedum rosea
Silene acaulis
Thalictrum alpinum
Trisetum spicatum
Woodsia ilvensis

Table 6. Species collected at bedrock sample site 31.

Androsace chamaejasme
Antennaria umbrinella
Cerastium beeringianum
Cystopteris fragilis
Draba lonchocarpa
Epilobium alpinum
Erigeron humilis
Festuca brachyphylla
Lloydia serotina
Polygonum viviparum
Petasites nivalis
Potentilla villosa
Salix reticulata
Saxifraga adscendens
Saxifraga oppositifolia
Saxifraga rivularis
Silene acaulis
Solidago multiradiata
Taraxacum kamschaticum
Thalictrum alpinum
Trisetum spicatum
Viola biflora

noncalcareous sites, including the sites of samples 1261, 1231 and 24, are listed in Table 7.

Insofar as is presently known, several species appear to grow only on soils derived from calcareous parent material in the alpine of Prince of Wales Island. These "calcicolous" species are listed in Table 8. A somewhat heterogeneous group of species is found on both calcareous and noncalcareous soils. These species are listed in Table 9.

Many areas of the world support interesting calcareous floras. Some countries or states containing widespread calcareous substrates are Great Britain (Salisbury, 1952; Louseley, 1950; Pigott and Walters, 1954), Yugoslavia (Grebenshchikov, 1960), Georgian S. S. R. (Sokhadze and Sokhadze, 1960), Montana, U. S. A. (Bamberg and Major, 1968), Norway (Gjaerevoll, 1950; Dahl, 1956), and California, U. S. A. (Mooney et al., 1962). Interesting pockets of limestone vegetation collected from Montana, U. S. A. (Bamberg and Pemble, 1968), California, U. S. A. (Major and Bamberg, 1963), Norway (Coombe and White, 1951) and the Queen Charlotte Islands, Canada (Calder and Taylor, 1968) have been studied and described.

Factors that operate in the calcareous alpine region of Prince of Wales Island, to produce a vegetation type markedly different from that on acid substrates, are many and varied. The effects of limestone upon vegetation are not so marked at lower elevations as in the

Table 7. Species found on noncalcareous sites.

Aconitum delphinifolium	Equisetum arvense	Ranunculus eschscholtzii
Actaea rubra	Erigeron peregrinus	Ranunculus occidentalis
Agrostis aequivalis	Eriophorum angustifolium	Ribes bracteosum
Agrostis borealis	Fauria crista-galli	Romanzoffia sitchensis
Agrostis thurberiana	Festuca brachyphylla	Rubus chamaemorus
Anemone narcissiflora	Fritillaria camschatcensis	Rubus pedatus
Angelica lucida	Gentiana platypetala	Rubus spectabilis
Aquilegia formosa	Geranium erianthum	Sanguisorba canadensis
Arnica latifolia	Geum calthifolium	Saxifraga ferruginea
Artemisia arctica	Habenaria saccata	Saxifraga lyallii
Aruncus sylvester	Heracleum lanatum	Saxifraga mertensiana
Asplenium viride	Heuchera glabra	Saxifraga punctata ssp. charlottae
Blechnum spicant	Hieracium triste	Saxifraga punctata ssp. pacifica
Caltha biflora	Hierochloe alpina	Saxifraga punctata ssp. pacifica X charlottae
Caltha leptosepala	Leptarrhena pyrolaefolia	Scirpus caespitosus
Campanula alaskana	Loiseleuria procumbens	Senecio cymbalarioides
Cardamine bellidifolia	Luetkea pectinata	Senecio triangularis
Cardamine umbellata	Lupinus nootkatensis	Sorbus sitchensis
Carex circinata	Luzula arcuata	Stellaria calycantha
Carex macrochaeta	Luzula parviflora	Streptopus roseus
Carex nigricans	Lycopodium alpinum	Thelypteris phegopteris
Carex stylosa	Lycopodium sabinaefolium	Tiarella trifoliata
Cassiope lycopodioides	Lycopodium selago ssp. miyoshianum	Tofieldia glutinosa
Cassiope mertensiana	Lycopodium selago ssp. selago	Trientalis europaea
Cassiope stelleriana	Menziesia ferruginea	Trisetum spicatum
Castilleja miniata	Osmorhiza purpurea	Tsuga heterophylla
Castilleja miniata X unalaschensis	Oxyria digyna	Tsuga mertensiana
Castilleja parviflora	Parnassia fimbriata	Vaccinium alaskense
Castilleja unalaschensis	Pedicularis lanata	Vaccinium caespitosum
Chamaecyparis nootkatensis	Pedicularis oederi	Vaccinium ovalifolium
Cladothamnus pyrolaeflorus	Pedicularis ornithorhyncha	Vaccinium uliginosum
Claytonia sibirica	Pedicularis verticillata	Vahlodea atropurpurea
Coptis aspleniifolia	Phleum alpinum	Valeriana sitchensis
Cornus unalaschensis	Phyllodoce glanduliflora	Veratrum eschscholtzii
Cryptogramma crispa	Picea sitchensis	Veronica wormskjoldii
Cystopteris fragilis	Pinguicula vulgaris	Viola glabella
Dodecatheon jeffreyi	Poa arctica	Viola langsdorffii
Dryopteris austriaca	Polygonum viviparum	
Empetrum nigrum	Ranunculus cooleyae	
Epilobium latifolium		

Table 8. Calcicolous species.

Abies lasiocarpa
Androsace chamaejasme
Anemone parviflora
Antennaria umbrinella
Arctostaphylos alpina
Arenaria rubella
Carex scirpoidea
Cerastium beeringianum
Draba lactea
Draba lonchocarpa
Dryas drummondii
Erigeron humilis
Lloydia serotina
Oxytropis campestris
Poa alpina
Poa macrocalyx
Polystichum lonchitis
Potentilla villosa
Salix arctica
Salix reticulata
Salix stolonifera
Saxifraga adscendens
Saxifraga caespitosa
Saxifraga nivalis
Saxifraga oppositifolia
Saxifraga rivularis
Sedum rosea
Senecio lugens
Silene acaulis
Solidago multiradiata
Taraxacum kamschaticum
Thalictrum alpinum
Tofieldia coccinea
Viola biflora
Woodsia glabella
Woodsia ilvensis

Table 9. Species found on both calcareous and noncalcareous soils.

Achillea millefolium	Lupinus nootkatensis
Aconitum delphinifolium	Lycopodium selago ssp. miyoshianum
Actaea rubra	Lycopodium selago ssp. selago
Adiantum pedatum	Mitella pentandra
Anemone narcissiflora	Oxyria digyna
Angelica lucida	Parnassia fimbriata
Aquilegia formosa	Pedicularis oederi
Arabis lyrata	Petasites nivalis
Arnica latifolia	Phyllodoce glanduliflora
Artemisia arctica	Picea sitchensis
Aruncus sylvester	Polygonum viviparum
Asplenium viride	Ranunculus eschscholtzii
Caltha biflora	Ranunculus occidentalis
Cardamine umbellata	Rubus pedatus
Cassiope mertensiana	Rubus spectabilis
Cassiope stelleriana	Saxifraga lyallii
Castilleja parviflora	Saxifraga punctata ssp. pacifica
Chamaecyparis nootkatensis	Senecio triangularis
Cladothamnus pyrolaeflorus	Streptopus roseus
Coptis aspleniifolia	Tiarella trifoliata
Cornus unalaschensis	Trisetum spicatum
Cystopteris fragilis	Tsuga heterophylla
Dodecatheon jeffreyi	Tsuga mertensiana
Dodecatheon pulchellum	Vaccinium alaskense
Empetrum nigrum	Vaccinium caespitosum
Erigeron peregrinus	Vaccinium ovalifolium
Festuca brachyphylla	Vaccinium uliginosum
Fritillaria camschatcensis	Valeriana sitchensis
Geum calthifolium	Veratrum eschscholtzii
Habenaria dilatata	Viola glabella
Heracleum lanatum	Viola langsdorffii
Heuchera glabra	
Leptarrhena pyrolaefolia	
Listera cordata	
Luetkea pectinata	

alpine zone. In the alpine zone extensive areas of moderate slope on Virginia Mountain are devoid of vegetation except for isolated individuals of Androsace chamaejasme ssp. lehmanniana and Saxifraga oppositifolia. Even during July, when snowmelt is greatest, very few meltwater channels are observed over the limestone, and those that do exist extend only a few meters along the ground surface and then go underground. Harris Peak and Granite Mountain possess great numbers of snowdrifts, each having its own drainage channels and pools. These pools often appear as small alpine lakes ten to fifteen meters wide. In contrast, on Virginia Mountain no pools were observed in the alpine zone although numerous concave surfaces were available to impound water. Consequent summer water stress on limestone substrates may therefore be a factor in restricting vegetation growth to those species that are able to withstand lengthy periods of less abundant soil moisture. Such periods do in fact occur in a region that receives 250 to 390 inches of precipitation per year. In the summer of 1971, on northern Prince of Wales Island, no precipitation was received between July 5 and August 16. Temperatures during this time attained a maximum of 94°F at sea level (84.3°F at 3000 feet elevation). In 1972 Weather Bureau records show a period of ten days on northern Prince of Wales Island with no precipitation and a maximum temperature of 91°F. Although they are generally cool and moist throughout the year, alpine limestone sites in Southeast Alaska provide what may be termed a seasonally xeric habitat with soil moisture characteristics more like continental areas than coastal areas. A significant number of the species growing on Prince of Wales Island limestone are "continental species" occurring as disjuncts in Southeast Alaska. These species will be discussed later, in the phytogeographical section.

Other possible reasons for the uniqueness of limestone floras are not clear and probably vary from species to species. Tansley (1917) has shown that competition may rule out the existence of certain species on calcareous soils. In Achillea atrata and Achillea moschata he demonstrated that in the absence of competition both species did well on calcareous soil, but when grown in competition Achillea atrata survived on the limestone and Achillea moschata did not. Butler (1918) indicates that certain calcicolous species of Iris are susceptible to severe attacks from the fungus Heterosporium gracile when grown in soil deficient in calcium. Along the same line of investigation, Rayner (1913) showed that Calluna mycorrhizae are adversely affected by certain bacteria only when grown on soils of a calcareous nature. Alkalinity is another important factor. High base content in soils can indirectly affect plants by neutralizing high acidity or allelopathic substances, thus favoring some species and selecting against others in that habitat. Humus is rapidly decomposed by increased soil organism activity on limestone while a lack of colloidal clays, combined with the flocculating effect of high Ca^{++} content and rapid water percolation, keeps only small amounts of nitrogen available for plant use at any one time.

Fernald (1907) further illustrated the complexity of the problem by showing that high calcium content depresses the potassium intake of some plants. Thus, some plants unable to grow on calcareous soils may demand a high potassium supply. In general, alkalinity and the xeric condition of alpine limestone would appear to be of major significance in determining what species will grow in such sites. Other factors, reported and unreported, are undoubtedly involved in selection as well.

Communities on Primitive Surfaces

On noncalcareous parent materials. Three general habitat types are recognized in the alpine area of Prince of Wales Island. These are alpine heath, alpine meadow, and alpine rock outcrops or other primitive surfaces.

Primitive surfaces occur as cliffs, bare ridgetops and knobs, walls of cirques and faces of peaks. Many north-facing slopes are abandoned cirques, the walls of which are steep cliffs that make collecting of plant specimens hazardous. These areas are all characterized by a lack of winter snow cover except in deep rock crevices, and no true community development exists. However, vegetation growing on rock outcrops is maintained by the active disintegration of the substrate which they colonize. Various allogenetic factors control the distribution of these species, including microclimate, composition of parent material, irregular topography and time. Table 10 is a list of the species found in this rocky habitat type on Prince of Wales Island. The most abundant species are Carex circinata, Cassiope lycopodioides, Festuca brachyphylla, Saxifraga ferruginea and Saxifraga mertensiana. Although all of the species listed as occurring on noncalcareous primitive surfaces may be found in crevices where little or no soil exists, several of them are more abundant where there has been a greater amount of soil development. These species include: Anemone narcissiflora ssp. alaskana, Polygonum viviparum, Actaea rubra ssp. arguta, Hieracium triste and Leptarrhena pyrolaefolia. Cardamine bellidifolia is found in rock crevices but its most luxuriant growth occurs in soil which has accumulated in fissures.

On calcareous parent materials. On limestone, primitive surfaces exist not only on cliffs, cirque walls and faces of peaks but also on numerous ridges and slopes of moderate to slight incline. These areas have apparently been bared by ice action (possibly restricted to higher levels during recent time). Crevices and broken level surfaces are marked by scattered groups of plants. The flora is quite diverse in these "rock garden" areas (Table 11). On Virginia Mountain extensive areas of this scattered vegetation occur, and of the total flora

Table 10. Species on noncalcareous primitive surfaces.

Actaea rubra
Agrostis borealis
Anemone narcissiflora
Asplenium viride
Campanula alaskana
Cardamine bellidifolia
Carex circinata
Carex macrochaeta
Cassiope lycopodioides
Cladothamnus pyrolaeflorus
Cryptogramma crispa
Cystopteris fragilis
Dryopteris austriaca
Epilobium latifolium
Erigeron peregrinus
Festuca brachyphylla
Heuchera glabra
Hieracium triste
Leptarrhena pyrolaefolia
Luetkea pectinata
Osmorhiza purpurea
Poa arctica
Polygonum viviparum
Ribes bracteosum
Romanzoffia sitchensis
Saxifraga ferruginea
Saxifraga lyallii
Saxifraga mertensiana
Saxifraga punctata ssp. pacifica
X charlottae
Vahlodea atropurpurea

Table 11. Species on calcareous primitive surfaces.

Abies lasiocarpa	Polygonum viviparum
Androsace chamaejasme	Polystichum lonchitis
Anemone parviflora	Potentilla villosa
Antennaria umbrinella	Ranunculus eschscholtzii
Aquilegia formosa	Salix arctica
Arabis lyrata	Saxifraga adscendens
Arenaria rubella	Saxifraga caespitosa
Asplenium viride	Saxifraga nivalis
Cerastium beeringianum	Saxifraga oppositifolia
Cystopteris fragilis	Saxifraga rivularis
Draba lactea	Sedum rosea
Draba lonchocarpa	Senecio lugens
Dryas drummondii	Silene acaulis
Epilobium alpinum	Solidago multiradiata
Erigeron humilis	Taraxacum kamschaticum
Erigeron peregrinus	Thalictrum alpinum
Festuca brachyphylla	Thelypteris phegopteris
Lloydia serotina	Tofieldia coccinea
Pedicularis oederi	Trisetum spicatum
Petasites nivalis	Viola biflora
Pinguicula vulgaris	Woodsia glabella
Poa alpina	Woodsia ilvensis

listed in Table 11, only four species (Saxifraga nivalis, Woodsia ilvensis, Saxifraga adscendens ssp. oregonensis and Saxifraga rivularis var. flexuosa) were not found there.

On Harris Peak and the Klawock Mountains, small areas with local outcrops of limestone or other calcareous parent materials exist. One area on the south ridge of the Klawock Mountains supports a flora closely resembling the "rock garden" flora of Virginia Mountain. Highly calcareous greywacke outcrops on the ridge from 3000 to 3500 feet, creating a distinct pocket in the alpine heath and talus vegetations that surround it. The species present at this site include: Androsace chamaejasme ssp. lehmanniana, Taraxacum kamschaticum, Saxifraga rivularis var. flexuosa, Saxifraga adscendens ssp. oregonensis, Viola biflora ssp. charlottae, Pinguicula vulgaris ssp. macroceras, Erigeron humilis, Antennaria umbrinella, Solidago multiradiata, Polygonum viviparum, Saxifraga oppositifolia, Epilobium alpinum, Cerastium beeringianum, Thalictrum alpinum, Draba lonchocarpa ssp. kamtschatica, Potentilla villosa, Silene acaulis var. exscapa and Petasites nivalis. The parent materials on Harris Ridge (soil samples 6, 17, 23 and 47) were less calcareous in nature, and their outcropping was not as extensive as on the Klawock Mountains. The above mentioned species may have been more abundant on Harris Ridge immediately after recession of ice, but autogenetic succession has taken place where the calcareous greywackes occur and, as a result, the number of calcicolous species found here is greatly reduced. The species common to all four of the calcareous sites in the Klawock Mountains and Harris Ridge are: Abies lasiocarpa, Erigeron humilis, Draba lonchocarpa ssp. kamtschatica, Silene acaulis var. exscapa, Potentilla villosa, Polygonum viviparum, Poa alpina, Poa macrocalyx, Sedum rosea ssp. integrifolium, Lloydia serotina, Saxifraga adscendens ssp. oregonensis, Thalictrum alpinum and Polystichum lonchitis.

The most abundant species found on the limestone primitive surfaces of Prince of Wales Island is Silene acaulis. It commonly occurs in the crevices of sheer cliffs and on slopes comprised of loose, cobble-sized material which is exposed to severe wind action. This same pattern has been observed in Monte Maiella, Italy (Whitehead, 1951) and in Montana (Johnson and Billings, 1962). Cushions of Silene trap soil particles and provide a suitable seedbed for many species which develop into a densly populated ring of mature flowering individuals. In time, wind erosion destroys the Silene mat, leaving the ring isolated. The following species were observed in flower in these cushions on Prince of Wales Island: Erigeron humilis, Draba lonchocarpa ssp. kamtschatica, Sedum rosea ssp. integrifolia, Androsace chamaejasme ssp. lehmanniana, Trisetum spicatum and Festuca brachyphylla.

No true community development is apparent on these primitive calcareous substrates. The scattered vegetation is remarkably heterogeneous, however. Small patches of plants make up a mosaic of groups of species that appear to be distributed in a random pattern, since no consistent groupings could be detected.

Meadow Communities

On noncalcareous parent materials. Alpine meadow vegetation can be classed according to length of snow-free season, moisture conditions and successional status. In general, meadows occur on steep, well-drained slopes. Snowbeds in some sites do not melt until very late in the season, and some remain year-round. Various types of flush areas are classed with this vegetation type.

Meadows occurring on moderate to very steep slopes, talus slopes and blockfields are in various stages of stabilization. The total vegetation type is composed of the species listed in Table 12.

Snow depth and length of snow cover are the most important factors controlling community development in the alpine zone. Ranunculus cooleyae, Ranunculus eschscholtzii and Luetkea pectinata are able to survive and flower in areas with a very long snow cover. Species which flower despite a moderately long snow cover are: Anemone narcissiflora, Ranunculus occidentalis, Cardamine umbellata, Epilobium alpinum, Viola glabella, Dodecatheon jeffreyi,

Table 12. Meadow species on noncalcareous parent materials.

Aconitum delphinifolium
Alnus crispa
Anemone narcissiflora
Angelica lucida
Aquilegia formosa
Arnica latifolia
Artemisia arctica
Cardamine umbellata
Castilleja miniata
Castilleja miniata X unalaschensis
Castilleja parviflora
Castilleja unalaschensis
Claytonia sibirica
Cryptogramma crispa
Dodecatheon jeffreyi
Epilobium alpinum
Equisetum arvense
Erigeron peregrinus
Fritillaria camschatcensis
Gentiana platypetala
Geranium erianthum
Heracleum lanatum
Hieracium triste
Luetkea pectinata
Luzula parviflora
Menziesia ferruginea
Oxyria digyna
Parnassia fimbriata
Pedicularis oederi
Pinguicula vulgaris
Poa arctica
Polygonum viviparum
Ranunculus cooleyae
Ranunculus eschscholtzii
Ranunculus occidentalis
Rubus spectabilis
Saxifraga punctata ssp. pacifica
Saxifraga punctata ssp. pacifica X charlottae
Senecio triangularis
Stellaria calycantha
Thelypteris phegopteris
Vaccinium alaskense
Vaccinium ovalifolium
Vahlodea atropurpurea
Valeriana sitchensis
Veratrum viride
Veronica wormskjoldii
Viola glabella
Viola langsdorffii

Aconitum delphinifolium, Artemisia arctica, Luzula parviflora, Castilleja parviflora, Castilleja miniata, Castilleja unalaschensis, Gentiana platypetala, Angelica lucida, Erigeron peregrinus, Vahlodea atropurpurea and Heracleum lanatum. The other species all require a minimum snow-free period of 60 days. Early snow-melt areas may be snow-free by the second week in July (the average date of snow-melt may be even earlier, since the two years in which observations were made were years of heavy snowpack). Late in the season, when the majority of the snowbeds have melted, the pattern is quite striking. A central mass of yellow Ranunculus cooleyae is surrounded by a ring of white flowers of Anemone narcissiflora with the diverse colors of the lush, flowering meadow vegetation spreading farther up slope.

Meadows occur at high elevations and extremely low elevations on both north and south slopes. Their descent to low elevations (1400 to 1500 feet) is correlated with steep slopes, snowslide paths and cool air drainage patterns. On north slopes and protected cirque valleys grow dense thickets of Alnus crispa ssp. sinuata. This vegetation type is found in areas with very late snow-melt. Alder stems are bent prostrate by the weight of winter snows. As the snow melts, the stems stand progressively more erect but retain a characteristic bow downslope from ground level to three or four feet above ground.

Devil's Club (Oplopanax horridus) is commonly mixed with the alder at lower elevations. Ground cover in these meadows consists predominantly of Viola glabella and Rubus spectabilis. This community was not studied extensively due to the very late snow-melt occurring both years when field studies were conducted. The soils underlying this vegetation are mapped as St. Nicholas and Lithic Cryaquepts (Gass et al., 1968).

Lush herbaceous meadows occur on slopes generally unaffected by avalanching or landslides. North slope vegetation in these meadows is somewhat less diverse, due probably to a lack of summer insolation and the effect this lack has on soil moisture, soil temperatures, etc. Species restricted to meadows with a southern exposure include: Arnica latifolia, Castilleja miniata, Castilleja unalaschensis, Claytonia sibirica, Senecio triangularis, Valeriana sitchensis and Menziesia ferruginea.

On calcareous parent materials. Small meadows occur on calcareous substrates wherever sufficient soil has developed: on north slopes, at the bases of cliffs, on stabilized talus slopes and in wide, shallow caverns. Species making up these meadows are listed in Table 13.

Ground cover is not continuous as it is in noncalcareous meadows. Cover ranges from 50 to 75 percent, and these meadows only rarely have cover values of less than 30 percent.

Table 13. Meadow species on calcareous parent materials.

Achillea millefolium
Actaea arguta
Androsace chamaejasme
Angelica lucida
Anemone narcissiflora
Anemone parviflora
Aquilegia formosa
Arnica diversifolia
Arnica latifolia
Artemisia arctica
Aruncus sylvester
Cardamine umbellata
Carex scirpoidea
Castilleja parviflora
Dodecatheon pulchellum
Epilobium alpinum
Erigeron peregrinus
Habenaria dilatata
Heracleum lanatum
Lloydia serotina
Oxyria digyna
Oxytropis campestris
Parnassia fimbriata
Pedicularis oederi
Pinguicula vulgaris
Polystichum lonchitis
Ranunculus occidentalis
Saxifraga caespitosa
Saxifraga punctata ssp. pacifica
Senecio triangularis
Thalictrum alpinum
Tofieldia coccinea
Valeriana sitchensis
Viola biflora
Viola langsdorffii

Heath Communities

On noncalcareous parent materials. Heath communities are the dominant vegetation type in the alpine zone of Southeast Alaska. Community composition varies due to snow cover and summer moisture regimes. Species making up the alpine heath vegetation on Prince of Wales Island are listed in Table 14.

Ridgetops which are blown free of snow during most of the winter maintain a vegetation cover of Empetrum nigrum, Loiseleuria procumbens, Vaccinium caespitosum, Vaccinium uliginosum, Geum calthifolium, Cornus unalaschensis, Lupinus nootkatensis, Pedicularis ornithorhyncha, Carex macrochaeta, Trientalis europaea, Luetkea pectinata, Lycopodium selago ssp. selago, Hierochloe alpina, Luzula arcuata ssp. unalaschcensis, Carex stylosa, Agrostis aequivalis and Agrostis thurberiana. Senecio cymbalarioides ssp. moresbiensis, Pedicularis lanata and Pedicularis verticillata are common elements in this community, but they are found only in the higher elevations of the Klawock Mountains. Scattered and stunted individuals of Picea sitchensis grow in this community. Once these individuals become established they can reproduce most vigorously by layering (Cooper, 1931b). Senecio cymbalarioides, Pedicularis lanata, Pedicularis verticillata and rupicolous species discussed earlier comprise the most frost-resistant group in the alpine zone on

Table 14. Heath species on noncalcareous parent materials.

Achillea millefolium	Lycopodium sabinaefolium
Agrostis aequivalis	Lycopodium selago ssp. selago
Blechnum spicant	Menziesia ferruginea
Caltha biflora	Pedicularis lanata
Caltha leptosepala	Pedicularis oederi
Carex macrochaeta	Pedicularis ornithorhyncha
Carex nigricans	Pedicularis verticillata
Carex stylosa	Phyllodoce glanduliflora
Cassiope mertensiana	Picea sitchensis
Cassiope stelleriana	Pinguicula vulgaris
Chamaecyparis nootkatensis	Poa arctica
Cladothamnus pyrolaeflorus	Rubus chamaemorus
Coptis aspleniifolia	Rubus pedatus
Cornus unalaschensis	Sanguisorba canadensis
Dodecatheon jeffreyi	Scirpus caespitosus
Empetrum nigrum	Senecio cymbalarioides
Erigeron peregrinus	Sorbus sitchensis
Eriophorum angustifolium	Streptopus roseus
Fauria crista-galli	Tiarella trifoliata
Geum calthifolium	Trientalis europaea
Hieracium triste	Tsuga mertensiana
Hierochloe alpina	Vaccinium alaskense
Leptarrhena pyrolaefolia	Vaccinium caespitosum
Listera cordata	Vaccinium ovalifolium
Loiseleuria procumbens	Vaccinium uliginosum
Luetkea pectinata	Valeriana sitchensis
Lupinus nootkatensis	Veratrum viride
Luzula arcuata	Veronica wormskjoldii
Lycopodium alpinum	

Prince of Wales Island. The sites they occupy are without snow cover and therefore are subjected to the full intensity of Alaskan alpine winters.

On south slopes and ridgetops up to 3100 feet small Sitka spruce (Picea sitchensis) and mountain hemlock (Tsuga mertensiana) grow in copses. Alaska yellow cedar (Chamaecyparis nootkatensis) is found on steep rocky slopes. Common understory species in these habitats are Cladothamnus pyrolaeflorus, Sanguisorba sitchensis ssp. grayi, Menziesia ferruginea and Veronica wormskjoldii. Less rocky sites where the two tree species occur also support a diverse herbaceous flora of common montane and subalpine species.

The "browning effect" (early snow-melt under trees) allows these plants to survive on south slopes under the protection of the tree groups. This environmental factor provides a much longer growing period for the areas immediately adjacent to any tree group. In early summer, when all areas except ridgetops and rock outcrops are covered with snow, melting around these tree groups has already taken place. The melting occurs rapidly around each tree, forming a snow-free area in the shape of a truncated, inverted cone which may be as deep as five or six feet. Here the following species begin their seasonal growth: Rubus pedatus, Vaccinium ovalifolium, Vaccinium alaskense, Streptopus roseus ssp. curvipes, Coptis aspleniifolia, Valeriana sitchensis, Tiarella trifoliata and Listera cordata.

Adjacent to this community and grading into it is another community with a slightly later snow release time. This community is made up of Cassiope mertensiana, Phyllodoce glanduliflora and Cassiope stelleriana.

Communities with late to very late snow cover survive in various habitats. Concave surfaces provide areas for snow accumulation and these sites possess distinct plant communities. Species occupying runnels are: Hieracium triste, Erigeron peregrinus, Veratrum viride ssp. eschscholtzii and Blechnum spicant. Alpine bogs, which are characteristic of the low alpine zone, contain various mosses (Worley, 1972) and the following vascular plants: Carex nigricans, Eriophorum angustifolium, Fauria crista-galli and Scirpus caespitosus. Meltwater channels are commonly bordered by Caltha biflora with Fauria crista-galli forming dense stands. Cassiope stelleriana and Trientalis europaea grow scattered at these sites. Surfaces and slopes that are flooded with meltwater support various groupings of species. These are made up of: Dodecatheon jeffreyi, Pinguicula vulgaris ssp. macroceras, Pedicularis oederi, Caltha biflora, Leptarrhena pyrolaefolia, Lycopodium alpinum, Lycopodium sabinaefolium ssp. sitchense, Poa arctica ssp. williamsii and, in the Klawock Mountains only, Caltha leptosepala.

The plant communities discussed in these heath habitat types form a mosaic in the alpine zone. Gradients of topography and length of snow cover provide a linear relationship between these plant communities. Empetrum heath is found on convex surfaces with no snow cover. Picea-Tsuga copses thrive on steep to moderate slopes with snow cover that provides insolation but melts early in the growing season. Phyllodoce-Cassiope heath grows on nearly level well-drained sites with moderate to late snow cover. The Carex nigricans community occurs on various concave surfaces which hold a snow cover until late in the year or even year-round. Work in Garibaldi Park in British Columbia (Archer, 1964) shows tree group communities (Abieto-Chamaecyparetum nootkatensis) with at least 110 snow-free days, the Phyllodoceto-Cassiopetum mertensianae with 100 snow-free days and Caricetum nigricantis with 60.

On calcareous parent materials. True alpine heath vegetation is extremely limited on calcareous parent materials. Since community development is slow in severe arctic-alpine climates, it is not surprising that the ericaceous heath species which dominate this vegetation type on acidic substrates are not present on calcareous substrates to any large extent. Calcareous soil development has proceeded far enough to provide suitable habitats for alpine heath only on some ridgetops in protected cirque basins and at much lower elevations. The species listed in Table 15 make up this vegetation type.

A unique association was seen on one ridgetop on Virginia Mountain. The vegetation forms a mat of at least 100 percent cover

Table 15. Heath species on calcareous parent materials.

Abies lasiocarpa
Achillea millefolium
Arctostaphylos alpina
Caltha biflora
Cassiope mertensiana
Cassiope stelleriana
Chamaecyparis nootkatensis
Coptis aspleniifolia
Cornus unalaschensis
Empetrum nigrum
Fauria crista-galli
Fritillaria camschatcensis
Geum calthifolium
Leptarrhena pyrolaefolia
Listera cordata
Luetkea pectinata
Lupinus nootkatensis
Lycopodium selago ssp. selago
Menziesia ferruginea
Mitella pentandra
Phyllodoce glanduliflora
Picea sitchensis
Rubus pedatus
Rubus spectabilis
Salix arctica
Salix reticulata
Salix stolonifera
Saxifraga lyallii
Streptopus roseus
Tiarella trifoliata
Tsuga mertensiana
Vaccinium alaskense
Vaccinium caespitosum
Vaccinium ovalifolium
Vaccinium uliginosum
Valeriana sitchensis
Veratrum viride

over a $20m^2$ area, which consists of Abies lasiocarpa, Tsuga mertensiana, Achillea millefolium, Fritillaria camschatcensis, Salix arctica, Salix reticulata ssp. reticulata, Salix stolonifera and Arctostaphylos alpina. This community may have survived from an association or community that was formerly more extensive. Gimingham, Pritchard and Cormack (1966) observed a similar relict plant association in Sweden. Heath vegetation more typical of Southeast Alaska's alpine regions is found on steep rocky slopes and ridgetops. The steep slopes support a vegetation dominated by Abies lasiocarpa, Tsuga mertensiana and Chamaecyparis nootkatensis, all in prostrate, semiprostrate or small shrub habits. Abies lasiocarpa forms a fringe around these copses, providing a striking blue-green outline to the tree copses on exposed slopes and ridges. Upright individuals grow up to 15 feet tall on more protected slopes and ridges. Characteristic herbaceous vegetation includes: Saxifraga lyallii ssp. hultenii, Luetkea pectinata, Vaccinium ovalifolium, Vaccinium alaskense, Mitella pentandra, Menziesia ferrűginea, Valeriana sitchensis, Streptopus roseus ssp. curvipes, Rubus pedatus, Listera cordata, Coptis aspleniifolia, Tiarella trifoliata and Rubus spectabilis.

At lower elevations this community type grades into the subalpine forest community. Calcareous subalpine forests on Prince of Wales and Dall Islands are often characterized by the presence of Abies lasiocarpa. The phytogeography of this species, with its insular disjunctions on these two islands of Southeast Alaska, has been more fully discussed by Harris (1965) and Worley and Jaques (in ed.).

Dry ridgetops, areas with moderate to late snow-melt, and very late snow-melt areas sustain floras similar to those found on noncalcareous substrates. Alpine heath vegetation is scarce on dry limestone ridgetops, but these ridgetops do support the following species: Achillea millefolium, Cassiope stelleriana, Geum calthifolium, Lycopodium selago ssp. selago, Cornus unalaschensis, Empetrum nigrum, Lupinus nootkatensis, Vaccinium caespitosum and Vaccinium uliginosum.

Late snow-melt areas adjacent to Abies-Tsuga-Chamaecyparis copses are dominated by Cassiope mertensiana associated with Phyllodoce glanduliflora, Cassiope stelleriana, Luetkea pectinata, Rubus pedatus and Vaccinium caespitosum. Late snow-melt areas and drainage channels in depressions and small sink holes are found only infrequently. The vegetation in these habitats consists of Fauria crista-galli, Caltha biflora, Luetkea pectinata and Veratrum viride ssp. eschscholtzii.

Snow appears to melt more rapidly on limestone alpine areas than on noncalcareous areas. During two field seasons snow was completely melted on north and south limestone slopes in the alpine zone, except for a few protected depressions, by July 15. However, by the same date in nearby noncalcareous alpine areas snowbeds were still abundant and providing substantial quantities of meltwater. No quantitative measurements were taken, but higher levels of heat absorption on limestone may contribute to the more xeric summer conditions found in the limestone areas of alpine sites.

Alpine Successional Patterns

In describing the alpine vegetation of Southeast Alaska, use of the temperate zone concept of "climatic climax" has severe limitations. Although not truly arctic in character, these alpine sites are generally physiographically unstable. Patterned ground phenomena in the form of solifluction lobes and terraces (Washburn, 1956) are common on gentle slopes above 3500 feet. Frost splitting is active in the alpine zone, sapping large boulders out of bedrock, forming cliffs, talus slopes and blockfields.

Various workers (Griggs, 1934; Raup, 1941, 1951; Sigafoos, 1951, 1952) have expressed serious doubts that arctic vegetation is ever formed from more than heterogeneous groups of pioneer species. Other workers have found little trouble in describing plant associations in arctic regions as static communities. In discussing alpine regions it is unfortunate that continual reference must be made to arctic studies. Historically, the two vegetation types (arctic and alpine) have been discussed together due to their apparent similarities in species composition. But physiologically, several arctic-alpine species have been shown to possess different biotypes, each adapted to its specific environment. Most notably, work with Thalictrum alpinum (Mooney and Johnson, 1965) and Oxyria digyna (Mooney and Billings, 1961) has shown this distinction. The differences between arctic and alpine environments are now beginning to be studied in detail.

Alpine successional schemes have been proposed by many workers. Where frost action is not the dominant controlling factor, these schemes are an accurate picture of the progression of succeeding vegetation types through time.

However, on sites where repeated severe disturbances are commonplace, no true "climax" vegetation is allowed to develop. In these cases the vegetation may be described as "permanently immature" (Hickman, 1968).

In alpine sites, topography appears to exert strong controls on what species can occur at a specific site. Talus slopes hold snowbeds which form in the same locations from year to year (Gjaerevoll, 1950). The plant communities discussed under meadow vegetation can all be viewed as topographic climax communities on these snowbed sites. However, there is a successional pattern which leads to these climax types when they are developed on noncalcareous and calcareous substrata.

On noncalcareous substrates, invasion of blockfields and talus slopes--both believed to be the result of rapid mechanical weathering of bedrock--begins with Luetkea pectinata, Ribes bracteosum, Osmorhiza purpurea, Rubus spectabilis, Oxyria digyna and Saxifraga punctata ssp. pacifica X charlottae. Once soil development occurs the various meadow communities can be formed on these sites.

Price (1969) described a process by which blockfields are vegetated. It involves the collapse of solifluction lobes upon the bare rock fragments of blockfields. This phenomenon was not observed by the author on Prince of Wales Island, but it may occur in the high alpine belt of the Klawock Mountains.

In early succession on calcareous sites different species are involved in vegetating the blockfields. On the limestone, seral species include: Polystichum lonchitis, Viola biflora ssp. charlottae, Oxyria digyna, Anemone parviflora, Adiantum pedatum var. aleuticum, Carex scirpoidea and Ranunculus eschscholtzii. When soil is developed the other meadow species become added to this assemblage, and several of the seral species, notably Viola biflora and Anemone parviflora, continue as abundant members of the meadow communities.

Areas with slopes more gentle than those supporting meadows produce vegetation which leads to the development of various heath communities. On noncalcareous sites no clear-cut scheme of succession is observed by the author. However, in Garibaldi Park, British Columbia, Archer (1964) recognizes the Luetkeatum pectinatae association as being the pioneer stage on the fine debris of dacite lava. Undoubtedly Luetkea pectinata plays a role in successional patterns; it is abundant in many habitats and may be involved in several different processes leading to the development of various vegetation types on Prince of Wales Island. At any rate, increasing soil development and acidification encourages the association of Phyllodoce glanduliflora and Cassiope mertensiana (Phyllodoce empetriformis in southern British Columbia).

Another successional sequence was observed by Archer in British Columbia. This involves succession on a quartz-diorite material similar to the quartz-diorite on Granite Mountain and Harris Peak in Southeast Alaska. The fact that all important species discussed by Archer also occur in Southeast Alaska's alpine vegetation indicates that the successional process he observed in British Columbia may also be operating here. Pioneer species on quartz-diorite include various lichens and bryophytes (Gymnomitrium, Polytrichum and Rhacomitrium) which precede the development of Carex nigricans bogs. Observations revealed that accumulated organic matter supports a Carex nigricans-Sphagnum stage which is followed by a Sphagnum stage. Further acidification will lead to establishment of the Phyllodoce-Cassiope mertensiana association.

On limestone, a different assemblage of species is involved in the development of the heath association. Bare limestone is invaded by *Saxifraga oppositifolia*, *Cerastium beeringianum*, *Arenaria rubella*, *Dryas drummondii*, *Festuca brachyphylla*, *Polygonum viviparum* and *Trisetum spicatum*. On more moist and protected sites with gentle slope a full meadow vegetation will develop. With increasing organic accumulation and acidification *Cassiope mertensiana*, *Cassiope stelleriana*, *Phyllodoce glanduliflora*, *Luetkea pectinata* and *Saxifraga punctata* ssp. *pacifica* will invade. After further soil development several tree species (*Abies lasiocarpa*, *Picea sitchensis* and *Chamaecyparis nootkatensis*), establish themselves; and, finally, all other associates of the heath vegetation type will develop under the cover of these tree copses.

It has been shown that tree species, including *Abies lasiocarpa*, *Tsuga mertensiana* and *Pinus albicaulis*, are in the process of invading treeless vegetation in timberline situations (Schmidt, 1957; Franklin, 1971; Brink, 1959, 1964). The process appears to be taking place in many areas of the Pacific Northwest and may be operating on Prince of Wales Island as well. However, insufficient samples were taken from Southeast Alaska to support the theory.

Brink (1959) and Franklin (1971) have correlated this invasion of meadow vegetation with a general glacial recession, which studies indicate has occurred over the past 100 years or more. With an amelioration of climate, snowpack will be reduced and suitable germination and growth conditions will develop. In the alpine, a reduction of snowpack over a period of many years will encourage invasion by subalpine fir and mountain hemlock into the Phyllodoce-Cassiope mertensiana heath vegetation of British Columbia (Archer, 1964).

Schmidt (1957) and Marshall (1956) speculate that the advance of white spruce (Picea glauca), western red cedar (Thuja plicata) and amabilis fir (Abies amabilis) has not proceeded north as far as present day climatic conditions would allow following Pleistocene glacial recession. They believe that these species are expanding their ranges--altitudinally and latitudinally--to include presently unoccupied territory.

A similar process appears to be operating in Southeast Alaska at timberline. On the Coast Range, and on some taller mountains on Prince of Wales Island (the Klawock Mountains) and on the Baranof-Chichagof Islands, an abrupt timberline of tall mountain hemlock is noted. This is interpreted as being the result of a recent rise in snowline and subsequent succession on the snow-free slopes (Heusser, 1960). With earlier snow-melt in more recent times these areas have been opened for colonization by alders and heath species. If present climatic conditions continue, the subalpine forests will probably advance into these newly released areas. Some evidence that this process is already operating on Prince of Wales Island may be observed. Many isolated copses of Tsuga mertensiana are found on south slopes growing above the elevation of the continuous subalpine forest. On calcareous sites these trees are found in association with Abies lasiocarpa.

Fire-caused meadows and other disturbances that have eliminated forests from areas they once occupied may be operating to bring about the patterns observed in some of the studies discussed above. However, fires occur infrequently in Southeast Alaska and are not viewed as major contributors to successional patterns.

PHYTOGEOGRAPHY

Distributional Affinities

The study of past and present distribution patterns of Southeast Alaskan plants is a large task made difficult because of 1) the lack of complete collection data, 2) a lack of understanding of phylogenetic relationships, especially at subspecific ranks and 3) limitations in understanding of past and present climatic factors.

Mention should be made of Hultén's (1927-1930, 1937a, 1937b, 1940, 1958, 1959, 1962, 1971) works on circumpolar and arctic plant distributions. His contribution to the knowledge of circumpolar plants is by far the greatest of any living botanist, and his studies serve as points of comparison with the present study.

The 166 alpine taxa on Prince of Wales Island have distributional affinities as plotted in Table 16. The circumboreal-

Table 16. General distributional affinities of alpine taxa of Prince of Wales Island.

Range	No. of Taxa	Percent of Flora
North American Only	72	43.4
North American and Asian	32	19.3
Circumboreal-circumarctic	62	37.3
Total	166	100.0

circumarctic group of plants includes the species listed in Table 17.

Some of the circumboreal-circumarctic, North American and North American-Asian species have distributions from the arctic regions of Alaska, Canada and Eurasia to scattered ranges in alpine tundra regions of North America and Eurasia. This group of species, called arctic-alpine plants, are listed in Table 18.

Another less well-defined group is composed of wide ranging cordilleran species. These species are of an alpine nature but do not occupy arctic regions of North America. This group includes the species listed in Table 19.

An important group of Southeast Alaskan species are those restricted to the coastal areas of Pacific Northwest America. Species with this distribution pattern are found in Table 20. Other widespread species having disjunct coastal populations in Southeast Alaska are given in Table 21. A few infraspecific taxa are endemics of Prince of Wales Island and the Queen Charlotte Islands. These are *Saxifraga punctata* ssp. *charlottae*, *Viola biflora* ssp. *charlottae* (see map 20 in Appendix) and *Senecio cymbalarioides* ssp. *moresbiensis* (see map 24 in Appendix).

Development of the Flora

The origins of the alpine flora on Prince of Wales Island and all

Table 17. Circumboreal-circumarctic species.

Achillea millefolium (S)[1]
Agrostis borealis (S)
Androsace chamaejasme
Arctostaphylos alpina
Arenaria rubella (S)
Ar uncus sylvester (S)
Asplenium viride (S)
Blechnum spicant (S)
Cardamine bellidifolia (S)
Carex scirpoidea
Cerastium beeringianum (S)
Cryptogramma crispa (S)
Cystopteris fragilis (S)
Drosera rotundifolia (S)
Dryopteris austriaca (S)
Empetrum nigrum (S)
Epilobium alpinum (S)
Epilobium angustifolium (S)
Epilobium latifolium (S)
Equisetum arvense (S)
Erigeron humilis
Eriophorum angustifolium (S)
Festuca brachyphylla (S)
Hierochloe alpina
Listera cordata (S)
Lloydia serotina (S)
Loiseleuria procumbens
Luzula parviflora (S)
Lycopodium alpinum
Lycopodium selago ssp. selago (S)
Oxyria digyna (S)
Oxytropis campestris
Pedicularis lanata
Pedicularis oederi
Pedicularis verticillata
Phleum alpinum (S)
Pinguicula villosa
Poa alpina (S)
Polygonum viviparum
Polystichum lonchitis (S)
Rubus chamaemorus
Salix arctica
Salix reticulata
Saxifraga adscendens (S)
Saxifraga caespitosa (S)
Saxifraga nivalis
Saxifraga oppositifolia
Saxifraga rivularis
Scirpus caespitosus (S)
Sedum rosea (S)
Silene acaulis (S)
Stellaria calycantha (S)
Thalictrum alpinum (S)
Thelypteris phegopteris (S)
Tofieldia coccinea
Trientalis europaea (S)
Trisetum spicatum (S)
Vaccinium uliginosum
Vahlodea atropurpurea (S)
Viola biflora
Woodsia glabella
Woodsia ilvensis

[1] (S) indicates species occurring south of the limits of continental glaciation in North America.

Table 18. Arctic-alpine species.

Achillea millefolium
Androsace chamaejasme
Anemone parviflora
Arctostaphylos alpina
Arenaria rubella
Artemisia arctica
Cardamine bellidifolia
Carex scirpoidea
Cerastium beeringianum
Cystopteris fragilis
Epilobium alpinum
Epilobium angustifolium
Epilobium latifolium
Erigeron humilis
Equisetum arvense
Festuca brachyphylla
Loiseleuria procumbens
Lycopodium selago ssp.
    selago
Oxyria digyna
Petasites nivalis
Poa alpina
Polygonum viviparum
Saxifraga caespitosa
Saxifraga oppositifolia
Scirpus caespitosus
Sedum rosea
Senecio lugens
Silene acaulis
Stellaria calycantha
Taraxacum kamtschaticum
Thalictrum alpinum
Trisetum spicatum
Vaccinium uliginosum
Viola biflora

Table 19. Wide-ranging cordilleran species.

Abies lasiocarpa
Actaea rubra
Agrostis borealis
Agrostis thurberiana
Antennaria umbrinella
Aquilegia formosa
Arnica latifolia
Asplenium viride
Caltha leptosepala
Castilleja miniata
Claytonia sibirica
Cornus stolonifera
Cryptogramma crispa
Dryas drummondii
Heuchera glabra
Hieracium triste
Luetkea pectinata
Mitella pentandra
Parnassia fimbriata
Ranunculus eschscholtzii
Saxifraga adscendens
Saxifraga ferruginea
Saxifraga mertensiana
Senecio triangularis
Solidago multiradiata
Thelypteris phegopteris
Tiarella trifoliata
Viola glabella

Table 20. Species endemic to coastal Pacific northwest America.

Agrostis aequivalis	Osmorhiza purpurea
Agrostis thurberiana	Pedicularis ornithorhyncha
Arnica latifolia	Phyllodoce glanduliflora
Blechnum spicant	Picea sitchensis
Caltha biflora	Pinguicula vulgaris
Campanula alaskana	Poa macrocalyx
Carex circinata	Potentilla villosa
Carex macrochaeta	Ranunculus cooleyae
Carex nigricans	Ranunculus occidentalis
Cassiope lycopodioides	Ribes bracteosum
Cassiope mertensiana	Romanzoffia sitchensis
Cassiope stelleriana	Rubus pedatus
Castilleja parviflora	Rubus spectabilis
Castilleja unalaschcensis	Salix stolonifera
Chamaecyparis nootkatensis	Saxifraga ferruginea
Cladothamnus pyrolaeflorus	Saxifraga mertensiana
Claytonia sibirica	Saxifraga punctata ssp. charlottae
Coptis aspleniifolia	Saxifraga punctata ssp. pacifica
Dodecatheon jeffreyi	Sorbus sitchensis
Erigeron peregrinus	Streptopus roseus
Fauria crista-galli	Tiarella trifoliata
Fritillaria camschatcensis	Tsuga heterophylla
Gentiana platypetala	Tsuga mertensiana
Heuchera glabra	Vaccinium alaskense
Leptarrhena pyrolaefolia	Vahlodea atropurpurea
Luetkea pectinata	Valeriana sitchensis
Lupinus nootkatensis	Viola glabella
Lycopodium selago ssp. miyoshianum	Viola langsdorffii
Menziesia ferruginea	

Table 21. Species having disjunct populations in southeast Alaska.

Abies lasiocarpa
Agrostis aequivalis
Agrostis thurberiana
Androsace chamaejasme
Anemone parviflora
Antennaria umbrinella
Arctostaphylos alpina
Arenaria rubella
Arnica diversifolia
Aruncus sylvester
Caltha leptosepala
Cassiope lycopodioides
Castilleja unalaschcensis
Cerastium beeringianum
Draba lactea
Draba lonchocarpa
Dryas drummondii
Erigeron humilis
Geum calthifolium
Hierochloe alpina
Loiseleuria procumbens
Lycopodium selago ssp. miyoshianum
Oxytropis campestris
Pedicularis lanata
Pedicularis oederi
Poa alpina
Poa arctica
Poa macrocalyx
Ranunculus eschscholtzii
Salix reticulata
Saxifraga adscendens
Saxifraga caespitosa
Saxifraga nivalis
Saxifraga oppositifolia
Saxifraga rivularis
Senecio lugens
Silene acaulis
Taraxacum kamschaticum
Thalictrum alpinum
Tofieldia coccinea
Woodsia glabella
Woodsia ilvensis

islands in the Archipelago are largely unknown. Fossil records of Cretaceous and Tertiary age in Alaska represent only the lowland facies. No remains of the montane flora of these times exists (Hollick, 1930). Cretaceous floras in central Alaska were apparently warm-temperate with significant subtropical and tropical elements such as Nilssonia, Podozamites and Ginkgo minor. During Paleocene time the flora of Southeast Alaska (Hamilton Bay, Kupreanof Island) maintained a strong subtropical and tropical aspect with Macaranga, Melanolepis, cycads, palms, Lauraceae and Dilleniaceae, indicating that the area was frost-free (Wolfe, 1966a). Some dicotyledonous species in this flora would suggest a warm-temperate climate, although the genera involved (Carya, Pterocarya and Acer) do have species existing in tropical regions today.

There is evidence that an "Arcto-Tertiary" flora existed in southcentral Alaska in lower Miocene time. Dominant families include Salicaceae, Juglandaceae, Betulaceae, Fagaceae, Ulmaceae, and Aceraceae. Wolfe (1966b) noted that Pinus and Picea are present but Abies, Tsuga and Ericales are rare. In the same study Wolfe discusses a late Miocene flora from Cook Inlet which lacks most of the warm-temperate elements seen in the early Miocene and in which Abies, Tsuga and Ericales are better represented.

Wolfe (1966b) also describes a deposit in Cook Inlet which may represent the youngest Tertiary rocks that are exposed in Alaska.

The fossils contained in this deposit are of plants closely related to species of the modern flora. One extant species, Alnus incana, has been identified in this Tertiary flora, which Wolfe states is "older than the glacial part of the Pleistocene epoch" (Wolfe, 1966b, p. 21).

During late Tertiary time the Coast Range Mountains and insular mountains of Southeast Alaska were beginning to be uplifted. These mountains are thought to have attained their present heights by the end of the Pliocene (Miller, 1958b). Significant elements of the modern flora probably existed in Southeast Alaska before complete uplift of the Coast Range and Pleistocene ice advance. This pre-Pleistocene flora of Alaska is known to have contained species of Salix, Betula, Alnus, Pinus, Picea, Abies, Ericales, Tsuga, Populus, Viburnum, Equisetum and Polypodiaceae. The number of alpine species presently restricted to coastal northwest North America (listed in Table 20) indicates that a large degree of autochthonous development of the alpine flora took place in Southeast Alaska. Although all of these species probably did not exist in late Tertiary time, their ancestral types did.

The fact that the earth experienced a period of extensive glacial activity in areas now devoid of ice has only been accepted since the mid-nineteenth century (Agassiz, 1841). Since this time four major advances of ice lobes have been recognized as having occurred in central North America. Four major advances also took place in southcentral Alaska (Karlstrom, 1961). Several minor pulses, which indicate advances of local glaciers, are recognized within the last two major advances. Their correlation with regional events is uncertain. Even today some ice lobes are advancing in Southeast Alaska; the most notable are Hole-in-the-Wall Glacier near Juneau and Hubbard Glacier in Yakutat Bay.

Records of the three oldest major advances are almost nonexistent in Southeast Alaska. Recent glacial activity has been intense, and any evidence that may have existed before the late Pleistocene ice advance was obliterated by it. The record of late Pleistocene glacial activity on Prince of Wales Island has been discussed earlier. Figure 8 shows the limits of Pleistocene ice in northwest North America.

In recent years there has been much discussion about refugia which may have existed during late Pleistocene glaciation. Coulter et al. (1962) indicated that the North Slope of Alaska was completely ice-free during the Pleistocene. They also describe a large ice-free corridor in central Alaska which extended into west central Yukon Territories. Cordilleran ice did not extend below the northern half of Washington and Idaho, and only isolated alpine glaciers affected the higher elevations of Oregon and California. The glacial map of Canada (Falconer et al., 1958) shows an ice-free area in southwest Alberta, and there is evidence that another such area existed along the eastern flanks of the Mackenzie Mountains during the Pleistocene.

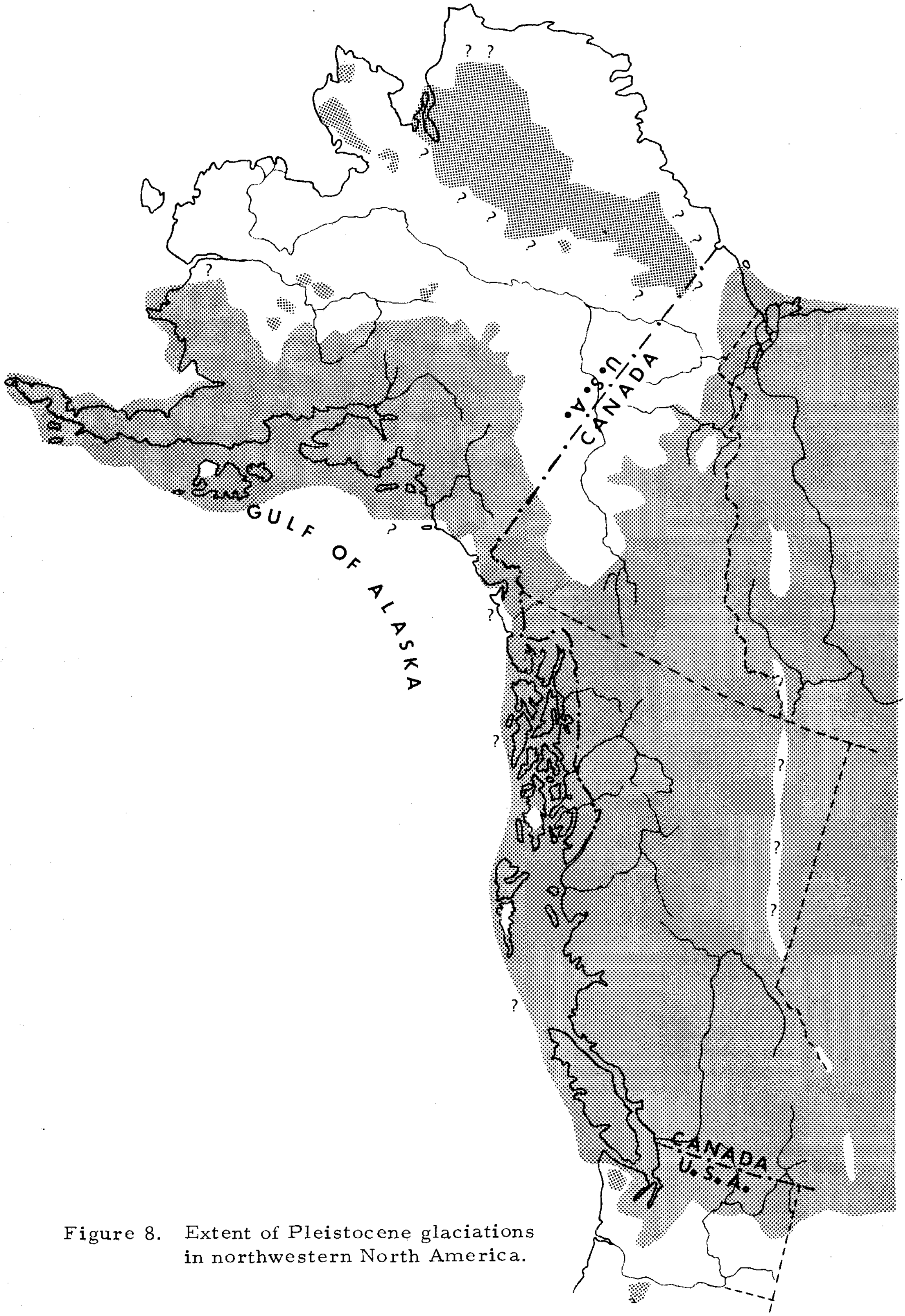


Figure 8. Extent of Pleistocene glaciations in northwestern North America.

Calder and Taylor (1968) and Heusser (1960) believe that parts of the Queen Charlotte Islands escaped Pleistocene glaciation. The fact that there are a significant number of endemics on the Islands supports this theory, although it is opposed by geological evidence (Brown and Nasmith, 1962).

Hultén's (1937b) monumental study of arctic and boreal plants of the Quaternary was made before there was much knowledge of glacial history, yet he spotted most of the ice-free areas mentioned above as major refugia for plants. A discussion of the concept of glacial refugia as it developed up to the time of Hultén's study and afterwards will be of value in evaluating the evidence for or against such an idea.

Glacial Age Refugia and Postglacial Plant History

Wherever ice does not obliterate vegetation, plants are capable of surviving. In many areas of Southeast Alaska plants grow right to the edges of the ice, and forests are presently existing on stagnating lobes of certain glaciers in Alaska.

It has been hypothesized that certain elements of the Scandinavian flora existed under these environmental conditions. Fries (1925) discussed disjunct elements which he felt had survived in "nunataks"[1]

[1] "Nunatak" is an Eskimo word meaning "lonely mountain." It was introduced by A. E. Nordenskjold to describe peaks which had escaped glaciation and therefore could have supported a glacial age flora.

during the Pleistocene. Many later workers have presented evidence to support the existence of such isolated areas as plant refugia (Fernald, 1925; Dahl, 1946, 1955, 1959; Faegri, 1963; Gjaerevoll, 1963; Hoppe, 1963; Nordhagen, 1963; Karlstrom and Ball, 1969).

In 1937, Hultén arrived at similar conclusions in explaining the survival of certain groups of arctic and boreal species. In mapping the ranges of Alaskan plants he noted certain "equiformal progressive areas" which he believed had served as refugia. Beringia, one such area which he described, has subsequently been discussed in detail (Hopkins, 1967). Though Pleistocene advances repeatedly disrupted their ranges, the species which Hultén believes survived in these ice-free centers could reradiate during interglacial periods. Although there are many specific problems with Hultén's analyses, his general concepts are valid. Isolation by Pleistocene ice has been instrumental in developing subspecific taxa and certain species as well.

Table 22 is a complete list of taxa collected on Prince of Wales Island's alpine areas. Their presence in each of the major refugia is noted. A few species collected in Prince of Wales Island's alpine ecosystems are not known to occur in any documented refugia. These species are: *Salix stolonifera*, *Saxifraga punctata* ssp. *pacifica*, *Geranium erianthum*, *Cassiope lycopodioides* and *Poa macrocalyx*. Hultén recognized six basic groups of radiants, each with a similar history. Plants from his arctic-alpine and boreal circumpolar

Table 22. List of alpine vascular plants on Prince of Wales Island, Southeast Alaska, and their occurrence in other refugial sites.

(Nomenclature after Calder and Taylor, 1968 and Hulten, 1968)

Key

M = Mackenzie
CA = Central Alaska
NA = North Alaska
QC = Queen Charlotte Is.
SA = Southwest Alberta
SI = South of the Ice
X = reported more than once or common
O = disjunct or rare occurrence

	M	CA	NA	QC	SA	SI
EQUISETACEAE						
Equisetum arvense L.	X	X	X	X	X	X
LYCOPODIACEAE						
Lycopodium alpinum L.	X	X			X	
Lycopodium sabinaefolium Willd. ssp. sitchense (Rupr.) Cald. and Tayl.				X		X
Lycopodium selago L. ssp. miyoshianum (Makino) Cald. and Tayl.				X		
Lycopodium selago L. ssp. selago	X			X	X	X
POLYPODIACEAE						
Asplenium viride Huds.	X			X	X	X
Blechnum spicant (L.) Roth				X		X
Cryptogramma crispa (L.) R. Br. ssp. acrostichoides (R. Br.) Christ	X			X	X	X
Cystopteris fragilis (L.) Bernh. ssp. fragilis	X	X	X	X	X	X
Dryopteris austriaca (Jacq.) Woynar	X	X		X	X	X
Polystichum lonchitis (L.) Roth ex Roem.				X	X	X
Thelypteris phegopteris (L.) Slosson		X		X		X
Woodsia glabella R. Br.	X	X	X		X	
Woodsia ilvensis (L.) R. Br.	X	X			X	
ABIETACEAE						
Abies lasiocarpa (Hook.) Nutt.	X				X	X
Picea sitchensis (Bong.) Carr.				X		X
Tsuga heterophylla (Raf.) Sarg.				X		X
Tsuga mertensiana (Bong.) Sarg.				X		X
CUPRESSACEAE						
Chamaecyparis nootkatensis (Lamb.) Spach				X		X
SALICACEAE						
Salix arctica Pall.	X	X	X		X	
Salix reticulata L. ssp. reticulata	X	X	X			
Salix stolonifera Cov.						

(continued)

Table 22. continued

	M	CA	NA	QC	SA	SI
BETULACEAE						
Alnus crispa (Ait.) Pursh ssp. sinuata (Regel) Hult.		X		X	X	X
POLYGONACEAE						
Oxyria digyna (L.) Hill	X	X	X	X	X	X
Polygonum viviparum L.	X	X	X	X	X	X
PORTULACACEAE						
Claytonia sibirica L.				X		X
CARYOPHYLLACEAE						
Arenaria rubella (Wahlenb.) Sm.	X	X	X		X	X
Cerastium beeringianum Cham. and Schlecht. var. beeringianum	X	X	X		X	X
Silene acaulis L. var. exscapa (All.) DC.	X	X	X	X	X	X
Stellaria calycantha Bong.	X	X		X	X	X
RANUNCULACEAE						
Aconitum delphinifolium DC.	X	X	X	X	X	
Actaea rubra (Ait.) Willd. ssp. arguta (Nutt.) Hult.	X			X	X	X
Anemone narcissiflora L. ssp. alaskana Hult.		X	X	X	X	
Anemone parviflora Michx.	X	X	X	X	X	X
Aquilegia formosa Fisch.				X		X
Caltha biflora DC. var. biflora				X		X
Caltha leptosepala DC.					X	X
Coptis asplenifolia Salisb.				X		
Ranunculus cooleyae Vasey and Rose				X		
Ranunculus eschscholtzii Schlecht.	X			X	X	X
Ranunculus occidentalis Nutt. ssp. occidentalis				X	X	X
Thalictrum alpinum L.	X	X	X	X	X	X
CRUCIFERAE						
Arabis lyrata L. ssp. kamchatica (Fisch.) Hult.	X	X		X	X	
Cardamine bellidifolia L.	X	X	X	X	X	X
Cardamine umbellata Greene		X		X	X	X
Draba lactea Adams	X		X		X	
Draba lonchocarpa Rydb. ssp. kamtschatica (Ledeb.) Cald. and Tayl.				X		
DROSERACEAE						
Drosera rotundifolia L.	X	X		X	X	X
CRASSULACEAE						
Sedum rosea (L.) Scop. ssp. integrifolium (Raf.) Hult.	X	X	X	X	X	X
SAXIFRAGACEAE						
Heuchera glabra Willd. ex R. and S.				X		X
Leptarrhena pyrolaefolia (D. Don) R. Br.				X	X	

Table 22. continued

	M	CA	NA	QC	SA	SI
Mitella pentandra Hook.				X	X	X
Parnassia fimbriata Konig	X			X	X	X
Ribes bracteosum Dougl.				X		X
Saxifraga adscendens L. ssp. oregonensis (Raf.) Baci.		X			X	X
Saxifraga caespitosa L.			X	X	X	X
Saxifraga ferruginea Grah.				X	X	X
Saxifraga lyallii Engl. ssp. hultenii Cald. and Tayl.	X			X	X	
Saxifraga mertensiana Bong.				X	X	X
Saxifraga nivalis L.	X	X	X		X	
Saxifraga oppositifolia L.	X	X	X	X	X	X
Saxifraga punctata L. ssp. charlottae Cald. and Sav.				X		
Saxifraga punctata L. ssp. pacifica Hult.						
Saxifraga punctata L. ssp. pacifica Hult. X charlottae Cald. and Sav.						
Saxifraga rivularis L.	X	X	X		X	
Tiarella trifoliata L.				X	X	X
ROSACEAE						
Aruncus sylvester Kostel.				X		X
Dryas drummondii Richards.	X	X			X	
Geum calthifolium Sm.				X		
Luetkea pectinata (Pursh) Kuntze				X	X	X
Potentilla villosa Pall. ex Pursh				X		
Rubus chamaemorus L.	X	X	X	X	X	
Rubus pedatus Sm.				X	X	X
Rubus spectabilis Pursh				X		X
Sanguisorba canadensis L. ssp. latifolia (Hook.) Cald. and Tayl.		X		X		X
Sorbus sitchensis M. Roemer ssp. grayi (Wenz.) Cald. and Tayl.				X		X
LEGUMINOSAE						
Lupinus nootkatensis Donn ex Sims				X		
Oxytropis campestris (L.) DC.	X	X	X	X	X	
GERANIACEAE						
Geranium erianthum DC.						
EMPETRACEAE						
Empetrum nigrum L.	X	X	X	X	X	X
VIOLACEAE						
Viola biflora L. ssp. charlottae Cald. and Tayl.				X		
Viola glabella Nutt.				X	X	X
Viola langsdorffii (Regel) Fisch.				X		X
ONAGRACEAE						
Epilobium alpinum L.	X	X		X	X	X
Epilobium angustifolium L.	X	X	X	X	X	X
Epilobium latifolium L.	X	X	X	X	X	X

Table 22. continued

	M	CA	NA	QC	SA	SI
UMBELLIFERAE						
Angelica lucida L.		X		X		X
Heracleum lanatum Michx.	X	X		X	X	X
Osmorhiza purpurea (Coult. and Rose) Suksd.				X	X	X
CORNACEAE						
Cornus stolonifera Michx.		X		X		X
Cornus unalaschensis Ledeb.		X		X		
ERICACEAE						
Arctostaphylos alpina (L.) Spreng.	X	X	X			
Cassiope lycopodioides (Pall.) D. Don ssp. lycopodioides						
Cassiope mertensiana (Bong.) D. Don ssp. mertensiana				X	X	X
Cassiope stelleriana (Pall.) DC.				X		O
Cladothamnus pyrolaeflorus Bong.				X		O
Kalmia polifolia Wang. ssp. polifolia	X			X		X
Loiseleuria procumbens (L.) Desv.	X	X	X	X		
Menziesia ferruginea Sm.				X		X
Phyllodoce glanduliflora (Hook.) Cov.	O			X	X	X
Vaccinium alaskense How.				X		O
Vaccinium caespitosum Michx.				X	X	X
Vaccinium ovalifolium Sm.				X	X	X
Vaccinium uliginosum L.	X	X	X	X	X	X
PRIMULACEAE						
Androsace chamaejasme Host ssp. lehmanniana (Spreng.) Hult.		X	X		X	O
Dodecatheon jeffreyi Van Houtte				X		X
Dodecatheon pulchellum (Raf.) Merrill				X	X	X
Trientalis europaea L.	X	X		X	X	X
GENTIANACEAE						
Fauria crista-galli (Menzies) Makino				X		
Gentiana platypetala Griseb.				X		
HYDROPHYLLACEAE						
Romanzoffia sitchensis Bong.				X	X	X
SCROPHYLARIACEAE						
Castilleja miniata Dougl.					X	X
Castilleja parviflora Bong.				X		O
Castilleja unalaschensis (Cham. and Schlecht.) Malte				X		
Castilleja miniata X unalaschensis						
Mimulus guttatus DC. ssp. suttatus		X		X	X	X
Pedicularis lanata Cham. and Schlecht.	X	X	X	O	X	
Pedicularis oederi M. Vahl.		X	X	O		X
Pedicularis ornithorhyncha Benth.				X		O
Pedicularis verticillata L.		X	X	X		
Veronica wormskjoldii Roem. and Schult. ssp. wormskjoldii		X		X		X

Table 22. continued

	M	CA	NA	QC	SA	SI
LENTIBULARIACEAE						
Pinguicula villosa L.	X	X	X	X		
Pinguicula vulgaris L. ssp. macroceras (Link) Cald. and Tayl.				X		X
CAPRIFOLIACEAE						
Viburnum edule (Michx.) Raf.	X	X		X	X	X
VALERIANACEAE						
Valeriana sitchensis Bong.	X			X	X	X
CAMPANULACEAE						
Campanula alaskana (Gray) Wight ex Anders.				X		
COMPOSITAE						
Achillea millefolium L.	X	X	X	X	X	X
Antennaria umbrinella Rydb.					X	X
Arnica diversifolia Greene					X	X
Arnica latifolia Bong.				X	X	X
Artemisia arctica Less. ssp. arctica	X	X	X	X	X	X
Erigeron humilis Grah.			X	O	X!	
Erigeron peregrinus (Pursh) Greene ssp. peregrinus				X		X
Hieracium triste Willd. ex Spreng. ssp. triste	X			X	X	X
Petasites nivalis Greene		X	X	X		X
Senecio cymbalarioides Buek ssp. moresbiensis Cald. and Tayl.				X		
Senecio lugens Richards.	X	X	X		X	O
Senecio triangularis Hook.	X			X	X	X
Solidago multiradiata Ait.	X	X	X	O	X	
Taraxacum kamschaticum Dahlstedt		X				
GRAMINEAE						
Agrostis aequivalis (Trin.) Trin.				X		
Agrostis borealis Hartm.		X		X	X	X
Agrostis thurberiana Hitchc.				X	X	X
Festuca brachyphylla Schult.	X	X	X		X	X
Hierochloe alpina (Sw.) Roem. and Schult. ssp. alpina	X	X	X		X	
Poa alpina L.	X	X	X		X	X
Poa arctica R. Br. ssp. williamsii (Nash) Hult.		X				
Poa macrocalyx Trautv. and Mey.						
Phleum alpinum L.	X			X	X	X
Trisetum spicatum (L.) Richt.	X	X	X	X	X	X
Vahlodea atropurpurea (Wahlenb.) Fr. ssp. paramushirensis (Kudo) Hult.	X			X		X
CYPERACEAE						
Carex circinata C. A. Mey.				X		
Carex macrochaeta C. A. Mey.				X		
Carex nigricans C. A. Mey.				X	X	X

Table 22. continued

	M	CA	NA	QC	SA	SI
Carex scirpoidea Michx.	X	X	X	X	X	X
Carex stylosa C. A. Mey.		X		X		
Eriophorum angustifolium Honck.	X	X	X	X	X	
Scirpus caespitosus L.	X	X		X	X	X
JUNCACEAE						
Luzula arcuata (Wahlenb.) Sw. ssp. unalaschcensis (Buch.) Hult.	X	X	X			
Luzula parviflora (Ehrh.) Desv.	X	X	X	X	X	X
LILIACEAE						
Fritillaria camschatcensis (L.) Ker-Gawl.				X		
Lloydia serotina (L.) Reichenb. ssp.. serotina	X	X	X			X
Streptopus roseus Michx. ssp. curvipes (Vail) Hult.				X		X
Tofieldia coccinea Richards.	X	X	X			
Tofieldia glutinosa (Michx.) Pers. ssp. brevistyla C. L. Hitchc.	X			X		X
Veratrum eschscholtzii Gray	X			X	X	X
ORCHIDACEAE						
Habenaria dilatata (Pursh) Hook.				X	X	X
Listera cordata (L.) R. Br.				X	X	X
Number of species (168)	71	73	51	132	96	104
Percentage total alpine flora	42.3	43.5	30.4	78.6	57.2	61.9

groups are included in Tables 17 and 18 of the present study. His "West American Coastal Radiants" category includes the species listed in Table 20. The "Continental West American Radiants," as Hultén describes them, have been included with various other distribution types. They appear to have had different histories but are similar in that they have very scattered or no coastal distributions. These species include all of Table 21. The distributions of most of these species are mapped in the appendix. Hultén's categories of "South Beringian" and "North Beringian" radiants have likewise been included in Tables 17, 18, 19 and 21.

The circumpolar species have the widest ranges. They are species which originally occupied large regions, but intruding Pleistocene ice created gaps in their ranges. Some circumpolar species, such as Thalictrum alpinum and Oxyria digyna, provide evidence for plant migration. Their ranges are very widespread, and both are morphologically remarkably uniform. These species undoubtedly did not always occupy their complete present ranges; rather, they have dispersed from the centers of their origin to many of their present localities. There are two important subgroups in the North American circumpolar flora--one which extends south of the ice and one which does not. Those species found in Washington and Oregon south of the limits of Pleistocene ice advance are marked by (S) in Table 17.

The arctic-alpine species include some circumpolar plants, together with those North American or North American and Asian species which occupy arctic regions and also possess biotypes in southern alpine regions (including the mountains of Prince of Wales Island). These species survived the Pleistocene age in several areas: northern Alaska, central Alaska, south of the ice and in refugia which existed within the glaciated area. The Beringian species are also found in areas known to have been unglaciated, so their presence on Prince of Wales Island is not surprising. However, the "West Coast Radiants" and many "Continental West American Radiants" contain interesting exceptions.

The "West Coast Radiants" are species with present-day ranges that do not include major known refugium areas. It is supposed that, following glacial recession, individuals of these west coast species remigrated from south of the ice to Southeast Alaska. Undoubtedly many species did this; however, even some of these species show interesting gaps in their coastal ranges south of the Panhandle. If the only center for dispersal was the vegetated area south of the ice, the gap areas should have been recolonized by these species. Coastal species whose ranges contain gaps include: _Agrostis aequivalis_, _Agrostis thurberiana_ and _Castilleja unalaschensis_. Coastal species collected in Southeast Alaska which are not found south of the limits of Pleistocene ice include: _Vahlodea atropurpurea_, _Poa macrocalyx_, Carex circinata, Carex macrochaeta, Salix stolonifera, Coptis aspleniifolia, Ranunculus cooleyae, Saxifraga punctata ssp. pacifica and ssp. charlottae, Potentilla villosa, Lupinus nootkatensis, Cassiope stelleriana, Cassiope lycopodioides, Gentiana platypetala, Fauria crista-galli, Pedicularis ornithorhyncha and Campanula alaskana. These species are not found in known refugia other than the Queen Charlotte Islands, but they must have survived as well in smaller coastal refugia and possibly on Prince of Wales Island.

The "Continental West American Radiants" (Table 21) provide some insight into this problem. For most of these species the present report represents a new range extension for Southeast Alaska (see Appendix). Many of these species are continental-arctic in nature, and this southernmost insular distribution is anomalous. The continental-arctic species include: Draba lactea, Hierochloe alpina, Erigeron humilis, Draba lonchocarpa, Saxifraga nivalis, Saxifraga oppositifolia, Silene acaulis, Poa alpina, Woodsia glabella, Woodsia ilvensis, Senecio lugens, Oxytropis campestris, Androsace chamaejasme, Tofieldia coccinea, Arctostaphylos alpina, Thalictrum alpinum, Saxifraga adscendens, Taraxacum kamschaticum, Pedicularis lanata, Pedicularis oederi, Loiseleuria procumbens and Lycopodium selago ssp. miyoshianum. A few continental species range southward into British Columbia, Alberta, or Washington and grow in disjunct stations on Prince of Wales Island. These disjunct species include:

Agrostis aequivalis, Agrostis thurberiana, Arnica diversifolia, Abies lasiocarpa and Antennaria umbrinella. Some north coastal species--Luzula arcuata ssp. unalaschcensis, Solidago multiradiata, Cerastium beeringianum, Cassiope lycopodioides, Salix reticulata, Dryas drummondii, Anemone parviflora and Poa arctica--also inhabit disjunct localities on Prince of Wales Island.

While the history of the disjunct and endemic coastal taxa is complex, the physical and ecological events of the Pleistocene era must have played a major rôle in determining distribution patterns. It is quite possible that Prince of Wales Island was included in the ranges of some of these pre-Pleistocene species. Ice advances could then have restricted the disjunct species to unglaciated areas on the Island. Worley (1972), in describing the Pleistocene refugia that could have existed in Southeast Alaska, postulated that unglaciated forelands and rocky coastal headlands adjacent to the open Pacific Ocean possibly were refugia. Forrester Island is believed to have escaped glaciation completely. Unglaciated areas on the continental shelf could also have served as refugia. Geological evidence indicates that certain segments of the coast of the northeast Gulf of Alaska between Prince William Sound and Lituya Bay may never have been glaciated (Miller, 1958a). The lowering of sea level during the Pleistocene would have exposed areas of continental shelf that are now 150 to 200 feet below sea level. The retreat of the ice at the end of the age exposed new areas of land which could have been resettled by plants migrating from the lower elevations. At the same time, with the rise in sea level, this lower elevation vegetation would be covered again with water. Eustatic readjustment of sea level following ice recession is generally believed to occur more slowly than isostatic uplift of land that has been depressed by the ice load (Twenhofel, 1952). Therefore, if plants did survive on these lower elevation shelves, they should have been able to colonize the uplifted land before being covered by rising sea water. Nunataks undoubtedly existed on Prince of Wales Island, and on Chichagof and Baranof Islands as well. Geological evidence (Swanston, 1967; Sainsbury, 1961) supports the possibility that late Pleistocene nunataks existed on the peaks and ridges of Prince of Wales Island above 3000 feet. Later advances of lesser dimensions left larger areas open for plant growth. Nunataks exist today in the Juneau Icefield and have been studied extensively (Heusser, 1954). Of the 102 vascular plants surviving on the isolated mountain peaks near Juneau, 57 are also found on peaks on Prince of Wales Island.

Evidence from Greenland indicates that nunatak floras become extremely depauperate under severe glacial conditions (Frederiksen, 1971). Nunataks are not considered to be major sites of post-Pleistocene plant dispersal; however, some species could have survived the Pleistocene on nunataks. Direct evidence that this survival did occur in a few cases is found in Saxifraga ferruginea (Randhawa and Beamish, 1972). A cytotaxonomic study of this species, conducted throughout its entire range, revealed that both diploid (N=10) and polyploid (N=19) populations occur. Polyploid populations were found throughout the area which had been covered by Pleistocene glaciation, whereas diploids occupy the area south of the ice sheets in Oregon, on the Queen Charlotte Islands, in southwestern Alberta, and on Kodiak Island--all refugial areas. The selective advantages which favor polyploids over diploids in previously glaciated terrain are undetermined, but it is apparent that diploid individuals are restricted to unglaciated areas (Randhawa and Beamish, 1972, p. 87). These authors state: "Diploids still mark approximately the locations of refugia in which they survived." I have made chromosome counts of Saxifraga ferruginea individuals collected from Harris Peak and Granite Mountain on Prince of Wales Island. All of these were diploids, thus supporting the existence of a refugium in this region. That these diploids are not composed only of narrowly adapted genotypes is shown by the fact that abandoned logging roads on Harris Ridge are commonly colonized by Saxifraga ferruginea as far down as 1400 feet elevation. With respect to this species, therefore, it appears that the capacity to spread and compete is great enough that the plants could have invaded newly emerged land from their lowland refugia on Prince of Wales Island. Yet, on a larger scale, it is the polyploids, rather than the diploids, which have been able to invade the large expanses opened up for colonization following glacial recession.

Post-Pleistocene climatic conditions and plant migrations could account for some of the distribution patterns observed on Prince of Wales Island. The disjunct arctic species discussed earlier probably expanded their ranges to include Southeast Alaska during cooling climatic conditions preceeding the Pleistocene. They possibly survived at higher elevations during the warmer interglacial periods. However, the history of species with a southern range in North America is probably reversed. With warmer and perhaps drier conditions than those of the ice advances, these southern continental species could have advanced northward to include Prince of Wales Island in their ranges. Abies lasiocarpa (see map 3 in Appendix) and Antennaria umbrinella (see map 22 in Appendix) are two examples of this distribution pattern. A warm Hypsithermal Interval following the last Pleistocene ice advance (10, 300$\pm$600 years B. P.) is hypothesized by Heusser (1960). He dates this interval as 7800$\pm$300 to 3500$\pm$250 years B. P. If this warming trend did indeed occur, many arctic species already in the area could have become progressively more restricted to cooler and moister alpine heights. At the same time, south-ranging plants would have been able to invade higher elevation areas. The past 3000 years or so have seen a return to cooler and more moist conditions. This return would again make the lower slopes favorable habitats for the arctic species while the southern species would become restricted to those remaining drier and warmer sites.

At this point mention should again be made of the earlier discussion of calcicolous vegetation. Almost all of the disjunct arctic and south-ranging species being discussed here are found only on calcareous substrates. Only the following disjunct species are found growing on noncalcareous sites: Agrostis aequivalis, Agrostis thurberiana, Aruncus sylvester, Caltha leptosepala, Cassiope lycopodioides, Castilleja unalaschcensis, Geum calthifolium, Hierochloe alpina, Loiseleuria procumbens, Lycopodium selago ssp. miyoshianum, Pedicularis lanata, Pedicularis oederi and Ranunculus eschscholtzii. It appears that, through one process or another, each disjunct species has become restricted to calcareous sites on Prince of Wales Island.

The historical schemes presented here have presumably operated singly or in conjunction with other processes to provide the distribution patterns observed today on Prince of Wales Island. In the case of rare alpine plants, another factor must be taken into consideration. Recent long-distance dispersal may have occurred in a few cases to provide highly disjunct distributions. In this regard Tolmachev (1960, p. 9) states:

> ...the hypothesis of the fast transport of plant rudiments over great distances...has not found many adherents among naturalists engaged in the study of Arcto-Alpine distribution

> of plants. All naturalists are agreed that the contemporary discontinuous distribution of the investigated plants has followed the dismemberment of a previously unbroken growth area...

However, individual species must be examined and evaluated as to the possibility that their presence is due to recent long-distance dispersal. In the present study one disjunct discovery appears to be readily explained in this way. One individual of *Dryas drummondii* was located on a limestone cliff on Virginia Mountain, a station which is disjunct by over 200 miles from its nearest known colonies at Glacier Bay. At Glacier Bay the plant is extremely abundant on recently deglaciated terrain (Cooper, 1939). Winter wind patterns commonly include strong northerlies, and these could have blown the plummed fruits of *Dryas drummondii* many miles to the south to bring about this disjunct occurrence.

SUMMARY AND CONCLUSIONS

A study was made of the alpine areas of Prince of Wales Island, in Southeast Alaska to determine what plants occur there and to describe basic vegetation patterns. Specific objectives included: 1) to describe the alpine vegetation, 2) to analyze the differences between vegetation on calcareous and noncalcareous soils, 3) to identify rare and disjunct taxa, and 4) to determine the history of the alpine flora in Southeast Alaska.

Southeast Alaska has been glaciated, and several workers have described two major late-Pleistocene ice advances on Prince of Wales Island. The bedrock geology of the region consists mainly of Paleozoic sediments and Cretaceous dioritic intrusive bodies. The following major soil types of Southeast Alaskan alpine areas have been mapped by the U. S. Forest Service: Sunnyhay soils (supporting *Empetrum*-heath vegetation), Hydaburg soils (supporting bog vegetation), St. Nicholas and Lithic Cryaquept soils (supporting meadow vegetation) and alpine rocklands (primitive surfaces).

Climate in the region is cool, moist and maritime. A large amount of precipitation falls as snow, and this is a dominant factor in the determination of vegetation patterns in the alpine and subalpine zones.

The subalpine zone is made up of two subzones: the subalpine forest subzone and the subalpine parkland subzone. The subalpine forest subzone begins at 1400 feet elevation where mountain hemlock (Tsuga mertensiana) becomes dominant. With increasing elevation (at about 1900 feet) and increasing snowpack, open parkland areas intrude into the forest. The parklands consist of heath vegetation, with Cassiope mertensiana, Cassiope stelleriana and Phyllodoce glanduliflora the principal species.

At about 2700 to 2800 feet, the treeless vegetation of the alpine becomes predominant. Three basic alpine habitat types were recognized: 1) alpine heath communities, 2) alpine meadow communities and 3) crevice plants on primitive surfaces.

Calcareous sites are located sporadically throughout the region, both as small outcrops and as extensive ridges and peaks. Thirty-six calcicolous species grow on Prince of Wales Island in the alpine zone. Talus slopes, rock outcrops and ledges provide habitats for these calcicoles; none of them occur in the climatic climax vegetation type.

On noncalcareous parent materials the climatic climax vegetation is Empetrum-heath. Strong controls on community placement are exerted by snow cover, as regulated by topography and climatic conditions. On dry ridgetops without snow cover Empetrum-Cassiope-Phyllodoce heaths are found. Caltha biflora grows in pure dense stands within drainage channels, while depressions without standing water support vegetation consisting of Dodecatheon jeffreyi and Fauria crista-galli. Carex nigricans bogs develop on concave surfaces.

Alpine heath vegetation grows sparingly on limestone, occupying a few ridgetops and other sites where succession has progressed to the heath stage. One unique patch of tundra-like heath mat covered a ridgetop of Virginia Mountain. This relict association was made up of Abies lasiocarpa, Tsuga mertensiana, Arctostaphylos alpina, and three dwarf willows--Salix reticulata, Salix arctica and Salix stolonifera.

Alpine meadows occur mostly on stabilized talus slopes where avalanching and soil movement do not allow heath vegetation to develop. Lush meadows are found on both calcareous and noncalcareous sites. No well defined communities exist in meadows; however, a distinction can be made between mesic and xeric sites.

Primitive surfaces exhibit the most distinctive vegetation differences between calcareous and noncalcareous sites. Here the physical and chemical properties of the substrate are not changed significantly by soil development and other processes. Only a few species occur on both calcareous and noncalcareous primitive surfaces; these are: Asplenium viride, Cystopteris fragilis, Festuca brachyphylla, and Polygonum viviparum.

Precise definition of alpine plant communities is made difficult by the fact that many species range widely from low to high elevations. On Prince of Wales Island, the topography is steep and the climate is moderated by maritime influences. These factors, combined with the great ecological tolerances of many of the species, apparently allow the plants to extend from sea level to high in the alpine zone.

Sixty-two of the alpine taxa on Prince of Wales Island are circumpolar species. Seventy-two species occur in North America while only 32 species range in North America and across the Bering Sea to Asia.

The history of Prince of Wales Island's alpine taxa is very complex. The discovery during this study of 57 species endemic to the coastal region of northwest North America, together with 42 widespread species with disjunct populations on Prince of Wales Island, indicates that glacial-age refugia did exist in Southeast Alaska. Unglaciated low elevation headlands, submerged continental shelf areas and other land surfaces that were unglaciated and above sea level during the Pleistocene probably served as refugial sites for at least some species of the present-day flora. Certain species (e. g. Saxifraga ferruginea and other crevice plants) may have persisted on nunataks; but in general, survival on nunataks probably accounts for a relatively insignificant number of present-day species on the Island. Post-Pleistocene migration from south of the ice sheets, central Alaska, west-central Yukon, the Queen Charlotte Islands and other refugial sites undoubtedly took place.

The occurrence of disjunct taxa on Prince of Wales Island could be correlated with post-Pleistocene stepwise migration patterns, with a subsequent restriction of the plants to various suitable habitats. Most of the 42 disjunct species grow only on calcareous substrates. It is possible to argue that recent long-distance dispersal, and establishment in ecologically suitable habitats accounts for these distribution patterns. However, this hypothesis is applicable to only a few rare cases (e.g. *Dryas drummondii*).

BIBLIOGRAPHY

Agassiz, Louis. 1841. Studies on glaciers. (translated and edited by Albert V. Carozzi). Urbana, University of Illinois Press. 213 p.

Anderson, J. P. 1916. Notes on the flora of Sitka. Proceedings of the Iowa Academy of Science 23:427-482.

__________ 1959. Flora of Alaska and adjacent parts of Canada. Ames, Iowa State University Press. 543 p.

Archer, Anthony Clifford. 1964. Some synecological problems in the alpine zone of Garibaldi Park. *In:* Ecology of the forests of the Pacific Northwest, 1962-1963, by V. J. Krajina. Vol. 2. Vancouver, University of British Columbia. p. 5-18.

Axelrod, D. I. 1958. Evolution of the Madro-Tertiary geoflora. Botanical Review 24:433-509.

Bakewell, A. 1943. Botanical collections of the Wood Yukon expeditions, 1939-1941. Rhodora 45:305-316.

Bamberg, S. A. and J. Major. 1968. Ecology of the vegetation and soils associated with calcareous parent materials in three alpine regions of Montana. Ecological Monographs 38:128-167.

Bamberg, S. A. and R. H. Pemble. 1968. New records of disjunct arctic-alpine plants in Montana. Rhodora 70:103-112.

Berry, F. A., Jr., E. Bollay and N. R. Beers (eds.). 1945. Handbook of meteorology. New York, McGraw-Hill. 1068 p.

Billings, W. D. 1969. Vegetational pattern near alpine timberline as affected by fire-snowdrift interactions. Vegetatio 10:192-207.

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.

Billings, W. D. and H. Mooney. 1968. The ecology of arctic and alpine plants. Biological Review 43:481-529.

Bishop, Daniel. 1972. Hydrologist, U. S. Forest Service. Personal communication.. Juneau, Alaska.

Bliss, L. C. 1956. A comparison of plant development in micro-environments of arctic and alpine tundras. Ecological Monographs 26(4): 303-337.

_______________ 1958. Seed germination in arctic and alpine species. Arctic 11: 180-188.

_______________ 1962. Adaptations of arctic and alpine plants to environmental conditions. Arctic 15: 117-144.

Bongard, H. G. 1833. Observations sur la vegetation de l'île de Sitcha. Memoirs of the Academy of Science St. Petersburg 6(2): 119-177.

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

_______________ 1964. Plant establishment in the high snowfall alpine and subalpine regions of British Columbia. Ecology 45: 431-438.

Brooke, R. C. 1965. The subalpine mountain hemlock zone. Part II. Ecotopes and biogeocoenotic units. Ecology of Western North America 1: 79-101.

_______________ 1966. Vegetation--environment relationship of subalpine mountain hemlock zone ecosystems. In: Progress Report on Ecology of the Pacific Northwest and Western Canadian Arctic and Subarctic, ed. by V. Krajina, Vancouver, University of British Columbia. p. 11-15.

Brooke, R. C., E. B. Peterson and V. J. Krajina. 1970. The subalpine mountain hemlock zone. Subalpine vegetation in southwestern British Columbia, its climatic characteristics, soils, ecosystems and environmental relationships. Ecology of Western North America 2(2): 153-349.

Brown, A. S. and H. Nasmith. 1962. The glaciation of the Queen Charlotte Islands. Canadian Field—Naturalist 76: 209-218.

Buddington, A. and T. Chapin. 1929. Geology and mineral deposits of Southeast Alaska. U. S. Geological Survey, Bulletin 800. 398 p.

Butler, E. J. 1918. Fungi and diseases in plants. Calcutta, Thacker, Sprenk and Company. 547 p.

Calder, J. A. and R. L. Taylor. 1968. Flora of the Queen Charlotte Islands. Part I. Canada Department of Agriculture, Monograph 4. 659 p.

Cantlon, J. E. 1961. Differences in plant abundance and cover in relation to macro-, meso-, and micro-relief. 128 numb. leaves. (Arctic Institute of North America. Final report of subcontracts Project ONR 208-212)

Churchill, E. D. and H. C. Hanson. 1958. The concept of climax in arctic and alpine vegetation. Botanical Review 24: 127-191.

Clements, F. E. 1928. Plant succession and indicators. New York, Wilson Company. 453 p.

Condon, W. H. 1961. Geology of the Craig quadrangle, Alaska. U. S. Geological Survey, Bulletin 1108-B. 43 p.

Coombe, D. E. and F. White. 1951. Notes on calcicolous communities and peat formation in Norwegian Lappland. Journal of Ecology 39(1): 33-62.

Cooper, W. S. 1931a. Seed-plants and ferns of the Glacier Bay National Monument, Alaska. Bulletin of the Torrey Botanical Club 57: 327-338.

__________ 1931b. The layering habits in Sitka spruce and the two western hemlocks. Botanical Gazette 91: 441-451.

__________ 1939. Additions to the flora of the Glacier Bay National Monument, Alaska, 1935-1936. Bulletin of the Torrey Botanical Club 66: 453-456.

__________ 1942. An isolated colony of plants on a glacier-clad mountain. Bulletin of the Torrey Botanical Club 69: 429-433.

Coulter, H. W. et al. 1965. Map showing extent of glaciations in Alaska. U. S. Geological Survey. Map I-415.

Coville, F. V. and F. Funston. 1895. Botany of Yakutat Bay, Alaska. Contributions to the U. S. National Herbarium 3(6): 325-356.

Dahl, Eilif. 1946. On different types of unglaciated areas during the ice ages and their significance to plant geography. New Phytologist 45:224-242.

_______________ 1951. On the relation between summer temperature and the distribution of alpine vascular plants in the lowlands of Fennoscandia. Oikos 3(1):22-52.

_______________ 1955. Biogeographical and geological indications of unglaciated areas in Scandinavia during the glacial ages. Bulletin of the Geological Society of America 66: 1499-1520.

_______________ 1956. Rondane mountain vegetation in Southern Norway and its relation to environment. Oslo, Aschehoug. 374 p.

_______________ 1959. Alpigenous and arctogenous plants. Pleistocene history of the flora of the North Atlantic region with special reference to Scandinavia. Recent Advances in Botany 1:919-925.

Douglas, G. W. 1971a. The alpine-subalpine flora of the North Cascade Range, Washington. Wasmann Journal of Biology 29(2):129-168.

_______________ 1971b. Effects of fire on alpine plant communities in the North Cascades, Washington. Ecology 52: 1058-1064.

Faegri, Knut. 1963. Problems of immigration and dispersal of the Scandinavian flora. In: North Atlantic biota and their history, by A. Löve and D. Löve. Oxford, Pergamon Press, Limited. p. 221-231.

_______________ 1966. A botanical excursion to Steens Mountain, southeastern Oregon, U. S. A. Blyttia 24: 173-181.

Falconer, G. et al. 1958. Glacial map of Canada. Toronto, Geological Association of Canada and Geological Survey of Canada.

Fernald, M. L. 1907. The soil preferences of certain alpine and sub-alpine plants. Rhodora 9:41-65.

__________ 1925. Persistence of plants in unglaciated areas of boreal America. American Academy of Arts and Sciences Memoirs 15:237-342.

Flint, R. F. 1945. Glacial map of North America. Geological Society of America Special Paper 60: 1-37.

Fonda, R. W. and L. C. Bliss. 1969. Forest vegetation of the montane and subalpine zones, Olympic Mountains, Washington. Ecological Monographs 39:271-301.

Franklin, Jerry F. 1971. Invasion of subalpine meadows by trees in the Cascade Range, Washington and Oregon. Arctic and Alpine Research 3:215-224.

Franklin, Jerry F. and R. G. Mitchell. 1967. Successional status of subalpine fir in the Cascade Range. U. S. Forest Service Research Paper PNW-46: 1-16.

Frederiksen, S. 1971. The flora of some nunataks in Frederikshab District, West Greenland. Botanisk Tidskrift 66: 60-68.

Fries, Th. 1925. The vertical distribution of some plants on Nuolja (Torne Lappmark). Botaniska Notiser 3:205-216.

Gass, C. R., et al. 1967. Soil management report for the Hollis area. U. S. Forest Service. In file report. Tongass National Forest. Alaska Region. 118 p.

Gimingham, C. H., N. M. Pritchard and R. M. Cormack. 1966. Interpretation of a vegetational mosaic on limestone in the Island of Gotland. Journal of Ecology 54:481-502.

Gjaerevoll, O. 1950. Snow-bed vegetation of the north of Sweden. Svensk Botanisk Tidskrift 44: 317-440.

__________ 1963. Survival of plants on nunataks in Norway during the Pleistocene glaciation. In: North Atlantic biota and their history, by A. Löve and D. Löve. Oxford, Pergamon Press. pp. 261-283.

Grebenshchikov, O. S. 1960. Vegetation of the high mountain areas of Yugoslavian Macedonia (the Vardar Basin). In: Studies on the flora and vegetation of high-mountain areas, ed. by V. N. Sukachev. Problems of Botany 5:104-117. (Israel Program for Science Translation. 1965. Jerusalem)

Griggs, R. F. 1934. The edge of the forest in Alaska and the reasons for its position. Ecology 15:80-96.

____________ 1938. Timberlines in the north Rocky Mountains. Ecology 19:548-564.

Grime, J. P. 1963. Factors determining the occurrence of calcifuge species on shallow soils over calcareous substrata. Journal of Ecology 51:375-390.

Harris, Arland. 1965. Subalpine fir on Harris Ridge near Hollis, Prince of Wales Island, Alaska. Northwest Science 39(4): 123-128.

Heusser, Calvin. 1953. Radiocarbon dating of the thermal maximum in Southeast Alaska. Ecology 34:637-640.

____________ 1954. Nunatak flora of the Juneau Icefield, Alaska. Bulletin of the Torrey Botanical Club 81:236-250.

____________ 1960. Late-Pleistocene environments of North Pacific North America. American Geographical Society Special Publication 35. 308 p.

____________ 1965. A Pleistocene phytogeographical sketch of the Pacific Northwest and Alaska. In: The quaternary of the United States, ed. by H. E. Wright, Jr. and D. G. Frey. p. 469-483.

Hickman, J. C. 1968. Disjunction and endemism in the flora of the central western Cascades of Oregon: an historical and ecological approach to plant distributions. Doctoral dissertation. Eugene, University of Oregon. 335 numb. leaves.

Hollick, A. 1930. The upper Cretaceous floras of Alaska with a description of the plant-bearing beds by G. C. Martin. U. S. Geological Survey Professional Paper 159:1-123.

__________ 1936. Tertiary floras of Alaska. U. S. Geological Survey Professional Paper 182: 1-185.

Hopkins, D. M. (ed.). 1967. The Bering land bridge. Stanford, University of California Press. 495 p.

Hoppe, G. 1963. Some comments on the "ice-free refugia" of northern Scandinavia. In: North Atlantic biota and their history, by A. Löve and D. Löve. Oxford, Pergamon Press. p. 321-335.

Hounsell, R. W. and E. C. Smith. 1968. Contributions to the flora of Nova Scotia. Part IX. Habitat studies of arctic-alpine and boreal disjunct species. Rhodora 70: 176-192.

Hultén, Eric. 1927-1930. Flora of Kamtchatka and the adjacent islands. Stockholm, Kunglinger Vetenskaps-Akademiens Handlinger. 5. 1135 p.

__________ 1937a. Flora of the Aleutian Islands and westernmost Alaska Peninsula with notes on the flora of the Commander Islands. Stockholm, Bokforlags Aktiebolaget Thule. 397 p.

__________ 1937b. Outline of the history of arctic and boreal biota during the Quaternary Period. Stockholm, Bokforlags Aktiebolaget Thule. 168 p.

__________ 1940. History of botanical exploration in Alaska and Yukon Territories from the time of their discovery to 1940. Botaniska Notiser, 1940, p. 289-346.

__________ 1958. The amphi-Atlantic plants and their phytogeographical connections. Stockholm, Kunglinger Svenska Vetenskaps Akademiens Handlinger Series 4. 7: 1-340.

__________ 1959. Alpigenous and arctogenous plants. Ranges of circumpolar arctic-montane plants. Recent Advances in Botany 1: 907-911.

__________ 1962. The circumpolar plants. Part I. Monocotyledons. Stockholm, Kunglinger Svenska Vetenskaps Akademiens Handlinger Series 4. 8: 1-275.

_______________ 1968. Flora of Alaska and neighboring territories. Stanford, University of California Press. 1008 p.

_______________ 1971. The circumpolar plants. Part II. Dicotyledons. Stockholm, Kunglinger Svenska Vetenskaps Akademiens Handlinger Series 4. 13: 1-463.

Johnson, A. W. and J. G. Packer. 1965. Polyploids and environment in arctic Alaska. Science 148:237-239.

Johnson, P. L. and W. D. Billings. 1962. The alpine vegetation of Beartooth Plateau in relation to cryopedogenic processes and patterns. Ecological Monographs 32: 105-135.

Karlstrom, Thor N. V. 1961. The glacial history of Alaska; its bearing on paleoclimatic theory. Annals of the New York Academy of Science 95:290-340.

Karlstrom, Thor N. V. and G. E. Ball (eds.). 1969. The Kodiak Island refugium. Its geology, flora, fauna, and history. Toronto, Ryerson Press. 262 p.

Kerr, F. A. 1936. Quaternary glaciation in the Coast Range, northern British Columbia and Alaska. Journal of Geology 44: 681-700.

Krajina, V. J. 1965. Biogeoclimatic zones and biogeocoenoses of British Columbia. Ecology of Western North America 1:1-17.

_______________ 1969. Ecology of forest trees in British Columbia. Ecology of Western North America 2: 1-146.

Kuramoto, R. T. and L. C. Bliss. 1970. Ecology of subalpine meadows in the Olympic Mountains, Washington. Ecological Monographs 40: 317-347.

Louseley, J. 1950. Wild flowers of the chalk and limestone. London, Collins. 316 p.

Löve, D. and N. J. Freedman. 1956. A plant collection from southwest Yukon. Botaniska Notiser 109: 153-211.

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. Madroño 17:93-109.

Marshall, Robert. 1956. Arctic Wilderness. Berkeley, University of California Press. 175 p.

McLean, A. 1970. Plant communities of the Similkameen Valley, British Columbia, and their relationships to soils. Ecological Monographs 40:403-424.

Meehan, Thomas. 1884. Catalogue of plants collected in July, 1883, during an excursion along the Pacific Coast in southeast Alaska. Proceedings of the Academy of Natural Sciences of Philadelphia, 1884, p. 76-96.

Miller, D. J. 1958a. Anomalous glacial history of the northeast Gulf of Alaska region. Bulletin of the Geological Society of America 96: 1613-1614.

______________ 1958b. Landscapes of Alaska--their geological evolution. Berkeley, University of California Press. 278 p.

Mooney, H. A. and W. D. Billings. 1961. Comparative physiological ecology of arctic and alpine populations of Oxyria digyna. Ecological Monographs 31:1-29.

Mooney, H. A. et al. 1962. Alpine and subalpine vegetation patterns in the White Mountains of California. American Midland Naturalist 68:257-273.

Mooney, H. A. and A. W. Johnson. 1965. Comparative physiological ecology of an arctic and alpine population of Thalictrum alpinum. Ecology 46:721-727.

Murray, D. F. 1968. A plant collection from the Wrangell Mountains, Alaska. Arctic 21:106-110.

______________ 1971. Notes on the alpine flora of the St. Elias Mountains. Arctic 24:301-304.

Neiland, Bonita. 1971. The forest-bog complex of Southeast Alaska. Vegetatio 22:1-63.

Nordhagen, R. 1963. Recent discoveries in the south Norwegian flora and their significance for the understanding of the history of the Scandinavian mountain flora after the last glaciation. In: North Atlantic biota and their history, by A. Löve and D. Löve, Oxford, Pergamon Press. p. 241-260.

Patric, J. H. and P. E. Black. 1968. Potential evapotranspiration and climate in Alaska by Thornthwaite's classification. U. S. Forest Service Research Paper PNW-71. 28 p.

Peterson, E. B. 1965. The subalpine mountain hemlock zone. Part I. Phytocoenoses. Ecology of Western North America 1:76-78.

Pigott, C. D. and S. M. Walters. 1954. On the interpretation of the discontinuous distributions shown by certain British species of open habitats. Journal of Ecology 42:95-116.

Polunin, Nicholas. 1959. Circumpolar arctic flora. Oxford, Clarendon Press. 514 p.

Porsild, A. E. 1945. The alpine flora of the east slope of the MacKenzie Mountains, Northwest Territories. National Museum of Canada Bulletin 101:1-35.

__________ 1951. Botany of southeastern Yukon adjacent to the Canol Road. National Museum of Canada Bulletin 121:1-400.

__________ 1966. Contributions to the flora of southwest Yukon Territory. Contributions to the National Museum of Canada 216:1-127.

Porter, S. C. 1971. Fluctuations of late Pleistocene alpine glaciers in western North America. In: Late Cenozoic glacial ages, ed. by K. K. Turekian, New Haven, Yale University Press. p. 307-329.

Presl, Karel B. 1825-1835. Reliquiae Haenkeanae seu descriptiones et icones plantarum quae in America meridionali et boreali, in insulis Phillipinis et Marianis collegit Thaddaeus Haenke. Prague, J. G. Calve. 2 vols.

Prest, V. K. 1969. Retreat of Wisconsin and recent ice in North America. Geological Survey of Canada Map 1257A.

Price, L. W. 1969. The collapse of solifluction lobes as a factor in vegetating blockfields. Arctic 22: 395-402.

Randhawa, A. S. and K. I. Beamish. 1972. The distribution of Saxifraga ferruginea and the problem of refugia in northwestern North America. Canadian Journal of Botany 50: 79-88.

Raup, Hugh M. 1934. Phytogeographical studies in the Peace and upper Liard River regions, Canada. Contributions to the Arnold Arboretum 6: 1-231.

__________ 1941. Botanical problems in boreal America. Botanical Review 7: 148-248.

__________ 1947. The botany of the southwest Mackenzie. Sargentia 6: 1-275.

__________ 1951. Vegetation and cryoplanation. Ohio Journal of Science 51: 105-116.

Rayner, M. C. 1913. The ecology of Calluna vulgaris. New Phytologist 12: 59-77.

Sainsbury, C. L. 1961. Geology of the northeast portion of the Craig quadrangle, Prince of Wales Island, Alaska. U. S. Geological Survey Bulletin 1058-H: 299-362.

Salisbury, E. J. 1952. Downs and dunes--their plant life and its environment. London, G. Bell and Sons, Ltd. 328 p.

Savile, D. B. O. 1956. Known dispersal rates and migratory potentials as clues to the origin of the North American biota. American Midland Naturalist 56: 434-453.

__________ 1960. Limitations of the competitive exclusion principle. Science 132: 1761.

Schmidt, R. L. 1957. The silvics and plant geography of the genus Abies in the coastal forests of British Columbia. British Columbia Forest Service Technical Publication T 46. 31 p.

Scofield, W. B. 1969. Phytogeography of northwestern North America: Bryophytes and vascular plants. Madroño 20: 155-207.

Shetler, Stanwyn. 1964. Plants in the arctic-alpine environment. Smithsonian Institute Publication 4584:473-497.

Sigafoos, R. S. 1951. Soil instability in tundra vegetation. Ohio Journal of Science 51:281-298.

_______________ 1952. Frost action as a primary physical factor in tundra plant communities. Ecology 33:480-487.

Sokhadze, E. V. and M. E. Sokhadze. 1960. Vegetation of Megrelia Highland (western Georgia) on limestone. In: Studies on the flora and vegetation of high-mountain areas, ed. by V. N. Sukachev. Problems of Botany 5:170-175. (Israel Progress for Science Translations. 1965. Jerusalem)

Stephens, F. R. 1969. A forest ecosystem on a glacier in Alaska. Arctic 22:441-443.

Stevens, M. E. 1965. Relation of vegetation to some soils in Southeastern Alaska. In: Forest soil relationships in North America, ed. by C. P. Youngberg, Corvallis, Oregon State University Press. p. 177-188.

Swanston, Douglas N. 1967. Geology and slope failure in the Maybeso Valley, Prince of Wales Island, Alaska. Doctoral dissertation. East Lansing, Michigan State University Press. 206 numb. leaves.

_______________ 1969. A late Pleistocene glacial sequence from Prince of Wales Island, Alaska. Arctic 22:25-33.

Tansley, A. G. 1917. On competition between *Galium saxatile* L. and G. *sylvestre* Poll. on different types of soil. Journal of Ecology 5:173-179.

Taylor, R. F. 1929. Pocket guide to Alaska trees. U. S. Department of Agriculture Miscellaneous Publications 55:1-39.

Thornthwaite, C. W. 1948. An approach toward a rational classification of climate. Geographical Review 38:55-94.

Tolmachev, A. I. 1960. The roles of migration and of autochthonous development in the formation of the high-mountain flora. In: Studies on the flora and vegetation of high-mountain areas, ed. by V. N. Sukachev. Problems of Botany 5:9-23. (Israel Progress for Science Translations. 1965. Jerusalem)

Twenhofel, W. S. 1952. Recent shoreline changes along the Pacific Coast of Alaska. American Journal of Science 250:523-548.

Vancouver, George. 1798. A voyage of discovery to the North Pacific Ocean and round the world; In which the coast of north-west America has been carefully examined and accurately surveyed. London, printed for G. G. and J. Robinson, Paternoster-Row Vol. 2, Book 4.

Viereck, L. A. and E. L. Little, Jr. 1972. Alaska trees and shrubs. U. S. Department of Agriculture. Agricultural Handbook 410. 265 p.

Walker, E. R. 1961. A synoptic climatology for parts of the western Cordillera. McGill University, Arctic Meteorological Research Group, Publications in Meteorology No. 35, Science Report 8:1-218.

Washburn, A. L. 1956. Classification of patterned ground and review of suggested origin. Bulletin of the Geological Society of America 67:823-866.

Weaver, J. E. and F. E. Clements. 1929. Plant ecology. New York, McGraw-Hill. 520 p.

Welsh, Stanley L. and J. K. Rigby. 1971a. Botanical and physiographic reconnaissance of northern Yukon. Brigham Young University Science Bulletin 14(2):1-64.

__________ 1971b. Botanical and Physiographic reconnaissance of northern British Columbia. Brigham Young University Science Bulletin 14(4):1-49.

Whitehead, F. H. 1951. Ecology of the Altipiano Monte Maiella, Italy. Journal of Ecology 39:330-355.

Wiggins, Ira L. and J. H. Thomas. 1962. A flora of the Alaskan arctic slope. Arctic Institute of North America Special Publications 4. 425 p.

Wolfe, J. A. 1966a. Tertiary plants from the Cook Inlet Region, Alaska. U. S. Geological Survey Professional Paper 398-B. 32 p.

__________ 1966b. Tertiary stratigraphy and paleobotany of the Cook Inlet region, Alaska. U. S. Geological Survey Professional Paper 398-A. 29 p.

Worley, Ian A. 1972. The bryo-geography of Southeast Alaska. Doctoral dissertation. Vancouver, University of British Columbia Press. 715 numb. leaves. (microfilm)

Worley, Ian A. and Dennis R. Jaques. 1973. Subalpine fir (Abies lasiocarpa) in coastal western North America. Northwest Science. (in press)

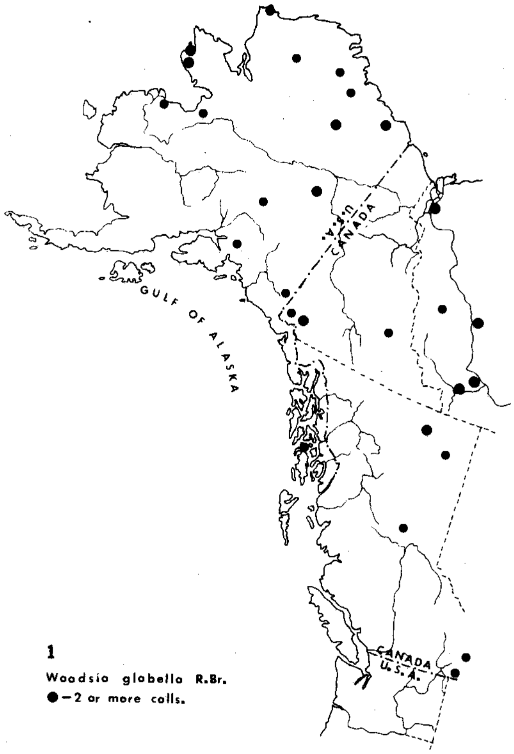
Wynne-Edwards, V. C. 1937. Isolated arctic-alpine floras in eastern North America: a discussion of their glacial and recent history. Transactions of the Royal Society of Canada 31:33-58.

__________ 1939. Some factors in the isolation of rare alpine plants. Transactions of the Royal Society of Canada 33:35-42.

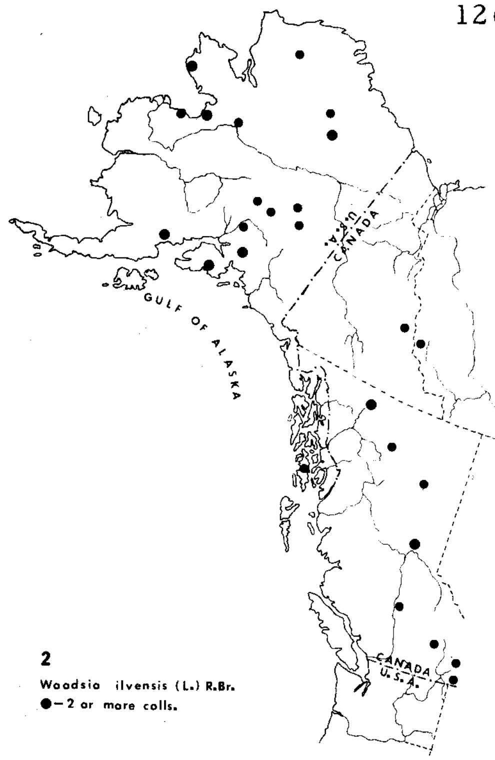
Young, S. B. 1970. On the taxonomy and distribution of Vaccinium uliginosum. Rhodora 72:439-459.

APPENDIX

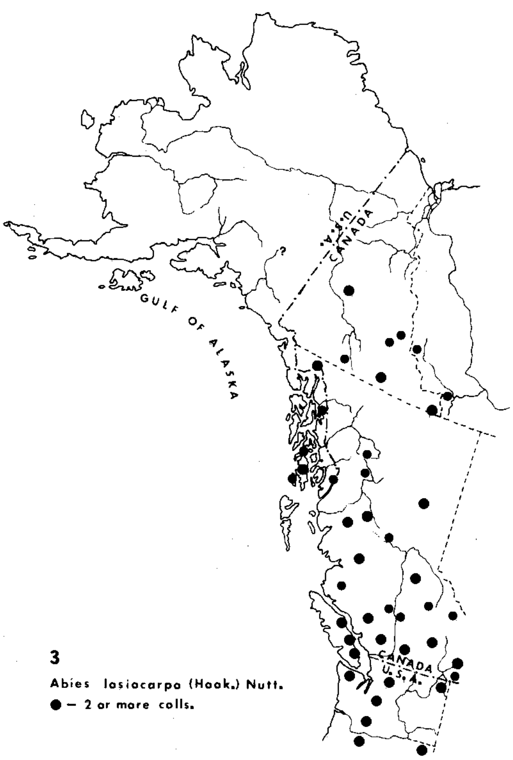
Distribution Maps of Disjunct Alpine Taxa,
Prince of Wales Island, Alaska



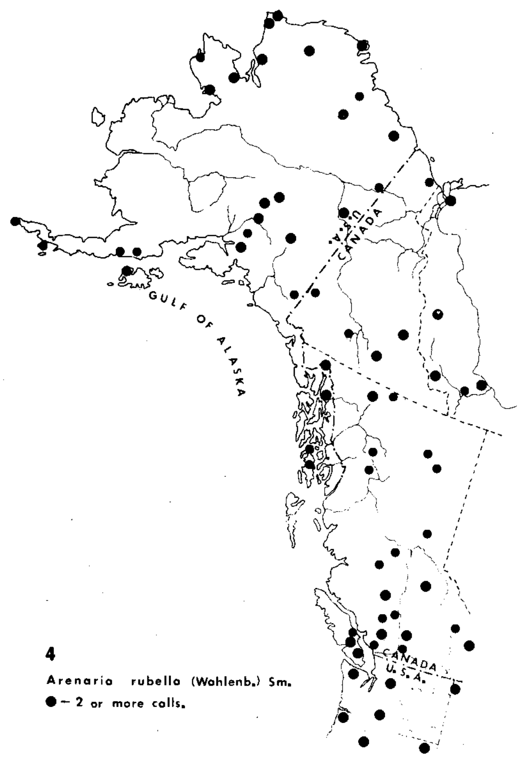
1
Woodsia glabella R.Br.
● – 2 or more colls.



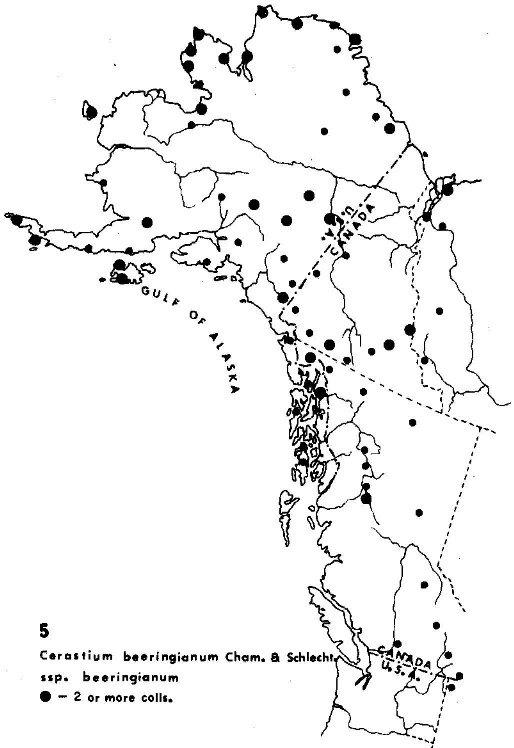
2
Woodsia ilvensis (L.) R.Br.
● – 2 or more colls.



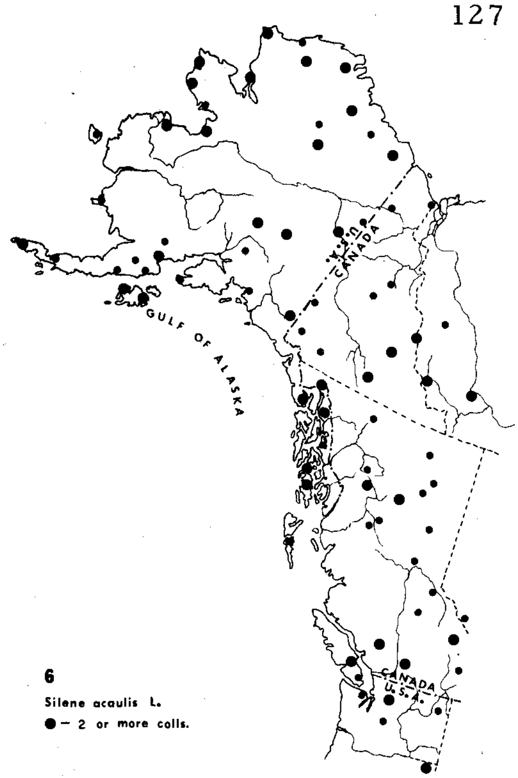
3
Abies lasiocarpa (Hook.) Nutt.
● – 2 or more colls.



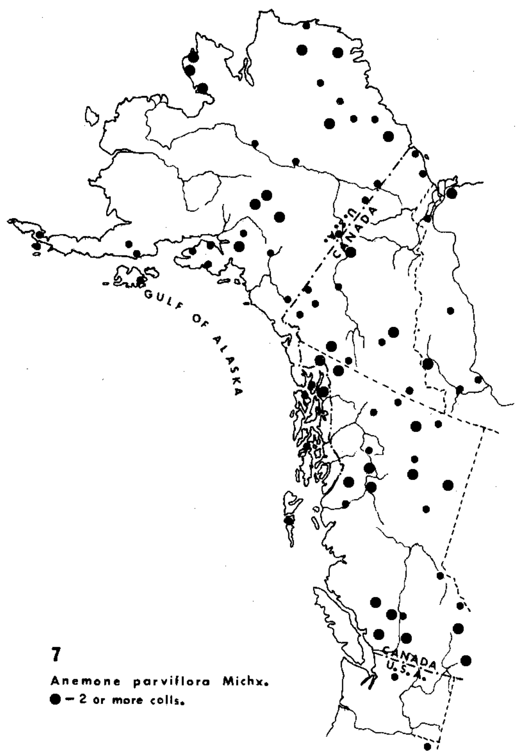
4
Arenaria rubella (Wahlenb.) Sm.
● – 2 or more colls.



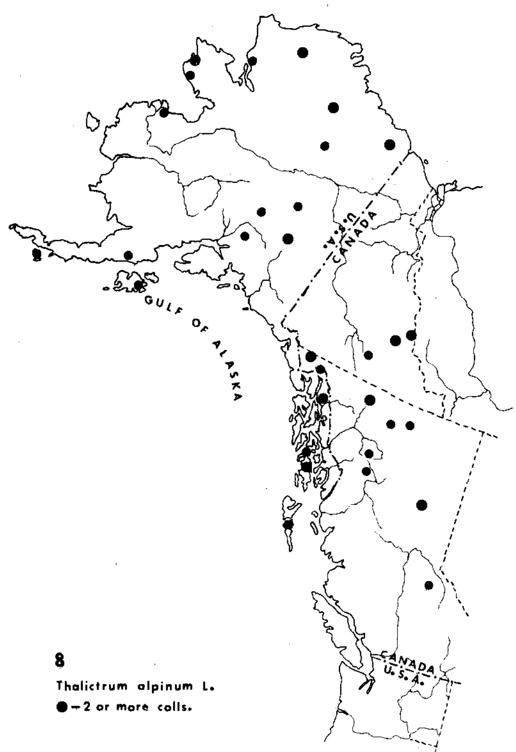
5
Cerastium beeringianum Cham. & Schlecht.
ssp. beeringianum
● – 2 or more colls.



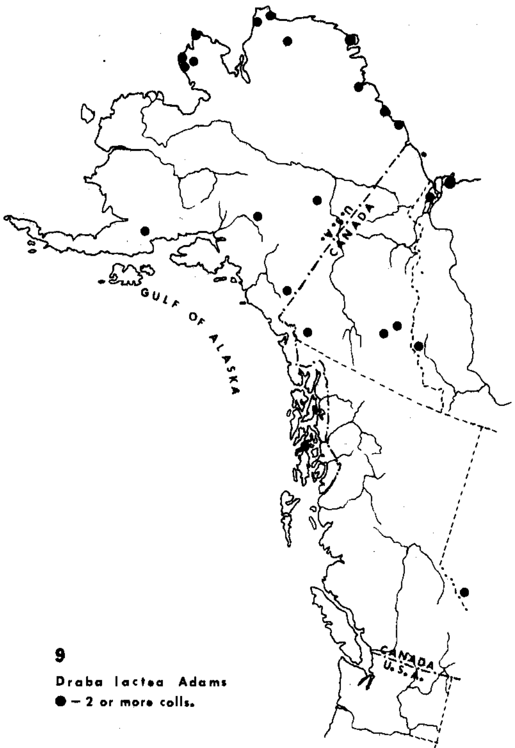
6
Silene acaulis L.
● – 2 or more colls.



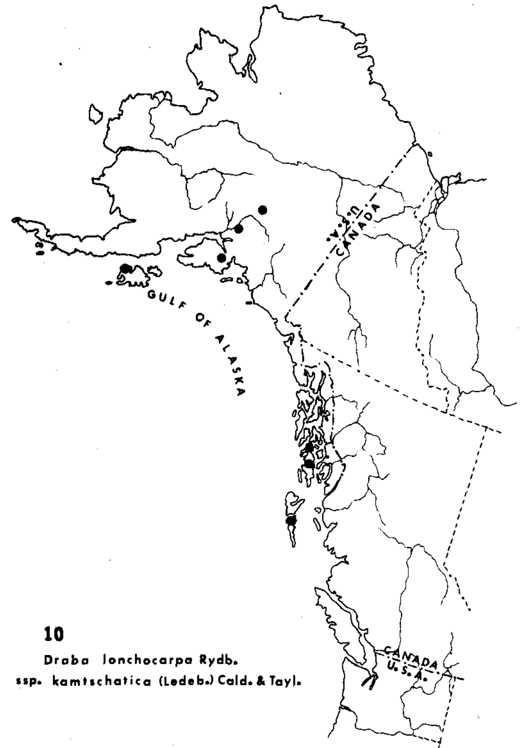
7
Anemone parviflora Michx.
● – 2 or more colls.



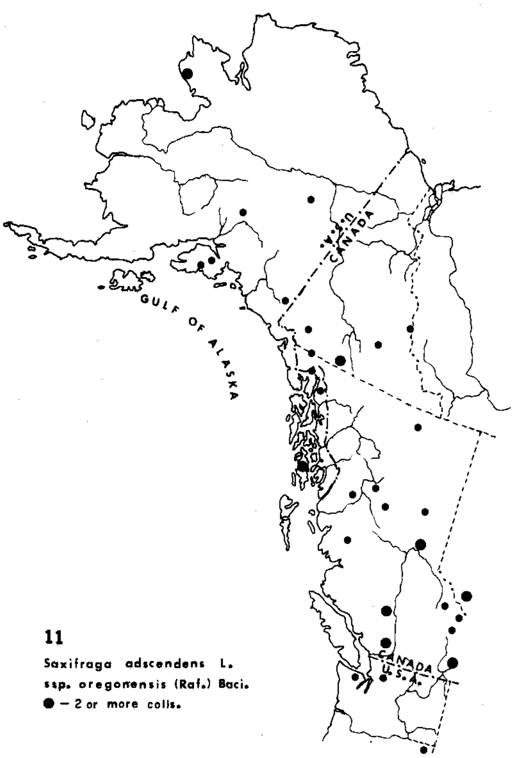
8
Thalictrum alpinum L.
● – 2 or more colls.



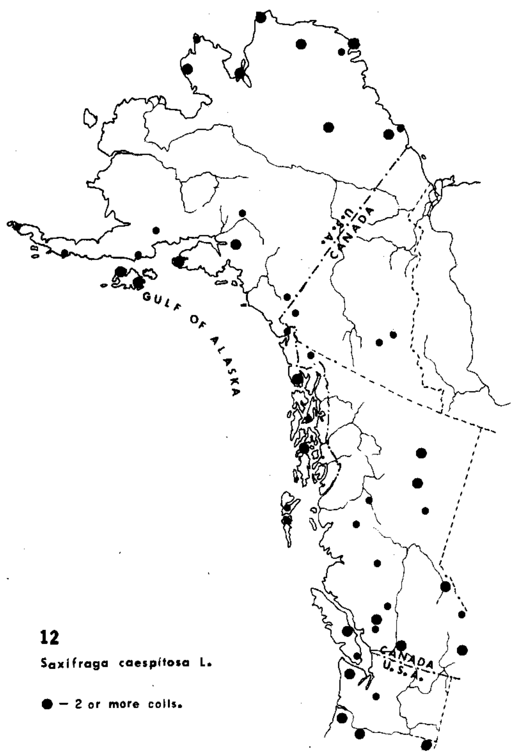
9
Draba lactea Adams
● – 2 or more colls.



10
Draba lonchocarpa Rydb.
ssp. kamtschatica (Ledeb.) Cald. & Tayl.

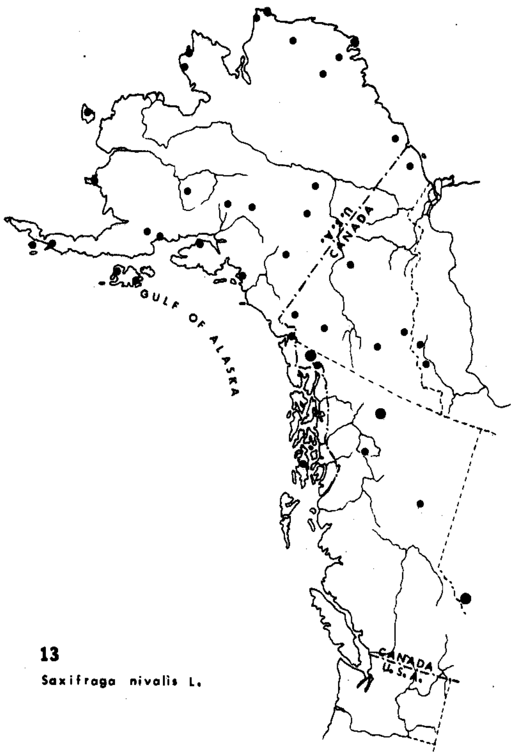


11
Saxifraga adscendens L.
ssp. oregonensis (Raf.) Baci.
● – 2 or more colls.

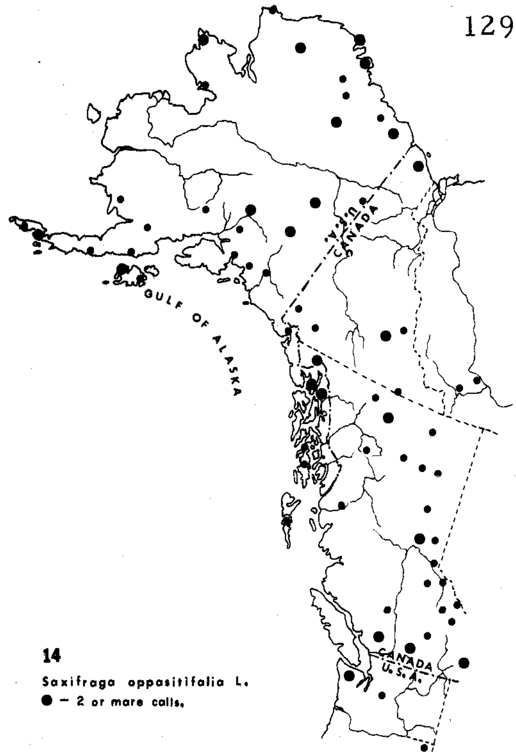


12
Saxifraga caespitosa L.

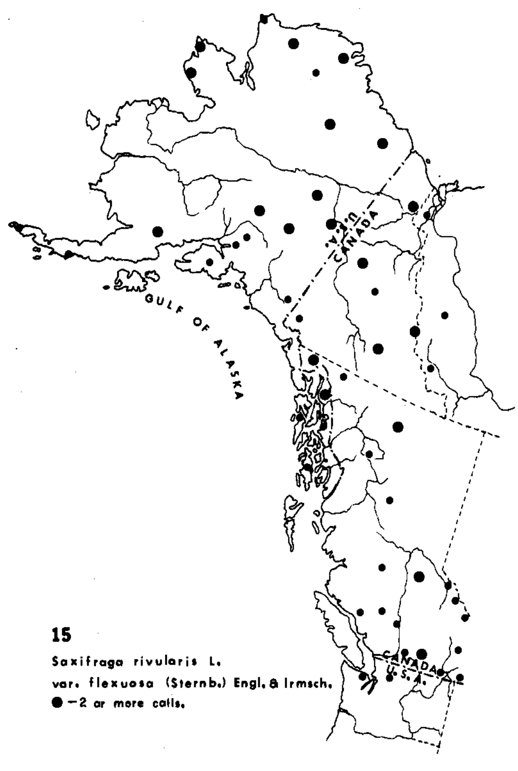
● – 2 or more colls.



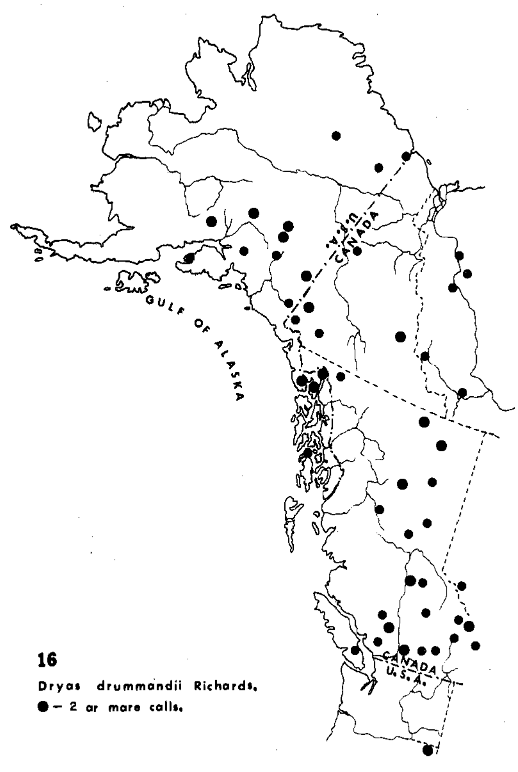
13
Saxifraga nivalis L.



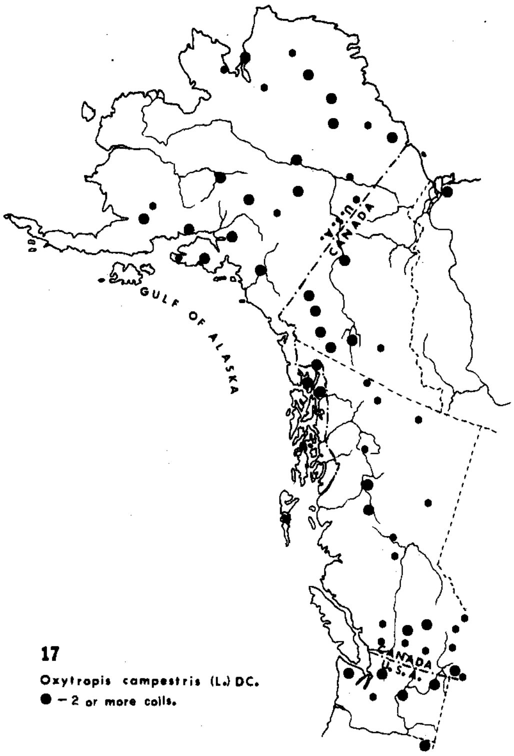
14
Saxifraga oppositifolia L.
● – 2 or more colls.



15
Saxifraga rivularis L.
var. flexuosa (Sternb.) Engl. & Irmsch.
● –2 or more colls.



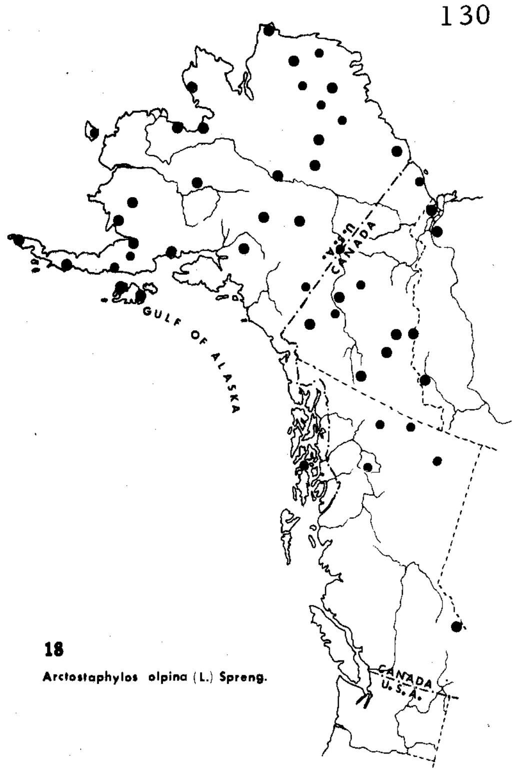
16
Dryas drummondii Richards.
● – 2 or more colls.



17

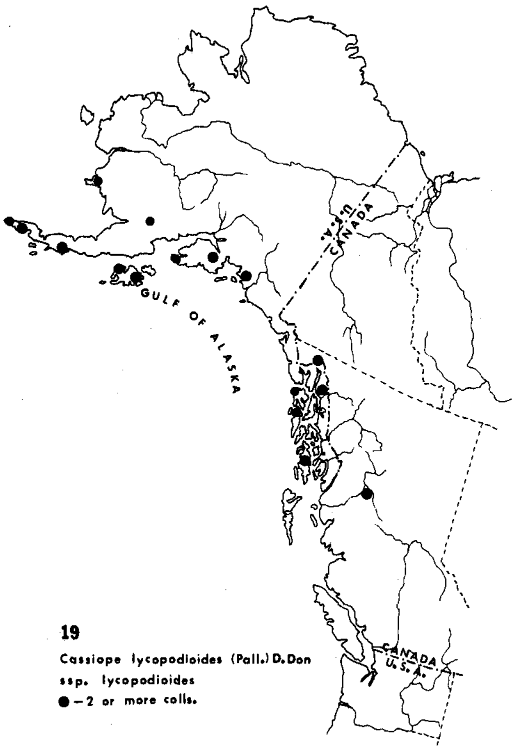
Oxytropis campestris (L.) DC.

● – 2 or more colls.



18

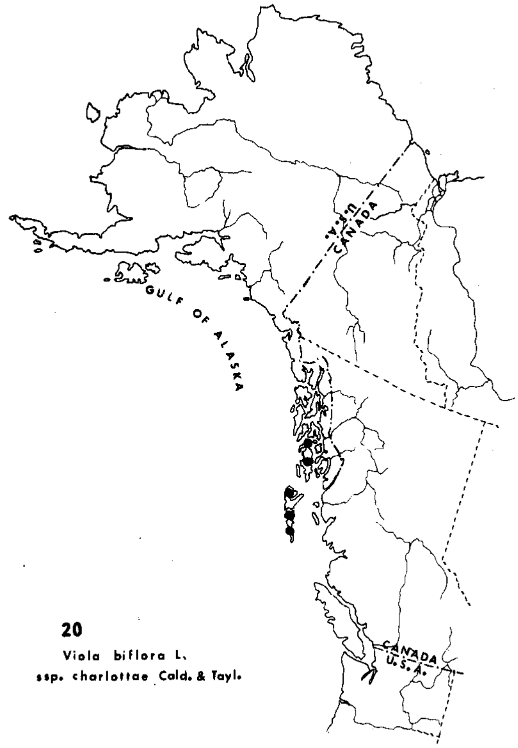
Arctostaphylos alpina (L.) Spreng.



19

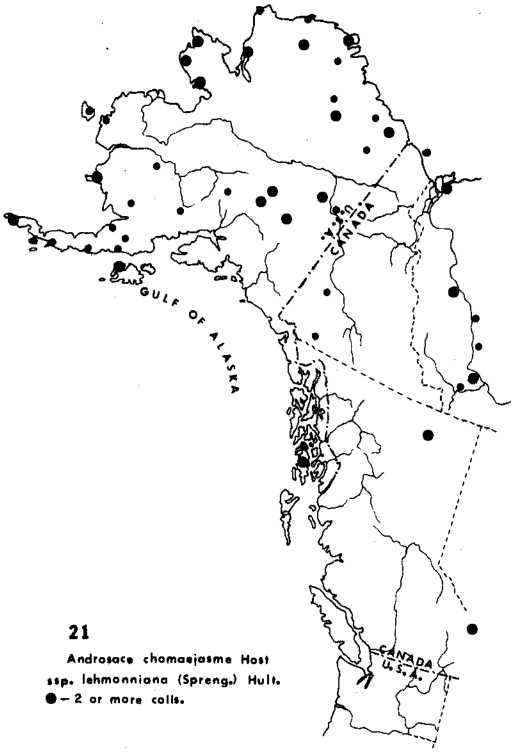
Cassiope lycopodioides (Pall.) D.Don ssp. lycopodioides

● – 2 or more colls.



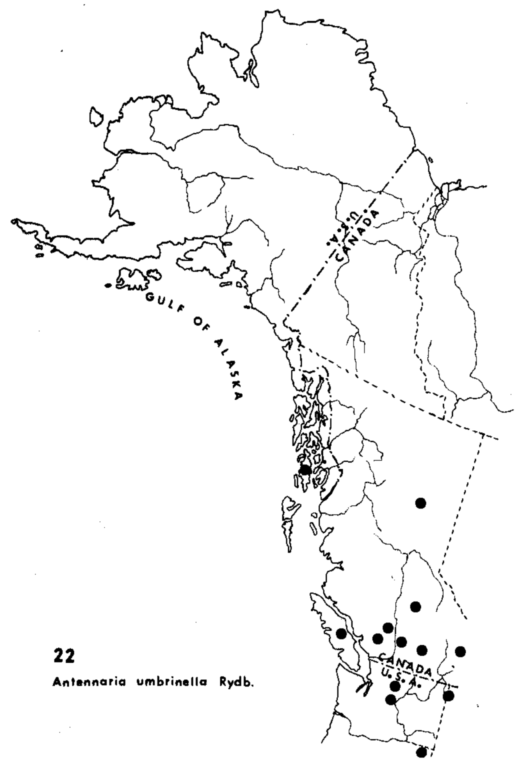
20

Viola biflora L. ssp. charlottae Cald. & Tayl.



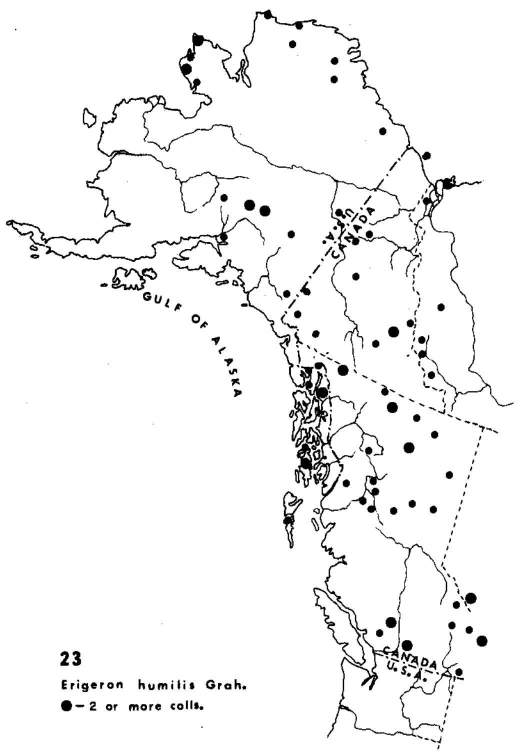
21

Androsace chamaejasme Host ssp. lehmanniana (Spreng.) Hult.
● – 2 or more colls.



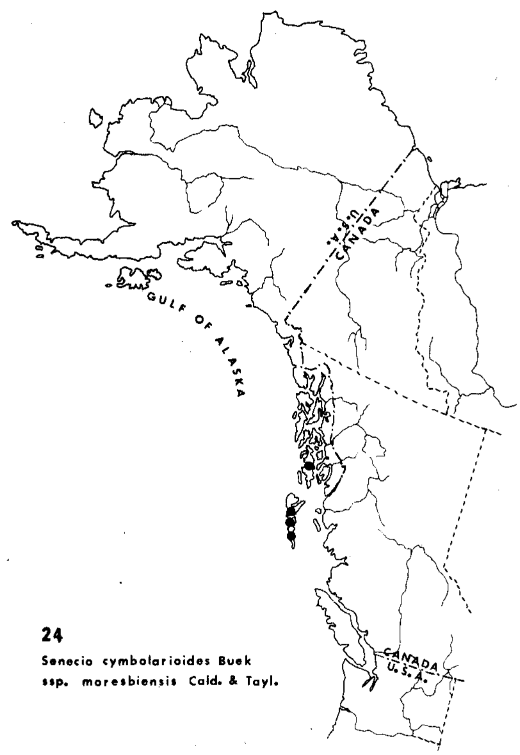
22

Antennaria umbrinella Rydb.



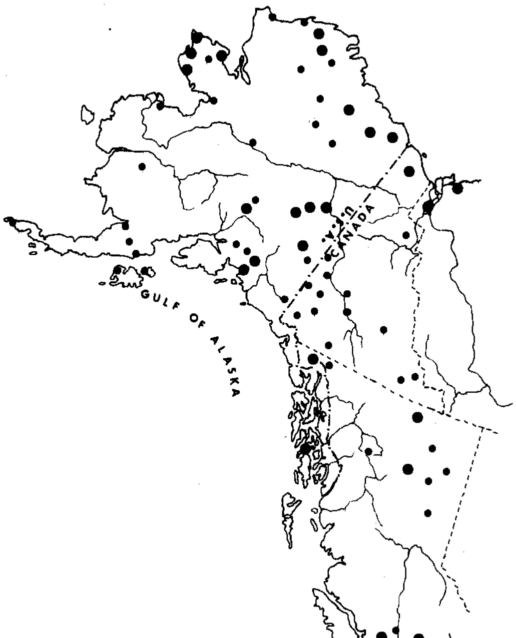
23

Erigeron humilis Grah.
● – 2 or more colls.



24

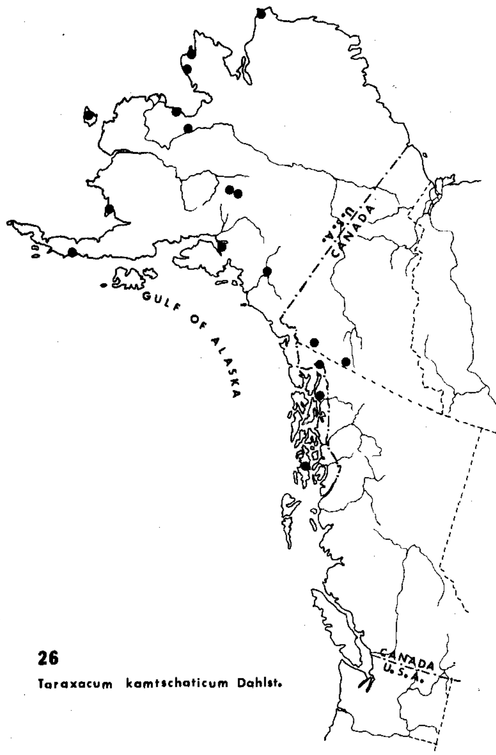
Senecio cymbalarioides Buek ssp. moresbiensis Cald. & Tayl.



25

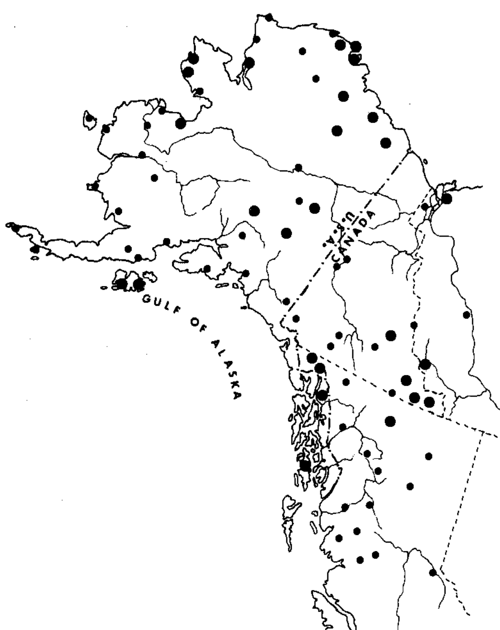
Senecio lugens Richards.

● – 2 or more colls.



26

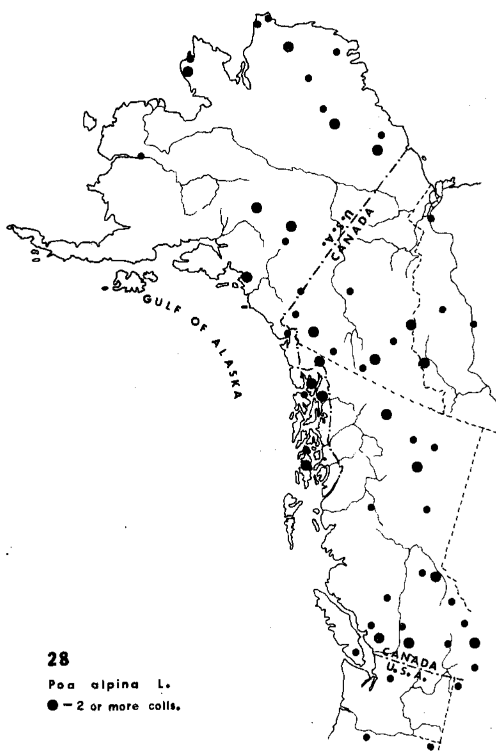
Taraxacum kamtschaticum Dahlst.



27

Hierochloë alpina (Sw.) Roem.&Schult.

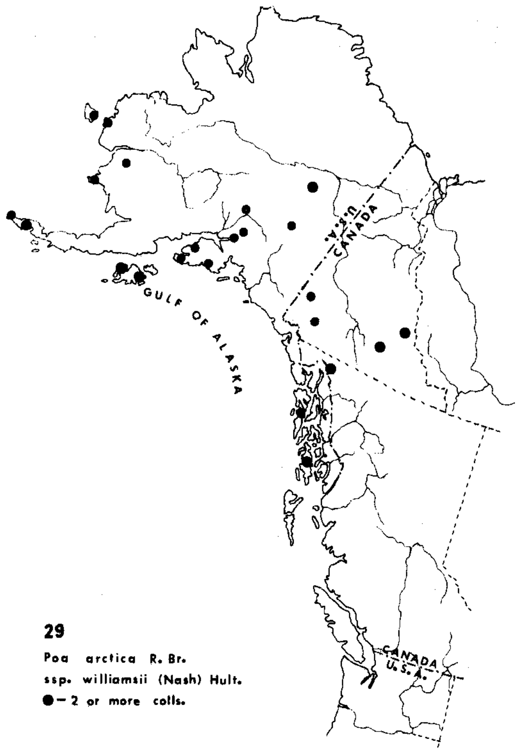
● – 2 or more colls.



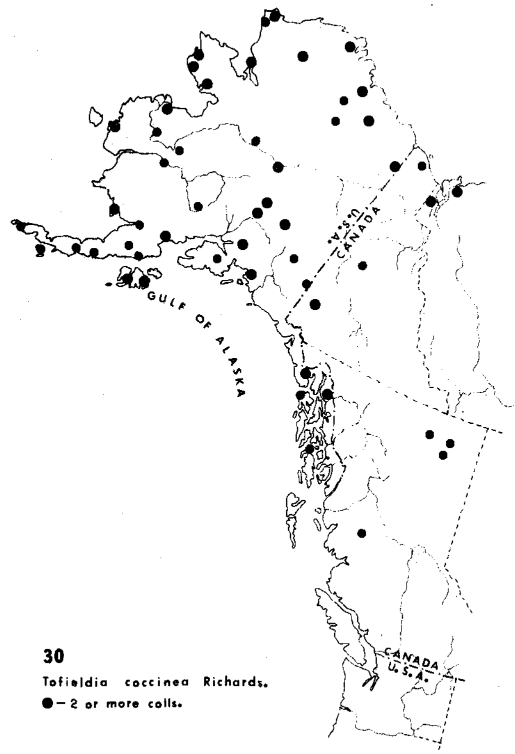
28

Poa alpina L.

● – 2 or more colls.



29
Poa arctica R. Br.
ssp. williamsii (Nash) Hult.
●— 2 or more colls.



30
Tofieldia coccinea Richards.
●— 2 or more colls.