AN ABSTRACT OF THE THESIS OF

Robert John Marquis for the degree of Master of Arts
in Botany and Plant Pathology presented on December 8, 1977
Title: AN INVESTIGATION INTO THE ECOLOGY AND DISTRIBUTION OF *KALMIOPSIS LEACHIANA* (HEND.) REHDER
Abstract approved: Redacted for Privacy
William W. Chilcote

Ecological factors associated with the relictual distribution of the endemic shrub *Kalmiopsis leachiana* (Ericaceae) were investigated. A prostrate evergreen species with small coriaceous leaves, *K. leachiana* is restricted to two disjunct populations in the Siskiyou Mountains and southern Cascade Mountains of southwestern Oregon, USA. Exact distributions of individual populations were mapped and were related to soils, geology, climate, and fire history using these factors to define in part this species' ecological range. Further investigation involved intensive sampling of associated vegetation, pressure chamber studies, seed germination and seedling growth experiments, and preliminary study of herbivore relationships and the heterostylous breeding system.

Associated vegetation of *Kalmiopsis* populations was sampled using a nested plot technique. Analysis showed there to exist three major vegetation units: (1) low elevation Siskiyou stands (300-600 m), characterized by a conifer, broadleaf sclerophyll tree, evergreen shrub, and herb layer; (2) high elevation Siskiyou stands (900 m), differing from low elevation site by the absence of a broadleaf sclerophyll canopy; and (3) Southern Cascades vegetation, having relatively low species diversity associated with a more dense conifer canopy. In the latter stands, Kalmiopsis is found to grow almost invariably only on exposed, silicified rock outcrops. Soil in the Cascades did not prove to be inhibitory to germination and seedling development. Thus it is suggested that competition for light, water, and nutrients plays an important role in the species distribution and especially in its exclusion from surrounding vegetation of Cascades rock outcrops. In turn loss of the broadleaf sclerophyll canopy at high elevations in the Siskiyous, and related decrease in overstory canopy cover, is correlated with the much greater abundance of Kalmiopsis at high elevations there. The nature of the growth form and morphology of this plant and how they appear to be advantageous for establishment and growth in rocky, competition low microhabitats is discussed.

Measurements of internal moisture stress were taken in the Siskiyou Mountains on Kalmiopsis and two sympatric sclerophyllous shrub species. Results of predawn and midday measurements at the height of the drought season indicate that Kalmiopsis undergoes higher stress levels than the other two species do in the same location, and appears to shut its stomata early in the day to avoid high stress

buildup. In contrast the two sympatric shrubs appear to be able to remain photosynthesizing longer into the day, and this combined with their ability to handle higher stress, might account for their occurrence at more xeric topographic positions where K. leachiana is not found.

Germination and growth experiments on natural soils showed that Kalmiopsis seeds can germinate under low light conditions, are heat sensitive, and resulting seedlings have relatively slow growth rates. The seedlings' small size and slow growth rates are suggested to account for the low reproductive rate observed in the field and to be a contributing factor in the restricted distribution of the species.

Kalmiopsis is distylous, this being the first reported case of heterostyly in the Ericaeae. In addition evidence is given that this morphological adaptation for outcrossing is strengthened by genetic self-incompatibility within and between plants of similar morphological types.

Evidence of herbivory was practically absent in all populations. Two seed eating species, a lygaeid bug in the genus Kleidocerys and a species of mite in Trichoribates, were found to be associated with the persistent capsules. These may play an important role in the reproductive output of this plant.

An Investigation into the Ecology and Distribution of *Kalmiopsis leachiana* (Hend.) Rehder

by

Robert John Marquis

A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Master of Arts

Completed December 1977

Commencement June 1978

APPROVED:

Redacted for Privacy

Professor of Botany
in charge of major

Redacted for Privacy

Chairman of Department of Botany and Plant Pathology

Redacted for Privacy

Dean of Graduate School

Date thesis is presented December 8, 1977

Typed by Mary Jo Stratton for Robert John Marquis

ACKNOWLEDGEMENTS

I would like to express my appreciation here to those who have helped in the realization of this study. First of all, the advice and encouragement of Dr. William Chilcote were invaluable. Dr. Kenton L. Chambers helped greatly with an initial introduction to the general Siskiyou area and his further technical advice was always present when needed. Greenhouse space for experimental studies was provided through the courtesy of Dr. Chambers. I would like to thank the ladies of the Limpy Rock Committee, and especially Jeanie Moore, for their aid and guidance in location of *Kalmiopsis* populations in the North Umpqua River area. Many members of the Siskiyou National Forest of the United States Forest Service also aided in numerous ways and are thanked as well. Mr. Len Ramp, through identification of collected rock samples, made possible an important part of this study. Field study of populations in the Big Craggies Botanical Area were made through a grant of the Northwest Scientific Association and through funds provided by Dr. Thomas C. Moore and the Department of Botany and Plant Pathology at Oregon State University. Additional funding was provided by Dr. J. Lattin of the Department of Entomology, OSU. And lastly, I would especially like to thank Cheryl A. Crowder for her valuable assistance and encouragement in the field, and discussion of ideas which are presented here.

TABLE OF CONTENTS

METHODS

Table of Contents (Continued)

APPENDICES

LIST OF TABLES

List of Tables (Continued)

List of Tables (Continued)

LIST OF FIGURES

List of Figures (Continued)

AN INVESTIGATION INTO THE ECOLOGY AND DISTRIBUTION OF *KALMIOPSIS LEACHIANA* (HEND.) REHDER

INTRODUCTION

The genus *Kalmiopsis* is a monotypic member of the Ericaceae. Its one species, *K. leachiana* (Hend.) Rehder, is a prostrate evergreen shrub with small, entire, coriaceous leaves, which are densely dotted beneath with golden glands but are otherwise glabrous. The bright pink flowers are borne on pedicels up to 2 cm long and are typically ericaceous, with a five-lobed gametopetalous corolla and ten stamens whose anthers open by terminal pores. The corolla is broadly campanulate and actinomorphic.

Kalmiopsis leachiana was first discovered on June 14, 1930 by Dr. and Mrs. J.R. Leach at Gold Basin, Curry County, in the south western corner of Oregon. Here it shares habitats with other three distinctive endemic species, *Picea breweriana*, *Quercus sadleriana*, and *Leucothoe davisiae*, in the rugged and ancient mountain range known as the Siskiyou Mountains. This area is well known for the number of species of restricted distribution which are found there, and for its possible importance as part of a floristic center of the Pacific Northwest (Whittaker, 1961). But unlike many Siskiyou mountain endemics, *K. leachiana* occurs in a second geographical province, skipping approximately 160 km to the northeast to a small area in the southern Cascade Mountains. This mountain range has had an entirely different geologic history and is covered by a different type of vegetation. Here, *Kalmiopsis* is almost invariably a rock-dweller on exposed, sunny outcrops of silicified tuffs. This modest disjunction in the range of *Kalmiopsis* itself is overshadowed by a much larger one between Kalmiopsis and its nearest relatives, *Rhodothamnus chamaecistus* and *R. sessifolius*. The latter two species grow in alpine and subalpine portions of the Eastern Alps of Europe and on two peaks of northeastern Turkey, respectively.

Previous study of the distribution of *Kalmiopsis leachiana* and its ecological and environmental limits has been limited to passing notes in vegetational studies of broader scope (Whittaker, 1960; Gratkowski, 1961; Stebbins and Major, 1965; Waring, Emmingham, and Running, 1975) and to general articles describing the plant's botanical features (Rehder, 1932; Steward, 1957; Lang, 1969; Gerdemann, 1972; Mulligan, 1973). It has been reported to occur in a wide range of habitats as: a cliff dweller of dry, sunny rocks (Mulligan, 1973); a member of cool, high elevation Brewer spruce forests (Waring, Emmingham, and Running, 1975); an inhabitant of dry, stony slopes of the mountains of Curry County (Peck, 1961); and an associate and indicator of southwestern Oregon chaparral fire climax vegetation (Gratkowski, 1961).

The purposes of the present study were to establish the exact distribution of *Kalmiopsis leachiana*, to describe the environmental conditions in which it is found, and to relate those environmental conditions to its distribution with the intention of developing a possible explanation for its present pattern of occurrence. The specific aspects of the environment of *Kalmiopsis* which were studied included both abiotic and biotic factors that were felt to be important as influencing agents and at the same time could be quantified with the facilities available. The climate, fire history, physiography and geology, and resulting soils of the sites where *K. leachiana* grows were singled out as abiotic factors for study. The biotic portion of the environment on which study was centered included the surrounding vegetation and macroscopic herbivores.

Both a synecological and an autecological approach were taken for answering the questions at hand. In the absence of detailed measurements of the abiotic environment, vegetation was considered to be a direct reflection of that portion of the environment. In this sense changes in vegetation were viewed as representing changes in the biotic environment of *Kalmiopsis* and, indirectly, the abiotic environment. For this reason, vegetation was sampled intensively to establish the environmental range of this plant and to study the details of vegetational patterns within its distribution.

The autecology of Kalmiopsis leachiana was studied to determine the reproductive and evolutionary strategies of this plant and how they are related to its environment and thus its distribution. Its morphology, growth habit, phenology, and floral ecology were investigated, with emphasis on how these characteristics are affected by the environment. Because the distribution of a plant is a direct result of its reproductive success, the seed and seedling aspects of the reproductive cycle were examined from the standpoint of how soil type, fire, light, and possible chemical inhibitors might affect germination and development. Pressure chamber measurements were made to determine how Kalmiopsis physiologically interacts with such environmental components as soil moisture levels and atmospheric demand and how these might limit its distribution. Emphasis was placed at all times on differences in the environment which exist between the Siskiyou Mountains and the Cascade Mountains and in what way these might be associated with ecotypic differences in the respective populations.

Systematics of Kalmiopsis leachiana

Kalmiopsis leachiana has been considered by taxonomists as constituting the monotypic genus Kalmiopsis or has been treated as a member of the genus Rhodothamus Reichb. under the name R. leachianum (Hend.) Copeland. It was first described, soon after its discovery, as *Rhododendron leachianum* (Henderson, 1931) because of its general similarity in appearance to *Rhododendron lapponicum* Whlbg. However, its bracts and bracteoles are persistent while those of *Rhododendron* are deciduous, its seeds are unwinged whereas *Rhododendron* seeds include an elongated testa which forms a fringed wing at the ends, and its corolla is actinomorphic while that of *Rhododendron* is generally weakly zygomorphic. Rehder (1932) considered the species distinctive enough to comprise a separate genus *Kalmiopsis*. This name suggests a link to *Kalmia*, with which it shares a morphologically similar corolla. Although there are folds in the corolla of *K. leachiana* that house the stamens during development of the floral buds, the anthers are not held in pouches of the corolla at anthesis as they are in *Kalmia*. In addition, bracts of *K. leachiana* are alternate while those of members of the genus *Kalmia* are opposite.

A different taxonomic placement was proposed by Copeland (1943, 1954; see also Cox, 1948), who reassigned *Kalmiopsis leachiana* to the European and West Asian genus *Rhodothamnus*. Copeland mainly emphasized similarities in development and anatomy, especially internal leaf anatomy and structure of the vascular system of the receptacle. More recent workers (Davis, 1962; Callan, 1971; Stevens, 1971; Harborne and Williams, 1973) have recognized *K. leachiana* as separate from the genus *Rhodothamnus*, and this is the interpretation I will follow as well.

The genus *Rhodothamnus* consists of two widely separated relictual endemic species: *R. chamaecistus* (L.) Reichb., which is confined to the Eastern Alps of Austria, eastern Switzerland, northern Italy, western Yugoslavia, and southern-most West Germany; and *R. sessifolius* P.H. Davis, which is known only from two peaks in northeastern Turkey (Davis, 1962). Both species of *Rhodothamnus* are low, spreading shrubs with adventitiously rooting stolons and small, evergreen leaves with ciliated margins. *Rhodothamnus chamaecistus* grows to a height of 40 cm and has acute petiolate leaves which are 5 to 15 mm long and are one-half to one-third as wide, with multicellular bristles pointing forward along the leaf margins. The leaves are scattered the length of the stem. *Rhodothamnus sessifolius* is smaller, only 10 cm tall, with obovate, obtuse, sessile leaves 7 to 12 mm long and 3 to 5 mm wide. The ciliation is composed of two types of hairs, multicellular glandular-capitate and unicellular glandular. The leaves are clustered to form rosettes at the stem apices. Flowers of both species are borne on the terminal portion of the stems, one to three in number. The corolla of *R. sessifolius* is lilac-pink to pink, perhaps darker in tone than that of *R. chamaecistus* (Davis, 1962). The corollas of both species are rotate, with short tubes (2 mm) and long, exerted styles and stamens, the style somewhat longer than the ten stamens.

The stamens of R. chamaecistus are longer on the upper side of the flower, making it slightly zygomorphic, while R. sessifolius is actinomorphic.

Callan (1971) has summarized the salient differences between Kalmiopsis leachiana and Rhodothamnus chamaecistus. The latter species exhibits a zygomorphic corolla with deep sinuses between the lobes, while the corolla of Kalmiopsis is shallowly lobed, with slight folds in the lobes, and actinomorphic. Rhodothamnus chamaecistus and R. sessifolius have ciliate leaf margins while those of K. leachiana are only minutely setose-puberulent with stalked glands. The "lepidote" glands of the lower leaf surfaces of K. leachiana are absent from leaves of both species of Rhodothamnus.

Though the intrageneric classification of the members of the family Ericaceae and other families closely associated with it varies with different authors (see Stevens, 1971), the genera Kalmiopsis and Rhodothamnus have always been placed together in the tribe Phyllodoceae (Rhodoreae of Hooker) in the subfamily Rhododendroideae (Hooker, 1876; Drude, 1897; Copeland, 1943; Cox, 1954; Schultze-Motel, 1964). The most recent treatment of the Ericaceae is by Stevens (1971) using numerical taxonomic characteristics. He divides the Rhododendroideae into seven tribes and includes in the Phyllodoceae along with Kalmiopsis and Rhodothamnus, the genera Kalmia, Bryanthus, Ledothamnus, Leiophyllum and

Loiseleuria. This is essentially the same as the Phyllodoceae of previous workers except Daboecia and Diplarche have been placed in separate tribes of their own. The results of chemical analysis of leaf flavonoids and simple phenols of the Ericaceae support Stevens' system (Harborne and Williams, 1973).

The Rhododendroideae is considered to be the most primitive of the Ericaceae subfamilies due to the large number of carpels, petals and stamens of some genera, the presence of free petals in many genera, and the primitive nature of the wood (Cox, 1948). Of the 19 genera of Stevens' Rhododendroideae, 13 contain three species or fewer, and eight are monotypic. Most are well isolated taxonomically from each other and show little speciation, the genus Rhododendron, which includes more than 800 species (Stevens, 1971) being an obvious exception. These characteristics, along with the many examples of isolated geographical distribution, demonstrate that the Rhododendroideae is composed of relatively ancient, phylogenetically well separated genera which have been evolving away from each other for a long time. Kalmiopsis leachiana, Loiseleuria procumbens (Rehder, 1932), and Rhodothamnus chamaecistus (Hegi, (1909-1931, Vol. 5) are all considered old taxa of the Tertiary age.

Within the Phyllodoceae, for those species whose chromosome counts have been made, the base number has been found to be x=12 (Stevens, 1971). For some species of Rhododendron, x=13 (Hagerup, 1928). The base number of both *Kalmiopsis leachiana* (Baldwin, 1938) and *Rhodothamnus chamaecistus* (Polatschek, 1966 in Hess, Landolt, and Hirzel, 1930) is reported to be x = 12, and for both 2n = 24. Cox (1948) considered there to be three phylogenetic lines within the Phyllodoceae, all derived from a common ancestor. *Loiseleuria*, *Ledothamnus*, and *Leiophyllum* represent one line, *Phyllodoce* and *Bryanthus* represent another, and *Rhodothamnus* (including *Kalmiopsis*) and *Kalmia* a third.

Habitats and Ecology of the Genus *Rhodothamnus*

The distribution of *Rhodothamnus chamaecistus* follows two east-lying geologic formations of the eastern Alps, which consist mainly of diolomite (Hegi, 1909-1931, Vol. 5). It occurs most commonly in crevices in calcareous rock derived from either limestone or dolomite (Davis, 1962; Hess, Landolt, and Hirzel, 1970). These rocky habitats are frequently part of steep, sunny talus slopes scattered with large boulders and much exposed bedrock. The calcareous soils show little development, and consequently are stony and highly susceptible to slippage. The common elevational range of *R. chamaecistus* coincides with the subalpine and lower portions of the alpine zone of the Eastern Alps from 1000 m to 2400 m (3000 feet to 7800 feet). Only rarely does it extend into the lower elevational montane forests, and then never below 350 m.

Rhodothamnus chamaecistus occurs in three different vegetational associations: a rock-crevice association on large rock outcroppings where little soil development has taken place, a krummholtz-shrub association, and as an understory species of decumbent Pinus montana forests (Hess, Landolt, and Hirzel, 1970). The krummholtz-shrub association occurs as a band extending from just above the tree-line of subalpine and alpine areas to about 50 m higher in elevation. It may also overlap with sparse subalpine forests, becoming the understory in that case. It is especially common on nutrient poor soils, either highly acidic or highly basic. Rhododendron hirsutum is the major component with which Rhodothamnus is associated on limestone derived soils, and Rhododendron ferrugeum predominates on acidic soils.

Pinus montana is characteristically found on sites of extreme environments where soils are stony and dry in the summer, and slopes are steep. In the western Alps P. montana assumes a normal erect tree form, but farther east it becomes decumbent and krumholtz in growth. In these eastern "Gebuschgesellschaften" Rhodothamnus chamaecistus occurs in P. montana forests which develop on dry, exposed, subalpine summits and ridges, where avalanches and slippage are common and exposed bedrock with small areas of poorly developed soils serve as the main substrate. Along with R. chamaecistus in the understory are often found Erica carnea, *Arctostaphylos uva-ursi*, and *Rhododendron hirsutum*. In sites where soils are less developed and the overhead canopy is very sparse, the common associates include such species as *Dryas octopetala*, *Primula auricula*, *Globularis cordifolia* and *Carex firma*.

The two known locations for *Rhodothamnus sessifolius* are both above timberline. At one of the sites it grows from ledges of a shady igneous cliff, with *Potentilla oweriana*, at 2150 m altitude. The second collection was from steep, moist banks at 2400 m elevation (Davis, 1962).

THE STUDY AREAS

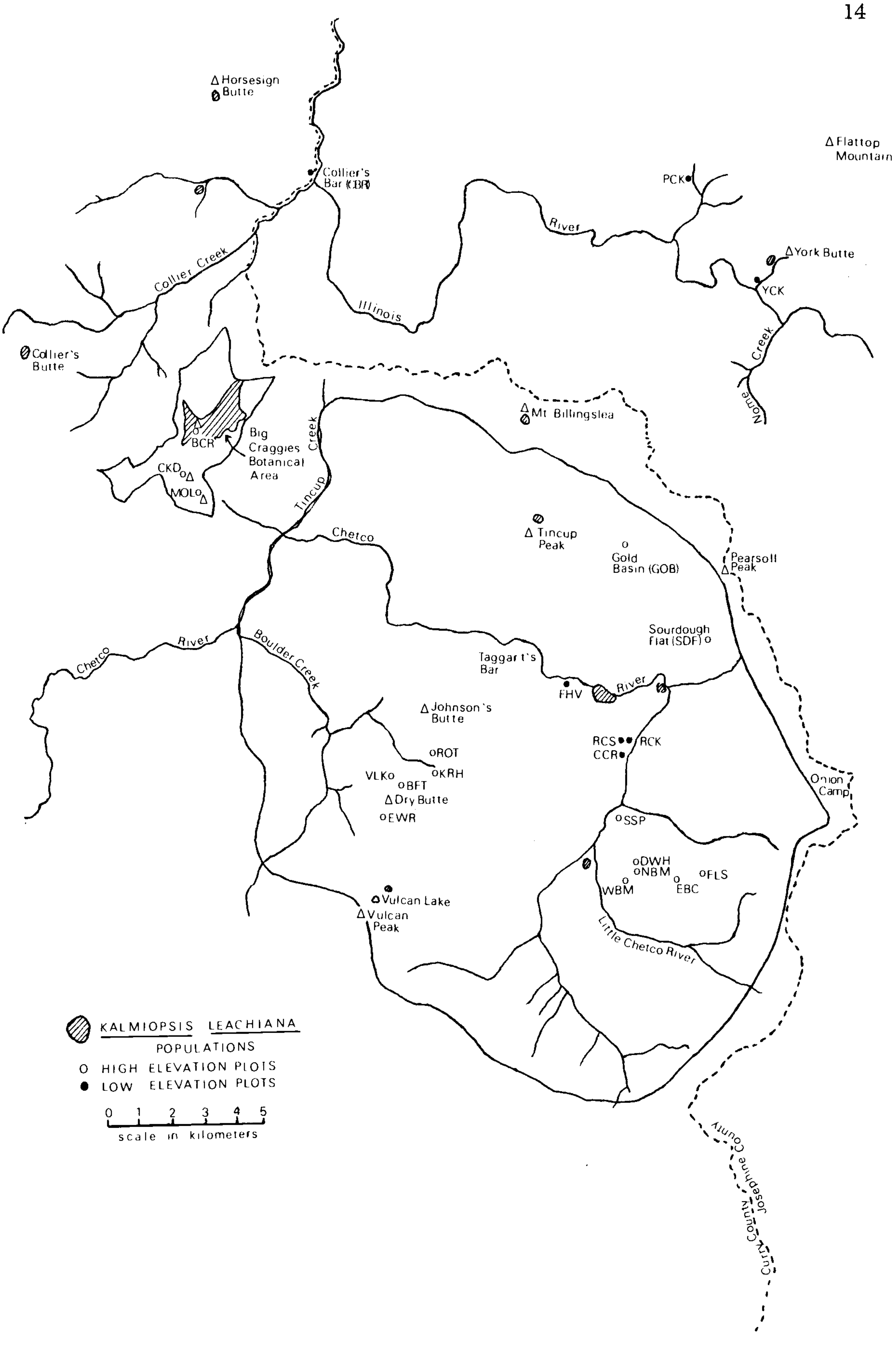
General Description

Siskiyou Study Area

Distribution of _Kalmiopsis leachiana_ in the Siskiyou Mountains is confined to a region 31 by 31 km in the Upper Chetco River drainage and a smaller portion of the Lower Illinois River drainage of southwestern Oregon. Within this area, its occurrence is subdivided into two smaller units, as shown in Figure 1. The pattern is due to the absence of _Kalmiopsis_ from the geologic formation known as the Dothan Formation. The most westerly location is at Collier Butte, 30 km from the Pacific Ocean, while the York Butte population marks the eastern boundary of distribution, 57 km from the ocean. There is an unconfirmed report of _Kalmiopsis_ at Flat Top Mountain 2 km to the east, and 5.5 km to the north of York Butte (Mansfield, H.R., 1975, pers. comm.). The northern limit of _Kalmiopsis_ in the Siskiyous is at Horse Sign Butte, and the southern outpost is marked by a population below Vulcan Lake.

The altitudinal limits of _Kalmiopsis leachiana_ in the Siskiyou study area range from 300 m to over 1400 m. Its most common occurrence is above 900 m (3000 feet), and it is found on many of the higher peaks of the area, for example, on the summit of Big

Figure 1. Distribution of _Kalmiopsis leachiana_ within the Siskiyou Mountains. Exact locations of plots which are identified here by abbreviations are given in Appendix I .


Δ Horsesign Butte
Δ Flattop Mountain
Collier's Bar (CBR)
PCK
River
Δ York Butte
YCK
Collier Creek
Illinois
Creek
Norne
Collier's Butte
BCR
Big Craggies Botanical Area
CKD
MOL
Creek
Tincup
Δ Mt Billingslea
Chetco
Δ Tincup Peak
Gold Basin (GOB)
Pearsoll Peak
Chetco
River
Boulder Creek
Sourdough Flat (SDF)
Taggart's Bar
FHV
River
Δ Johnson's Butte
RCS
RCK
CCR
ROT
KRH
VLK
BFT
Δ Dry Butte
EWR
Onion Camp
SSP
DWH
NBM
FLS
WBM
EBC
Vulcan Lake
Δ Vulcan Peak
Little Chetco River
KALMIOPSIS LEACHIANA POPULATIONS
O HIGH ELEVATION PLOTS
● LOW ELEVATION PLOTS
0 1 2 3 4 5
scale in kilometers
Curry County
Josephine County

Craggies, at 1408 m. The two peaks taller than Big Craggies (Pearsoll Peak, 1554 m, and Chetco Peak, 1437 m) are both masses of peridotite, a parent material on which *Kalmiopsis* was rarely found to grow.

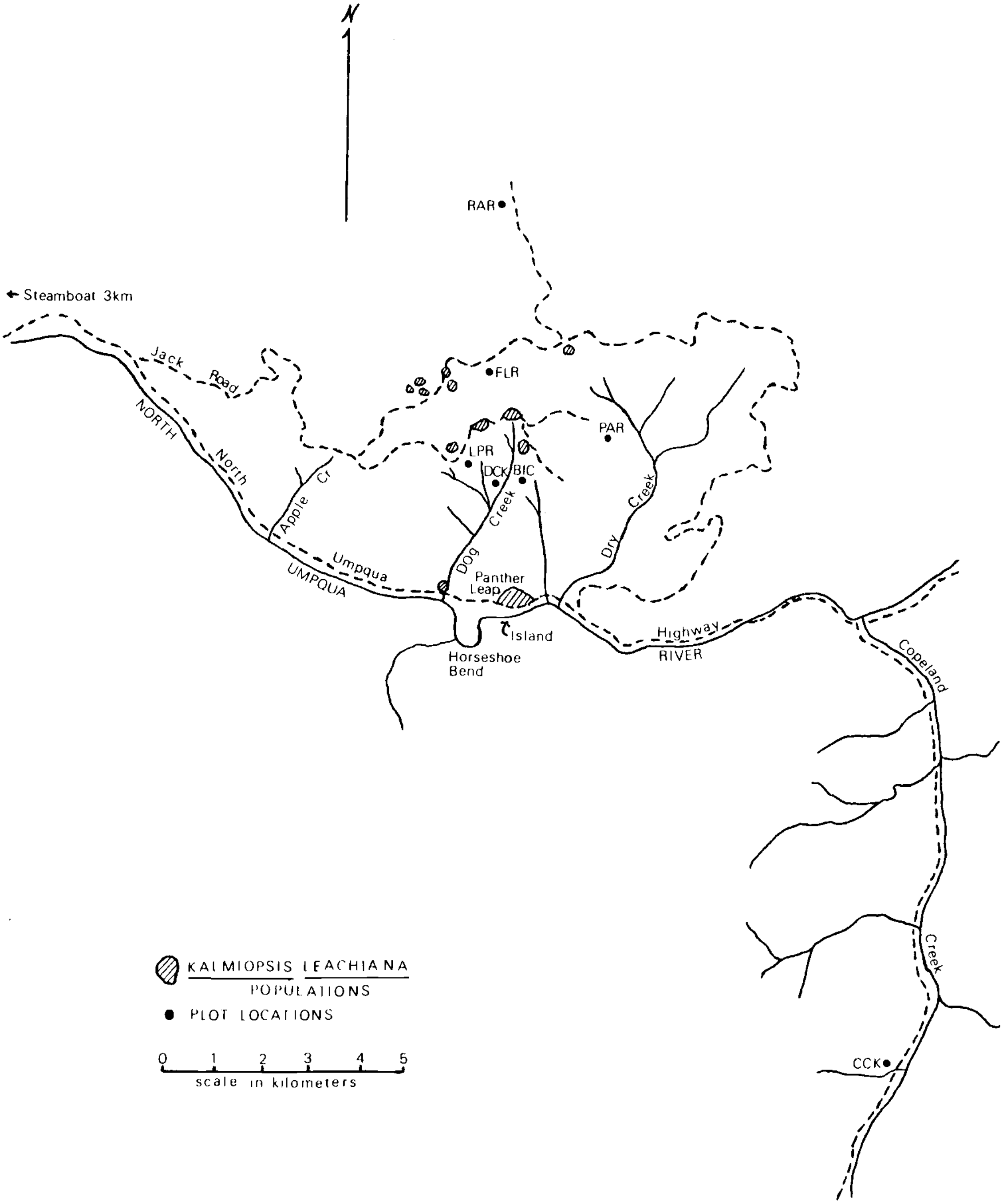
Except for the northwestern corner of the range most sites fall within one of three specially designated limited use areas of the U.S. Forest Service. These include the York Creek and Big Craggies Botanical Areas, and the Kalmiopsis Wilderness Area. Figure 1 marks the location of confirmed locations and includes others which have been reported by reliable sources and are considered likely to exist.

Southern Cascades Study Area

The populations of *Kalmiopsis leachiana* in the southern Cascade Mountains lie approximately 165 km (90 miles) from the nearest known location to the southeast in the Siskiyou Mountains. There are no known intermediate populations. The general location is in the North Umpqua River valley in Douglas County, approximately 85 km east of Roseburg along the North Umpque Highway 138, and 10 km east of Steamboat (Figure 2).

Several separate populations of *Kalmiopsis* are concentrated within an area of about 29 km (8 square miles) on the watershed of Dog Creek, a tributary of the North Umpqua River that drains the south-facing slope. The drainage is bounded to the north by Ragged

Figure 2. Distribution of Kalmiopsis leachiana within the Southern Cascade Mountains. Exact locations of plots which are here identified by abbreviations are given in Appendix I.


N
RAR
Steamboat 3km
Jack Road
FLR
PAR
LPR
DCK
BIC
NORTH
North
Apple Cr
Dog Creek
Dry Creek
Umpqua
UMPQUA
Panther Leap
Island
Horseshoe Bend
Highway
RIVER
Copeland
Creek
CCK
▨ KALMIOPSIS LEACHIANA POPULATIONS
● PLOT LOCATIONS
0 1 2 3 4 5
scale in kilometers

Ridge, which runs from 1350 m to 1450 m elevation and meets the North Umpqua River at 425 m elevation. Populations of *Kalmiopsis* occur at the ridgeline and at separate locations all the way down to the river. Probably the most notable occurrence here is in the crevices and on the sides of Limpy Rock, a huge silicified tuff outcrop that rises out of the surrounding conifer forest. The lowest location is on a small island in the North Umpqua River itself, about 0.9 km west of the mouth of Happy Creek and 0.6 km east of the beginning of Horseshoe Bend. There, a few plants of *Kalmiopsis* cling to the side of a huge boulder on the edge of the island, overhanging the river.

At this time there are only two verified locations which fall outside the southwest-facing steep slopes of Dog Creek drainage. The first is a boulder outcrop on Copeland Creek approximately 9.45 km south of its junction with the North Umpqua River. There are logged clearcuts on either side of this outcrop. The other outlying *Kalmiopsis* occurrence is on the north side of Ragged Ridge about 1.8 km downslope from the ridgeline, on deeply shaded outcrops within a forest dominated by western hemlock, *Tsuga heterophylla*.

Climate

Siskiyou Study Area

The climate of the Siskiyou Mountains is one in which the ameliorating effect of the Pacific Ocean plays an important role in plant distribution (Whittaker, 1960; Waring, 1969). There exists a gradient of precipitation levels from the coastal area, where rainfall can exceed 250 cm of rain per year, to the eastern boundary, which receives 50 cm or less annually. As in most of western Oregon, the rainfall is distributed unevenly throughout the year, with the summer months of June through October receiving the least and December through February the most. At the six Siskiyou stations for which data are available, rainfall amounts for June through September represented ten per cent or less of the annual total (Table 1). All soils throughout the Siskiyous are at field capacity during the winter (Waring, 1969), but as the dry summer months proceed less water becomes available and moisture-laden maritime air masses influence greatly the evaporative demand of the atmosphere over plant communities.

Total rainfall data show that there is a reduction in precipitation at low elevation sites inland. Rainfall at the Kerby station was slightly less than that at Gold Beach and Brookings, while Galice measured 60 cm less and Grants Pass 115 cm less (Table 1). At

Table 1. Average precipitation for Siskiyou weather stations (Gregg, 1936; USDA Weather Bureau, 1955-1975).

Station	Elevation (m)	Length of record (years)	Precipitation amounts (cm)												
			J	F	M	A	M	J	J	A	S	O	N	D	Total
Brookings	37	26	30.1	22.5	23.0	15.4	8.2	6.9	1.3	1.1	7.3	14.0	28.3	28.7	187.0
Gold Beach	18.5	20	31.5	26.4	27.8	12.9	9.9	6.0	1.0	0.6	4.6	11.5	29.7	29.6	191.6
Grants Pass	290	40	13.6	11.5	7.5	4.9	3.1	1.8	0.4	0.5	2.1	5.5	11.2	12.1	74.2
Sexton Summit	1170	30	14.2	10.5	8.1	4.7	5.6	3.9	0.8	0.6	3.2	8.7	11.1	12.1	84.1
Kerby	401	10	35.3	35.8	22.6	7.8	5.9	2.5	0.4	0.9	3.1	10.0	28.2	29.6	181.1
Galice	617	6	30.7	11.1	8.3	8.2	4.7	1.7	1.1	0.2	4.3	9.6	24.4	18.4	122.9
Agness	61	8	28.4	22.1	20.2	12.1	4.7	2.8	0.9	0.8	6.7	7.4	23.9	21.8	151.8

Grants Pass there is much higher temperature range in the summer than occurs on the coast, resulting in higher atmospheric demand and higher transpiration rates (Table 2). As rainfall levels drop off in the summer, increasing transpiration causes stomatal closure and consequent reduction in growth. It would thus be expected that at the eastern edge of the Kalmiopsis distribution and farther east, growth would be reduced to a larger degree compared to sites nearer the ocean where maritime air masses would tend to keep atmospheric demand at lower levels. Waring (1969) used these differences in temperature extremes to define two floral subunits within the Siskiyou Mountains, the Eastern Siskiyous and the Western Siskiyous. Thermographs placed in plots on a transect from west to east showed that the daily temperature ranges were greater than 11°C (20°F) for 95 per cent of the time in the Eastern Siskiyous. For the Western Siskiyous, one-third of the daily summer months' temperature variations averaged less than 11°C. The distribution of K. leachiana in the Siskiyou Mountains falls entirely within Waring's Western Siskiyou province.

Precipitation gauges at Snow Camp Mountain (elevation 1290 m) and Buzzard's Roost (elevation 885 m), just on the western edge of the Kalmiopsis distribution, and the weather at Sexton Mountain (elevation 1170 m) represent the transition in climate at higher elevations. Monthly averages could not be determined for the two

Table 2. Temperatures for Siskiyou and Southern Cascade stations (Gregg, 1936; USDA Weather Bureau, 1955-1975).

Station	Elevation (m)	Distance from coast (km)	Length of record (years)	January average (°C)	July average (°C)	Maximum (°C)	Minimum (°C)
Brookings	37	10	26	7.8	14.5	37.8	- 8.3
Gold Beach	18.5	5	22	7.8	14.0	36.7	- 6.7
Grants Pass	290	88	27	3.9	21.1	45.6	-17.8
Sexton Summit	1170	84	30	1.1	17.7	37.8	-18.9
Idleyld Park	333	-	14	3.5	18.9	39.4	- 7.8
Roseburg	479	-	40	5.0	19.4	41.7	-21.1
Toketee Falls	617	-	20	1.7	20.0	42.8	-20.6

Table 3. Growing season for Siskiyou and Southern Cascade stations (Gregg, 1936; USDA Weather Bureau, 1955-1975).

Station	Elevation (m)	Length of record (years)	Mean number of days between recorded temperatures in fall and spring				
			0°C	-2.2°C	-4.4°C	-6.7°C	-8.9°C
Brookings	37	14	298	*	*	*	*
Gold Beach	18.5	15	238	*	*	*	*
Grants Pass	290	32	167	217	277	324	351
Sexton Summit	1170	30	149	200	252	301	343
Idleyld Park	333	15	143	211	291	320	*
Roseburg	479	40	219	278	328	346	*
Toketee Falls	617	20	143	187	273	315	*

*Temperatures never fell below this temperature on average less than 10 days per year.

former stations since the gauges are checked infrequently, and at times, rain levels were not recorded. However, for two periods complete data exist. Between January 18, 1965 and November 16, 1971, total annual rainfall at Snow Camp was 269.0 cm. At Buzzard's Roost, annual precipitation for a period from January 18, 1965 to November 26, 1972 was 323.3 cm (USDA Weather Bureau, 1965-1972). The nearest Kalmiopsis location at Collier's Butte is only 2.2 km to the east of Snow Camp and at approximately the same elevation. In the interior annual rainfall for Sexton Summit, 84.2 cm per year, is two-thirds to three-quarters less than for these sites. The extreme difference in rainfall amounts at higher elevation are accompanied by higher summer temperatures and shorter growing season than are found at Gold Beach and Brookings.

Snow pack levels at elevations below 600 m are probably negligible (Table 4). For higher elevations, information on snow pack levels comes only through indirect sources. Ramp (1975) states that above 4000 feet (1200 m), snow pack levels over 10 feet (3 m) are not uncommon in the Kalmiopsis Wilderness Area. Forests of Picea breweriana, which is associated with Kalmiopsis on more protected slopes at high elevations, are reported to accumulate usually more than 2 m of heavy snow in the winter (Waring, Emmingham, and Running, 1975). The highest recorded monthly snow depth at Sexton Summit is only 70.1 cm. Thus distance from

Table 4. Mean monthly snowfall for Siskiyou and Southern Cascade stations (Gregg, 1936). T = trace amount.

Station	Length of record (years)	Elevation (m)	Snowfall (cm)												
			J	F	M	A	M	J	J	A	S	O	N	D	Total
Gold Beach	15	18.5	3.8	0	2.0	0	0	0	0	0	0	0	0	0	5.8
Brookings	18	37.0	1.5	1.3	T	T	0	0	0	0	0	0	0	0	2.8
Grants Pass	69	290	7.9	3.8	1.8	T	T	0	0	T	T	1.0	2.5	17.0	40.9
Sexton Summit	30	1170	70.1	37.8	51.8	17.5	5.6	0.5	0	0	T	4.8	21.8	49.3	251.7
Agness	7	61.0	1.8	0.5	2.0	0.3	0	0	0	0	0	0	0	0	4.6
Roseburg	8	146	13.7	0.8	4.1	1.3	0	0	0	0	0	0	2.8	2.0	16.5
Toketee Falls	7	617	51.3	22.4	12.4	3.3	T	0	0	0	0	0.5	6.6	16.8	112.3

the coast strongly affects snow pack as well as annual rainfall, temperature extremes, and the length of the growing season.

Southern Cascades Study Area

Distribution of rainfall for stations in the Southern Cascades study area parallels the pattern that occurs in the summer months in the Siskiyou Mountains (Table 5). Between seven and nine per cent of the total rainfall occurs in the summer months of June through September. But total amount of precipitation at these stations is 50 cm less than that for Gold Beach and Brookings, and at least 100 cm less than that of Snow Camp and Buzzard's Roost. It would be expected that precipitation levels at the eastern limits of Kalmiopsis in the Siskiyous would more closely approximate those occurring for populations in the Cascades.

Temperatures and temperature ranges for weather stations in the Limpy Rock area approximate those at Sexton Summit and Grants Pass (Tables 2 and 3). The Southern Cascades stations are much closer to the actual Kalmiopsis populations than most of those in the Siskiyous, so it is difficult to make exact comparisons for temperature conditions. It can be concluded however that the close proximity to the Pacific Ocean of Siskiyou Kalmiopsis populations appears to reduce the extremes in temperature which might occur there as compared to that in the Cascades. Cooler temperatures

Table 5. Average precipitation for Southern Cascade weather stations (Gregg, 1936; USDA Weather Bureau, 1955-1975).

Station	Elevation (m)	Length of record (years)	Precipitation amounts (cm)												
			J	F	M	A	M	J	J	A	S	O	N	D	Total
Roseburg	146	40	25.0	10.1	7.8	5.6	4.3	2.9	0.6	0.8	3.1	6.1	12.0	11.8	77.4
Idleyld Park	333	20	27.1	14.9	19.7	11.4	7.7	4.2	0.8	1.8	5.3	13.8	26.6	30.3	162.9
Upper Steamboat Creek	565	20	25.3	16.1	17.9	10.1	6.7	3.6	0.6	1.9	4.9	10.5	22.0	25.7	146.2
Steamboat Ranger Station	365	20	22.4	14.5	16.5	9.4	7.7	3.7	0.7	1.5	4.7	13.0	20.8	22.8	136.7
Toketee Falls	617	20	19.9	13.0	14.4	8.4	6.5	4.6	1.0	1.9	4.0	10.5	19.0	21.2	123.8

throughout most of the year result in a shorter growing season for the Cascades populations of Kalmiopsis. This generally cooler climate is coupled with lower rainfall amounts which affect snow depth levels (Tables 4 and 6). Snow depths at Quartz Mountain and Red Butte are considered to approximate those at the Limpy Rock area. Snow depths are all less than a meter, and comparable to the lower elevation Siskiyou stations, the data show that there is also little snow accumulation for Kalmiopsis populations occurring at the elevations less than 600 m in the Southern Cascades.

Geology and Physiography

Siskiyou Mountain Study Area

The Siskiyou Mountain study area falls within the geologically ancient area known as the Klamath Region. The Klamath Mountains, as first outlined by Diller (1902), represent the connecting range of mountains between the Coast Range Mountains of Oregon to the north and the Coast Ranges of California to the south. They are geologically older, and thus distinct from both of these mountain ranges, as well as from those mountains that form the eastern boundary of the Klamath Region, the Southern Cascade Mountains. The Siskiyou Mountains form part of the northern portion of the Klamath Region, bounded to the north by the Rogue River and the Rogue River

Table 6. Snow depths at stations in the Southern Cascade Mountains (Grant, 1973).

Site	Length of record (years)	Elevation (m)	Depth (cm)					
			Jan 1	Feb 1	Mar 1	Apr 1	May 1	June 1
Red Butte 1	13	1430	61.0	76.2	76.3	96.9	73.9	4.7
Red Butte 2	12	1219	38.4	47.0	50.9	55.9	21.9	0.0
Red Butte 3	12	1079	36.2	32.5	41.1	41.3	5.1	0.0
Red Butte 4	12	925	26.5	17.8	13.9	14.1	0.0	0.0
Red Butte 5	13	771	24.4	5.1	3.1	0.0	0.0	0.0
Red Butte 6	12	617	8.9	1.2	1.4	0.0	0.0	0.0
Quartz Mountain	12	1641	29.6	49.7	46.1	30.2	3.0	0.0

Mountains and to the south by the Klamath River (Whittaker, 1960; Waring, 1969).

The nature of the geology is important for understanding vegetation patterns for the Siskiyou Mountains because it is an area of extreme diversity in parent materials and consequently in the soils derived from them (Whittaker, 1960; Peck, 1961; Waring, 1969; Emmingham, 1973; Ramp, 1975). Superimposed on this high geological diversity is the steep gradient of climatic change from west to east as affected by the influence of Pacific maritime air masses. A complex topography, which offers every conceivable exposure and land form, provides terrain that is generally steep as a result of uplift and consequent erosion by deep-cutting streams. This erosion has produced vertically walled canyons and sharp ridgelines. Slopes commonly have a 30° grade or more providing a high rate of erosion and thus a constant source of microhabitats open for colonization. These are added to the already extreme variation in habitats available as a result of the diversity in climate, geology and topography.

The study area itself encompasses portions of five different geologic formations (Wells, Holtz, and Cater, 1949; Coleman, 1972; Ramp, 1975). The oldest is the late Jurassic Rogue Formation. It consists of flow breccias, flows, tuffs and conglomerates which have been largely altered to metavolcanics ranging from basalt to andesite and dioritic dikes (Ramp, 1975). Its time of origin marks it as just prior to the uplift, folding and metamorphism known as the Nevadan Orogeny, which produced the first development of the Klamath land mass (Beaulieu, 1971). The Rogue Formation forms the eastern boundary and interdigitates to the north and east in a still unclear pattern with the Galice Formation (Wells, Holtz, and Cater, 1949; Ramp, 1975).

The central and north-central portion of the Siskiyou study area is occupied by a heterogeneous plutonic formation called the Chetco River Complex by Holtz (1971) and the Illinois-Chetco gabbro-diorite complex by Brooks and Ramp (1968). It is between 6 and 8 km in width and extends north for about 40 km, almost to the Rogue River. Consisting of gabbro, diorite, and metagabbro rocks, and sometimes intruded by peridotite and pyroxenite, the rocks of the Chetco River Complex have been age determined at about 150 million years old (Holtz, 1971), thus including them in the plutonism which took place during the middle and late Nevadan Orogeny. The Chetco River Complex, in addition to the Rogue Formation, runs in a northeast trending line.

There are two main areas of ultramafics within the study area aside from the irregular intrusions already mentioned. One of these, the Josephine Ultramafic Sheet, occupies the southwestern corner of the *Kalmiopsis* study and thrusts over the Chetco River

Complex at the line known as the Madstone Cabin thrust fault (Ramp, 1975). This particular formation extends south into California, and most of the peridotite of which it consists is relatively serpentinized.

The other region of serpentinite represents the northwest corner of the study area, extending from Snow Camp to Agness and is part of the formation known as the Colebrooke Schist (Coleman, 1972). Harzburgites and dunite make up the main composition of the ultramafics of this mass. Through indirect evidence of age, Coleman (1972) suggests that these serpentinite masses were intruded during the Late Jurassic, having been transported from their original positions in the Pacific Ocean to the west by repeated tectonic movements.

The last major formation, and perhaps the youngest geologically, is the Dothan Formation, which is considered to have originated in the Late Jurassic. The older Rogue and Galice Formations are believed to have been thrust over the Dothan (Ramp, 1975) which is composed of up to about 18,000 feet of dark-grained greywacke sandstone and siltstone with some volcanic chert and conglomerates intermixed (Baldwin, 1974). The Dothan Formation is important because of the fact that there are no known locations for _Kalmiopsis_ within it. The Dothan Formation divides the range of _Kalmiopsis_ within the Siskiyous into two smaller geographical subunits.

Special mention should be made of the geology of the Big Craggies area. Both Coleman (1972) and Ramp (1975) consider these peak formations to be the result of an overthrust klippe whose nearest association is with areas to the east, showing affinities with Dry Butte and Bailey Mountain (Ramp, 1975). The Big Craggies area itself consists of gneissic metagabbro sitting on a sheet of serpentinite overlaying the Dothan Formation. This band of gneissic metagabbro draws out to the north to Collier's Bar and the Illinois River.

Southern Cascades Study Area

The geology of the North Umpqua study area is much more recent than that of the Siskiyou Mountains. The Limpy Rock area is included in the geological province known as the Western Cascades, a north-south trending line of volcanic rocks, flows, tuffs, and intrusions of Cenozoic origin, as opposed to the Mesozoic origin of Klamath Mountains rock (Peck, Griggs, Schicker, Wells, and Dole, 1964). The main formations of the Western Cascades, which are mainly late Eocene to late Miocene in development, are continuous with those composing the metamorphic and volcanic rocks of the Klamath Mountains, as they interfinger with them to the southwest.

The earliest rocks of the Western Cascades are of Eocene age and belong to the marine Umpqua, Tyee and Spencer Formations

(Peck et al., 1964). They consist of sandstones, mudstones, and conglomerates with interbedded basaltic flows and pyroclastic rocks. During the latter part of the Eocene, the Colestine Formation, which averages 3000 feet in thickness, was laid down as pyroclastic rocks and flows of basaltic andesite and pyroxenes. Continued volcanic activity into the Oligocene and early Miocene led to the formation of the Little Butte Volcanic Series over the earlier Eocene layer. The Little Butte Volcanic Series averages between 5000 and 10, 000 feet in thickness and is made up of massive beds of andesite and dacite lapillie tuff, less abundant flows of basaltic and andesitic breccia, welded tuffs, and flows of dacite and rhydacite, along with rhydacitic tuffs. Two later formations of volcanic origin, Columbia River Basalt and the Sardine Formation, were formed in the middle and late Miocene. They are of much greater importance in the northern reaches of the Western Cascades and have not influenced the geology and physiography of the North Umpqua River area. In even later times the eastern edge of the Western Cascades has been influenced by flows of Boring Lava and other volcanic rocks from the High Cascade Range, which occurred during the Pliocene and Pleistocene eras.

Locally from the extreme western edge of the Western Cascades on up the North Umpqua River to Little River, the rocks consist almost entirely of Eocene and Oligocene tuffs and flows of the Colestine and Little Butte Volcanic Series (Peck *et al.*, 1964; Baldwin, 1976), with older rocks present to the north and south but absent here (Kays, 1970). The Little Butte Volcanic Series is the youngest in the Limpy Rock area and reaches its greatest depth for the entire Western Cascades here at 15,000 feet (Peck *et al.*, 1964). The Limpy Rock study area overlaps partially an area of local propylitic alteration that is associated with a smaller diorite dike located above Horseshoe Bend in the North Umpqua River and extends east about 0.8 km.

The large standing craggy and pinnacled outcrops, jutting steep, vertical ridges, and huge, irregular boulders with which the distribution of *Kalmiopsis leachiana* in the North Umpqua River area is associated all are composed of rocks of variously altered and unaltered siliceous tuffs, with the amount of silica varying as well. Though there have been no specific geologic studies of the rock outcrops in the study area, a large, craggy peak 17 km to the south called Quartz Mountain has been studied geologically on the basis of its composition, history of formation, and relation to the surrounding geology (Ramp, 1960).

According to the Quartz Mountain study and the identification of rock of outcrops on which *Kalmiopsis* grows (Table 8), the rocks at the North Umpqua River area, and Quartz Mountain itself, represent point locations in the volcanic flows in which the tuffs have been replaced to varying degrees with silica (Ramp, 1960; Kays, 1970). Outcropping occurs as a product of differential weathering between the surrounding non-silicified and the much smaller areas of silicified tuffs. The process by which silicification occurred is not completely understood. The most plausible explanation given is that the outcrops were sites of vertically and laterally moving highly reactive siliceous thermal waters that ascended through the porous tuff layers, which in time came to be replaced by the silica of the hot springs (Ramp, 1960). These partially silicified tuffs have in turn in some areas been largely altered to clay. Cavernous weathering, and the formation of caves, comes about as the result of the partial porosity of the differentially silicified tuffs. Places in the rock where silicification is not complete and clay is present are more porous than the silica itself, will absorb more water, and consequently are subjected to a higher amount of weathering and breakdown by frost action. Many cracks, irregular crevices, fissures, and pockets in the body of the outcrop result which provide points of moisture and organic matter accumulation.

Weathering of rocks through frost action brings about the chipping and fracturing of an entire range of sizes of silicified tuff pieces. These collect in the soil and on the soil surface surrounding the outcrop of their origin, with the extent of rockiness depending on the size of the outcrop itself and the rate of weathering which is taking place. There is seen a definite change in the structure and composition of the surrounding vegetation correlated with the increase in rock fragments closer to the base of an outcrop.

Fire History

Siskiyou Mountain Study Area

Fires have had an important influence on vegetation patterns in the study areas within the Siskiyou Mountains. Every site provides abundant evidence, in the form of charred stumps, dead snags, and charcoal littered ground, that fires have been frequent and severe. Lightning fires were common throughout the entire summer season in early settlement days as well as now, and it is safe to assume that they have always been a major factor under the present climatic conditions. The high flammability of the forest, shrub, and grassland vegetation during the long, dry summers only increases the degree to which fires are likely to occur.

Little is known about fire frequency and the influence on it by American Indians in pre-settlement days, but it is certain that when Europeans first entered the area frequency of fires increased over the already high rate due to lightning storms (Mansfield, 1972). Miners and prospectors practiced burning off slopes before beginning prospecting in order to ease their task (Butler and Mitchell, 1916; Haefner, 1975). Cattlemen and ranchers burned brush to promote the growth of grass as feed for cattle (Haefner, 1912, 1975), while pig farmers would burn to increase the amount of tanoak flowering, as pigs relished the inflorescence of this species (Waller, J., 1976, pers. comm.). Hunters used fire to drive game and clear undergrowth to make traveling easier (Haefner, 1912; Whittaker, 1960). Neglected campfires and careless misuse of fire, a miner's need for Saturday night entertainment, and the feeling that it was an inalienable right to set fire all were part of the forces increasing fire frequency during early settlement and mining days.

Specific fire records for the study area are almost non-existent. The Siskiyou National Forest retains records only for ten years previous. However, through personal communication with retired Forest Service personnel once associated with the Siskiyou National Forest and through limited literature records and U.S. Forest Service records, a partial fire history has been gathered for the Chetco River and Lower Illinois River drainage areas from the year 1909 to the present (Table 7).

Between 1909 and 1924 many small fires occurred in the area but were suppressed soon enough that they never exceeded 200 acres in extent. On September 1, 1924, very dry forest conditions led to a lightning fire which burned between 5,000 and 5,500 acres along the Tincup-Collier Creek divided. Starting near Collier's Bar on the Illinois River it moved up the north slope as a ground fire

Table 7. Summary of the fire history in the Chetco and Lower Illinois River drainages: 1900-1975.

Date	Name	Extent of burn (acres)	Cause	Information source
Sept. 1, 1924	Craggies Fire	5,000- 5,500	lightning	Haefner (1975); Haefner, H.E. (pers. comm.)
Sept., 1936	-	5,000	unknown	Haefner, H.E. (pers. comm.)
late June, 1938	Nome Creek Fire	4,000	man-caused	Covill, L.L., G.W. Morey (pers. comm.)
July 14, 1938	Big Chetco Fire	34,627	lightning	Covill, L.L., G.W. Morey (pers. comm.); Siskiyou National Forest Record
" "	Little Chetco Fire	3,000	lightning	Morey, G.W. (pers. comm.)
1940	Little Chetco Fire	18,412- 22,000	man-caused	Philbrook, J.R. (pers. comm.) Siskiyou National Forest Service record
about 1955	Mislatnah Creek	70-80	lightning	Philbrook, J.R. (pers. comm.)
late 1950's	Bailey Cabin Fire	400	unknown	Philbrook, J.R. (pers. comm.)
about 1962	Tincup Creek	70-80	lightning	Philbrook, J.R. (pers. comm.)

along Collier's Creek and two miles south of that stream. Appearing to be controlled by the efforts of a few Forest Service foresters, it crowned out during the night as an intensely hot fire and swept up Collier's Creek to the summit of the Big Craggies, destroying all vegetation in its path. By the tenth or eleventh day it had slowed to a ground fire and was extinguished by the fourteenth day when the rains came. At this time H.E. Haefner, the forester in charge of the fire fighting crew, described the vegetation that was burned in the Craggies area as "a sea of heavy manzanita brush. Loss of timber--mostly young growth fir and pine--was nil. This was brush country--manzanita and tanoak brush" (Haefner, 1975, p. 49).

In September of 1935 a large brush fire again burned in the Big Craggies area, this time sweeping over about 5,000 acres in the lower Tincup Creek drainage, south across the Chetco River to Boulder Creek and northwest to the Craggies.

In 1938, a total of almost 45,000 acres burned as a result of three different fires. In late June, the Nome Creek fire burned about 4,000 acres. It was man-caused, starting near the Illinois River and burning most of the Nome Creek drainage. It also crossed the Illinois River and burned to the east to Panther and Briggs creeks. Compared to the other two 1938 fires it destroyed little timber and ground cover.

On July 14, 1938, a severe lightning storm started two fires, both of which damaged much of the present day Kalmiopsis Wilderness Area. The first was the Big Chetco Fire which began near Cedar Springs, burning to the northeast to the top of Green Craggie. The vegetation at this time was extremely inflammable and the fire burned in all directions for three weeks. It extended from Cedar Springs south and southeast to the Chetco River, Dry Butte and Johnson Butte, and east to Heather Mountain, Mount Billingslea, and Box Canyon Creek, burning 35, 000 acres total in area. Almost all ground cover was destroyed. This was considered at that time to be the largest and most difficult to control in any national forest since 1910.

The little Chetco Fire began on the same day as the Big Chetco Fire, burning from Chetco Bar north towards Tincup Peak and covering 3000 acres total. The degree to which vegetation was destroyed is not known. L.L. Covill, in a Siskiyou National Forest Service memorandum, states that the Kalmiopsis population on the north side of Tincup Peak was burned over, probably as a result of the Nome Creek fire a month earlier. Instead the Little Chetco Fire was more likely to have been responsible for the burning of this site, since the Nome Creek Fire was limited to an area much farther north. However, Covill does postulate in the same memorandum that Kalmiopsis is like other "brush species" in its ability to sprout shoots following a fire, evidence being that the Tincup Peak population was not destroyed even though fire swept through the area.

The second Little Chetco Fire, taking place two years later in 1940, was "caused by a brush-happy miner who lit a signal fire to summon help for imagined problems." It burnt between 1800 and 2200 acres in total. It was started near the mouth of the Little Chetco River and burnt across to Box Canyon Creek, entirely confined within the boundaries of the present day Kalmiopsis Wilderness Area. The Bailey Cabin fire also burned entirely within Wilderness boundaries, covering about 400 acres in the late 1950's.

Lightning fires were apparently numerous throughout the fire season in both the Chetco and Illinois drainages, but with the development of more rapid transportation and the advent of the Smoke Jumpers, these later fires did little damage compared to those of earlier dates. A lightning fire on Mislatnah (Miss Latney) Creek about 1955 consumed some 70 to 80 acres and a similar fire at Tincup Creek occurred about 1962.

From these reports, it appears that natural lightning fires have had a very significant impact on the vegetation of the Siskiyou Mountain study area. The Big Craggies area burned at least three times during the last 50 years. J.R. Philbrook (pers. comm., 1977) feels that the present day Big Craggies vegetation has its origin in ancient fires. Human-caused fires certainly have added to the total burned acreage in earlier time, but both natural and human-caused fires are suppressed to a great deal today. Fires burned through or very near to 12 different known Kalmiopsis populations according to information provided in these reports.

Southern Cascades Fire History

As was true for the Siskiyou Mountains, fire has been a dominant factor in the shaping of the vegetation of the Limpy Rock area, as it has for the entire Cascade range (Franklin and Dyrness, 1973). A report of a sea captain in 1868 mentions that he sailed for seven days along the Oregon Coast and never moved out of sight of one tremendous fire (Mansfield, 1972). Present vegetation structure and patterns suggest that fire frequency and intensity has not been as great as that which occurred in the Siskiyou study area, at least for the more moist sites in the North Umpqua River drainage. However, each site does bear evidence of burned stumps and scarred snags that are marks of fires that once swept through the area.

Specific reports as to fire history for the Cascade study area and the southern Cascade Mountain range in general are limited to a reconnaissance report of the area of the Southern Cascades drained by the South Umpqua, Rogue, and Klamath rivers (Leiberg, 1900). At the time of the report there existed no old growth stands of less fire resistant species and those that did occur were found singly or in small groups. This, plus the fact that all forest tracts were fire-marked to some degree, suggest that fire was a prevalent and widespread feature before settlement by Europeans. However, the great diversity in age structure which existed in these forests showed that fire was not as frequent and of the same magnitude as when only American Indians occupied the area. The largest burned stand attributable to Indians was 60,000 acres in expanse, an area systematically burned for over 300 years. Reasons given for deliberate burning by Indians included the facilitation of hunting at low elevations through the reduction of brush, and the maintenance of grass growth for camping and huckleberry and blackberry growth at high elevations.

Fire frequency has increased as well in the Cascades with the settlement by Europeans. This has resulted in large even-aged stands of forest. Fires were set to destroy underbrush, to facilitate traveling, and to clear the way for new roads being built. High fire frequency was associated with the need for increase of grass growth and brush growth for grazing. In addition fires were set to attract game, to burn away windfalls, and through sheer carelessness.

Thus it appears that fire history has been similar for both study areas. Human-caused fires increased greatly with settlement by Europeans and this increase has caused a reduction in the structural heterogenity of the vegetation, at least in the Cascades. More recently, human-related fires have decreased considerably through fire prevention, but the high occurrence of naturally caused fires, especially those initiated by lightning, suggests that fire has always been a chief factor in vegetation patterns under present day climatic conditions.

METHODS

Geology and Soils

Because changes in parent material type and associated differences in soils derived from them are known to be extremely important in their effect in vegetation patterns in the Siskiyou Mountains (Whittaker, 1960), and thus in individual plants, both rock and soil samples were collected from each Kalmiopsis population visited.

Three rock samples were collected for each site. These were broken from larger rock formations or from exposed bedrock which were considered typical for the site. All samples were identified through the courtesy of Mr. Len Ramp, state geologist of the Oregon Department of Geology and Mineral Industries, Grants Pass Office.

At each site where the surrounding vegetation was to be sampled, a soil sample was collected for both later chemical analysis and Kalmiopsis seed germination and seedling growth experiments. A minimum of five subsamples, each collected from different areas within a site, were sifted through an 8 mm wire mesh screen. All samples were collected from the root zone vicinity of Kalmiopsis and consisted only of mineral soil. Five of the samples, each representing a different parent material type, were treated to chemical analysis by the soil testing laboratory of the Oregon State University Agricultural Extension Service, according to the methods of that laboratory (Kauffman and Gardner, 1976). Soils were analyzed for total quantities of potassium, phosphorus, calcium, magnesium, ammonia, nitrates, and total exchange capacity.

Soil description and site physiognomy description included estimation of per cent cover of site surface represented by exposed bedrock and bare mineral soil. Surface soil color was determined with Munsell soil color charts. Surface soil rockiness was estimated by per cent represented by three size classes of rocks: 0.25 cm to 1.0 cm in diameter, 1.0 cm to 3.0 cm in diameter, and rocks over 3.0 cm in diameter.

Synecology

Vegetation Sampling

Intensive sampling of vegetation associated with *Kalmiopsis leachiana* populations was performed to quantify the biotic and abiotic aspects of the environment in which *Kalmiopsis* is found to grow. Without direct means of thoroughly measuring the abiotic environment itself, changes in the composition and structure of vegetation are considered to be a direct reflection of the abiotic environmental complex in which it occurs, within the scope of modification by biotic factors. Known environmental limits of species found associated with Kalmiopsis would aid in the definition of this plant's distribution. Discovery of the changes in abundance and species composition of vegetation of Kalmiopsis stands from one site to the next will reveal the biotic influence, as represented in part by the plants themselves, and the abiotic environmental factors operating on the population distribution of this one species.

Reconnaissance and Stand Selection. Information as to the possible location of populations of Kalmiopsis leachiana was attained through various sources, including the Kalmiopsis Wilderness Map (Mansfield, 1972), Siskiyou National Forest Service files on "vanishing species" and the wilderness area itself, herbarium specimens of the Oregon State University Herbarium (OSC) and the University of Oregon Herbarium (ORE), and personal reports of local naturalists, botanists and U.S. Forest Service personnel.

Sites were chosen for sampling within the geographical range of Kalmiopsis leachiana with three purposes in mind. First, it was intended to derive information about as many locations as possible which are typical of Kalmiopsis populations. At the same time as many habitats as possible which represent deviations from the typical were visited and sampled to encompass the entire variety of types in which Kalmiopsis is found to occur. And lastly, sites were chosen for sampling so that the entire geographical range of

Kalmiopsis was represented as it is now known. It was felt that these criteria would allow a nearly complete delineation of the abiotic and biotic factors influencing the distribution of this plant within its range. Certainly, not all reported locations were visited because of the time involved in reaching them, a limitation compounded by the fact that much time was spent simply in the attempt to locate reported populations.

When a Kalmiopsis population had been located in the field, a rectangular nested plot system as put forth by Daubenmire (1968) was established to sample the associated vascular plant species and bryophytes. In those cases in which the Kalmiopsis population sampled was smaller or only slightly larger than the 375 m^2 plot, the topographical center of the population served as the plot center. If the Kalmiopsis population was instead relatively large compared to the plot, a portion of the population was subjectively chosen for sampling. The choice was made with the intention of deriving as complete as possible a representative sampling of variation in site location as influenced by elevation, topography, parent material, and fire history. For those larger populations the plot center was made to coincide with the center of the sub-population chosen. All plots were established perpendicular to the direction of the slope.

Except in the case of one sampled population, Kalmiopsis leachiana in the North Umpqua River area was found to be restricted to rock outcrops, steep cliffs, or large, irregular boulders. This made it physically impossible to use the topographic center of the *Kalmiopsis* population as the center of the plot. Instead, plots were established immediately adjacent to rock outcrops where the vegetation appeared homogeneous, again perpendicular to the direction of the slope. Frequently *Kalmiopsis* grows in the immediate rocky soil at the base of these rock outcrops. It was on the side of the rock outcrops in which *Kalmiopsis* was the most abundant, either at the base of the rock or on the rock itself, that the plot was established.

Sampling System and Site Description. Measurement of vegetation was focused on the determination of the importance of each individual species associated with *Kalmiopsis leachiana*. A species importance is defined here as its density, cover, frequency, and constancy. The nested plot system used for vegetation sampling consisted of three contiguous 25 m x 5 m macroplots, lying with their longest edge perpendicular to the direction of the slope (Figure 3). In each of these three macroplots all trees over 1 m in height were counted and their diameter measured at breast height (DBH). Individual tree species density, defined as the number of stems per relevé, was thus determined. Total DBH for each tree species per relevé was considered to be a representative value of the total ground surface area covered by the canopy of that species. In the

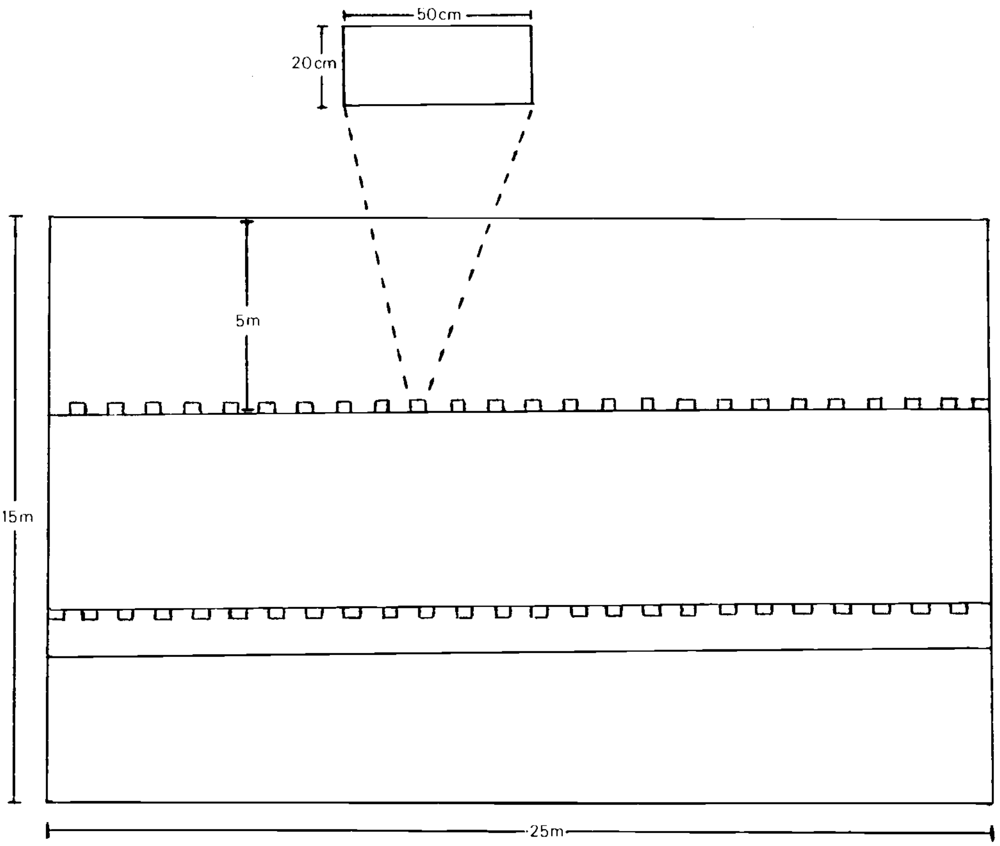


Figure 3. Nested plot system employed for vegetation sampling. Adopted from Daubenmire (1968).

past most workers have used total basal area of a tree species to represent tree cover (Daubenmire, 1968). For this study it was felt that basal area overestimates the cover of large trees as a result of the conversion of the diameter measurement to area.

Numbers of trees less than 1 m in height and numbers of stems of shrubs and herb species were tallied in two strips 1 m in width each running the length of the boundaries of the center macroplot (Figure 3). This allowed determination of the density of seedlings and saplings of tree species, and of herb and shrub species per relevé. Cover values were determined for herb and shrub species as well as for bryophytes by estimation of the per cent ground surface (to the nearest five per cent) covered by a species within 20 cm x 50 cm microplots. (The total cover represented by bryophytes was always less than one per cent, so cover of individual species was combined with all other species and reported as a total estimated cover for the entire class.) A total of 50 microplots was tallied for an entire site, 25 each spaced at 1 m intervals along the two boundaries of the center macroplot (Figure 3). Frequency of herb and shrub species was determined by tallying the number of microplots within a releve in which the species was found to occur. Constancy, defined as the percentage of releves of a major vegetation unit in which a species is found, was also determined for herb, shrub, and tree species. All taxonomy is based on

Peck (1961), except where felt to be superceded by Hitchcock and Cronquist (1973) or Munz and Keck (1959). Voucher specimens have been placed in the Oregon State University Herbarium.

In addition to classifying plant species associated with Kalmiopsis leachiana on the basis of their density, cover, frequency, and constancy, species were placed into one of the following categories: those species found to occur within one or more of the microplots; those species absent from all microplots but present in at least one of the macroplots; and those species in the very near vicinity of the three macroplots but not actually found in them. In this way a crude measure of the degree of clumping in vegetation patterns could be made as well as the degree to which local topography changed adjacent to the plot as measured by differences in neighboring vegetation. Observations and notes of the immediate vicinity were made to determine the latter category of species, as well as associated land forms, immediately adjacent vegetation types, extent of local Kalmiopsis distribution, and the degree of homogeneity in vegetation patterns that each site supported. Additional notes were made at each site on the phenology of Kalmiopsis, growth habit and morphology, and herbivore and pollinator activity associated with this plant.

Site aspect was determined for each sampled site by compass and the degree of slope was obtained with an Abney handlevel.

Altitude and plot location were determined from United States Geological Survey maps, United States Forest Service fire survey maps, and the Kalmiopsis Wilderness Area map (Mansfield, 1972).

A total of 28 plots was sampled according to the above outlined methods. Twenty-six of these plots were sampled between June 18, 1976 and September 14, 1976. The two remaining plots, one at Gold Basin and one in the Big Craggies Botanical Area, were sampled in the spring of 1977, on May 22 and June 7 respectively. Two additional _Kalmiopsis_ populations were sampled in the Big Craggies Botanical Area in June, 1977, according to the reconnaissance method of Franklin, Dyrness, and Moir (1970). In this case species were given cover values based on cover classes and no specific plot was established. Instead, cover values were estimated for species over a general area of 15 m x 25 m.

Vegetation Analysis

After density, cover, frequency, and constancy had been calculated for each species, more rigorous analysis of vegetation data was conducted, taking two forms. First, the manual-visual association table method of Braun-Blanquet, as described in detail by Mueller-Dombois and Ellenberg (1974), was used to differentiate patterns and changes among the various vegetation types sampled. This was supplemented by reference stand two-dimensional ordination (Whittaker, 1967) using a computer program SIMORD as first developed and applied by Dick-Peddie and Moir (1970) in the description of the vegetation of the Organ Mountains, New Mexico. Emphasis in analysis was directed towards consideration of what plants are associated with Kalmiopsis with the intention of discovering specific factors involved in its distribution.

The Braun-Blanquet method of vegetation analysis by manual-visual tables allows sorting of sample stands or relevés on the basis of presence and absence of species (Mueller-Dombois and Ellenberg, 1974). Relevés were first placed temporarily in a synthesis table, with each relevé represented by the cover values of the species of which it is comprised. Species were also differentiated as to whether they occurred in the macroplots but were absent from all microplots, and if they were present in the immediate vicinity of a macroplot but did not actually occur in it. The synthesis table allows easy calculation of species constancy, and when this had been completed the original table was rewritten to form a constancy table in which species were arranged from highest to lowest relative constancy.

Actual determination of vegetation units was accomplished by the grouping of relevés on the basis of shared species composition and on shared absence of certain species. Species which are highly ubiquitous and those that only rarely occur are of little utility in differentiating vegetation units, though both may be of use in final description of the vegetation under analysis. For this study all species with greater than 60 per cent and less than 10 per cent constancy were excluded from the formation of further partial tables. From the remaining set of species were chosen groups of differential species, those which were used to define vegetation units by their shared occurrence in some relevés and absence from others. The differential species allow a re-ordering of relevés in a final classification table into units which are compositionally similar. Further comparison was made within and between established units for more detailed description based on presence or absence of all species involved.

The disadvantage of the above method is that sample stand affinities are determined for the most part on the basis of recorded presence and absence of species alone. Species importance values can be used, but only to a limited and subjective degree. Computerized similarity ordination analysis (SIMORD) instead compares relevés quantitatively on a species numerical basis. Vegetation analysis by this method has been widely used in the past for a variety of different studies involved in vegetation distribution and description (Dick-Peddie and Moir, 1970; Franklin, Dyrness, and Moir, 1970; Emmingham, 1973), as well as for a number of unpublished thesis studies in Oregon vegetation patterns (Hawk, 1972; Mitchell, 1972; Juday, 1977).

The SIMORD program develops a two-dimensional graphical ordination of sampled stands by computing similarity values between each stand and every other stand on quantitative species similarity. Stands are ordered with respect to reference end stands, one at each end of the Y- and X-axes. The similarity between two stands I and J was computed according to the following formula (Dick-Peddie and Moir, 1970):

$$\mathrm{SIM}\ (I, J) = \frac{1}{n} \sum_{k=1}^{n} \left(\frac{2\mathrm{MIN}(a_i k, a_j k)}{a_i k + a_j K} \right), \text{ for } a_i k \text{ or } a_j k \geq 0.1\%$$

where $a_i k$ and $a_j k$ are cover measurements of the k^{th} species in stands I and J, and n is equal to the number of stands, in this case 28. The summation is performed for only those species whose cover value equals or exceeds 0.1 per cent. Previous workers (e.g., Dick-Peddie and Moir, 1970; Franklin, Dyrness, and Moir, 1970; Hawk, 1972) have set this limit at a cover value of 3.0 per cent. For this study most herb species would be excluded from the ordination developmental process at a 3.0 per cent level because of their very low cover values. In order to base ordination results on a representative number of species, and to include those which were felt to be an integral part of the vegetation, the cover limit was reduced. Herb and shrub cover values used are actual per cent cover estimates, while the tree cover values are represented by total measured DBH values for a particular species.

Species which occurred in the macroplots but not in any microplots were given cover values of 0.09 per cent. Those found in the very near vicinity but not in any microplots were given a cover value of -1.0 per cent. The effect on the resultant ordination of the inclusion of these last two groups was determined by a stepwise inclusion of them into the ordination process. Exclusion of both groups was accomplished by setting the cover limit at 0.1 per cent. Inclusion of the first group but not the second was brought about by setting a cover limit of 0.0 per cent and inclusion of both groups was done by setting the cover limit at -1.0 per cent.

Both hand-picking and computer choice of end stands were employed for this study. In addition, two different modes of Y-reference stand choice, as allowed by SIMORD analysis (Dick-Peddie and Moir, 1970), were also employed. The independent mode of selection allows a maximum separation of stands over the ordination plane, and thus was used to determine vegetation patterns of similarity and dissimilarity based on species cover values. The results were compared with those obtained through the use of manual-visual association tables. On the other hand, the dependent mode of Y-end stand selection produces a more linear ordination of stands, for relatively similar relevés are chosen as Y- and X-axis reference stands. An attempt was made to relate the resulting ordination to an inferred environmental gradient.

Autecology

Plant Moisture Stress

Investigations of moisture stress patterns within plants using a pressure chamber and following the methods of Schollander, Hammel, Bradstreet, and Hemmingson (1965) have been conducted both in the Siskiyou Mountains (Waring, 1969; Waring, Emmingham, and Running, 1975) and the western Cascade Mountains (Hickman, 1968, 1970). These studies have shown that plant species distribution patterns, especially in the Siskiyou Mountains, are strongly correlated with the ability of plants to withstand moisture stress as it increases during the summer drought season. Initial reconnaissance of sites of *Kalmiopsis* populations suggested that pressure chamber measurements could aid in the explanation of distribution patterns of *Kalmiopsis*, both within its geographical range as well as in explanation of the restricted geographical range itself. The proposed site of measurement was Rattlesnake Creek in the Kalmiopsis Wilderness Area. Here *Kalmiopsis* is entirely confined to a north-facing slope of a tent-like projecting ridge, never occurring on the opposite south slope. Thus measurement of internal xylem sap tension for associated plants occurring on both north and south slope as well as for *Kalmiopsis* would demonstrate the degree to which moisture stress affects plant distribution there.

Pressure chamber measurements were made at the peak of the dry season on September 7, 1976. The pressure chamber used was a portable one, manufactured by PSI Precision Instruments, Inc., of Corvallis, Oregon, and is described by Waring and Cleary (1967). Air pressure was provided by a five-pound capacity oxygen tank.

Two transect lines along which plants were to be measured were established the day previous to measurement. Twelve stations were marked along these transects by attaching clothespins to twigs of plants that were to be measured. The clothespins themselves had been marked with fluorescent sticky tape and plastic tape to facilitate finding them by flashlight in the dark. Non-flowering twigs were chosen which were always on the same level and general exposure on the plant (either Kalmiopsis leachiana, Arctostaphylos canescens, or Quercus vaccinifolia) and showed no evidence of recent new growth. Sites were picked such that all three species were growing in close proximity.

The first transect was established 65 m down from the ridgeline on the north slope, and following a line parallel to the slope direction, went to the top of the ridgeline and down the south slope a distance of 52 m. The other transect began approximately 20 m below the ridgeline on the north side of the previous transect, followed a contour going around the east slope, and ended 20 m below the ridgeline on the south end of the first transect (Figure 14).

Two sets of measurements were made. The first took place at predawn, with measurements beginning at 4:00 A.M. and continuing until 6:00 A.M. The sun rose on that day at 6:15 A.M. Pressure chamber measurements were also made at midday between 1:30 P.M. and 2:30 P.M. to determine maximum stress levels that the plants were undergoing. All measurements, recorded in pounds of pressure per square inch and later converted to atmospheres of pressure, were made according to the methods of Waring and Cleary (1967).

Because of the steepness of the terrain and type of vegetation, up to five minutes occurred between cutting of the twig and actual measurement of internal stress. To reduce the chances of possible increased stress values before measurements occurred, twigs were carried to the site of the pressure chamber in an airtight bag which had been moistened on the interior.

Seed Germination

To determine the germinability of seeds of Kalmiopsis leachiana under different conditions and in that way gain insight into the conditions necessary for reproduction of this species, a series of seed germination tests were conducted. These tests took two basic forms: (1) germinating seeds in petri dishes between filter paper, and (2) sowing seeds on soils collected from the natural habitats of Kalmiopsis.

Petri Dish Experiments. Experiments were run between December 1976 and July 1977. All seeds were collected between July and September of 1976, using capsules that had matured during the growing season of the previous year (1975). If stratification is necessary for germination, this sampling method gives seeds that were stratified naturally and to the same degree. Immature capsules that were developing at the time of collection at most sites had not reached the point of dehiscence, so there was no chance of collecting ripe seeds that had not overwintered. All capsules and seeds were stored until use in dry petri dishes in the absence of light and at room temperature.

Preliminary experiments with seed germination in petri dishes involved allowing seeds to sit in approximately 1.0 cm of distilled water for three weeks. A high amount of germination occurred (20 to 30 per cent) and it was concluded that any further stratification was not needed.

After preliminary trials had been performed, seed germination was tested under the following procedure. All seeds were sorted under a dissecting microscope to remove misshapen, miscolored, abnormally small, or otherwise visibly nonviable seeds.

Cleaned and sorted seeds were placed on a single piece of No. 1, 7 cm diameter filter paper in a sterilized 1.5 cm x 19 cm petri dish. Another piece of filter paper of the same size was placed over the seeds to reduce evaporation and maintain high moisture levels. The dishes were initially watered with 5 ml of distilled water with needleless sterile plastic syringes. Subsequent watering occurred in 3 ml amounts. Replicates of 25 seeds each were prepared, with equal numbers of replicates for Cascade and Siskiyou seed sources. Germination was considered to have occurred when the radicle broke through the seed testa. Experiments were continued until no further germination occurred after one week's time.

All seed germination experiments in petri dishes were run in a walk-in growth chamber. Temperature was kept constant at 23°C. The light cycle alternated between 16 hours of light and 8 hours of total darkness.

Seeds were tested for their ability to germinate in the dark. As before, seeds from both major populations were placed between filter paper of the same size in petri dishes; however, the top and bottom halves of the dishes were wrapped in aluminum foil. All watering followed the schedule outlined above and was done in the dark. Water levels were monitored by checking a control dish, prepared in the same manner as the dark dishes but without seeds. When water level was low in the control dish, it and the dark dishes containing seeds were watered. Germination amounts were tallied only after light germination tests had been terminated.

Because seedlings of Kalmiopsis are very rare in nature (only one was ever found), experiments were performed to determine if auto-toxic compounds are released through the leaves of this species which inhibit the germination of its seeds and early growth of seedlings. Three different leaf extracts were prepared. For the first, fresh leaves were collected at Rattlesnake Creek in the Kalmiopsis Wilderness Area on May 20, 1977 and were stored in an airtight bag under refrigeration until time of use two days later. A 40 g fresh weight sample of these leaves was mechanically stirred in 150 ml of distilled water for three hours, and the solution was then filtered through a Büchner funnel. The resulting filtrate was kept frozen until the actual germination test was conducted in order to minimize any degradation of active compounds.

A filtrate was made in a similar manner from a 40 g weight of litter consisting almost entirely of Kalmiopsis leaves. The litter sample was pre-sorted to remove obvious contaminants such as pine needles, moss fragments, and small twigs. The sorted sample was mechanically stirred for three hours, filtered and the filtrate frozen until germination tests were initiated. The litter sample was collected on May 21, 1977, at Rattlesnake Creek from below a number of Kalmiopsis plants.

The last extract was prepared from a leaf spray collected from a greenhouse-grown plant of *Kalmiopsis*. Distilled water was sprayed through a plastic sprayer onto the foliage of the plant. The pot in which it was growing was tipped on its side, and spraying continued until one liter of water was collected dripping into a plastic pan below the plant. The plastic sprayer and pan both had been previously rinsed with one-tenth strength Chlorox bleach, which was followed by several washings with distilled water. In addition, one liter of water was collected straight, after having been sprayed through the plastic sprayer as a control. Both the actual collected leaf spray and the distilled water control were then evaporated to a volume of 200 ml each using a rotary evaporator at temperatures kept between 25°C and 30°C. The final distilled preparations were kept under refrigeration until seed germination experiments were initiated, one day later.

Petri dishes and seeds were prepared in the same manner as for the light and dark germination tests. Dishes were watered initially with 5 ml of each extract, and when extract levels became low, subsequent 3 ml quantities were added. All extracts were refrigerated between waterings and allowed to come to room temperature before watering took place.

Soil Germination Experiments. To determine the effect of soil type on seed germination, five separate soil tests for germination were performed in replicates of 25 seeds each for seeds from plants of the Southern Cascades and the Siskiyou Mountains. Test soils from Kalmiopsis habitats included: mineral soil or soil of gabbro origin collected from the plot site above Valen Lake, Kalmiopsis Wilderness; a mineral soil of metavolcanic origin from the plot site at Limpy Rock; mineral soil of peridotite origin from the plot site at Sourdough Flat, Kalmiopsis Wilderness; and an organic material and humus sample from a rock crevice in Limpy Rock. All mineral soils had been previously sifted through an 8 mm wire mesh screen. A fifth soil substrate consisted of an autoclaved equal-parts mixture of sand, finely ground peat, and perlite. This was used as a control soil substrate because it was considered to provide few if any germination stimulating or inhibiting substances and was found to be a satisfactory substrate for germination of Kalmiopsis seeds in previous nursery practice (H. Greer, pers. comm., 1976).

Clean and sorted seeds were sown on the surface of the different soil types in plastic trays 6 cm deep by 18 cm long. Soil levels were at least 2 cm deep for all tests. The plastic trays had been first washed thoroughly and then rinsed with one-tenth Chlorox bleach followed by distilled water rinses. Watering was done with tap water by placing the plastic trays, which had several evenly spaced holes in the bottom, in large, flat, metal trays of water for the duration of the experiment. In this way there was minimum disturbance of the seed and soil surface interface. The plastic trays themselves were covered with glass plates to maintain high humidity and reduce the influx of moss and fungal spores.

These soil germination tests were conducted under greenhouse conditions in which temperatures were controlled at 65°F for the day and 60°F at night. All lighting was natural except for those lights in an adjoining hall which provided diffuse light at night. A germination event was counted when a seedling appeared on the soil surface. Experiments were continued until no new germination took place for a two week period.

Effect of Fire on Germination. Vegetation sampling during the field season of 1976 suggested that fire has strongly affected vegetation associated populations of Kalmiopsis leachiana. To determine the effect of fire upon germination of Kalmiopsis seeds, seeds were subjected to moist heat and then allowed to germinate under conditions previously shown to be conducive to a high percentage of germination. Previous work with legume seeds has shown that moist heat, rather than dry heat, more closely simulates the conditions that occur in the litter layer during a fire (Martin, Miller, and Cushwa, 1975). Maximum germination for the fire-adapted legume genera tested was found to occur after heating to 70°C. In their experiments, seeds were placed under insulated cover baskets hanging over water baths which had been heated to a range of different temperatures. Quick (1935, 1959, 1961) tested germination response to heat in Ceanothus integerrimus and C. cordulatus by subjecting seeds to boiling water for different periods of time. He also placed seeds in 4-liter containers of water that had been previously heated to different temperatures. The water was allowed to cool to room temperature and seeds were removed and then placed under conditions which were known to allow germination. His findings showed that moist heat treatments of 70°C to 80°C promoted the greatest amount of germination in these two species of Ceanothus, while boiling seeds more than 30 seconds will likely kill the embryo when the integument opens to imbibe water. For Ceanothus velutinus var. laevigatus, Gratkowski (1962) found that germination amount was maximum for seeds steeped in water at temperatures between 80°C and 90°C.

To test for germination response to heat in Kalmiopsis, 100 previously sorted seeds from both the Cascades and Siskiyou Mountains were placed in 2.0 cm lengths of clear plastic tubing cut from disposable pipettes. Both ends of the plastic were then covered with a small piece of filter paper by means of rubber bands to prevent escape of the seeds. A 600 ml beaker of distilled water was heated to 70°C and the two plastic sections, wrapped in cheesecloth to weigh them down, were placed in the water after the heat source was removed. The water was allowed to cool to room temperature in a place free from draft and the seeds were then removed. Subsequently the seeds were sown in two separate plastic flats as described previously, in the sterilized mixture of equal parts finely ground peat, perlite, and sand. The plastic flats were covered with glass plates and placed in water in a shallow metal tray to keep the soil mixture moist for the duration of the experiment. These germination tests were conducted under the same greenhouse conditions for those of seed germination tests on different soils.

Seedling Growth

To determine the ability of *Kalmiopsis* seedlings to grow on the different soil types on which this species occurs and in this way discover the effect of parent material on its distribution, young seedlings were grown on different soils of actual *Kalmiopsis* habitats. These included soils derived from ultramafic, gabbro, and metavolcanic parent materials, in addition to organic material from the crevices of Limpy Rock.

Two- to three-week-old seedlings from germination tests were transferred to 7.5 cm high plastic pots containing soil to the depth of at least 6 cm. Most seedlings were those germinated in the mixture of equal parts sand, peat, and perlite. At the time of transfer the seedlings were still young enough that no secondary roots had yet developed. Seedling growth was allowed to continue for a period between four and seven months from December 1976 to July 1977. At the end of July all seedlings were removed from the pots and the soil surrounding their roots was carefully washed off. Measurements were taken of root and shoot length, length of the largest leaf, number of leaves, and number of shoots.

Phytochemistry

In visited populations of *Kalmiopsis leachiana*, only a very few leaves out of the entire population ever showed evidence of herbivory. This observation of low incidence of herbivory prompted an initial investigative study of possible secondary compounds concentrated in the leaves of *Kalmiopsis* which might deter feeding of herbivores.

Leaves of *Kalmiopsis leachiana* were collected from Limpy Rock on May 15, 1977. Leaf extracts were prepared and analyzed for presence of gravanotoxins I, II, and III by comparison thin-layer chromatography according to the methods outlined by Constantine, Sheth, and Catalfomo (1967), under the direction of Dr. G.H. Constantine, Jr., of the Oregon State University Department of Pharmacognosy.

RESULTS AND DISCUSSION

Geology and Soils

The results of identification of rock samples from Kalmiopsis populations are presented in Table 8. The dominant rock types for the Siskiyou Mountains stands are gabbro and metagabbro. The exceptions to this are the sites Sourdough Flat and Vulcan Lake on peridotite, Collier's Bar on metavolcanic rock, Pine Creek on altered quartz diorite, Bailey Cabin partially on a diorite dike, the Fawn Lily Slope on serpentinite, and Fire Heaven and Kurt's Reading Hole on secondary serpentine. The rock type of the rock outcrops on which Kalmiopsis leachiana was found to grow in the Southern Cascades consisted of silicified tuff.

Characteristics measured at each of the vegetation sample sites, including pH, color, and stone content, are presented in Appendix IV. The results show that soils of the Siskiyou Mountains almost without exception were high in stone content. The surface soil on average was composed of 2.5 per cent fragments between 0.25 cm and 1.0 cm diameter, 11.0 per cent fragments of 1.0 cm to 3.0 cm in diameter, and 1.9 per cent fragments over 3.0 cm. Exposed bedrock composed at least five per cent of the total ground surface in all sites of the Siskiyou Mountains except for Bailey Cabin, and ranged up to 90 per cent at the Rock of Taurus. Acidity for

Table 8. Rock types associated with sampled sites of Kalmiopsis populations as identified by Len Ramp, Oregon Department of Geology and Mineral Industries. Explanation of vegetation units is found in the vegetation section of Results and Discussion. Location of sample sites listed Appendix I. (LS = low elevation Siskiyous; HS = high elevation Siskiyous; SC = Southern Cascades.)

Site name	Vegetation unit	Rock type
Collier's Bar	LS	Siliceous metavolcanic rock related to the Rogue Formation
Chetco Crossover	LS	Metagabbro composed of hornblende, plagioclase, and quartz
Pine Creek	LS	Coarse-grained altered quartz diorite with secondary green amphibole (uralite), probably occurring in the contact zone of gabbro and quartz diorite
Rattlesnake Creek	LS	Gneissic metagabbro
Rattlesnake Creek Slope	LS	Greatly altered metagabbro
Fire Heaven	LS	Pyroxenite of almost entirely clinopyroxene and some olivine and secondary serpentine; plus one piece of quartz diorite, possibly from a dike
York Creek	LS	Coarse-grained olivine gabbro containing pyroxene and magnetite
Vulcan Lake	HS	Olivine-rich peridotite (harzburgite)
Kurt's Reading Hole	HS	Pyroxenite of almost entirely clinopyroxene and some olivine and secondary serpentine
Valen Lake	HS	Medium-grained gabbro with pyroxenes partially altered to green amphibole

(Continued on next page)

Table 8. (Continued)

Site name	Vegetation unit	Rock type
East West Ridge	HS	Metagabbro, coarse-grained plagioclase-amphibole in composition
Fawn Lily Slope	HS	Serpentinite, altered clinopyroxene
Rock of Taurus	HS	Gabbro pegmatite, very coarse-grained hornblende plagioclase
East Bailey Cabin	HS	Dike rock, dacite porphyry and fine-grained diorite or diabase
Sourdough Flat	HS	Weathered peridotite
Dried Waterhole	HS	Gneissic metagabbro with some secondary quartz
Bailey Mountain	HS	Gneissic metagabbro
Burnt Forest	HS	Metagabbro, in part gneissic
Sewell Spring	HS	Metagabbro
Gold Basin	HS	Gabbro, magnetite and basic plagioclase
Copeland Creek	SC	Porous iron-stained quartz
Limpy Rock	SC	Fractured iron and manganese oxide-stained quartz
Dog Creek	SC	Altered tuff with abundant quartz, some pyrite and clay
Knobcone Pine Ridge	SC	Iron-stained, altered silicified tuff
Ragged Ridge	SC	Iron-oxide-stained druzzy vein quartz and iron-stained silicified tuff
Bradley Indian Cave	SC	Silicified tuff, porous with iron oxide, clay and some manganese oxide
Four Ladies' Rock	SC	Silicified pinkish brown crystal tuff

gabbro soils ranged between pH 5.6 and pH 6.4, with an average of pH 5.8. The heavier the forest canopy development which was present, the more acidic was the soil underneath. All ultramafic soils had a pH of 6.4. The diorite soil at Pine Creek had a measured pH of 5.8. The peridotite soils were more yellow in color than the gabbro derived soils with a hue value of 5Y/R as opposed to 10Y/R for the gabbro soils. Values for all Siskiyou soils were medium in lightness ranging from 4 to 6. Chroma numbers ranged between 6 and 2.

For soils of forest stands sampled near *Kalmiopsis* rock outcrops in the Southern Cascades, all three size classes of stone fragments usually represented less than ten per cent of the surface soil amount. In those cases there the plot was established very near an outcrop, rock fragments under 1.0 cm sometimes approached a ten per cent value. Exposed bedrock always represented less than five per cent of the total ground surface. Soil color measurement showed a hue of 10Y/R, a value of 5 to 6, and a chroma between 4 and 2. The only exception to the above statements for Southern Cascades plots is that at Knobcone Pine Ridge and this is discussed in more detail in the vegetation section.

Soil analyses results (Table 9) show that the peridotite soil from the Sourdough Flat *Kalmiopsis* population proved to be lowest in the essential minerals tested for (calcium, potassium, phosphorus,

Table 9. Soil analysis results of soils collected from sites of selected _Kalmiopsis_ populations. (ppm = parts per million; meq = milliequivalents)

Parent material	Site	P (ppm)	K (ppm)	Ca (meq/100 g)	Mg (meq/100 g)	Cation exchange capacity (meq/100 g)	NO_3^- (ppm)	NH_4^+ (ppm)
Serpentinite	KRH	14	54	1.8	1.5	7.31	6.72	12.81
Peridotite	SDF	9	44	1.3	2.7	8.27	2.94	42.00
Metavolcanic	BIC	9	180	1.5	1.3	27.35	1.89	11.30
Gabbro	VLK	17	54	1.8	1.1	10.67	1.05	16.21
Diorite	PCK	11	490	5.0	2.2	38.57	59.22	11.55
Organic matter	LPR	29	418	0.13	0.03	-	-	-

and nitrates) as well as having the highest magnesium to calcium ratio. These are consistent with results found by Walker (1954) to be true for serpentine soils. The diorite soil nitrate content and cation exchange capacity, as well as the concentrations of phosphorus, potassium, and calcium, were the highest recorded for any of the soils tested. The gabbro and metavolcanic soils show levels intermediate between those of the diorite and ultramafic soils.

Vegetation

Introduction

Manual-visual table analysis of vegetation patterns of the sampled areas in which Kalmiopsis leachiana was found to occur yielded three major vegetation units. Each is distinctly defined by the characteristics of species composition, vegetation structure, soils, elevation, and topographic position. More precisely, one vegetation unit consists of Kalmiopsis populations and associated vegetation occurring only at low elevations (300 to 600 m) in the Siskiyou Mountains; another is composed of those Kalmiopsis stands occurring at high elevation in the Siskiyous (over 900 m); and a third is of stands sampled in the Southern Cascade Mountains. The species used to define these units were those whose constancy fell between 10 and 60 per cent. Location, elevation, slope, aspect, and date of sampling for each population sampled are given in Appendix I.

Distribution of populations according to slope, aspect, elevation, and vegetation unit are presented in Figure 4.

The three vegetation units are defined by six different sets of species. Each vegetation type was found to contain a group of species which is exclusive to that type alone (Table 10). There are ten species characteristic of low elevations in the Siskiyou Mountains, 16 species which are associated with high elevation plots in the Siskiyous, and six species which occur with *Kalmiopsis* only in the Southern Cascade Mountains. Although these 32 exclusive species establish the identity of the three vegetation units, there exist additional plant species which were used to delineate the three *Kalmiopsis* vegetation associations. These are species which occur in two of the vegetation units but are excluded from the third (Table 11).

All vascular plant species associated with *Kalmiopsis* are tabulated in Appendix III by constancy and cover value for each of the stands. Seven of these species were consistently found in all three vegetation types, with constancies of 60 per cent or more. These include *Kalmiopsis leachiana*, *Pseudotsuga menziesii*, *Rosa gymnocarpa*, *Vaccinium parvifolium*, *Gaultheria shallon*, *Pinus lambertiana*, and *Whipplea modesta*. Douglas-fir (*Pseudotsuga menziesii*) and sugar pine (*Pinus lambertiana*) tended to be the dominant conifers throughout all these units. *Kalmiopsis* was in

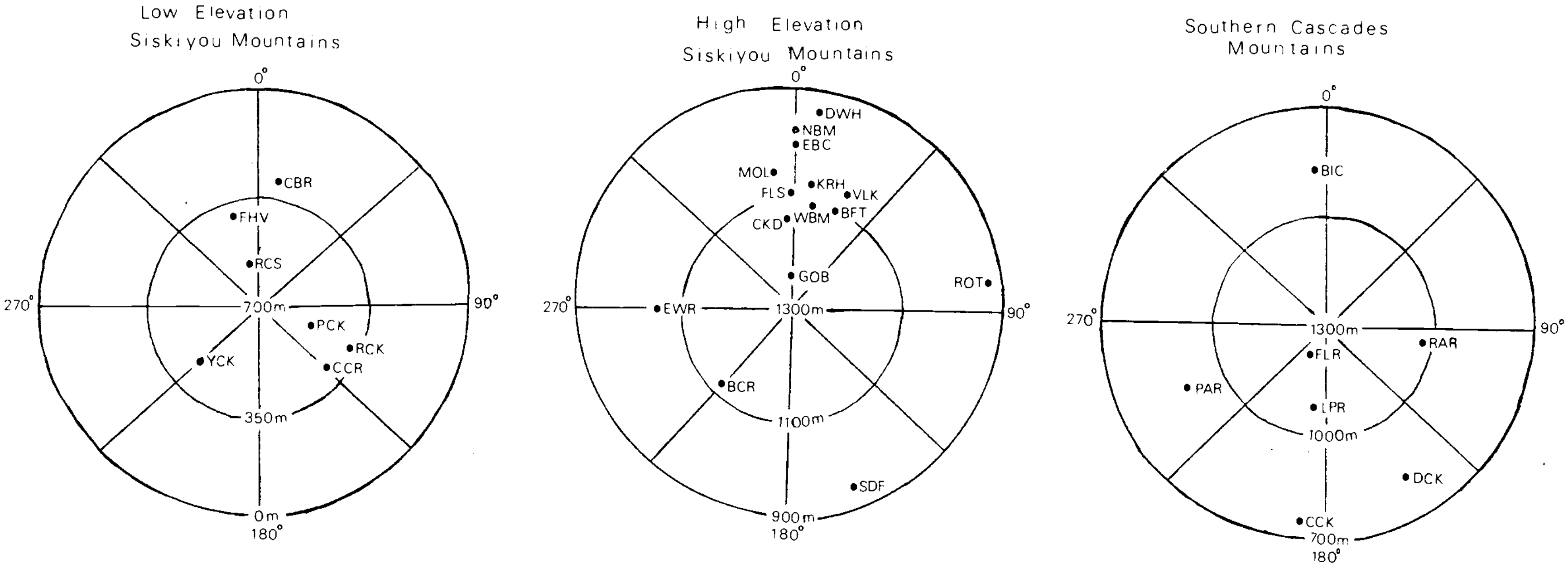


Figure 4. Distribution of sampled Kalmiopsis populations according to associated vegetation, stand elevation, and slope position. Key to site abbreviations, and actual stand elevations and slope positions are given in Appendix I.

Table 10. Distribution among sampled vegetation of differential samples which are common to a single vegetation. X represents presence of a species in a stand. Key to site abbreviations is given in Appendix I.

	High elevation Siskiyous																Low elevation Siskiyous							Southern Cascades						
	ROT	FWR	SDF	FLS	VLK	SSP	EBC	KRH	CKD	BCR	MOK	BFT	WBM	NBM	DWH	GOB	RCS	FHV	CBR	YCK	RCK	CCR	PCK	FLR	LPR	RAR	RIC	DCK	CCK	PAR
Quercus vaccinifolia	X	X	X	X	X	X	X	X	X	X	X		X	X	X		X	X												
Pinus monticola	X	X	X	X		X	X	X	X	X	X		X	X			X													
Garrya buxifolia	X	X	X	X	X	X		X	X	X	X	X																		
Lilium bolanderi	X	X	X	X	X		X		X	X							X	X												
Arctostaphylos patula	X							X	X	X	X		X			X														
Gaultheria ovatifolia							X	X	X	X	X					X														
Veratrum insolitum						X	X	X						X	X	X														
Quercus sadleriana							X				X	X	X	X	X	X														
Berberis pumila		X	X	X	X	X	X	X							X							X								
Picea breweri												X	X	X	X	X														
Asarum hartwegi					X								X	X	X															
Pinus contorta	X			X				X	X							X								X						
Senecio canus	X	X	X	X																										
Festuca ovina				X									X	X																
Nothochelone nemorosa													X	X	X															
Eriogonum ternatum	X	X						X																						
Linocera hispidula																	X	X	X	X	X	X	X							
Rhus diversiloba																		X	X	X	X	X	X							
Galium ambiguum			X														X	X	X	X	X									
Quercus chrysolepis																	X		X	X	X	X	X							
Vancouveria planipetala																	X	X	X		X									
Galium bolanderi																	X	X		X	X									
Chamaecyparis lawsoniana																	X	X			X	X								
Polygala californica																	X	X	X	X										
Festuca californica																		X		X	X	X								
Brodaea sp.																		X	X	X										
Iris chrysophylla																								X	X	X		X	X	
Tsuga heterophylla																								X	X	X	X			
Thermopsis montana																								X	X		X		X	
Campanula scouleri																								X				X	X	
Collomia heterophylla																								X				X	X	
Acer circinatum																								X				X	X	

Table 11. Distribution among sampled vegetation of differential species which are common to two vegetation units but absent from the third. X represents presence for species in a stand. Key to site abbreviations is given in Appendix I.

	High elevation Siskiyous																Low elevation Siskiyous							Southern Cascades						
	ROT	EWR	SDF	FLS	VLK	SSP	EBC	KRH	CKD	BCR	MOL	BFT	WBM	NBM	DWH	GOB	RCS	FHV	CBR	YCK	RCK	CCR	PCK	FLR	LPR	RAR	BTC	DCK	CCK	PAR
Lithocarpus densiflora	X	X	X	X	X	X	X	X	X	X	X		X	X	X	X	X	X	X	X	X	X	X							
Arctostaphylos canescens	X	X	X	X	X	X	X	X				X	X	X			X	X	X	X	X									X
Rhamnus californica	X	X	X	X	X	X			X	X							X	X	X	X	X	X	X							
Iris thompsonii	X	X		X	X	X	X	X							X			X	X	X		X	X							
Amelanchier pallida	X	X		X	X	X											X	X	X		X	X								
Vaccinium ovatum		X	X		X	X											X	X	X	X	X	X							X	
Arnica parviflora	X						X	X	X	X							X	X	X		X	X								
Umbellularia californica	X	X		X		X											X			X	X	X								
Aster brickellioides	X	X			X	X		X									X	X		X										
Pinus attenuata	X				X	X		X	X	X	X							X	X											X
Ceanothus pumilus	X	X		X				X	X	X										X										
Juniperus sibirica	X			X					X	X									X	X										
Berberis nervosa					X						X													X	X	X	X	X	X	
Chimaphila umbellata							X					X	X	X	X								X	X					X	
Rhododendron macrophyllum						X		X					X	X	X	X										X			X	
Symphoricarpus albus						X							X	X	X									X	X			X		
Arctostaphylos nevadensis				X			X	X	X		X		X	X		X			X					X						
Smilacina stellata	X	X																									X		X	
Achlys triphylla					X										X														X	
Arenaria macrophylla												X												X				X		
Arbutus menziesii															X			X	X			X	X		X		X	X		X
Pteridium aquilinum						X												X		X	X	X	X	X				X	X	
Rubus ursinus																					X	X		X	X	X		X	X	
Cornus nuttallii															X		X		X	X	X	X			X					
Garrya fremontii																	X	X			X	X			X			X		

high concentration in most stands except those in the Southern Cascades. Salal (*Gaultheria shallon*) was in heavy abundance but was restricted to those plots which through evidence of topographic position and soil conditions, appeared to be more mesic in nature. Salal and *Kalmiopsis* appeared to be major competitors at the low shrub level when they occurred together. *Rosa gymnocarpa* and *Vaccinium parvifolium* both were highly constant for all stands, but usually represented only a small portion of the total cover of the shrub layer. *Xerophyllum tenax* was by far the most constant and dominant herb of any one of those associated with *Kalmiopsis*.

A total of 161 vascular plant species representing 44 families were found to be closely associated with *Kalmiopsis leachiana* in the 30 sites sampled. These are listed in Appendix II by family and according to the vegetation units in which they are found. The species of each vegetation unit are also classified on a general life-form basis in Table 12. Eighty-seven species were exclusive to Siskiyou plots and 24 were found only with *Kalmiopsis* in the Southern Cascades. A total of 49 species were shared by Siskiyou and Cascade stands.

Low Elevation Siskiyou Vegetation

Seven sites were sampled in which *Kalmiopsis leachiana* was found to occur at low elevation in the Siskiyou Mountains. Location,

Table 12. Composition of the three major vegetation units on general life-form basis.

Vegetation unit	Total species	Conifer tree species	Sclerophyll tree species	Deciduous tree species	Evergreen shrub species	Deciduous shrub species	Herb species
Low elevation Siskiyous	87	9	3	2	10	10	28
High elevation Siskiyous	114	12	3	1	18	8	67
Southern Cascades	82	9	2	2	8	9	43

elevation, slope, aspect, and date of sampling for each of these stands are given in Appendix I. Plots are distributed in almost equal numbers to both steep north and south slopes which form the deepcut valleys of the Chetco and Illinois Rivers (Figure 4). Four of these occur in the Kalmiopsis Wilderness Area and thus are part of the Chetco River drainage, while the remaining three plots are located on the sharply inclined slopes just above the near vertical canyons of the Lower Illinois River (Figure 1). Five sites are at elevations between 300 m and 430 m, while the stands at Rattlesnake Creek Slope and Pine Creek are approximately 550 m and 600 m in elevation, respectively.

Structure and composition characteristics of the tree canopies, along with herb layer cover values, of low elevation Siskiyou stands are outlined in Tables 13 and 14. The composition of the shrub layers by major shrub species of these stands is given in Table 15. Cover and constancy values for all species of this vegetation unit are listed in Appendix III.

These results show that the vegetation of low elevation sites is one dominated by conifers and sclerophyll trees and shrubs (Tables 13, 14, and 15). The general vegetation spectrum is one of a few scattered and large fire-scarred conifers in amongst which is a relatively open canopy, smaller in stature and consisting of broad-leaved evergreen sclerophyll trees and shrubs. Herbs,

Table 13. Relative tree canopy size, conifer representation, species totals, and total herb cover for low elevation Siskiyous <u>Kalmiopsis</u> populations. All values based on a 375 m^2 area for each site.

Site	Total DBH (cm)	Total conifer DBH (cm)	% Conifer DBH of total DBH	Number conifer stems $>$ 20 cm DBH	Total species per plot	Total herb cover (%)
PCK	813.0	355.0	43.7	5	29	1.8
RCK	746.9	228.8	30.6	5	36	1.7
CBR	601.4	140.5	25.3	2	35	1.1
CCR	577.8	113.2	18.8	3	40	1.3
YCK	353.0	135.5	38.3	3	40	3.0
Submean	618.4	194.6	31.5	3.6	36	1.8
RCS	250.3	242.5	84.6	4	42	0.5
FHV	206.0	168.3	87.7	2	40	5.9
Total mean	507.9	197.7	47.0	3.4	37	2.1

Table 14. Representation of major tree species by total diameter at breast height (cm) of low elevation Siskiyous *Kalmiopsis* populations for 375 m^2 plots. Numbers in parentheses are per cents of total stand DBH represented by the indicated species.

Site	*Pseudotsuga menziesii*	*Pinus lambertiana*	*Lithocarpus densiflora*	*Quercus chrysolepis*	*Arbutus menziesii*
PCK	267.5 (32.9)	87.5 (10.8)	357.4 (44.0)	94.6 (11.6)	3.2 (0.4)
RCK	162.4 (21.7)	66.4 (8.9)	320.1 (42.9)	198.0 (26.5)	- -
CBR	85.2 (14.7)	55.3 (9.6)	428.0 (74.1)	9.3 (1.6)	- -
CCR	89.7 (14.9)	23.5 (3.9)	202.2 (33.6)	138.6 (14.9)	86.3 (14.3)
YCK	95.3 (27.0)	40.2 (11.4)	71.6 (20.3)	131.4 (37.2)	- -
Submean	140.0 (22.2)	54.6 (8.9)	275.9 (43.9)	114.4 (18.4)	17.9 (7.35)
RCS	115.5 (46.1)	79.1 (31.6)	18.0 (7.2)	7.8 (3.1)	- -
FHV	52.4 (31.1)	38.2 (22.7)	37.7 (18.3)	- -	- -
Total mean	124.0 (26.9)	55.7 (14.1)	194.8 (34.3)	82.8 (13.6)	12.8 (2.1)

Table 15. Cover distribution of major shrub species of low elevation Siskiyous *Kalmiopsis* populations for 375 m^2 plots. Cover values are per cent ground surface shaded by a species' foliage.

Site	*Vaccinium ovatum*	*Gaultheria shallon*	*Kalmiopsis leachiana*	*Quercus vaccinifolia*	*Lithocarpus densiflora*	*Vaccinium parvifolium*	Total shrub cover
PCK	-	12.0	8.4	-	13.3	-	43.8
RCK	23.3	1.6	12.6	-	12.2	2.7	83.8
CBR	19.9	-	27.1	-	12.9	0.1	61.3
CCR	4.2	2.9	47.7	-	15.2	-	79.1
YCK	9.2	-	17.9	-	0.2	-	28.4
Sub-mean	11.3	3.3	22.7	-	11.0	0.5	51.5
RCS	1.4	-	25.1	10.9	13.3	2.1	58.8
FHV	8.2	-	25.1	2.0	37.7	0.3	65.7
Total mean	9.5	2.4	23.4	1.8	15.1	0.8	54.6

though present in a large number of species, only account for 2.2 per cent of the ground cover on average (Table 13). A total species count shows that average number of species is greatest for this set of plots compared to the other two major vegetation units (Table 12). These stands averaged 36 species for the 375 m^2 plots, while a total of 40 species were recorded for two sites (Table 13).

The conifers are almost entirely dominated by two species, *Pseudotsuga menziesii* and *Pinus lambertiana*, the former playing the more important role (Table 14). *Juniperus sibirica*, *Taxus brevifolia*, *Pinus monticola*, *Pinus attenuata*, *P. ponderosa*, *Calocedrus decurrens* and *Chamaecyparis lawsoniana* are found in low elevation stands, but to a much lesser degree (Appendix III). Of the broadleaf sclerophyll species characteristic of these stands which show potential for growth to tree size on other sites in the Siskiyou Mountain study area, only canyon live oak (*Quercus chrysolepis*) and madrone (*Arbutus menziesii*) reach what can be considered normal tree height. Canyon live oak has a relatively high cover value, approximately twice that of sugar pine (based on total DBH) but is less important on average than Douglas-fir. Madrone was found to occur to a much smaller extent, representing only 2.9 per cent of the total tree canopy (Table 14).

By far the greatest portion of the cover of the overstory canopy on these sites is attributed to tanoak, *Lithocarpus densiflora*.

On average its total DBH represented 43.0 per cent of the total DBH for the plots (Table 14). Though Lithocarpus is capable of attaining much greater heights under other conditions (personal observation; Peck, 1961), it rarely exceeded 3 m in these Kalmiopsis stands. Thus it could almost be relegated to the shrub layer, but it was such a dominant factor and still of considerable height that it was included in the broadleaf sclerophyll canopy. In fact, as a member of the shrub layer, Lithocarpus stems less than 1.0 cm in DBH accounted for 15.1 per cent of the cover of that stratum. Only Kalmiopsis showed a higher cover value (Table 15). The growth form of this plant encountered at these sites was one of a highly branched, greatly spreading, tall shrub or small tree whose thick and stiffly branched form allowed some growth of smaller shrubs and herbs beneath it. Most commonly the stems of Lithocarpus reclined at an angle as they grew out of the rocky soil.

Deciduous trees were present to only a small extent at these low elevation sites (Table 14). Cornus nuttallii was confined to only those three sites which were near stream drainages and Acer macrophyllum was present only at Pine Creek in the Illinois River drainage.

The shrub layer of this vegetation unit is highly diverse, but two evergreen Ericaceae, Vaccinium ovatum and Gaultheria shallon, along with Kalmiopsis leachiana, rated the highest in cover values (Table 15). From the standpoint of direct competition with

Kalmiopsis for water, nutrients, and light, these two species appear to be the most direct competitors in the shrub layer at low elevations. In all but two sites, as the cover of Kalmiopsis leachiana decreases with an increasing thickness in the overstory canopy, V. ovatum becomes the dominant shrub. At Pine Creek, G. shallon becomes the important shrub species with increasing canopy density, while at Chetco Crossover, V. ovatum and G. shallon share this role. Other important shrubs include Rhus diversiloba, Umbellularia californica, Garrya fremontii, Rubus ursinus, and Rhamnus californica var. occidentalis. In species numbers evergreen shrubs equal deciduous shrubs (Table 12), but in terms of cover, the sclerophyll shrubs played a much more dominant role (Table 15).

Four of the seven stands at low elevation occur on south-facing slopes (Figure 4). General observations indicate that north-facing sites which are adjacent to these four are much more heavily vegetated. Two of the Kalmiopsis populations which are on north-facing slopes at low elevation are near very exposed ridgelines (Rattlesnake Creek Slope and Collier's Bar) and the third, Fire Heaven, is on ultramafic-derived parent material.

The low elevation Siskiyou stands occur on a relatively high number of different parent materials, with gabbro or altered forms of it the most common type (Table 8). Parent material had been shown to be extremely important in the development of a particular vegetation in the Siskiyous (Whittaker, 1960). For that reason it is difficult to single out the effects that change in topography, elevation, and influence of fire have on these low elevation Kalmiopsis stands, since they occur on such a wide range of parent materials.

Upon examination of geologic maps (Wells, Holtz, and Cater, 1949; Wells and Walker, 1953; Coleman, 1972; Ramp, 1975), and the exact rock type which underlies the vegetation, the dominant theme which holds true for these sites is that they are located on major transition zones between one parent material type and another. Geologically, this results in a hybridization of rock types and a large degree of alterations at the point of intrusion and movement between one zone and another (Ramp, 1975). A gradation in degree of metamorphism and thus a gradation in rock structure and chemical composition will occur from those rocks which are most extremely altered at the point of contact to those farther away which experienced less severe conditions and as a consequence are less altered (Flint and Skinner, 1974). From a vegetation standpoint, one can expect vegetation types of intermediate composition and structure (Whittaker, 1960). This has special significance for this study because many stands of Kalmiopsis leachiana occur on transition zones between one igneous parent material and another.

Six of the seven Siskiyou sites at low elevation occur on alteration zones between two parent material types. Stands at

Rattlesnake Creek, Chetco Crossover, and the slope above the Rattlesnake Creek site are located in the Chetco River Complex. They are found on the gabbro side of a contact area between large zones of gabbro and an ultramafic intrusion consisting of the harzburgite form of peridotite. The parent material as a result is highly altered metagabbro. The site named Fire Heaven in the Taggart's Bar vicinity of the Chetco River is also located in the Chetco River Complex but is instead on the ultramafic side of the contact zone. In this case the parent material is pyroxenite, an altered form of peridotite. Vegetatively, these three sites are in transition areas between the relatively open and exposed vegetation characteristic of ultramafic parent materials and the denser, more closed types of vegetation common on soils of gabbro derivation.

The Kalmiopsis population at Collier's Bar occurs at a ridgeline which marks the transition zone between a large sheet of serpentine and what Coleman (1972) maps as amphibolic gneiss. Ramp, however, identified rock samples from this stand as siliceous metavolcanic rocks similar to those of the Rogue Formation (Table 8). This would apparently account for the relatively dense Pseudotsuga-Lithocarpus-Quercus forest just down slope from the ridge. Kalmiopsis only occurs near the ridge where the apparent proximity to the open exposed vegetation on serpentine has reduced the density of the vegetation found on soils derived from metavolcanic parent material. It is here that *Kalmiopsis* was observed to grow to its greatest length and density, trailing out from underneath a very thick layer of *Lithocarpus densiflora*.

Two sites, the *Kalmiopsis* populations at Rattlesnake Creek Slope and at Fire Heaven, represent significant deviations from the general vegetation pattern of low elevation Siskiyou sites. For this reason they have been treated separately in Tables 13, 14, and 15. These stands are characterized by an almost complete absence of a broadleaf sclerophyll tree layer. The two main components of this stratum are instead represented in the shrub layer: *Quercus chrysolepis* by *Q. vaccinifolia* and *Lithocarpus densiflora* by a shrubby, low-statured form of the same species which rarely exceeds 1 m in height (Table 15). At Rattlesnake Creek Slope there is a transition in growth form in the oak from a thickly-branched, tall shrub at the bottom of the slope to a many-branched form which occurs near the ridgetop and is indistinguishable from *Q. vaccinifolia*. The plot itself lies in the middle of the transition. The loss of the broadleaf tree sclerophylls results in a decrease in total DBH for both stands (Table 13), and this loss in canopy density is correlated with a general increase in the cover of *Kalmiopsis* (Table 15).

The change in structure of the Rattlesnake Creek Slope and Fire Heaven stands is accompanied by a change in species composition. Four of the differentiating species of low elevation vegetation, Polygala californica, Garrya fremontii, Lonicera hispidula, and Festuca californica, are absent from the Rattlesnake Creek Slope (Table 10). In their place are three indicator species of high elevation Kalmiopsis stands, Pinus monticola, Lilium bolanderi, and Quercus vaccinifolia. Most differentiating species of low elevation are present at Fire Heaven, although in comparatively low abundance. In addition the high elevation indicator species, Lilium bolanderi, is present. For the shrub layer of both sites, Arctostaphylos canescens and Vaccinium parvifolium increase in cover values while Vaccinium ovatum and Gaultheria shallon decrease in importance (Table 15).

The differences in composition and structure of the latter two stands appear to be the result of two different sets of environmental factors. The Rattlesnake Creek Slope site is near a very exposed ridgeline and at a higher elevational level away from the direct ameliorating influence of a stream or river drainage. For Fire Heaven recent fires, as evidenced by the presence of knobcone pine, Pinus attenuata, along with a serpentine-related parent material are correlated with the differences observed. In the Siskiyou Mountains knobcone pine is an indicator of sites where fire has repeatedly occurred, and is not restricted to any one particular soil type (Whittaker, 1960; Emmingham, 1973; Franklin and Dyrness, 1973).

In general, a movement towards what appear to be more xeric sites at low elevation *Kalmiopsis* stands results in the depression of a relatively dense broadleaf sclerophyll tree layer found on more mesic sites to a sclerophyll shrub layer. This is associated with a decrease in the density of the canopy and is affected by soil type, topographic position, and elevation. *Pseudotsuga menziesii* and *Pinus lambertiana* dominate all stands but total DBH is lowest for the most xeric sites. Under relatively moist conditions *Acer macrophyllum* and *Cornus nuttallii* are present, while at the most xeric sites deciduous trees drop out. *Vaccinium ovatum* and *Gaultheria shallon* are the most important shrubs at the mesic end of the moisture gradient, but lose importance to *Quercus vaccinifolia*, *Arctostaphylos canescens*, *Vaccinium parvifolium*, and the shrub form of *Lithocarpus densiflora* on the more xeric sites. *Kalmiopsis leachiana* also has a higher cover value at the more xeric sites. A change in cover from 8.4 per cent at Pine Creek (on diorite) to 25.1 per cent at Rattlesnake Creek Slope and Fire Heaven for *Kalmiopsis* is associated with a concommitant increase in the amount of non-vegetated ground present.

High Elevation Siskiyou Mountains

Kalmiopsis leachiana was found to occur most frequently in the Siskiyou Mountains at elevations of 900 m (3000 feet) and greater. Location, elevation, aspect, slope, and date of sampling of the 16 vegetation plots which compose this vegetation unit are listed in Appendix I. Cover and constancy values are given for each species in Appendix III. The composition and structure of the tree canopy, plus herb stratum covers, are reported in Tables 16 and 17. The composition of the shrub layer of high elevation stands according to the major shrub species which compose it is given in Table 18.

A total of 114 vascular plants were recorded for high elevation stands and as was true for lower elevation sites, more than one-half of this total (67 species) are herb species (Table 12). Twelve species of conifers alone were recorded in high elevation _Kalmiopsis_ habitats. Twenty-six shrub species are associated with _Kalmiopsis_ in the sites sampled, but with the increase in elevation there is a correlated doubling of the number of evergreen shrubs compared to deciduous shrubs (Table 12).

The total average DBH for sites at high elevations is approximately 150 cm less than that for low elevation plots (Tables 14 and 17). This does not appear to be due to a thinning of large-stemmed conifers or a decrease in their size. The average number of conifer stems per plot which measure over 20 cm DBH is even somewhat larger for higher elevation sites, 3.9 stems compared to 3.4 stems per low elevation plot (Tables 13 and 16). Thus the

Table 16. Relative tree canopy size, conifer representation, species totals, and total herb cover for high elevation Siskiyou *Kalmiopsis* populations. All values are based on a 375 m^2 area for each site.

Site	Total DBH (cm)	Total conifer DBH (cm)	% Conifer DBH of total DBH	Number conifer stems >20 cm DBH	Total species per plot	Total herb cover (%)
GOB	576.5	559.6	97.1	3	26	6.9
DWH	692.6	580.4	83.8	15	29	1.0
NBM	264.0	262.8	99.5	3	22	0.6
WBM	342.5	342.5	100.0	6	29	1.6
BFT	227.4	227.4	100.0	3	23	1.2
MOL	41.3	41.3	100.0	0	27	1.9
BCR	0.0	0.0	0.0	0	25	1.6
CKD	37.5	37.5	100.0	0	29	5.4
KRH	476.3	463.1	97.2	1	33	6.8
EBC	506.0	498.7	98.6	9	29	4.3
SSP	264.9	263.5	99.5	3	35	1.4
VLK	86.9	86.9	100.0	0	29	1.8
SDF	1094.2	1094.2	100.0	0	28	11.3
FLS	466.6	465.4	99.7	12	33	5.4
EWR	266.7	266.7	100.0	2	25	0.5
ROT	95.9	95.9	100.0	2	37	1.9
Mean	362.6	330.4	92.2	3.9	28.7	3.3

Table 17. Representation of major tree species by total diameter at breast height (cm) of high elevation Siskiyous *Kalmiopsis* populations for 375 m^2 plots. Numbers in parentheses are per cents of total stand DBH represented by the indicated species.

Site	*Pseudotsuga menziesii*	*Pinus lambertiana*	*Pinus contorta*	*Pinus monticola*	*Pinus attenuata*	*Castanopsis chrysophylla*
GOB	75.7 (13.1)	68.4 (10.8)	346.3 (60.2)	30.6 (6.4)	-	16.9 (2.9)
DWH	580.4 (83.8)	-	-	-	-	13.5 (1.9)
NBM	149.8 (45.4)	105.4 (40.0)	-	15.2 (5.8)	-	1.2 (0.5)
WBM	254.9 (83.2)	57.6 (16.8)	-	-	-	-
BFT	227.4 (100.0)	-	-	-	-	-
MOL	38.4 (93.0)	-	-	-	2.9 (7.6)	-
BCR	-	-	-	-	-	-
CKD	-	-	-	-	37.5 (100.0)	-
KRH	79.7 (16.3)	-	354.8 (74.5)	30.6 (6.4)	-	13.2 (2.8)
EBC	150.4 (29.7)	348.3 (68.8)	-	-	-	7.3 (1.4)
SSP	13.9 (5.2)	34.0 (12.8)	-	204.7 (77.3)	8.5 (3.2)	3.8 (1.4)
VLK	-	-	-	-	86.9 (100.0)	-
SDF	-	-	1094.2 (100.0)	-	-	-
FLS	199.5 (42.5)	-	-	160.0 (34.3)	-	-
EWR	21.1 (7.9)	35.4 (13.3)	-	210.2 (78.8)	-	-
ROT	54.3 (56.6)	-	-	34.4 (35.9)	7.2 (7.5)	-
Mean	123.0 (41.1)	43.3 (28.1)	48.5 (14.7)	41.4 (11.8)	7.0 (7.4)	2.4 (0.7)

Table 18. Cover distribution of major shrub species of high elevation Siskiyou *Kalmiopsis* populations for 375 m^2 plots. Cover values are per cent ground surface shaded by a species foliage.

Site	*Quercus vaccinifolia*	*Kalmiopsis leachiana*	*Lithocarpus densiflora*	*Rhododendron macrophyllum*	*Quercus sadleriana*	*Arctostaphylos canescens*	*Vaccinium parvifolium*	Total shrub cover
GOB	-	30.6	-	3.4	5.0	2.5	0.2	42.7
DWH	9.5	47.5	27.4	13.9	2.8	-	8.5	125.0
NBM	2.5	45.5	14.0	4.8	4.8	0.4	5.3	76.5
WBM	20.8	16.1	5.5	4.1	2.7	-	19.6	62.8
BFT	4.4	33.0	-	-	-	0.3	2.7	11.1
MOL	9.8	24.0	9.6	2.5	2.3	-	1.8	76.1
BCR	1.0	16.0	15.0	-	2.3	-	1.1	42.5
CKD	15.0	15.0	2.5	1.0	-	-	2.5	60.0
KRH	7.4	28.4	24.2	5.6	-	9.5	2.4	88.7
EBC	6.8	51.8	18.9	-	15.1	-	4.6	107.7
SSP	0.1	34.0	27.5	11.3	-	-	3.0	85.1
VLK	2.4	17.4	12.3	-	-	2.8	-	51.1
SDF	-	9.9	7.4	-	-	2.4	0.9	20.9
FLS	31.9	26.9	12.6	-	-	-	8.3	95.4
EWR	23.3	18.9	1.7	-	-	10.8	1.2	58.1
ROT	9.6	8.4	-	-	-	1.9	-	26.5
Mean	9.6	26.5	11.9	2.9	2.1	1.9	3.9	68.4

difference in DBH must be due to the loss of the broadleaf sclerophyll tree stratum. However, relationships are certainly obscured by the fact that high elevation sites show a whole range in the total DBH present, from chapparal-like shrub associations where no trees are present to sites where the DBH total equals that of more mesic low elevation sites (Table 17).

With the loss of the broadleaf trees, the higher elevation vegetation is dominated by a few medium to large-sized conifers which are more diverse in species compared to low elevation sites (Table 17 and Appendix III). The combined per cent total DBH represented by *Pseudotsuga menziesii* and *Pinus lambertiana*, still the most common canopy species, increases on average for these sites (Table 17). Together they account for 69.2 per cent of the total DBH at higher elevation, compared to 41.0 per cent of the total for low elevation stands (Table 14). On an absolute basis, however, their respective DBH totals change very little. The average total *Pseudotsuga* DBH was only 1.0 cm less for high elevation sites (Tables 14 and 17). The difference between the amount of cover represented by these two species and the total canopy itself is accounted for by the appearance and increase in DBH of other conifer species, especially *Pinus attenuata*, *P. contorta*, *P. jeffreyi*, and *P. monticola*.

GO TO 101

Within the vegetational composition of sites of high elevation Kalmiopsis populations is encompassed a gradient of composition and cover values for the indicator species which were used to delineate this major vegetation unit from the other two. Table 19 shows this gradient for indicator species shared by high and low elevation Siskiyou stands, and for those species present only at high elevation.

Although precise correlations do not exist between changes in species composition along the gradient and associated changes in environmental conditions, certain trends do appear. Observation of individual species distribution within the study area with respect to topography, moisture, soils, and elevation suggest that the gradient portrayed in Table 19 represents a change in moisture conditions from those stands which appear to be relatively mesic in nature to those which are relatively xeric. Kalmiopsis thus appears to grow in a relatively wide range of moisture conditions at high elevation sites in the Siskiyou Mountains.

High Elevation Mesic Vegetation. At the mesic end of the gradient, the first five stands are delineated by the presence of Brewer spruce, Picea breweriana, in the forest canopy (Table 19). Waring, Running, and Emmingham (1975) have shown that Brewer spruce is limited to sites in the Siskiyous where snowfall is heavy and deep (2 to 6 m) and cool maritime air masses reduce evaporative

Correlated with the decrease in total DBH in higher elevation Kalmiopsis stands is an increase in total cover of the shrub layer to an average 68.4 per cent (Table 18). This is compared to 54.6 per cent for stands below 600 m (Table 15). Three species consistently dominate the shrub stratum, which averages 1.0 to 1.5 m in height. Kalmiopsis leachiana averages 26.5 per cent (nearly equal to that at Fire Heaven and Rattlesnake Creek Slope), while Lithocarpus densiflora and Quercus vaccinifolia share equal portions of the remaining shrub canopy, averaging 11.9 per cent and 9.6 per cent respectively (Table 18). Thus the move to higher elevation results in an increase in abundance of Kalmiopsis from an average 22.7 per cent for the five sites more typical of low elevation vegetation. Herb cover values were again low, only 3.3 per cent average for the 16 plots.

It is significant that all Kalmiopsis populations sampled at high elevations except two occur on north to north-east facing slopes (Figure 4). The two exceptions are a direct west-facing slope called East West Ridge and a southwest slope in the Big Craggies Botanical Area, both of which are on the western extreme in the range of Kalmiopsis. Thus they receive the direct and immediate influence of maritime breezes originating from the Pacific Ocean located less than 35 km away. In contrast, four of the seven lower elevation sites are on south-facing exposures.

demand in the summer. This low tolerance of high atmospheric evaporation demand is seen as the limiting factor in its distribution.

Along with Brewer spruce, other species which appear to be more mesic in distribution and are found in these stands are *Achlys triphylla*, *Nothochelone nemorosa*, *Asarum hartwegi*, *Berberis nervosa*, and *Symphoricarpos albus*. Douglas-fir and sugar pine dominate the overhead canopies of these stands. The site at Gold Basin has a canopy atypical of high elevation sites, in that it includes, in addition to *Pseudotsuga* and *Pinus lambertiana*, both *Abies concolor* and *Pinus contorta* as substantial representatives of the tree stratum (Table 17 and Appendix III).

Lithocarpus densiflora and *Quercus vaccinifolia* are present throughout the gradient (Table 19). In addition, *Rhododendron macrophyllum* and *Quercus sadleriana*, two shrub species distributed towards the mesic end of the gradient, are abundant (Table 18). All five of these mesic *Kalmiopsis* populations are on gabbro or metagabbro-derived soils (Table 8).

High Elevation Sub-xeric Vegetation. For the six middle stands of the species compositional gradient, which appear to be sub-xeric in vegetation composition, *Pinus monticola* is a prominent member of the overstory canopy (Table 17). Species such as *Aster brickellioides*, *Garrya buxifolia*, *Rhamnus californica* and *Arctostaphylos canescens* begin to appear. But at the same time more

Table 19. Distribution of differentiating species among high elevation Siskiyou Mountains stands. X represents presence of a species in a stand.

	GOB	DWH	NBM	WBM	BFT	MOL	BCR	CKD	KRH	EBC	SSP	VLK	SDF	FLS	EWR	ROT
Festuca ovina			X	X										X		
Nothochelone nemorosa		X	X	X												
Picea breweriana	X	X	X	X	X											
Berberis nervosa		X			X	X						X				
Asarum hartwegi		X	X	X												
Achlys triphylla		X	X		X											
Symphoricarpos albus		X	X	X							X					
Chimaphila umbellata	X	X	X	X	X	X				X						
Gaultheria ovatifolia	X					X	X	X	X	X						
Arctostaphylos nevadensis	X		X	X		X	X	X	X	X				X		
Rhododendron macrophyllum	X	X	X	X		X	X	X	X		X					
Quercus sadleriana	X	X	X	X		X	X	X	X	X						
Arctostaphylos patula	X			X		X	X	X	X							X
Castanopsis chrysophylla	X	X	X						X	X	X					
Veratrum insolitum	X						X		X	X	X					
Lithocarpus densiflora	X	X	X	X		X	X	X	X	X	X	X	X	X	X	X
Quercus vaccinifolia	X	X	X	X		X	X	X	X	X	X	X	X	X	X	X
Vaccinium parvifolium	X	X	X	X	X	X	X	X	X	X	X		X	X	X	X
Iris thompsonii	X	X				X			X	X	X	X		X	X	X
Pinus monticola			X	X		X	X	X	X	X	X		X	X	X	X
Arctostaphylos canescens			X	X					X	X	X	X	X	X	X	X
Garrya buxifolia					X	X	X	X	X		X	X	X	X	X	X
Holodiscus discolor					X		X					X	X	X	X	X
Pinus attenuata						X	X	X	X		X	X				
Amelanchier pallida						X		X	X		X	X		X	X	X
Lilium bolanderi							X	X		X		X	X	X	X	X
Arnica parviflora								X	X	X						X
Pinus contorta								X	X				X			X
Rhamnus californica							X				X	X	X	X	X	X
Berberis pumila		X							X	X	X	X		X	X	X
Aster brickellioides									X		X	X			X	X
Umbellularia californica											X			X	X	X
Senecio canus													X	X	X	X

mesic species, most importantly *Rhododendron macrophyllum* and *Quercus sadleriana* remain abundant, while others like *Picea breweriana*, *Nothochelone nemorosa* and *Achlys triphylla* drop out. *Arctostaphylos patula*, *A. columbiana*, *Veratrum insolitum*, and *Arnica parviflora* are almost totally restricted to this center sub-xeric group.

A particular feature of these sub-xeric sites is that they represent vegetation which has burned recently and at a high enough frequency such that *Pinus attenuata* comprises a significant portion of the overstory canopy (Table 12). For some sites, the effect of the fire appears to have been to increase the xeric nature of the vegetation. As an example, the only conifer species on the north-facing slope above Valen Lake is knobcone pine (Table 17) and shrubs cover only one-half of the ground surface (Table 18). However a *Pseudotsuga*-*Pinus lambertiana* forest occurs in the ravine about 300 m below. Large, dead snags in the plot plus a few scattered mesic species at the base of rock outcrops indicate that the forest probably once extended to the same elevational height of the plot. These species include *Asarum hartwegii*, *Berberis nervosa*, *Gaultheria shallon*, and *Polystichum munitum*. The rockiness of the site (Appendix IV) in conjunction with the influence of repeated fires have allowed a more xeric element, including *Arctostaphylos canescens*, *Lilium bolanderi*, *Berberis pumila*, Castilleja pruinosa, and Aster brickellioides, to exist at this site as well (Table 19).

Stems of Kalmiopsis gathered from the Valen Lake stand were aged at least 55 years (Table 23). This indicates that they were present in the stand during the Big Chetco Fire of 1938 which probably swept through this site (Table 7). It appears then that Kalmiopsis has the ability to remain established in areas where fires may alter the vegetation, and indirectly the abiotic environment, to a very significant degree. The high amount of rock-outcropping is hypothesized as the factor which has allowed Kalmiopsis to exist here under the more mesic conditions of the past.

For three of these sub-xeric sites past fires appear to have been severe enough that a relatively dense shrub stratum exists in the absence of a once-present tree canopy. The specific sites are those sampled in the Big Craggies Botanical Area and are essentially less densely vegetated areas in a thick "sea of brush": Morrison's Lament (MOL), Cookie Drop (CKD), and Big Craggie (BCR).

The brush vegetation or chaparral as it has been termed and described by Gratkowski (1961) consists of a number of shrub species which attain a height of 1 to 2 m. Most important in this area are the shrub species Arctostaphylos columbiana, A. patula, Quercus vaccinifolia, Lithocarpus densiflora, and to a lesser degree Castanopsis chrysophylla, Rhododendron macrophyllum, and Quercus sadleriana. In almost every situation herb cover and the conifer tree canopy is restricted to a few scattered and very dwarfed knobcone and western white pines (Pinus monticola).

In areas near the coast where rainfall approaches 150 cm a year, Gratkoswki (1961) believes chaparral brushfields are a fire-maintained vegetation formation, or perhaps permanent only on extreme southwest slopes where soil types are limiting. Repeated fires act to destroy seed sources for continued conifer production, and at the same time favor those shrub species which are capable of resprouting after a fire. This chaparral-like formation with which Kalmiopsis is associated in the Big Craggies Botanical Area is thus seen as a changing mosaic of forest and shrub-dominated vegetation. The specific pattern is influenced by the frequency of fire, topographic position, and soil type.

The three specific sites where Kalmiopsis stands were sampled within this chaparral formation are all areas where the shrub density and stature are much less than the surrounding vegetation. One location is a bench area near the peak 4116 (Cookie Drop). It is the site of a small azonal and thin-soiled serpentinite outcrop that supports a highly diverse herb layer and a few dwarfed trees and shrubs (Appendix III). It is surrounded by the zonal gabbro parent material which in turn supports an almost impenetrable sclerophyll shrub vegetation.

The other two sites sampled in the Big Craggies are on steep, shrub-covered slopes, one a southwest-facing slope (Big Craggie) and the other north-facing (Morrison's Lament). Both are located on shallow, stony soils and are at or near a ridgeline. The decrease in density of the chaparral associated with these two latter sites is apparently due to increasing exposure and shallowness of the soil. The conditions at these two stands suggest that it is not a specific change in parent material that allows *Kalmiopsis* to occur in otherwise dense vegetation. Instead the common denominator appears to be a requirement for environmental conditions which result in an open vegetation where competition for light, water, and nutrients is reduced.

High Elevation Xeric Vegetation. Four stands in which *Kalmiopsis* is found to occur at high elevations exhibit species compositions which appear to be relatively xeric compared to the sites previously discussed (Table 19). Two of these, East West Ridge and Rock of Taurus, are both very rocky, steep ridgelines and as a consequence show a high percentage of rock outcropping (Appendix IV). At both sites *Kalmiopsis* is almost entirely restricted to rock crevices and the base of trees and shrubs, all places where organic material and moisture can accumulate and the degree of exposure is less extreme.

The remaining sites, Sourdough Flat and Fawn Lily Slope, plus an unsampled population below Vulcan Lake (Figure 1), all occur on ultramafic-derived soils (Table 8). Though xeric in nature relative to other Kalmiopsis high elevation stands, these sites appear to be relatively mesic compared to the range of conditions found on ultramafic soils in the Siskiyou Mountains. The Vulcan Lake population is on the rocky banks of the headwaters of Box Canyon Creek, while the presence of Rhododendron occidentale and Gentiana affinis at Sourdough Flat (Appendix III) suggests that this location is part of a seepage area (Peck, 1961). The stand at Fawn Lily Slope is on the protected north-facing edge of an open and very exposed serpentinite outcrop, exhibiting a relatively high shrub cover (Table 18), compared to the herb-dominated understory of the main body of the outcrop.

Southern Cascades Vegetation

Vegetation sampling in the North Umpqua River area was directed towards measuring quantitatively and qualitatively the vegetation immediately adjacent to Kalmiopsis rock populations. It was initially observed that this surrounding vegetation appeared to be much greater in density and canopy coverage than vegetation sampled in the Siskiyou Mountains. These factors appeared to be resulting in a decrease in site exposure and a concomitant increase in dominance of the microsite environment. This suggested that competition for light, water, and nutrients is playing a pronounced role in the nature of the distribution of Kalmiopsis there. Accompanying analysis was directed towards determining how different this vegetation is from that of the Siskiyous and if these differences could be related to possible factors which result in the segregation of Kalmiopsis to practically competition-free rock outcrops.

The location, elevation, slope, aspect, and date of sampling of Southern Cascades plots are given in Appendix I. Structure and composition of the tree canopy, in addition to herb layer cover values for each of the plots, are listed in Tables 20 and 21. The composition of the shrub layer by major shrub species is given in Table 22. Cover and frequency values for all species of the Southern Cascades stands are found in Appendix III.

A major difference between Southern Cascades sampled stands and those of the Siskiyous, especially high elevation stands, is that all Cascades plots with one exception are located on south-facing slopes (Figure 4). It is significant that in this apparently cooler, more mesic environment Kalmiopsis is largely restricted to the south-facing slopes of the river valley (Figure 2). In addition, within this general distribution all microsites which were sampled occurred on south-facing slopes. The exception to this is the population at Bradley Indian Cave. Here, Kalmiopsis grows

Table 20. Relative tree canopy size, conifer representation, species totals, and total herb cover for Southern Cascade *Kalmiopsis* populations. All values based on a 375 m^2 area for each site.

Site	Total DBH (cm)	Total conifer DBH (cm)	% Conifer DBH of total DBH	Number conifer stems >20 cm DBH	Total species per plot	Total herb cover (%)
DCK	731.9	616.3	84.2	15	33	4.1
CCK	923.3	902.2	97.7	7	32	4.4
RAR	684.5	684.5	100.0	8	13	4.2
FLR	847.8	847.8	100.0	17	29	1.1
BIC	650.0	650.0	100.0	14	19	0.6
LPR	1157.2	1000.2	86.4	11	35	1.1
sub-mean	832.5	783.5	94.7	12.0	26.8	2.6
PAR	331.3	317.2	95.7	0	6	0
total mean	760.9	716.9	94.9	10.8	23.8	2.2

Table 21. Representation of major tree species by total diameter at breast height (cm) of Southern Cascades *Kalmiopsis* populations for 375 m^2 plots. Numbers in parentheses are per cents of total stand DBH represented by the indicated species.

Site	*Pseudotsuga menziesii*	*Pinus lambertiana*	*Tsuga heterophylla*	*Arbutus menziesii*
DCK	488.4 (66.0)	132.9 (18.2)	-	70.7 (9.6)
CCK	619.8 (67.1)	44.8 (4.9)	38.2 (4.1)	-
RAR	51.9 (7.6)	32.8 (4.8)	599.8 (87.6)	-
FLR	847.8 (100.0)	-	-	-
BIC	391.9 (60.3)	-	222.3 (34.2)	-
LPR	767.6 (63.3)	232.6 (20.1)	-	62.6 (5.4)
Submean	529.1 (60.7)	73.9 (8.0)	143.4 (21.0)	22.2 (2.5)
PAR	6.6 (2.0)	-	-	9.5 (2.9)
Total mean	452.7 (52.3)	63.3 (4.0)	122.9 (18.0)	20.4 (2.6)

abundantly on the exposed rock outcrop itself but also in the stony soil at the base of the rock which runs the length of a north slope. It was on this slope that the plot was located.

The change towards a more mesic climate for the Cascades sites is also reflected in an increase in total average DBH to 832.5 cm for six sites and 760.9 cm for all seven (Table 20). This is a greater total value than for either of the Siskiyous vegetation types (Tables 13 and 16). This increase in DBH is due simply to the increase in size and density of the overstory conifers, which account for 95 per cent of the total DBH of the sites (Table 20). The number of conifers stems over 20 cm in DBH averages 10.2 per plot for all Cascades plots compared to 3.4 and 3.0 stems respectively for the low and high elevation Siskiyous plots (Table 20). The overwhelming impression which is conveyed is that the entire microclimate is much cooler and more moist, less light reaches the understory strata, and in short, a more complete influence is exerted by the overstory conifer canopy. There is no longer a thick shrub layer or broadleaf sclerophyll or deciduous tree layer present, probably the result of a decrease in available light under the thick conifer canopy. The only understory sclerophyll species present is Castanopsis chrysophylla, which occurs only at low abundance as a very small tree or tall shrub (Appendix III).

The forests that were sampled in the Southern Cascades in general were dominated by Pseudotsuga menziesii and Pinus lambertiana, as was true for the Siskiyous (Table 21). But sugar pine was found to be less important, averaging only 12 per cent of the total DBH of the stands in which it was found (Table 21). In those sites where sugar pine was least important western hemlock (Tsuga heterophylla) occurred at its greatest abundance in the overstory canopy (Table 21). Franklin and Dyrness (1973) rank Tsuga heterophylla as the least tolerant of moisture stress of the major tree species of southwestern Oregon. Thus the presence of western hemlock in Southern Cascades vegetation and its absence from the Siskiyous stands again suggests that the former sites are much more mesic in nature.

Along with the conifer species already mentioned, Taxus brevifolia, Abies grandis, Abies concolor, Calocedrus decurrens, Thuja plicata, and Pinus attenuata are also present (Appendix III). Though it is never more than a low reclining shrub in the Siskiyou Mountain stands, Taxus brevifolia is present in tree growth form in Cascades stands and represented a substantial portion of the tree canopy at Bradley Indian Cave (Appendix III). The only true sclerophyll tree present is Arbutus menziesii and it is restricted to more open sites where it is present in low amounts (Table 21).

The shrub layer of Southern Cascades stands consists of a fewer number of species than for either Siskiyous vegetation units (Table 12). It is also of much less importance as part of the total vegetation in terms of the cover that it represents. The total average shrub cover for the Umpqua sites is 35 per cent compared to 55 per cent and 68 per cent, respectively, for low and high elevation Siskiyous sites (Table 22). Its abundance on the ground is a direct reflection of the rockiness of the substrate and the density of the overhead canopy (Tables 20 and 22; Appendix IV).

The major shrub species include Gaultheria shallon, Rhododendron macrophyllum, and Berberis nervosa (Table 22). The only sclerophyll shrub common to the stands of the Southern Cascades and the more xeric-appearing sites of the Siskiyous is Arctostaphylos canescens. In the Cascades it was found only in the very rocky sites and those which were very exposed. At Limpy Rock, the scattered, dead stems of A. canescens suggest that the vegetation surrounding that outcrop was once more open than it is now.

Total number of species was less per plot than for the two Siskiyous vegetation groups (Table 12). Because the number of species of conifers, broadleafed trees, both deciduous and evergreen, and shrubs in the Cascades site nearly equaled that of the Siskiyous stands, the difference in species numbers is accounted for by the decrease in herbaceous species. Mosses, when present,

Table 22. Cover distribution of major shrub species of Southern Cascades *Kalmiopsis* populations for 375 m^2 plots. Cover values are per cent ground surface shaded by a species foliage.

Site	*Kalmiopsis leachiana*	*Gaultheria shallon*	*Berberis nervosa*	*Rhododendron macrophyllum*	Total shrub cover
DCK	0.2	18.7	7.8	-	31.4
CCK	0.1	7.6	4.2	15.3	40.2
RAR	0.4	36.8	-	24.4	62.0
FLR	0.0	-	0.7	-	5.1
BIC	18.9	38.8	1.1	-	59.9
LPR	0.0	36.1	0.9	-	38.0
sub-mean	3.3	23.0	2.5	6.6	38.7
PAR	13.4	-	-	-	13.4
Total mean	4.7	19.7	2.1	5.7	35.1

were confined almost completely to shaded rock surfaces and accounted for mostly less than 2.0 per cent cover (Appendix III).

All sites in the Southern Cascades showed ample evidence of past fires, mostly in the form of fire scars on large, veteran Douglas-firs and sugar pines. Slopes were steep, all over 25^{o} grades, and most trees usually bent at the base, indicating a rocky substrate prone to slippage. This was most evident in the vicinity of the rock outcrops themselves.

The site at Knobcone Pine Ridge is distinctly different in vegetation from the general pattern just described for Kalmiopsis locations in the Southern Cascades. For that reason and because Kalmiopsis is found to grow there extensively and directly on the ground surface, this site is treated separately in the vegetation tables for the Southern Cascades (Tables 20, 21, and 22), and will be discussed in detail.

Knobcone Pine Ridge appears to be a rock outcrop like those so far described, but in this case the processes of weathering and frost action have proceeded to a larger extent. There is very little exposed bedrock. Instead this southerly-exposed protruding knob is covered with fractured platey pieces of silicified tuff, and to a lesser degree, a coarse-grained, very immature soil. At one time this site was presumably like the other rock outcrops of the area, with fractured stone limited to the very base of the rock outcrop.

But here, only a few consolidated rock mounds remain protruding from the rock mass which underlies the surface of fractured tuff.

The vegetation of this site is as different and unique as the geological formation. Only seven species of vascular plants were recorded for the ridge itself. These include *Kalmiopsis leachiana*, *Pinus attenuata*, *Pseudotsuga menziesii*, *Arbutus menziesii*, *Arctostaphylos canescens*, *Castanopsis chrysophylla*, and *Gaultheria shallon* (Appendix III). Ground surface covered by shrubs is only 13.4 per cent. Bryophytes comprise almost five per cent of the total cover but are limited to stable rock surfaces. *Gaultheria* and *Arctostaphylos* are scattered very infrequently over the ridgeline, with salal almost completely restricted to the edge between the forest and open ridge. But more importantly, *Kalmiopsis* is growing here on the ground surface just as it does in the Siskiyou Mountains. With the exception of *Arctostaphylos*, the shrub layer consists entirely of *Kalmiopsis leachiana* (Table 22).

The canopy of this stony, thin-soiled ridge is overwhelmingly composed of dwarfed knobcone pines, *Pinus attenuata*, which never attain a DBH greater than 15 cm (Table 21). Distributed sparingly through these knobcone pines are a few dwarfed Douglas-firs. Madrone, like salal, is limited to the edge marking the boundary between the surrounding forest and the open talus ridge. The total canopy cover is very low compared to that of the other sites, totaling only 331 cm total DBH (Table 20). The likely effects associated with this decrease in cover of all vegetation strata are that (1) the amount of light reaching the ground surface is higher, (2) lower strata plants are subjected to desiccating winds to a greater degree, and (3) there occur more rapid changes in temperature which in turn fluctuate between higher maxima and lower minima.

The forest from which this exposed ridge projects is not unlike those already described. Douglas-fir and sugar pine are heavily represented, along with Abies grandis and Calocedrus decurrens. The presence of the latter species suggests that locally the site is more xeric than those sampled previously. The understory is a mixture of Acer circinatum and A. macrophyllum, Berberis nervosa, Gaultheria shallon, Symphoricarpos albus, Holodiscus discolor, and Rosa gymnocarpa in the shrub layer.

The striking feature of the adjacent surrounding forest, however, is the presence of a few standing, large knobcone pines and the many more which are scattered about the ground. The stems of these trees measure 10 cm to 15 cm in diameter and are all much larger than any growing presently on the slope. Though most of the branches have broken off, the cones still remain on the main stem, unopened. Consequently there is an absence of Pinus attenuata seedlings, both within forest, the transition zone, and on the ridge itself. In contrast to this, there is much young

Pseudotsuga and sugar pine reproduction intermixed among the *Arbutus* and *Castanopsis,* and especially prominent in the transition area between the ridge and the forest. *Kalmiopsis* occurs in this transition area, but immediately drops out as the trees become larger at distances farther from the main portion of the ridge.

Differences in soil are as dramatic as those found in the vegetation patterns. *Kalmiopsis* is growing in a substrate composed of at least 75 per cent sharp-angled and flat rock fragments, about half of which measured between 2 and 7 cm, with the remaining fraction under 2 cm (Appendix IV). The rest of the substrate consists of a soil high in sand content and very poor in any form of organic matter. Depth to bedrock varies between 25 cm and appearance right at the soil surface. The only place an organic and litter layer is present on the ridge is where litter has collected in exposed rock crevices and at the base of rocks, or in and amongst patches of *Kalmiopsis*. In the latter case, measurements showed the organic and litter layers together to average 1.5 to 2.5 cm in depth, and sometimes as much as 4 cm deep. In contrast to this poorly developed ridge soil, the soil associated with a sugar pine root-throw in the surrounding forest measured is at least 1 m in depth. Organic matter and litter layer average together about 4 cm in depth and are omnipresent. Though the lower soil horizons are fairly sandy and light colored in composition, the soil consists of only five per cent stones, all mostly less than 2 cm in diameter.

Besides the effect of differences found to occur in soil development there is strong evidence that fire has played a major role in perpetuating the vegetation differences found on and off the ridge. The abundance of knobcone pine indicates that past fires were frequent enough to maintain this fire-dependent species and to reduce competition from young Douglas-fir and sugar pine seedlings on the ridge. The highly spreading and dead stems of *Arctostaphylos canescens* found in the forest amongst the fallen knobcone pines imply that the forest itself was once more open than at present. Increase in fire frequency would probably push back the limits of the surrounding mesic forest and increase the size of the open, exposed stand *Pinus attenuata*. Encroachment of the forest would be hindered by the arrestment of soil development through the combined effect of removal of collected organic matter and direct reduction in growth of plants on the ridge, leading to lower organic matter accumulation and soil development.

It appears from the above observations that the ability of *Kalmiopsis leachiana* to grow on the ground in the Southern Cascades populations is strongly affected by the frequency of fire and the degree of soil development. Associated with these factors is a correlated decrease in the cover of the overstory canopy. Since canopy cover values are less for the Siskiyou Mountain plots, where Kalmiopsis does grow on the ground, than for the Cascades where it does not, it would appear that competition for light is a very influential factor in the distribution of this plant.

Quantitative Similarity Analysis (SIMORD Analysis)

Analysis of vegetation patterns associated with Kalmiopsis by the manual-visual association table method is a qualitative, somewhat subjective approach. As a means of checking the validity of the conclusions arrived at with this method, the vegetation data were subjected to similarity ordination analysis (SIMORD). Because relevés are compared on a quantitative value (the similarity index), a relatively objective analysis takes place. In addition patterns may be made apparent which were not elucidated by previous manual-visual table analysis. Similarity ordination was performed with two goals in mind: (1) to determine whether relevés cluster together on the basis of their quantitative similarity value and if these groupings match those established in manual-visual analysis, and (2) to determine if, in the ordination of relevés, there is some discernible environmental gradient which appears which might represent that ordination. For the first goal, the independent mode of Y-end stand choice was employed, and for the latter the dependent mode was used.

The first seven ordinations were produced by using the independent mode of Y-axis reference stands choice. The first step in analysis was to allow the computer to pick end stands. All species present in the macroplot or its immediate vicinity were given an ordination value of 1.0 per cent and similarity values were computed on this basis. In this way stands were compared simply on the presence or absence of species. The resulting ordination is seen in Figure 5. A large degree of clumping occurred in the center of the ordination plane along the Y-axis. This is the result of the computer choosing the Knobcone Pine Ridge plot (PAR) as the first end stand. The center clustering took place because all other stands were very dissimilar to this site (similarity values of PAR with all other sites never exceeded 3.1). However, this preliminary ordination did suggest which plots might be chosen for maximum separation and grouping of releves.

After this initial ordination end stands were hand-picked, the choice made on the basis of knowledge gained from the previous ordination and that gained from operation of manual-visual tables. By hand-picking end stands, those stands very dissimilar to all others, in particular Knobcone Pine Ridge, could be left in the ordination process so that their position relative to the remaining stands could be clarified. All species present were given a cover value of 1.0 per cent. The result, seen in Figure 6, groups plots

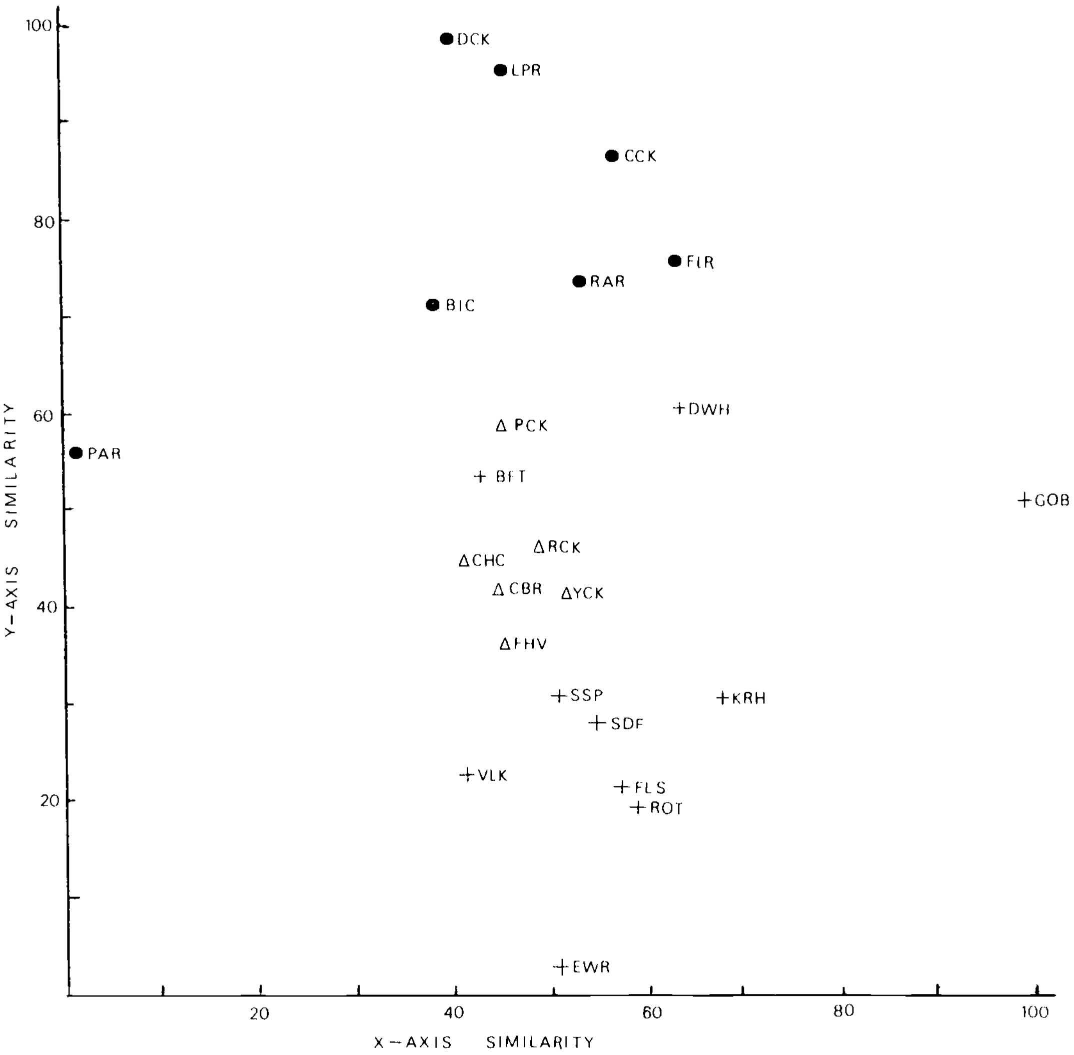


Figure 5. Similarity ordination of sampled Kalmiopsis stands with end stands computer-picked and all species having ordination values of 1.0 per cent. Y-axis stands chosen by independent mode. ▵ : low elevation Siskiyou stands; +: high elevation Siskiyou stands; ●: Southern Cascades stands.)

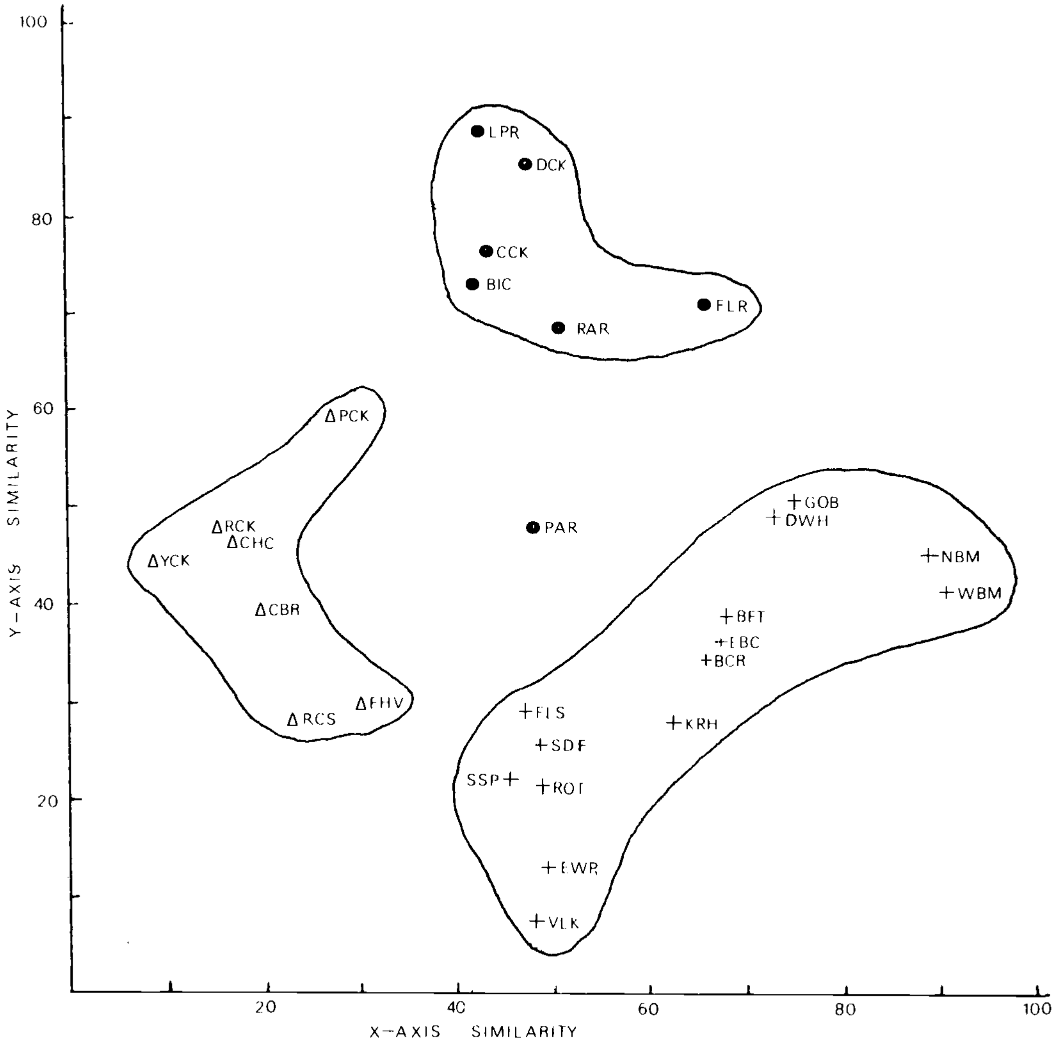


Figure 6. Similarity ordination of sampled Kalmiopsis stands with end stands hand-picked and all species having ordination values of 1.0 per cent. (▲: low elevation Siskiyou stands; +: high elevation Siskiyou stands; ●: Southern Cascades stands.)

exactly in the manner manual-visual tables suggested. Three clusters were produced, one each for high and low elevation plots in the Siskiyou Mountains and one for plots in the Cascades. The stand sampled at Knobcone Pine Ridge falls exactly in the middle of the ordination plane, again the result of its complete dissimilarity with all other sites sampled. Rattlesnake Creek Slope (RCS) and Fire Heaven (FHV) lie on the outside of the low elevation stand cluster nearest to Siskiyous high elevation plots. This agrees with the relationship suggested by manual-visual tables.

The next three ordinations compared stands on the basis of actual quantitative values given to species found within or in the neighborhood of the macroplots. The first of these involved only species which occurred in one or more microplots. Figure 7 shows the ordination. The three basic vegetation groups, developed in the previous ordination on the basis of species presence-absence alone, are preserved. However, the positions of stands within the individual clusters change relative to each other. The most obvious change occurs in the position of the plots Rattlesnake Creek Slope and Fire Heaven with respect to the two main clusters of high and low elevation Siskiyou vegetation. These two stands no longer group with the other low elevation plots, but instead fall much closer to the Kalmiopsis plots located at elevations over 900 m. Floristically they appear to be much more similar to this latter

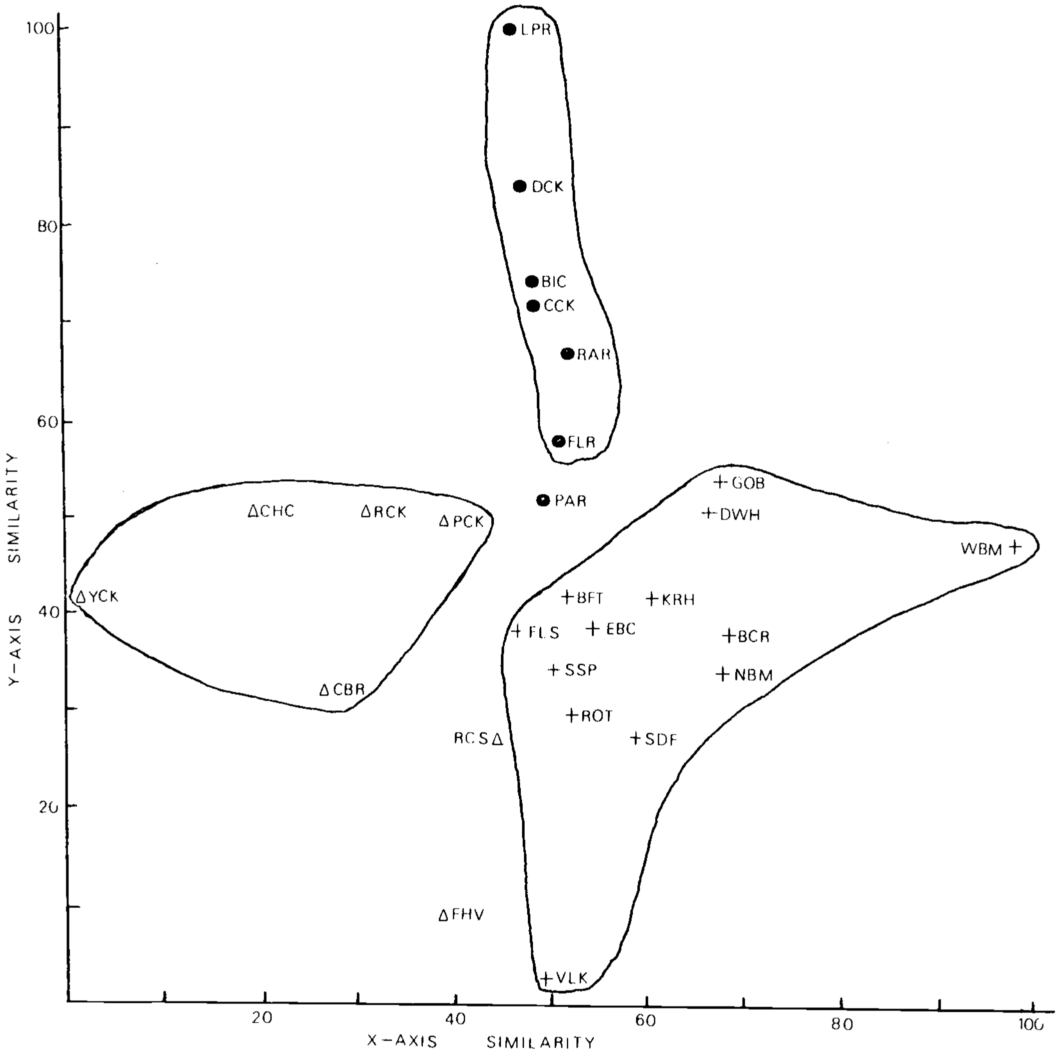


Figure 7. Similarity ordination of sampled Kalmiopsis stands, with end stands hand-picked. Only species actually occurring in one or more microplots were included in the ordination. Stand similarity values were computed on actual cover values. (Δ: low elevation Siskiyou stands; +: high elevation Siskiyou stands; ●: Southern Cascades stands.)

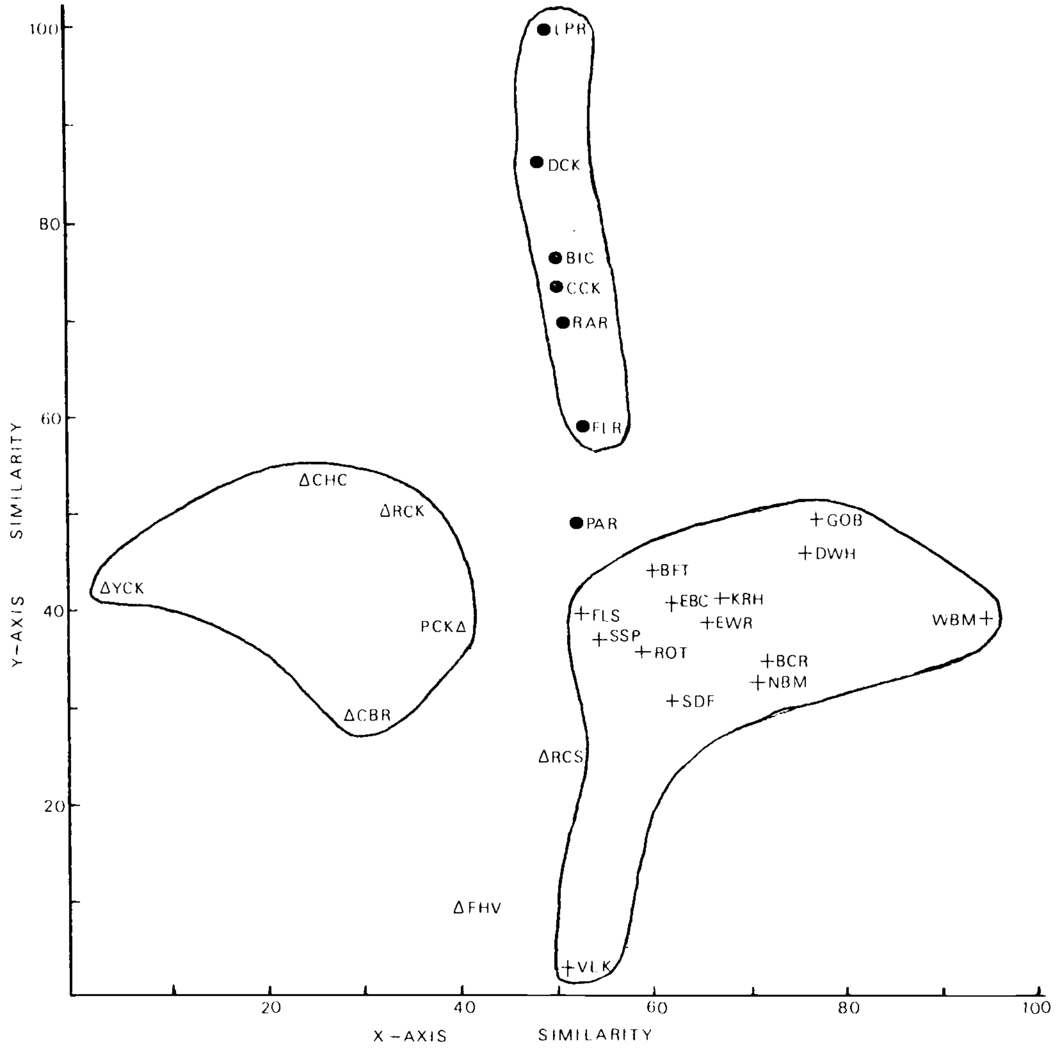


Figure 8. Similarity ordination of sampled stands, with end stands hand-picked. Species found in macroplots but not within a microplot are included. Δ : low elevation Siskiyou stands; + : high elevation Siskiyou stands; ●: Southern Cascades stands.)

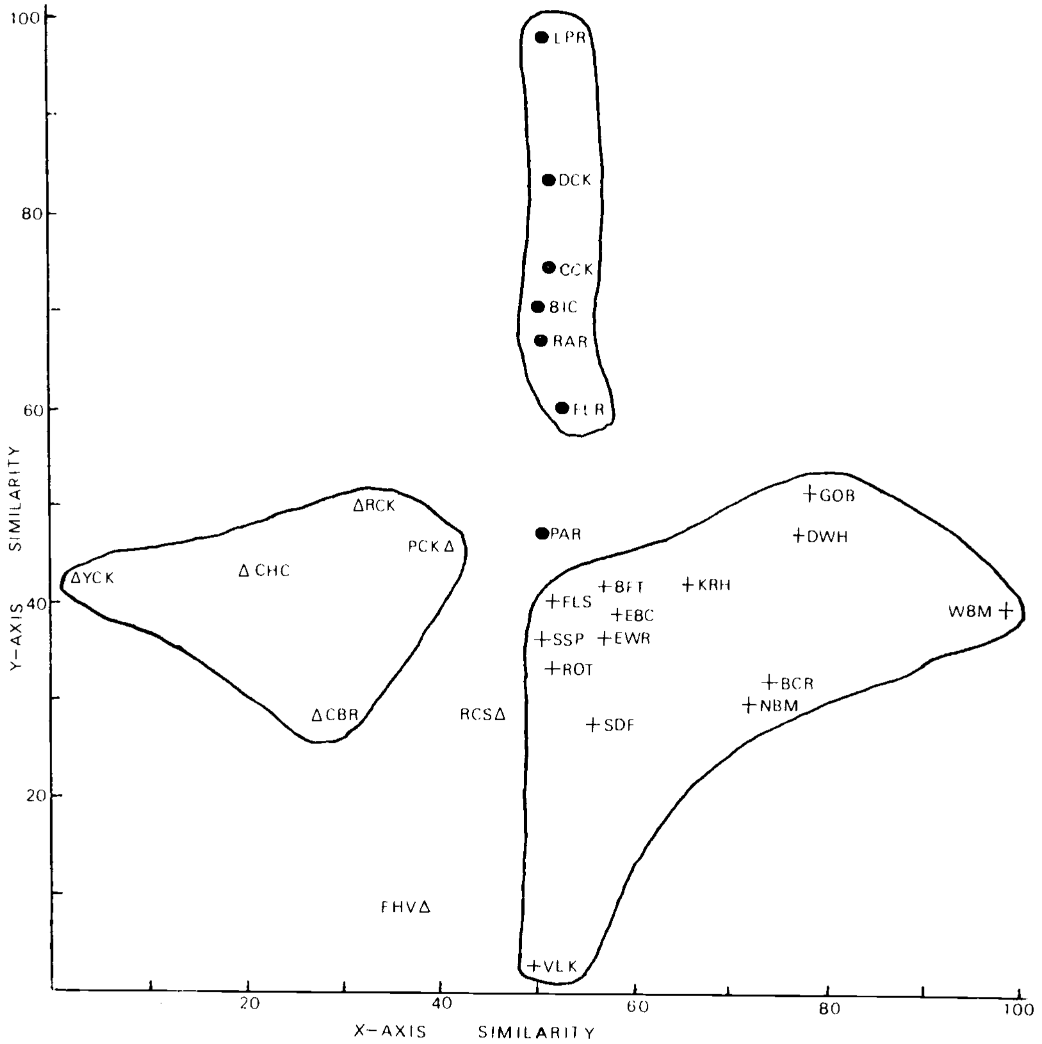


Figure 9. Similarity ordination of sampled Kalmiopsis stands with end stands hand-picked. Species found in vicinity of macroplot but not within it and species found in macroplot but not in a microplot are included. (▲: low elevation Siskiyou stands; +: high elevation Siskiyou stands; ●: Southern Cascade stands.)

group of plots than presence or absence of species would suggest. The differences were explained in terms of fire history, increase in slope exposure, and change in soil type.

Figure 9 shows the two dimensional ordination of plots which results when species which were located in the macroplot but not in any microplots were included in the calculation of similarity values. Figure 9 gives the ordination when all the previously included species, plus those found in the near vicinity of macroplots but not within them, are used in the calculation of similarity values. It can be seen that these ordinations differ very little from Figure 7 for which these last two groups of species were excluded. This points out the value of the manual-visual table method of vegetation classification. It allows one to make qualitative, as well as quantitative, decisions during the vegetation analysis procedure. Decisions can be made based on the presence or absence of species which do not fall directly in any of the microplots, either because they are highly clumped or simply low in density. Consideration can also be given to those species which fall outside the macroplot but could be used as possible indicators of the plot's topographic position, and in that way aid in its classification. Because these species must necessarily be assigned low importance for similarity ordination, they have little influence in the relative positioning of stands via computer data programs such as SIMORD.

Figures 10 and 11 represent ordinations with hand-picked end stands for Siskiyous plots only. Clear differentiation occurs between low elevation and high elevation stands. Choosing different high elevation end stands (the difference between ordination plots in Figure 10 and 11) only shifts patterns within the clustered groups in the middle of the graph. This substantiates that a large amount of variability exists in floristic composition within the high elevation group, the result being that all plots cluster to the center regardless of the particular plots used as reference stands. Thus each stand within this group shares high dissimilarity with every other stand. In this way the heterogeneity of vegetation, especially that at high elevation, is portrayed. Numerous other combinations of reference stands were used, all with the same general result. Thus, as was the case for manual-visual table analysis, further breakdown of high elevation stands into smaller, more homogeneous groups was not possible.

In the attempt to produce an ordination of plots which may reflect changes along only one environment gradient, end stands for the Y-axis were computer picked using the "best axis" procedure. In this case the stand at Knobcone Pine Ridge was omitted because of its high degree of dissimilarity relative to all other plots. By using the "best axis" procedure, the Y-axis stands picked are similar to the X-axis reference stands. Thus, if the X-axis

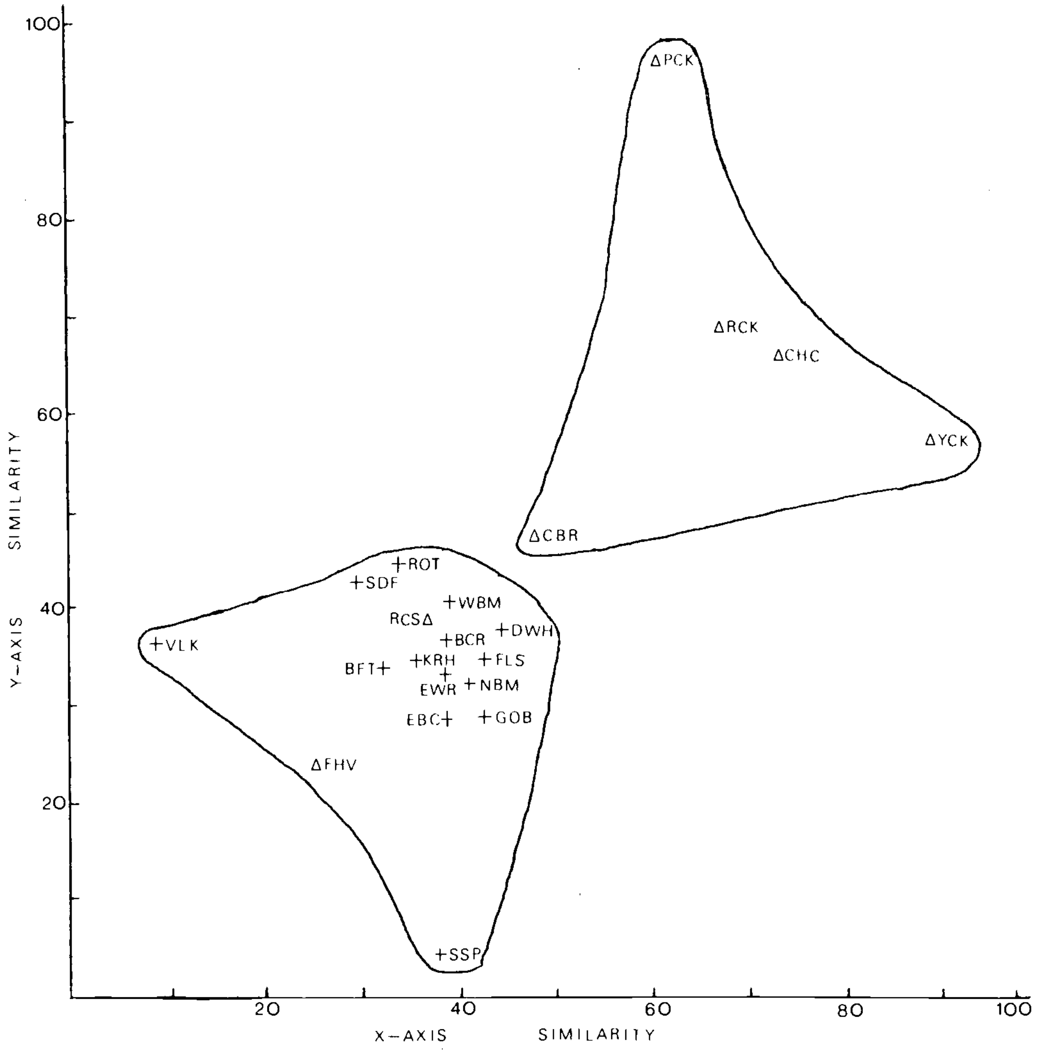


Figure 10. Similarity ordination of Siskiyou Kalmiopsis sampled stands alone, with end stands hand-picked. (Δ: low elevation Siskiyou stands; +: high elevation Siskiyou stands.)

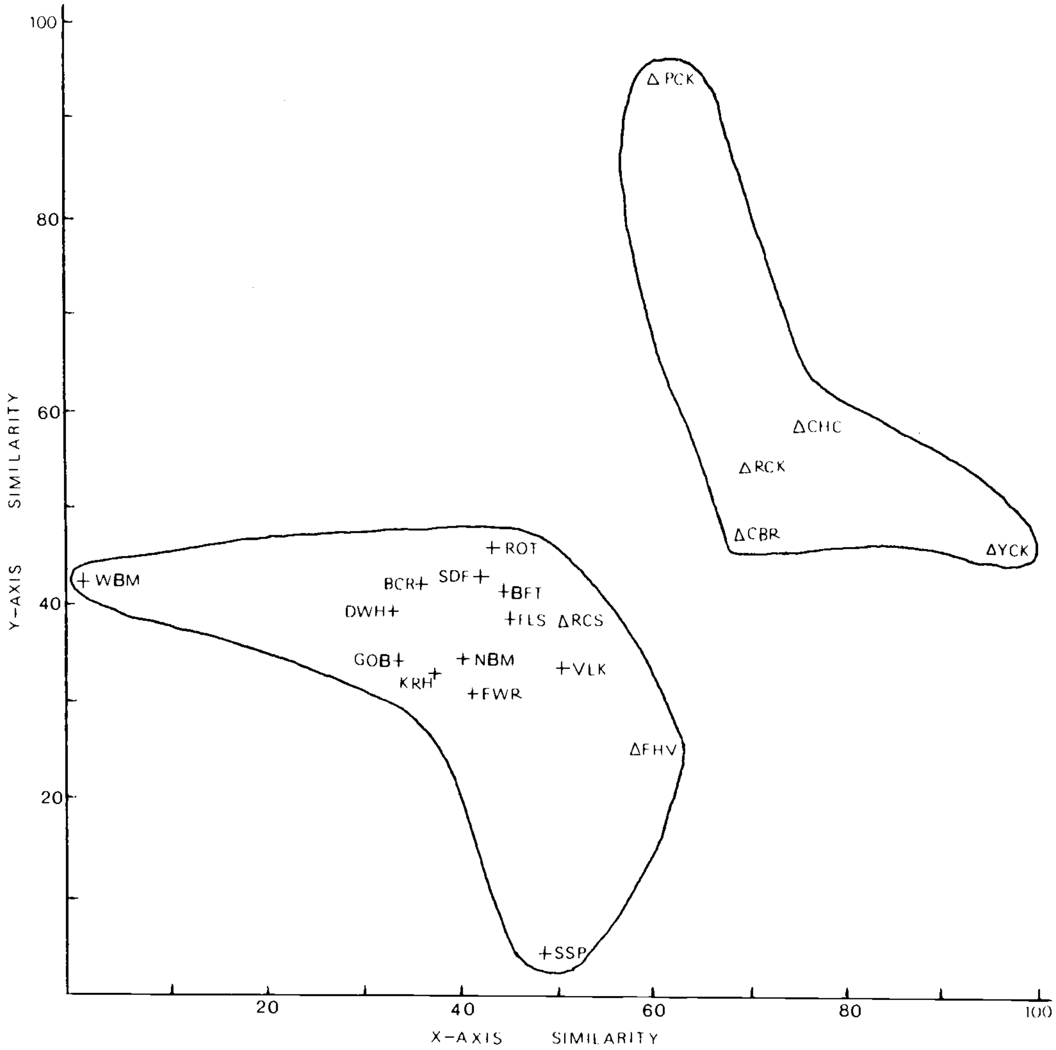


Figure 11. Similarity ordination of Siskiyou *Kalmiopsis* sampled stands alone, with change in end stand choice. (Δ: low elevation Siskiyou stands; +: high elevation Siskiyou stands.)

represents a gradient change in some environmental factor, or a complex gradient of factors, the choice of Y-axis end stands similar to those of the X-axis should reinforce the distribution of stands along the simple or complex gradient (Goff and Cottam, 1967; Dick-Peddie and Moir, 1970). Independent choice of Y-end stands, on the other hand, may instead order stands about a different gradient than the X-axis represents and in that way obscure meaning of the ordination without detailed environmental measures to supplement analysis.

The resulting ordination is portrayed in Figure 12. As can be seen no clear differentiation of previously recognized groups occurs. Cascades plots are segregated to one end while a mixture of high and low elevation stands are concentrated at the other end. The line of plots from the left-hand corner to the top right of the graph represents only crudely a complex moisture gradient. The lack of demonstration of any clear relationship by this method is due to the high amount of floristic variability represented by these plots and the lack of stands intermediate in composition between those of the Siskiyous and the Cascades sample stands.

The final step was to allow the computer to pick end stands using the "best axis" method for Siskiyous plots only. The gradient resulting (Figure 13) appears to represent a change from mesic (the left bottom corner) to more xeric environments (top right

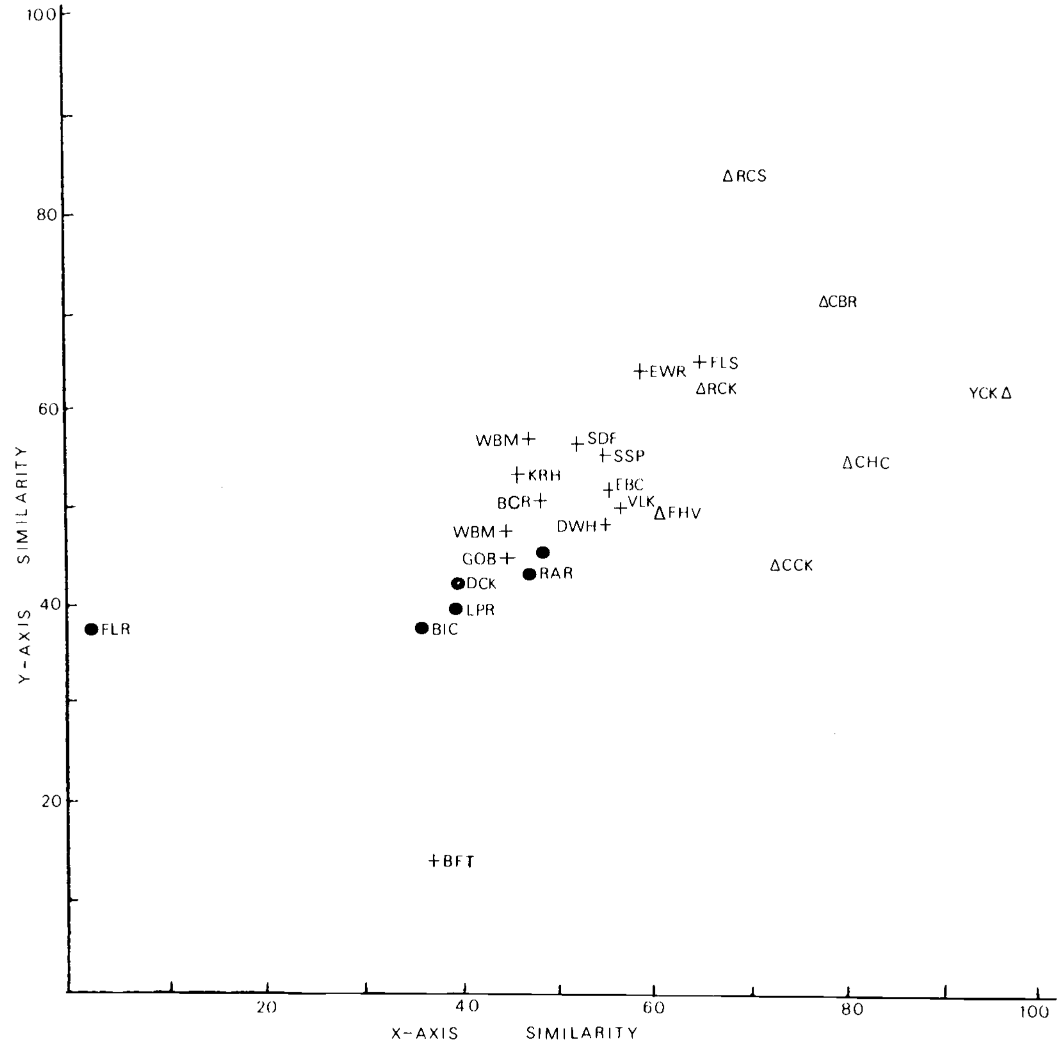


Figure 12. Similarity ordination of sampled Kalmiopsis stands with end stands computer-picked and dependent mode of Y-end stand choice. (Δ: low elevation Siskiyou stands; +: high elevation Siskiyou stands; ●: Southern Cascades stands.)

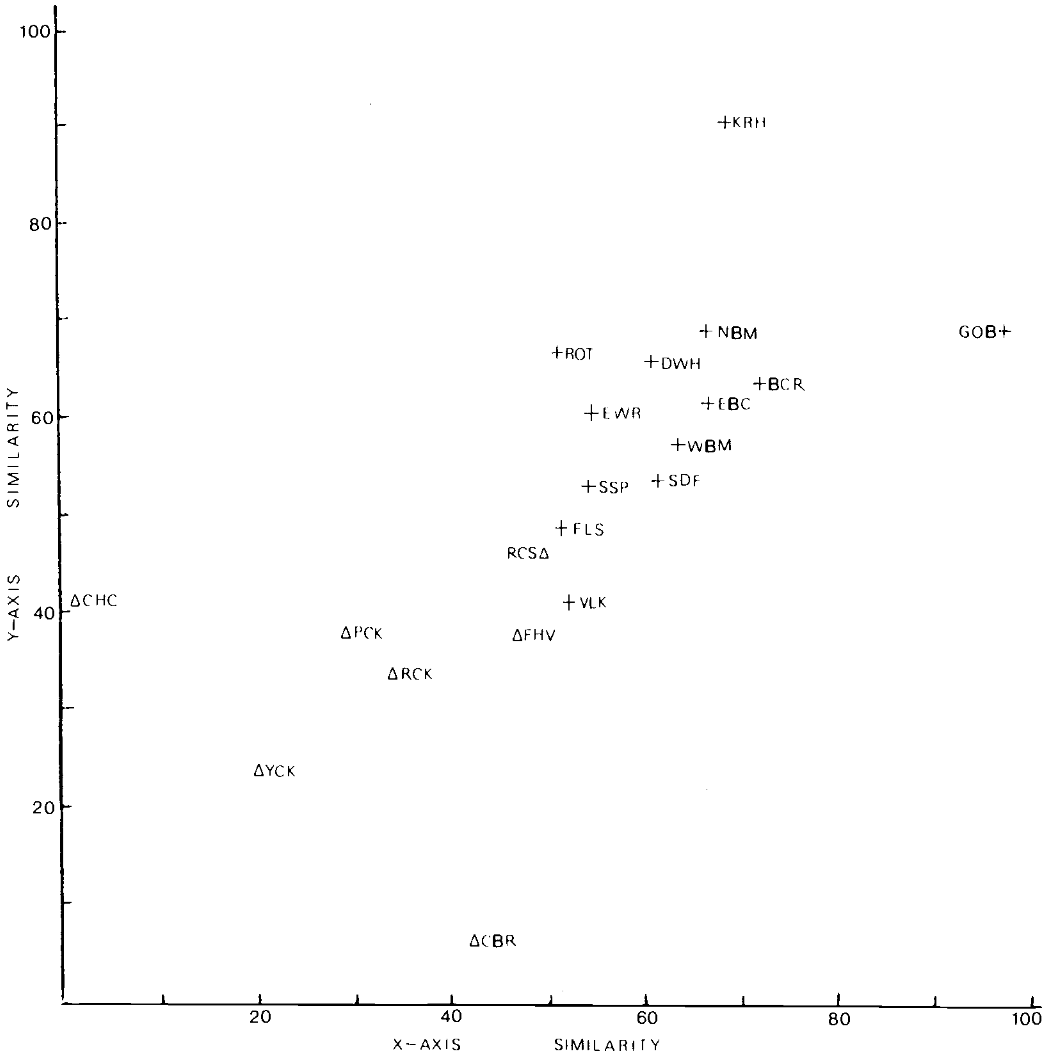


Figure 13. Similarity ordination of Siskiyou *Kalmiopsis* stands alone with end stands computer-picked and dependent mode of Y-end stand choice. (▲: low elevation Siskiyou stands; +: high elevation Siskiyou stands; ●: Southern Cascades stands.)

corner). Low elevation plots are distributed toward the mesic end and high elevation plots, which have lower biomass and lesser amount of canopy cover, are found toward the xeric end. The two low elevation plots, Rattlesnake Creek Slope and Fire Heaven, whose environments represent the extremes of those low elevation sites, are located in the very center of the gradient marking the floristic transition from the relatively mesic to the relatively xeric end of this complex gradient.

Morphology, Phenology, and Age

Morphology and Growth Form in Relation to Environment

Observations of growth form and morphology in Kalmiopsis were made at each site visited. Emphasis focused on correlation of differences in environment with changes in these specific plant characteristics and how this relates to the general ecology of the plant. Investigation was also directed towards discovery of possible differentiation patterns in morphology between Siskiyous and Southern Cascades populations.

Kalmiopsis leachiana is a low-growing evergreen shrub whose relatively small ericaceous leaves are confined to the terminal portions of highly clustered to loosely spreading stems. These stems arise almost at ground level from a central, thickened stem, or in older plants, from a complex of larger, twisted and gnarled stems whose origin at one time was the main axis of the plant. The aerial portions reach a height between 15 and 40 cm, although exceptions are found at both extremes. On very dry, wind exposed, rocky ridgelines height development can be restricted to 5 cm or less, while in more mesic situations near streambanks, plants have been measured over 70 cm tall. The central stem axis and larger stems deriving from it are covered by a multitude of papery, thin layers of reddish-brown to dark grey bark, underlain by a smoothly striated, red-purple to deeply reddish-tan surface. The actual base of the plant is usually small in length and at times difficult to ascertain due to a large number of central stems arising from above it and the proliferation of large and small roots which generate from below. The main root system is spreading divaricate in pattern with root branches developing from a short, compact central rootstock.

The pattern of growth which develops in the above-ground portions of Kalmiopsis leachiana is highly dictated by the environment in which the plant is found to occur, both when growing on rocks and directly on the ground. In more mesic situations and under certain soil conditions, stems may grow to relatively great lengths. On the metavolcanic soils at Collier's Bar on the Illinois River, stems were measured to be over 1.75 m in length.

However, even the longest stems rarely increase in diameter much over 0.5 cm. As a result the great majority of the stems, as represented by the older portions which have long since lost their leaves and smaller side branches, are rather flexuous and trail in a decumbent manner parallel to the surface of the ground. From these decumbent stem portions develop a mass of fine, adventitious roots which provide anchorage and a source of water and nutrients closer than the main root system. This ability to produce adventitious roots leads to the possibility of vegetative reproduction, either through mechanical damage to the stem portion separating the growing shoot and the primary plant growth center or by the death of the central plant axis itself.

The terminal growing portions are oriented perpendicular to the axis of the declining sections and consist of numerous, very thin and closely crowded branches. On the ends of these are clustered the leaves. Further growth begins from terminal buds or from the axils of terminal leaves. Growth may also be initiated as shoots developing from further down the stem, portions from which leaves have long since been lost.

On level terrain and gentle slopes, stem growth will develop in a dense manner in all directions from the main axis. With the juxtaposition of many plants together, a relatively thick, mat-like shrub layer will be formed as a result. The density of this low growing shrub layer will be determined by the proximity of spacing between plants. When an entire patch is connected spatially from one end to another it becomes very difficult to determine how many separate individuals are represented and if those individuals are actually genetically different.

Kalmiopsis is more commonly found on steep slopes than on flat terrain and on these occasions an entirely different pattern develops from this rhizomatous form of growth. Most stems will tend to grow in a downslope direction from their point of anchorage, with those growing upslope all concentrated near the plant axis. The result is an elongated semi-circle of growth originating from the central rooted portion of the plant. On very mesic slopes where vegetation is relatively dense and there is little overt slope movement through erosional processes, growth can extend farther upslope as well. In this case organic material collected and produced in the mass of downslope growing stems, all variable in length and intermixed with adventitiously produced shoots, is held in place by the proliferation of adventitious rootlets which penetrate throughout. This entire mass of Kalmiopsis stems, adventitious roots, organic material, and bryophyte growth which may become established on top can be lifted from the surface of the underlying soil layers. The majority of roots are concentrated in this collected organic material with only a few connecting this mass to the soil below.

This type of growth form, where an extensive system of adventitious roots comprised the majority of the underground growth and is concentrated in the upper organic layers of the soil, has been reported for ericaceous members of *Calluna* heaths in Great Britain, specifically *Calluna vulgaris*, *Erica tetralix*, *E. cinerea*, and *Vaccinium myrtillus* (Heath and Luckwill, 1938). In the dense shrub vegetation of *Kalmia* bogs of Newfoundland, 97.5 per cent of the rhizomes and roots under 1 cm thick of *Kalmia angustifolia* were found to be concentrated in the top organic layers of the soil (Dammon, 1972). As a result, *K. angustifolia* is almost completely independent of mineral soil for nutrition, the source instead being precipitation and the decomposing organic material. This situation is analogous to that described for *Kalmiopsis*, and in these particular examples *Kalmiopsis* must likely derive a large portion of its nutrition in a similar manner.

On open, exposed talus and scree slopes where erosion and slippage are commonplace occurrences and highly evident by the long trails of loose cobble and stone, *Kalmiopsis* is frequently located on the downslope side of trees and other taller shrubs and large boulders. Litter and organic matter falling and washed down from above easily become trapped in the dense low growth of *Kalmiopsis*. Where no more than 0.5 cm of litter had accumulated on the open talus of the slopes of Rattlesnake Creek, up to 3.5 cm of undecomposed litter and 2.5 cm of humus had accumulated in the living and dead stems of *Kalmiopsis*. The major portion of litter input will consist of dried or partially decomposed leaves from the plants growing above.

Unlike the example of the bog and heath plants, *Kalmiopsis* derives a further benefit from this collected organic matter relative to its associated plants. On dry, open talus slopes, where little soil development occurs and that which is generated is soon washed away, collected litter may provide a rich source of nutrients in an otherwise nutrient poor environment. And further, this dense, low growth habit allows an additional chance to recover nutrients which may be lost through leaf drop by *Kalmiopsis* itself. Not only are talus slopes poor in nutrients, but water is at a premium and a dense layer of litter and organic matter would absorb and hold a relatively large amount of water compared to other soil types (Brady, 1974), as well as retard evaporation from the roots and soil below.

Kalmiopsis will also grow in the much more open portions of a talus slope. As a result of its growth form and the fact that there are no obstructions upslope in these places, soil and talus will build up behind the plant itself. No longer protected from above, it initially will have to bear the force of this material moving down on it. But valuable nutrient-releasing and moisture-holding soil will build up around the plant, while at the same time litter is collecting in the stems. In this way, if a plant can become established in such locations a relatively competition-free environment will have developed. Here, stems do not exhibit the matted form common on steep but more mesic slopes, perhaps because of the lower litter input. Instead, the long, trailing stems may actually become covered by talus originating from above. A whole series of relatively small plants may lie in a trailing line downslope from each other, appearing to be completely separate. In actuality they will be connected through rhizomes to which they are attached. At Rattlesnake Creek Slope the leafy tip portions of rhizomes averaging in height between 30 cm and 40 cm were separated from the parent plant by as much as 0.5 m. The rhizomes themselves were found to travel parallel to the surface of the slope and were covered with adventitious roots.

At even more exposed sites, especially at higher elevations, growth appears to be limited, and a long, trailing rhizome system will not develop to the degree it does in more mesic habitats. Here much shorter, leaf-covered stems will arise directly from the main axis of the plant. These highly clustered stems will still cause eroding soil and rock debris to back up. When a long line of these plants occurs perpendicular to the direction of the slope, a slightly terraced terrain results.

Growth of Kalmiopsis among rocks and rock crevices shows the same general forms of development as that on soil. A crevice in a rock or a gap between rocks provides an anchorage point for the root system. Frequently the roots will appear to grow out of pure rock in these situations. The crevices themselves and any depressions around them, however, provide collection points for litter, runoff water, and nutrients from above. Soil production may never occur to any degree but the amount of litter accumulation, and the continued source of nutrients through slow decomposition which it provides, is certainly enhanced by the low level and thickly branched growth form of Kalmiopsis.

On more mesic rock exposures the development of long, trailing stems from a main stem system will also occur. This is most dramatic when plants are found to be sweeping down vertical rock faces from ledges above. On two outcrops approximately 3 km up the Dog Creek drainage from the North Umpqua River Kalmiopsis was found growing in crevices of the straight, vertical faces of these outcrops. Sweeping down these perpendicular faces, the plants were completely alone, but were absent from the level portion of the summit of the outcrop. In these situations, organic material builds up among the stems through litter collection with the possibility of providing a substrate upon which bryophytes may colonize. As happened on the ground surface of more mesic slopes, a thick mat develops. The mat becomes a cohesive entity by continued production of adventitious roots and stems throughout it, and will be anchored to the rock by these stem-derived roots. The result is that a substrate rich enough to support the growth of a relatively large plant has been generated on pure rock simply through the characteristic growth form of *Kalmiopsis* and its ability to provide a source of water and nutrients.

On rock exposures where plants are continually subjected to high light intensities, desiccating winds, and great extremes in temperature, especially on top of outcrops where there is no benefit of runoff from above, total height and stem length of the plants are small. Here growing out between large rock pieces in many places, separate shoots may be connected underneath by hidden, twisting rhizomes. But large, bushy growth does not develop and litter accumulation and adventitious root production is held to a minimum. In solid rock, crevice-grown plants are almost always small, while those developing in hollow depressions will become relatively larger presumably because the microhabitat provides a substantially greater amount of litter and runoff accumulation, and at the same time protection from constant exposure to environmental extremes.

The leaves of *Kalmiopsis leachiana* are thick and relatively small in size. They have a thick cuticle on both the upper and lower surfaces (Copeland, 1943), and are completely glabrous except for occasional sparse setoseciliations on the margins. They range in average size from 10 to 25 mm in length and 6 to 8 mm wide, with variations occurring between sun and shade grown plants. Average leaf length proved to be significantly greater for sun and shade grown plants of the Southern Cascade Mountains than for their respective counterparts in the Siskiyou Mountains (Table 23). The leaves of shade grown plants of the Cascades were much thinner in texture, as well as being larger. The largest leaves measured averaged 39.7 mm and were found on shade plants growing in rock outcrops on the north side of Ragged Ridge in the North Umpqua River drainage.

The larger difference in leaf size between sun and shade plants of Cascades populations than those of the Siskiyous (Table 23) suggests that there exists a greater difference in microclimate between the extremes as represented by exposed rock outcrops and the closed canopy conifer forest. Significantly, leaves of _Kalmiopsis_ growing on diorite at Pine Creek had the largest leaf lengths for all Siskiyou populations and very nearly equaled the means of Cascades populations (Table 23).

The corolla of _Kalmiopsis_ is five-lobed and open campanulate in form, narrowing to the base to a very short tube surrounding the superior ovary. Each of the corolla lobes contains two slight folds

Table 23. Length (mm) of sun and shade leaves of Siskiyous and Southern Cascades populations of Kalmiopsis. Values based on 30 leaves of each type from at least five different plants per population. Means for sun and shade leaves between the two main populations are significantly different at $\alpha = 0.001$.

Siskiyous site	Sun leaves	Shade leaves	Southern Cascades site	Sun leaves	Shade leaves
NBM	10.9	17.9	PAR	12.8	20.0
WBM	9.2	15.7	RAR	16.3	39.1
DWH	12.8	19.2	LPR	20.3	30.2
SSP	8.7	20.8	CCK	16.9	29.8
FHV	13.8	24.6	DCK	18.4	34.3
SDF	11.5	24.7	BIC	14.3	33.1
CCR	16.4	18.9	FLR	17.6	29.5
YCK	15.5	19.5	mean	16.6	30.9
EBC	11.0	15.2			
CBR	14.3	21.2			
ROT	13.4	22.5			
FLS	11.0	14.0			
KRH	11.4	19.0			
PCK	16.3	27.5			
RCK	13.3	19.9			
VLK	12.1	17.4			
EWR	11.3	18.3			
BFT	12.5	18.7			
mean	12.5	19.7			

which, when the flower is still in bud, slightly house two each of the ten stamens. In the North Umpqua River populations corolla color never appeared to vary from a pale pink. In the Siskiyou Mountains both a pale pink and a deeper rose color form occur. Plants exhibiting both color forms were found growing side by side in the Big Craggies Botanical Area, but otherwise all visited populations were of a single color. In addition, the corollas of Cascades populations were found to be significantly larger than those of the Siskiyous plants, on average measuring between 21 and 23 mm, as opposed to 14 and 18 mm for the latter populations (Table 24).

Phenology

Information regarding phenological patterns in Kalmiopsis was obtained through actual observation of patterns at each visited site, coupled with that retrieved from inspection of herbarium specimens.

Initiation of flowering and new shoot growth in Kalmiopsis occurs relatively early in the spring of the year. Both flower buds and vegetative growth buds are produced in the preceding growing season and overwinter in the bud form. Flowering begins very early in May and late April at lower elevations (300 m) and will proceed to mid-June at the highest elevations. A few isolated instances of late flowering plants occurring in late June were

Table 24. Age determination of growth rings of stems of *Kalmiopsis leachiana*.

Site	Largest diameter (mm)	Number of growth rings	Average diameter increase per growth ring
Valen Lake (Siskiyous)	14.0	55	0.255
Valen Lake	9.0	35	0.257
Valen Lake	11.0	53	0.208
Valen Lake	7.5	32	0.234
Valen Lake	8.5	32	0.266
Valen Lake	9.0	38	0.237
Valen Lake	8.5	31	0.274
Valen Lake	16.0	46	0.345
Valen Lake	7.0	33	0.212
Valen Lake	6.0	14	0.429
Valen Lake	9.0	35	0.257
Valen Lake	6.5	14	0.203
Valen Lake	11.5	53	0.217
York Creek (Siskiyous)	9.0	41	0.220
York Creek	8.5	59	0.144
Siskiyous mean			0.250
Limpy Rock (Southern Cascades)	20.5	60	0.342

found. Time of shoot elongation and new leaf size increase parallel the period of flowering.

The observations made during the study period were not continuous enough to determine unequivocally whether there exist differences in flowering phenology between Cascades and Siskiyous populations. On January 24, 1977, in the North Umpqua River area, a few plants found growing in an exposed, sunny location at 1250 m were ready to burst flower bud, while one had three open flowers. That particular day was clear and sunny, and only a few patches of snow had accumulated as a result of a relatively dry winter. Plants were found in full flower at the same site on May 15, 1977. This was also true for populations located at the bottom of the Dog Creek drainage and the cliffs above Horseshoe Bend in the North Umpqua River. Flowering specimens have been collected as late as June 19 from the North Umpqua area (Chambers 4218; Davis, laPiniec, McMullen, and Wilson 29638, OSC).

The earliest recorded flowering in the Siskiyou Mountains is of blooming plants collected from Horse Sign Butte, Curry County, at 1130 m on May 1, 1931 (Leach 2915, in part, ORE) and on May 14, 1932 (Applegate 7229, OSC). Populations at York Creek, Josephine County, at an elevation of 430 m, were found in peak bloom on May 8, 1977, and with most corollas dropping on May 30, 1976. However, plants were still in bud at Gold Basin, Curry

County, in the Kalmiopsis Wilderness Area at 1220 m on May 30, 1977, and were collected in flower there by Mrs. Leach on June 14, 1930 (Leach 2915, in part, ORE). The time of flowering is also apparently later for higher elevations (1200-1400 m) in the Big Craggies Botanical Area. Plants were at their blooming peak beginning the second week of June 19, 1977. A Siskiyou National Forest Service memorandum dates a Leach collection of flowering Kalmiopsis as June 19, 1938 (Leach 22824, OSC). According to this memorandum by G.E. Mitchell the time of collection was "approximately two weeks too late to find the plant in the prime of blooming period." A flowering specimen was also collected in the Big Craggies on June 12, 1932 (Leach 4336, ORE). Certainly specific habitat affects the exact time of flowering and new vegetative growth, in addition to the influence of elevation and geographical location.

Age

Counts of growth rings of Kalmiopsis stems of plants from two sites in the Siskiyou Mountains and one large stem collected from Limpy Rock (Chambers 4041, OSC) showed that not only is Kalmiopsis capable of relatively great longevity but annual growth increments during those years, as measured by the increase in diameter, are very small (Table 24). The number of growth rings counted in the stems represents only approximate total life spans of the plants from which they came due to the fact that stem sections usually were not from the base of the plant and that for many of the sections, rings tended to be obscured by their close proximity. For this reason age determinations all underestimate to some degree the true age of the plant. Those stems collected from Siskiyou Mountain populations were from plants which had been pulled up by either vandals or members of the Siskiyou National Forest trail crew.

Two important conclusions can be made from the results. First, the environment in which Kalmiopsis grows, at least those from which stems were analyzed, severely limits growth so that the increase in diameter per season is less than 0.35 mm per year. Though sample size is certainly small for plants of the North Umpqua area, the environment may be less stressful there compared to that in the Siskiyou Mountains, where a smaller average annual growth increment occurs. Secondly, despite the fact that environmental stress is very growth limiting in these sampled habitats, Kalmiopsis is able to survive the environmental conditions for long periods of time, in some cases at least 60 years.

Plant Moisture Stress Studies

Site Description

The site of soil moisture and plant moisture stress studies was located on the slopes of an unmapped tributary creek of the Chetco River, christened Rattlesnake Creek, within the Kalmiopsis Wilderness Area (Figure 14). Initial reconnaissance of this area suggested that it would be ideal for determining the role of soil moisture availability as affected by topography and exposure in the distribution of _Kalmiopsis leachiana_. At this location _Kalmiopsis_ is relatively evenly distributed along the north-facing slope of the ridge which forms one-half of the Rattlesnake Creek watershed. It occurs right up to the ridgeline, but stops there and does not extend down the south-facing slope which forms the other side of the ridge. In addition, it occurs around the slope to the east but stops again, approximately half way before the more open southeast-facing slope is reached (Figure 14).

The ridge and adjoining slope are found at the southwest corner of the Rattlesnake Creek and Chetco River junction. Rattlesnake Creek flows directly east into the Chetco River from the latter's east-facing slope. The ridge on which pressure chamber studies were conducted is actually a tent-like projection from a much higher ridge which forms the demarcation between the Chetco River drainage and the Box Canyon Creek drainage. This tent-like

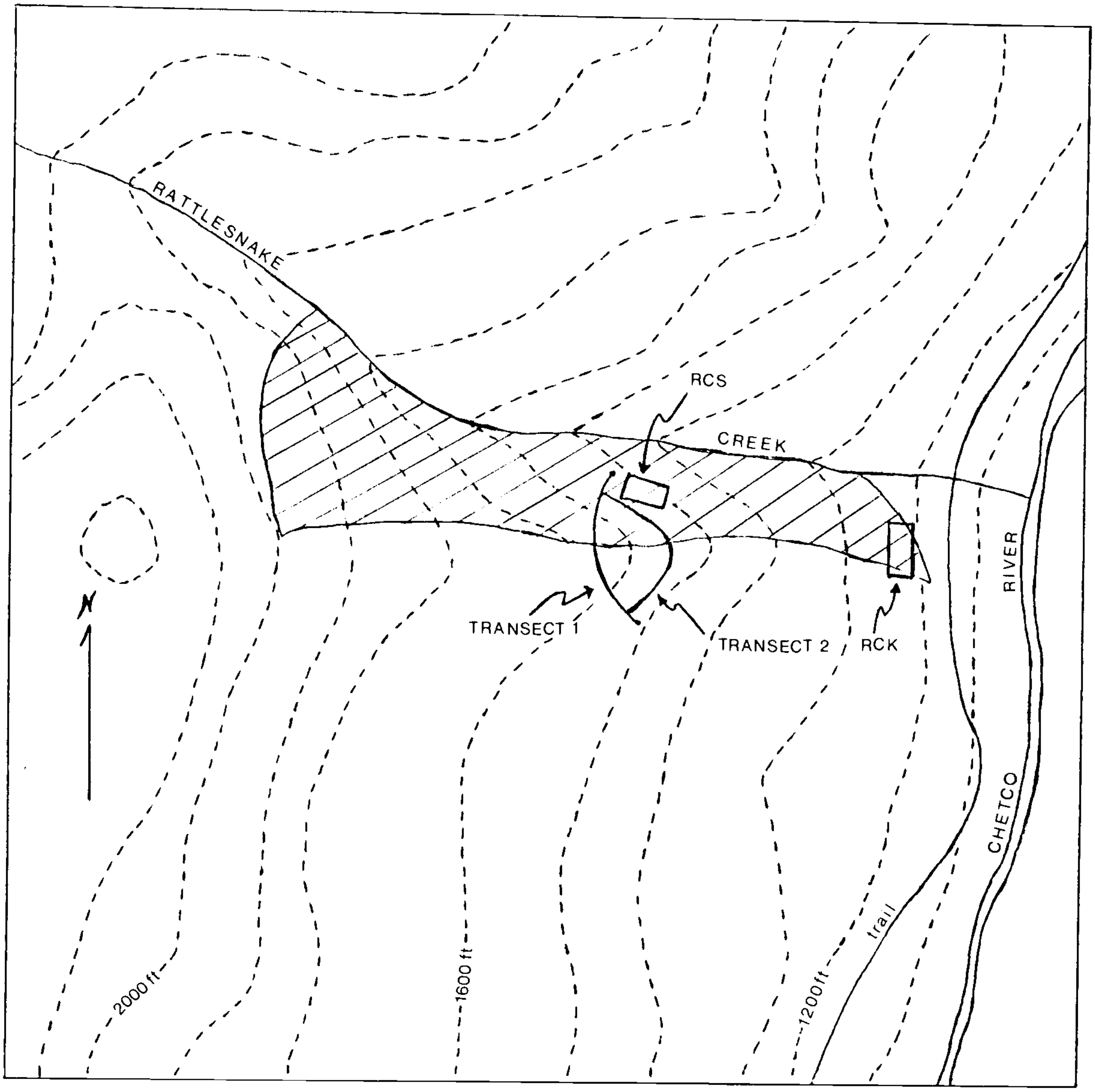


Figure 14. Distribution of *Kalmiopsis leachiana* and location of vegetation plots (RCK and RCS) and moisture stress transects at Rattlesnake Creek, Kalmiopsis Wilderness Area.

▨ : *Kalmiopsis* distribution

projection consists of three steep talus slopes, each facing a different compass direction and culminating to a sharp east-west running ridgeline about 580 m in elevation. The slope which forms part of the Rattlesnake Creek drainage is north-facing with a 344° aspect and a 35° grade. Opposite is a south-facing slope which is 152° in aspect and falls at a 33° grade. On the front end of the projecting ridge is a rounded, generally east-facing slope at 90° and having a 33.5° grade. There are no ridgelines projecting south and parallel to the one in question. Thus the slope is not protected topographically from any higher ridges. In contrast to this the slope forming the other half of the Rattlesnake Creek drainage is slightly higher in elevation than the north-facing slope and runs parallel to it, thus reducing the degree of exposure to which plants on the north slope would be subjected if it were not there (Figure 14).

Geologically, this whole portion of the Chetco River canyon represents an area of intense metamorphosis associated with the contact zone of a peridotite intrusion into a generally gabbro dominated formation (Ramp, 1975). The slope in question is in the zone of metamorphosed gabbro, and the north-south running ridge above is mostly part of the peridotite intrusion. A stepwise collection of rock samples was made along the line of pressure chamber readings, from both slopes, the ridgeline and down to Rattlesnake Cree, as well as at the bottom of the east-facing slope. All rocks were identified as highly altered metagabbro types (Ramp, pers. comm.). Thus, vegetation changes along the established transects cannot be attributed to changing parent material types.

Two vegetation plots were established and sampled here. One, named Rattlesnake Creek, was located at the bottom of the east-facing slope where it is intersected by the trail which parallels the Chetco River. The other, termed the Rattlesnake Creek Slope plot, was located on the north-facing slope below the ridgeline at 550 m (Figure 14). The results of these samplings have been discussed earlier, but will be referred to in relation to the general vegetation of the projecting ridge.

The north-facing slope of the projecting ridge represents a gradual change from a very mesic to a very xeric conditions, but with a sharp transition taking place at the edge of Rattlesnake Creek. Along this stream Chamaecyparis lawsoniana is the prominent canopy representative. Underneath, the shrub layer is dominated by Rhododendron occidentale and Salix sp. Along the banks and among rocks of the boulder-strewn stream are found Darlingtonia californica, Cypripedium californicum, Tofieldia glutinosa, Pinguicula vulgaris, Habenaria sparsifolia, and Balsamorhiza sp. Away from the immediate edge of the stream all of these species drop out except for a few young Chamaecyparis. In their place is a thick shrub layer of Kalmiopsis, Vaccinium ovatum, Umbellularia californica, and Vaccinium parvifolium. Additional shrub species include Gaultheria shallon, Rhamnus californica, Garrya fremontii, and Lonicera hispidula. The genus Quercus is represented by a thick stemmed, heavily branched but dwarfed form of Quercus chrysolepis. Intermixed are Lithocarpus densiflora, again of small stature, and Cornus nuttallii. Overhead the canopy consists of Pseudotsuga menziesii and Pinus lambertiana. Herb species near the bottom of the slope are relatively mesic in composition and include Polystichum munitum, Trientalis latifolia, Disporum hookeri, Iris thompsonii, Polypodium vulgare, and Smilacina racemosa.

Towards the ridgeline there is a noticeable change in the stature of the broadleaf sclerophylls. Quercus takes on the much shrubbier form of Q. vaccinifolia, being highly branched from the base with stems much thinner than those at the slope bottom. Lithocarpus densiflora as well is much lower in stature and shrubbier in growth form. This change in the two shrub layer dominants is accompanied by a decrease in the amount of Vaccinium ovatum and Gaultheria shallon, and the increasing predominance of Arctostaphylos canescens, which comes to dominate the shrub layer at the ridgeline. The amount of nonvegetated ground surface increases as well, from less than 5 per cent at the slope bottom to between 10 and 15 per cent near the ridgeline. The vegetated areas are mostly separated by talus flow. *Kalmiopsis* occurs at the base of those flows or at the base of larger shrubs and small rock outcrops. Although decreasing in density and in height farther up the slope, *Kalmiopsis* is found all the way to the ridgeline, but does not proceed down the opposite slope.

The vicinity of the ridgeline supports an herb layer of a more xeric type as well. *Hieracium albiflorum*, *Xerophyllum tenax*, *Lomatium howellii*, *Allium falcifolium*, *Cheilanthes gracillima*, *Arnica cernua*, *Galium bolanderi*, *Erigeron foliosus* var. *confinis*, and *Aster brickelioides* are the most common, though they are very scattered and represent very little cover. *Pinus monticola* occurs at the top end of the slope among Douglas-fir and sugar pine, which are present at lower density and are somewhat smaller in size than those found near the stream.

The south and southeast-facing slopes are more open and less stabilized talus slopes. Douglas-fir and sugar pine represent much less of the canopy, which is thinner than on the north-facing side. In their place are both *Pinus monticola* and *Calocedrus decurrens*. The shrub layer is composed mainly of *Quercus vaccinifolia* and *Arctostaphylos canescens* but also includes *Umbellularia californica*, *Rhamnus californica*, *Berberis pumila*, and *Lithocarpus densiflora*. At the bottom of the east and south slopes the vegetation is like that sampled by the Rattlesnake Creek plot: much more dense than the slope vegetation and dominated by *Lithocarpus*, *Quercus chrysolepis*, *Pseudotsuga*, *Pinus lambertiana*, and *Vaccinium ovatum*.

Theoretical Considerations

Pressure chamber studies were initiated at this site to determine the role of soil moisture level and its effect on leaf moisture stress in limiting *Kalmiopsis* to the north slope of the described projecting ridge. Because leaf moisture levels could not be measured for *Kalmiopsis* growing on the south slope since it was not there, an indirect approach was taken. A transect was established from the midpoint of the north slope up over the ridgeline and 50 m down the opposite slope. On the north slope measurements were to be made at different stations along the transect on *Kalmiopsis leachiana*, *Arctostaphylos canescens*, and *Quercus vaccinifolia*. On the south slope stations were established such that *A. canescens* and *Q. vaccinifolia* were present together. Measurements for these latter two shrubs on the south-facing slope would then be compared with those for the north slope and with those obtained for *K. leachiana*. In this manner, it can be established what the general stress levels are which *Kalmiopsis* might experience on the south slope, and in so doing, if soil moisture levels during some part of the season are preventing establishment there.

The pressure chamber theoretically is able to measure the amount of negative pressure built up in the xylem of a plant as the result of limited access to water (Schollander, Hammel, Bradstreet, and Hemmingsen, 1965). The longer the period of time that a plant is subjected to conditions of low water and high transpirational demand, the greater the tension there exists in the water column represented by the xylem. When a twig is cut the water column snaps back into the xylem tissue. By placing the twig into an eirtight chamber, pressure can be exerted on the xylem water column until water is just forced out the cut stem portion. At this point the amount of pressure required to force the water out equals the negative pressure existing in the stem previous to its cutting. The amount of pressure applied to the twig is measured by an attached pressure gauge.

To determine the relation between soil moisture content and internal water stress and its effect on plant distribution, pressure chamber measurements were made at dawn. At this time internal water balance is relatively stable (Slatyer, 1961), and the plant has recovered to the fullest extent allowed by its root system depth and density, from the soil moisture level and stress conditions experienced the day previous (Waring and Cleary, 1967; Waring, 1969). Soil moisture generally has been found to correlate strongly with internal stress (e.g. Slayter, 1961; Waring and Cleary, 1967;

Sucoff, 1972), but for honey-mesquite, Prosopsis glandulosa var. glandulosa, daily water stress and water stress at predawn were not related to soil moisture content, but instead to the vapor pressure deficit of the atmosphere at the time of measurement (Haas and Dodd, 1966). Assuming that internal water stress is a direct reflection of soil moisture content, for climates of annual summer drought such as the Pacific Northwest the relation between vegetation and the moisture gradient can be determined by measuring stress values at the high point of the drought period (Waring and Cleary, 1967).

Results and Discussion

Predawn Measurements. For pressure chamber measurements made at predawn hours, results show that there is a general increase in the internal stress for all three species of shrubs, from the lowest point on the north slope up to the ridgeline (Figure 15). The lowest reading for any of the plants was -4.4 atm, measured for Kalmiopsis at the lowest station. The highest stress reading for the entire north-south transect again was for Kalmiopsis, at -16.7 atm, a measurement made for a plant growing at the ridgeline. For measurements of moisture stress levels from the mesic end of the transect to the more xeric ridgeline, Kalmiopsis shows in general a consistently higher stress value than both Arctostaphylos canescens

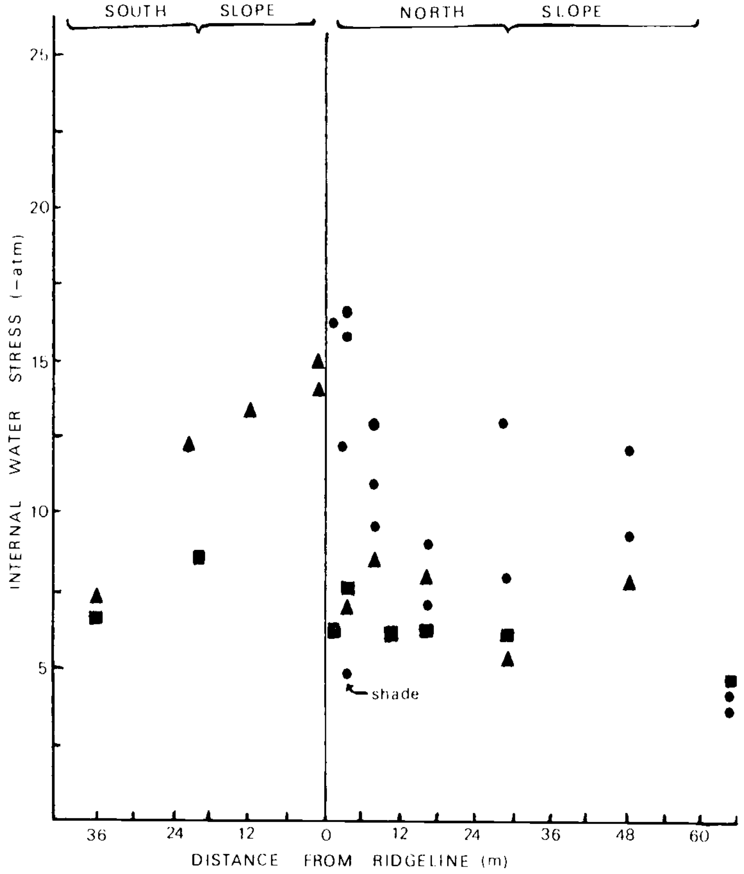


Figure 15. Predawn moisture stress as a reflection of slope position along the north-south Transect 1 at Rattlesnake Creek, Kalmiopsis Wilderness Area, Curry County, Oregon. Measurements made from 4:00 to 6:00 A.M., September 7, 1976. (●: Kalmiopsis leachiana; ▲: Arctostaphylos canescens; ■: Quercus vaccinifolia.)

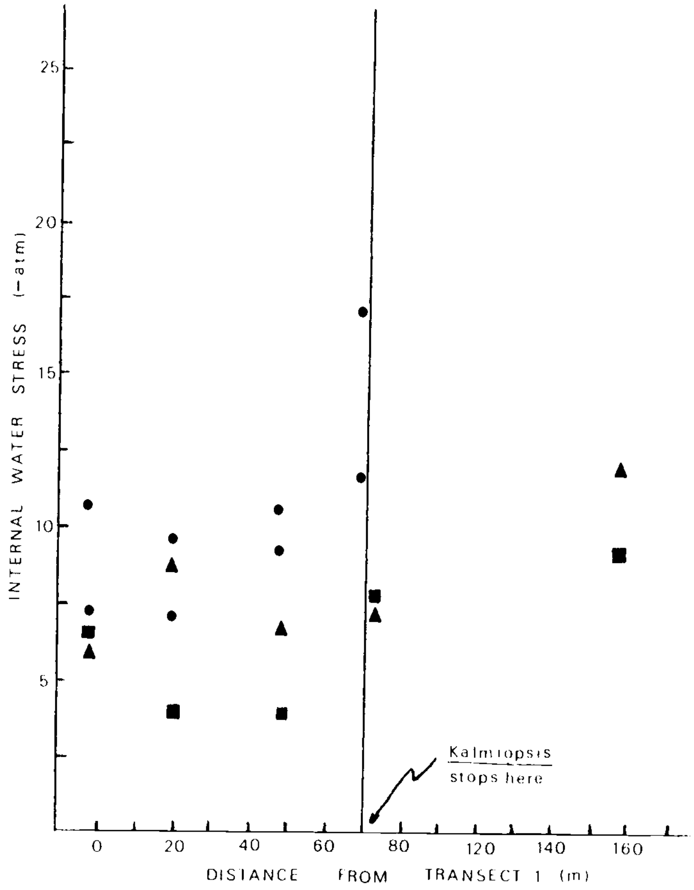


Figure 16. Predawn moisture stress as a reflection of slope position along the horizontal Transect 2 at Rattlesnake Creek, Kalmiopsis Wilderness Area, Curry County, Oregon. Measurements made from 4:00 to 6:00 A.M., September 7, 1976. (●: Kalmiopsis leachiana; ▲: Arctostaphylos canescens; ■: Quercus vaccinifolia.)

and Quercus vaccinifolia. The obvious exception to this is at the station 18 m below the ridgeline where stress values in Kalmiopsis are approximately equal to that in A. canescens and Q. vaccinifolia. This may in part be explained by a more sheltered microclimate experienced by Kalmiopsis, a condition perhaps not obvious when the station was chosen. The important effect of microclimate is seen for the measurement made on Kalmiopsis growing in the shade of a manzanita bush at the top of the slope (Figure 15). There is a difference of 11.6 atm between it and the exposed plant occurring just 1 m away.

For the south slope of this north-south transect, readings for Quercus vaccinifolia are only slightly higher than those for the same species on the north slope. For Arctostaphylos canescens, moisture stress levels increased exceptionally for the south slope for plants near or at the ridgeline and remained higher down the slope.

The same general trends hold true for the transect which runs parallel to the direction of the slope and around it (Figure 16). Moisture stress increases for all three species as the distance from the vertical transect increases. Kalmiopsis exhibits higher values than both of the other shrubs, and Arctostaphylos again reaches higher values than Quercus vaccinifolia. Levels of stress are comparable to those along the north-south transect as well. On the south end of this second transect where Kalmiopsis does not grow, moisture stress is greater for both *Arctostaphylos* and *Quercus* than for any measured on the north side of the gradient.

Indications are that moisture levels increase for *Kalmiopsis leachiana* with the degree of exposure of the site on which it is growing and the distance from the stream drainage. For those same sites, stress levels are less for *Arctostaphylos canescens* and *Quercus vaccinifolia*. At more exposed sites where *Kalmiopsis* does not grow (the south slope) stress levels are higher for *Arctostaphylos* and *Quercus* than those values for the same species on the north slope where *Kalmiopsis* does grow. Thus soil moisture levels appear to be less on the south slope than on the north slope since the plants are able to recover to a lesser degree on these more exposed topographic positions. *Kalmiopsis leachiana* is limited to only the more mesic topographic positions where soil moisture levels allow a certain amount of overnight recovery from the previous day's high stress levels.

Midday Measurements. The most striking trend resulting from midday pressure chamber measurements is that relative to the stress values in *Arctostaphylos* and *Quercus*, difference in stress values for *Kalmiopsis* between predawn and midday are relatively low (Figure 17). For *Kalmiopsis* the highest value recorded at midday was -22.8 atm compared to -17.0 atm, the maximum value at predawn. For *Arctostaphylos* the maximum for midday was

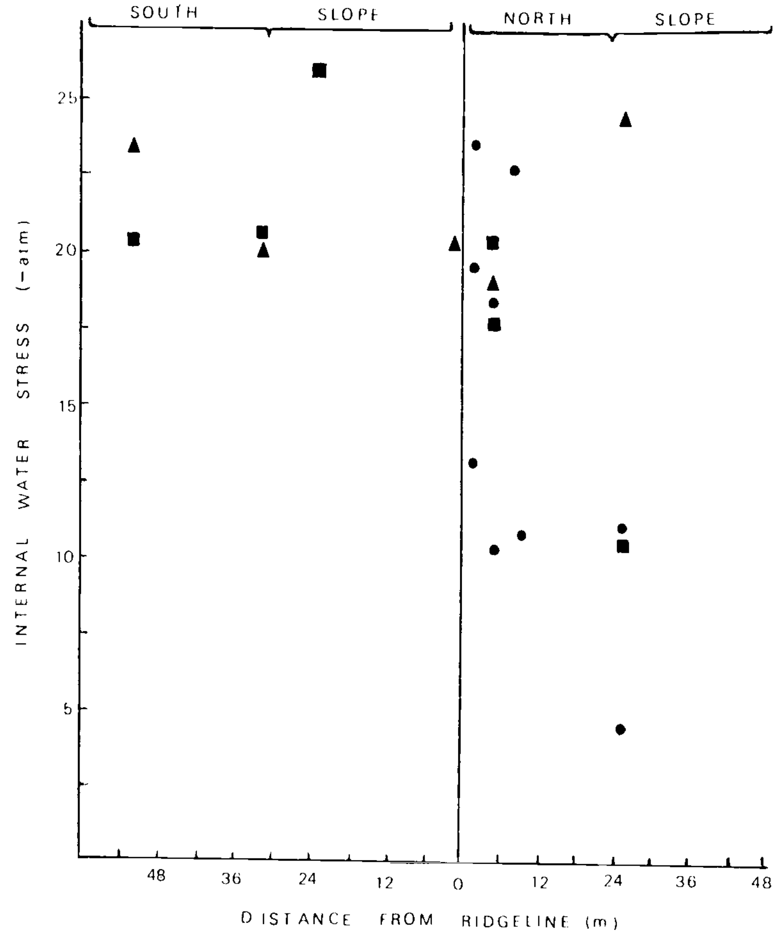


Figure 17. Midday moisture stress as a reflection of slope position along the north-south Transect 1 at Rattlesnake Creek, Kalmiopsis Wilderness Area, Curry County, Oregon. Measurements made from 1:30 to 2:30 P.M., September 7, 1976. (●: Kalmiopsis leachiana; ▲: Arctostaphylos canescens; ■: Quercus vaccinifolia.)

-24.8 atm, while only -15.3 atm at predawn. The difference is even more striking for *Q. vaccinifolia*, the values for which were -27.9 atm and -8.5 atm respectively. This trend holds for stations along both transects (Figure 18). Where *K. leachiana*, *A. canescens*, and *Q. vaccinifolia* occur together, midday stress values for the latter two species are equal to or greater than those of *Kalmiopsis*. For the south end of the transects where *Kalmiopsis* does not grow stress values increased greatly for both *A. canescens* and *Q. vaccinifolia* over those measured at predawn. This suggests that *A. canescens* and *Q. vaccinifolia* are continuing to transpire for a longer time during the day, taking in carbon dioxide through open stomata for photosynthesis and to allow leaf cooling to occur. The result is that relatively great negative pressure builds up in the conductive system of these plants. The stress values are highest on the south and more exposed slope, where soil moisture levels appear to be lower, so that the plant is unable to meet the high atmospheric demand by taking up larger amounts of water.

For *Kalmiopsis*, midday stress values do not increase much over those found to occur for predawn. A probable explanation is that unlike *Arctostaphylos canescens* and *Quercus vaccinifolia*, higher stress values cause early stomatal closure which stops any further increase in transpirational demand. In that way continued buildup of internal water stress in the plant is prevented. As the

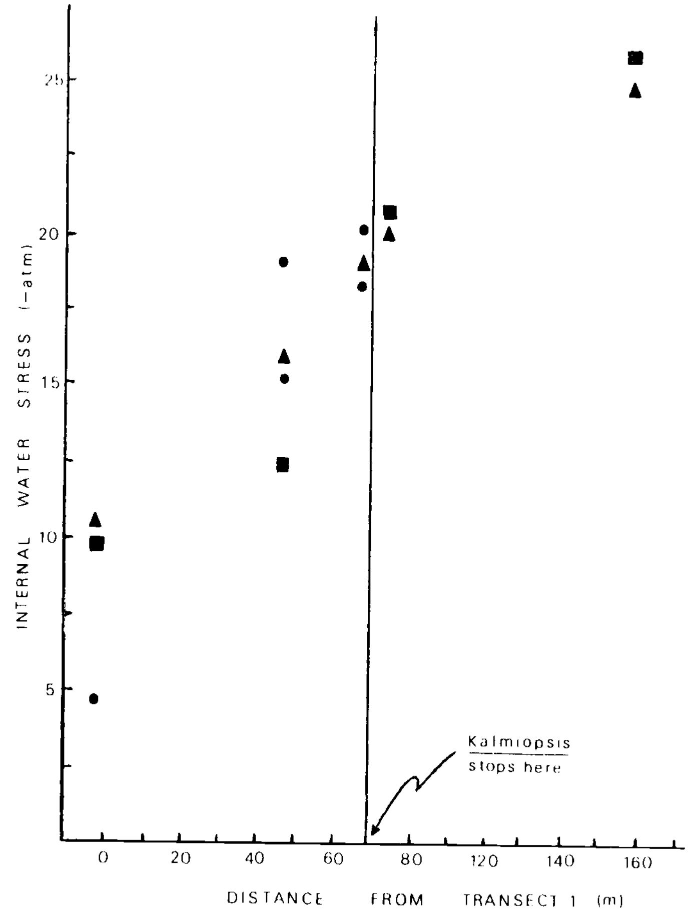


Figure 18. Midday moisture stress as a reflection of slope position along the horizontal Transect 2 at Rattlesnake Creek, Kalmiopsis Wilderness Area, Curry County, Oregon. Measurements made from 1:30 to 2:30 P.M., September 7, 1976. (●: *Kalmiopsis leachiana*; ▲: *Arctostaphylos canescens*; ■: *Quercus vaccinifolia*.)

sun rises, stress values begin to increase with increasing temperature and atmospheric demand. Since the stress values for *Kalmiopsis* are not much higher than those recorded for predawn, the stomates of *Kalmiopsis* probably closed very soon after opening. The exact pattern of stress buildup and stomatal closure can only be determined by measuring stress values throughout the morning.

The effect is that for this particular site, *Kalmiopsis* is limited to a portion of the total habitats available, those which have high enough soil moisture levels and relatively low atmospheric demand. At the high point of the drought season indications are that moisture stress builds up in this species to the point such that it recovers only to a small degree from the previous day's high stress. Photosynthesis, and thus growth, is limited during this time of high stress, since the high moisture stress that *Kalmiopsis* experiences causes stomatal closure early in the day before stress can build up. Young seedlings may simply be physiologically unable to tolerate high levels of stress which accompany living on the south slope.

The pattern is wholly different for two associated species, *Arctostaphylos canescens* and *Quercus vaccinifolia*. During the day they are able to withstand stress values at least as high as *Kalmiopsis* on shared sites at the more mesic slope positions. On more xeric topographic positions these two species are able to withstand stress values even greater than *Kalmiopsis* does in any of the locations in which it occurs. Unlike *Kalmiopsis*, *A. canescens* and *Q. vaccinifolia* are able to recover during the night to much lower stress values. This, plus the fact that they can withstand higher daily internal water stress, could account for their ability to grow on more exposed topographic positions where soil moisture content is low and atmospheric demand during the day is high. The stomata of *K. leachiana* appear to shut down early, thus limiting growth, with a maximum of 5.8 atm increase measured between predawn and midday. For *A. canescens* the maximum difference was 8.5 atm, and for *Q. vaccinifolia* the value was 19.4 atm. The ability to recover overnight allows a much longer photosynthetic period during the day, since there is a greater gap between stress measured at predawn and that maximum stress as represented by measurements at midday.

In addition to differing physiologically, *Arctostaphylos* and *Quercus* differ morphologically from *Kalmiopsis* in ways which are suspected to allow them to grow on more xeric sites. Both of these species, plus *Berberis pumila*, *Lithocarpus densiflora*, and *Umbellularia californica*, all found on the south slope, have leaves oriented vertically to the sun. In *A. canescens* and *Q. vaccinifolia* the leaves form almost a box-like formation enclosing the twig. The leaves of *Kalmiopsis*, on the other hand, are oriented perpendicular to the stem and horizontally to the sun. The vertical orientation of leaves is considered to dissipate heat load buildup during times when transpiration is limited because stomata are closed (Gates, 1966). Hickman (1970) has shown that Arctostaphylos nevadensis, Juniperis communis var. montana, and Pachystima myrsinites, three species which all have small coriaceous leaves that can be vertically oriented, are able to withstand increasingly high xylem sap tension during the growing season despite the fact that they do not have deep root systems. In addition, Daubenmire (1974, p. 225) suggests that vertical orientation of leaves in Arctostaphylos and other genera reduces injury due to supraoptimal light intensities.

The moisture stress values measured were high enough to affect growth. In general, most physiological process fall to very low levels at -14 to -15 bars, especially photosynthesis and cell enlargement (Hsiao, 1973; Noggle and Fritz, 1976; 1 bar = 0.987 atm). But considerable variability exists from plant to plant in the degree to which negative xylem pressures are correlated with reduction in metabolic activity. Zahner (1968) found that needle elongation in Pinus taeda seedlings was directly correlated to water stress values, with total 30 day elongation at -10.2 atm less than half that at -3.6 atm. For cambial tissue of Pinus sylvestris, a 30 per cent decrease in the amount of incorporation of labeled glucose in tracheid cell walls occurred with a change in stress levels from -3.1 atm to -5.9 atm. Further decrease was less dramatic in effect until -28.4 atm was reached and the incorporation level was 46 per cent less than at -3.1 atm (Whitmore and Azhner, 1967). For Douglas fir seedlings cambial growth stops after stress levels reach -18 atm at sunrise irrespective of other conditions (Waring, 1969). At -45 atm, Pseudotsuga seedlings normally die, depending upon the particular genetic race. After -26 atm has been reached, very little night recovery takes place, at least on the coarser textured soils.

Seed and Seedling Ecology

Adaptive Nature of the Seeds

Seeds of Kalmiopsis leachiana are small, and are produced in prodigious numbers. An average of 104.7 viable-appearing seeds per capsule was attained for ten undehisced capsules collected from each of ten different plants at Limpy Rock. When those seeds which were collapsed, discolored, or misshapen are included in the tally, the value is increased to 123.6 seeds per capsule. This latter amount does not include the numerous underdeveloped ovules which were present in the capsule and are probably the result of lack of fertilization (Callan, 1971). When it is considered that three to ten flowers are produced per flowering shoot, and that there are many flowering shoots per plant, the number of seeds produced per plant is seen to be very large indeed. A greenhouse grown plant collected from Limpy Rock and measuring 40 cm in diameter produced 63 flowers in one flowering period.

Seeds from Siskiyous plants are larger than those produced by plants of the Southern Cascades. Siskiyous seeds weighed an average 0.016 mg per seed and measured 1.68 mm by 0.86 mm, while seeds from plants of the Limpy Rock area weighed one-fourth less at 0.012 mg and measured an average 1.17 mm by 0.61 mm. The increase in weight is not due to an increase in seed coat thickness since the testa of seeds of both sources measured approximately 0.0155 mm in thickness. All measurement values are averages for 30 seeds of each seed source, while weight values are averages for 100 seeds of each source.

Kalmiopsis seeds show no specially adapted dispersal morphology or structure. On the surface of the seed coat there exists a reticulate pattern of slight ridging, but no wing is present which would aid in wind dispersal. There may be dispersal in limited amounts by foraging ants, but there is no elaiosome or caruncle common to ant-dispersed seeds (Stebbins, 1971). No birds have been observed foraging for capsules, and it is unlikely anyway that the seeds would pass through their gut unharmed, for the seed is quite fragile and easily punctured by forceps. The seed's small size and light weight indicate, however, that wind and gravity are the main dispersal agents. Seeds of *Rhodothamnus chamaecistus* are elliptical in shape, but somewhat smaller than those of *Kalmiopsis*, measuring 0.5 to 0.6 mm in length and are reported to be wind dispersed (Hegi, 1909-1931, Vol. 5).

In relation to other genera of the Ericaceae, *Kalmiopsis* falls in the class which are small-seeded (Table 25; H.G. Baker, pers. comm.). Two of the small-seeded genera, *Cassiope* and *Phyllodoce*, are characteristic alpine and arctic species. Baker (1972) has found that for the flora of California seed weight decreases with an increase in the altitude of a taxon's habitat. The genus *Arctostaphylos*, which is relatively large-seeded compared to other Ericaceae and is abundant at low elevation both in species numbers, habitat diversity, and importance in floral composition, is replaced by smaller-seeded heath family members (such as *Phyllodoce* and *Cassiope*) at higher elevations. *Kalmiopsis* is closely related to *Rhodothamnus chamaecistus* and *R. sessifolius* which are both species of subalpine and alpine affinities. This fact, along with *K. leachiana*'s small seeds, suggests strongly that at least from a seed size standpoint *Kalmiopsis* is derived from or has affinities for plants which were once distributed at higher altitude.

Small, light-weight seeds are of extreme adaptive significance in habitats such as rocky ridgelines, high montane rock outcrops, and talus slopes. Here wind is everpresent, and provides a

Table 25. Mean seed weight of various members of the Ericaceae. Values based on 100 or more seeds.[1]

Species	Seed weight (mg)	Species	Seed weight (mg)
Arbutus menziesii	1.728	*Comarostaphylos diversifolia*	6.612
Arctostaphylos canescens	10.491	*C. planifolia*	2.260
A. columbiana	13.080	*Cassiope mertensiana*	0.014
A. elegans	25.380	*Gaultheria humifusa*	0.054
A. glandulosa	43.457	*G. shallon*	0.013
A. glauca	13.130	*Kalmia polifolia* var. *microphylla*	0.012
A. mariposa	14.166	*Leucothoe davisiae*	0.022
A. nevadensis	37.790	*Ledum glandulosum* var. *columbianum*	0.015
A. patula	26.046	*Phyllodoce breweri*	0.012
A. pumila	6.172	*P. empetriformis*	0.021
A. standfordiana	18.012	*Rhododendron macrophyllum*	0.297
A. standfordiana var. *bakeri*	7.600	*R. occidentale*	0.143
A. uva-ursi var. *coactilis*	14.759	*Kalmiopsis leachiana* (Siskiyous)	0.016
A. viscida	19.630	*K. leachiana* (Southern Cascades)	0.012

---

[1] All data, except those for *K. leachiana*, courtesy of H.G. Baker.

dependable dispersal agent for seeds which are small and can be transported from outcrop to rock outcrop where they may lodge in cracks and crevices. The fact that Kalmiopsis plants are growing Limpy Rock 100 m or more above the ground surface certainly suggests that wind is an effective dispersal agent and that the seeds of Kalmiopsis are generally wind dispersed. Kalmiopsis grows in a number of rock outcrop areas in the Siskiyou Mountains as well.

For plants of rocky habitats, production of relatively small seeds as opposed to large seeds is important from another standpoint. On a constant and limited energy budget, many more small seeds can be produced than larger seeds for the same energy cost. A larger number of seeds in habitats where potential germination sites are few and restricted to crevices, under rock overhangs, and infrequent spots of organic material accumulation and moisture collection, increases the chance that a seed will land in one of these favorable but relatively rare germination sites.

The Kalmiopsis populations in the Siskiyous and the Southern Cascades have been segregated long enough for selection for changes in seed size to have resulted in significant differences for the two populations, with those of the Siskiyous larger and weighing more. Baker (1972) found that in California there is an increase in seed weight within taxa for herbs and trees of habitats where the chance of drought during establishment is greater. However, for shrub species, shading and competitive stress were the significant factors correlated with seed weight. Baker found a general increase in seed weight of shrub species with the likelihood that a seedling would have to become established among grass or other shrubs. An increase in altitude also correlated with smaller seed weight, and it was suggested that the shorter growing season might be a ruling factor in limiting the total season's photosynthesis and in that way be important. Salisbury (1942), in a study of plants of England, found that seed weight increased for those seeds more likely to germinate in the shade and also for species of late successional stages. For the case of differing seed weights in *Kalmiopsis*, the nature of the vegetation and the limited climatic data which are available suggest that seedlings becoming established in the Siskiyous may be more likely to experience moisture stress. This would correlate with the larger seed size. An additional factor might be the poorer nutrient content of the Siskiyous soils in general (Table 8). Increase in seed size would mean a greater nutrient source for the young embryo to draw upon until it was large enough that it could survive despite the low nutrient edaphic situation.

Seed Germination

Viability. Germination of Kalmiopsis seeds in distilled water under controlled conditions gives an estimate of the viability of seeds from each of the major populations, as well as the seed viability of the species in general. Seeds of the Siskiyou Mountains plants gave a significantly higher per cent germination ($\alpha = 0.05$) under the conditions tested than seeds of plants growing in the Southern Cascades (Table 26).

Two to three weeks occurred between the time of moisture introduction to seeds of Southern Cascades plants and when the first ones germinated. The main peak of germination of Siskiyous seeds was delayed approximately one week. The earliest germination recorded for either seed source from the point of water introduction was 20 days.

Callan (1971) observed that a number of seeds which she examined were abnormal, either in that they were "empty" (containing a degenerated embryo) or collapsed due to probable insufficient fertilization. Her composite tally of capsules collected from the North Umpqua area gave a total of 59.7 per cent normal looking seeds of those examined, the rest being collapsed in form. Empty seeds, because they appear to look normal, by necessity are included in the total normal looking seeds. The study included examination of seeds from plants of six different sites in the Siskiyou and Southern Cascade Mountains (Table 27). Of the total number of Cascades seeds examined 55.9 per cent were normal looking, while 53.8 per cent of Siskiyous seeds appeared normal.

Table 26. Results of germination experiments in petri dishes of Kalmiopsis seeds from both Siskiyou and Cascade seed sources. SK = Siskiyous population seeds; SC = Southern Cascades population seeds.

Treatment	Light germination distilled water		Leaf spray		Leaf spray control		Fresh leaf extract		Litter extract		Dark germination distilled water	
	SK	SC	SK	SC	SK	SC	SK	SC	SK	SC	SK	SC
Per cent germination	62.0	36.7	42.0	36.0	62.0	42.0	60.0	36.0	38.0	44.0	44.0	20.0
Number of replicates	6	6	2	2	2	2	2	2	2	2	1	1
Number of seeds per replicate	25	25	25	25	25	25	25	25	25	25	25	25
Per cent of control	100	100	67.7	85.7	100	100	96.8	98.1	61.3	119.9	71.0	54.5

Table 27. Viability, on basis of normal appearance, of *Kalmiopsis* seeds from the two major geographic populations.

Site	Total seeds counted	Number of normal appearing seeds	Per cent normal
Copeland Creek	580	322	55.5
Bradley Indian Cave	190	109	57.4
Southern Cascades population total	770	431	55.9
Pine Creek	527	317	60.2
Valen Creek	116	641	55.2
Taggert's Bar	1094	481	44.0
Collier's Bar	1175	690	58.7
Siskiyous population total	3957	2129	53.8

Combining this information with germinability percentages determined for the germination of seeds in distilled water, gives a total of 33.4 per cent germinable seeds of those produced by Siskiyous plants under the conditions tested. For the Southern Cascades, the germinability value amounts to 20.5 per cent. Viability in *Rhodothamnus chamaecistus*, whose seeds also are slow to germinate, has been reported as rarely as high as 20 per cent (Hegi, 1909-1931, Vol. 5).

Autotoxicity. Only one seedling of *Kalmiopsis leachiana* was ever found in the field. Even though the seedlings are small and perhaps easily overlooked, this suggested that autotoxicity may be occurring through the release of compounds from the plant to its immediate environment which would be inhibitory to seed germination. By this means competition for water, light, and nutrients between parent and offspring would be reduced, and would appear perhaps to be of high selective value for a long-lived perennial such as *Kalmiopsis*. Autotoxicity has been shown to exist only in a limited number of cases, notably for *Typha latifolia* (McNaughton, 1968), *Eucalyptus pilularis* (Florence and Crocker, 1968), and *Grevillea robusta*, a tropical tree of mature canopies (Webb, Tracey, and Haydock, 1967). Leaf extracts of *Rhododendron maximum* did not inhibit germination of this species' seeds (Romancier, 1970).

Kalmiopsis leachiana seeds which were watered with extracts made from fresh leaves, from litter samples collected below *Kalmiopsis*, and from a leaf spray of *Kalmiopsis* foliage showed no significant decrease in germination amount compared to seeds watered with distilled water (Table 26). Thus the low level of seedling establishment observed in the field suggests that other factors besides possible autotoxic effects are involved.

Light. Seeds of *Kalmiopsis leachiana* when given adequate moisture are able to germinate in the dark or at very low light intensities (Table 26). Germination was somewhat reduced compared to light germinated seeds, representing 54.5 per cent and 71.0 per cent of the distilled water controls for Cascades and Siskiyous seeds respectively. The resultant seedlings were very spindly in growth form with the stem-root axis four to five times longer than for seedlings germinating in the light. The cotyledons were green, but approximately one-fourth smaller than those of light grown seedlings.

The adaptive significance of low light intensity germinable seeds and subsequent seedling growth under the same conditions may lie in the nature of the common habitat of *Kalmiopsis*. In exposed rock outcrops and otherwise very rocky terrain, for the most part only cracks and crevices would provide collection spots for nutrients and water and enough protection against evaporation such that seedling establishment would take place. In these sites light intensity would tend to be low and would necessitate an ability to terminate under those light conditions. In contrast to *Kalmiopsis*, seeds of *Rhodothamnus chamaecistus* are reported to germinate only in the light (Hegi, 1909-1931, Vol. 5).

The only seedling of *Kalmiopsis leachiana* ever found (within the Big Craggies Botanical Area, June 14, 1977) was growing on moist, bare, mineral soil underneath the shade of a rock ledge from which was overhanging a larger plant of *Kalmiopsis*. It had not as yet developed the first true leaves. The soil in the vicinity of the seedling supported no plant life other than a few fern gametophytes. No other *Kalmiopsis* seedlings were found on the mineral soil or growing up through the litter which formed the perimeter boundary of the exposed soil. Ability to germinate and become established under the low light condition of this microhabitat certainly may provide a means for avoidance of competition.

Effect of Soil Type. Germination tests of seeds sown on different soils were conducted to determine the role of the edaphic factor in the distribution of *Kalmiopsis leachiana* as it affects germination and early establishment of young seedlings. This represents the most critical stage in the sexual reproductive process of the plant: the dispersal portion of the life cycle and the point at which its geographical distribution is most likely to be affected. The intention was also to determine if seeds differed ecotypically between the Southern Cascades and the Siskiyous in their germination response to the spectrum of soil types on which Kalmiopsis is found to occur. Results have been expressed as straight per cent germination as well as compared to per cent germination on the sand-peat-perlite mixture and petri dish germination (Table 28).

Kalmiopsis seeds from plants of the Siskiyou Mountains showed a greater germination amount for all tests than did seeds from plants of the Limpy Rock area (Table 28). The major portion of these differences no doubt, are simply a reflection of the higher viability of seeds from the former source. The largest differences in germination amounts, and the only ones which proved to be significantly different for the two seed sources were for germination on peridotite derived soil and on the organic material substrate of Limpy Rock ($\alpha = 0.001$). Eighteen per cent of the Siskiyous seeds sown on peridotite soil germinated while only four per cent of Limpy Rock seeds did so. This is evidence for the existence of some ecotypic differentiation.

The lower germination rates for seeds of both sources on peridotite is correlated with the relatively high magnesium to calcium ratio of this soil type (Table 9). This factor has been shown to be important in plant distribution with relation to serpentine

Table 28. Seed germination (per cent) of Kalmiopsis leachiana on various soil types. SC = seeds of the Southern Cascades populations; SK = seeds of Siskiyous populations.

Soil type	Sand-peat-perlite		Metavolcanic		Gabbro		Peridotite		Organic matter	
	SC	SK	SC	SK	SC	SK	SC	SK	SC	SK
Per cent germination	42.5	49.4	21.9	25.0	33.8	35.6	4.0	18.0	47.5	84.4
Per cent of sand-peat-perlite	100.0	100.0	51.5	50.6	80.0	72.1	9.4	34.2	111.8	170.8
Per cent of distilled water petri dish[1]	115.8	79.7	59.7	40.3	92.6	57.4	8.5	29.0	129.4	136.1
Number of replicates	4	4	4	4	2	4	4	2	4	4
Number of seeds per replicate	40	40	40	40	40	40	40	40	40	40
Date	11/19/76- 1/31/77		11/19/76- 1/31/77		11/19/76- 1/31/77		11/19/76- 1/31/77		4/23/77- 6/21/77	

[1] See Table 25.

soils in the Siskiyous (Walker, 1954) and serpentine soils in general (Proctor and Woodwell, 1975). Toxic levels of magnesium, nickel, and chromium have also been shown to correlate with plant distribution on Siskiyou Mountains serpentine soils (White, 1971), although there is much question as to what represents actual available amounts of these elements and how to measure this availability (Proctor and Woodwell, 1975).

Associated with the low rates of germination on peridotite, there was in addition a relatively high amount of early mortality for seedlings of both seed sources. Two of four seedlings which had germinated from the Cascades seeds died within a week of germination. Six of 14 Siskiyous seedlings died within five days.

In contrast, of the non-ultramafic soils only seeds sown on gabbro soil produced a mortality rate higher than five per cent for the entire first month of growth. Thus, not only do both Siskiyous and Cascades seeds demonstrate very reduced germination on the peridotite soil, but coupled with this, very young seedlings just becoming established show an almost 50 per cent mortality rate within the first week of germination. This inhibition of germination and early growth were not found to be true for the other soil types on which Kalmiopsis is known to occur.

Kalmiopsis was found to be growing only to a limited amount on soils of ultramafic origin. Only two of the study sites were on unaltered ultramafic rock and both were on the mesic end of the moisture gradient for serpentine soils, one near a streambed in a *Chamaecyparis*-mixed conifer association (Vulcan Lake) and the other in a hollowed seepage area (Sourdough Flat). White (1971) found that the effect of the adverse chemistry of ultramafic-derived soils is ameliorated by local topographic situations, as influenced by elevation, exposure, and moisture seepage. This would allow species to exist there when otherwise excluded from more xeric sites which demonstrated equivalent levels of magnesium, nickel, and chromium. Thus tests for germination of *Kalmiopsis* seeds on soils show that the lowest germination occurs on peridotite derived soil and that this is correlated with the low occurrence of *Kalmiopsis* populations on soils of ultramafic origin compared to those from gabbro. On those ultramafic sites which *Kalmiopsis* does occur, most commonly the ultramafic rock is highly metamorphosed. With this metamorphosis can be expected a change in the chemistry of the derived soils (Flint and Skinner, 1974). On unaltered peridotite, *Kalmiopsis* was found only in very mesic topographic positions.

Germination on soils of gabbro parent material and those derived from the metavolcanics of the Southern Cascades sites was relatively high, thus confirming the ability of *Kalmiopsis* seeds to germinate and establish themselves on bare mineral soil (Table 28). The amount of germination on gabbro soil was higher than on metavolcanic soil, but not to a significant degree for seeds of either source ($p > 0.1$). There appeared no inhibiting effect of the soils of the North Umpqua area on germination or early seedling growth. This then eliminates the possibility that an edaphic factor is preventing establishment of Kalmiopsis on the ground under the forest canopy.

Germination totals were highest for seeds of both sources on organic material and mixed humus collected from a crevice in Limpy Rock (Table 28). In fact, a higher germination percentage was obtained for this substrate than occurred in petri dishes or on the sand-peat-perlite substrate. Thus, organic matter accumulating in rock crevices may provide substances that stimulate germination in Kalmiopsis seeds. From these results it would appear that seeds of Kalmiopsis show adaption to germination in moist pockets of accumulating organic material, such as in between or surrounding rocks, below trees and taller shrubs, and in crevices and cracks of larger rock outcrops.

Effect of Fire. No seeds which were heat treated in 70°C distilled water, either from the Southern Cascades or the Siskiyou Mountains, germinated (Table 29). Thus the seeds of Kalmiopsis leachiana are not fire-adapted like some of the plants with which it is now to be associated such as Arctostaphylos spp. (Gratkowski, 1961) and Pinus attenuata (Harlow and Harrar, 1968). Of course, fires of much lower intensity may not be as harmful to the seeds,

Table 29. Germination amounts (per cent) of heat-treated seeds of Kalmiopsis leachiana. SC = seeds of the Southern Cascades populations; SK = seeds of Siskiyous populations.

Treatment	Control		Heat treatment	
	Seed source		Seed source	
	SC	SK	SC	SK
Per cent germination	40.1	52.0	0.0	0.0
Per cent of control	100.0	100.0	0.0	0.0
Number of replicates	2	2	1	1
Number of seeds per replicate	40	40	120	120
Date	4/13/77 - 6/21/77		4/13/77 - 6/21/77	

but it would be expected that the extremely thin and fragile testa of the seeds would be able to withstand only those fires of very low intensity, if any at all.

Seedling Growth

General Growth Patterns. Germination in *Kalmiopsis leachiana* is epigeal in pattern. As expected the emergent seedlings are very small and vary in size depending on the seed source. For newly germinated seedlings of the Siskiyou Mountains, each cotyledon measured an average 0.96 mm and the root-shoot axis 5.33 mm. Seedlings developing from Southern Cascades seed were even smaller, their cotyledons measuring only 0.57 mm and their root-shoot axis less than one-half that of Siskiyous seedlings at 2.53 mm. Values are based on measurement of 30 seedlings each.

The cotyledons serve as a primary photosynthetic organ for a long period during the development of the young seedling. For most plants, the cotyledons were still actively photosynthesizing after six months. In some cases, the first true leaf appeared as early as three weeks after germination on metavolcanic and organic soils, but usually the time period required was four or five weeks. The early true leaves of young seedlings are different than the glabrous and eglandular cotyledons, in that they are finely ciliated on the margins with glandular hairs and soon develop a few scattered glands on the leaf undersurface. These glandular hairs occur relatively infrequently on leaves of mature plants.

The first few leaves are normally crowded very close together but by the time six or seven leaves have been produced (a process which requires an average of four months or more) further new leaves are generally separated by much longer internodes. Presumably, elongation occurs when the root system has developed to an extent which can support a larger photosynthetic area. Some of the seedlings grown on gabbro and serpentinite soils never reached the stage at which the stem began to elongate. Their leaves were crowded into a terminal rosette-formation. Others, especially seedlings grown on the organic matter substrate, had developed side shoots arising from the axils of the tightly clustered basal leaves by the end of the experimental period.

The root system is represented in newly germinated seedlings by a radicle that accounts for only one-fifth of the total length of the root-shoot axis. It is demarcated by a short hypocotyl region, from which arises an upright, photosynthetic epicotyl. Typically the radicle will lie parallel to the ground as the stem rises in the air. Growth of the young root begins almost immediately, but again at a slow rate. About the time that the length of the seedling has been doubled as a consequence of growth in the young root, a small branch will appear somewhere along its length. The primary root will develop more side branches near the base of the seedling. These, in turn, will also develop branches of their own and in so doing will assume importance equal to that of the initial developing root from which they arose. From these two or three main roots will develop a highly branched, fibrous root system.

Growth Rates, Seed Source, and Soil Type. Growth rates of transplanted seedlings of both Cascades and Siskiyous seeds on the major soil types tested are given in Tables 30 and 31. Results of statistical comparison for differences in growth rates due to seed source and soil type are presented in Tables 32 and 33, respectively.

The striking feature about growth in young Kalmiopsis seedlings is that it is relatively slow even under greenhouse conditions and a constant water supply. The highest growth rate exhibited was for seedlings of Southern Cascades seed source growing on metavolcanic soil. These attained a total growth of about 10 cm in six months. Seedlings of Siskiyous seeds growing on soil of serpentine origin attained a total growth of just over one-half that value, at 5.5 cm, the lowest mean for all tests (Table 33).

These growth rates under greenhouse conditions can be compared to that of Arctostaphylos canescens and A. patula under field conditions, both of which are associated species found growing with Kalmiopsis in some areas. After a controlled burn the previous September, seedlings of these two manzanita species had developed

Table 30. Relationship between seedling growth and soil type for *Kalmiopsis leachiana*.

Soil type	Seed source	Number of seedlings	Total growth per month (mm)	Shoot growth per month (mm)	Root growth per month (mm)	Root-shoot ratio
Serpentinite	Siskiyous	4	9.45	1.45	8.00	5.56
	S. Cascades	17	10.69	1.14	9.55	8.30
	Combined	21	10.46	1.20	9.26	7.78
Gabbro	Siskiyous	66	11.41	2.37	9.05	4.02
	S. Cascades	21	9.70	1.92	7.79	4.48
	Combined	87	10.18	2.09	8.10	4.13
Metavolcanic	Siskiyous	20	11.88	2.93	8.98	3.38
	S. Cascades	16	17.95	2.84	15.11	6.20
	Combined	36	14.58	2.89	11.70	4.63
Organic matter	Siskiyous	20	12.21	3.71	8.50	2.36
	S. Cascades	16	13.41	4.82	8.32	2.24
	Combined	36	13.18	4.20	8.43	2.30

Table 31. Relationship between soil type, seedling mortality, and leaf growth of *Kalmiopsis leachiana*.

Soil type	Seed source	Number of seedlings planted	Final number of seedlings	Percent mortality	Number of leaves produced per month	Largest leaf after 6 months (mm)
Serpentinite	Siskiyous	5	4	20.0	1.65	3.6
	S. Cascades	20	17	15.0	1.68	4.2
	Combined	25	21	16.0	1.67	4.1
Gabbro	Siskiyous	70	66	5.7	2.27	4.6
	S. Cascades	25	21	16.0	2.26	5.1
	Combined	95	87	8.4	2.26	4.3
Metavolcanic	Siskiyous	23	20	13.0	4.16	6.1
	S. Cascades	17	16	5.9	3.64	8.2
	Combined	40	36	10.0	3.93	7.0
Organic matter	Siskiyous	-	20	-	4.13	5.4
	S. Cascades	-	16	-	6.00	10.4
	Combined	-	36	-	4.96	7.6

Table 32. Student's t-test comparison results for *Kalmiopsis* seedling growth on various soil types for seeds of the two main populations. NS = not significant at $\alpha \geq 0.01$.

Comparison	Total growth	Shoot growth	Root growth	Root-shoot ratio	Number leaves produced per month	Largest leaf after 6 months
Serpentinite Siskiyou vs. Cascade seed	NS	t=2.69 α=0.02	NS	NS	NS	NS
Gabbro Siskiyou vs. Cascade seed	NS	NS	NS	NS	NS	NS
Metavolcanic Siskiyou vs. Cascade seed	t=2.31 α=0.05	NS	t=2.59 α=0.02	t=3.00 α=0.01	NS	t=2.14 α=0.05
Organic matter Siskiyou vs. Cascade seed	NS	NS	NS	NS	t=2.20 α=0.05	t=3.75 α=0.001

Table 33. Student's t-test comparison results for *Kalmiopsis* seedling growth on various soil types. NS = not significant at $\alpha \geq 0.01$.

Comparison	Total growth	Shoot growth	Root growth	Root-shoot ratio	Number leaves produced per month	Largest leaf after 6 months
Gabbro vs. serpentinite growth	NS	$t=2.69$ $\alpha=0.01$	NS	$t=6.51$ $\alpha=0.01$	$t=2.15$ $\alpha=0.05$	NS
Gabbro vs. metavolcanic growth	$t=3.60$ $\alpha=0.001$	$t=2.92$ $\alpha=0.01$	$t=3.36$ $\alpha=0.01$	$t=1.72$ $\alpha=0.1$	$t=14.15$ $\alpha=0.001$	$t=5.36$ $\alpha=0.001$
Gabbro vs. organic matter growth	$t=3.37$ $\alpha=0.001$	$t=6.92$ $\alpha=0.001$	NS	$t=4.32$ $\alpha=0.001$	$t=8.94$ $\alpha=0.001$	$t=5.30$ $\alpha=0.001$
Serpentinite vs. metavolcanic growth	$t=1.71$ $\alpha=0.1$	$t=5.69$ $\alpha=0.001$	NS	$t=3.32$ $\alpha=0.01$	$t=4.79$ $\alpha=0.001$	$t=3.77$ $\alpha=0.001$
Serpentinite vs. organic matter growth	$t=3.43$ $\alpha=0.001$	$t=7.12$ $\alpha=0.001$	NS	$t=7.95$ $\alpha=0.001$	$t=5.56$ $\alpha=0.001$	$t=3.28$ $\alpha=0.01$
Metavolcanic vs. organic matter growth	NS	$t=3.32$ $\alpha=0.01$	$t=2.37$ $\alpha=0.02$	$t=4.29$ $\alpha=0.001$	$t=1.80$ $\alpha=0.01$	NS

roots of at least eight inches (over 20 cm) by the following September (Gratkowski, 1960). Presumably, the seeds had germinated at the beginning of the growing season. Based on growth rates determined in the experimental studies, the largest root growth Kalmiopsis would attain after six months would be 5.7 cm. From a growth standpoint therefore, Kalmiopsis would not be able to compete favorably with seedlings of associated species for space and its resultant rewards of light, water, and nutrients.

The relatively long period in which a Kalmiopsis seedling is very small, plus the length of time which is required for germination to occur, represent the stage in the life cycle when the seedling is most vulnerable and least buffered against environmental stress (Stebbins, 1971). A quickly developed root system and a large photosynthetic surface all aid in combating sudden changes in moisture level, temperature, and mechanical damage due to wind and erosion. Moisture levels may remain high enough to allow germination to occur, but because seedlings demonstrate such a slow growth rate a sudden loss in water from the upper soil levels would quickly mean the death of the newly germinated seedling. For Kalmiopsis an exceptionally slow growth rate means a very extended period of vulnerability and this is correlated with the very low rate of reproduction observed in the field season of 1976-1977.

Comparison of performance of Siskiyous and Cascades seedlings on the different soil types suggests that ecotypic differentiation may exist between the two on the basis of their respective leaf size. The largest leaves of both seedling groups growing on serpentinite and gabbro soils were not significantly different in length. However, the largest leaf of Cascades seedlings was statistically greater than those of Siskiyous seedlings growing on metavolcanic soils and almost three times that on the organic material substrate (Table 32). Thus leaf growth of Cascades seedlings appears to be inhibited on the Siskiyous soils, but not so on the metavolcanics and organic material substrate of the Limpy Rock area. In contrast to this, the largest leaves produced on Siskiyous seedlings did not increase to the same degree with this change in soil type. In addition, size of the largest leaf was always greater for Cascades seedlings on all soil types. These considerations suggest that measured differences in the field of leaf size are in part genetically controlled.

Besides those in leaf growth, other differences in growth measurements are few which prove to be statistically significant for seedlings of the two main populations (Table 32). For those that do exist the pattern is difficult to interpret. It may be that longer growth periods would allow development of growth patterns that would indicate further evidence for ecotypic differentiation.

In general, growth response of Kalmiopsis leachiana is different for each soil type (Table 32). Combined averages for growth of seedlings of both seed sources show that growth rates on serpentinite and gabbro soils were significantly less than for metavolcanic soil and organic material. This is most dramatically reflected in shoot growth rates, as well as the root-shoot ratio, the number of leaves produced per month, and the size of the largest leaf after a six month period. Thirty-one of 36 plants grown on organic material had one or more side shoots after six months for an 86 per cent total. For plants grown on metavolcanic soil this number was also high at 55 per cent. But only 18.9 per cent of the gabbro grown plants had any side shoots at the end of the experiment and no serpentinite grown plants ever branched after six months time.

The root-shoot ratio of Kalmiopsis varied according to the soils in which seedlings were growing. This variation was generally manifested by increasing growth rates for shoots on organic matter and metavolcanic soil and not increased root growth rate (Table 30). Except for the extraordinarily high rate of root growth for Cascades seedlings on metavolcanic soil, all other plants were very close to the average of 8.6 mm per month of root length increase. In contrast, shoot growth increased four times, from a low of 1.14 mm per month on serpentinite to 4.82 mm on the organic material substrate. It thus appears that environmental conditions, at least the soil type, have a relatively smaller influence on the rate of root length increase compared to that of above ground parts. Root system development would be expected to be very critical for young seedlings growing in rocky habitats and on soils which are very poorly developed, conditions in which *Kalmiopsis* grows.

Although demonstrating the lowest ratio of root to shoot growth, *Kalmiopsis* grown on serpentinite had roots that were not significantly shorter than *Kalmiopsis* grown on metavolcanic soil (Table 33). Metavolcanic soil allowed the greatest rate of root growth and had the highest root to shoot ratio of any soil. In comparison, growth rates are certainly limited on serpentinite soil, but the growth inhibition for the measurements taken is reflected in the development of above ground parts (leaf size, the number of leaves produced, and shoot growth), and not in the length of root growth. On a biomass basis, however, root growth as well as shoot growth was observed to be inhibited on serpentine and gabbro soils. The result is that growth inhibition is reflected in all parts of the young seedling. Root development is small so that water and nutrient uptake is reduced, which limits the photosynthetic area that can be produced, and in turn limits further root development. When the observed differences are combined with the already known low germination rates and lower survival of very young seedlings on serpentine, it is seen that soils of ultramafic origin do strongly inhibit early stages of growth of *Kalmiopsis* more than any other soil type on which it is found to occur.

Just as germination of *Kalmiopsis* seeds was not inhibited on the soils surrounding the rock outcrops of the North Umpqua River sites, neither is growth of young seedlings inhibited. In fact, total growth was on average greater than that for all soils, including the organic matter substrate. This is further support that *Kalmiopsis* is not limited edaphically to the rock outcrops of the Umpqua area.

Heterostyly and Floral Ecology

The first report of variation in style length in *Kalmiopsis leachiana* was made by Rehder (1932) from his observations of plants collected at Horse Sign Butte and Collier's Bar, Curry County, in 1931 (*Leach 2915*, in part, ORE). These collections included flowers with styles 3.5 mm long and others with styles 8 mm in length. Rehder discounted the possibility that *K. leachiana* could be heterostylous, attributing the variation in style length to "seminal variation" (p. 34). He suggested instead that style length variation might be concomitantly related to differences in leaf shape and size that he had observed in collected specimens. His apparent basis for disregarding heterostyly as a possibility is the fact that there are no reported heterostylous species in the Ericaceae. However, the flowers of *Epigaea repens*, a dioecious member of the

Ericeae, exist in both long and short styled forms (Darwin, 1877). This species is considered to have evolved directly from a previously heterostylous reproductive system (Darwin, 1877; Darlington, 1958; Crowe, 1964; Vuilleumier, 1967).

Although isolated evolution of heterostyly within a family is relatively rare, four other angiosperm families have been reported to contain only one or two heterostylous species. These include Nivenia binata Klall. of the Iridaceae (Mulcahy, 1965), Gelsemium rankii Small and G. sempervirens of the Loganiaceae (Duncan and Dejong, 1964) and Fagopyrum esculentum of the Polygonaceae (Schoch-Bomer, 1934). In addition, the three species which compose the genus Jepsonia, all considered to be relictual endemics, represent the only heterostylous species of the Saxifragaceae (Ornduff, 1969).

Callan (1971) made measurements of styles of plants growing in the North Umpqua River area and grouped her results into different flower types. Flowers found at Dry Creek had style lengths of 6-7 mm and 10-13 mm and flowers at Copeland Creek exhibited style lengths of 13-17 mm. She did not report having made any corresponding measurements of stamen lengths.

Persistent Style Measurements

Initial investigation of possible heterostyly in Kalmiopsis took the form of measurement of persistent styles on developing capsules.

This provided a general picture of the distribution of heterostylous forms (Table 34). For the Siskiyou Mountains the data show that two general forms exist. The average short style length for a particular population ranges from 1.7 mm to 3.2 mm, while the average length for long styled forms measures between 6 mm and 10 mm. The exception to this is the population found on the west side of Bailey Mountain in the Kalmiopsis Wilderness Area. Plants fall into two categories for this site, those with styles approximately 9 mm long and those with styles averaging 14 mm. It appears also that for the Siskiyou Mountains the smaller a population is the more likely it will be represented by plants of only one style length. The stands at Sourdough Flat and Bailey Cabin are both relatively small (less than 300 m^2 in area) and contain plants with only short styles.

The Kalmiopsis populations of the North Umpqua River differ in two ways with respect to measured style length from those of the Siskiyou Mountains. First of all, measurements of persistent styles show that there is a much greater variability in style length, not only between plants within a single population, but also between populations (Table 34). Significantly, this variation is spread over a much smaller geographical area. Style lengths average from 3.9 mm all the way to 16.7 mm, with modes at approximately 6 mm, 8 mm, 10-11 mm, and 13-14 mm. This then points to the second difference: style lengths for Cascades populations are greater than

Table 34. Distribution of persistent style lengths (means) in populations of *Kalmiopsis leachiana*.

Site	Length of long styles (mm)	Length of short styles (mm)
	Siskiyou Mountains	
WBM	14	9
NBM	6	2
ROT	7.5-9	1.5-3.0
KRH	7-9	2-4
FHV	10	2
DWH	9	3
SSP	9	3
SDF	-	2-3
VLK	9-11	2-2.5
EWR	7-9	1.5-3.0
EBC	-	2
CBR	9-11	2-3
BFT	9-11	2-3.5
Vulcan Lake	-	2-4
	Southern Cascade Mountains	
LPR	11.1, 13.8, 16.0	5.5, 8.0, 10.9
DCK	11.5	-
RAR	7	4
CCK	12.5	-
PAR	14	-
FLR	12.2, 13.0, 14.1	6.0, 8.0, 10.5

those of the Siskiyou Mountains. Thus there has been an evolutionary divergence in flower morphology between the two disjunct populations.

It is difficult to determine from these data but it appears, as Callan suggests (1971), that more than two general style lengths may exist within the Umpqua population thus making Kalmiopsis tristylous. For plants in the immediate vicinity of Limpy Rock, there are three groupings for this single but large population, one between 5-6 mm, one set of styles measuring 8-11 mm, and another measuring 16 mm. Alternatively, there may be only two general flower morphological types within the Cascades. In this case the measurements would simply indicate a larger degree of variance about the short and long style means than was found in the Siskiyous. As was true for the Siskiyou Mountains, small populations, specifically those associated with the two large boulders in the Copeland Creek drainage and those at the intersection of Dog Creek and the North Umpqua Highway, consisted of plants of only one general style length.

Flower Measurements

Measurements of styles and stamens of flowers substantiate that Kalmiopsis is heterostylous in flower morphology for populations in both the Cascades and Siskiyou Mountains (Table 35). The terminology applied here relates to the early classic studies of

Table 35. Style, stamen, and corolla measurements in pin and thrum forms of *Kalmiopsis leachiana*.

			Thrum plants			Pin plants		
Site	Date sampled	Mean corolla width (mm)	Mean style length (mm)	Mean stamen length (mm)	Number plants	Mean style length (mm)	Mean stamen length (mm)	Number plants
BCR	6/15/77	16.16	2.62	8.45	25	10.60	7.23	13
BCR[1]	6/15/77	-	2.39	6.99	12	9.70	5.86	13
RCK	5/20/77	14.27	3.79	8.32	20	8.38	6.22	8
MOL	6/11/77	18.50	3.30	10.17	10	-	-	-
SDF	5/21/77	14.17	3.02	8.23	13	-	-	-
YCK	5/ 9/77	14.80	-	-	-	8.56	6.62	10
CKD	6/ 8/77	18.10	-	-	-	10.55	8.56	10
LPR	5/15/77	23.10	7.05	13.12	11	13.57	12.11	13
PAR	5/15/77	21.30	7.08	11.15	12	12.21	9.93	26
DCK	5/14/77	21.20	-	-	-	14.27	11.72	5

[1] Measurements made on partially open or unopened flowers.

heterostyly in Primula (Darwin, 1877). Pin plants are those with long styles and short stamens, while thrum plants have flowers with short styles and long stamens. Legitimate crosses are defined as those which occur only between opposite forms.

For the Siskiyou Mountains two populations visited were large enough to contain both long-styled and short-styled plants. In the Kalmiopsis Wilderness Area at Rattlesnake Creek the styles of pin plants were significantly greater than those of thrum plants (α = 0.001; Table 35). The mean stamen length of pin plants was also significantly different than those of thrum plants (α = 0.01), measuring 2.1 mm less. The stamens of pin plants are at a relatively greater height above the style of the average thrum plant (Figures 19 and 21). Thus there is much greater chance for illegitimate pollen flow from thrum stamens to thrum styles than there is for flow between pin stamens and pin styles. There appear to be about equal numbers of pin and thrum forms at Rattlesnake Creek.

Both long- and short-styled plants were also found to occur on the slopes and ridges in the general vicinity of the tallest peak in the Big Craggies Botanical Area (4616 ft). Pin and thrum plants were again in approximately equal numbers, but plants of a single segregated rock outcrop were not uncommonly of the same form. This probably shows the influence of vegetative reproduction. The styles of the two forms were of significantly different mean length, as was

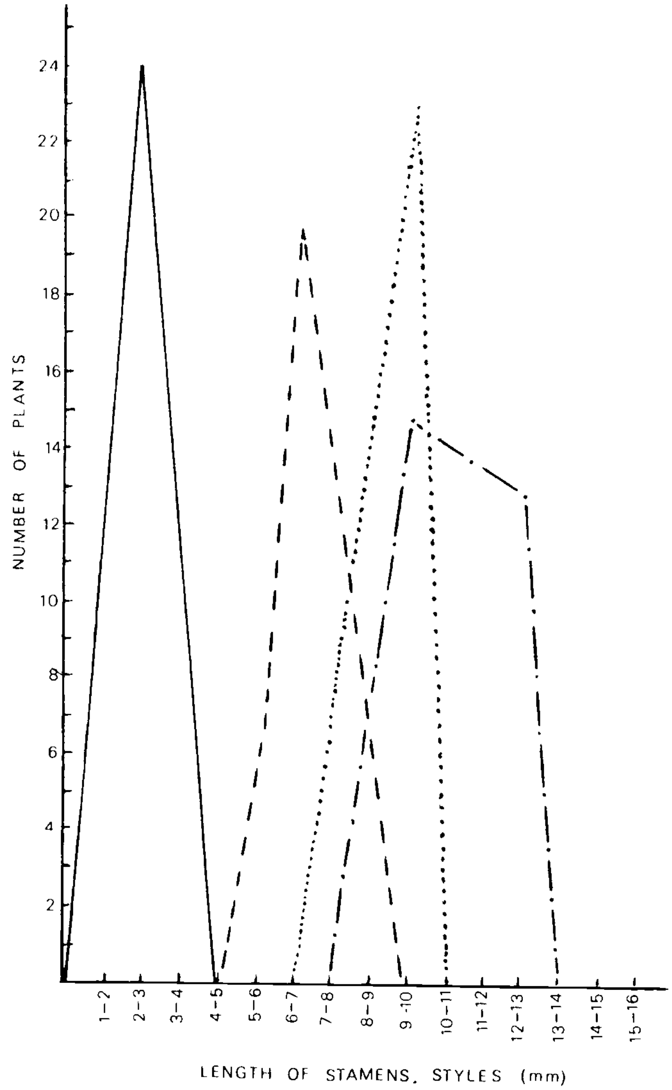


Figure 19. Distribution of style and stamen lengths of pin and thrum forms of *Kalmiopsis leachiana* of the Siskiyou Mountains. Each value represents one flower of a single randomly selected plant at the Siskiyou populations listed in Table 34. (____ thrum styles; _ _ _ thrum stamens; _._._ pin styles; . . . pin stamens.)

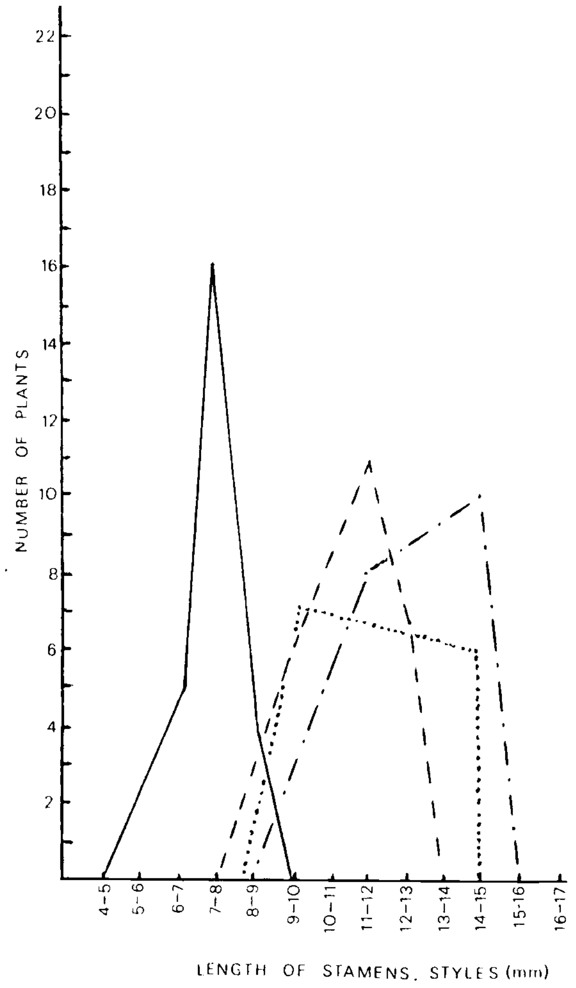
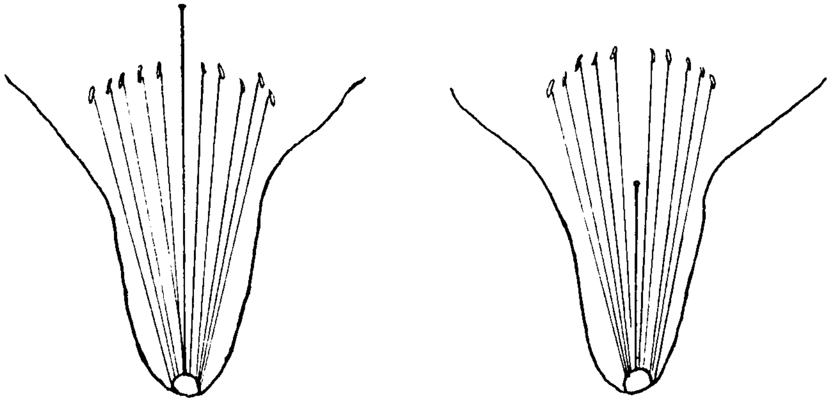
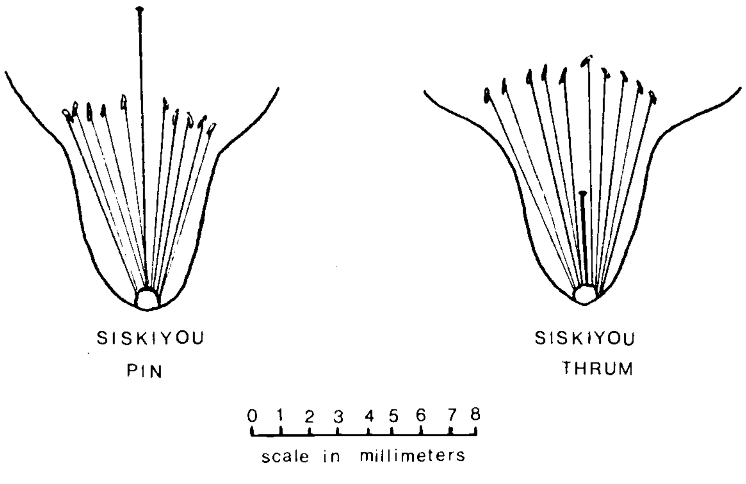


Figure 20. Distribution of style and stamen lengths of pin and thrum forms of Kalmiopsis leachiana of the Southern Cascades Mountains. Each value represents one flower of a single randomly sampled plant at the Southern Cascades populations listed in Table 34. (___ thrum styles; _ _ _ thrum stamens; _._._ pin styles; . . . pin stamens.)



SOUTHERN CASCADES
PIN

SOUTHERN CASCADES
THRUM



SISKIYOU
PIN

SISKIYOU
THRUM

Figure 21. Relative size of Southern Cascades and Siskiyous flower forms of Kalmiopsis leachiana. Actual sizes based on mean values obtained for single flowers of randomly sampled individual plants (see Table 35).

true for the stamens ($\alpha = 0.001$). The relative position of stamens of pin and thrum plants with respect to the styles of opposite and alike forms was the same as that found at Rattlesnake Creek.

Four plants were found growing in the vicinity of the Big Craggies which had intermediate style lengths at 5 mm, 5.5 mm, 6 mm, and 7 mm to give an average of 5.8 mm. The average stamen length for these four plants was 6.01 mm. Four other smaller populations were also sampled in the Siskiyou Mountains. Kalmiopsis plants at Morrison's Lament of the Big Craggies Botanical Area were found to be short-styled while the population on the edge of a serpentinite outcrop at Cookie Drop, also in the Big Craggies, contained only pin plants (Table 35).

For Kalmiopsis populations at Limpy Rock and Knobcone Pine Ridge of the North Umpqua River area, plants again fall into two different morphological forms. However, there is a large amount of variance in the length of pin styles. This would appear to account for the earlier impression that tristyly might exist in these populations (Table 35 and Figure 20). The variance in both stamen and style length is much greater than for Siskiyous plants.

At Knobcone Pine Ridge, styles of thrum plants averaged 7.1 mm and those of pin plants 12.2 mm. These two means were significantly different at a one per cent significance level, but average stamen length between the two forms was statistically different only at a ten per cent probability level. The same general situation was true for Kalmiopsis at Limpy Rock. Average style lengths of pin and thrum plants were significantly different at the one per cent level but stamen lengths of the two forms overlapped to such a degree that the average stamen lengths for pin and thrum plants did not differ significantly ($p < 0.1$; Table 35 and Figure 20). Thus it appears that selection for stamen length differences in the two flower forms has been less in Cascades populations than for those in the Siskiyou Mountains. The small, isolated Kalmiopsis population at the intersection of Dog Creek and the North Umpqua Highway contains only pin plants (Table 35). Placement of stamens relative to styles of pin and thrum plants takes the same general form in the two different geographical provinces.

As was the case for Siskiyous plants, stamens of pin plants are much closer to pin styles than thrum stamens are to thrum styles (Figure 21). There is a probable additional amount of illegitimate pollen flow for Umpqua plants of thrum form since there is a larger amount of overlap in style and stamen lengths in these plants. Duhlberger (1973) has shown that for Linum pubescens and L. mucronatum, in which anther height is the same for pin and thrum plants and approximately equal to that of the pin styles, a combination of morphological and physiological barriers together aid in the efficacy of the heteromorphic system. Crosses between pin styles and pin stamens produce relatively little mature seed. Thus this pathway is blocked physiologically. For crosses between thrum styles and thrum stamens seed production is relatively high, but natural illegitimate crosses of this type would occur only rarely since thrum styles and stamens are widely separated spacially. In this way illegitimate crosses are prevented morphologically.

Stigma and Style Morphology

Commonly, the different flower forms of heterostylous plants differ in the nature of the stylar stigmatic surfaces, either in the number of papillae, size of the stigmatic surface, or orientation with respect to the rest of the flower parts (Darwin, 1877; Vuilleumier, 1971). Observation of different stigmas of styles of pin and thrum plants of *Kalmiopsis* showed no apparent differences in the nature or size of the stigmatic surface. For both pin and thrum plants the stigma measured 0.5 mm in width, was convex in general outline, and was obscurely five-lobed on the shiny surface. This is true for both plants in the Cascades and Siskiyou Mountains. Normally styles are straight for both pin and thrum plants, projecting directly out from the center of the ring of stamens. However, some pin plants were found both in Cascades and Siskiyous populations in which styles curved such that the stigmas of these flowers were positioned outside the stamen ring. This was most commonly observed in the very long-styled pin plants of the North Umpqua populations.

Pollen Tetrad Shape and Size

In many heterostylous plants the pollen from anthers of one form will differ in shape, texture, or size from that of the other form. In all cases where size differentiation of pollen is known to exist pollen from anthers of thrum plants will be larger than pollen from pin anthers (Darwin, 1877). *Kalmiopsis* pollen tetrads (in the Ericaceae individual pollen grains do not separate from each other but remain attached in tetrad form) do not differ significantly in shape, texture, or size for pin and thrum plants. For Cascades populations, pin tetrads measured 56.5 μ and tetrads of thrum anthers measured 55.5 μ. These values were 41.5 μ and 41.7 μ respectively for Siskiyous plants. Values are based on measurements of 15 tetrads from flowers of five different plants for each flower form.

In comparison with the above results, Duhlberger (1973) has shown that *Linum pubescens*, which is distylic in morphology and is incompatible within same forms, shows no difference in pollen morphology between forms. However, pollen tetrads of *Kalmiopsis leachiana* growing in the Cascades proved to be significantly larger than those of the Siskiyou Mountains, measuring approximately 14.2 μ greater. The reason most commonly invoked to explain larger thrum pollen is that the pollen tube must travel farther down the long pin styles than pin pollen tubes must travel to reach the ovary via the shorter thrum styles (Darwin, 1877). The longer styles in both pin and thrum forms of Cascades _Kalmiopsis_ could explain the existence of larger pollen grains in those plants.

Crossing Experiments

The results of artificial self-pollinations on a greenhouse grown _Kalmiopsis_ plant of Limpy Rock are presented in Table 36. Of 35 artificially pollinated flowers all but one failed to produce normal-sized capsules. For flowers which were left undisturbed 18 out of 28 flowers produced such a capsule. But for each of the three pollinated types, within flower pollinated, between flower pollinated, and undisturbed flowers, the highest number of normal-looking seeds produced in one capsule was five (Table 36). This is compared to an average of 104.7 normal seeds per capsule counted for 30 capsules collected at Limpy Rock on January 24, 1977. This latter value probably represents a somewhat smaller number than were actually produced since capsules had already partially dehisced when the seeds were counted. The capsules of the selfed plants were collected before dehiscence began. Thus there was an almost

Table 36. Seed production and capsule size in relation to pollen source for a cultivated plant of *Kalmiopsis* from the Southern Cascade Mountains.

Cross	Number capsules	Capsule width (mm)	Range	Number good seeds per capsule	Range	Number partially developed seeds per capsule	Range
Selfed-within flowers	18	3.90	3.0-4.5	0.9	0-4	3.8	1-12
Selfed-between flowers	16	3.85	3.0-4.5	1.1	0-4	1.5	0-5
"Undisturbed" flowers	28	3.63	3.0-3.5	0.8	0-5	0.8	0-7
Capsules from the wild (Southern Cascades)	10	5.00	4.5-5.5	104.7	69-154	18.9	8-31

100 per cent reduction in seed production with the elimination of out-crossing for this pin form of Kalmiopsis leachiana. It would then appear that strong incompatibility barriers do exist preventing self-fertilization in this flower form of Kalmiopsis in the Cascades populations.

In almost every example of a heterostylous species, self-incompatibility is associated with the morphological differences between different flower forms (Vuilleumier, 1967). In fact this was originally proposed as a criterion for defining a heterostylous species (Darwin, 1877). However, there are no reports of artificial pollination studies in Kalmiopsis.

Mulligan (1973) reports that a single plant of Kalmiopsis of stock collected in Curry County and grown in a lath house of the University of Washington Arboretum "flowers freely each year" and "also produced seeds regularly" (p. 132). He does not mention whether the plant was available to pollinators, how many seeds were produced, or the condition of the seeds and the capsules in which they developed. The crossing experiments conducted for this study suggest that the number of seeds produced was probably limited. Further evidence for this is that the Kalmiopsis population at Gold Basin in the Kalmiopsis Wilderness Area in May 1977, was found to have no capsules whatsoever from the previous seasons, even though a near normal amount of flower buds were present on the plants at the time. It may be that the entire population is represented by a single clone. When Kalmiopsis was first discovered at Gold Basin on June 14, 1930, no fruits were available either (Henderson, 1931). It was not until the following year that fruits were first collected at Horse Sign Butte.

There appeared to be no difference in seed set for flowers which were pollinated shortly after onset of anthesis or just before the corolla had withered. Thus it appears that the stigma is receptive through the entire anthesis period. The styles of Rhodothamnus chamaecistus are reported to be receptive to their own pollen late in anthesis. Self-pollination and subsequent fertilization can be effected when, at the end of the flowering period, the flower is commonly in a drooping position and the stigma is below the anthers (Hegi, 1909-1931, Vol. 5).

Pollinator Observations

For heterostyly to be effective in the promotion of outcrossing between opposite morphological forms, it has been considered that reciprocal lengths in styles and stamens must be accompanied by a tubular-shaped corolla (Baker, 1964). In its search for nectar or pollen, the pollinator, due to the constriction of the corolla throat, is forced to approach and enter the flower from a specific direction every time. In this way pollen will be transferred differentially to specific areas on the pollinator's body and illegitimate pollen flow will be reduced to a minimum. For a heterostylous species with a relatively open corolla a pollinator may brush against anthers and stigmas with more than one area of its body, increasing the chance for illegitimate pollen flow. If the tube is large flower visitors may completely miss contact with anthers and stigmas. For these reasons it becomes very difficult to explain how there has been selection for reciprocal lengths of anthers and styles in the very open corolla of Fagopyrum esculentum (Baker, 1964).

Kalmiopsis leachiana possesses a relatively open corolla, but the ring of ten stamens essentially forms a tube that larger pollinators must approach always from one direction. Bumblebees (Bombus sp.) appear to be the chief pollinators, and in their approach to the corolla, the edges of the corolla are grabbed and the bumblebees insert their upper body into the center of the ring of stamens. They come in contact with both the anthers and the stigmas on their way to the nectary at the upper side of the base of the ovary. As a result, it appears that pollen would be distributed differentially on portions of the head and upper thorax of the bee. However, the fact that the corolla does not completely force approach from a specific direction is pointed out by observation of foraging activity of honeybees. Normally these bees would approach the flower in the manner described for bumblebees and the same conclusions would hold. But occasionally honeybees were observed to bypass the stigmas and anthers completely, reaching the nectary by slipping in between the ring of stamens and the corolla itself.

Observations of pollinators' activity in the Big Craggies Botanical Area from June 12 to June 16, 1977 suggests that differential visitation of flower visitors to partially open flowers might additionally serve in the efficacy of heterostyly in Kalmiopsis. In populations in which approximately equal numbers of fully open flowers and flowers still in bud or just opening existed, bumblebees and honeybees appeared to be directing their activities differentially to the latter group. Flowers of both groups were producing nectar, and for closed to partially open flowers some but not all of the anthers were always found to have dehisced. Measurements of style and dehisced stamen lengths in this latter group show that mean style length and mean stamen length are significantly different ($\alpha = 0.001$; Table 35).

On two consecutive days the number and type of flowers visited by bumblebees were counted in which the bee landed and attempted to extract nectar. Flowers were classed subjectively into two forms: open flowers and partially open flowers (including those still unopened). On both days five separate counts were made. Visits were tallied into one or the other flower categories until 50 visits to flowers of one form had been counted. In each case no more than 15 open or almost fully open flowers were visited before 50 closed or partially closed flowers had been recorded. These observations suggest that promotion of legitimate pollen flow may be increased in *Kalmiopsis* by attraction of pollinators to flowers at a stage in development when they are tubular-shaped.

Herbivore Interactions

Insects

During the period of study insects were never observed on the foliage of *Kalmiopsis leachiana*. In conjunction with this, at every population only a very few leaves of *Kalmiopsis* out of all the plants present ever showed evidence of herbivory. In the few cases of herbivory observed, small semicircles of tissue from the leaf margins appeared to have been chewed away. From these observations it appears that *Kalmiopsis leachiana* is well protected against possible herbivores. This is especially significant for an evergreen species in which foliage is available for attack over a long period of time.

During the initial summer field season collections of mature capsules yielded larvae of the hemipteran family Lygaeidea, the seedbugs. Additional capsule collections were made subsequent to this which contained more larvae, but adults were not found until June 11, 1977, in the Big Craggies Botanical Area, NE 1/4 Sec. 25, T37$^{1}/_{2}$S R12W, Curry County, Oregon. They were found crawling over developing capsules, presumably in the egg laying process. These were identified as belonging to the genus *Kleidocerys* near *ovalis* Barber. *Kleidocerys ovalis* is known from *Rhododendron*. Identification was made through the courtesy of Dr. J.D. Lattin, Department of Entomology, Oregon State University. Insects were deposited in the insect collection of Oregon State University. Dates and sites of collection of larvae of this species are listed in Table 37.

Mites

In addition to the seed-eating bugs, mites were also inadvertently collected with capsules. The sites and dates of collection are also listed in Table 37. These were identified by Dr. G.W. Krantz of the Department of Entomology of Oregon State University as belonging to the genus *Trichoribates*, near *striatus* Hammer of the Oribatidae of the family Ceratozetidae. No positive species identification can be made at the present. Interestingly enough, sites of mite collection are mutually exclusive of those where lygaeid bugs were collected.

Mites are suspected to be nectar feeders in *Rhododendron* (Stevens, 1976) and known to be so for two members of the Vaccinioideae, *Mailearia glabra* and *Cavendishia smithii* (Colwell, 1973).

Table 37. Site and date of collection of suspected *Kalmiopsis* seed predators.

Site	*Trichoribates* sp.	*Kleidocerus* sp.	Date
Bradley Indian Cave	X		7/19/76
Conway Creek	X		7/20/76
Valen Lake	X		7/26/76
East West Ridge		X	7/27/76
Rock of Taurus		X	8/12/76
Vulcan Lake	X		8/12/76
Pine Creek		X	8/26/76
Bailey Mountain	X		8/29/76
Limpy Rock		X	1/20/77
Four Ladies' Rock		X	1/20/77
Limpy Rock		X	5/14/77
Rattlesnake Creek		X	5/21/77
Big Craggies		X	6/17/77

For the latter two species, mites are dispersed from flower to flower on the bills of pollinating hummingbirds. The mites in both cases belong to the family Amerosiidae, whose members are exclusively nectar and pollen feeders. Mites were not observed on live flowers or herbarium specimens of Kalmiopsis leachiana. It is more likely that they are possible seed feeders, since they were only found to be associated with seed-containing capsules. The possibility exists that they may as well be dispersed from plant to plant by pollinators.

Phytochemistry

The low incidence of herbivory on foliage of Kalmiopsis prompted an initial investigative study of possible secondary compounds concentrated in the leaves of Kalmiopsis which might deter feeding. Previously, leaves of seven ericaceous species, all known to be poisonous to humans, had been analyzed for the presence of grayanotoxins I, II, and III (Constantine, Sheth, and Catalfomo, 1967). The grayanotoxins (acetylandromedol) are a set of related compounds known to be family specific to the Ericaceae (Hegenaurer, 1966). For those species analyzed, Rhododendron albiflorum, R. macrophyllum, R. occidentale, Kalmia polifolia var. microphylla, and K. polifolia var. polifolia were found to contain in their leaves grayanotoxin I. This compound was absent in the leaves of Ledum *glandulosum* and *Menziesia ferruginea*. None of the seven species contained grayonatoxins II and III. Results of analysis of leaves of *Kalmiopsis leachiana* showed an absence of all three grayanotoxins.

SUMMARY AND CONCLUSIONS

Kalmiopsis leachiana is a low-growing shrub and monotypic member of the Ericaceae. Its nearest affinities are with the genus *Rhodothamnus*, whose two species have relictual distributions in the eastern Alps of Europe and two mountain summits in northeastern Turkey. *Kalmiopsis* is a long-lived, slow-growing plant which is capable of exceeding 60 years in age. It blooms in the spring from May to June, with new vegetative growth taking place at approximately the same time. Capsules are mature and begin to dehisce in August. Seeds are numerous and very minute, suggesting that wind and gravity are the main dispersal agents.

Kalmiopsis leachiana is restricted in its present distribution to two separate geographical areas in southwestern Oregon. It is found in the Siskiyou Mountains in a small area of the Upper Chetco and Lower Illinois River drainages, 30 km to 57 km from the Pacific Ocean. A much smaller population is restricted to local rock outcrops in the North Umpqua River Valley in the Southern Cascade Mountains, 167 km to the northeast. Distribution of single populations within these two geographical areas has been compiled and mapped, with the investigation directed towards relating the distribution of *Kalmiopsis* with the environment it now occupies. Specific areas of study focused on seed germination, soil moisture stress relationships, seedling growth and establishment, the nature of the associated vegetation, floral ecology, and plant-herbivore interactions.

Vegetation associated with *Kalmiopsis leachiana* was sampled intensely, since it represents in part the biotic environment in which *Kalmiopsis* occurs and indirectly reflects the abiotic environment. Through combined analysis by manual-visual association table methods and subsequent two-dimensional reference stand ordination using the computer program SIMORD, three major vegetation units were established. One unit consisted of vegetation sampled from low elevation stands (300 to 600 m) in the Siskiyou Mountains. These stands exhibit the greatest species diversity (species numbers per stand) compared to the other two vegetation units. Four major strata were represented in this vegetation. A conifer layer dominated by *Pseudotsuga menziesii* and *Pinus lambertiana,* and a shorter, broadleaf evergreen sclerophyll tree layer consisting of *Quercus chrysolepis* and *Lithocarpus densiflora*, composed the overstory canopies. Underneath a diverse but mostly evergreen shrub layer was dominated by *Vaccinium ovatum*, *Kalmiopsis leachiana*, and *Gaultheria shallon*. There was no dominant and everpresent set of herb species, but as a group the herbs represented over one-half of the total associated species in these stands.

The second vegetation unit could be characterized physiognomically by the loss of the broadleaf sclerophyll tree layer. These stands occurred at higher elevations in the Siskiyou Mountains (over 900 m). In this second vegetation unit *Quercus chrysolepis* and *Lithocarpus densiflora* are replaced by *Q. vaccinifolia* and a dwarfed form of *L. densiflora*, respectively, as the major shrub dominants. For intermediate elevations there is seen a transition of growth form in these two species, as well as in overall species composition and physiognomy of the vegetation itself.

For higher elevation Siskiyous plots, the conifer canopy is more diverse in species composition, but still dominated by *Pseudotsuga menziesii* and *Pinus lambertiana*. The number of of evergreen shrub species increases over that of deciduous shrubs. Besides *Q. vaccinifolia* and *Lithocarpus*, *Kalmiopsis*, *Rhododendron macrophyllum*, *Quercus sadleriana*, *Arctostaphylos canescens*, and *Vaccinium parvifolium* are the major shrub stratum species. A wide variety of topographic positions, parent material types, and overall stand diversities are represented at high elevations. These sites include very mesic and cool Brewer spruce forests, fire-associated sclerophyll shrub associations, mesic ultramafic stands, and ridgeline and summit rock outcrop asspcoations.

The third and last major vegetation unit represents stands associated with *Kalmiopsis* rock outcrops in the Southern Cascades.

Here the overstory canopy dominates the vegetation spectrum to a much larger degree. Average total DBH is greater than for the two Siskiyous vegetation units. As a result the understory shrub layer is reduced in species composition, cover, density, and height. Pseudotsuga and Pinus lambertiana still dominate the conifer layer. In addition, Tsuga heterophylla, a species relatively intolerant of moisture stress, is important in some stands. The shrub layer is composed mainly of Gaultheria shallon, Berberis nervosa, and Rhododendron macrophyllum. The herb layer is much less diverse than in either of the other two vegetation units.

Kalmiopsis is found on soils of a number of different parent material types. In the Southern Cascades, the rock of the outcrops on which it grows is silicified quartz, and the soil of the surrounding forest is of metavolcanic origin. For the Siskiyou Mountains, the most common parent material types are gabbro and metagabbro. In a few instances, it was found on ultramafic parent materials but only in very mesic streamside and seepage locations. This low frequency on ultramafic soils is correlated with low seed germination, high seedling mortality, and lowered growth on the same soil in the greenhouse.

Chemically the soils derived from the range of soil types represented are different and their particular nutrient composition and cation exchange capacity suggest a connection with the frequency with which Kalmiopsis occurs on them. Definitive statements are difficult to make for present chemical analysis methods fall short of measuring actual availability of soil elements to plants (Waring, 1975). Kalmiopsis appears to be restricted from soils which are more "fertile" in chemical composition and structure, especially those derived from metavolcanics and diorite. Though Kalmiopsis is able to flourish in these more "fertile" soils in greenhouse experiments, it is hypothesized that the higher vegetation density and coverage on these soils excludes this species. Within its distribution in the Siskiyou Mountains, Kalmiopsis is absent from an entire geological formation, the Dothan Formation, which is of metavolcanic origin and has much denser vegetation than the surrounding geologic formations dominated by gabbro and serpentine.

Conclusions concerning comparative climates between major Kalmiopsis populations and within each separate distribution are limited because of the lack of on-site environmental data. Data from weather stations in the general vicinity of Kalmiopsis populations show that the climate is cooler for the Southern Cascades populations than those in the Siskiyous, with a resultant shorter growing season. Related to this cooler climate may be the significantly smaller seed weight and size for the Southern Cascades populations. It is hypothesized that the higher summer temperature in the Siskiyous increases the probability of seedlings being exposed to high moisture stress. One may speculate that larger seeds produce larger seedlings that are likely to be more resistant to drought.

For Kalmiopsis populations in the Siskiyou Mountains, the effects of proximity to the Pacific Ocean are seen in the species' distribution. With increasing distance from the ocean, absolute and relative daily changes in the temperature increase, while humidity, snowfall and snowpack, and total annual rainfall decrease. The result is that atmospheric demand is higher farther inland and there is a limitation on growth due to high moisture stress levels in the summer. Those plants which are not adapted to high stress levels, either through simple toleration, as in the case of Arctostaphylos nevadensis (Hickman, 1970), or through the ability to maintain low internal xylem tension despite dry environmental conditions, are physiologically excluded.

Kalmiopsis leachiana is found in the western portions of the Siskiyou Mountains where atmospheric demand as affected by temperature and humidity level is kept relatively low by moisture-laden maritime breezes. Within its distribution, and excluding those stands located at low elevations in the river canyons, Kalmiopsis is restricted to north-trending slopes. Here again moisture stress is less likely to be as high as on south-facing xeric slopes during the summer drought, the limiting period in the climate of the Pacific Northwest. Pressure chamber measurements of moisture stress levels along a moisture gradient suggest that Kalmiopsis is restricted to more mesic slope positions because of at least three factors. It appears to show a physiological intolerance of high stress, a condition which leads to early stomatal closure and consequent lowered growth during the summer season. It has a limited capacity to recover overnight from the previous day's high level of moisture stress compared to sympatric shrub species distributed throughout the extent of the moisture gradient. And in addition, for Kalmiopsis there is an absence of adapted morphological structure such as vertical leaf orientation common to more tolerant species. This adaptation is known to reduce heat load and thus the necessity for higher rates of transpiration for leaf cooling.

In those low elevation stands in the Siskiyou Mountains at or near the canyon edges of the Chetco and Illinois Rivers, Kalmiopsis occurs on south-facing slopes. Here there is an increase in the density of the overstory canopy associated with the occurrence of a broadleaf sclerophyll tree layer. It would be expected from evidence of direct observation that the north-facing slopes along the canyon bottoms would support a richer and denser canopy than on adjacent, more xeric sites. Kalmiopsis is restricted to more exposed and south-facing slopes at low elevation where vegetation is not as dense for both the overstory and shrub canopies. With increase in elevation and a movement away from the influence of the river canyons, there is a loss of the broadleaf trees and a resulting increase in light available to the understory. High elevation *Kalmiopsis* locations are much more numerous, probably because of lower levels of competition for light, water, and nutrients.

Kalmiopsis in the Southern Cascade Mountains represents the extreme mesic end of vegetation types in which it occurs. The overstory canopy density, as measured by total DBH, is on average higher than for sampled Siskiyous stands. This increase in overstory density is correlated with an observed dominance of the microsite environment, resulting in cooler temperatures and lower temperature extremes in general, lower light intensities, and a decrease in the density of the shrub layer. Here *K. leachiana* is restricted to exposed rock outcrops of point locations of silicification in the surrounding metavolcanic rock parent material. It is only these almost competition-free habitats which provide a suitable habitat.

Seed germination tests and seedling growth experiments have shown that surrounding soils of Southern Cascades populations are not inhibitory to growth. Thus *Kalmiopsis* is not restricted to rock outcrops for that reason. The only site where it does grow on the ground in the North Umpqua River area is in a very open and exposed stand of *Pinus attenuata*. Here fire and soil type have produced a microclimate which has high understory light level, temperature, and temperature extremes, and is low in understory growth. There are very few species adapted to this particular situation in which soil depth is shallow, stone content is high, and moisture-holding capacity and organic content of the soil are very low. Here again, compared to the surrounding forest, competition for light, water, and nutrients is much less.

Thus Kalmiopsis appears to be associated with those sites within its geographical distribution where competition is low. Various aspects of its seed and seedling ecology and growth morphology are adaptive to such a life strategy. Seeds are light and wind dispersed, allowing a high rate of colonization of scattered rock outcrops and open sites on talus slopes. The seeds are able to germinate under the low light conditions which probably exist in rock crevices. Crevices, fissures, and depressions in outcrops, and rock piles on talus slopes provide points of organic matter and moisture accumulation. Here competition for the developing seedling is practically nil. Seeds of Kalmiopsis were found to show the greatest germination percentage on moist organic matter. Growth on organic material collected from Limpy Rock, along with that for metavolcanic derived soils, was the highest for any soil type tested.

The seedling phase of the life cycle of Kalmiopsis leachiana is adapted to sites relatively free of competition, and seedling establishment is probably largely restricted to such habitats. Seeds germinate only after an incubation period of at least three weeks. Subsequent growth of seedlings is very slow compared to some associated species (Arctostaphylos canescens and A. patula). Small seed size, and resulting small seedlings, a long period of time in which seedlings are vulnerable to environmental stress, and low competitive ability due to slow growth are all factors which probably cause the low numbers of seedlings found in the field. The low reproductive success observed must be due to factors other than autotoxicity, as fresh leaf, litter, and leaf spray solutions did not decrease the germination amounts compared to controls.

The sites at which seedling establishment may occur normally provide little in the form of nutrients and water for future growth. The growth form of Kalmiopsis allows it to establish its own nutrient and water supply in an otherwise harsh environment. The highly clustered stems collect litter from sources above the plant, and breakdown of this material provides a continual source of nutrients. This material is high in moisture-holding capacity as well. The vigorous adventitious shoot sprouting is an aid in absorbing nutrients from the organic mat as well as preventing their loss from the plant itself.

There is indirect evidence which suggests that Kalmiopsis can withstand by forming root sprouts the high fire frequency of its present geographical range. Fires have occurred repeatedly in areas where it is now established. Through growth ring aging it was determined that plants now alive were present in at least one area before major fires burned through it. However, the heat level generated by an average fire would appear to be lethal to the seeds of this species.

Kalmiopsis is practically free of herbivore damage, so that predators and parasites do not appear to be a factor limiting its distribution. However, an insect species of the seed-eating family Lygaeidae may cause a significant amount of seed destruction. This bug is associated with developing and mature capsules. A single unidentified species of mite was also found in Kalmiopsis capsules. Many seeds are held within the capsule for a year or more, providing a dependable food source which could have favored the evolution of certain seed predators.

Kalmiopsis is distylous, this being the first reported case of heterostyly for the Ericaceae. In the open campanulate corolla, the morphological structure of the stamen ring and differential attraction of pollinators to partially open flowers may increase the amount of legitimate crossing. The morphological barrier to selfing and crossing between plants of the same form is probably strengthened by genetic self-incompatibility. Self-pollination in the greenhouse produced very reduced seed set compared to capsules collected from populations in the field. Pollen tetrads and the stigmatic surface do not show morphological differences between pin and thrum plants.

Populations of Kalmiopsis in the Southern Cascade Mountains differ from those in the Siskiyou Mountains in having larger leaves, seeds of smaller size and weight, lower rates of seed germination under tested conditions, larger corollas, and different stamen and style lengths in pin and thrum plants. In addition there is some slight evidence that seeds and seedlings of the two populations may differ in their ability to germinate and become established on the different soil types on which Kalmiopsis occurs. The differences observed between the two major populations of Kalmiopsis, especially the clearcut morphological differences, suggest that the disruption in gene flow between the two geographical areas may have occurred a relatively long time ago.

Kalmiopsis leachiana not only demonstrates very close morphological similarities with the genus Rhodothamnus, but their ecology and nature of distribution are closely related as well. Kalmiopsis frequently occurs near ridgelines where soil depth is shallow, or in areas of mixed parent material types. From a vegetation standpoint these represent intermediate zones between a dense vegetation where competition is great and a much more open situation. In the latter, vegetation is sparse and the principle factors influencing plant growth are abiotic. In turn R. chamaecistus often occurs in habitats of thin forest canopy and shrub associations of krummholtz between subalpine and lower alpine zones. They mark a transition from high forest canopy to areas of little or no overstory canopy where vegetation is scattered and sparse. Rhodothamnus chamaecistus, R. sessifolius, and K. leachiana all are able to exist in crevices and rock fissures and can produce stolons from which adventitious shoot production takes place. In addition, all three are very limited in distribution. Because they are so closely related it must be assumed that their ranges were once much more widespread and continuous than they are today, and their present restricted ranges represent only a fraction of past geographical affinities. In this sense they are examples of depleted species of Stebbins (1942).

Although there are no fossil records of Kalmiopsis and fossil pollen of the Ericaceae is difficult to identify at the generic level (Hansen, 1947), K. leachiana may have been present in the Pacific Northwest as early as the Miocene. Fossils of Rhododendron, which is considered to be closely related to Kalmiopsis and Rhodothamnus, are known from Oregon and Washington as early as that period (Wolfe, 1969). Its present restricted distribution is perhaps then the result of climatic changes which occurred during Pleistocene glaciation and the xerothermic period following (Detling, 1968).

BIBLIOGRAPHY

Baker, H.G. 1964. Variation in style length in relation to outbreeding in Mirabilis (Nyctaginaceae). Evol. 18:507-512.

________________. 1972. Seed weight in relation to environmental conditions in California. Ecol. 53:997-1010.

Baldwin, E.M. 1976. Geology of Oregon. Corvallis, OSU Bookstores Inc. 167 p.

________________. 1974. Eocene stratigraphy of southwestern Oregon. Ore. Dept. Geo. and Min. Ind. Bull. 83. 40 p.

Baldwin, J.T., Jr. 1938. Chromosomes of Kalmiopsis. Rhodora 40:278-279.

Beaulieu, J.D. 1971. Geologic formations of western Oregon. Dept. of Geol. and Min. Ind. Bull. 70. 72 p.

Brady, N.C. 1974. The nature and properties of soils. 8th ed. New York, Macmillan. 639 p.

Brooks, H.C. and L. Ramp. 1968. Gold and silver in Oregon. Ore. Dept. Geo. and Min. Ind. Bull. 61. 337 p.

Butler, G.M. and G.S. Mitchell. 1916. Preliminary survey of the geology and mineral resources of Curry Co., Oregon. Min. Resources, Ore. 2:1-132.

Callan, N.W. 1971. An investigation of the floral biology of Kalmiopsis leachiana (Hend.) Rehder. M.S. thesis. Ashland, Southern Oregon College. 41 numb. leaves.

Coleman, R.G. 1972. The Colebrooke Schist of southwestern Oregon and its relation to the tectonic evolution of the region. U.S. Geol. Survey Bull. 1339. 61 p.

Colwell, R.H. 1973. Competition and coexistence in a simple tropical community. Amer. Nat. 107:737-750.

Constantine, G.H., Jr., K. Sheth, and P. Catalfomo. 1967. Grayanotoxin I. Occurrence in additional Ericaceae species. J. Pharm. Sci. 56:1518-1519.

Copeland, H.F. 1943. A study, anatomical and taxonomic, of the genera of the Rhododendroideae. Am. Midl. Nat. 30:533-625.

Cox, H. T. 1948. Studies in the comparative anatomy of the Ericales. I. Ericaceae - subfamily Rhododendroideae. Am. Midl. Nat. 39:220-245.

Crowe, L.K. 1964. The evolution of outbreeding in plants. I. The angiosperms. Heredity 19:435-457.

Dammon, A.W.H. 1971. Effect of vegetation changes on the fertility of a Newfoundland forest site. Eco. Mono. 41:253-270.

Darlington, C.D. 1958. Evolution of genetic systems. 2nd ed. Oliver and Boyd, London and Edinburgh.

Darwin, C. 1877. Different forms of flowers in plants of the same species. London. 352 p.

Daubenmire, R. 1974. Plants and environment. John Wiley and Sons, New York. 422 p.

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

Davis, P.H. 1962. *Rhodothamnus sessifolius*. Hoo. Icones. Plant 36: tabula 3575.

Detling, L.E. 1968. Historical background of the flora of the Pacific Northwest. Oregon Museum of Nat. Hist. Bull. 13. 57 p.

Dick-Peddie, W.A. and W.H. Moir. 1970. Vegetation of the Organ Mountains, New Mexico. Colo. State Univ. Range Ser. Dept. Sci. Ser. 4. 28 p.

Diller, J.S. 1902. Topographic development of the Klamath Mountains. U.S. Geol. Survey Bull. 196:1-69.

Drude, D. 1889. Ericaceae. In: A. Engler and K. Prantl. Nat. Pflanzenfamilien. 2nd ed. Berlin 12.

Duhlberger, R. 1973. Distyly in *Linum pubsecens* and *L. mucronatum*. Bot. J. Linn. Soc. 17:349-351.

Duncan, W.H. and D.W. Dejong. 1964. Taxonomy and heterostyly of North American *Gelsemium* (Loganiaceae). Sida 1:341-557.

Emmingham, W.H. 1973. Lower Illinois River forest ecosystem study. U.S. Dept. of Agriculture, Forest Service, Siskiyou National Forest. 74 p.

Flint, R.F. and R. Skinner. 1974. Physical geology. John Wiley and Sons, New York. 454 p.

Florence, R.G. and R.L. Crocker. 1968. Analysis of blackbutt (*Eucalyptus pilulans* Sin.) seedling growth in a blackbutt forest soil. Ecol. 42:670-679.

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

Franklin, J.F., C.T. Dyrness, and W.H. Moir. 1970. A reconnaissance method for forest site classifications. Shinrin Richi 12:1-14. Meguro, Tokyo, Japan.

Gates, D.M. 1966. Transpiration and energy exchange. Quant. Rev. Biol. 41:353-364.

Gerdemann, J.W. 1972. *Kalmiopsis leachiana*. Quarterly Bull. Amer. Rhododendron Soc. 20:199-200.

Goff, F.G. and G. Cottam. 1967. Gradient analysis--the use of species and synthetic indices. Ecol. 48:793-806.

Grant, K.E. 1973. Summary of snow survey measurements for Oregon. USDA Soil. Cons. Serv. 564 p.

Gratkowski, H. 1960. Brush seedlings after controlled burning of brushlands in southwestern Oregon. J. Forest. 59:885-888.

________________. 1961. Brush problems in southwestern Oregon. USDA Forest Serv. Pac. NW Range Exp. Sta. Portland, Oregon. 53 p.

________________. 1962. Heat as a factor in germination of seeds of *Ceanothus velutinus* var. *laevigatus* T. & G. Ph.D. thesis. Corvallis, Oregon State University. 131 numb. leaves.

Gregg, W.R. 1936. Climatic summary of the United States. Sec. 3 - western Oregon. USDA Weather Bureau. U.S. Environmental Data Service, 1957.

Haas, R.H. and J.D. Dodd. 1972. Water-stress patterns in honey mesquite. Ecol. 53:674-680.

Haefner, H.E. 1912. Chaparral areas of the Siskiyou National Forest. Soc. Amer. Foresters Proc. 7:82-95.

__________________. 1975. Reminiscence of an early forester. Ore. Hist. Quart. 76:39-88.

Hagerup, O. 1928. Morphological and cytological studies of Bicornes. Dansk Bot. Ark. 6:1-26.

Hansen, H.P. 1947. Post-glacial forest succession, climate and chronology in the Pacific Northwest. Trans. Amer. Philo. Soc. 37:1-130.

Harborne, J.B. and P.A. Williams. 1973. A chemotaxonomic survey of flavanoids and single phenols in leaves of the Ericaceae. J. Linn. Soc. Bot. 66:37-54.

Harlow, H.M. and E.S. Harrar. 1968. Textbook of dendrology. McGraw-Hill. 512 p.

Hawk, G.M. 1972. Forest vegetation and soil of terraces and floodplains along the McKenzie River, Oregon. M.S. thesis. Corvallis, Oregon State University. 188 numb. leaves.

Heath, G.H. and L.C. Luckwill. 1938. The rooting system of heath plants. J. Ecol. 26:331-352.

Hegi, G. 1909-1931. Illustrierte Flora von Mittel-Europa. 7 vols. Carl Hanser, Munich.

Hegnauer, R. 1966. Chemotaxonomie der Pflanzen. Birkhäuser, Bagel. 551 p.

Henderson, L.F. 1931. New plants from Oregon. Rhodora 34:203-206.

Hess, H.E., E. Landolt, and R. Hirzel. 1970. Flora der Schweiz: Nymphaceae bis Primulaceae. Vol. 2. Birkhäuser Verlag, Basel. 912 p.

Hickman, J.C. 1968. Disjunction and endemism in the flora of the central western Cascades: an historical and ecological approach to plant distribution. Ph.D. thesis. Eugene, University of Oregon. 345 numb. leaves.

__________. 1970. Seasonal course of xylem sap tension. Ecol. 51:1052-1056.

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

Holtz, P.E. 1971. Plutonic rocks of the Klamath Mountains, California and Oregon. U.S. Geol. Sur. Prof. Paper 684-B.

Hooker, J.D. 1876. Ericaceae. In: G. Bentham and J.D. Hooker. Genera Plantarum. 2.2. London.

Hsiao, T.S. 1973. Plant response to water stress. Ann. Rev. Plant Physio. 24:519-570.

Juday, G.P. 1977. The location, composition, and structure of old-growth forest of the Oregon Coast Range. Ph.D. thesis. Corvallis, Oregon State University. 206 numb. leaves.

Kauffman, M.D. and E.H. Gardner. 1976. Methods of soil assays used in the soil testing laboratory at Oregon State University. Special Report, 321, Ag. Exp. Sta. Corvallis, Oregon State University. 39 p.

Kays, M.A. 1970. Western Cascades volcanic series, South Umpqua Falls region, Oregon. OREBIN 32:81-94.

Lang, L.F. 1969. Asplenium septentrionale in Oregon. Amer. Fern Jour. 59:45-57.

Leiberg, J.B. 1900. Cascade Range and Ashland Forest reserves and adjacent regions. U.S. Geol. Sur. 21st Annual Rpt. 1899-1900. Pt. 5, Forest reserves, 211-498.

Mansfield, H.R. 1972. Kalmiopsis Wilderness Area map. Siskiyou Nat. For. Ser. Publ. 796-033.

Martin, R.E., R.L. Miller, and C.Y. Cushwa. 1975. Germination response of legume seeds subjected to moist and dry heat. Ecol. 56:1441-1445.

McNaughton, S.E. 1968. Autotoxic feedback in relation to germination and seedling establishment and growth in Typha latifolia. Ecol. 49:367-369.

Mitchell, R.J. 1972. An analysis of the vegetation of the Abbott Creek Natural Area, Oregon. Ph.D. thesis. Corvallis, Oregon State University. 132 numb. leaves.

Muhlcahy, D.L. 1965. Heterostyly within Nivenia (Iridaceae). Brittonia 17:349-351.

Mueller-Dombois, E. and H. Ellenberg. 1974. Aims and methods of vegetation ecology. John Wiley and Sons, New York. 547 p.

Mulligan, B.O. 1973. Kalmiopsis leachiana. Quart. Bull. Alp. Gard. Soc. 41:131-134.

Munz, P.A. and D.D. Keck. 1959. A California flora. Univ. Calif. Press, Berkeley. 1681 p.

Noggle, E.R. and G.S. Fritz. 1976. Introductory plant physiology. Prentice-Hall, Inc., Englewood Cliffs, N.J. 688 p.

Ornduff, R. 1969. Ecology, morphology and systematics of Jepsonia (Saxifragaceae). Brittonia 21:286-298.

Peck, D.L., A.B. Griggs, H.G. Schlicker, G.G. Wells, and H.M. Dole. 1964. Geology of the central and northern parts of the western Cascade Range in Oregon. U.S. Geol. Surv. Prof. Paper 449.

Peck, M.E. 1961. A manual of higher plants of Oregon. 2nd ed. Binfords and Mort, Portland, Oregon.

Procter, J. and S.R.J. Woodwell. 1975. Ecology of serpentine soils. Adv. in Eco. Res. 9:255-366.

Quick, C.R. 1935. Notes on the germination of Ceanothus seeds. Madroño 3:135-140.

__________________. 1959. Ceanothus seeds and seedlings on burns. Madroño 15:79-81.

Quick, C.R. and A.S. Quick. 1961. Germination of Ceanothus seeds. Madroño 16:23-30.

Ramp, L. 1960. The Quartz Mountain silica deposit, Oregon. OREBIN 22:109-114.

______________, 1975. Geology and mineral resources of the Upper Chetco Drainage area, Oregon. Dept. Geol. and Min. Ind. Bull. 88. 47 p.

Rehder, A. 1932. Kalmiopsis, a new genus of Ericaceae from Northwest America. J. Arnold Arb. 13:31-35.

Romancier, R.M. 1970. Ecology of the seedling establishment of Rhododendron maximum L. in the Southern Appalachians. Ph.D. thesis. Durham, N.C., Duke University. 189 numb. leaves.

Salisbury, E.S. 1942. The reproductive capacity of plants; studies in quantitative biology. Bell, London.

Schollander, P.F., H.T. Hammel, E.D. Bradstreet, and E.A. Hemmingsen. 1965. Sap pressure in vascular plants. Science 148:339-346.

Schoch-Bomer, H. 1934. Heterostylie Problem: Griffelbeschaffenheit und Pollenschaubwachsten bei Fagopyron esculentum. Planta 22:149-152.

Schultze-Motel, W. 1964. Ericales. In: H. Melchior (ed.). A. Engler's Syllabus der Pflanzenfamilien. 2nd ed. Berlin.

Slayter, R.O. 1961. Internal water balance of Acacia aneura F. Muell. in relation to environmental conditions. p. 137-146. In: Plant-water relationships in arid and semi-arid conditions. Proc. Madrid Symp. Paris, UNESCO.

Stebbins, G.L., Jr. 1942. The genetic approach to problems of rare and endemic species. Madroño 6:210-226.

______________. 1971. Adaptive radiation of reproductive characteristics in angiosperms. II. Seeds and seedlings. Ann. Rev. Eco. Syst. 2:237-260.

Stebbins, G.L. and J. Major. 1965. Endemism and speciation in the California flora. Ecol. Mono. 35:1-35.

Stevens, P.F. 1971. A classification of the Ericaceae: subfamily and tribes. J. Linn. Soc. Bot. 64:1-53.

________________. 1976. The altitudinal and geographical distribution of flower types in Rhododendron, section Vireya especially in the Papusian species, and their significance. Bot. J. Linn. Soc. 72:1-33.

Steward, A.N. 1957. Kalmiopsis and other botanical items from the Siskiyou region. Mazama 3:1-4.

Sucoff, E. 1972. Water potential in red pine: soil moisture, evapo-transpiration, crown position. Ecol. 53:681-686.

USDA Weather Bureau. 1955-1975. Climatological data of the United States: Oregon. Annual Summary.

________________. 1955-1975. Climatological data of the United States: Precipitation data from storage-gauge stations.

Vuilleumier, B.S. 1967. The origin and evolutionary development of heterostyly in the angiosperms. Evol. 21:210-226.

Walker, R.B. 1954. Ecology of serpentine soils. II. Factors affecting plant growth on serpentine soils. Ecol. 35:259-266.

Waring, R.H. 1969. Forest plants of the Eastern Siskiyous: their environmental and vegetational distribution. Northwest Sci. 43:1-17.

Waring, R.H. and B.D. Cleary. 1967. Plant moisture stress: evaluation by pressure bomb. Science 155:1248-1254.

Waring, R.H., W.H. Emmingham, and S.W. Running. 1971. Environmental limits of the endemic Brewer spruce, Picea breweriana. Can. J. Bot. 53:1599-1613.

Webb, L.J., J.G. Tracy, and K.P. Haydock. 1967. A factor toxic to seedlings of the same species associated with living roots of the non-agregarious subtropical rain forest tree Grevillea robusta. J. Appl. Ecol. 84:13-25.

Wells, F.G. and G.W. Walker. 1953. Geology of the Galice quadrangle, Oregon. U.S. Geological Survey in cooperation with the Oregon Dept. Geology and Mineral Industries. (Map)

Wells, F.G., P.F. Holtz, and F.W. Cater, Jr. 1949. Preliminary description of the geology of the Kerby quadrangle, Oregon. Oregon Dept. Geol. and Mineral Indus. Bull. 40. 23 p. and geol. map.

White, C.D. 1971. Vegetation-soil chemistry correlations in serpentine ecosystems. Ph.D. thesis. Eugene, University of Oregon. 232 numb. leaves.

Whitmore, F.W. and R. Zahner. 1967. Evidence for direct effect of water stress on tracheid cell wall metabolism in pine. Forest Sci. 13:397-400.

Whittaker, R.H. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. Ecol. Monogr. 30:279-338.

__________________. 1961. Vegetation history of the Pacific coast states and the "central" significance of the Klamath Region. Madroño 16:5-22.

__________________. 1967. Gradient analysis of vegetation. Biol. Rev. 42:207-264.

Wolfe, J.A. 1969. Neogene floristic and vegetational history of the Pacific Northwest. Madroño 20:32-110.

APPENDICES

APPENDIX I. Location and relevant data of sampled populations of <u>Kalmiopsis</u> <u>leachiana</u>.

Site name	Symbol	Location	Elevation	Aspect	Slope	Date sampled
York Creek	YCK	NW 1/4 Sec. 1, T37S, R10W, Josephine Co., Oregon	430 m (1400 ft)	330°	32° (68%)	6/26/76
Collier's Bar	CBR	west Sec. 32, T36S R11W, Curry Co., Oregon	305 m (1000 ft)	30°	31° (60%)	7/23/76
Pine Creek	PCK	NE 1/4 Sec. 27, T36S R10W, Josephine Co., Oregon	610 m (2000 ft)	130°	24° (46%)	8/26/76
Chetco Crossover	CCR	NE 1/4 Sec. 28, T38S R10W, Kalmiopsis Wilderness Curry Co., Oregon	430 m (1400 ft)	135°	25° (45%)	9/ 1/76
Rattlesnake Creek	RCK	south center Sec. 21, T38S R10W, Kalmiopsis Wilderness Curry Co., Oregon	430 m (1400 ft)	112°	26° (48%)	9/ 1/76
Rattlesnake Creek Slope	RCS	south center Sec. 21, T38S R10W, Kalmiopsis Wilderness Curry Co., Oregon	550 m (1800 ft)	344°	34° (68%)	9/ 1/76
Fire Heaven	FHV	center Sec. 17, T38S R10W, Kalmiopsis Wilderness Curry Co., Oregon	365 m (1200 ft)	322°	33° (63%)	9/ 3/76
Valen Lake	VLK	SE 1/4 Sec. 27, T38S R11W, Kalmiopsis Wilderness Curry Co., Oregon	1070 m (3500 ft)	22°	45° (98%)	7/26/76

(Continued on next page)

Appendix I (Continued)

Site name	Symbol	Location	Elevation	Aspect	Slope	Date sampled
Burnt Forest	BFT	SE 1/4 Sec. 27, T38S R11W, Kalmiopsis Wilderness Curry Co., Oregon	1100 m (3600 ft)	40°	40° (85%)	7/26/76
East West Ridge	EWR	center Sec. 34, T38S R11W, Kalmiopsis Wilderness Curry Co., Oregon	1070 m (3500 ft)	270	40 (85%)	7/27/76
Kurt's Reading Hole	KRH	center Sec. 26, T38S R11W, Kalmiopsis Wilderness Curry Co., Oregon	1070 m (3500 ft)	10	30 (52%)	8/11/76
Rock of Taurus	ROT	NW 1/4 Sec. 26, T38S R11W, Kalmiopsis Wilderness Curry Co., Oregon	975 m (3200 ft)	76	31 (59%)	8/12/76
Fawn Lily Slope	FLS	west center Sec. 2, T39S R10W, Kalmiopsis Wilderness Curry Co., Oregon	1100 m (3600 ft)	350	22 (51%)	8/28/76
west slope Bailey Mountain	WBM	center Sec. 4, T39S R10W, Kalmiopsis Wilderness Curry Co., Oregon	1100 m (3600 ft)	20	43 (90%)	8/29/76
East Bailey Cabin	EBC	west center Sec. 3, T39S R10W, Kalmiopsis Wilderness Curry Co., Oregon	975 m (3200 ft)	360	24 (45%)	8/29/76

(Continued on next page)

Appendix I (Continued)

Site name	Symbol	Location	Elevation	Aspect	Slope	Date sampled
north slope Bailey Mountain	NBM	west center Sec. 4, T39S R10W, Kalmiopsis Wilderness Curry Co., Oregon	975 m (3200 ft)	360°	24° (45%)	8/30/76
Dried Water Hole	DWH	NE 1/4 Sec. 4, T39S R10W, Kalmiopsis Wilderness Curry Co., Oregon	915 m (3000 ft)	20	33 (63%)	8/31/76
Sewell Spring	SSP	center Sec. 33, T38S R10W, Kalmiopsis Wilderness Curry Co., Oregon	975 m (3200 ft)	43	21 (38%)	8/31/76
Sourdough Flat	SDF	SW 1/4 Sec. 11, T38S R10W, Kalmiopsis Wilderness Curry Co., Oregon	945 m (3100 ft)	160	7 (13%)	9/ 4/76
Gold Basin	GOB	S 1/2 Sec. 33, T37S R10W, Kalmiopsis Wilderness Curry Co., Oregon	1220 m (4000 ft)	0	0	5/22/77
Cookie Drop	CKD	SW 1/4 Sec. 36, T37S R12W, Big Craggies Botanical Area Curry Co., Oregon	1190 m (3900 ft)	350	8 (17%)	6/ 8/77
Big Craggie	BCR	south center Sec. 27, T37S R12W, Big Craggies Botanical Area Curry Co., Oregon	1160 m (3800 ft)	225	25 (40%)	6/14/77

(Continued on next page)

Appendix I (Continued)

Site name	Symbol	Location	Elevation	Aspect	Slope	Date sampled
Morrison's Lament	MOL	E 1/2 Sec. 25, T37S R12W, Big Craggies Botanical Area Curry Co., Oregon	1040 m (3400 ft)	340°	28° (45%)	6/17/77
Dog Creek	DCK	W 1/2 Sec. 7, T26S R2E, Douglas Co., Oregon	915 m (3000 ft)	155	29 (35%)	7/15/76
Four Ladies' Rock	FLR	SW 1/4 Sec. 6, T26S R2E, Douglas Co., Oregon	1295 m (3640 ft)	200	25 (47%)	7/18/76
Bradley Indian Cave	BIC	SE 1/4 Sec. 7, T26S R2E, Douglas Co., Oregon	865 m (2800 ft)	345	34 (66%)	7/19/76
Copeland Creek	CCK	NW 1/4 Sec. 13, T27S R2E, Douglas Co., Oregon	741 m (2400 ft)	210	25 (56%)	7/20/76
Limpy Rock	LPR	SW 1/4 Sec. 7, T26S R2E, Douglas Co., Oregon	1125 m (3640 ft)	190	31 (61%)	7/20/76
Knobcone Pine Ridge	PAR	NW 1/4 Sec. 9, T26S R2E, Douglas Co., Oregon	865 m (2800 ft)	250	33 (64%)	9/10/76
Ragged Ridge	RAR	east center Sec. 31, T25$^{1/2}$S R2E, Douglas Co., Oregon	1110 m (3600 ft)	94	30 (56%)	9/11/76

APPENDIX II

Partial checklist of vascular plant species associated with *Kalmiopsis leachiana*. Major vegetation unit in which a species was found to occur is reported. All taxonomy based on Peck (1961), unless otherwise specified by (M) for Munz and Keck (1959), or by (H) for Hitchcock and Cronquist (1973). (LS = low elevation Siskiyous stands; HS = high elevation Siskiyous stands; SC = Southern Cascades stands.)

	Polypodiaceae		
	Cheilanthes gracilima D. C. Eat.	Lace-fern	HS
	C. siloquosa Maxon	Oregon cliffbrake	HS
	Cryptogramma crispa (L.) R. Br. var. *acrostichoides* R. Br.) Clarke	Parsley-fern	LS
(H)	*Polypodium glycyrrhiza* D. C. Eat.	Licorice fern	LS, HS, SC
	Polystichum munitum (Kaulf.) Presl.	Western sword-fern	LS, HS, SC
	Pteridium aquilinum (L.) Kuhn var. *pubsecens* Underw.	Western braken	LS, HS, SC
	Selaginellaceae		
	Selaginella wallacei Hieron.	Wallace's selaginella	HS
	Taxaceae		
	Taxus brevifolia Nutt.	Western yew	LS, SC
	Pinaceae		
	Abies concolor Lindl.	White fir	HS, SC
	A. grandis Lindl.	Grand fir	SC
	Picea breweriana Wats.	Brewer spruce	HS
	Pinus attenuata Lem.	Knobcone pine	LS, HS, SC
	P. contorta Dougl.	Lodgepole pine	HS
	P. jeffreyi Murr.	Jeffrey pine	HS
	P. lambertiana Dougl.	Sugar pine	LS, HS, SC
	P. monticola Dougl.	Western white pine	LS, HS
	P. ponderosa Dougl.	Ponderosa pine	LS
(H)	*Pseudotsuga menziesii* (Mirb.) Franco	Douglas-fir	LS, HS, SC
	Tsuga heterophylla (Raf.) Sarg.	Western hemlock	SC
	Cupressaceae		
(H)	*Calocedrus decurrens* (Torr.) Florin.	Incense cedar	LS, HS, SC
	Chamaecyparis lawsoniana Parl.	Port Orford cedar	LS, HS
	Juniperus sibirica Burgsd.	Dwarf juniper	LS, HS
	Thuja plicata Donn.	Western red cedar	SC

(Continued on next page)

Appendix II (Continued)

Gramineae

Bromus vulgaris (Hook.) Shear	Narrow-leaved bromegrass	SC
Calamagrostis koeleroides Vas.	Tufted pinegrass	HS
Festuca californica Vas.	California fescue	LS
F. occidentalis	Western fescue	HS, SC
F. ovina	Sheep fescue	HS
F. rubra	Red fescue	HS, SC
(H) *Poa sandbergii*	Sandberg's bluegrass	HS
Trisetum canescens Buddl.	Tall trisetum	SC

Cyperaceae

Carex sp.	Sedge	HS
C. concinnoides Mack.	Northwestern sedge	HS

Juncaceae

Luzula campestris (L.) DC. var. *multiflora* (Ehr.) Celak.	Common woodrush	SC

Liliaceae

Allium falcifolium H. & A.	Sickle-leaved onion	LS
A. watsoni How.	Watson's onion	HS
Brodiaea sp.	Brodiaea	LS, SC
Disporum hookeri (Torr.) B. & H.	Hooker's fairy bells	LS, HS, SC
Erythronium sp.	Fawn lily	HS
Lilium bolanderi Wats.	Bolander's lily	LS, HS
Trillium ovatum Pursh.	Western trillium	HS
T. rivale Wats.	Brook trillium	HS
Smilacina racemose (L.) Desf.	False Solomon's seal	LS, HS, SC
(H) *S. stellata* (L.) Desf.	Star flowered Solomon's seal	HS, SC
Veratrum insolitum Jeps.	Siskiyou false hellebore	HS
Xerophyllum tenax (Pursh.) Nutt.	Beargrass	LS, HS, SC
Zigadenus micranthus Eastw.	Small flowered zigadenus	HS

Iridaceae

Iris chrysophylla How.	Slender-tubed iris	SC
I. thompsonii Foster	Thompson's iris	LS, HS

Orchidaceae

Corallorhiza maculata Raf.	Spotted coral root	SC
Goodyera oblongifolia Raf.	Giant rattlesnake plantain	LS, HS, SC
Habenaria unalaschensis (Spring.) Wats.	Short-spurred rein orchid	LS, HS, SC

Betulaceae

Corylus cornuta Marsh. var. *californica* (DC.) Sharp	Hazelnut	SC

(Continued on next page)

Appendix II (Continued)

Fagaceae

Castanopsis chrysophylla (Dougl.) A. DC.	Chinquapin	LS, HS, SC
Lithocarpus densiflora (H. & A.) Rehd.	Tan oak	LS, HS
Quercus chrysolepis Liebm.	Canyon oak	LS
Q. sadleriana R. Br.	Sadler oak	HS
Q. vaccinifolia Kell.	Huckleberry oak	LS, HS

Aristolochiaceae

Asarum hartwegii Wats.	Marbled wild ginger	HS, SC

Polygonaceae

Eriogonum nudum Dougl.	Naked eriogonum	LS
E. ternatum How.	Waldo eriogonum	HS

Portulacaceae

Montia parviflora (Moc.) Greene	Streambank spring beauty	HS
M. perfoliata (Donn.) How.	Miner's lettuce	SC

Caryophyllaceae

Arenaria macrophylla Hook.	Large-leaved sandwort	HS, SC

Ranunculaceae

Anemone deltiodea Hook.	Columbia wildflower	LS, SC
A. lyallii Butl.	Lyall's anemone	HS

Berberidaceae

Achlys triphylla (Smith) DC.	Vanilla-leaf	HS, SC
Berberis nervosa Pursh.	Oregon grape	HS, SC
B. pumila Greene	Dwarf western barberry	HS, SC
Vancouveria hexandra (Hook.) Morr. & Dcne.	Inside-out flower	LS
V. planipetala Calloni	Small inside-out flower	LS, HS

Lauraceae

Umbellularia californica Nutt.	California laurel	LS, HS

Fumariaceae

Dicentra formosa (Andr.) DC.	Western bleeding-heart	SC

Cruciferae

Streptanthus tortuosus Kell. var. *oblongus* Jeps.	Twisted streptanthus	LS

(Continued on next page)

Appendix II (Continued)

	Crassulaceae		
	Sedum laxum (Britt.) Berger	Lax stonecrop	HS
	S. spathulifolium Hook.	Broad-leaved stonecrop	HS, SC
	Hydrangeaceae		
	Philadelphus lewisii Pursh. var. *gordonianus* (Linell.) Jeps.	Western syringa	SC
	Whipplea modesta Torr.	Whipple vine	LS, HS, SC
	Rosaceae		
(H)	*Amelanchier alnifolia* Nutt.	Western serviceberry	LS, SC
	A. pallida Greene	Pale serviceberry	LS, HS
	Holodiscus discolor (Pursh.) Maxim.	Ocean spray	LS, HS, SC
	Rosa gymnocarpa Nutt.	Little wild rose	LS, HS, SC
	Rubus parviflorus Nutt.	Thimbleberry	LS
(H)	*R. ursinus* C. & S.	Pacific blackberry	LS, SC
	Leguminosae		
	Lathyrus californicus Wats.	California pea	LS
	L. polyphyllus Nutt.	Leafy pea	SC
	Psoralea physodes Dougl.	California tea	SC
	Thermopsis argentata (Greene) Jeps.	Silvery thermopsis	HS
	T. montana Nutt.	Mountain thermopsis	SC
	Polygalaceae		
	Polygala californica	California milkwort	LS
	Anacardiaceae		
	Rhus diversiloba	Poison oak	LS, HS
	Aceraceae		
	Acer circinatum Pursh.	Vine maple	SC
	A. macrophyllum Pursh.	Big-leaved maple	LS
	Rhamnaceae		
	Ceanothus pumilus Greene	Dwarf ceanothus	LS, HS
	Rhamnus californica Esch. var. *occidentalis* (How.) Jeps.	California coffee berry	LS, HS
	R. purshiana DC.	Cascara	SC
	Violaceae		
	Viola cuneata Wats.	Wedge-leaved violet	HS
	V. douglasii Steud.	Golden violet	HS

(Continued on next page)

Appendix II (Continued)

Viola glabella Nutt.	Smooth woodland violet	HS
V. lobata Benth.	Pine violet	LS, HS

Onagraceae

Oenothera oblongifolia		

Umbelliferae

Lomatium howellii (Wats.) Jeps.	Howell's desert parsley	HS
L. macrocarpum (Nutt.) C. & R.	Gray desert parsley	LS, HS
L. martindalei C. & R.	Few-fruited desert parsley	HS
Osmorhiza chilensis (Hook.) Arn.	Western sweet cicely	SC

Cornaceae

Cornus nuttallii Aud.	Western flowering dogwood	LS, HS, SC

Garryaceae

Garrya buxifolia Gray	Box-leaved garrya	LS, HS
G. fromontii Torr.	Bear brush	LS, SC

Ericaceae

Allotropa virgata T. & G.		
Arbutus menziesii Pursh.		
Arctostaphylos canescens Eastw.		
A. columbiana Piper		
A. nevadensis Gray		LS, HS, SC
A. patula Greene		HS
Chimaphila menziesii (R. Br.) Spreng	Little prince's pine	LS, HS, SC
C. umbellata (L.) Nutt. var. *occidentalis* (Rydb.) Blake	Western prince's pine	LS, HS, SC
Gaultheria ovatifolia Gray	Slender gaultheria	HS
G. shallon Pursh	Salal	LS, HS, SC
(H) *Ledum glandulosum* Nutt. var. *columbianum* (Piper) Hitchc.	Smooth labrador tea	HS
Leucothoe davisiae Torr.	Western leucothoe	HS
Pterospora andromedea Nutt.	Pine drops	HS
Pyrola picta J. E. Sm.	White-veined pyrola	LS, HS, SC
Rhododendron macrophyllum G. Don.	Western rhododendron	HS, SC
R. occidentale (T. & G.) Gray	Western azalea	LS, HS
Sarcodes sanguinea Torr.	Snow plant	HS
Vaccinium membranaceum Dougl.	Thin-leaved huckleberry	HS
V. ovatum Pursh	Shot huckleberry	LS, HS, SC
V. parvifolium J. E. Sm.	Red huckleberry	LS, HS, SC

Primulaceae

Trientalis latifolia Hook.	Broad-leaved starflower	LS, HS, SC

(Continued on next page)

Appendix II (Continued)

Gentianaceae		
Gentiana affinis Griseb.	Oblong-leaved gentian	HS
Apocynaceae		
Apocynum androsaemifolium L.	Spreading dogbane	LS, HS, SC
Polemoniaceae		
Collomia heterophylla Hook.	Varied-leaved collomia	SC
Phlox adsurgens Torr.	Woodland phlox	SC
P. diffusa Benth.	Spreading phlox	LS, HS
Scrophulariaceae		
Castilleja pruinosa Fern.	Frosted paintbrush	LS, HS
Collinsia torreyi Gray	Torrey's collinsia	LS
(H) *Nothochelone nemorosa* (Dougl.) Straw.	Woodland beard tongue	HS
Penstemon cardwellii How.	Cardwell's penstemon	HS
P. rupicola How.	Rock penstemon	HS
Synthyris reniformis Benth.	Snow-queen	SC
Orobanchaceae		
Boschniakia hookeri Walp.	Ground-cone	LS, HS
Rubiaceae		
Galium ambiguum Wight var. *siskiyouense* Ferris	Obscure bedstraw	LS, HS
G. bolanderi Gray	Bolander's bedstraw	LS
G. multiflorum Kell.	Many-flowered bedstraw	HS
G. triflorum Michx.	Fragrant bedstraw	LS
Caprifoliaceae		
Linnaea borealis L. var. *americana* (Forbes) Rehder	American twinflower	LS, HS, SC
Lonicera hispidula Dougl.	Hairy honeysuckle	LS
Symphoricarpos albus (L.) Blake	Snowberry	HS, SC
Campanulaceae		
Campanula prenanthoides Dur.	California harbell	LS
C. scouleri Hook.	Scouler's campanula	SC
Compositae		
Antennaria suffrutescens Greene	Shrubby everlasting	HS
Arnica cernuua How.	Nodding arnica	HS
A. parviflora Gray	Small-flowered arnica	LS, HS

(Continued on next page)

Appendix II (Continued)

(M)	*Aster brickellioides* Greene		LS, HS
	Cacaliopsis nardosmia Gray	Silver-crown	HS
	Erigeron foliosus Nutt. var. *confinis* (How.) Jeps.	Leafy erigeron	LS, HS
	Hieracium albiflorum Hook.	White-flowered hawkweed	LS, HS, SC
	Madia madioides (Nutt.) Greene	Woodland tarwood	SC
	Senecio canus Hook.	Gray senecio	HS

APPENDIX III

Cover and constancy (C) values for plant species of the three major vegetation units associated with *Kalmiopsis leachiana*. Values based on 375 m^2 samples plots, with total DBH given as the cover value for tree species. (++: species found within a macroplot but not in any microplot; +: species found in the vacinity of but not within a macroplot).

Low Elevation Siskiyou Vegetation:

	YCK	PCK	CCR	RCK	RCS	CBR	FHV	C(%)
Kalmiopsis leachiana	17.9	8.4	47.7	12.6	25.1	27.1	25.1	100.0
Lithocarpus densiflora	71.6	357.4	202.2	320.1	18.0	428.0	37.7	100.0
Rhamnus californica	1.3	0.2	1.8	2.1	0.3	0.2	0.4	100.0
Polystichum munitum	++	0.2	0.1	0.1	++	++	+	100.0
Disporum hookeri	0.3	++	++	++	0.1	++	0.6	100.0
Iris thompsonii	0.2	+	0.1	0.3	0.1	0.1	0.8	100.0
Lonicera hispidula	0.1	0.6	0.5	0.4	++	++	++	100.0
Pseudotsuga menziesii	95.3	267.5	89.8	162.4	115.5	85.2	52.4	100.0
Pinus lambertiana	40.2	87.5	23.5	66.4	79.1	55.3	38.2	100.0
Whipplea modesta	1.2	1.0	0.5	2.5		++	++	85.7
Vaccinium ovatum	9.2		4.2	23.3	1.4	19.9	8.2	85.7
Trientalis latifolia	0.2		0.1	++	0.1	++	+	85.7
Hieracium albiflorum		++	++	++	++	++	++	85.7
Rhus diversiloba	++	1.4	2.4	0.1		++	+	85.7
Arnica parviflora	++		++	0.1	0.1	+	0.2	85.7
Quercus chrysolepis	131.4	94.6	138.6	201.5	7.8	9.3		85.7
Cornus nuttallii	14.5	++	4.8	++	12.8	++		85.7
Vancouveria planipetala			++	1.8	++	++	++	71.4
Pteridium aquilinum	+	++	+	0.9			0.1	71.4
Amelanchier pallida			0.5	++	0.3	++	0.1	71.4
Galium ambiguum	++			+	+	0.1	++	71.4
Xerophyllum tenax	0.2		+		++	1.0	1.1	71.4
Arctostaphylos canescens				0.1	6.0	0.2	0.2	71.4
Gaultheria shallon	++	12.0	2.9	0.9		+		71.4

continued --

Appendix III (continued)

Low Elevation Siskiyou Vegetation:

	YCK	PCK	CCR	RCK	RCS	CBR	FHV	C(%)
Polypodium glycyrrhiza	++	++	++	++	++			71.4
Vaccinium parvifolium				2.7	2.1	0.1	0.3	57.1
Rosa gymnocarpa		++	0.4	0.1			++	57.1
Polygala californica	0.1				+	++	++	57.1
Goodyera oblongifolia		++	++	++			0.1	57.1
Arbutus menziesii		3.2	86.3			+	+	57.1
Garrya fremontii		3.0	0.2	+	0.5			57.1
Smilacina racemosa	0.3		++		++	+		57.1
Umbellularia californica	0.4		4.2	++	0.1			57.1
Holodiscus discolor	0.5				+		0.2	42.9
Chamaecyparis lawsoniana			+		++		++	42.9
Aster brickellioides	++					0.1	0.3	42.9
Calocedrus decurrens	++				+	++		42.9
Festuca californica	++	0.1	0.1					42.9
Pyrola picta			++	+	++			42.9
Galium bolanderi	++			++	++			42.9
Brodiaea sp.	++					+	+	42.9
Lilium bolanderi					+		++	28.6
Quercus vaccinifolia					10.9		2.0	28.6
Viola lobata	++						1.4	28.6
Pinus attenuata						++	77.7	28.6
Amelanchier alnifolia	0.1	++						28.6
Boschniakia hookeri	++	++						28.6
Juniperus sibirica	+					+		28.6
Taxus brevifolia	+			++				28.6
Garrya buxifolia							++	14.3
Streptanthus tortuosus							+	14.3
Eriogonum nudum							++	14.3
Anemone deltoidea							0.7	14.3
Vancouveria hexandra		++						14.3
Acer macrophyllum		+						14.3

continued --

Appendix III (continued)

Low Elevation Siskiyou Vegetation:

	YCK	PCK	CCR	RCK	RCS	CBR	FHV	C(%)
Rubus parviflorus		+						14.3
Erigeron foliosus	+							14.3
Galium triflorum		+						14.3
Chimaphila umbellata		++						14.3
Campanula prenanthoides						0.1		14.3
Arctostaphylos nevedensis					+			14.3
Allotropa virgata					++			14.3
Linnaea borealis	0.4							14.3
Chimaphila menziesii	++							14.3
Ceanothus pumilus	+							14.3
Erythronium sp.	+							14.3
Apocynum androsaemifolium		++						14.3
Rubus ursinus						++		14.3
Berberis pumila		++						14.3
Rhododendron occidentale		3.7						14.3
Lathyrus californica		++						14.3
Cryptogramma crispa					+			14.3
Sedum spathulifolium					+			14.3
Arnica cernuua					+			14.3
Allium falcifolium					+			14.3
Lomatium howellii					+			14.3
Collinsia torreyi					+			14.3
Pinus monticola					17.1			14.3
Castilleja pruinosa				++				14.3
mosses	2.3	3.7	1.1	0.9	1.3	1.2	0.8	100.0

continued --

Appendix III (continued)

High Elevation Siskiyou Vegetation (first 8 plots of the moisture gradient):

	GOB	DWH	NBM	WBM	BFT	MOL	BCR	CKD	C(%)
Kalmiopsis leachiana	30.6	47.5	45.5	10.1	3.3	24.4	10.0	11.2	100.0
Vaccinium parvifolium	1.9	8.5	5.3	19.6	2.7	1.8	0.4	2.5	100.0
Quercus vaccinifolia		9.5	2.5	20.8	4.4	9.8	0.3	16.1	93.8
Lithocarpus densiflora	0.4	27.4	14.0	5.5		9.8	15.0	2.5	87.5
Pyrola picta	0.1		0.4	++		0.3	0.1	++	81.3
Psuedotsuga menziesii	75.7	580.4	119.8	284.9	227.4	38.4			75.0
Arctostaphylos canescens	++		0.4	++	0.3				75.0
Iris thompsonii	0.2	++				+			68.8
Garrya buxifolia					1.8	0.4	0.5	2.0	68.8
Xerophyllum tenax	5.9					0.9	2.5	8.5	62.5
Pinus lambertiana	68.4	+	105.5	57.6					56.3
Pinus monticola			15.2	+		++		+	56.3
Arctostaphylos nevadensis	5.1		0.3	++		0.6	0.3	11.3	56.3
Lilium bolanderi							++	++	56.3
Goodyera oblongifolia	0.1	0.2	0.1	0.1					56.3
Gaultheria shallon		8.7	1.9		1.4				50.0
Whipplea modesta				++	0.3			++	50.0
Amelanchier pallida						++		2.3	50.0
Castanopsis chrysophylla	16.9	13.5	1.2			++	++		50.0
Chimaphila menziesii	++	0.2	++	0.1		++			50.0
Rhododendron macrophyllum	3.4	13.9	0.6	4.1		2.5		+	50.0
Rosa gymnocarpa		++	+	0.1	++				43.8
Berberis pumila		+							43.8
Chimaphila umbellata	0.2	0.3	++	0.2	0.1				43.8
Quercus sadleriana	5.0	2.8		2.7		23.0	0.5		43.8
Rhamnus californica							++		43.8
Calocedrus decurrens		+							37.5
Pinus attenuata						2.9		15.6	37.5
Ceanothus pumilus							++	1.1	37.5
Berberis nervosa		0.4			1.6	+			31.3

continued --

Appendix III (continued)

High Elevation Siskiyou Vegetation (first 8 plots of the moisture gradient):

	GOB	DWH	NBM	WBM	BFT	MOL	BCR	CKD	C(%)
Juniperus sibirica						+	++	2.5	31.3
Pinus contorta	347.3							+	31.3
Arctostaphylos patula						2.8	2.5	++	31.3
Veratrum insolitum	0.1						++		31.3
Gaultheria ovatifolia	++					0.4	++	0.2	31.3
Polystichum munitum		++	+		0.2				25.0
Hieracium albiflorum					0.1			++	25.0
Trientalis latifolia					0.1				25.0
Polypodium glycyrrhiza		++	++	0.1					25.0
Arnica parviflora							++		25.0
Symphoricarpus albus		++	+	++					25.0
Asarum hartwegi		+	0.1	++					25.0
Picea breweri	+	+	22.3	+	+				25.0
Selaginella wallacei			++	++	0.1				25.0
Holodiscus discolor					0.9		++		25.0
Castilleja pruinosa							++		25.0
Disporum hookeri						0.1			18.8
Nothochelone nemorosa		++	++	1.3					18.8
Arctostaphylos columbiana						0.3	15.0	2.8	18.8
Thermopsis argentata						0.6	++		18.8
Festuca ovina			++	0.1					18.8
Boschniakia hookeri						+			12.5
Pterospora andromedea			+						12.5
Festuca occidentalis					0.1				12.5
Lomatium martindalei						++		++	12.5
Smilacina racemosa					+				12.5
Arbutus menziesii		+							6.3
Cornus nuttallii		+							6.3
Achlys triphylla		0.3							6.3
Linnaea borealis		+							6.3

continued --

Appendix III (continued)

High Elevation Siskiyou Vegetation (first 8 plots of the moisture gradient):

	GOB	DWH	NBM	WBM	BFT	MOL	BCR	CKD	C(%)
Viola cuneata	+								6.3
Luzula campestris					0.1				6.3
Vaccinium membranaceum						1.2			6.3
Lewisia cotyledon								++	6.3
Arnica cernuua								1.1	6.3
Allium watsoni								0.5	6.3
Poa sandbergii								++	6.3
Sedum laxum					0.5				6.3
Arenaria macrophylla					0.1				6.3
Trillium ovatum					++				6.3
Montia parviflora					0.1				6.3
Anemone lyallii	++								6.3
Viola glabella	0.1								6.3
Leucothoe davisiae	+								6.3
Abies concolor	68.2								6.3
Penstemon cardwellii							+		6.3
mosses	0.1	2.4	1.1	0.4	0.3	0.1	0.2	0.1	100.0

High Elevation Siskiyou Vegetation (second 8 plots of the moisture gradient):

	KRH	EBC	SSP	VLK	SDF	FLS	EWR	ROT	C(%)
Kalmiopsis leachiana	28.4	51.8	31.0	17.9	9.9	26.9	19.9	8.4	100.0
Vaccinium parvifolium	2.4	4.6	3.0	++	0.9	8.3	1.2	++	100.0
Quercus vaccinifolia	7.4	6.8	0.1	2.4	+	31.9	23.3	9.6	93.8
Lithocarpus densiflora		18.9	27.5	12.3	7.4	12.1	1.7	++	87.5
Pyrola picta	0.2	0.2	+	++	0.1	++	+		81.3
Psuedotsuga menziesii	77.7	150.4	13.9			199.5	21.1	54.3	75.0
Arctostaphylos canescens	9.5	++	+	2.8	2.4	++	10.8	1.9	75.0
Iris thompsonii	0.4	++	++	++	2.3	0.4	++	+	68.8
Xerophyllum tenax	5.6	3.2	1.1	1.8	4.7	3.5			62.5

continued --

Appendix III (continued)

High Elevation Siskiyou Vegetation (second 8 plots of the moisture gradient):

	KRH	EBC	SSP	VLK	SDF	FLS	EWR	ROT	C(%)
Pinus lambertiana	24.2	348.3	34.0				35.4	+	56.3
Pinus monticola	30.6		204.7			160.0	210.2	34.4	56.3
Arctostaphylos nevadensis	1.4	+				0.2			56.3
Lilium bolanderi		++	++	++	0.1	0.1	++	++	56.3
Goodyera oblongifolia	++	++	0.2			0.1		++	56.3
Gaultheria shallon	8.7	++	+	+					50.0
Whipplea modesta	0.4		+	++		0.7		0.2	50.0
Amelanchier pallida	0.1		++	0.5		0.1	++	0.1	50.0
Castanopsis chrysophylla	13.2	7.3	3.8						50.0
Chimaphila menziesii		0.1				++	0.2		50.0
Rhododendron macrophyllum	5.6		11.3						50.0
Rosa gymnocarpa	++	++	0.1	1.8		0.2			43.8
Berberis pumila	0.2	++	0.1	++		0.5	+		43.8
Chimaphila umbellata		0.9						+	43.8
Quercus sadleriana	+	15.1							43.8
Rhamnus californica			++	0.1	++	++	+	++	43.8
Calocedrus decurrens		++	+	+		++		+	37.5
Pinus attenuata	+		8.5	86.9				7.2	37.5
Ceanothus pumilus	+					0.1	+	++	37.5
Berberis nervosa				+				0.1	31.3
Aster brickellioides	0.1		+	++			++	+	31.3
Juniperus sibirica						+		++	31.3
Pinus contorta	354.8				1094.2			+	31.3
Arctostaphylos patula	++				++				31.3
Veratrum insolitum	0.1	++	++	+					31.3
Gaultheria ovatifolia	3.2	5.5							31.3
Polystichum munitum				++					25.0
Hieracium albiflorum					0.4	++			25.0
Trientalis latifolia			+	++		0.1			25.0
Vaccinium ovatum			11.1	14.3	+		2.0		25.0
Polypodium glycyrrhiza								+	25.0

continued --

Appendix III (continued)

High Elevation Siskiyou Vegetation (second 8 plots of the moisture gradient):

	KRH	EBC	SSP	VLK	SDF	FLS	EWR	ROT	C(%)
Umbellularia californica			+			2.0	++	++	25.0
Arnica parviflora	+	++						0.1	25.0
Symphoricarpus albus			++						25.0
Asarum hartwegi			++						25.0
Senecio canus					++	++	+	++	25.0
Selaginella wallacei								0.2	25.0
Holodiscus discolor							+	0.2	25.0
Castilleja pruinosa	++			+					25.0
Disporum hookeri		+				1.2			18.8
Festuca ovina						++			18.8
Erythronium sp.					++	+			12.5
Boschniakia hookeri					+				12.5
Smilacina stellata							++	0.1	12.5
Lomatium howellii				++				+	12.5
Pterospora andromeda		+							12.5
Festuca occidentalis	++								12.5
Smilacina racemosa				+					12.5
Cheilanthes siloquosa				+			++		12.5
Habenaria unalaschensis		+			++				12.5
Pteridium aquilinum			++						6.3
Rhus diversiloba			++						6.3
Oenothera oblongifolia			+						6.3
Apocynum androsaemifolium	+								6.3
Galium ambiguum					0.6				6.3
Gentiana affinis					0.6				6.3
Calamogrostis koeleroides					2.3				6.3
Rhododendron occidentale					0.3				6.3
Viola douglasii					0.2				6.3
Vancouveria planipetala					+				6.3
Carex sp.					+				6.3

continued --

Appendix III (continued)

High Elevation Siskiyou Vegetation (second 8 plots of the moisture gradient):

	KRH	EBC	SSP	VLK	SDF	FLS	EWR	ROT	C(%)
Zygadenus micranthus					++				6.3
Viola cuneata					+				6.3
Chamaecyparis lawsoniana					+				6.3
Galium multiflorum								0.1	6.3
Cheilanthes gracilima								++	6.3
Sedum spathulifolium								++	6.3
Antennaria suffrutescens								++	6.3
Phlox diffusa			++						6.3
Sarcodes sanguinea		+							6.3
Carex concinnoides	++								6.3
Lomatium macrocarpum							+		6.3
Eriogonum ternatum							+		6.3
Erigeron foliosus						+			6.3
Collinsia torreyi								+	6.3
Trillium rivale						+			6.3
Cacaliopsis nardosmia						+			6.3
Pinus jeffreyi						107.1			6.3
Penstemon rupicola								+	6.3
mosses	0.5	0.3	0.2	+	++	0.9	0.1	+	100.0

continued --

Appendix III (continued)

Southern Cascades Vegetation:

	RAR	CCK	BIC	DCK	PAR	FLR	LPR	C(%)
Kalmiopsis leachiana	0.4	0.1	18.9	0.2	13.4	+	+	100.0
Gaultheria shallon	36.8	7.6	38.8	18.7	++	++	36.1	100.0
Pseudotsuga menziesii	51.9	619.8	391.9	483.4	6.6	847.8	767.6	100.0
Pinus lambertiana	32.8	44.8	+	132.9	+	+	232.6	100.0
Castanopsis chrysophylla	1.3	13.2	1.1	1.6	+		90.2	85.7
Vaccinium parvifolium	0.1	0.1	++		+	+	++	85.7
Berberis nervosa	++	4.2	1.1		7.8	0.7	0.9	85.7
Iris chrysophylla	++	++		0.6		++	+	71.4
Rubus ursinus	++	2.1		0.4		0.2	+	71.4
Rosa gymnocarpa		++	++	1.2		++	++	71.4
Linnaea borealis	++	2.6	0.6				+	57.1
Polystichum munitum	++		+	+		+		57.1
Tsuga heterophylla	599.8	38.2	34.2				+	57.1
Arbutus menziesii			+	70.7	9.5		62.6	57.1
Pyrola picta		++	++			++	++	57.1
Disporum hookeri		++	+	++			+	57.1
Thermopsis montana		+	+			+	++	57.1
Hieracium albiflorum		0.1		++		++	+	57.1
Acer circinatum		2.1		44.9		+	+	57.1
Whipplea modesta		0.6	++				++	42.9
Goodyera oblongifolia			++	++		++		42.9
Pteridium aquilinum		1.0		1.3			0.9	42.9
Collomia heterophylla		0.1		+			+	42.9
Campanula scouleri		0.1		0.5		0.1		42.9
Symphoricarpus albus			2.7			4.2	+	42.9
Apocynum androsaemifolium		0.3				+	+	42.9
Rhododendron macrophyllum	24.4	15.3						28.6
Xerophyllum tenax	4.2	1.0						28.6

continued --

Appendix III (continued)

Southern Cascades Vegetation:

	RAR	CCK	BIC	DCK	PAR	FLR	LPR	C(%)
Smilacina stellata			++			++		28.6
Habenaria unalascensis			++	+				28.6
Taxus brevifolia		+	5.5					28.6
Garrya fremontii		++					1.3	28.6
Chimaphila umbellata		0.1				++		28.6
Corylus cornuta		++		+				28.6
Achlys triphylla		0.1					+	28.6
Luzula campestris		1.6		+				28.6
Synthyris reniformis		0.1					+	28.6
Smilacina racemosa				++		+		28.6
Arenaria macrophylla				++		0.2		28.6
Trientalis latifolia				0.6			0.1	28.6
Rhamnus purshiana				++			0.7	28.6
Chimaphila menziesii						0.2	++	28.6
Amelanchier alnifolia						++	++	28.6
Psoralea physodes						++	+	28.6
Arctostaphylos canescens					+			14.3
Pinus attenuata					315.2			14.3
Anemone deltoidea		0.1						14.3
Vaccinium ovatum		7.6						14.3
Festuca rubra		++						14.3
Brodiaea sp.		0.1						14.3
Abies grandis		199.4						14.3
Osmorhiza chilensis				++				14.3
Bromus vulgaris				0.2				14.3
Montia perfoliata				0.3				14.3
Dicentra formosa				+				14.3
Lathyrus polyphyllus				++				14.3
Trisetum canescens				+				14.3

continued --

Appendix III (continued)

Southern Cascades Vegetation:

	RAR	CCK	BIC	DCK	PAR	FLR	LPR	C(%)
Thuja plicata				+				14.3
Phlox adsurgens				+				14.3
Actostaphylos nevadensis						++		14.3
Holodiscus discolor						1.3		14.3
Polypodium glycyrrhiza						++		14.3
Asarum hartwegii						0.1		14.3
Corallorhiza maculata						+		14.3
Festuca occidentalis							++	14.3
Philadelphus lewisii							+	14.3
Cornus nuttallii							+	14.3
mosses	4.5	1.1	0.5	0.7	3.0	++	++	100.0

APPENDIX IV. Results of surface soil description of sampled sites of *Kalmiopsis* populations. (LS: low elevation Siskiyou sites; HS: high elevation Siskiyou sites; SC: Southern Cascades sites).

Site	Vegetation unit	Color	pH	% Exposed bedrock	% Bare soil	Soil stone content (diameter) %0.25-1.0 cm	%1.0-3.0 cm	% > 3.0 cm
RCS	LS	10Y/R 4.4	5.8	10.0	40.0	30.0	5.0	5.0
PCK	LS	10Y/R 5.3	6.0	2.0	---	10.0	10.0	---
RCK	LS	10Y/R 4.2	5.8	5.0	15.0	20.0	5.0	5.0
CCR	LS	10Y/R 4.2	6.0	5.0	20.0	10.0	10.0	---
YCK	LS	10Y/R 5.4	5.6	5.0	60.0	15.0	10.0	---
CKD	HS	10Y/R 4.4	5.8	2.0	40.0	45.0	40.0	---
FHV	HS	10Y/R 6.4	6.4	5.0	30.0	10.0	---	---
FLS	HS	5Y/R 3.2	6.4	2.0	2.0	10.0	10.0	---
MOL	HS	10Y/R 5.4	5.8	2.0	10.0	40.0	15.0	5.0
ROT	HS	10Y/R 4.4	5.9	40.0	85.0	30.0	20.0	5.0
SSP	HS	10Y/R 4.4	5.6	1.0	25.0	20.0	5.0	---
NBM	HS	10Y/R 6.4	5.4	5.0	15.0	25.0	10.0	5.0
DWH	HS	10Y/R 4.2	5.4	2.0	---	20.0	5.0	---
VLK	HS	10Y/R 6.4	5.9	25.0	50.0	30.0	10.0	---

continued --

APPENDIX IV (continued)

Site	Vegetation unit	Color	pH	% Exposed bedrock	% Bare soil	Soil stone content (diameter) %0.25-1.0 cm	%1.0-3.0 cm	%>3.0 cm
EWR	HS	10Y/R 5.4	5.8	40.0	30.0	30.0	20.0	5.0
BFT	HS	10Y/R 5.4	5.6	25.0	80.0	40.0	10.0	5.0
SDF	HS	5Y/R 4.3	6.4	15.0	5.0	20.0	5.0	1.0
EBC	HS	10Y/R 4.4	5.8	---	5.0	20.0	5.0	---
KRH	HS	5Y/R 4.3	6.4	5.0	5.0	30.0	10.0	1.0
WBM	HS	10Y/R 6.4	5.4	5.0	20.0	15.0	5.0	1.0
PAR	SC	10Y/R 3.2	5.4	5.0	75.0	30.0	30.0	20.0
FLR	SC	10Y/R 5.2	5.3	---	40.0	5.0	5.0	---
LPR	SC	10Y/R 5.3	6.4	5.0	10.0	10.0	10.0	---
RAR	SC	10Y/R 5.4	6.3	2.0	15.0	5.0	---	---
BIC	SC	10Y/R 6.4	6.3	---	20.0	10.0	5.0	---
CCK	SC	10Y/R 6.4	5.4	---	10.0	5.0	2.0	---
DCK	SC	10Y/R 5.3	6.2	---	20.0	5.0	---	---