

AN ABSTRACT OF THE THESIS OF

Daniel L. Luoma for the degree of Master of Science in Geography presented on July 1, 1987.

Title: Synecology of the Monotropeidae within Limpy Rock Research Natural Area, Umpqua National Forest, Oregon

Abstract approved: _____

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Four aspects of the ecology of members of the Monotropeidae (achlorophyllous Ericaceae, referred to here as "monotropes") are presented: (1) a clarified conceptualization of monotrope nutrition based on a detailed literature review, (2) the relationship of monotrope populations to the plant communities of Limpy Rock RNA, (3) a test of Vreeland's hypothesis concerning the influence of overstory trees on the number of *Sarcodes sanguinea* plants in a forest stand, (4) the population dynamics of the northernmost known occurrence of *Sarcodes sanguinea*.

A literature survey provides insight into the development of concepts concerning the nutritional mode of monotropes. The experimental evidence reviewed showed that the fungi involved have little saprobic ability but are ectomycorrhizal with autotrophic plants. Hence, the concept "epiparasite" can be used to describe an indirect relationship in the life history of monotropes. With consideration of the operational environment of monotropes, however, it can be concluded that the term "epiparasite" is not appropriately used in the context of the nutritional mode of monotropes. Members of the Monotropeidae can be viewed as parasites of their mycorrhizal fungi. Some evidence showed growth of the fungi was stimulated by the presence of monotropes. Since the term "parasite" has negative connotations in general usage, the terms "obligate mycotroph" and "mycotrophic" may be preferred when referring to members of the Monotropeidae. "Mycotrophic" could be strictly applied to only those organisms which depend on fungi for energy; however, the term has long been used in a broad sense interchangeably with "mycorrhizal."

Limpy Rock Research Natural Area is located in the south central portion of the Cascade Mountains in Oregon. The 751 ha (1879 ac.) tract encompasses most of the

drainage of Dog Creek. Elevation ranges from 525 to 1305 m (1750 - 4350 ft.). The high species diversity of the Limpy Rock area and local concentration of all eight western monotrope species, provided excellent and possibly unique research opportunities.

Coniferous forest vegetation was classified by TWINSPAN into six community types: *Pseudotsuga menziesii/Acer circinatum* (PSME/ACCI), *Pseudotsuga menziesii/Cornus nuttallii/Berberis nervosa* (PSME/CONU/BENE), *Pseudotsuga menziesii-Arbutus menziesii/Gaultheria shallon-Berberis nervosa/Pteridium aquilinum* (PSME-ARME/GASH-BENE/PTAQ), *Pseudotsuga menziesii-Calocedrus decurrens/Gaultheria shallon-Berberis nervosa* (PSME-CADE/GASH-BENE), *Pseudotsuga menziesii-Calocedrus decurrens/Gaultheria shallon-Berberis nervosa* (PSME-PILA/GASH-BENE), *Pseudotsuga menziesii-Abies concolor/Berberis nervosa/Xerophyllum tenax* (PSME-ABCO/BENE/XETE). Community types were related to several general environmental measures by detrended correspondence analysis and correlation analysis.

Allotropa virgata is strongly preferential to plots at the dryer end of the moisture gradient. *Monotropa hypopithys* shows a preference for higher elevation and cooler types. *Pterospora andromedea* was not found in any plots but was noted to be widespread throughout the RNA. *Hemitomes congestum*, *Monotropa uniflora*, *Pityopus californica*, and *Pleuroscopora fimbriolata* were largely restricted to dryer types. No monotropes were found in plots of the PSME/CONU/BENE or PSME-ARME/GASH-BENE/PTAQ community types.

Vreeland's (1980) hypothesis concerning predicting the number of *Sarcodes* in a stand was reviewed and discussed. In particular, his "Influence Factor" was tested with a data base of over 2000 measurements. The results show his hypothesis to be invalid.

Population monitoring of the northernmost known population of *Sarcodes sanguinea* showed that flowering of individual plants in subsequent years was low in frequency. Despite the low rate of flowering recurrence, population levels were relatively stable over the five years of monitoring.

Synecology of the Monotropoideae Within
Limpy Rock Research Natural Area,
Umpqua National Forest, Oregon

by

Daniel L. Luoma

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SYNECOLOGY OF THE MONOTROPOIDEAE WITHIN
LIMPY ROCK RESEARCH NATURAL AREA,
UMPQUA NATIONAL FOREST, OREGON

INTRODUCTION

The botanical importance of the Limpy Rock area was first made known through the efforts of the Limpy Rock Botanical Committee (Moore et al., 1976). The Committee's work documented the high species diversity of the Limpy Rock area and local concentration of many "special interest" vascular plant species. These "special interest" plants were recognized as rare, threatened or endangered by the Oregon Natural Area Preserves Advisory Committee (Siddall et al., 1979) and the Oregon Natural Heritage Data Base (The Nature Conservancy, 1983). The species and reasons for special interest are listed in Table 1.

Based on the Limpy Rock Botanical Committee's work and comments of many regional scientists, the U. S. Forest Service established a Research Natural Area (RNA) in 1980 to protect the natural values of the Limpy Rock area. The Research Natural Area program is designed to

...provide baseline areas against which the effects of human activities in similar environments can be measured; provide sites for study of natural processes in undisturbed ecosystems; and to provide gene pool preserves for plant and animal species, particularly of rare and endangered types. (Franklin et al., 1973, p. 2.).

The investigation reported here is a first step in establishing baseline vegetational data as background for future studies and adds to ecological knowledge of a group of plants, members of the Monotropeae, four of which are special interest species.

The Monotropeae is a taxon of sub-family rank within the Ericaceae (Wallace, 1975a). It consists of 10 genera and 12 species. Seven genera and 8 species are found in the western United States (Wallace, 1975b). All eight western species are represented within Limpy Rock RNA, providing excellent and possibly unique research opportunities.

TABLE 1. Status of special interest vascular plant species of Limpy Rock RNA.

Species	Status ^a
<i>Phacelia verna</i>	Candidate threatened, U. S. Fish and Wildlife Service; needs active protection measures to insure survival throughout its range.
<i>Asplenium septentrionale</i>	Endangered in Oregon, disjunct population. More common elsewhere.
<i>Astragalus umbraticus</i>	Threatened in Oregon, disjunct population. More common elsewhere.
<i>Polystichum californicum</i>	Threatened in Oregon, disjunct population. More common elsewhere.
<i>Kalmiopsis leachiana</i>	Endemic in southwest Oregon, limited in abundance, populations thought to be stable.
<i>Orobanche pinorum</i>	Limited in abundance but stable in Oregon, more common elsewhere.
<i>Pellaea brachyptera</i>	Limited in abundance but stable in Oregon, more common elsewhere.
<i>Pityopus californica</i>	Limited in abundance but stable in Oregon, more common elsewhere.
<i>Sarcodes sanguinea</i>	Peripheral population, scattered and scarce in southwestern Oregon; northernmost known occurrence at Limpy Rock.

Table 1. Continued.

Species	Status ^a
<i>Equisetum fluviatile</i>	Potential for concern, status under review, disjunct population.
<i>Montia diffusa</i>	Potential for concern, status under review, reported from few stations recently.
<i>Hemitomes congestum</i>	Potential for concern, status under review, specialized biology - very susceptible to habitat modification.
<i>Pleuricospora fimbriolata</i>	Potential for concern, status under review, specialized biology - very susceptible to habitat modification.
<i>Calypto bulbosa</i>	Currently abundant or widespread but declining; populations need monitoring.
<i>Cephalanthera austiniiae</i>	Currently abundant or widespread but declining; populations need monitoring.
<i>Lilium pardalinum</i>	Currently abundant or widespread but declining; populations need monitoring.
<i>Lilium washingtonianum</i>	Currently abundant or widespread but declining; populations need monitoring.

^a Sources: Siddall et al., 1979; The Nature Conservancy, 1983

Objectives

This investigation of the Monotropeoideae (members of which may hereafter be referred to informally as "monotropes") has three objectives. The first objective is to describe and classify the forest plant communities within the RNA. Non-forest vegetation, the riparian zone, and "oak savanna" stands were not examined. Community analysis was a necessary precursor for the species-centered study of the Monotropeoideae.

The second objective is to analyze the distribution of monotropes in relation to the forest community types identified in the vegetational study. The third objective is to test the usefulness of H. Vreeland's (1980) "Influence Factor" hypothesis to explain the abundance of monotropes in the plant community types. H. Vreeland (1980, p. ii) suggested that his approach "should be tested in other ecosystems on other achlorophyllous species and on this species [*Sarcodes sanguinea*] to determine the validity or lack thereof ... " of his model.

Study Area

Limp Rock RNA is located in the North Umpqua River drainage, about 75 km (45 mi.) east of Roseburg, and 10 km (6 mi.) east of Steamboat (Figure 1). The 751 ha (1879 ac.) tract encompasses most of the drainage of Dog Creek (Figure 2). Elevation ranges from 525 to 1305 m (1750 - 4350 ft.). The general aspect is southerly, but northeast aspects are often encountered.

Climate

The regional climate is classified as a Temperate Oceanic type by Trewartha and Horn (1980). This type is characterized by average temperatures greater than or equal to 10 °C (50 °F) for four to seven months, and mild winters, with the average temperature of the coldest month greater than or equal to 0 °C (32 °F). The type is latitudinally located between the Subtropical Dry-summer and Boreal climatic types. The idealized location of the type is on the west coast of continents poleward of 40° latitude. The relative position of the study area in its climatic type region is equatorward and inland from the ocean. Therefore, the study site is in an area transitional to the Subtropical Dry-summer (Mediterranean) climatic type.

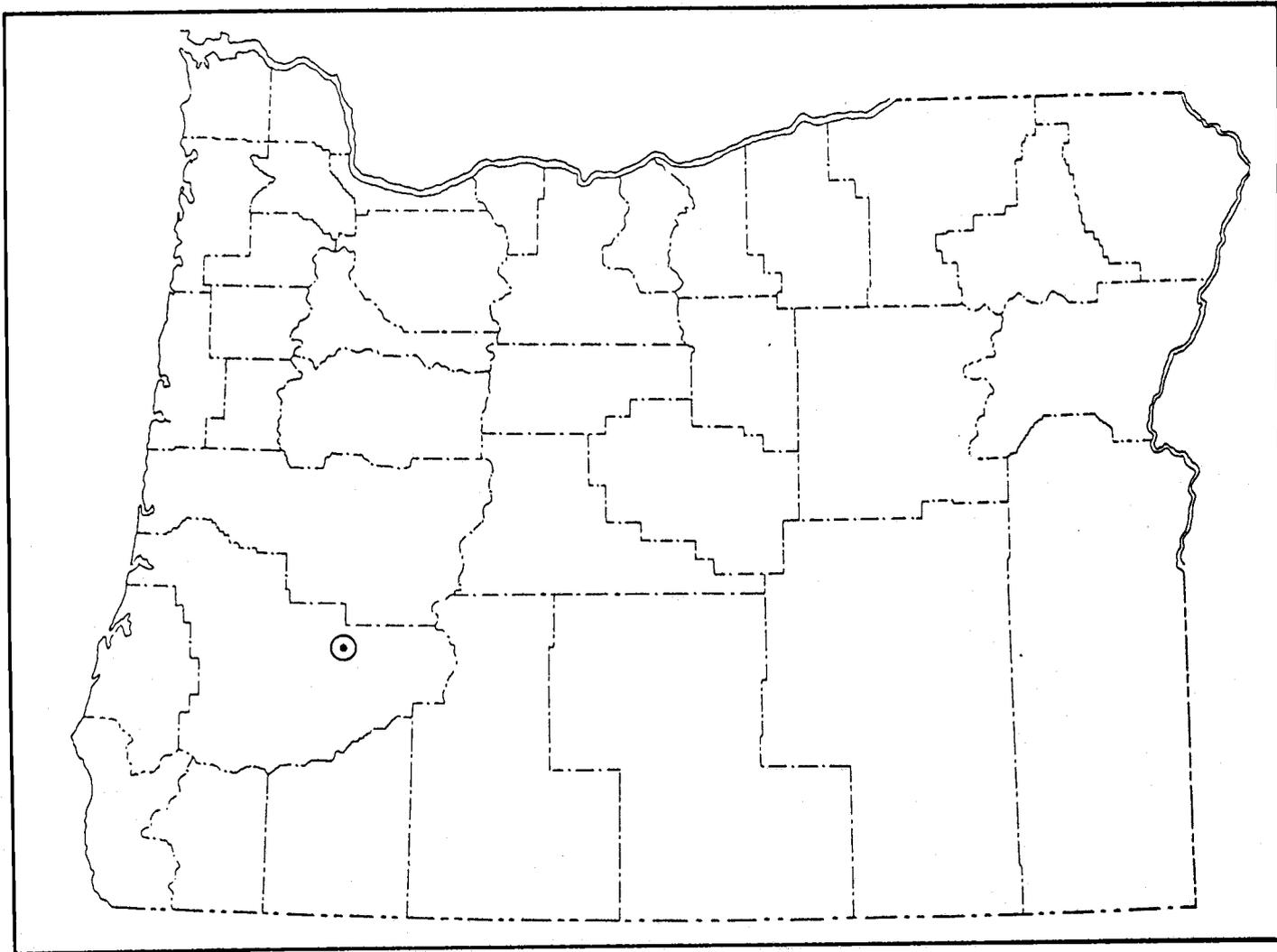


Figure 1. General location of Limpy Rock RNA, Douglas County, Oregon.

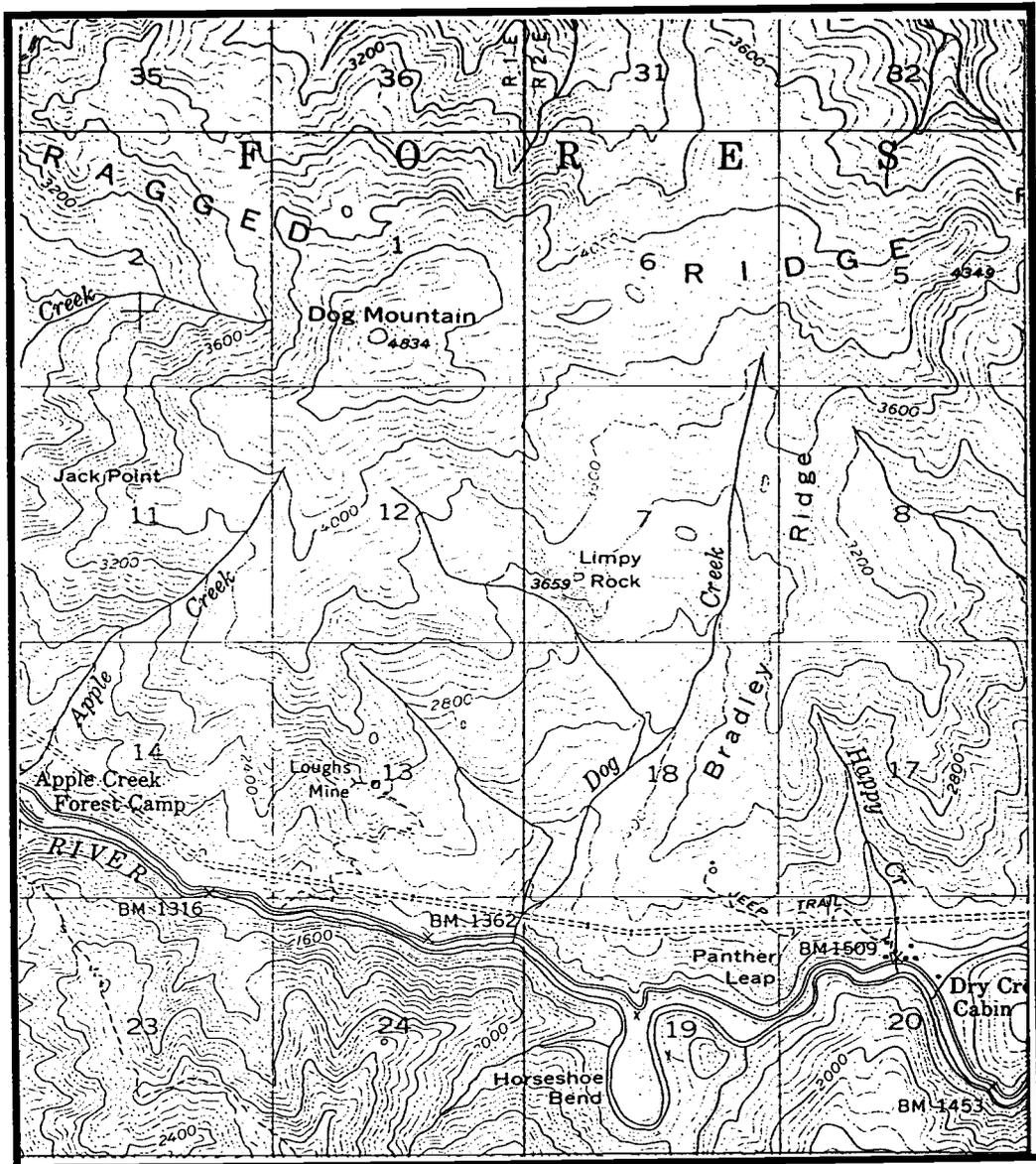


Figure 2. Topography of Limpy Rock RNA.

The nearest weather station with complete information is Roseburg. A climatic diagram for Roseburg is included to illustrate the seasonal progression of the climate (Figure 3). The values at Limpy Rock would be cooler and moister, but the relative changes through the year are similar.

In the summer, cool but stable air commonly moves onshore bringing fog and/or cloudy skies to the Western Cascades. Little rainfall occurs because of the stability of the air. Less than ten percent of the average annual precipitation occurs in June through September (Table 2). Occasionally a continental air mass will prevail, raising temperatures to 32 °C (90 °F) or more, greatly increasing evapotranspiration (Waring and Franklin, 1979). Due to the interplay of climatic elements, weather during the growing season at Limpy Rock fluctuates greatly. As can be seen in Table 2, the intensity of the summer drought is seldom near "normal" (average), but shows high variance from year to year or month to month.

Unfortunately, temperature data are not recorded at the Steamboat station. During this study, air temperatures in the forest were recorded during July and August of 1982, near the summit of Dog Mountain at 1372 m (4500 ft.) elevation. Low temperatures ranged from 3 to 15 °C (38 to 60 °F) and highs from 12 to 21 °C (55 to 70 °F) during July. Temperatures during August were slightly warmer; lows ranged from 6 to 19 °C (42 to 66 °F) and highs from 10 to 25 °C (50 to 77 °F). The lower part of the RNA probably experienced maximum air temperatures near 27 °C (84 °F) based on a temperature lapse rate of -0.5 °C/100 m (Zobel et al., 1976). Holms (1987) reports temperature data from Williams Ridge (Table 3), located 14.4 km (9 mi.) to the NW of Limpy Rock, at an elevation of 975 m (3200 ft.). The data from Table 3 were gathered in a west facing, open grass "bald" which may have higher temperatures than those of the forest habitats of Limpy Rock RNA. Zobel et al. (1976) report a maximum air temperature on warmer sites of 38 °C at comparable elevations in the Willamette National Forest, indicating that the summer of 1982 may have been much cooler as well as wetter than average.

Winters are cool and wet. Eighty percent of the 140 cm (55 in.) average annual precipitation occurs primarily as rain from October through March. Above 1076 m (3500 ft.) snow may accumulate with depths up to 75 cm.

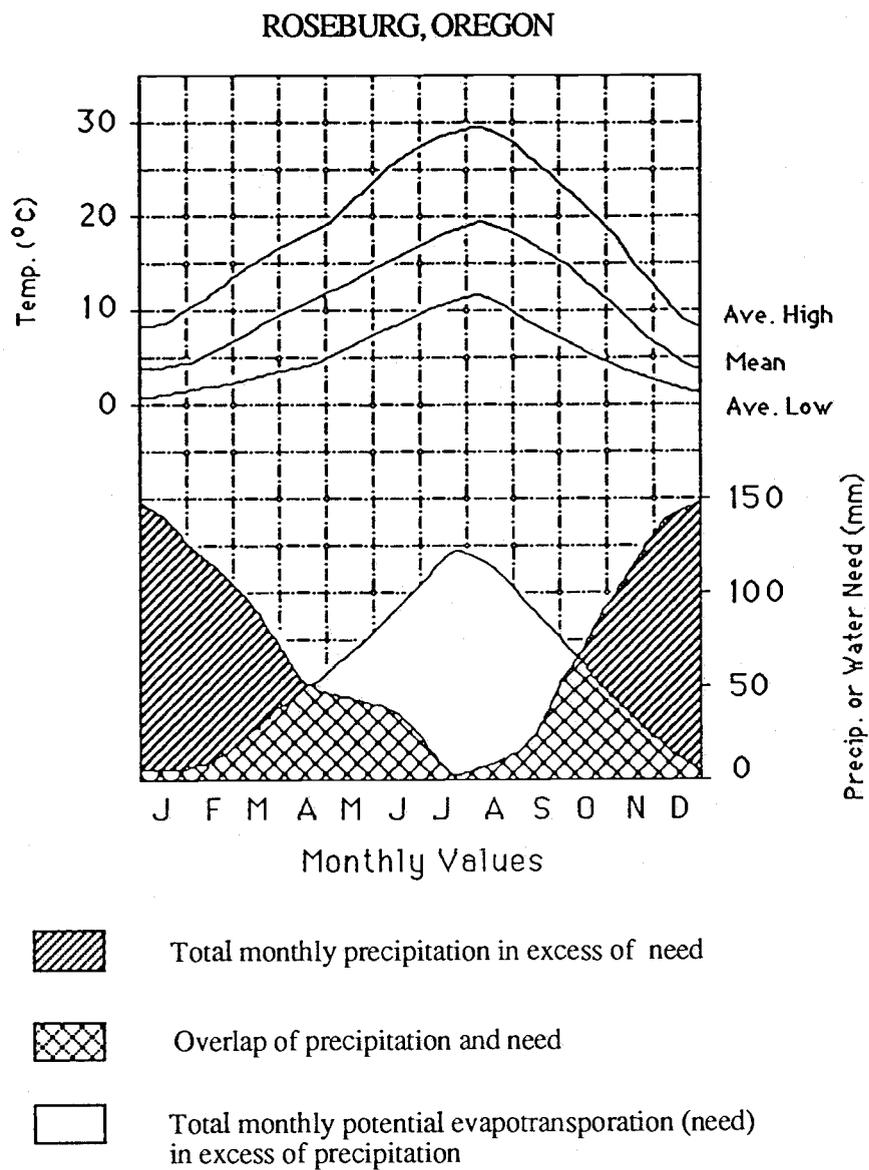


Figure 3. Climatic Diagram, after Loy (1976).

Table 2. Precipitation data, Steamboat Ranger Station. Source: U. S. Forest Service.

Month	Precipitation (cm)				
	1981	1982	1983	1984	28 yr. mean
January	5.6	17.4	13.9	7.1	20.2
February	18.0	16.5	30.3	24.3	16.6
March	11.2	16.0	24.1	18.4	18.1
April	8.6	14.5	12.1	20.0	10.2
May	11.0	0.7	7.2	12.5	7.6
June	7.9	5.3	3.7	11.2	3.8
July	1.4	1.9	8.2	0.8	1.0
August	0.0	1.4	5.3	0.7	2.3
September	7.5	11.5	1.4	2.1	5.1
October	12.6	17.6	5.6	19.0	12.0
November	21.1	15.0	31.6	43.5	20.4
December	49.4	33.6	37.8	17.4	25.3
Total	154.3	151.4	181.2	177.0	142.6
(inches)	(60.7)	(59.6)	(71.3)	(69.7)	(56.1)

Table 3. Monthly temperatures (°C), Williams Ridge. Source: Holmes, 1987.

Month	Mean High			Mean Low		
	1982-83	1983-84	1984-85	1982-83	1983-84	1984-85
October	16.2	17.4	11.3	4.6	5.0	1.6
November	6.8	4.2	4.5	-1.4	-0.6	-1.0
December	4.5	1.0	5.1	-2.0	-3.7	-4.0
January	nr	10.3	15.4	nr	-1.0	-0.9
February	nr	7.6	5.6	nr	-1.5	-3.4
March	7.4	10.2	6.6	0.4	0.7	-3.1
April	12.3	8.9	14.5	-0.5	-1.6	1.8
May	17.9	14.8	16.3	4.7	2.0	2.3
June	19.2	18.1	23.2	5.7	4.7	7.4
July	20.2	27.2	30.0	7.5	9.9	12.2
August	23.7	26.3	26.3	10.6	9.0	9.1
September	21.8	23.4	19.4	6.9	6.7	5.7

nr = no record

Geology and Soils

Limpy Rock RNA is within the Western Cascades physiographic province (Baldwin, 1964). Massive beds of andesitic and dacitic tuff ash flow, with lesser amounts of basaltic rock, characterize the basement geology. These flows are part of the older-Tertiary Little Butte Volcanic Series (Peck et al.; 1964). Limpy Rock itself is a monolith (probably andesitic, Peck et al.; 1964) over 76 m (250 ft.) high.

Rock outcrops and cliffs are common along the ridges. These ridges run generally NW-SE off Dog Mt., and are marginal to Ragged Ridge, which forms the divide between the N. Umpqua River and Steamboat Creek. The Dog Creek drainage forms a wide bowl tipped to the south and set in the side of Ragged Ridge. Bradley Ridge and Lough's Ridge form the east and west rims, respectively. Where the two ridges curve toward each other, Dog Creek breaks through, emptying into the N. Umpqua River (Figure 2).

Several unnamed southeasterly-flowing perennial streams feed Dog Creek. The progressively steepened slopes, from ridges to creeks, suggest accelerated incision rates (Patton et al., 1974). Associated landforms include earth flows, slumps, scarps, small ponds and seeps, particularly in the drainages west of Limpy Rock.

Soils of the study area have not been surveyed. Inceptisols are the most extensive order in the region (Mitchel, 1979). Shallow, gravelly loams are common. Deeper, more clayey Ultisols are found on gentler, more stable slopes (Simonson, 1976).

Radtke and Edwards (1976) provide landtype maps and descriptions of the mapping units for the Umpqua National Forest. Nineteen landtypes are found within Limpy Rock RNA. The five predominant landtypes are summarized here:

Landtype 13 is comprised of deep soils which are derived from colluvial materials.

Surface horizons are thin, gravelly loams. The type occurs on uneven to hummocky benches, terraces and valley bottoms.

Landtype 22 soils are shallow over weathered volcanic breccia. The surface is a shotty loam. The type occurs on undulating to hilly topography. It is found on low ridgetops, gentle sideslopes, and stabilized landflows.

Landtype 25 is comprised of deep soils associated with inactive land flows. Soil profiles are mixed. The surface is a thin, gravelly to cobbly loam. The type occurs on uneven landforms and is indicated by pressure ridges, leaning trees and sag ponds.

Landtype 41 consists of shallow colluvial and residual soils. Thin gravelly to clayey loams comprise the surface soil. The type occurs on steep upper side slopes and ridges

Landtype 46 contains shallow residual soils. The surface horizon is a thin gravelly to shotty loam. The type is found on steep to very steep, deeply incised topography. Rock outcrops cover up to ten percent of the area.

Overall, surface horizons are thin and gravelly while the sub-horizons are thick in older colluvial soils, or otherwise thin and residual.

Biological Features

Limp Rock RNA is within the *Tsuga heterophylla* Zone of Franklin and Dyrness (1973). K uchler (1964) vegetation types are: Cedar - Hemlock - Douglas-fir Forest (93% cover), Mixed Conifer Forest (3.5%), and Fescue - Oatgrass (3.5%).

The Fescue - Oatgrass type contains *Quercus garryana* and was referred to in the introduction as "oak savanna". *Alnus rubra* (with occasional *Thuja plicata*) dominates the riparian zone. Riparian vegetation was not investigated, but *Aralia californica* was noted to be a dominant tall herb along creeks. Other non-forest habitat includes rocky outcrops (where *Arctostaphylos* spp. or *Kalmiopsis leachiana* may dominate) and small ponds bordered by wetland vegetation.

Forest cover dominated by *Pseudotsuga menziesii* characterizes most of the RNA. *Pinus lambertiana* and *Calocedrus decurrens* are co-dominants in some stands. Two early-seral stage stands are dominated by *Arbutus menziesii*. *Calocedrus decurrens*, *Abies grandis*, and *Tsuga heterophylla* are the most commonly reproducing trees. Other tree species in the RNA are: *Acer macrophyllum*, *Castanopsis chrysophylla*, *Abies concolor*, *Taxus brevifolia*, *Pinus attenuata*, and *Pinus ponderosa*.

In addition to the special interest plants already mentioned, the RNA has an exceptionally high diversity of vascular plant species, with nearly 400 taxa represented. More specific vegetational information will be presented in the results section.

Disturbances in the area include wildfire and timber harvest. The most recent fire seems to have occurred in the 1890's. However, scattered old trees remain in some areas and two stands of old-growth Douglas-fir forest, in the upper part of the drainage, escaped burning. Three areas of old-growth were logged just prior to RNA establishment. Logging activities included: (a) commercial thinning of 40 ha (99 ac.) along the northern boundary in 1971 with subsequent shelterwood cutting in 1980 and (b) shelterwood cutting of 27 ha (66 ac.) along Forest Road 2643 in 1974 with subsequent broadcast burning, replanting, and erosion control. Analysis of pre-disturbance areal photographs shows that the logging units were placed in dense old-growth forest habitat.

LITERATURE SURVEY

General Vegetation

Studies of forest communities within the *Tsuga heterophylla* Zone reveal a generalized pattern of occurrence along a moisture gradient (Franklin and Dyrness, 1973). Characteristic understory species are used to describe the community types. *Lysichitum americanum* indicates wet forest sites with the water table near or above the surface. Abundant *Polystichum munitum* and *Oxalis oregana* typify very moist sites. Mesic sites may be occupied by *Berberis nervosa* and/or *Rhododendron macrophyllum*. Towards the dry end of the scale, *Gaultheria shallon* increases in dominance.

Forest communities in the central Western Cascades of Oregon were classified by Dyrness et al. (1974). Their study area is located about 100 km (62 mi.) north of Limpy Rock RNA. Eleven *Tsuga heterophylla* Zone climax associations and three seral communities were described. Their results conform to the general pattern with respect to a moisture gradient. Additionally, they noted a temperature gradient reflecting elevation. The hot, dry *Pseudotsuga/Holodiscus discolor* association represents one extreme of the temperature gradient. Passing through the types previously noted, the coolest extreme is represented by the *Tsuga-Abies amabilis/Linnaea borealis* association (Figure 4).

Dyrness et al. (1974) found classification of communities to be challenging because of the wide geographic and ecologic distribution of most plant species. In modal communities, the difference in relative abundance of shared species was the basis for community recognition.

Means (1980) further investigated dry site community types; describing (among others) a *Pseudotsuga menziesii/Holodiscus discolor-Acer circinatum* type. Halpern et al. (1984) recognized a *Tsuga heterophylla* Series of community types at lower elevations in the west central portion of the Three Sisters Biosphere Reserve/Wilderness Area where moisture was found to be an important gradient influencing community composition. At the dry end of this gradient is the *Pseudotsuga menziesii-Calocedrus decurrens/Symphoricarpos mollis* community type. Modal stands are typified by *Tsuga/Acer circinatum/Berberis nervosa*, *Tsuga/Berberis nervosa*, *Tsuga/Rhododendron macrophyllum/Berberis nervosa*, *Tsuga/Rhododendron macrophyllum/Gaultheria shallon*, and *Tsuga/Rhododendron/Linnaea borealis* community types. Moister stands belong to the *Tsuga/Acer circinatum/Polystichum munitum* community type. *Tsuga heterophylla-Abies amabilis* stands were classified in a separate Series.

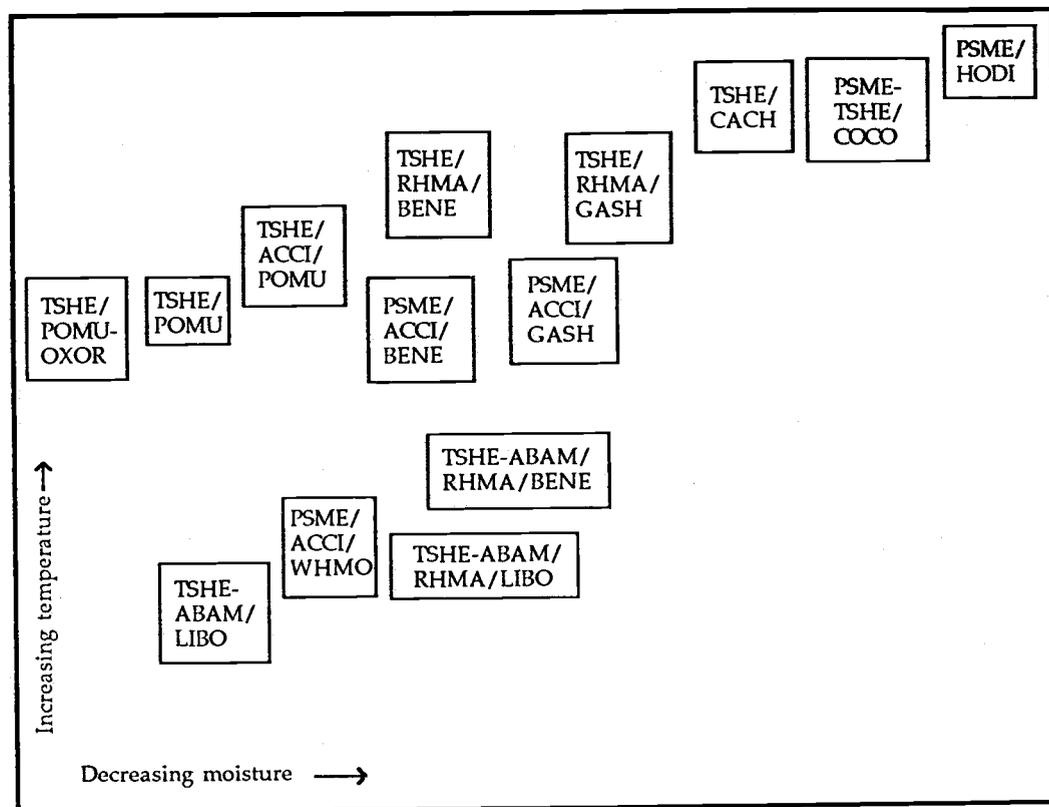


Figure 4. Inferred relative position along moisture and temperature gradients among forest communities of the *Tsuga heterophylla* Zone (after Dymess et al., 1974). Acronyms are given in Table 4.

Limpy Rock RNA is near the southern limit of the *Tsuga heterophylla* Zone in the Cascades. Franklin and Dyrness (1973) locate the limit at the divide between the North and South Umpqua Rivers. To the south is found the Mixed-Conifer Zone. Forests in the southern Cascades are northern extensions of Sierran montane communities.

A *Pseudotsuga menziesii*-*Tsuga heterophylla*/*Gaultheria shallon* community type is described from more mesic habitats in the South Umpqua Experimental Forest, 32 km (19 mi.) south of Limpy Rock. Although in the Mixed-Conifer Zone, community composition indicates this type has strong affinities with types in the *Tsuga heterophylla* Zone (Franklin and Dyrness, 1973).

Abbott Creek Research Natural Area is located 45 km (28 mi.) south of Limpy Rock RNA. There, stream terraces and the lower slopes of major drainages provide mesic habitat for an *Abies concolor*-*Tsuga heterophylla*/*Acer circinatum*-*Taxus brevifolia* community type. This type has high floristic similarity to *Tsuga heterophylla* Zone types (Mitchell, 1972; Mitchell and Moir, 1976). Farther south, in the Eastern Siskiyou Mountains, forest communities containing significant *Tsuga heterophylla* are apparently absent (Waring, 1969; Atzet, 1979).

Forest vegetation in the Oregon Coast Range has been studied by numerous investigators e. g., Spilsbury and Smith, 1947; Becking, 1954; Corliss and Dyrness, 1965; Bailey, 1966; Hines, 1971; Juday, 1976; Luoma, 1982; Hemstrom and Logan, 1986. Seven generalized climax associations within the *Tsuga heterophylla* Zone have been arranged along a moisture gradient by Franklin and Dyrness (1973). Very moist stands are typified by the *Tsuga*/*Polystichum*/*Oxalis* association; dryer sites by *Tsuga*/*Acer circinatum*/*Gaultheria*, and the driest sites are occupied by the *Pseudotsuga*/*Holodiscus*/*Gaultheria* association. When compared with similar communities from the Western Cascades, the Coast Range communities show a shift towards greater cover values for moisture-indicating species. Presumably, this reflects the overall lower moisture stress in the Coast Range.

Monotropoideae

The Monotropoideae is recognized as a sub-family of the Ericaceae by Wallace (1975a). In his monograph of the group, Wallace (1975b) recognizes ten genera, eight of which are monotypic, and twelve species, all achlorophyllous. The eight species which occur in western North America and Limpy Rock RNA are:

Allotropa virgata
Hemitomes congestum
Monotropa hypopithys
Monotropa uniflora
Pityopus californica
Pleuricospora fimbriolata
Pterospora andromedea
Sarcodes sanguinea

Mycotrophy

Since the plants are achlorophyllous their mode of nutrition is of interest. Fries (1832) has often been credited with the first description of the mycorrhizal roots of *Monotropa hypopithys* (MacDougal and Lloyd, 1900; Francke, 1934; Hatch, 1937; Björkman, 1960; Vreeland et al., 1981). This is a mistake, apparently traceable to MacDougal and Lloyd (1900). They may have misread Rylands' (1842, p. 347) quote of Fries' description of a smut parasite of *Monotropa* roots and stems or relied on secondary sources. This longstanding error was noted by Trappe and Berch (1985).

Unger (1840, in Trappe and Berch, 1985, p. 4) describes the relationship between the roots of *Monotropa hypopithys* and *Picea abies*. He concluded "... by virtue of the intimate root contact of the two plants, an exudation on the part of one and an ensuing absorption of the nutritious exudate on the part of the other ... a genuine dependent relationship ... take[s] place." He did not perceive the intermediating fungal connection. Lees (1841, p. 100) after observing a collection of *Monotropa hypopithys* from a beech forest states:

These hairy fibers, however, appear to me to be really part of the economy of the plant, imbibing nutriment from the rootlets of the beech, to which

they are closely applied, and conveying it to the succulent radicles of the *Monotropa*, with which they are also connected.

Lees rejected a fungal origin for the hairy fibers and considered *Monotropa* to be a direct root parasite, though he noted the hirsuture "... appears like a byssoid fungus." Rylands (1842, p. 343) described the mycelium on the roots of *Monotropa hypopithys*, but concluded the substance "... performs no essential function in the economy of the *Monotropa*." Vittadini (1842, in Trappe and Fogel, 1977) proposed that the fungal mantle of certain tree roots provided benefit to the tree. Kamienski (1881, 1882) established that *Monotropa hypopithys* is not a root parasite. He noted the complete envelopment of the roots by mycelium and the consequent necessity for *Monotropa* to obtain nutrients from the fungus. He felt the symbiosis was mutualistic, though what the fungus received, other than lodgement, was unknown. It was his opinion that the same fungus formed parasitic associations with nearby tree roots which were similar morphologically to *Monotropa* roots. The fungus then served as an intermediary in the nutrition of *Monotropa*.

The associations of the fungal mantle with tree roots of distinctive branching morphology were termed "Mykorrhizen" by Frank (1885). Frank (1887) further categorized "Mykorrhizen" of beech and pine trees as "ectotrophisch" or ectotrophic mycorrhiza, referring to the fungal mantle sheathing the root tips. By 1894 Frank's experiments had shown the presence of ectomycorrhizae to benefit the growth of pines (in Harley and Smith, 1983). Ectomycorrhizae are further characterized by hyphae from the fungal sheath penetrating between the cells of the root epidermis and cortex. Usually, little intracellular penetration by the hyphae occurs (Harley and Smith, 1983).

Oliver (1890), described the "...close-fitting sheath of fungal mycelium..." on the roots of *Sarcodes sanguinea* and noted "...that the roots here, as in *Monotropa*, display in a marked degree the phenomenon of Mycorrhiza..." (p. 307). However, he speculated that monotropes were "...dependent on organic matter in the substratum..." (p. 306) and that they "...obtain most of their food in the form of complex organic substances..." (p. 314). He considered *Sarcodes* to be a saprophyte because he considered its mycorrhizal fungus to be saprobic. He noted it had been impossible to cultivate the plants in botanic gardens, yet did not question why a "saprophyte" should be so difficult to cultivate.

The relationship of *Monotropa* to its root-fungi is considered to be strictly parasitic by Kerner (1894, p. 253): "If the mycelium subsequently withdraws any material whatever from the still living or decaying *Monotropa*, the process is only one of restitution and not of exchange". Since instances of fungi parasitic on flowering plants are so much more common, he believed the idea of a flowering plant as a mycoparasite was difficult for people to accept. He attributed some writers' regard of *Monotropa* as a root parasite or

saprophyte to this difficulty. In Kerner's concept, the mode of nutrition of the fungi is irrelevant when conceptualizing the mode of nutrition of *Monotropa*.

He does not state his view of the mode of nutrition of the fungi which form mycorrhizae with *Monotropa*, but he notes the significance of discussing the mycorrhiza of *Monotropa* in the same section as the mycorrhiza of some forest trees. Kerner (1894, p. 254) states: "As a parasite *Monotropa* ought to have been discussed at the same time as others in earlier pages, but it was not without intention that the description of this plant was reserved for this place..."; implying an agreement with Kamienski's (1882) view that the same fungi form mycorrhizae with overstory trees.

Groom (1895, p. 149) defines saprophytes as "...plants which are dependent for their existence on the presence in the substratum of decaying organic matter." MacDougal (1899, p. 2) states: "It is customary to designate all species that have lost the chlorophyll-apparatus as holosaprophytes." He proposed the term "symbiotic saprophytism" for the method by which a higher plant gains complex organic food-substances from fungi interposed with the "nutritive substratum."

In a study of roots and mycorrhizas of monotropes, MacDougal and Lloyd (1900, pp. 420-421) continue the concept that monotropes are symbiotic saprophytes by virtue of the assumed saprobic ability of their mycorrhizal fungi. For example: "...all energy of the plant in the form of organic substances is taken in through the roots by the co-operation of the sheathing fungus..." and "...the real absorbing organs are the branching strands and hyphae, which radiate from the sheathing mycelium..."

The confusing concepts as to the nutritional "status" of monotropes is reflected in Bergen's (1908) flora. In the description of *Monotropa* he leaves it up to the reader to choose whether the plants are "...root parasites or saprophytes or fed by slender fungus threads which cluster on the roots." This does illustrate his conceptual distinction between saprobic and mycotrophic existence, though he is unsure as to which to apply to *Monotropa*.

In a morphological and taxonomic study of the Pyroloideae and Monotropoideae, Henderson (1919) accepts without comment MacDougal's concept of symbiotic saprophytism. Peklo (1908), Neger (1913), Rexhausen (1920), and Christoph (1921) expressed similar concepts of the nutritional mode of monotropes (in Björkman, 1960). The acceptance of the concept is expressed by Coulter et al. (1911):

The relation here pictured also has been termed *symbiotic saprophytism*, since the relation of the symbiotic complex to the soil is saprophytic. Most cases of so-called holosaprophytism in the higher plants (such as in

Lycopodium, *Monotropa*, and *Corallorhiza*) are to be referred to symbiotic saprophytism or mycophytism.

The only report of successful germination of monotrope seeds is that of Francke (1934). His study revealed many important insights into the biology of *Monotropa hypopithys*. The process of fungal mantle formation on germinated seedlings was observed. Haustorium-like hyphae which penetrate epidermal cells were described. He cultivated the fungus from the mantle and found it was unable to use cellulose or starch but depended on soluble carbohydrates. Nevertheless, he thought the fungus was saprobic on humus and used the term "holosaprophytische" to describe the nutritional strategy of *Monotropa*. He reviewed Oliver (1890) and MacDougal (1899) and apparently accepted the concept of symbiotic saprophytism. Francke did note the symbiosis was very one-sided in favor of *Monotropa*.

Weaver and Clements (1938) considered *Monotropa uniflora* to be parasitic on its mycorrhizal fungi. They did not comment on the nutritional strategy of the fungi.

The taxonomic and morphological studies of Copland (1934, 1935, 1937, 1938, 1939, 1941) and Doyel and Goss (1941) refer to members of the Monotropoideae simply as saprophytes. They were well aware of the mycorrhizal condition of the plants and followed Oliver (1890) and MacDougal's (1899) concepts.

It appears that Oliver's speculation, amplified and named "symbiotic saprophytism" by MacDougal, developed into a nearly teleological argument which, for many, hindered thought and inquiry concerning the nutritional biology of monotropes.

Romell (1939) offered an alternative view. Of the authors reviewed here, he refers only to Francke (1934). It is not known if he was expressly refuting the concept of symbiotic saprophytism. Romell noted research had shown that ectomycorrhizal fungi of forest trees obtain carbohydrates from the trees and that the mycotrophic roots of *Monotropa* are entangled with tree mycorrhizae. He concluded: "The writer ventures the hypothesis that the monotropas are energetically epiparasites on woody plants associated with the same fungus. This could be tested by trenching experiments." (Romell 1939, p. 166).

The textbook portrayal of monotropes as plants which absorb nourishment from decaying organic matter in the soil received comment from Herrick (1957). He concluded the saprophytic "status" of *Monotropa* in some texts could be traced to Luxford's (1842) suggestion that nourishment was obtained from the humus. However, Luxford's concept was not the same as "symbiotic saprophytism" in which the presence of the fungus is understood. Herrick rejected the use of the term saprophyte and maintained monotropes

are best considered parasites, noting that if the fungus receives some benefit the symbiosis would be mutualistic.

Bakshi (1959) studied the ecology and morphology of *Pterospora andromedea*. Attempts to isolate the mycorrhizal fungi were made. Root segments were washed and placed on agar. When the hyphae which grew from the roots on the agar were severed from the root the hyphal tips ceased growing and degenerated after thirty-six hours. This suggested some type of dependency on the *Pterospora* root.

He also reviewed the various concepts concerning the nutrition of monotropes. Of twenty-one mainly floristic works, only one was found to consider *Pterospora* other than a saprophyte or root-parasite. Gleason (1952) described *Pterospora* as parasitic on soil fungi. Bakshi concluded *Pterospora* is "parasitic on the root fungi" (p. 216) and if the reciprocal aspects of the relationship (monotrope to fungus) were over-emphasized, then *Pterospora* would be a "symbiotic" parasite rather than the "symbiotic saprophyte" of MacDougal (1899).

Apparently, Bakshi had not read Romell (1939) nor appreciated the subtle suggestions of Kamienski (1882) and Kerner (1894) with regard to the similarity between the mycorrhizae of forest trees and *Monotropa* and the potential for nutrient flow.

The hypothesis of Kamienski (1882) and Romell (1939) — that the mycorrhizal fungi of *Monotropa hypopithys* also form mycorrhizae with overstory trees, thereby acting as a nutrient bridge between the two — was tested by Björkman (1960). First, *Monotropa* plants were isolated from tree roots with sheet metal. The following year the isolated plants showed no or very weak growth of flowering stems. Untreated plants developed normally.

In the next experiment, ^{14}C -labeled glucose was induced into the phloem of pine and spruce trees. Within five days *Monotropa* plants near the trees showed radioactivity 3 to 10 times above background radiation. Finally, ^{32}P was used in a similar experiment. *Monotropa* received significant amounts while surrounding chlorophyllous vegetation received little or no radioactive ^{32}P .

Björkman (1960) also isolated a fungus from the roots of *Monotropa* and used it to form ectomycorrhizae with pine seedlings. Extracts from *Monotropa* were found to have a "powerful stimulating effect" on growth of cultures of the fungus and on cultures of *Boletus* spp.

In order to counter the deeply ingrained concept of monotropes as "symbiotic saprophytes", Björkman (1960, p. 323) emphasized Romell's (1939) concept of epiparasitism: "*Monotropa* is accordingly to be regarded chiefly as an epiparasite on the roots of certain trees with ectotrophic mycorrhizae." Björkman stressed the role of the

shared mycorrhizal fungus. He found it to be non-saprophytic. The fungus, in effect, provides a nutrient bridge by obtaining its energy from trees, and then giving up energy to *Monotropa*. One result of this definitive study could have been the elimination of the commonly held idea that monotropes were saprophytic.

However, teleological arguments do not die easily. Harley (1969), even while relating the work of Björkman (1960), refers to monotropes as saprophytes. This leads to confusion on the part of the reader as to what Harley's concept of "saprophyte" entails.

Furman (1966) tested the reciprocal nature of the monotrope/fungus relationship. He injected ^{32}P into flowering stems of *Monotropa uniflora* and found it passed into the ectomycorrhizae of *Quercus*.

Went (1971) referred to *Pterospora andromedea* as a saprophyte, partially in the tradition of MacDougal (1899). He claimed the decomposer fungi *Mucor* and *Penicillium* form mycorrhizae. His conclusion is based only on xenic culture of litter, roots and rhizomorphs in "moist cool chambers" and on agar. No mycorrhizal syntheses with the fungi and potential hosts were attempted. There is no basis for his conclusion, here or in the literature.

Furman and Trappe (1971, p. 219) clarified the conceptualization of the nutritional mode of monotropes:

Productivity rates of most such [achlorophyllous] plants cannot be satisfactorily explained by the saprophytic niche which is often assumed as theirs but is inadequately nutritious. Rather, they parasitize their mycorrhizal fungi. When a mycorrhizal fungus is shared by roots of an achlorophyllous angiosperm and those of a photosynthesizing plant the former can indirectly parasitize the latter via the connecting mycelium (epiparasitism).

In the tradition of Kamienski (1882), Romell (1939), and Björkman (1960); Furman and Trappe conceptualize the niche of monotropes as being mycotrophically determined, requiring the presence of compatible fungi which are mycorrhizal with autotrophic plants.

Despite the work of Björkman and the others, MacDougal's (1899) concept persisted. Smith (1973), Hitchcock and Cronquist (1973), and Steele and Stickney (1974), use the term "saprophyte" when referring to monotropes. Khan (1972, p. 188) blended the two concepts with "saprophytic epiparasitic." Daubenmire (1974, p. 317), however, adopted Björkman's (1960) concept and further stated: "There is no evidence vascular plants are ever saprophytes."

Jimerson's (1980) report on *Pityopus californica* illustrates the confused state of concepts even at this late date. He first presents monotropes in the conceptual traditions of

Lees (1841) and Rylands (1842): "This group of achlorophyllous plants...are (sic) saprophytic (feeding on dead plant material) or parasitic (feeding on live plants)." He then goes on to present its actual mycotrophic niche (cf. Björkman, 1960). A textbook (Raven et al., 1981) describes the "recent discovery" of nutrient transfer from tree through fungus to *Monotropa*. The previous editions treated *Monotropa* as a saprophyte. Abandoning traditional concepts seems to be intimidating.

Vreeland et al. (1981) reported experiments similar to Björkman's (1960). Four ectomycorrhizal tree species were supplied with ^{32}P to the phloem. Subsequent transfer of radioactive phosphorus to *Sarcodes sanguinea* was demonstrated.

Conard and Radosevich (1982) refer to monotropes as "root parasites." It is unclear if they intend a literal interpretation or if they are transforming the concept of "epiparasite". Similarly when "saprophyte" is used, the concept could be different from MacDougal's, in which the presence of the fungus was acknowledged. Many users of "saprophyte" may have a concept similar to Luxford's (1842), in which *Monotropa* was thought to absorb complex organic substances directly from the humus.

Under the heading "Saprophytic Herbs", Barrows (1984, p. 22) states monotropes "...are known to require a symbiotic fungus to grow in association with their roots, which enables them to obtain nutrients from the soil." This statement seems to have a direct link with MacDougal's concept.

Harley and Smith (1983, p. 261) do nothing to lessen the confusion by referring to monotropes as "holosaprophytes" (cf. Groom, 1895). This is done in the context of reviewing research which shows that the roots of monotropes are sheathed by mycorrhizal fungi, and that the fungi obtain their nutrients in mycorrhizal associations with overstory trees.

Harley and Smith (1983) point out that discussion on nomenclature may be pedantic unless it leads to clearer questions, experiments and answers. The preceding discussion documents the existence of a persistent, confusing, nearly teleological argument which presented monotropes as "saprophytes"; an argument which hindered the development of clear concepts of the nutritional "status" of the Monotropeidae. Such a situation cannot be helpful to the formulation of clear questions and experiments.

The confusion stems from the tradition established by MacDougal's (1899) concept of "symbiotic saprophytism." Some workers ignored tradition and treated monotropes as parasites of their mycorrhizal fungi. Björkman (1960) chose to emphasize the role of the fungus as a nutrient bridge and applied Romell's (1939) concept "epiparasite" to *Monotropa*.

By using Mason and Langenheim's (1957) concept of "operational environment" confusing terminology can be eliminated, and communication facilitated. Mason and Langenheim (1957, p. 325)

...have become convinced that where controversy reigns for long periods in science, in spite of the discoveries and new techniques developed by generations of scientists, the difficulty is probably not so much inherent in the material as in the language in which it is being discussed.

Through analysis of the concept "environment" they determine that "...only those phenomena that actually enter a relation with a particular organism, constitute the environment of that organism..." (Mason and Langenheim, 1957, p. 330). "Indirect factors" which do not enter directly in reaction with an organism are excluded from the concept of operational environment.

To introduce indirect factors into causal relations within the environment is to introduce an infinite regress into the system of explanation....The only reaction the organism makes is directly with the phenomenon of the environment as it finds it at the moment of reaction [p. 336].

They recognize that indirect relations of an organism are equally important and necessary to understand. "This in no sense diminishes the importance of these facts; it only places them in a context in which they are important and removes them from a context in which they can only serve to confuse" (p. 336).

When considering members of the Monotropoideae, using the operational environment concept, their mode of nutrition involves a direct relation only with their mycorrhizal fungi. The mode of nutrition of these fungi is irrelevant to the operational environment of a monotrope. Whether the fungi are saprobic, pathogenic or mycorrhizally nourished is within the realm of the operational environment of the fungi.

The experimental evidence reviewed shows that the fungi involved have little saprobic ability and are ectomycorrhizal with autotrophic plants. Hence, the concept "epiparasite" can be used to describe an indirect relationship in the life history of monotropes. "Epiparasite" is not appropriately used in the context of the nutritional mode of monotropes. Members of the Monotropoideae can be viewed as parasites of their mycorrhizal fungi. Some evidence showed that growth of the fungi was stimulated by the presence of monotropes. Gogala (1972) discovered two cytokinins in *Monotropa hypopithys* which enhance the growth rate of ectomycorrhizal fungi. Since the term "parasite" has negative connotations, the terms "obligate mycotroph" and "mycotrophic" may be preferred. This, essentially, is the view offered by Furman and Trappe (1971). "Mycotrophic" could be strictly applied to only those organisms which depend on fungi for

energy. However, the term has long been used in a broad sense interchangeably with "mycorrhizal."

Questions concerning the transfer of nutrients from fungus to plant fall within the realm of the operational environment. Francke (1934) described hyphae from the fungal sheath and Hartig net as forming haustoria and penetrating (one per cell) the epidermal cells of the *Monotropa* root. The tip of the haustorium swells and bursts. The contents are then digested and the haustorium sealed off. Francke viewed this process as the major means of nutrient transfer. Campbell (1971) reports similar observations for *Monotropa uniflora* and *M. hypopithys*. Lutz and Sjolund (1973) found inward projections of the root cell wall in the region of fungal invasion and note the similarity to transfer cells described by Gunning and Pate (1969). Those cells transfer material from one cell to another.

Recently, more refined interpretations of the process with *M. hypopithys* are presented by Duddridge and Read (1982) and with *Pterospora andromedea* and *Sarcodes sanguinea* by Robertson and Robertson (1982). Mainly because the epidermal cell wall is not breached but invaginates around the intruding hypha, they conclude the hyphal intrusion into the cell is not a true haustorium. They term the intrusion a "fungal peg." The development of fungal pegs, which induce the outer cortical cells to function as transfer cells, was followed ontogenetically. The number of cells with fungal pegs increases rapidly as shoot elongation occurs. Duddridge and Read (1982) describe fungal cytoplasm "bursting" into a "membranous sac" made up of the cortical cell plasmalemma. During flowering most outer cortical cells contain "burst" pegs. During shoot senescence, degeneration of the fungal sheath and Hartig net occurs. Robertson and Robertson (1982) contend the contents of the membranous sack are not identical to the contents of the fungal peg.

Duddridge and Read (1982) and Robertson and Robertson (1982) agree that the mycorrhizae of monotropes are different from those of *Arbutus* and *Pyrola* which exhibit extensive intracellular penetration in the outer cortical cells. Such ectendomycorrhizae have been classified as "arbutoid" (Harley and Smith, 1983). Duddridge and Read (1982) proposed a separate class "monotropoid" for the mycorrhizae of *Monotropa*. Robertson and Robertson (1982) concur for *Pterospora* and *Sarcodes*.

Since the fungal peg does not breach the cell wall during the active period of symbiosis, monotropoid mycorrhizae may be viewed as a modification of the typical ectendomycorrhizae that the shared fungi form with autobionts. The term "ectendomycorrhizae" is used as a descriptive name for a heterogenous group of mycorrhizae which exhibit various combinations and development of the fungal sheath, Hartig net, and coiled hyphae within cortical cells (Harley and Smith, 1983).

Encompassing monotropoid mycorrhizae by the term "ectendomycorrhizae" could obscure functional and evolutionary relationships.

Synecology

Relatively few community ecology studies of monotropes have been conducted. Howell (1950) (regarding the plants as saprophytes) provides an account of the life history of *Pityopus* through a growing season. The plants were growing in a dense *Abies grandis*-*Pseudotsuga menziesii* forest with little understory. A bumblebee (*Bombus* sp.) was observed working the flowers. Initial collections were kept for a month, during which time the flower buds developed and bloomed. Utilization of stored nutrient reserves was indicated. This agreed with Björkman's (1960) finding that some *Monotropa* isolated from tree roots were able to develop weakly the following year.

A great deal of animal predation of the plants during the season was noted. It was necessary to put wire mesh cages over plants to ensure the development of mature fruit. Howell expected the fruit to be a capsule but found it to be a berry. The odor of the mature plants was said to resemble overripe Brie cheese. The odor "...would undoubtedly be attractive to some animals..." (Howell, 1950, p. 60). Which animals were involved as potential seed vectors was unknown.

Pterospora andromedea, as noted by Bakshi (1959), occurs in almost all temperate coniferous forests in North America. Bakshi specifically recorded it in northern Idaho and adjacent Washington in five plant associations (cf. Daubenmire and Daubenmire, 1968):

- 1) *Pinus ponderosa*/*Physocarpus malvaceus*
- 2) *Pseudotsuga menziesii*/*Physocarpus malvaceus*
- 3) *Picea engelmannii*-*Abies grandis*/*Pachistima myrsinites*
- 4) *Thuja plicata*/*Pachistima myrsinites*
- 5) *Tsuga heterophylla*/*Pachistima myrsinites*

Attempts to germinate seeds were conducted with 33 treatments, each with 45 lots of 250 seeds. None of the 370,000 seeds germinated. Bakshi's (1959) biochemical tests showed seeds to be viable for 3 to 9 weeks. The smallest shoot he found in nature was 3 mm tall, 5 mm wide, and attached to a mass of roots 11 mm in diameter.

In greenhouse transplant studies, all potted *Pterospora* died within four days. Attempts to transplant *Pterospora* upto a distance of 15 m from growing sites were also unsuccessful. Bakshi (1959) concluded *Pterospora* has a wide ecological amplitude, but abundance is restricted by specific germination requirements and sensitivity to disturbance.

Riley and Eichenmuller (1970b) report *Monotropa uniflora* from four different tree cover types in West Virginia. The month during which *Monotropa* attained maximum scape height is shown in parentheses:

- 1) *Carya glabra*-*C. alba* (July)
- 2) *Sassafras veriifolium* (August)
- 3) *Tsuga canadensis*-*Betula lutea* (Sept.)
- 4) *Quercus velutina*-*Q. muhlenbergii*-*Q. alba* (Oct.)

All of these trees belong to genera reported to have ectomycorrhizal species (Trappe, 1962).

Campbell (1971) in a Michigan study, reported *Monotropa uniflora* under single species of trees growing in groves. The size of the "pure" groves was not given. The trees were: *Fagus grandifolia*, *Acer saccharum*, *Quercus rubra*, *Pinus strobus*, and *Tsuga canadensis*. She also found *Monotropa hypopithys* growing under *Betula papyrifera*, *Picea glauca*, *Populus grandidentata*, and *P. tremuloides*. Various unknown fungi formed ectomycorrhizae with the trees and *M. hypopithys*.

The association of *Sarcodes sanguinea* with other plants was investigated in Nevada by Vreeland (1975) who reported finding *Sarcodes* in moist meadow, grassy meadow, and brush habitats. Of ten forested habitats, *Pinus jeffreyi* was the dominant tree in six and co-dominant with *Abies concolor* in one. *Pinus contorta* var. *latifolia* dominated two habitats and *Populus tremuloides* one. No conclusions were reached regarding the synecology of *Sarcodes*.

The clumped distribution of plants suggested *Sarcodes* could reproduce vegetatively. The perennial root mass of *Sarcodes* may be 60 cm in diameter (Wallace, 1975b). Only annual flowering stems appear above ground. A definition of how flowering stems were considered to represent "the plant" should have been made. Did Vreeland (1975) consider each flowering stem a "plant"? Although the relationship between "plants" and "locations" was unclear, it was noted that the recurrence of plants at their original locations declined to 40% after one year, and to 24% after two. However, the total number of plants in the study areas was greater in years two and three of the study.

Wagner (1979) made a field study of *Pityopus californica* in a fifty year old *Pseudotsuga menziesii* forest in Oregon. Occasional *Thuja plicata* of the same age were scattered in the forest. The area was clear-cut and burned shortly before 1929. Occasional hardwoods were *Acer macrophyllum*, *Cornus nuttallii*, and *Castanopsis chrysophylla*. Tree reproduction was dominated by *Tsuga heterophylla*. There was a prevalence of *Gaultheria shallon* over *Polystichum munitum* and *Berberis nervosa*. *Pityopus* sites were characterized by a lack of dense understory. Wagner conceptualized a *Pityopus* "plant" as

being a discrete group of one or more flowering stalks. Other monotropes sparingly present were: *Monotropa hypopithys*, *Hemitomes congestum*, and *Pleuricospora fimbriolata*.

As reported by Howell (1950), Wagner (1979, p. 5) also found small mammals grazed heavily on the plants: "On 20 July only a pit remained where the flowering stalks [15] had been and rodent trails had entrances in this pit." He found that by September, 50% of the fruits had been grazed or removed. *Hemitomes* was also grazed. The mature fruits had a strong "musky-yeasty" odor. Trails and holes of small mammals were common around plant sites; evidence that small mammals are potential seed dispersal vectors.

The study covered two seasons. Of the total 55 plants, 18 were observed in both years, 20 plants in the first year only, and 17 plants in the second year only. Of the 18 observed in both years, 5 had fewer stalks, 7 an equal number, and 6 increased. Wagner hypothesized the non-recurrence and "new" occurrence of flower stalks could be accounted for in four ways:

- 1) Death of plants
- 2) Subterranean predation of immature stalks
- 3) Plants not producing stalks every year
- 4) First production of flowering stalks

Wagner proposed continued study of the dynamics of this population.

H. Vreeland's (1980) record of *Sarcodes* population levels in the Nevada study area is of interest. Over the five year study period, the number of snow plants in locations was relatively stable with an average of 180 and extremes of 159 and 204 "plants". He also noted that the root mass of *Sarcodes* contains immature buds of flowering stalks. The different sizes of the buds suggested that the maturation process may cover more than one year.

Jimerson (1980) reported *Pityopus californica* from various conifer and hardwood forests in northwest California, but no specific data are presented. Heavy predation of flower stalks is also reported but, again, no data are presented. Contrary to other workers, he feels mycorrhizal fungi are not limiting to the occurrence of *Pityopus* "...due to the prolific spore production and efficient spore dispersal mechanisms..." (p. 12). No data as to the identity of the fungi or spore production and dispersal efficiency were presented to substantiate the conclusion.

Vreeland et al. (1981) report differential transfer rates between *Sarcodes sanguinea* and different tree species including *Pinus jeffreyi*, *Abies concolor*, *Pinus contorta* v. *latifolia*, and *Populus tremuloides*. Their data are difficult to interpret because the first

monitoring of radioactivity did not occur until seven days after injection of the trees. This information had to be calculated from the distance and transport rate data of P. Vreeland (1980). Neither P. Vreeland (1980) nor Vreeland et al. (1981) specifically state the time elapsed before the monitoring of individual *Sarcodes*. The distances transported at the time of the first monitoring ranged from 0.5 to 5 m. The "slower" transport rates could be underestimated by an order of magnitude. This situation was not discussed in their results.

Luoma (1982) reported on a large population of *Pleuricospora fimbriolata* in the Oregon Coast Range associated with a 90-year-old *Pseudotsuga menziesii*/*Acer circinatum*/*Polystichum munitum*-*Gaultheria shallon* community. Friedman (1982) studied the same *Pleuricospora* population, finding shrub abundance (density) and cover to be the most effective separators of *Pleuricospora* presence/absence. Number of flowering stalks increased with increase of soil pH from 5.2 to 5.9. At another study site in the Oregon Cascade Range with an old-growth *Pseudotsuga* overstory, Friedman (1981) found that in plots where *Berberis nervosa* cover was greater than 300 cm²/19.2 m (line intercept) *Pleuricospora* was absent.

Vreeland hypothesis

In a continuation of his 1975 studies, H. Vreeland (1980, p. 2) attempted to "...establish a rank ordering of tree species with respect to relative importance to Snow Plant [*Sarcodes sanguinea*] occurrence...." He first tried to apply the theory of island biogeography (MacArthur and Wilson, 1967) to the distribution of *Sarcodes* in the forest. The island model of analysis was determined to be inappropriate for his data.

In the second part of his study, Vreeland established "Experimental Locations" containing populations of *Sarcodes*. "Experimental Sites" were established within each Location by establishing a circle 1.5 m in radius about each *Sarcodes* "plant" as it emerged from the ground. Ninety-three "Experimental Sites" were established, but there were 163 "Snow Plants". No explanation was given as to why the number of "plants" greatly exceeded the number of "Experimental Sites", nor is an operational definition of "Snow Plant" given. The tree species, diameter-at-breast-height (dbh), and distance to all trees within 10 m of each "Experimental Site" were recorded.

For analysis of the data, two statistical terms "Influence Factor" and "Consistency Factor" were developed. The influence factor (IF) was obtained by multiplying the dbh of a tree times an inverse distance weighting factor. The consistency factor (CF) for a tree species was computed as the number of sites in a location with the tree species (S_i) present

within 10 m, divided by the total number of sites in the location (S), multiplied by the total number of *Sarcodes* found in the location (N_S); or $S_t/S \times N_S = CF$ for tree species t.

For example:

Location "A" might have nine sites,	$S = 9$
<i>Abies concolor</i> might occur within	
ten meters of six sites,	$S_t = 6$
The total number of <i>Sarcodes</i> within	
the location might be sixteen,	$N_S = 16$
CF (ABCO) at location "A" = $(6/9) \times 16 = 10.67$	

The consistency factor was meant to measure of the "preponderance" of one tree species relative to the number of *Sarcodes*. It is actually a qualitative relative frequency (presence/absence) measure, not a preponderance (quantitative) measure. Such relative qualitative parameters have limited information value (Mueller-Dombois and Ellenberg, 1974). Multiplication of the relative frequency (S/S_t) by N_S confounds the precise meaning in the index. Different relative frequencies could have the same CF index value.

Conversely, different CF values could contain the same relative frequency values.

H. Vreeland (1980) used step-wise regression to analyze the data. The number of snow plants in a location (N_S) was treated as the dependent variable. The influence factor (IF) and consistency factor (CF) of four tree species (*Abies concolor*, *Pinus jeffreyi*, *Pinus contorta* v. *latifolia*, *Populus tremuloides*) were treated as independent variables. The full model had a coefficient of multiple determination (R^2) of 0.99.

He then subjectively selected various combinations of four and six of the independent variables and developed regression models with R^2 values ranging from 0.85 to 0.96. Vreeland subjectively decided that a model using IF *Abies concolor*, CF *A. concolor*, IF *Pinus jeffreyi*, and CF *P. jeffreyi* as independent variables was the "best" for "predicting" "Snow Plant" occurrence ($R^2 = 0.94$).

Vreeland's approach contains many flaws. Only the most important will be addressed.

1. The consistency factor does not distinguish between the relative contribution of S_t/S and N_S to the CF index. As pointed out by Goodall (1970) it is generally preferable to enter variables separately in regression analysis.
2. The consistency factor (CF) contains the term N_S which is the number of "Snow Plants" in a location which is the dependent variable. In cases where the relative frequency is 100%, the dependent variable is entered as an independent variable (CF). CF *Pinus jeffreyi* alone had a correlation coefficient (r) of 0.91 with N_S . *P. jeffreyi* was present in all but one location

and since the CF value can be N_S the resulting high correlation is an artifact of the method.

3. As previously noted, "Snow Plant" is not defined. "Experimental Sites" were said to be defined by "a circle 1.5 m in radius about each Snow Plant" (p. 14) but there are 70 more snow plants than sites. This situation is not explained.
4. The number of observations (10) is not substantially larger than the maximum number of potential parameters (8).
5. No criteria for selecting the "best" set of independent variables were followed (e.g., R^2_p , MSE_p , C_p , F^* ; Neter and Wasserman, 1974). Vreeland claimed to use R^2 as a criterion for model selection. Use of R^2_p would indicate CF *Pinus jeffreyi*, IF *Abies concolor*, and IF *Pinus contorta v. latifolia* as the independent variables of choice ($R^2=0.99$). However, he subjectively chose another model ($R^2=0.94$) based on preconceived ideas from the results of other research (P. Vreeland, 1980). The significance (probability of Type I error) of any of the models is not reported.
6. The IF and CF for a species are highly intercorrelated, having r values of 0.74 to 0.96. When the main purpose of regression analysis is to assess the effects of each of the independent variables (here to be ranked as to importance to snow plant occurrence), multicollinearity is a serious problem. "Thus a regression coefficient does not reflect any inherent effect of the particular independent variable on the dependent variable but only a marginal or partial effect..."(Neter and Wasserman, 1974, p. 252). Furthermore, "...the regression coefficients may be subject to large roundoff errors as well as large sampling variances" (Neter and Wasserman, 1974, p. 347). Testing of the statistical significance of intercorrelated variables must be done carefully. In Vreeland's study no significance tests were done or were not reported.
7. Use of the influence factor in the analysis was invalid as is shown in part of the present study and will be presented in the Results and Discussion.

It appears CF *Pinus jeffreyi* is the basis of the entire regression model. Yet, this index merely reflects the widespread occurrence of *Pinus jeffreyi* in the study area. Additional parameters may do little to explain or reduce the variance. Without more information, Vreeland's conclusion that his model is "...accurate in predicting Snow Plant presence and number..." (p. 52) cannot be accepted; the fundamental flaw being that the "independent" variables cannot be measured without knowledge of the dependent variable (presence of Snow Plants).

Fungal Symbionts

The identity of fungi forming mycorrhizae with members of the *Monotropeoideae* has received some attention over the last 100 years. Reess (1885) observed *Elaphomyces granulatus* associated with *Monotropa hypopithys* (in Trappe and Berch, 1985). Trappe (1976) reported the same fungus associated with the roots of *Monotropastrum humile* (a species of Japan and eastern Asia). *Boletus* spp. have been reported as probable associates of *Monotropa hypopithys* by Francke (1934) and Björkman (1960). Khan (1972) traced direct hyphal connection between *Boletus* sp. and *Monotropa hypopithys*. Sterile mycelium of a fungus found on the roots of *Monotropa hypopithys* was shown to be strongly antagonistic to the root rot fungus *Heterobasidion annosum* (Trofast and Wickberg, 1977).

Campbell (1971) reports visually observing rhizomorphs of a fungus assumed to be *Armellaria mellea* connecting the mycorrhizae of *Monotropa uniflora* with rotting wood and parasitized tree roots. *Armellaria* has been reported to form endomycorrhizae with orchids, but Warcup (1981, p. 61) points out that a: "...problem is that *Armellaria* rhizomorphs tend to invest any plant structures in their vicinity whether [they be] roots, potato tubers, carrots, etc., so presence of rhizomorphs is not necessarily proof that the fungus is mycorrhizal...". Campbell (1971) concludes *Monotropa* can also form mycorrhizae with saprobic/parasitic higher fungi. No attempts to isolate, culture or synthesize mycorrhizae with the fungus were made. Although intriguing, her conclusion must be regarded as tentative.

Riley and Eichenmuller (1970a) found apothecia on the ectomycorrhizae of *Monotropa uniflora*. The fungus belonged to the order Helotiales (Ascomycotina) and was to be tested for mycorrhizal formation potential. However, Kerns and Finocchino (1983) described a similar fungus (*Hymenoscyphus monotropae*) as a probable parasite of *Monotropa uniflora*. Riley et al. (1987) reported on the culture of their fungus (as *Peizizella*) but have yet to test for mycorrhizal formation potential.

Castellano and Trappe (1985) observed sporocarps directly connected to fungal mantles of monotropoid roots: *Elaphomyces muricatus* associated with *Monotropa hypopithys* and *Truncocolumella citrina* with *Pleuricospora fimbriolata*. They also noted *Rhizopogon vinicolor* mycorrhizae on *Allotropa virgata*, *Pleuricospora fimbriolata*, and *Hemitomes congestum*; and minor amounts of *Cenococcum geophilum* mycorrhizae on *Pleuricospora fimbriolata*, *Pterospora andromedea*, and *Hemitomes congestum*.

METHODS

Vegetation

Field Methods

The vegetation reconnaissance method developed by Franklin et al. (1971) was adapted for use in this study. Vegetation was systematically sampled with eighty-one, 500 m² circular plots (Hawk et al., 1979), to obtain an unbiased sample of the major variations in vegetation. Seventy-six plots were located at approximately 120 m intervals along four transects and five plots were located in selected stands. The transects ran from southwest to northeast (54°, TN) through the RNA, approximately perpendicular to the trend of the major ridges. Transects were parallel and were spaced approximately 400 to 800 m apart. Transects and plot locations were recorded on a topographic map (Figure 5).

Plots were located systematically (with few exceptions) and without consideration of the degrees of floristic homogeneity or stand development. Often this approach has been avoided because it is assumed to produce so much variation in the data that classification of community types is very difficult (Mueller-Dombois and Ellenberg, 1974); however, this approach is consistent with the goal of examining the existing vegetation rather than the erection of more abstract "climax association" or "habitat type" classifications.

Plot placement was subjectively modified only when obvious excessive external heterogeneity would be introduced by strict systematic placement. At such points, the plot was moved forward or backward along the transect the minimum distance necessary to exclude the discordant element. Such discordant elements might be non-forest vegetation, geologic substrate boundary, abrupt change in slope, fire boundary (structure), logging boundary, and, in one case, the near impossibility of establishing a plot in a gigantic pile of windthrow. The degree of internal homogeneity in species composition, *per se*, in and around a plot was not a criterion for moving a plot. The location of major ecotones along the transect was noted. Additionally, five plots were installed to record vegetation of special interest, not encountered on the transects (plots # 69 - 72, 81).

Site physical measurements for each plot included: elevation, slope, aspect, landform, and soil characteristics determined as described in Hawk et al. (1979). Trees were recorded by species and percent cover by diameter class and height class. Shrubs and herbs were recorded by species and percent cover. Cover values were estimated at the following levels: 0.01%, 0.1%, nearest 1% from 1 to 10%, nearest 5% above 10%.

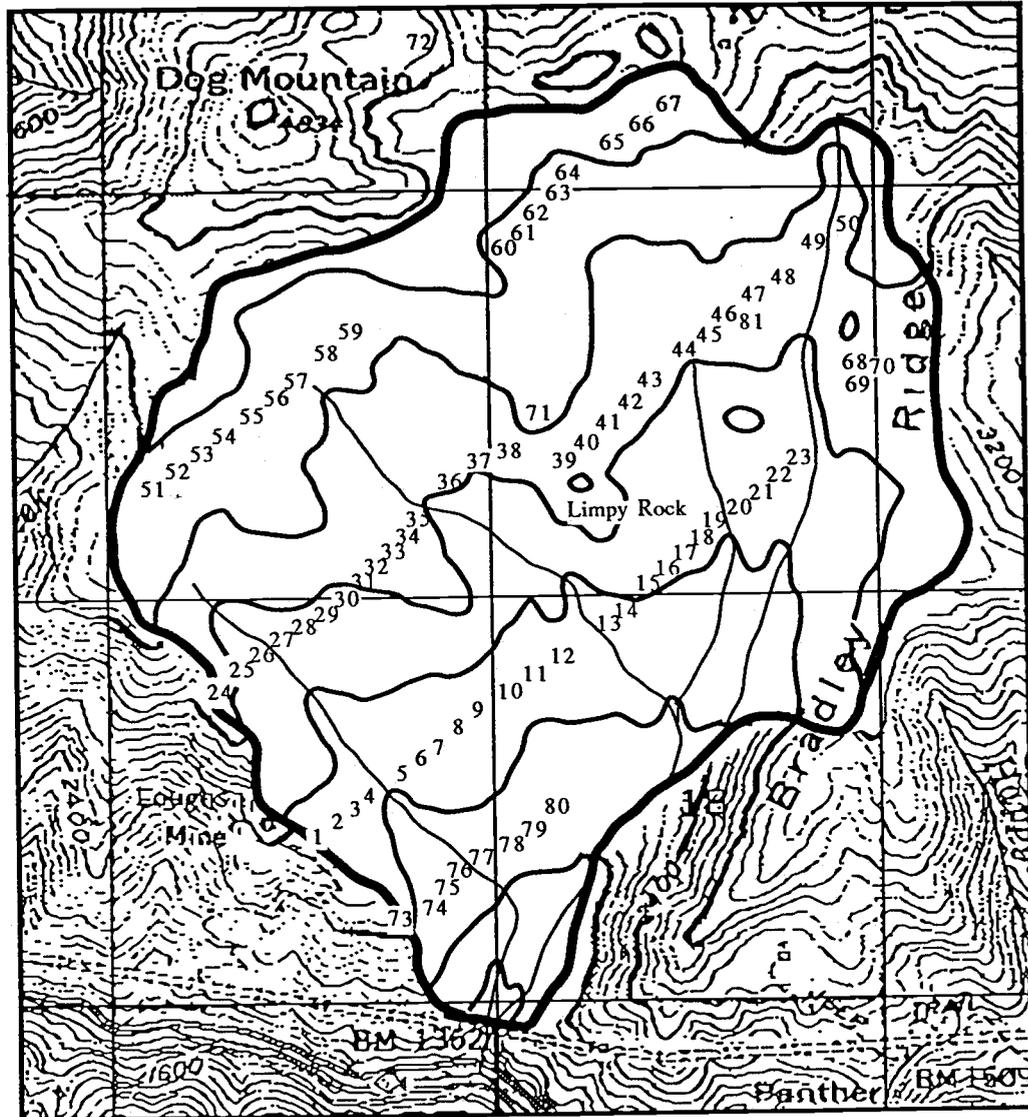


Figure 5. Vegetation transects with approximate plot locations (numbered) in Limpy Rock RNA. Major contour interval is 400 ft. (120 m).

One dominant tree per plot was cored and its height and dbh recorded. If a stand contained post-fire mature trees and trees remnant from fires, fire scars were carefully searched for and a dominant post-fire tree cored. This permitted analysis of vegetational trends considering the amount of time since the last fire. Some fire-scarred stands were intact with no mature post fire trees. To get a good core in that situation, the tree which seemed least damaged was sampled. Cores were stored in labeled straws and the rings were later counted using a stereoscopic microscope. One measurement of basal area was taken per plot with a 4.9 factor metric prism.

Analytical Methods

To increase the influence of attributes (species) which would be obscured by the overall dominance of *Pseudotsuga menziesii* or *Berberis nervosa*, percent cover was transformed to an octave scale (Gauch, 1982). Plant communities were classified into community types using a combination of two analytical computer programs, TWINSPAN and TABORD. TWINSPAN is a polythetic divisive method of classification providing a two-way table in which species as well as samples are classified (Hill, 1979a). TABORD (Maarel et al., 1978) is a program for structuring phytosociological tables according to floristic similarity. Vegetation data were ordinated with DECORANA to provide environmental interpretation and as a means of displaying classification by superimposition of the classification upon the ordination. Nomenclature generally follows Hitchcock and Cronquist (1973), or occasionally Peck (1961) for species not covered in the former. The following nomenclatural changes are accepted: *Maianthemum racemosum* and *M. stellatum* for *Smilacina racemosa* and *S. stellata* (LaFrankie, 1986), *Cephalanthera austiniiae* for *Eburophyton austiniiae* and *Piperia unalascensis* for *Habenaria unalascensis* (Luer, 1975), *Claytonia perfoliata* and *C. sibirica* for *Montia perfoliata* and *M. sibirica* (McNeill, 1975). Wallace (1975) is used for the Monotropoideae except his change of *Pityopus californica* to *P. californicus* is not accepted because it was unnecessary.

DECORANA (Hill, 1979b; Hill and Gauch, 1980) is a computer program that performs calculations for "detrended correspondence analysis". This technique represents and improvement of reciprocal averaging by removing any systematic relations between axes (detrending) and by rescaling segments of the axes such that equal distances in the ordination correspond to equal differences in species composition. (Gauch, 1982, pp. 153-154). DECORANA scores for the principal axes were correlated with environmental and structural variables using the statistical package SIPS (Rowe and Brenne, 1982).

Aerial photographs in conjunction with the classification of plot data were used to produce a map of generalized cover types. Black and white (1:12,000), true color (1:24,000), and false color infrared (1:16,000) photographs were used to interpret vegetation for mapping purposes.

Monotropeoideae

Field Methods

H. Vreeland (1980, p. ii) suggested that his approach "[s]hould be tested in other ecosystems on other achlorophyllous species and on this species [*Sarcodes sanguinea*] to determine the validity or lack thereof..." of his model. A portion of this study tested the validity of Vreeland's approach. In particular his "Influence Factor" (IF) was examined.

H. Vreeland (1980) recorded tree species, diameter-at-breast-height (dbh), and distance to all trees within 10 m of each *Sarcodes* "plant". As noted, his concept of a *Sarcodes* "plant" was unclear. The "Influence Factor" was obtained by multiplying the dbh of a tree by a decreasing (3, 2, or 1) distance "Weighting Factor".

In this study, a *Sarcodes* "plant" is considered to be a group of one or more caespitose clusters of annual flowering stems (or stem) which are each other's nearest neighbors and can be encompassed within a circle of 1 m diameter. This definition is based on Wallace's (1975b) report of *Sarcodes* perennial root mass being up to 60 cm in diameter. This study also tested the IF concept with *Allotropia virgata*. The same "plant" operational definition was used with reservations because *Allotropia* was observed to be strongly rhizomatous.

One population each of *Sarcodes* and *Allotropia* was observed. Measurements were made from ten "plants" in each population. When a "plant" consisted of more than one caespitose cluster of annual flowering stems, measurements were made from the midway point between clusters. Data recorded were distance to, and dbh of, all trees over 5 cm dbh occurring within one and ten meters of the target "plant". In order to test the significance of H. Vreeland's (1980) IF concept, the same data were also recorded from ten "random" sample points within the aerial extent of each population of target "plants". Approximately 2000 distance and diameter measurements were obtained.

Random sample points were obtained as follows. A transect was established through the main axis of each population. Ten numbers between 0.05 and 20.00 (to the nearest 0.05) were obtained from a random numbers table. These numbers were used to establish 10 points along a transect by starting at one end of the transect and measuring the

given random number in meters to the transect location next point. For each point a random departure distance from the transect between 0.05 and 20 m was also obtained. Departure direction was determined in the course of obtaining the data by orienting a wristwatch in the direction of the transect and stopping the sweep second hand with the face of the watch covered. From the transect point, the direction the second hand pointed was followed the departure distance to the sample point. This procedure provided an efficient way to obtain a well-dispersed, unbiased selection of points. No sample points were rejected. This constitutes a comparative mensurative experiment where appropriate dispersal of the measurements is the critical aspect of design (Hurlbert, 1984).

Analytical Methods

Data collected at each sample point consisted of paired sets of distance to tree and dbh of tree measurements. 2116 observations were recorded. The dbh was divided by distance to obtain an influence factor (IF) value. The mean IF value from "plant" points was compared with the mean IF value from "random" points by a two-sample *t*-test (Snedecor and Cochran, 1980). A parametric two-group unpaired *t*-statistic for comparison of means was obtained through use of SIPS (Rowe and Breene, 1982).

RESULTS AND DISCUSSION

Vegetation

Plant Communities

Similarity analysis (TABORD) and divisive classification (TWINSpan) identify six groups or clusters of plots and one distinct single plot cluster. Seventy-three of the 81 plot samples (90%) are assigned to the same groups by both classification techniques. The six groups are considered community types of existing vegetation, as opposed to hypothesizing future "climax" status. The single distinct stand is described and its affinities with one of the abstract community types discussed.

At the first division by TWINSpan three community types identified as the *0 group are separated from the other three, identified as the *1 group. Affinities of the borderline plots to community types were studied in the *0 group and *1 group ordinations. Only three plots are finally placed in community types other than those assigned by one of the classification techniques.

Community names follow the format of Franklin and Dyrness (1973, p. 61). Because the focus is on existing vegetation, only high constancy ($\geq 80\%$) species are considered for inclusion in syntaxa. A list of species with their acronyms is presented in Table 4. Communities are discussed in order of occurrence across the (TWINSpan) ordered two-way table (Table 5). Constancy and average percent cover of all species is shown by community type in Table 6. Species richness for each community type is summarized in Table 7.

Pseudotsuga menziesii/Acer circinatum (PSME/ACCI) community type.

This is a cool, mesic community type within the context of the study area. Species richness is relatively high (mean 37, max. 50, total 89). The number of high constancy species (occurrence $\geq 80\%$) is 15. *Acer circinatum* is the only shrub of importance with an average cover (cov.) of 22%. *Berberis nervosa* reaches its lowest importance with respect to other Limpy Rock types in this community type with an average cover of 4% and 80% constancy (const.). The minor importance of *Gaultheria shallon* is distinctive of this community type.

Table 4. Vascular plant species and acronyms.

TREES		<i>Vaccinium parvifolium</i>	VAPA
<i>Abies amabilis</i>	ABAM	<i>Whipplea modesta</i>	WHMO
<i>Abies concolor</i>	ABCO		
<i>Abies grandis</i>	ABGR	HERBS/GRASSES	
<i>Acer macrophyllum</i>	ACMA	<i>Achlys triphylla</i>	ACTR
<i>Alnus rubra</i>	ALRU	<i>Adenocaulon bicolor</i>	ADBI
<i>Arbutus menziesii</i>	ARME	<i>Allotropa virgata</i>	ALVI
<i>Calocedrus decurrens</i>	CADE	<i>Anemone deltoidea</i>	ANDE
<i>Castanopsis chrysophylla</i>	CACH	<i>Anemone lyallii</i>	ANLY
<i>Cornus nuttallii</i>	CONU	<i>Anemone oregana</i>	ANOR
<i>Pinus attenuata</i>	PIAT	<i>Apocynum androsaemifolium</i>	APAN
<i>Pinus lambertiana</i>	PILA	<i>Aquilegia formosa</i>	AQFO
<i>Pinus ponderosa</i>	PIPO	<i>Arenaria macrophylla</i>	ARMA
<i>Pseudotsuga menziesii</i>	PSME	<i>Arnica latifolia</i>	ARLA
<i>Taxus brevifolia</i>	TABR	<i>Asarum caudatum</i>	ASCA
<i>Thuja plicata</i>	THPL	<i>Asarum hartwegii</i>	ASHA
<i>Tsuga heterophylla</i>	TSHE	<i>Aster radulinus</i>	ASRA
		<i>Boykinia elata</i>	BOEL
SHRUBS		<i>Bromus orcuttianus</i>	BROR
<i>Acer circinatum</i>	ACCI	<i>Bromus suksdorfii</i>	BRSU
<i>Acer glabrum</i> v. <i>douglasii</i>	ACGL	<i>Bromus vulgaris</i>	BRVU
<i>Amelanchier alnifolia</i>	AMAL	<i>Calypso bulbosa</i>	CABU
<i>Arctostaphylos canescens</i>	ARCA	<i>Campanula prenanthoides</i>	CAPR
<i>Arctostaphylos nevadensis</i>	ARNE	<i>Campanula scouleri</i>	CASC
<i>Berberis aquifolium</i>	BEAQ	<i>Carex concinnoides</i>	CACO
<i>Berberis nervosa</i>	BENE	<i>Carex deweyana</i>	CADE2
<i>Ceanothus integerrimus</i>	CEIN	<i>Carex</i> sp.	CAREX
<i>Chimaphila menziesii</i>	CHME	<i>Cephalanthera austiniiae</i>	CEAU
<i>Chimaphila umbellata</i>	CHUM	<i>Claytonia perfoliata</i>	CLPE
<i>Corylus cornuta</i> v. <i>californica</i>	COCO	<i>Claytonia sibirica</i>	CLSI
<i>Gaultheria shallon</i>	GASH	<i>Clintonia uniflora</i>	CLUN
<i>Holodiscus discolor</i>	HODI	<i>Collomia heterophylla</i>	COHE
<i>Kalmiopsis leachiana</i>	KALE	<i>Coptis laciniata</i>	COLA
<i>Linnaea borealis</i>	LIBO	<i>Corallorhiza maculata</i>	COMA
<i>Lonicera ciliosa</i>	LOCI	<i>Corallorhiza mertensiana</i>	COME
<i>Lonicera hispidula</i>	LOHI	<i>Cynoglossum grande</i>	CYGR
<i>Oemleria cerasiformis</i>	OECE	<i>Disporum hookeri</i>	DIHO
<i>Prunus emarginata</i>	PREM	<i>Epilobium angustifolium</i>	EPAN
<i>Rhamnus purshiana</i>	RHPU	<i>Equisetum fluviatile</i>	EQFL
<i>Rhododendron macrophyllum</i>	RHMA	<i>Erythronium oregonum</i>	EROR
<i>Rhus diversiloba</i>	RHDI	<i>Festuca occidentalis</i>	FEOC
<i>Ribes lacustre</i>	RILA	<i>Festuca subuliflora</i>	FESU
<i>Ribes sanguineum</i>	RISA	<i>Fragaria vesca</i>	FRVE
<i>Rosa gymnocarpa</i>	ROGY	<i>Galium aparine</i>	GAAP
<i>Rubus lasiococcus</i>	RULA	<i>Galium triphyllum</i>	GATR
<i>Rubus parviflorus</i>	RUPA	<i>Goodyera oblongifolia</i>	GOOB
<i>Rubus ursinus</i>	RUUR	<i>Hemitomes congestum</i>	HECO
<i>Salix scouleriana</i>	SASC	<i>Hieracium albiflorum</i>	HIAL
<i>Symphoricarpos mollis</i>	SYMO	<i>Hierochloe occidentalis</i>	HIOC
<i>Vaccinium membranaceum</i>	VAME	<i>Hypericum perforatum</i>	HYPE

Table 4. continued.

HERBS/GRASSES cont.			
<i>Iris chrysophylla</i>	IRCH	<i>Polystichum munitum</i>	POMU
<i>Lathyrus polyphyllus</i>	LAPO	<i>Psoralea physodes</i>	PSPH
<i>Ligusticum apiifolium</i>	LIAP	<i>Pteridium aquilinum</i>	PTAQ
<i>Lilium columbianum</i>	LICO	<i>Pyrola aphylla</i>	PYAP
<i>Listera caurina</i>	LICA	<i>Pyrola asarifolia</i>	PYAS
<i>Luzula parvifolia</i>	LUPA	<i>Pyrola dentata</i>	PYDE
<i>Maianthemum racemosum</i>	MARA	<i>Pyrola picta</i>	PYPI
<i>Maianthemum stellatum</i>	MAST	<i>Pyrola secunda</i>	PYSE
<i>Matricaria matricarioides</i>	MAMA	<i>Sanicula crassicaulis</i>	SACR
<i>Melica hartfordii</i>	MEHA	<i>Sarcodes sanguinea</i>	SASA
<i>Melica subulata</i>	MESU	<i>Synthyris reniformis</i>	SYRE
<i>Mitella ovalis</i>	MIOV	<i>Thermopsis montana</i> v. <i>venosa</i>	THMO
<i>Monotropa hypopithys</i>	MOHY	<i>Tiarella trifoliata</i> v. <i>trifoliata</i>	TITR
<i>Monotropa uniflora</i>	MOUN	<i>Tiarella trifoliata</i> v. <i>unifoliata</i>	TIUN
<i>Montia diffusa</i>	MODI	<i>Trientalis latifolia</i>	TRLA
<i>Nemophila parviflora</i>	NEPA	<i>Trilium ovatum</i>	TRÖV
<i>Osmorhiza chilensis</i>	OSCH	<i>Trisetum canescens</i>	TRCA
<i>Oxalis oregana</i>	OXOR	<i>Trisetum cernuum</i>	TRCE
<i>Pedicularis racemosa</i>	PERA	<i>Vancouveria hexandra</i>	VAHE
<i>Phacelia</i> sp.	PHACE	<i>Veratrum californicum</i>	VECA
<i>Phlox adsurgens</i>	PHAD	<i>Vicia americana</i>	VIAM
<i>Piperia unalascensis</i>	PIUN	<i>Viola glabella</i>	VIGL
<i>Pityopus californica</i>	PICA	<i>Viola howellii</i>	VIHO
<i>Pleuricospora fimbriolata</i>	PLFI	<i>Viola sempervirens</i>	WISE
<i>Polystichum imbricans</i>	POIM	<i>Xerophyllum tenax</i>	XETE

Table 5. TWINSpan ordered two-way table. Acronyms are given in Table 4.

	Community Type					
	PSME/ACCI	PSME-CONU/ BENE	PSME-ARME/ GASH-BENE/ PTAQ	PSME-CADE/ GASH-BENE	PSME-PILA/ GASH-BENE	PSME-ABCO/ BENE/XETE
	45555522555	.7.22277.7	.123477...378331	35245111111222344133346	.13444477648	66667666
	2345845167	23446785653	9092078678090178	50349234569012417136854	179236801991	01232567
ANOR	--11--1-					
AQFO	-----1-					
ARMA	23---11-32	-----1	-----1	-----1-1-----2-3	1--1-1-	
CAPR	1--2--1-1-	--1-1----			1	
CAREX	-----1					
CLPE	-----2					
EROR	--1-1-1-					
FESU	--2--3-2-					
FRVE	-2-13-2122		-----2121--122-			-----1-
LIAP	-2-----22		-----21	-----1		
LICA	-2-----					
LICO	132--11-			-----1		
MESU	1-2--33333	-----2	--1--2--22	-----1-2--2--2	2--2--	
NEPA	-1--1-1-	--2-----		-----1	1	
PHACE	-----1					
PYSE	-3-----					
SACR	-----1	-----1				
VAHE	2322--1-22	2-2-----	-----11--12-	-----1	-----1	-----2
VECA	2221-----2					
RILA	-----2					
CYGR	-----1		-----1		2	
CEAU	11-----	1-----	1-----1-1-			
GAAP	-----	-----1--2-			1	
HAUN	-----		-----1-		1	
POIM	-----2		-----121		21	
VIGL	-----1	--2-----	-----1			
VIHO	-----2		-----211			
OECE	-----1		2-----			
MOHY	1121-----					1--1
CLSI	-1--1--1-	-1-1-----	-----1	-----2	-----2	-----1
COMA	1--1-1-1-	-1-1-----1	--2-1-----1-	-1-----1	-----1	-----1
OSCH	21-1-12-22	2212--12-	-----2-1-1-1-	11-----		-----1
VIAM	2-1--1222	1-1-1-	-----1-1--23	-----13		
AMAL	-3322--222	--21--1-	--2-3-1--3-	--2-----2-	-----1-3-	
LOCI	-2122-----	--21-----		-----2	-----1	
HYPE	-----1	--1-----				
LUPA	1-----	-----1-1-	-----1		1	
PYDE	-----	-----1				
ACGL	-----	-----3				
BROR	-----		-----2			
BRSU	-----		-----1			
EPAN	-----		-----1-1			
FEOC	-----		-----1			
MEHA	-----		-----1-21	-----1		-----1
PYAP	-----		-----1			
SADO	-----		-----12--11-			
TRCA	-----		-----1			
BEAQ	-----2-2	-----2	-----2-23-3-333-	-----2		
CEIN	-----		-----2			
RHPU	-----		11-----1			
SASC	-----		-----2			
PREM	-----		2-----2			
ASHA	-----	-----1-322-1-	--2-----	-----2	-----2	
ASRA	-----2		-----2	-----113-	-----2	1-----2
COHE	-2-2--11-	-----1--2-	-----1-2	-----222	-----3	1-1--2-2
LAPO	-----222	222-----	-----23252	-----5	-----4-32	-----2
COCO	-22--332-	--33-----	33-3-33-3-2343-	-----22-234	-----3	
HODI	-2222-4322	--4-2--2-	223-3246352-3-34	-----2-2-2-2-2	-----32-3	-2-3-3-2
LOHI	-----1	--2-----	-----2		1	
RHDI	-----	-----1-1-1-	-3-1-22	-----23-	-----13	-----1-2-
SYMO	32222-3333	42-22212-21	2-223423322212-	12--1-----2	-----2	1-2-2-222--2-2--1-
ACMA	-----	5-75334--1	664-457--3-5-	-----4	-----7	1-----
CONU	-----	2-343334512	344--3-4-2-43-	-----32-4	-----3-44-3-	
MODI	-----		-----1-1			-----1
PTAQ	23-2-124--	3232-23--22	3333334436352233	2-----2-2232-2222223-23	2222222-233-	222--2-
RUPA	-----	-----2-2	-----2			
ARME	-----3	-----3753--	3-53-36748733443	-----1--3434--4--4-	-----3534553423	
APAN	-----1		-----2-11		-----2	-----2-1-1
POMU	-2322-3-23	323342-2332	-33333--2-2422	33623-2223322-33222-2-2	-2-22-----	-22-----
TRCE	12112-1111	223111-222	-11-1-1-1--2-1	-1-21322221-1111--3-2	-1-2--2232--	-1--22--
TRLA	--2-----	-----222-1-2-	1--222311--232-	-----3-223222221-1-1-1-	12122--32--	-----3
CHME	22-2--122	--1--11-	-1-111-11-1-1-2-	-11-11--1-1-11-112-	-----112-1-	112-111-
WHMO	-2-22--233	--2--2--	-21322-222-2222	232--2323--3232322--322	-2-3-22232-1-	-1-----2

Table S. continued

PSME	9978898899	79888888799	8888897796899889	7778899788888897889888	988998878877	78776878
ADBI	2-23222	2233-121	12-12-3	32-122-322-2-1	2-3-2	2-2
BRVU	21-12222-2	-3-11-2	-1-221-2112	-1-12-222-21	-1-21-21	-1-1
CASC	2322-23222	1-2-2222	122-22-11-2	1-1-2223222	-2-2	1-223-2132
COLA		-32-24				-12-12
DIHO	2223-3222	2232222222	112-22111222-22	-32-1-22-2-222-2	-2-2	1-2-2-2
GATR	2-11-2122	22212-2	111-2-111-22-1	-1-1-22112	-1-1-1	2-21
HIAL	2222-12122	112321-11	-2-11-1222	-11-2222211	-1-3	1-12-32
IRCH	-11-1-1	-1-1-1	-2-11-12	-1-1-1	1111-11-1	-1-212
ROGY	3322313232	222-32222-1	-2222223-3222233	22232132-23-323-2232-2	22222-222	-22-121
RUUR	3222-122-2	22-222222	232232233423-232	-2232-323-322232322-22	-21-2	1-2-2
ANDE	3222112122	-222-3	-1-1-2-1	21-11-2-2-2	-2	1-2-22
ARLA	2323-34-3			1-1-2-22-2	1-2	1-22
CACO	-211			-2		
MAST	33221-12			22		-2
ACTR	-1-1	-4-2-12	-21-2-1	-32-2-122-22-2	-11	1-1
MAMA	-1-1	-1-1	-1-1	-2-2-1		
BENE	55444-4-24	77754556642	4473474864775425	46554355546667744646544	44773344421	35433144
ALRU			-4	-4		
MARA	-2-22	-222-2	-1-2	22122-1-1-2	-1-111	-1
SYRE	2223323223	123-2212212	-2-2	232-3-3233-21-21-3-3	1-3-1-2-1	22-2-23
ACCI	75818-263	38-576745	5-1-3	47449-33-324-8-873454		-534
PHAD	-1-1-32			1-2	1	2-1-133
PYPI	2222-121	-1-1-1	-1-1-2	2-1-1-11-2-1-2	-1221-2-2-1	12-21-2
GOOB	1211112-21	-22211221	-2-11-22	12211211122221-1-11	11-11-12-2	122-1122
TROV	3332-2	-2211-2	-1-1	23222-1-2-222-1-1	-1	2-2122
VISE	-322	123-23	-1-1-1-2	-422-1-2-122-2-1	-1-2-2-2	2-33
VAPA	-3-32-3	-2-2	-2-2	2322-2-32-2-2		212-2
THMO	-2		4-2-2	-2-1-12		22-122
PERA	11					-232
PSPH			1-2			-222
TIUN	-2			1		-23
VAME	-3-2			-2-2		1-2-223
LIBO	2534-23	-33-33134-2		2334-23333443-43222-2	-24332-4-2	22323264
CLUN	2312	-2		244-21-21-22		-2-33
PLFI	-1-1			1		
CHUM	-2211	-11-11	-1-1	22-2-2-2-22-22	1-2-2-1-11	-21222
ABGR	-85-2	-14-77	-3-2	4-24-4462237334	-2-26-232	
CACH	-2	-2	-17-2	2-222-2-3-33-23-2	-31-42-332	-2
ASCA			1	2		
GASH	-3	-23-3	78378-7378372-75	3668736674878768678948	-356687-3367	486-3
KALE			3	3	83	
PILA	-4	-2-2-145	-7	26252-76-3-5-664	465554364346	347-35
CADE2				-2		-1
CADE		-2-4	-3-4	-435-746356665353214-44	-2-3-42321-2	22--264
TSHE	-2	1-1		88863-364435-46-8-4-3	-2	62 74388
EQFL				2		
HECO				-1-2		
HIOC		1				
MOUN				-1		
PICA				1		
SASA					1	
TITR				1		
RISA				2		
RULA				2		
RUNI				44		
PIAT						6
PIPO						6
TABR				-442-2-1-2		-1
THPL				5		
ALVI				1	1111	-2-1
ARCA					4	2
ARNE					6	72
ANLY						12
BOEL						2
CABU						1-1
COME						1
MIOV						2
PYAS					2-3-3	223-353
XETE						24724
RHMA				6		77545557
ABCO				-3	2	

b 0000000000|0000000000|0000000000000000|11111111111111111111|11111111111|11111111
 0000000000|1111111111|1111111111111111|0000000000000000000000|00000000000|11111111
 0000111111|0000000000|1111111111111111|0000000000000000000000|11111111111|00000011
 a5555522555|.7.22277.7|.123477...378331|3524511111222344133346|.13444477648|66667666
 2345845167|23446785653|9092078678090178|50349234569012417136854|179236801991|01232567

a Plot number (vertical)
 b TWINSpan division group code, i.e. *0, *011 (vertical)

Table 6. Species average percent cover and percent constancy by community type. Community type acronyms are given in text (+ = 0.1-0.8% ave. cov., \diamond < 0.1% ave. cov.).

Species	Community type											
	PSME/ACCI		PSME-CONU/ BENE		PSME-ARME/ GASH-BENE/ PTAQ		PSME-CADE/ GASH-BENE		PSME-PILA/ GASH-BENE		PSME-ABCO/ BENE/XETE	
	cov.	const.	cov.	const.	cov.	const.	cov.	const.	cov.	const.	cov.	const.
TREES												
<i>Abies concolor</i>							\diamond	9	+	42	17	100
<i>Abies grandis</i>	6	30	7	36	\diamond	13	3	59				
<i>Acer macrophyllum</i>			5	64	5	50	2	9	\diamond	8		
<i>Alnus rubra</i>					+	6	+	5				
<i>Arbutus menziesii</i>	+	20	3	36	12	88	+	27	3	83		
<i>Calocedrus decurrens</i>			+	18	+	13	7	91	+	58	3	63
<i>Castanopsis chrysophylla</i>	\diamond	10	\diamond	9	\diamond	19	+	50	+	58	\diamond	13
<i>Cornus nuttallii</i>			2	91	1	50	+	27	\diamond	8		
<i>Pinus attenuata</i>									2	8		
<i>Pinus lambertiana</i>	+	10			1	38	6	55	8	100	6	63
<i>Pinus ponderosa</i>									2	8		
<i>Pseudotsuga menziesii</i>	79	100	68	100	67	100	63	100	70	100	39	100
<i>Taxus brevifolia</i>							+	27	\diamond	8		
<i>Thuja plicata</i>							+	5				
<i>Tsuga heterophylla</i>	\diamond	10	\diamond	18			14	73	2	17	21	63
SHRUBS												
<i>Acer circinatum</i>	22	80	16	73	+	19	13	73	+	8	2	38
<i>Acer glabrum v. douglasii</i>			\diamond	9								
<i>Amelanchier alnifolia</i>	+	70	\diamond	27	+	25	\diamond	5	\diamond	25		
<i>Arctostaphylos canescens</i>									+	8	\diamond	13

Table 6. continued.

Species	Community type											
	PSME/ACCI		PSME-CONU/ BENE		PSME-ARME/ GASH-BENE/ PTAQ		PSME-CADE/ GASH-BENE		PSME-PILA/ GASH-BENE		PSME-ABCO/ BENE/XETE	
	cov.	const.	cov.	const.	cov.	const.	cov.	const.	cov.	const.	cov.	const.
<i>Arctostaphylos nevadensis</i>									◇	8	5	25
<i>Berberis aquifolium</i>	◇	20	◇	9	+	44	◇	5				
<i>Berberis nervosa</i>	4	80	16	100	16	100	12	100	7	92	3	100
<i>Ceanothus integerrimus</i>					◇	6						
<i>Chimaphila menziesii</i>	◇	60	◇	27	◇	56	◇	50	◇	33	◇	75
<i>Chimaphila umbellata</i>	◇	40	◇	18	◇	6	◇	41	◇	50	◇	63
<i>Corylus cornuta v. californica</i>	+	50	+	18	+	63	+	27				
<i>Gaultheria shallon</i>	+	10	+	27	28	88	33	95	16	92	13	50
<i>Holodiscus discolor</i>	+	80	+	27	3	81	+	27	+	33	◇	13
<i>Kalmiopsis leachiana</i>					+	6	◇	5	4	17		
<i>Linnaea borealis</i>	2	60	+	73			1	82	+	50	3	100
<i>Lonicera ciliosa</i>	◇	40	◇	18			◇	9				
<i>Lonicera hispidula</i>	◇	10	◇	9	◇	6	◇	5				
<i>Oemleria cerasiformis</i>	◇	10			◇	6						
<i>Prunus emarginata</i>					◇	13						
<i>Rhamnus purshiana</i>					◇	19						
<i>Rhododendron macrophyllum</i>							1	5			6	100
<i>Rhus diversiloba</i>			◇	18	+	38	◇	14	◇	17		
<i>Ribes lacustre</i>	◇	10										
<i>Ribes sanguineum</i>							◇	5				
<i>Rosa gymnocarpa</i>	+	100	+	82	+	88	+	77	◇	67	◇	63
<i>Rubus lasiococcus</i>							◇	5				
<i>Rubus nivalis</i>							+	9				
<i>Rubus parviflorus</i>					◇	13	◇	5				
<i>Rubus ursinus</i>	+	80	◇	73	+	94	+	86	◇	33	◇	25
<i>Salix scouleriana</i>					◇	6						

Table 6. continued.

Species	Community type											
	PSME/ACCI		PSME-CONU/ BENE		PSME-ARME/ GASH-BENE/ PTAQ		PSME-CADE/ GASH-BENE		PSME-PILA/ GASH-BENE		PSME-ABCO/ BENE/XETE	
	cov.	const.	cov.	const.	cov.	const.	cov.	const.	cov.	const.	cov.	const.
<i>Symphoricarpos mollis</i>	+	70	+	82	+	88	◇	23	◇	33	◇	38
<i>Vaccinium membranaceum</i>	+	20					◇	9	◇	8	+	63
<i>Vaccinium parvifolium</i>	+	40	◇	9	◇	6	+	41			◇	50
<i>Whipplea modesta</i>	+	60	◇	18	+	75	+	73	+	67	◇	25
HERBS/GRASSES												
<i>Achlys triphylla</i>	◇	10	+	36	◇	25	◇	50	◇	17		
<i>Adenocaulon bicolor</i>	+	60	+	64	◇	19	+	50	◇	17	◇	13
<i>Allotropa virgata</i>							◇	5	◇	33	◇	25
<i>Anemone deltoidea</i>	+	100	+	36	◇	25	◇	32	◇	8	◇	50
<i>Anemone lyallii</i>											◇	25
<i>Anemone oregana</i>	◇	30										
<i>Apocynum androsaemifolium</i>	◇	10			◇	19	◇	5	◇	33	◇	13
<i>Aquilegia formosa</i>	◇	10										
<i>Arenaria macrophylla</i>	+	60	◇	9	◇	6	◇	14	◇	25		
<i>Arnica latifolia</i>	1	70					◇	27	◇	25	◇	38
<i>Asarum caudatum</i>							◇	6	◇	5		
<i>Asarum hartwegii</i>			+	45			◇	6	◇	9	◇	8
<i>Aster radulinus</i>	◇	10			◇	25	◇	5	◇	17		
<i>Boykinia elata</i>											◇	13
<i>Bromus orcuttianus</i>					◇	6						
<i>Bromus suksdorfii</i>					◇	6						
<i>Bromus vulgaris</i>	◇	80	+	36	◇	50	◇	41	◇	33	◇	13
<i>Calypso bulbosa</i>											◇	25
<i>Campanula prenanthoides</i>	◇	40	◇	18			◇	5				

Table 6. continued.

Species	Community type											
	PSME/ACCI		PSME-CONU/ BENE		PSME-ARME/ GASH-BENE/ PTAQ		PSME-CADE/ GASH-BENE		PSME-PILA/ GASH-BENE		PSME-ABCO/ BENE/XETE	
	cov.	const.	cov.	const.	cov.	const.	cov.	const.	cov.	const.	cov.	const.
<i>Campanula scouleri</i>	+	90	◇	55	◇	50	◇	45	+	67	◇	50
<i>Carex concinnoides</i>	◇	30					◇	5			◇	13
<i>Carex deweyana</i>							◇	5				
<i>Cephalanthera austiniiae</i>	◇	20	◇	9	◇	19						
<i>Claytonia perfoliata</i>	◇	10										
<i>Claytonia sibirica</i>	◇	20	◇	18	◇	13	◇	5			◇	13
<i>Clintonia uniflora</i>	+	40	◇	9			+	41			+	38
<i>Collomia heterophylla</i>	◇	40	◇	18	◇	31	◇	9	◇	25		
<i>Coptis laciniata</i>			+	36								
<i>Corallorhiza maculata</i>	◇	40	◇	27	◇	19	◇	9	◇	8		
<i>Corallorhiza mertensiana</i>											◇	13
<i>Cynoglossum grande</i>	◇	10			◇	6		◇	8			
<i>Disporum hookeri</i>	+	80	+	100	◇	81	◇	50	◇	42	◇	85
<i>Epilobium angustifolium</i>					◇	13						
<i>Equisetum fluviatile</i>							◇	5				
<i>Erythronium oregonum</i>	◇	30										
<i>Festuca occidentalis</i>					◇	6						
<i>Festuca subuliflora</i>	+	30										
<i>Fragaria vesca</i>	+	70			◇	44			◇	8		
<i>Galium aparine</i>			◇	18			◇	5				
<i>Galium triphyllum</i>	◇	70	◇	55	◇	63	◇	45	◇	8	◇	25
<i>Goodyera oblongifolia</i>	◇	90	◇	82	◇	31	◇	77	◇	58	◇	88
<i>Hemitomes congestum</i>							◇	5				
<i>Hieracium albiflorum</i>	◇	90	+	73	◇	44	◇	45	+	50	◇	50
<i>Hierochloa occidentalis</i>			◇	9								
<i>Hypericum perforatum</i>			◇	9								

Table 6. continued.

Species	Community type											
	PSME/ACCI		PSME-CONU/ BENE		PSME-ARME/ GASH-BENE/ PTAQ		PSME-CADE/ GASH-BENE		PSME-PILA/ GASH-BENE		PSME-ABCO/ BENE/XETE	
	cov.	const.	cov.	const.	cov.	const.	cov.	const.	cov.	const.	cov.	const.
<i>Iris chrysophylla</i>	◇	40	◇	18	◇	19	◇	14	◇	58		
<i>Lathyrus polyphyllus</i>	◇	30	◇	27	1	38	+	14	◇	8		
<i>Ligusticum apiifolium</i>	◇	30			◇	13	◇	5				
<i>Lilium columbianum</i>	+	50					◇	5				
<i>Listera caurina</i>	◇	10										
<i>Luzula parvifolia</i>	◇	10	◇	18	◇	6			◇	8		
<i>Maianthemum racemosum</i>	◇	10	◇	36	◇	13	◇	50	◇	17		
<i>Maianthemum stellatum</i>	+	70					◇	14			◇	13
<i>Matricaria matricarioides</i>	◇	10	◇	9	◇	13	◇	14			◇	13
<i>Melica hartfordii</i>					◇	25					◇	13
<i>Melica subulata</i>	+	70	◇	9	◇	25	◇	18	◇	17		
<i>Mitella ovalis</i>											◇	13
<i>Monotropa hypopithys</i>	◇	40									◇	25
<i>Monotropa uniflora</i>							◇	5				
<i>Montia diffusa</i>					◇	13			◇	8		
<i>Nemophila parviflora</i>	◇	30	◇	9	◇	13	◇	9				
<i>Osmorhiza chilensis</i>	◇	70	◇	55	◇	25	◇	9			◇	13
<i>Pedicularis racemosa</i>	◇	20									+	38
<i>Phlox adsurgens</i>	+	40					◇	14	◇	8	+	63
<i>Piperia unalascensis</i>					◇	6	◇	5	◇	8		
<i>Pityopus californica</i>							◇	5				
<i>Pleuricospora fimbriolata</i>	◇	10					◇	5	◇	8		
<i>Polystichum imbricans</i>	◇	10			◇	19	◇	5	◇	8		
<i>Polystichum munitum</i>	+	70	1	91	+	63	1	82	◇	33	◇	25
<i>Psoralea physodes</i>					◇	13			◇	8	◇	38
<i>Pteridium aquilinum</i>	+	60	+	73	3	100	+	68	+	83	◇	50

Table 6. continued.

Species	Community type					
	PSME/ACCI	PSME-CONU/ BENE	PSME-ARME/ GASH-BENE/ PTAQ	PSME-CADE/ GASH-BENE	PSME-PILA/ GASH-BENE	PSME-ABCO/ BENE/XETE
	cov. const.	cov. const.	cov. const.	cov. const.	cov. const.	cov. const.
<i>Pyrola aphylla</i>			◇ 6			
<i>Pyrola asarifolia</i>						◇ 13
<i>Pyrola dentata</i>		◇ 9				
<i>Pyrola picta</i>	◇ 70	◇ 18	◇ 19	◇ 36	◇ 58	◇ 63
<i>Pyrola secunda</i>	+ 10					
<i>Sanicula crassicaulis</i>	◇ 10	◇ 9				
<i>Sarcodes sanguinea</i>						
<i>Satureja douglasii</i>			◇ 25			
<i>Synthyris reniformis</i>	+ 100	+ 91	◇ 13	+ 59	+ 42	+ 63
<i>Thermopsis montana</i> v. <i>venosa</i>	◇ 10		+ 19	◇ 18	◇ 8	◇ 63
<i>Tiarella trifoliata</i> v. <i>trifoliata</i>				◇ 5		
<i>Tiarella trifoliata</i> v. <i>unifoliata</i>	◇ 10			◇ 5		+ 25
<i>Trientalis latifolia</i>	◇ 10	◇ 45	+ 63	+ 55	+ 67	+ 13
<i>Trilium ovatum</i>	+ 50	◇ 45	◇ 13	◇ 55	◇ 8	◇ 75
<i>Trisetum canescens</i>			◇ 6			
<i>Trisetum cernuum</i>	◇ 90	+ 82	◇ 44	+ 64	+ 50	◇ 38
<i>Vancouveria hexandra</i>	+ 70	◇ 18	◇ 25	◇ 5	◇ 8	◇ 13
<i>Veratrum californicum</i>	◇ 50					
<i>Vicia americana</i>	◇ 60	◇ 27	◇ 25	◇ 9		
<i>Viola glabella</i>	◇ 10	◇ 9	◇ 6			
<i>Viola howellii</i>	◇ 10		◇ 19			
<i>Viola sempervirens</i>	+ 30	+ 45	◇ 31	+ 45	◇ 25	+ 38
<i>Xerophyllum tenax</i>					+ 25	3 88

Table 7. Species richness by community type in Limpy Rock RNA. Community acronyms are given in text.

	Community type					
	PSME/ACCI	PSME-CONU/ BENE	PSME-ARME/ GASH-BENE/ PTAQ	PSME-CADE/ GASH-BENE	PSME-PILA/ GASH-BENE	PSME-ABCO/ BENE/XETE
Max.	50	34	35	40	32	33
Mean	37	26	26	27	22	25
Min.	16	16	13	11	14	21
Total	89	69	87	94	71	62
N	10	11	16	22	12	8

Max. = maximum number of species in a plot

Mean = mean number of species per plot

Min. = minimum number of species in a plot

Total = number of species found in the type

N = number of plots from each type

Veratrum californicum is a species with important fidelity. It occurs with 50% constancy and does not occur in other Limpy Rock community types. Other high fidelity species are: *Anemone oregana*, *Arenaria macrophylla*, *Carex concinnoides*, *Erythronium oregonum*, *Festuca subuliflora*, and *Lilium columbianum*.

The PSME/ACCI community is further distinguished from the subsequent two communities by the presence of *Arnica latifolia* and *Smilacina stellata* and the absence of *Acer macrophyllum* and *Cornus nuttallii*. Of special interest is *Monotropa hypopithys* which occurs with 40% constancy in this community.

Tree cover is dominated by *Pseudotsuga menziesii* with an average cover value of 79%. The next most important tree is *Abies grandis* with only 30% constancy, however, it dominated one plot with 50% cover.

Pseudotsuga menziesii/*Cornus nuttallii*/*Berberis nervosa*
(PSME/CONU/BENE) community type.

In ordination space (Figure 6) this community is transitional between the PSME/ACCI community and the PSME-ARME/GASH-BENE/PTAQ community; however, a number of features make it distinctive.

Species richness averages 26 with a maximum of 34 and total of 69, considerably lower than the PSME/ACCI community type. Ten species show high constancy. *Polystichum munitum* reaches its greatest constancy in this type (91%). *Coptis laciniata* (37% const.) has exclusive fidelity to this community. The presence of only one high fidelity species markedly contrasts with both the PSME/ACCI and PSME-ARME/GASH-BENE/PTAQ community types. The strong presence of *Acer macrophyllum* (cov. 5%, const. 64%) further distinguishes this community from the PSME/ACCI type. The constancy of *Synthyris reniformis* and *Acer circinatum* link the PSME/ACCI and PSME/CONU/BENE community types. Shrub cover is dominated by *Acer circinatum* (73% const.) and *Berberis nervosa* (100% const.), each with 16% average cover. *Cornus nuttallii* (2% cov, 91% const.) and *Asarum hartwegii* (45% const.) are preferential species for this community type.

TABORD and TWINSPAN placed plot #3 in the PSME/ACCI community type. However, examination of the ordinations (Figures 7 and 8) shows plot # 3 has its closest affinities with the PSME/CONU/BENE community type. The Z axis of the whole data-set ordination and the Y axis of the *0 group ordination clearly demonstrate this. High *Berberis nervosa* cover and the presence of *Coptis laciniata* are strong components of the linkage of plot #3 with the PSME/CONU/BENE type.

Plot #76 was placed in the PSME/ACCI community type by TABORD and in the PSME-CADE/GASH-BENE community type by TWINSPAN. The plot is unusual in that it is dominated by *Abies grandis*. This seems to be the link to the PSME/ACCI community type which contains *A. grandis* as an important codominant. However, none of the high fidelity species of the PSME/ACCI type are present and the high constancy species of this type are either not present or in low abundance, e.g., *Acer circinatum*. The link to the PSME-CADE/GASH-BENE community type (to be described below) is through the presence of *Calocedrus decurrens* but the absence of *Gaultheria shallon* reduces the strength of the linkage. Examination of the ordinations (Figures 7 and 8) shows the closer affinity of plot #76 to the PSME/CONU/BENE community type. The link is formed by relatively low *Acer circinatum* cover and by relatively high *Cornus nuttallii* and *Berberis nervosa* cover.

***Pseudotsuga menziesii*-*Arbutus menziesii*/*Gaultheria shallon*-*Berberis nervosa*/*Pteridium aquilinum* (PSME-ARME/GASH-BENE/PTAQ) community type.**

This community is relatively warm and mesic in the context of this study. *Pseudotsuga* has an average cover of 67%. *Arbutus* is an important tree with 12% average cover and 88% constancy. *Pinus lambertiana* begins to achieve some importance in this community with 38% constancy and 1% average cover. Notable by its absence is *Tsuga heterophylla*.

The dominant shrubs are *Gaultheria* (28% cov., 88% const.) and *Berberis nervosa* (16% cov., 100% const.). *Holodiscus discolor* is of moderate importance (3% cov., 81% const.) and has preference for this community. *Pteridium aquilinum* is the only non-woody species of much importance, with 3% average cover and 100% constancy.

Ten species have high constancy in the PSME-ARME/GASH-BENE/PTAQ community. A total of 87 species was found in the community type. Plots in this community type had an average of 26 species and a maximum of 35.

An interesting group of twelve high fidelity and unique species is found in this community. The species with unique occurrences include *Bromus orcuttianus* and *B. suksdorfii*. These two grasses are noteworthy in that Hitchcock et al. (1969, p. 501) state that they are not found west of the Cascade crest. Limpy Rock lies just south of the area covered by their flora, and the occurrence of these two species may represent outlier populations or part of the northern extent of their range west of the Cascade crest. Their occurrence in only this community reinforces its distinctiveness. Furthermore, maintenance of the distinction between *Bromus suksdorfii* and morphologically similar *B.*

vulgaris at the species level is reinforced on the basis of habitat differences, *B. vulgaris* occurring through all communities in the RNA.

Montia diffusa is a special interest species with high fidelity to this community type. It has one occurrence in the PSME-PILA/GASH-BENE community type. *Satureja douglasii*, with 25% constancy, is not found in the other community types. *Berberis aquifolium* (44% const.) is strongly preferential to this community type though it is found in three other community types. *Fragaria vesca*, *Melica subulata*, and *Vancouveria hexandra* form a group of species preferential to the PSME/ACCI community type but are also frequent in the PSME-ARME/GASH-BENE/PTAQ community type.

As noted earlier, the absence of *Smilacina stellata* and *Arnica latifolia* differentiates this community type (and the PSME/CONU/BENE community type) from the PSME/ACCI community type. The low importance of *Smilacina racemosa*, *Synthyris reniformis*, and *Acer circinatum* as a group also serves to distinguish this community type. This is the only community type in which *Linnaea borealis* was not found.

Plot # 77 was placed in the PSME/CONU/BENE community type by TABORD and TWINSPAN. Although this plot does have strong affinity with that type, as indicated by the ordination of the whole data set (Figures 6 and 7). The split data (*0 group) ordination (Figure 8) shows this to be a result of the influence of its affinity with the PSME-CADE/GASH-BENE community. The *0 group ordination demonstrates the strong affinities of plot #77 with the PSME-ARME/GASH-BENE community.

Plot #77 illustrates the similarity of the PSME/CONU/BENE and PSME-ARME/GASH-BENE communities as demonstrated by the TWINSPAN divisions. *Cornus nuttallii* is present and *Gaultheria shallon* is absent in plot #77 but the high fidelity species *Melica hartfordii* and the preferential species *Rhus diversiloba* are present. The combined absence of *Acer circinatum*, *Goodyera oblongifolia*, and *Trillium ovatum* further distance plot #77 from the PSME/CONU/BENE community type.

***Pseudotsuga menziesii-Calocedrus decurrens/Gaultheria shallon-Berberis nervosa* (PSME-CADE/GASH-BENE) community type.**

It is in this community type that *Calocedrus* and *Tsuga heterophylla* attain their greatest importance (7%/91%; 14%/73%; average cover and constancy, respectively). *Pinus lambertiana* has moderate importance with 6% average cover and 55% constancy. *Gaultheria* and *Berberis nervosa* show 33%/95% and 12%/100% average cover and constancy respectively.

Acer circinatum (13% cov., 73% const.), *Trillium ovatum* (55% const.), *Smilacina racemosa* (50% const.), *Galium triphyllum* (45% const.) *Clintonia uniflora* (41% const.)

Vaccinium parvifolium (41% const.), *Cornus nuttallii* (27% const.), and *Corylus cornuta* (27% const.) distinguish this community from the PSME-PILA/GASH-BENE community in which they are absent.

Taxus brevifolia and *Rubus nivalis* have high fidelity. Seven species show high constancy including *Rubus ursinus* (86%) and *Polystichum munitum* (82%) which also separate the PSME-CADE/GASH-BENE community type from the PSME-PILA/GASH-BENE community type in which they have low constancy.

In terms of species richness, an average of 27 species per plot was found in the community type. The maximum number of species in a plot was 40 and the total number of species in the type was 94. This community had the greatest diversity of monotrope species with *Allotropa virgata*, *Hemitomes congestum*, *Monotropa uniflora*, and *Pityopus californica* present.

***Pseudotsuga menziesii*-*Pinus lambertiana*/*Gaultheria shallon*-*Berberis nervosa* (PSME-PILA/GASH-BENE) community type.**

This type tends to represent dry-warm conditions within the RNA. It is often associated with the shallow rocky soils of topslope topographic positions. *Pinus lambertiana* (with 100% constancy and 8% average cover) reaches its maximum importance in the RNA within this type. *Pseudotsuga* has 70% average cover and 100% constancy. *Arbutus menziesii* has 83% constancy and 3% average cover. *Pinus ponderosa* and *P. attenuata* occur in this type but were not found in any other community type.

In the shrub layer, *Gaultheria* and *Berberis nervosa* each have 92% constancy with 16% and 7% average cover respectively. *Kalmiopsis leachiana* has 4% average cover only because it had 50% cover in plot #49.

The PSME-PILA/GASH-BENE community has an average of 22 species per plot with a maximum of 32 in one plot and a total of 71 species. There are six high constancy species and no high fidelity or preferential species.

Arbutus menziesii is considerably more important in this type than in the PSME-CADE/GASH-BENE community type. The only other species of note is *Castanopsis chrysophylla* which achieves its greatest importance in this type (58% constancy, 0.6% average cover). The PSME-PILA/GASH-BENE community type is defined more by differences in the relative abundances of species which occur with some importance in either the PSME-CADE/GASH-BENE or the PSME-ABCO/BENE/XETE community types than by distinctive occurrences in this community type. Ordination indicates the PSME-PILA/GASH-BENE community type is a topographic (drier) extension of the PSME-CADE/GASH-BENE type.

***Pseudotsuga menziesii*-*Abies concolor*/*Berberis nervosa*/*Xerophyllum tenax* (PSME-ABCO/BENE/XETE) community type.**

This community type represents cool-dry conditions within the study area. It is restricted to elevations above 1200 m (4000 ft.) in the RNA. *Abies concolor* shows strong preference for this type, occurring in only two plots in other types and with 100% constancy and 17% average cover in this type. In seven of eight plots, *A. concolor* showed signs of introgression with *Abies grandis*, differing from typical *A. concolor* by the following characters:

1. Needles more spreading, arrangement flat
2. Bark mostly brick red and hard, some brown and yellow, flaky
3. Few needles with stomata on top, and then, only some with stomata the full needle length

Typical *A. concolor* was found only at plot #72, 150 m (500 ft.) higher in elevation than the other plots and outside the RNA.

Tsuga heterophylla achieves its greatest importance in this community, 21% average cover, 63% constancy. *Pseudotsuga* reaches its least importance, 39% average cover, 100% constancy. This is the only community type lacking *Arbutus menziesii*.

In the shrub layer, *Gaultheria shallon* has 13% average cover but just 50% constancy. *Berberis nervosa* and *Linnaea borealis* each has 3% average cover and 100% constancy. *Rhododendron macrophyllum* has 6% average cover and 63% constancy. *Vaccinium membranaceum* shows strong preference for this community type.

Xerophyllum tenax is the most important herbaceous species with 3% average cover and 88% constancy. *Phlox adsurgens* attains its maximum importance in this community; it is mostly absent from other community types except the PSME/ACCI type. This implies an elevational component to the distribution of *Phlox adsurgens*. *Goodyera oblongifolia* is another high constancy species in this type. This is the only type lacking *Iris chrysophylla* and *Achlys triphylla*. *Rhododendron macrophyllum* has high fidelity for this community. *Boykinia elata*, *Corallorhiza mertensiana*, *Mitella ovalis* and *Pyrola asarifolia* make unique occurrences in this type. *Anemone lyallii* and *Calypso bulbosa* show high fidelity with two occurrences each.

The PSME-ABCO/BENE/XETE community type is most different from the PSME/ACCI type in terms of non-shared (b and c) species. This lack of similarity is somewhat surprising since the two communities occupy the highest elevations in the RNA. However, the PSME/ACCI community type occurs on deeper soils in a midslope position on Dog Mt. while the PSME-ABCO/BENE/XETE community type occurs on shallow

rocky soils on an upper slope position on Ragged Ridge. *Pedicularis racemosa* is the only species shared exclusively by the two community types. The two community types are separated by one of the unsampled logged areas within the RNA.

The PSME-ABCO/BENE/XETE community type is differentiated from the PSME-PILA/GASH-BENE type by the absence of *Abies concolor*, *Rhododendron macrophyllum*, *Phlox adsurgens*, and *Clintonia uniflora* from the latter. Additionally, *Abies grandis*, *Arbutus menziesii*, and *Achlys triphylla* are absent from the former.

Important species shared between the two types are: *Pinus lambertiana*, *Calocedrus decurrens*, *Gaultheria shallon*, *Linnaea borealis*, *Arctostaphylos canescens*, and *A. nevadensis*. *Xerophyllum tenax* occurs in both, but is strongly preferential to the PSME-ABCO/BENE/XETE community type.

Arbutus menziesii-*Pseudotsuga menziesii*-*Pinus attenuata*/*Arctostaphylos* (ARME-PSME-PIAT/ARCTO) stand.

Plot # 68 is not classified with the other community types and represents the extreme of moisture stress found in the conifer vegetation of the RNA. The stand is located at the top of a south trending, rocky ridgeline/cliff, 120 m (400 ft.) above Dog Creek. The elevation is 1073 m (3500 ft.). *Arbutus menziesii* (20% cover), *Pseudotsuga menziesii* (18% cover), *Pinus attenuata* (16% cover) co-dominate the tree canopy. This plot had the lowest cover of *Pseudotsuga* of any plots.

Arctostaphylos nevadensis dominated the shrubs with 30% cover. *A. canescens* had 3% cover. An *Arctostaphylos* which appeared to be a hybrid between the two had 10% cover. It was distinguished primarily by its intermediate growth form and morphological characters (especially pubescence). Table 8 presents a comparison of characters observed from fresh material. Kruckeberg (1977) used pubescence characters (among others) to identify hybrids between *Arctostaphylos columbiana* and *A. nevadensis*. *Pyrola picta* and *Sarcodes sanguinea* were the only herbs observed. However, spring annuals, not evident at the time of sampling (Sept.), may be present.

In order to document the relationship of this stand to the classified community types the following information is presented. *Pinus attenuata* is near the northern limit of its range here (Little, 1971). In the Siskiyou Mountains, Atzet (1979, p. 89) notes that *P. attenuata* stands are associated with intense fires because of the heat needed to induce seed germination. In his study, *Abies concolor* was replacing *Pinus attenuata* at about age fifty. The dominant *P. attenuata* in this stand is 24 m tall, 36 cm dbh, and has 115 annual growth rings. Basal area by species is: *P. attenuata*, 24.5 sq. m/ha; *Pseudotsuga menziesii* 14.7 sq. m/ha; *Arbutus menziesii* 9.8 sq. m/ha. The low basal area for *Arbutus* compared to its

Table 8. Morphological characteristics of *Arctostaphylos* spp. indicating hybridization.

<i>A. canescens</i>	<i>A. canescens</i> x <i>nevadensis</i>	<i>A. nevadensis</i>
Young stems densely hairy	hairy	sparsely hairy
Petiole and leaf hairy	hairy	pubescence only on leaf margins and mid-nerve
Flower pedicel hairy	glabrous	glabrous
Sepals revolute	not revolute	not revolute
Ovary densely hairy	glabrous	glabrous
Stature (growth-form) erect (to 1.5 m), dendritic	ascending (to 0.5 m), spreading	prostrate, spreading

canopy cover is attributed to crown sprouting following fire. Several smaller diameter stems support the crown and these were not counted with the prism as a single larger stem would be.

Plots #69 and #70 are located nearby, off the ridge crest, to the south and east respectively. Both of these stands belong to the PSME-PILA/GASH-BENE community type. Plot #69 contains *Pinus attenuata* with 20% cover. Standing dead and numerous down stems are also present. It is being succeeded by *Pseudotsuga* (55% cover). *Pinus attenuata* was more widely distributed after a fire 115+ years BP and is now being replaced except on the most harsh sites (i. e., plot #68). Plot 70 was located on an east facing slope in the middle of the *Sarcodes* population. *Pinus attenuata* is not present. *Pseudotsuga* (35% cov.), *Pinus lambertiana* (20% cov.), and *Abies grandis* (20% cov.) dominate the canopy.

Plot #81 has the closest floristic affinity to plot #68. It was chosen for sampling because of the two large (95 cm DBH) *Pinus ponderosa* noted from the ridge upon which plot 68 is located. The similarity lies in the low value for *Pseudotsuga* (35%), the amount of *Arctostaphylos nevadensis* (15%) and the presence of *Chimaphila umbellata* and *Pyrola picta*. The vegetation of plot #81 is also part of the PSME-PILA/GASH-BENE community type.

The ARME-PSME-PIAT/ARCTO stand has the most affinity with the PSME-PILA/GASH-BENE community type, and can be considered an expression of its most dry phase at the extreme of the moisture gradient for coniferous vegetation. At lower elevations in the RNA, similar habitat supports *Quercus garryana* "savanna", a type not investigated. Non-forested rocky habitat is dominated by *Kalmiopsis leachiana*.

Interpretation of Ordinations

Ordination is used to derive "low" (2-3) dimensionality environmental space from "high" dimensional field data (Gauch, 1982). This summary of community pattern is compared with environmental and other types of variables to provide interpretation of vegetation pattern across an environmental gradient. Interpretation of the community types and display of the classification is also facilitated.

Dyrness et al. (1974) used 2-dimensional polar ordination to display vegetation pattern over complex environmental gradients in the central Western Cascades. The end stands of the ordination were chosen to represent extremes of predefined gradients related to temperature and moisture.

In this study, detrended correspondence analysis (DECORANA) was used to ordinate the sample stands in three dimensions. This was done for the entire data set and for two subgroups defined by the first TWINSPAN division as the *0 and *1 groups. Plots classified differently by TABORD than TWINSPAN or that were otherwise borderline were tried in each split group for "best fit".

Entire Data Set Ordination. The ordination of the entire data set is plotted in Figures 6 and 7. The eigenvalue of the DCA 1(X) axis is 0.39 and it covers a length of 3 standard deviations (sd.). Plot #25 has the lowest score on the X axis and occupies a cool mesic site on an 18° slope with a SSE aspect. Its macroposition is upper midslope tending NE, so it is well shaded by the trees and ridge above. *Pseudotsuga menziesii* is the only tree species (80% cover). *Holodiscus discolor* and *Berberis nervosa* co-dominate the shrubs. The herbs are diverse with 31 species present.

Plot #68 has the highest X axis score and is established on the dry site discussed in the previous section. The X axis is interpreted as representing a complex gradient related to moisture availability.

To further define the potential factors represented by the ordination gradients, plot scores are correlated with environmental and structural variables. Among environmental variables, elevation (ELEV) ($r=0.44$) is the most highly correlated with X axis scores (Table 9). This relation is mostly a function of the two dryer community types being above 3200 ft. elevation. Macro-topographic position (TPOS1) is also significantly correlated ($r=0.42$) with the X axis. Macro-topographic position is often related to moisture but the actual moisture index, which incorporates macrotopographic position with other variables, is not significantly correlated.

Tree reproduction cover (REPRO) was the most significant structural variable associated with the X axis ($r=.49$). The dryer stands tend to stay open longer during succession, hence have more tree cover in the understory.

The DCA 2 (Y) axis, with a eigenvalue of 0.24 and length of 2.5 sd., is also positively correlated with elevation ($r=0.48$). The Y axis is negatively correlated with the aspect ($r= -0.44$) and insolation ($r= -0.35$) indices (ASIND and INSOL) and is interpreted to reflect a complex gradient related to a decreasing thermal gradient.

Plot #78 has the lowest score on the Y axis. It is one of the lowest elevation samples and has a southern aspect. *Berberis aquifolium*, *Holodiscus discolor*, *Rhus diversiloba*, and *Satureja douglasii* are all present and are regarded as warm site indicators.

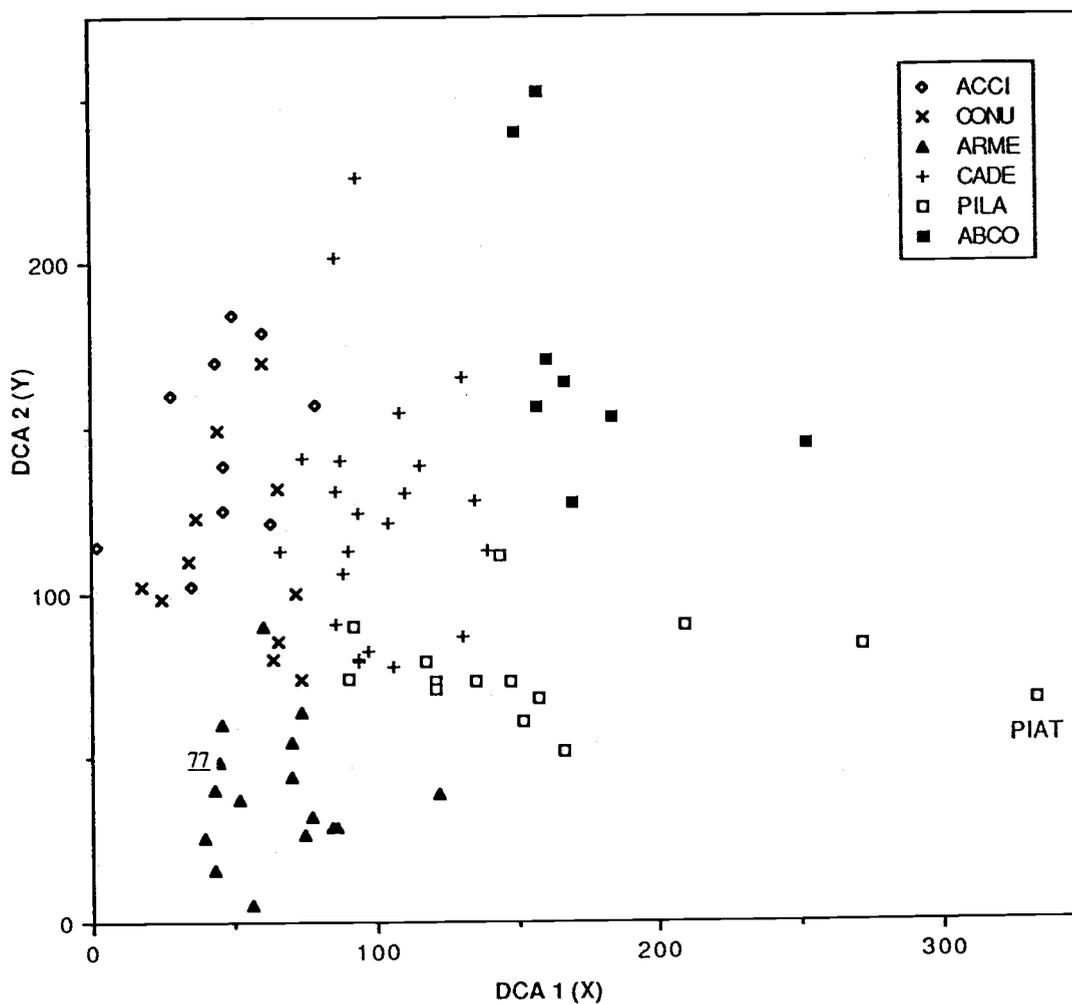


Figure 6. Ordination of the entire data set, X and Y axes. Community type symbols coded by acronym of the second species in type name. Plot # 77 shown.

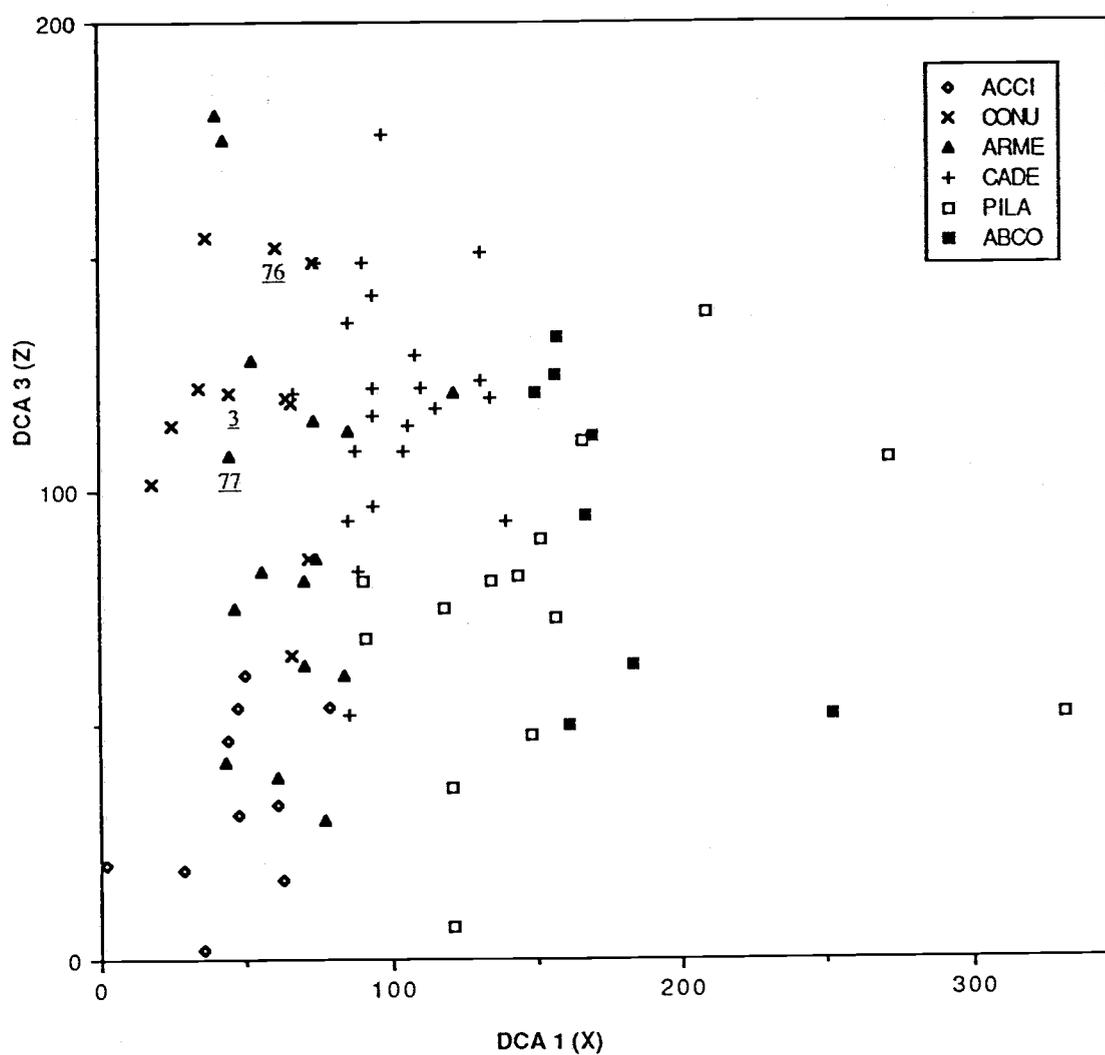


Figure 7. Ordination of the entire data set, X and Z axes. Community type symbols coded by acronym of the second species in type name. Selected plots shown.

Table 9. Single correlations with the entire data set ordination scores.

Variable	Axis 1 (X)		Axis 2 (Y)		Axis 3 (Z)	
	r	p^1	r	p	r	p
ELEV	0.44	****	0.48	****	-0.30	**
SLOPE						
ASIND			-0.44	****		
INSOL			-0.35	***	-0.35	***
TPOS1	0.42	****			-0.27	**
TPOS2	0.22	*			-0.30	**
TPOG						
MOIST			0.23	*		
PH	-0.36	***	-0.30	*		
CORFRG					0.26	*
GRAVEL					0.24	*
COBBEL						
TRECOV	-0.30	**				
TSHCOV	-0.25	*	0.26	*		
LSHCOV			-0.34	***	0.42	****
HERB					-0.23	*
REPRO	0.49	****				
TBA						
YEARS	0.29	**	0.51	****		

- ¹ **** $p \leq 0.0001$
 *** $p = 0.005-0.0001$
 ** $p = 0.01-0.005$
 * $p = 0.05-0.01$

Acronym Legend

ELEV	elevation	GRAVEL	% gravel in soil
SLOPE	slope	COBBEL	% cobble in soil
ASIND	aspect index	TRECOV	tree layer cover
INSOL	insolation index	TSHCOV	tall shrub layer cover
TPOS1	macro-topographic position	LSHCOV	low shrub layer cover
TPOS2	micro-topographic position	HERB	herb layer cover
TPOG	topographic index	REPRO	tree reproduction cover
MOIST	moisture index	TBA	total basal area
PH	soil pH	YEARS	years in tree core
CORFRG	% coarse fragments in soil		

The highest score on the Y axis was assigned to plot #72. It is the highest elevation plot and has a slight north aspect. *Xerophyllum tenax* and *Tiarella trifoliata* v. *unifoliata* dominate the herb layer and often occur in the cooler *Abies amabilis* Zone (Dyrness et al., 1974).

The DCA 3 (Z) axis has an eigen value of 0.14 and covers 1 sd. It is most effective in displaying the gradient between the PSME/ACCI and PSME/CONU/BENE types. The environmental variable most highly correlated with the Z axis is the insolation index with an r value of -0.35. Most of the PSME/ACCI plots are on southerly slopes and are better illuminated. Most of the PSME/CONU/BENE plots face easterly and are more shaded. The other community types are not well separated on the Z axis (Figure 7).

The low shrub cover (LSHCOV) structural variable was the most highly correlated with the Z axis ($r=0.42$). The PSME/ACCI community has an average low shrub cover of 6% compared with the PSME/CONU/BENE community average of 17%.

Stepwise regression was used to determine which combinations of variables formed significant correlations with the ordination axes plot scores. A p value of 0.05 was used as a stopping criteria for adding variables except when addition of the last variable resulted in a small increase in r at a cost of a large increase in p to near 0.05, in which case the smaller p value was preferred. Table 10 shows the results of stepwise multiple correlations. The coefficient of multiple correlation (r) is used to emphasize the non-predictive nature of the relationships and generalized level of the interpretations. Time since last disturbance, expressed as "years in tree core" (YEARS), was treated as both an environmental and structural variable since both types of variables are subject to change through time.

The significant environmental variables for the X axis were elevation, macro-topographic position, and years in core. They produced an r value of 0.60, $p = 0.029$. Together the structural variables tree reproduction cover, tree cover (TRECOV), and tall shrub cover (TSHCOV) were significant with an r value of 0.57, $p = 0.05$. When the structural and environmental variables were combined; reproduction cover, elevation, macro-topographic position, tree cover, and soil pH (PH) were significant with an r value of .73, $p = 0.039$.

The X axis is interpreted as representing a complex gradient related to increasing elevation and decreasing moisture (topographic position) accompanied by increasing stand age, increasing tree reproduction cover and decreasing tree cover and soil pH. The elevational component of the gradient is partly an artifact of the location of the dryer types and does not reflect a consistent thermal gradient. This gradient is most useful in separating the TWINSPAN *0 and *1 groups of community types.

Table 10. Multiple correlations with the entire data set ordination scores.

	<u>r</u>	<u>p</u>
DCA Axis 1 (X)		
Environmental variables		
ELEV, TPOS1, YEARS	0.60	0.029
Structural variables		
REPRO, -TRECOV, TSHCOV	0.57	0.05
All variables		
REPRO, ELEV, TPOS1, -TRECOV, -PH	0.73	0.039
DCA Axis 2 (Y)		
Environmental variables		
ELEV, YEARS, -INSOL	0.70	0.0006
Structural variables		
YEARS, TSHCOV, LSHCOV	0.63	0.007
All variables		
YEARS, ELEV, -INSOL, LSHCOV	0.74	0.0004
DCA Axis 3 (Z)		
Environmental variables		
-INSOL, CORFRG, -TPOS1, -TPOS2	0.60	0.044
Structural variables		
LSHCOV, -HERB	0.49	0.015
All variables		
-INSOL, -HERB, LSHCOV, -TPOS1, CORFRG	0.74	0.002

Acronym Legend

ELEV	elevation	GRAVEL	% gravel in soil
SLOPE	slope	COBBEL	% cobble in soil
ASIND	aspect index	TRECOV	tree layer cover
INSOL	insolation index	TSHCOV	tall shrub layer cover
TPOS1	macro-topographic position	LSHCOV	low shrub layer cover
TPOS2	micro-topographic position	HERB	herb layer cover
TPOG	topographic index	REPRO	tree reproduction cover
MOIST	moisture index	TBA	total basal area
PH	soil pH	YEARS	years in tree core
CORFRG	% coarse fragments in soil		

The significant environmental variables for the Y axis were elevation, years in core, and insolation index (negative). They produced an r value of .70, $p = 0.0006$. The structural variables with significant multiple correlation to the Y axis were: years in core, tall shrub cover, and low shrub cover (negative). They had an r value of 0.63, $p = 0.007$.

Multiple correlation based on both sets of variables produced a model with years in core, elevation, insolation (negative), and low shrub cover (negative) as the significant variables and an r value of 0.74, $p = 0.0004$. The Y axis is interpreted as a complex thermal gradient (increasing elevation, decreasing insolation) with a temporal (successional) component and over which low shrub cover decreases.

The decrease in insolation along the Y axis is reflected in the response of the PSME-ARME/GASH-BENE/PTAQ and PSME/CONU/BENE types (which occur at about the same elevation). The PSME/CONU/BENE community type generally receives less insolation and is found on higher insolation slopes only as elevation increases.

The significant environmental variables for the Z axis were: insolation (negative), percent coarse fragments in soil, macro-topographic position (negative), and microtopographic position (negative). The r value of this model was 0.60, $p = 0.044$. Low shrub cover and herb cover (negative) were the significant structural variables. The structural model had an r value of 0.49, $p = 0.015$. In the combined correlation model insolation (negative), herb cover (HERB) (negative), low shrub cover, and macro-topographic position (negative), were the significant variables. The r value was .74, $p = 0.002$.

The PSME/ACCI and PSME/CONU/BENE types are separated on the Z axis. The PSME/ACCI and PSME-CADE/GASH-BENE types are well separated with only one overlapping plot. The PSME-CADE/GASH-BENE and the PSME-PILA/GASH-BENE types are mostly separated on this axis with only five plots overlapping. The Z axis is interpreted as a complex moisture gradient (increasing) over which low shrub cover increases and herb cover decreases.

The environmental gradients of elevation, insolation, and macro-topographic position are each significant in two axes implying that the gradient space defined by these factors is not orthogonal with the DECORANA axes. The imposed orthogonal nature of the DECORANA ordination axes introduces constraints which may obscure the relative position of plots with respect to these factors.

Ordinations of the split data set are presented in Figures 8 and 9. They are essentially ordinations of the left (*0) and right (*1) groups formed by the first TWINSpan division, with the exception of plot #'s 1, 38, 43, 64, 71, and 76; which are assigned to the opposite group from their original TWINSpan designation.

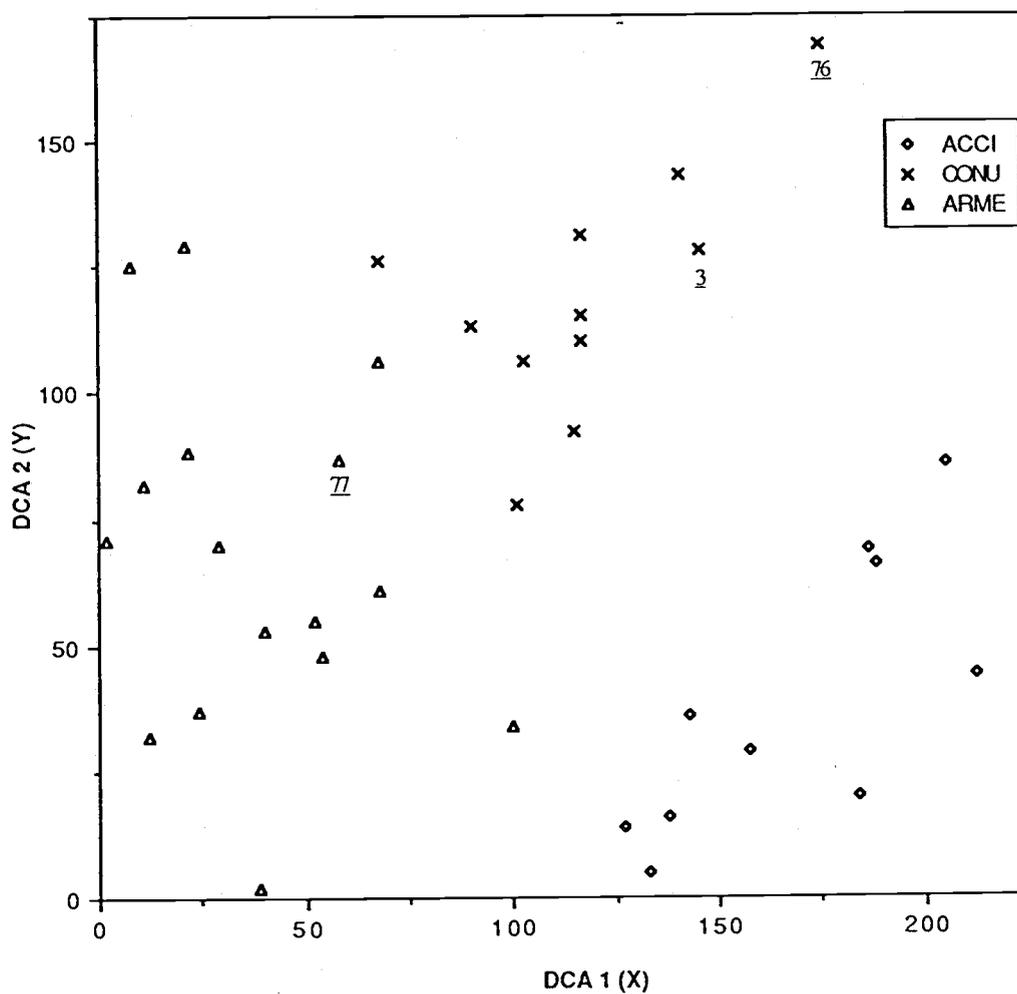


Figure 8. Ordination of the TWINSPAN *0 group. Community type symbols coded by acronym of the second species in type name. Selected plots shown.

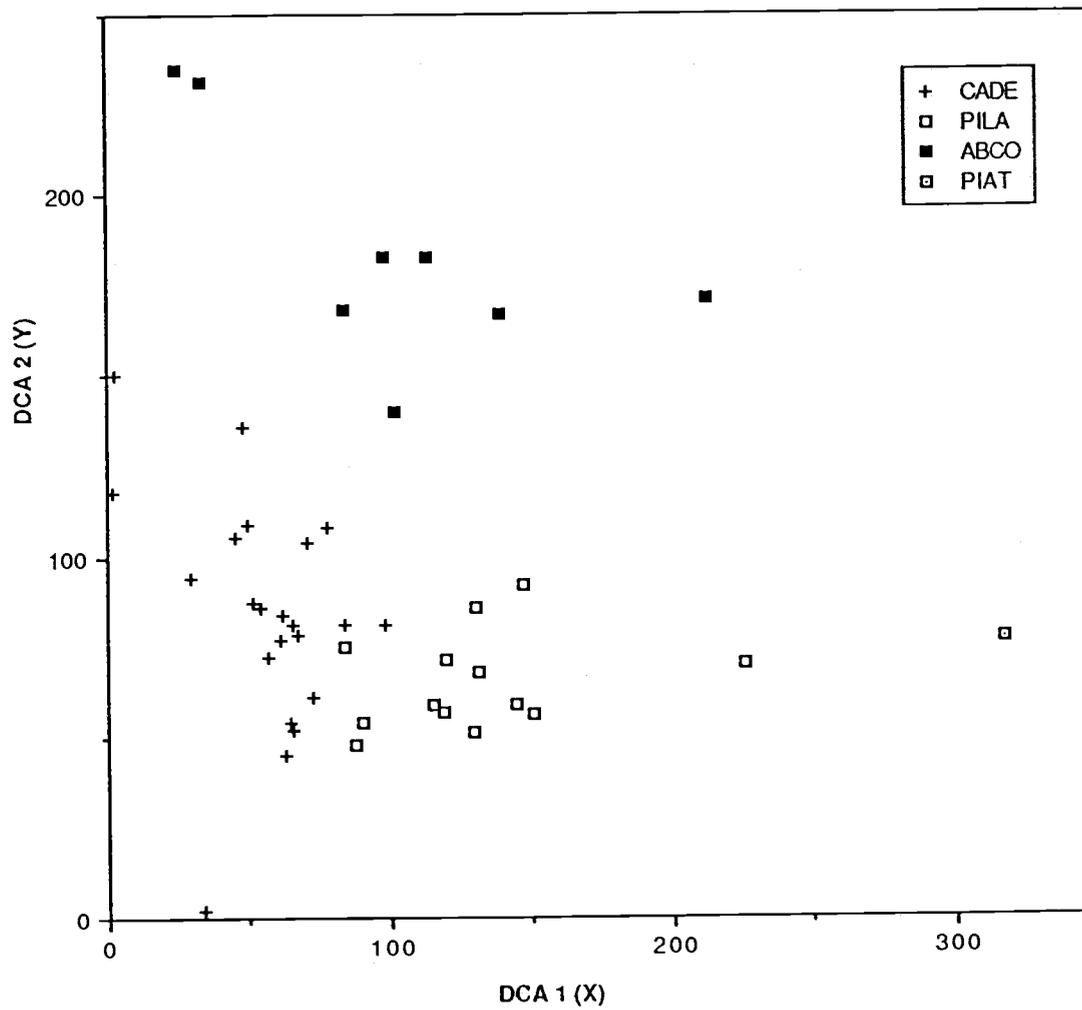


Figure 9. Ordination of the TWINSPAN*1 group. Community type symbols coded by acronym of the second species of type name.

Clearer understanding of the relationships between plots of the communities in the *0 group can be obtained without influence of the plots from the other community types and vice-versa. Additionally, borderline plots can be tried in both ordinations to see which community relationships are stronger. The single correlations between the ordination scores and the environmental and structural variables are presented in Table 11.

TWINSPAN *0 Group Ordination. The ordination of the *0 group shows the communities occupy discrete areas of the ordination space in the first two dimensions (Figure 8). The DCA 1 (X) axis has an eigenvalue of 0.30 and covers 2 sd. Elevation is the most significant environmental variable. Decreasing low shrub cover is very significant as a structural variable. The temporal variable "years in core" is also significant.

In multiple correlation (Table 12) elevation, insolation (negative), and years in core were significant with an r value of 0.77, $p = .007$. Structurally, low shrub cover (negative) and tree reproduction cover (negative) were important with an r value of 0.74, $p = 0.019$. The combined correlation produced a model in which low shrub cover (negative), aspect index (negative), elevation, and tree reproduction cover (negative) were significant variables with an r value of 0.86, $p = 0.035$.

The X axis is interpreted as a decreasing thermal gradient with increasing elevation and decreasing insolation. It is accompanied by decreasing low shrub and tree reproduction cover which may reflect a successional gradient implicit in the correlation with years in core. This axis is essentially interpreted as the Y axis of the entire data set ordination (Figure 6).

The DCA 2 (Y) axis has an eigenvalue of 0.14 and covers 1.5 sd. Elevation is the most significant variable in single correlation. Insolation and aspect are also significant. No structural variables correlated significantly with this axis.

In multiple correlation, elevation (negative) and aspect (negative) were significant with an r value of 0.60, $p = 0.039$. There are indeed two opposed thermal gradients along the Y axis. One is the increasing gradient with decreasing elevation from the PSME/ACCI plots to the PSME/CONU/BENE plots. The other is the decreasing insolation/aspect gradient from the PSME-ARME/GASH-BENE/PTAQ plots to the PSME/CONU/BENE plots. The strongest trends in the elevation and insolation gradients are then at angles to the DECORANA axis.

The result is that the PSME/ACCI and PSME-ARME/GASH-BENE/PTAQ types occupy the same end of the axis. The PSME/ACCI community type is distinguished from the PSME/CONU/BENE community type by increased elevation. The PSME-ARME/GASH-BENE/PTAQ community type is less well separated from the

Table 11. Single correlations with the TWINSpan #0 group ordination scores.

Variable	Axis 1 (X)		Axis 2 (Y)		Axis 3 (Z)	
	r	p ¹	r	p	r	p
ELEV	0.46	***	-0.52	***		
SLOPE					0.37	*
ASIND	-0.40	*	-0.40	*		
INSOL	-0.34	*	-0.44	**		
TPOS1						
TPOS2						
TPOG						
MOIST						
PH						
CORFRG					0.45	**
GRAVEL						
COBBEL					0.58	***
TRECOV						
TSHCOV	0.36	*			0.34	*
LSHCOV	-0.69	****				
HERB						
REPRO	-0.44	**				
TBA						
YEARS	0.53	***				

- ¹ **** $p \leq 0.0001$
 *** $p = 0.005-0.0001$
 ** $p = 0.01-0.005$
 * $p = 0.05-0.01$

Acronym Legend

ELEV	elevation	GRAVEL	% gravel in soil
SLOPE	slope	COBBEL	% cobble in soil
ASIND	aspect index	TRECOV	tree layer cover
INSOL	insolation index	TSHCOV	tall shrub layer cover
TPOS1	macro-topographic position	LSHCOV	low shrub layer cover
TPOS2	micro-topographic position	HERB	herb layer cover
TPOG	topographic index	REPRO	tree reproduction cover
MOIST	moisture index	TBA	total basal area
PH	soil pH	YEARS	years in tree core
CORFRG	% coarse fragments in soil		

Table 12. Multiple correlations with the TWINSpan *0 group ordination scores.

	<u>r</u>	<u>p</u>
DCA Axis 1		
Environmental variables		
ELEV, -INSOL, YEARS	0.77	0.007
Structural variables		
-LSHCOV, -REPRO,	0.74	0.019
All variables		
LSHCOV, ASIND, ELEV, REPRO	0.86	0.035
DCA Axis 2		
Environmental variables		
ELEV, ASIND	0.60	0.039
Structural variables		
no significant combinations		
All variables		
ELEV, ASIND, HERB	0.70	0.007
DCA Axis 3		
no significant combinations		

Acronym Legend

ELEV	elevation	GRAVEL	% gravel in soil
SLOPE	slope	COBBEL	% cobble in soil
ASIND	aspect index	TRECOV	tree layer cover
INSOL	insolation index	TSHCOV	tall shrub layer cover
TPOS1	macro-topographic position	LSHCOV	low shrub layer cover
TPOS2	micro-topographic position	HERB	herb layer cover
TPOG	topographic index	REPRO	tree reproduction cover
MOIST	moisture index	TBA	total basal area
PH	soil pH	YEARS	years in tree core
CORFRG	% coarse fragments in soil		

PSME/CONU/BENE community type by aspect. The PSME/CONU/BENE community type occupies the relatively low elevation, low insolation end of the axis. There were no significant combinations of structural variables. Herb cover was added to the all variable model.

The DCA 3 (Z) axis has an eigenvalue of 0.11. Percent cobble in the soil fraction was most highly correlated with the axis scores. In multiple correlation there was no significant combination of variables. Since plots from all three communities are distributed over the gradient and given the low eigenvalue, little interpretation is possible. Plot #58 accounts for much of the correlation with cobbles in soil. It occurred on a moss covered rocky substrate of fractured bedrock or colluvium with almost no soil. Its herb layer was relatively depauperate. *Aspidotis densa* and *Cheilanthes gracillima* characteristic of rocky habitats, were found nearby, but out of the plot on the same substrate.

The PSME/CONU/BENE community type tended to occur on steep slopes. Its position at the upper end of the Z axis may account for the correlation with slope.

TWINSPAN *1 Group Ordination. The ordination of the *1 group (Figure 9) shows stronger ordination space partitioning between the PSME-CADE/GASH-BENE and the PSME-PILA/GASH-BENE community types in two dimensions as compared to the ordination of the entire data set (Figure 6).

The DCA 1 (X) axis has an eigenvalue of 0.39 and covers 3 sd. In single correlations, topographic position and the moisture index were significant environmental variables (Table 13). Tree cover (negative) was the most significant structural variable.

In multiple correlation (Table 14), micro-topographic position represents the moisture-related variables. The axis can readily be interpreted as a decreasing moisture gradient over which tree and tall shrub cover decrease. This axis is not greatly different than the X axis of the entire data set ordination (Figure 6). Most of the PSME-CADE/GASH-BENE plots are separated on this gradient from plots of the other community types.

The DCA 2 (Y) axis has an eigenvalue of 0.24 and covers 2 sd. The axis was strongly correlated with elevation ($r = 0.71$, $p = 0.0001$). The two end plots of the axis (#13 and #72) are the lowest and highest elevation plots in the data set respectively. Structurally, total basal area was significantly correlated with this axis.

In the combined multiple correlation, elevation and insolation index were significant ($r = 0.76$, $p = 0.015$) when the environmental data set was used. The structural data set produced no significant combination of variables. When all variables were entered into the model, elevation and years in core were significant ($r = 0.74$, $p = 0.02$).

Table 13. Single correlations with the TWINSpan *1 group ordination scores.

Variable	Axis 1 (X)		Axis 2 (Y)		Axis 3 (Z)	
	r	p ¹	r	p	r	p
ELEV			0.71	****		
SLOPE						
ASIND			-0.34	*	-0.38	*
INSOL					-0.40	**
TPOS1	0.54	***				
TPOS2	0.47	***				
TPOG	0.34	*				
MOIST	0.43	***				
PH			-0.33	*		
CORFRG						
GRAVEL						
COBBEL					0.30	*
TRECOV	-0.57	***				
TSHCOV	-0.34	*				
LSHCOV					0.36	*
HERB					0.40	**
REPRO					-0.33	*
TBA			0.45	***		
YEARS					-0.32	*

- ¹ **** $p \leq 0.0001$
 *** $p = 0.005-0.0001$
 ** $p = 0.01-0.005$
 * $p = 0.05-0.01$

Acronym Legend

ELEV	elevation	GRAVEL	% gravel in soil
SLOPE	slope	COBBEL	% cobble in soil
ASIND	aspect index	TRECOV	tree layer cover
INSOL	insolation index	TSHCOV	tall shrub layer cover
TPOS1	macro-topographic position	LSHCOV	low shrub layer cover
TPOS2	micro-topographic position	HERB	herb layer cover
TPOG	topographic index	REPRO	tree reproduction cover
MOIST	moisture index	TBA	total basal area
PH	soil pH	YEARS	years in tree core
CORFRG	% coarse fragments in soil		

Table 14. Multiple correlations with the TWINSPAN *1 group ordination scores.

	<u>r</u>	<u>p</u>
DCA Axis 1		
Environmental variables		
TPOS2, INSOL	0.60	0.013
Structural variables		
-TRECOV, TSHCOV	0.68	0.002
All variables		
TPOS2, -TRECOV, TSHCOV	0.73	0.002
DCA Axis 2		
Environmental variables		
ELEV, INSOL	0.76	0.015
Structural variables		
no significant combinations		
All variables		
ELEV, YEARS	0.74	0.02
DCA Axis 3		
Environmental variables		
INSOL, YEARS, COBBEL	0.66	0.014
Structural variables		
LSHCOV, TSHCOV	0.50	0.043
All variables		
INSOL, YEARS, LSHCOV, COBBEL	0.72	0.032

Acronym Legend

ELEV	elevation	GRAVEL	% gravel in soil
SLOPE	slope	COBBEL	% cobble in soil
ASIND	aspect index	TRECOV	tree layer cover
INSOL	insolation index	TSHCOV	tall shrub layer cover
TPOS1	macro-topographic position	LSHCOV	low shrub layer cover
TPOS2	micro-topographic position	HERB	herb layer cover
TPOG	topographic index	REPRO	tree reproduction cover
MOIST	moisture index	TBA	total basal area
PH	soil pH	YEARS	years in tree core
CORFRG	% coarse fragments in soil		

The PSME-ABCO/BENE/XETE community type is clearly distinguished in elevation from the other communities (except for anomalous plot #64). The trees tend to be older and larger in this community. The Y axis is interpreted as a complex thermal gradient.

The DCA 3 (Z) axis had an eigenvalue of 0.15. In single correlations the most important environmental variable was insolation. The most important structural variable was herb cover. Since plots from all three community types occur over the length of the axis and the types are well defined on the first two axes, no interpretation of the Z axis is offered. The X and Y axes of the *1 group ordination (Figure 9) are essentially slightly rotated, with respect to community positions, from their relative positions in the ordination of the entire data set (Figure 6).

Relations to Other Plant Communities

In the context of the *Tsuga heterophylla* Zone, the vegetation at Limpy Rock is in the mesic to drier end of the spectrum of associations in the Zone. Species with high constancy in the entire data set were *Pseudotsuga menziesii* (100%), *Berberis nervosa* (95%) and *Rosa gymnocarpa* (79%). Species with more than 10% average cover were *Pseudotsuga* (64%), *Gaultheria shallon* (18%), and *Berberis nervosa* (10%). *Polystichum munitum* was fairly widespread (63% const.) but with low average cover (0.6%), and *Vaccinium parvifolium* was infrequent (23% const.). *Oxalis oregana*, an important species in low moisture stress associations of the Zone in the Coast Range, was not encountered.

Separate ordinations of the TWINSPAN *0 and *1 groups assisted the interpretation of community relationships to complex environmental gradients related to temperature and moisture. *Symphoricarpos mollis* was strongly preferential to the *0 group. *Calocedrus decurrens* and *Tsuga heterophylla* were strongly preferential to the *1 group. However, both groups are too heterogeneous for recognition of series level syntaxa. The community types are transitional in composition to communities of the Mixed Conifer Zone of Franklin and Dyrness (1973). The *1 group demonstrates this affinity by the strong presence of *Pinus lambertiana*, *Calocedrus decurrens*, *Abies concolor*, and *A. grandis*; however, *Tsuga heterophylla* is also strongly preferential to this group.

Based on overstory composition, the PSME-PILA/GASH-BENE community type would seem to have the closest ties to the Mixed Conifer Zone vegetation, but no similar communities could be found in the literature. The PSME-ABCO/BENE/XETE community type would seem to have connection to communities of the *Abies concolor* Zone (Franklin and Dyrness, 1973). The understory of *Rhododendron macrophyllum*, *Berberis nervosa*, *Vaccinium membranaceum*, and *Xerophyllum tenax* seem to link it more strongly to

communities transitional between the *Tsuga heterophylla* Zone and the *Abies amabilis* Zone (Dyrness et al., 1974). The PSME-CADE/GASH-BENE community type may have affinities to a tentative *Pseudotsuga menziesii*-*Tsuga heterophylla*/*Gaultheria shallon* community type in the South Umpqua Experimental Forest (Franklin and Dyrness, 1973). It is in the PSME-CADE/GASH-BENE community type that *Tsuga heterophylla* reaches its greatest importance in the RNA.

Communities in the *0 group seem to have floristic connections to previously described associations and communities in the *Tsuga heterophylla* Zone (except for the general absence of *Tsuga* in the *0 group). The PSME/ACCI and PSME/CONU/BENE types are probably closest to the PSME/ACCI/BENE community type of Dyrness et al. (1974). They hypothesized a *Tsuga heterophylla*/*Rhododendron macrophyllum*/*Berberis nervosa* climax association for their community type. The PSME-ARME/GASH-BENE/PTAQ community type is at a rather early successional stage and comparable communities have not been described by others.

Mapping Vegetation Cover Types

The cover type map (Figure 10) was generalized from some 70 mapping units identified through interpretation of aerial photography. Slope, aspect, canopy density, and canopy texture were the primary criteria for defining mapping units. Integration of the mapping units was strongly guided by the distribution of the community types. The map is a rough approximation useful for general impressions only.

Much of the shape of the cover type units is influenced by the trend of the major ridge systems. The trends of the ridges in turn influence the pattern induced by fires. For instance, the cool moist NE slope of the PSME/CONU/BENE community type escaped fire while the hot SW slope of the PSME-ARME/GASH-BENE/PTAQ community type burned. Approximate correlations between cover types and community types are as follows:

1. Old growth *Pseudotsuga*-*Abies* = PSME-ABCO/BENE/XETE
2. Mature *Pseudotsuga* = PSME/ACCI
3. Old/mature *Pseudotsuga*-*Pinus* = PSME-PILA/GASH-BENE
4. Mixed conifer has several types represented
5. Old growth *Pseudotsuga* with hardwoods = PSME/CONU/BENE
6. *Pseudotsuga*-*Tsuga* = PSME-CADE/GASH-BENE
7. *Pseudotsuga*-*Arbutus* = PSME-ARME/GASH-BENE/PTAQ
8. *Pinus*-*Pseudotsuga* = ARME-PSME-PIAT/ARCTO

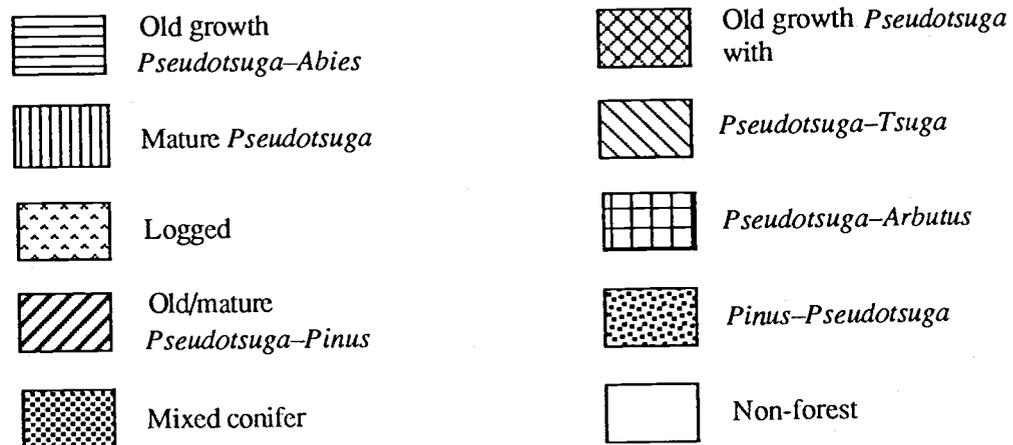
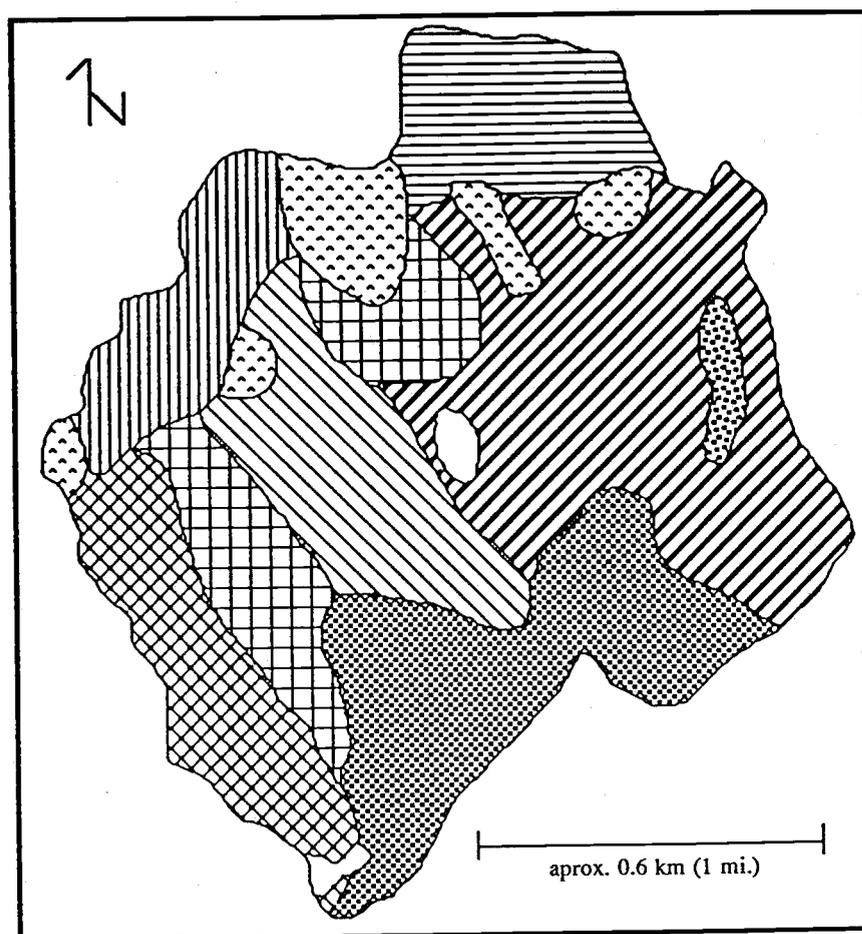


Figure 10. Vegetation cover types in Limpy Rock RNA.

Monotropeidae

Vegetation/Monotrope Relationships

A descriptive analysis of monotropes as they were encountered in the course of the vegetation survey is presented. Figure 11 shows the generalized areas occupied by the plant community types in the entire data set ordination of the first two axes. Monotrope species are coded and positioned by the location of the plots in which they occurred. Species codes in parentheses indicate plants which were located within one meter of the plot.

Allotropia virgata was the most frequently encountered monotrope in vegetation plots. It was found in seven plots and was always found in the *1 group of community types. The occurrence of *Pinus lambertiana* and *Calocedrus decurrens* is strongly characteristic of these communities. *Allotropia* tended to be found on the dryer sites. It was observed to be rhizomatous in decaying coarse woody debris on several occasions. This has also been reported by Steele and Stickney (1974).

The PSME-PILA/GASH-BENE community type had four plots containing *Allotropia* (33% constancy). Additionally, it was observed near two other plots in the community type. The PSME-ABCO/BENE/XETE community type supported *Allotropia* in two plots (25% constancy). *Allotropia* was found in one plot in the PSME-CADE/CASH-BENE community type. Soil pH in the plots with *Allotropia* ranged from 4.4 to 5.8 with an average of 5.3. *Allotropia* has also been recorded in 17 locations out of the plots (13 by Moore et al., 1977).

Hemitomes congestum occurred in one plot and near another in the PSME-PILA/GASH-BENE community type. It also occurred within 1 m of a plot in the PSME-CADE/GASH-BENE community type. *Hemitomes* was locally abundant in plot #17. The soil consisted mostly of coarse fragments (90% > 2 mm) infused with mycelium. Soil taken from the root zone of *Hemitomes* had a pH of 5.8. *Pleuricospora fimbriolata* also occurred in this plot. Nine out-of-plot locations are recorded for *Hemitomes* (5 by Moore et al., 1977). One of the sites was discovered in one of the freshly logged areas in 1980. When the site was revisited during the course of this study no flowering stalks of *Hemitomes* could be found.

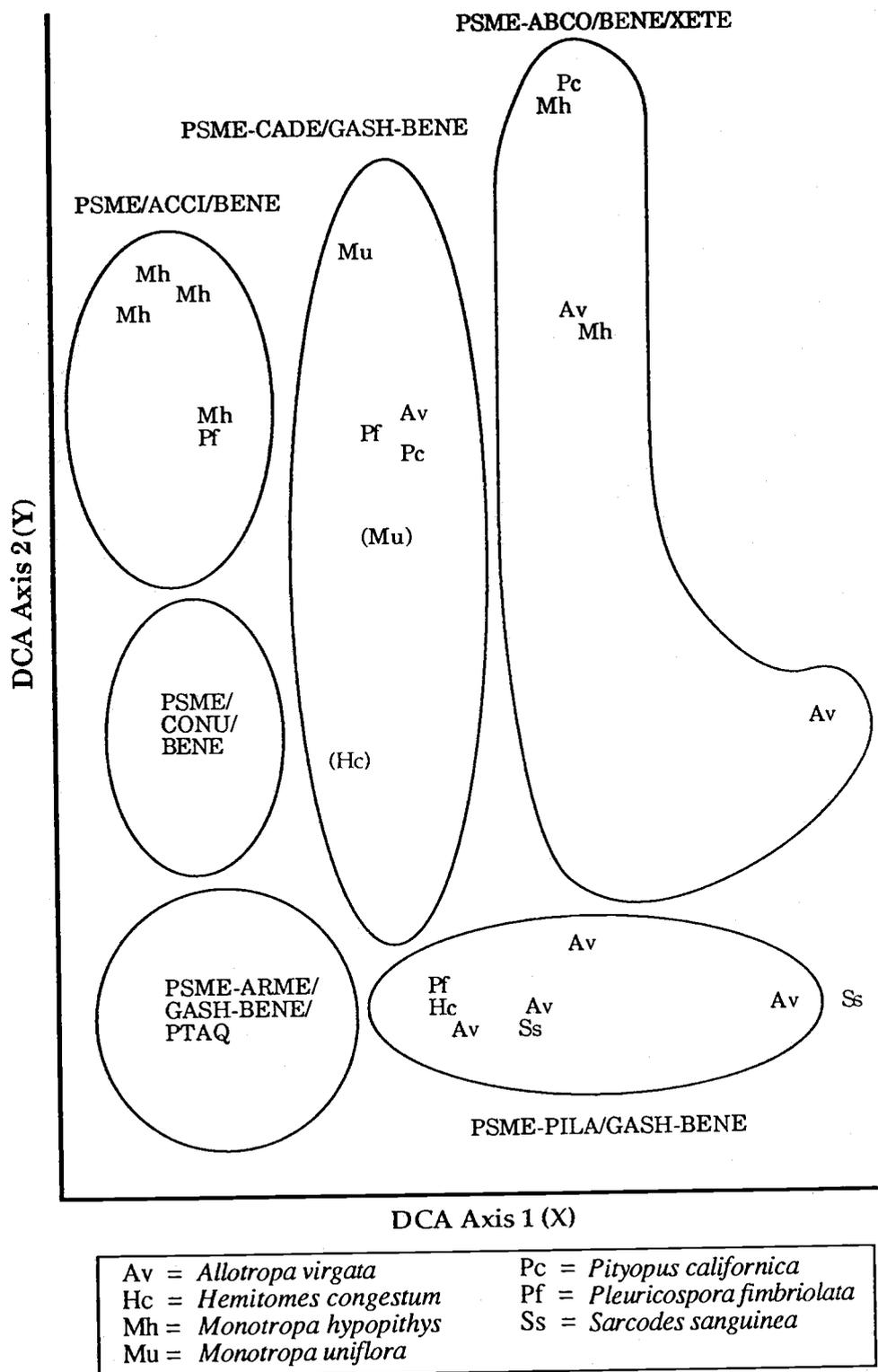


Figure 11. Schematic of monotropes in the entire data set ordination. Figures enclose the general areas the indicated community types occupy in the ordination space. Monotrope species are shown by location of the plots in which they occur.

Monotropa hypopithys was predominantly found above 3000 ft in elevation (17 of 18 occurrences). It occurred in four plots in the PSME/ACCI community type (40% constancy). Two plot soil pH samples were 5.4 and 5.6. The pH of soil samples taken from the root zone of *M. hypopithys* were 4.8 and 5.6. The pH of an underground stem of *M. hypopithys* was 5.4.

The PSME-ABCO/BENE/XETE community type had 2 plots containing *M. hypopithys* (25% constancy). Soil samples had pH's of 4.8 and 5.2. Of the 12 out of plot occurrences, ten were located by Moore et al. (1977).

Monotropa uniflora was found in one plot in the PSME-CADE/GASH-BENE community type. Soil pH from underneath a plant was 6.2. *M. uniflora* was also found near this plot and between two others of this community type.

In the PSME-PILA/GASH-BENE community type, it was located near plot #70. Moore et al. (1977) report two additional sightings in the RNA

Pityopus californica occurred in one plot in the PSME-CADE/GASH-BENE community type. Moore et al. (1977) report *P. californica* from four sites in the RNA, one of which was subsequently logged. It also occurred in plot #72 in the PSME-ABCO/BENE/XETE community type. Soil pH was 4.6. Plot #72 was located near my tent site on Dog Mt. just out of the RNA. The plot was established to sample the upper elevational aspect of the forest left out of the RNA. The stand was old-growth (300+ yrs.) *Pseudotsuga menziesii* and *Abies concolor* with *Tsuga heterophylla* dominating in total cover and reproduction. Unfortunately these highest slopes in the Dog Creek Drainage were not included in the RNA, so they will be logged.

Pleuricospora fimbriolata occurred in one plot in each of three types: PSME/ACCI, PSME-CADE/GASH-BENE, PSME-PILA/GASH-BENE. *Pleuricospora* was also found just out of a plot in the PSME-ABCO/BENE/XETE community type. Soil pH ranged from 4.8 to 5.8. Three of the remaining four out-of-plot locations were reported by Moore et al. (1977).

Pterospora andromedea did not occur in any plots. However, out-of-plot occurrences were widespread in the RNA. *Pterospora* would probably be associated with all the described community types. Moore et al. (1977) reported 6 of the 12 sites.

Sarcodes sanguinea at Limpy Rock represents the northernmost known population of the species. *Sarcodes* occurs in the PSME-PILA/GASH-BENE community type and its extreme expression, the ARME-PSME-PIAT/ARCTO plot (# 68) described earlier. Plot #70 was established at the center of the *Sarcodes* population, specifically to type the associated vegetation. *Pseudotsuga menziesii*, *Pinus lambertiana*, and *Abies grandis* dominate the overstory. *A. grandis* and *Pseudotsuga menziesii* are the main

reproducing species. *Berberis nervosa* and *Linnaea borealis* comprise most of the shrub layer. The soil is a sandy loam with 35% coarse fragments and a pH of 5.7. Tree core rings showed about 125 years have past since the last fire, which some old growth *Pinus lambertiana* and *Pseudotsuga menziesii* survived.

Influence Factor Tests

As noted in the literature review, H. Vreeland (1980) attempted to establish an "Influence Factor" and a "Constancy Factor" which could be used in regression to "predict" the number of "Snow Plants" in a forest stand. He urged others to attempt to duplicate his results.

Data obtained from 10 points randomly placed in a stand compared with data from 10 points centered on *Sarcodes* showed no statistically significant difference between the mean values of the influence factor (Table 15). Likewise, in a different stand, 10 *Allotropa*-centered points produced influence factor values which were not statistically significantly different from the influence factor values generated by data from 10 points randomly placed in the same area (Table 15). Over 2000 distance and diameter observations are the basis of this analysis. The greater departure of values obtained from *Allotropa* centered points from random point values may be attributed to its rhizomatous habit. This incompatibility with the definition of "plant" used may produce a clustered sampling pattern which is an artifact of the "plant" definition. H. Vreeland (1980) did not collect data from randomly placed points for comparison.

These results indicate Vreeland's method was inappropriate and his conclusions unsubstantiated. His sampling method approximates a muddled mixture of a general count plot method (Mueller-Dombois and Ellenberg, 1974) and a point-centered quarter analysis (cf. Cottam and Curtis, 1956). The methodology merely (over) samples at each point (monotrope or random) the data related to mean area occupied by the trees in a stand and their mean diameter. Vreeland's model cannot be meaningfully interpreted, particularly in the absence of information regarding the incorporation of data into his model or the chance of a Type I error.

Table 15. Influence factor *t*-tests, *Sarcodes* and *Allotropa* populations, respectively.

VARIABLE	Influence Factor	
	<i>Sarcodes</i>	Random
Mean	0.034	0.035
Std. Error	0.002	0.002
Variance	0.002	0.002
Std. Deviation	0.041	0.043
Range	0.394	0.365

<i>t</i> -Value	0.370
D. F.	705
<i>t</i> -Table Value (.95)	1.963
<i>t</i> -Table Value (.99)	2.582

VARIABLE	Influence Factor	
	<i>Allotropa</i>	Random
Mean	0.076	0.060
Std. Error	0.007	0.006
Variance	0.008	0.007
Std. Deviation	0.088	0.081
Range	0.541	0.511

<i>t</i> -Value	1.704
D. F.	351
<i>t</i> -Table Value (.95)	1.967
<i>t</i> -Table Value (.99)	2.590

The relationship the data would actually reflect is the well documented $-3/2$ power "law" of self thinning (cf. Reinecke, 1933; Yoda et al., 1963; Perry, 1984). As the trees in a stand grow, mean tree diameter increases while density decreases. Drew and Flewelling (1977) refer to this phenomenon as the "maximum size-density relationship" and present Reinecke's (1933) formula as: $\ln(p) = \ln(c) - 1.67\ln(\text{DBH})$, where p is current density of trees per unit area, c is a constant, and DBH is mean tree diameter at breast height. Perry (1984) developed a generalized model in which the slope of the log-linear approximation of the self thinning curve is a function of (1) photosynthetic response to density and (2) the relation between leaf area and total aboveground biomass.

To accept H. Vreeland's (1980) hypothesis would be to accept the proposition that the number of monotropes in a stand influences the mean area trees occupy. With the invalidation of Vreeland's model, the intended comparative regression analysis between monotropes and host trees within the various community types is not possible.

Population Dynamics of *Sarcodes sanguinea*

The population has been monitored annually since its discovery in 1982. Plants have been numbered and marked with flags. In this study, a *Sarcodes* "plant" is considered to be a group of one or more caespitose clusters of annual flowering stems (or stem) which are each other's nearest neighbors and can be encompassed within a circle of 1 m diameter. This definition was used fully only with plant # 3 in 1983, indicated in Table 16 by "2+2" flowering stems. All other occurrences were of single or nearly touching stalks and recurrences within a few centimeters of the previous years stalks.

Number of plants and number of flowering stalks were recorded. In 1983 and 1984 some plants were numbered with a letter postscript. These plants occurred near the plant with the original number. It was anticipated some groupings might be necessary if plants in intermediate locations were found. However, distinguishing individual plants with the operational definition did not become a problem and the practice was discontinued.

The results of five years monitoring are displayed in Table 16. The recurrence of flowering by *Sarcodes* plants is variable and low in frequency. Flowering in the subsequent year ranged from 3% to 35%. Only one recurrence beyond the subsequent year was recorded. Plant # 14 produced two flowering stalks in 1982 and one in 1985. Plant # 4 provides some limited insight on flowering dynamics. It was discovered in 1982 only because a dead *Pinus attenuata* had toppled over. The lifting of the root was exposed a

Table 16. Population dynamics of *Sarcodes sanguinea*.

Plant #	Flowering stems/plant/year				
	1982	1983	1984	1985	1986
5	1	—	—	—	—
6	2	—	—	—	—
7	1	—	—	—	—
8	1	—	—	—	—
9	1	—	—	—	—
10	2	—	—	—	—
11	1	—	—	—	—
13	1	—	—	—	—
15	1	—	—	—	—
16	2	—	—	—	—
14	2	—	—	1	—
1	3	1	—	—	—
2	4	1	—	—	—
3	2	2+2	—	—	—
4	bud	bud	—	—	—
12	1	1	—	—	—
18	1	2	—	—	—
3a	—	1	—	—	—
7a	—	1	—	—	—
19	—	1	—	—	—
20	—	1	—	—	—
8a	—	1	1	—	—
9a	—	1	1	—	—
2a	—	—	2	—	—
7b	—	—	1	—	—
7c	—	—	1	—	—
7d	—	—	1	—	—
9b	—	—	1	—	—
11a	—	—	1	—	—
11b	—	—	1	—	—
19b	—	—	2	—	—
20a	—	—	1	—	—
22	—	—	3	—	—
32	—	—	1	—	—
8b	—	—	1	1	—
23	—	—	1	1	—
24	—	—	2	1	—
28	—	—	1	1	—
25	—	—	—	1	—
26	—	—	—	1	—
27	—	—	—	1	—
29	—	—	—	1	—
30	—	—	—	1	—

Table 16. continued

<u>Plant #</u>	<u>Flowering stems/plant/year</u>				
	<u>1982</u>	<u>1983</u>	<u>1984</u>	<u>1985</u>	<u>1986</u>
31	--	--	--	1	--
33	--	--	--	2	--
34	--	--	--	1	--
35	--	--	--	1	--
36	--	--	--	2	--
37	--	--	--	1	--
38	--	--	--	1	--
39	--	--	--	2	--
40	--	--	--	1	--
41	--	--	--	1	--
42	--	--	--	1	--
43	--	--	--	1(+ 2 buds)	--
44	--	--	--	1	--
45	--	--	--	1	1
46	--	--	--	--	1
47	--	--	--	--	1
48	--	--	--	--	1
49	--	--	--	--	1
50	--	--	--	--	1
51	--	--	--	--	1
52	--	--	--	--	1
53	--	--	--	--	2
54	--	--	--	--	1
55	--	--	--	--	1
56	--	--	--	--	1
57	--	--	--	--	1
58	--	--	--	--	4
59	--	--	--	--	1
<hr/>					
Total					
Stems	27	16	22	29	19
Plants	17	12	17	24	15
<hr/>					
Mean #					
Stems/Plant	1.6	1.3	1.3	1.2	1.3

Flowering recurrence

1982-1983	35%	1982-1985	6%
1983-1984	17%		
1984-1985	24%		
1985-1986	3%		

flower stalk bud (Figure 12). The bud did not flower that year and was killed over the winter. It was replaced by another bud which also did not flower or survive. No further activity has been observed.

Plant # 3 consisted of two flowering stalks in 1982. In 1983 two flowering stalks appeared in the original place and two more appeared about 50 cm away. They were considered from one plant based on the operational definition which is based on the potential size of the root mass (up to 60 cm diameter, Wallace, 1977). Neither group flowered subsequently. Plant # 43 had 1 flowering stalk and two stalk buds but has yet to reflower.

Number of flowering stems per plant was markedly higher in 1982 than in subsequent years (1.6 vs. 1.2 - 1.3). 1985 had the most plants and flowering stems but was followed by the lowest flowering recurrence percentage. The characteristics of the flowering population which were monitored appear relatively stable from over time. The data emphasize the point that true population levels of these plants can not be known short of digging up an entire site.

It was observed that the flower stalks and indurate seed capsules of *Sarcodes* persist for two or three years. Many of the capsules had no openings. Some had holes near the attachment of the style (presumably the "circumscissile" dehiscence described by Oliver, 1890, p. 320) or a small hole apparently chewed in the side. The capsules mostly sit and decompose in place with no particular seed dispersal mechanism. The migration potential of the species appears to be quite low. Little is known of the life cycle of *Sarcodes*.



Figure 12. Photograph of *Sarcodes* flowering stalk bud.

SUMMARY

Vegetation

Coniferous forest vegetation at Limpy Rock Research Natural Area was classified into six types:

Pseudotsuga menziesii/Acer circinatum (PSME/ACCI) community type.

Pseudotsuga menziesii/Cornus nuttallii/Berberis nervosa
(PSME/CONU/BENE) community type.

Pseudotsuga menziesii-Arbutus menziesii/Gaultheria shallon-Berberis nervosa/Pteridium aquilinum (PSME-ARME/GASH-BENE/PTAQ) community type.

Pseudotsuga menziesii-Calocedrus decurrens/Gaultheria shallon-Berberis nervosa (PSME-CADE/GASH-BENE) community type.

Pseudotsuga menziesii-Pinus lambertiana/Gaultheria shallon-Berberis nervosa (PSME-PILA/GASH-BENE) community type.

Pseudotsuga menziesii-Abies concolor/Berberis nervosa/Xerophyllum tenax (PSME-ABCO/BENE/XETE) community type.

An *Arbutus menziesii-Pseudotsuga menziesii-Pinus attenuata/Arctostaphylos* (ARME-PSME-PIAT/ARCTO) stand, represented by a single plot, with strong affinities to the PSME-PILA/GASH-BENE community, was also identified.

The entire vegetational data set was divided into two TWINSPAN groups (*0, *1). Subsequent classification showed each group contained three communities. The *0 group consists of the PSME/ACCI, PSME/CONU/BENE, and PSME-ARME/GASH-BENE/PTAQ communities. The *1 group contains the PSME-CADE/GASH-BENE, PSME-PILA/GASH-BENE, and PSME-ABCO/BENE/XETE communities.

Separate ordinations of the *0 and *1 groups assisted the interpretation of community relationships to complex environmental gradients related to temperature and moisture. *Symphoricarpos mollis* was strongly preferential to the *0 group. *Calocedrus decurrens* and *Tsuga heterophylla* were strongly preferential to the *1 group; however, both groups are too heterogeneous (due, in part, to the different successional status of the community types) for recognition of series level syntaxa. The community types are transitional in composition to communities of the Mixed Conifer Zone of Franklin and Dyrness (1973). The strong presence of *Pinus lambertiana*, *Calocedrus decurrens*, *Abies concolor*, and *A. grandis* demonstrates that the *1 group has more affinity to Mixed

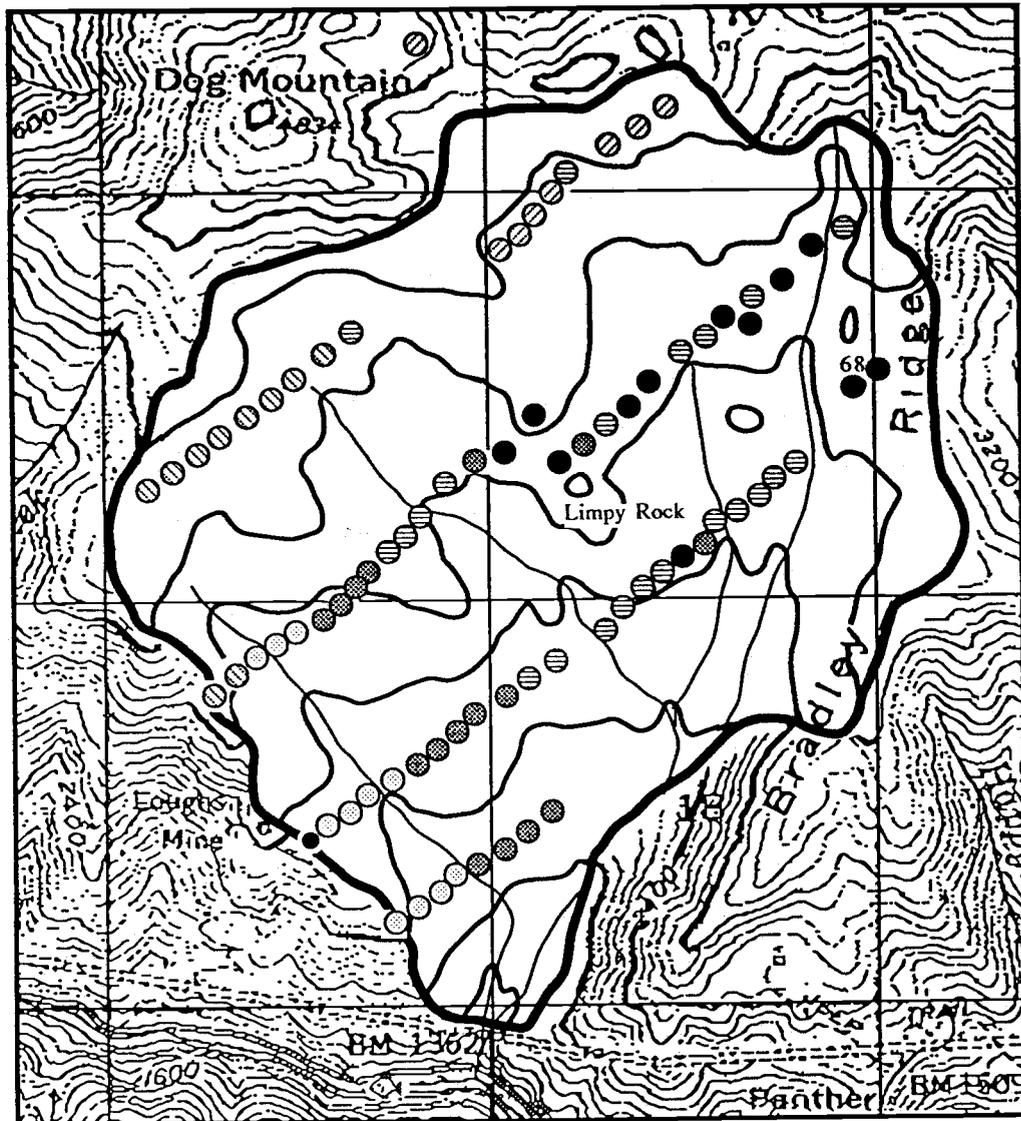
Conifer Zone types than the *0 group has. However, *Tsuga heterophylla* is also strongly preferential to the *0 group.

Communities in the *0 group seem to have floristic connections to previously described associations and communities in the *Tsuga heterophylla* Zone (except for the general absence of *Tsuga* in the *0 group). The PSME/ACCI and PSME/CONU/BENE community types are probably closest to the PSME/ACCI/BENE community type of Dyrness et al. (1974). They hypothesized a *Tsuga heterophylla/Rhododendron macrophyllum/Berberis nervosa* climax association for their community.

The relationships between the community types and the complex temperature and moisture gradients revealed by the ordinations are summarized in Figure 13. The PSME-CADE/GASH-BENE community would seem to be the "central" type with variations in the gradients resulting in the other communities.

At the dry end of the moisture gradient is found the PSME-PILA/GASH-BENE community type. An earlier seral stage, persistent on rocky ridges is represented by the ARME-PSME-PIAT/ARCTO stand sample. The PSME/CONU/BENE and PSME/ACCI community types are found at the mesic end of the gradient.

The thermal (elevation) gradient starts with the warm, low elevation, relatively early seral stage, PSME-ARME/GASH-BENE/PTAQ community type. Two paths lead upward to cooler types. The first goes through the PSME/CONU/BENE type to the PSME/ACCI type. The second passes through the PSME-CADE/GASH-BENE type to the PSME-ABCO/BENE/XETE community type. Where strong gradients between types were not evident, they are not delineated in Figure 13. Vegetation plot locations are coded by community type in Figure 14 to summarize the distribution of the types. Plot numbers were presented in Figure 5.



Community Types

- | | |
|----------------------------|-----------------------|
| ⊙ PSME/ACCI | ⊖ PSME-CADE/GASH-BENE |
| ○ PSME/CONU/BENE | ● PSME-PILA/GASH-BENE |
| ⊗ PSME-ARME/GASH-BENE/PTAQ | ⊘ PSME-ABCO/BENE/XETE |

Figure 14. Vegetation plot locations coded by community type, Limpy Rock RNA. Major contour interval is 120 m (400 ft.).

Monotropoideae

Allotropia virgata is strongly preferential to plots in the *1 group at the dryer end of the moisture gradient. *Monotropa hypopithys* shows a preference for higher elevation plots. *Pterospora andromedea* was not found in any plots but was noted to be widespread throughout the RNA. *Hemitomes congestum*, *Monotropa uniflora*, *Pityopus californica*, and *Pleuricospora fimbriolata* were largely restricted to the *1 group. No monotropes were found in plots of the cool mesic, PSME/CONU/BENE type or the young warm PSME-ARME/GASH-BENE/PTAQ community type.

Analysis and testing (with over 2000 observations from *Sarcodes*, *Allotropia*, and randomly centered points) of H. Vreeland's (1980) hypothesis concerning predicting numbers of "Snow Plants" in a location, showed his model (which incorporated a "Constancy Factor" and an "Influence Factor") and conclusions to be inappropriate. The "Influence Factor" data obtained by this methodology are related to the $-3/2$ power law of self thinning (Yoda et al., 1963).

The northernmost known population of *Sarcodes sanguinea* was discovered in the PSME-PILA/GASH-BENE community type. Population monitoring demonstrated a low percentage of flowering recurrence from year to year. Actual population levels of these perennial subterranean mycotrophic organisms were shown to be unpredictable. During the five years observed, number of flowering plants and flowering stems was relatively stable, with a two-fold difference in minimum and maximum values.

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