AN ABSTRACT OF THE THESIS OF

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Title: THE RELATION OF SOIL CHARACTERISTICS TO GROWTH AND DISTRIBUTION OF *CHAMAECYPARIS LAWSONIANA* AND *THUJA PLICATA* IN SOUTHWESTERN OREGON

Abstract approved:
Donald B. Zobel

Twelve plots at six sites in southwestern Oregon were studied to determine the degree to which various soil characteristics are related to the occurrence and growth of *Chamaecyparis lawsoniana* and *Thuja plicata*. Soil profiles and vegetation were described in each plot; and measurements were made of insolation, soil and litter temperature, creek and groundwater characteristics, and litter accumulation. Growth was estimated by measurement of age, height, DBH, 10-year basal area increment, and foliage elongation between July, 1979, and January, 1980. In July and September, 1979, and January, 1980, mineral soils from the 0-10 cm level were analyzed for pH, moisture holding capacity, loss-on-ignition, and concentrations of nitrate, ammonium and total N. Nitrate and ammonium concentrations were also determined in stream and groundwater. In July and January, fine litter was analyzed for pH, nitrate and ammonium. On each sample date, soils and litter were incubated aerobically for five weeks at 28°C to determine their potential for ammonification and nitrification. Ammonium was added to some samples

before incubation. Total N concentration was determined for individual foliage samples (collected in September) in most plots; foliage and mineral soil samples were composited for each plot and analyzed for P, Ca, K and Mg concentrations. The various soil and other measurements were related to basal area increment by multiple regression analysis.

Occurrence of *Thuja* was associated with higher availability of N, particularly nitrate, and soils which were at or near field capacity in July and September. Within each locality *Thuja* also was most important on soils which were more basic and had higher Ca content than soils of sites dominated by *Chamaecyparis*. Litter under *Thuja* generally contained higher levels of extractable N and exhibited more vigorous N mineralization, particularly nitrification, than did litter under *Chamaecyparis*. *Chamaecyparis* was associated with higher soil C/N ratios and had significantly higher foliar K corresponding to higher soil K levels. No consistent relationship occurred between distribution of *Thuja* and *Chamaecyparis* and total soil N or loss-on-ignition.

Variability in basal area growth was best explained for *Chamaecyparis* by soil nitrate concentration in July ($R^2 = 0.30$), and for *Thuja* by soil Ca concentration and clay content ($R^2 = 0.37$), after variability due to age had been removed. Growth of both *Chamaecyparis* and *Thuja* (and *Pseudotsuga* and *Tsuga*) was best where N (especially nitrate) was most available, and poorest on sites where N availability was lowest. Although growth at an early age appears lower, growth of older *Thuja* exceeded that of *Chamaecyparis* on most sites studied.

It appears that water and N availability are the primary factors limiting distribution of *Thuja* in southwestern Oregon. Low availability of soil Ca and Ca/Mg ratio may also restrict *Thuja* from some soils. In contrast, *Chamaecyparis* tolerates a wider range in most of the soil characteristics measured. The sites studied seem to exhibit higher nutrient availability and better growth of *Chamaecyparis* than in most of its range; however, soil N appears more limited than in soils outside its range farther north. None of the factors measured here, with the possible exception of soil Mg availability, are correlated with *Chamaecyparis*' northern range boundary. Therefore, it seems likely that as conditions improve for growth farther north, growth of *Chamaecyparis* is less affected than that of *Thuja* or other species; and it may be eliminated by competitive exclusion.

In general, distribution of *Thuja* seems more limited by physical site characteristics, in contrast to *Chamaecyparis*, which is more subject to competitive stress. *Chamaecyparis* is often important on sites where soil conditions are not suitable for other species. It is doubtful whether *Thuja* will replace *Chamaecyparis* over most of its range, as *Chamaecyparis*' importance declines due to disease and commercial harvest.

The Relation of Soil Characteristics to Growth and Distribution of *Chamaecyparis lawsoniana* and *Thuja plicata* in Southwestern Oregon

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THE RELATION OF SOIL CHARACTERISTICS TO GROWTH AND DISTRIBUTION OF CHAMAECYPARIS LAWSONIANA AND THUJA PLICATA IN SOUTHWESTERN OREGON

INTRODUCTION

Chamaecyparis lawsoniana (A. Murr.) Parl. (Port-Orford-cedar) and Thuja plicata Donn (western redcedar), members of the Cupressaceae, grow together infrequently in southwestern Oregon and northwestern California. Chamaecyparis lawsoniana is endemic to a coastal strip extending about 200 km from Reedsport, Oregon, to Eureka, California, and about 55 km inland at its widest near the latitude of Powers, Oregon (Figure 1; Hawk, 1977). Isolated populations occur near the headwaters of the Sacramento and Trinity rivers in northern California, about 150 km inland. Generally, populations are most widespread in the north, becoming increasingly disjunct and small farther south. The tree grows from sea level to about 1500 m on seaward slopes of the Coast Range and Klamath Mountains.

In contrast, the geographical range of Thuja plicata is large, with a coastal distribution extending from southeastern Alaska to northern California and east to the eastern slope of the Cascade Mountains. It also has an inland distribution extending from southern British Columbia to central Idaho along the west side of the Rocky Mountains (Figure 2; Fowells, 1965). Elevation ranges from sea level to 2300 m near Crater Lake, Oregon. In southern Oregon and northern California, the species occurs sporadically, largely within or near the fog belt.

Macroclimate is similar for the two species. Precipitation in Chamaecyparis' range varies from 102 cm in the south and east to nearly 305 cm at higher elevations near the coast. Average annual temperature at weather stations varies from about 10°C at high elevation near Mt. Shasta to 13.3°C in the inland regions of the Coast Range (Hawk, 1977).

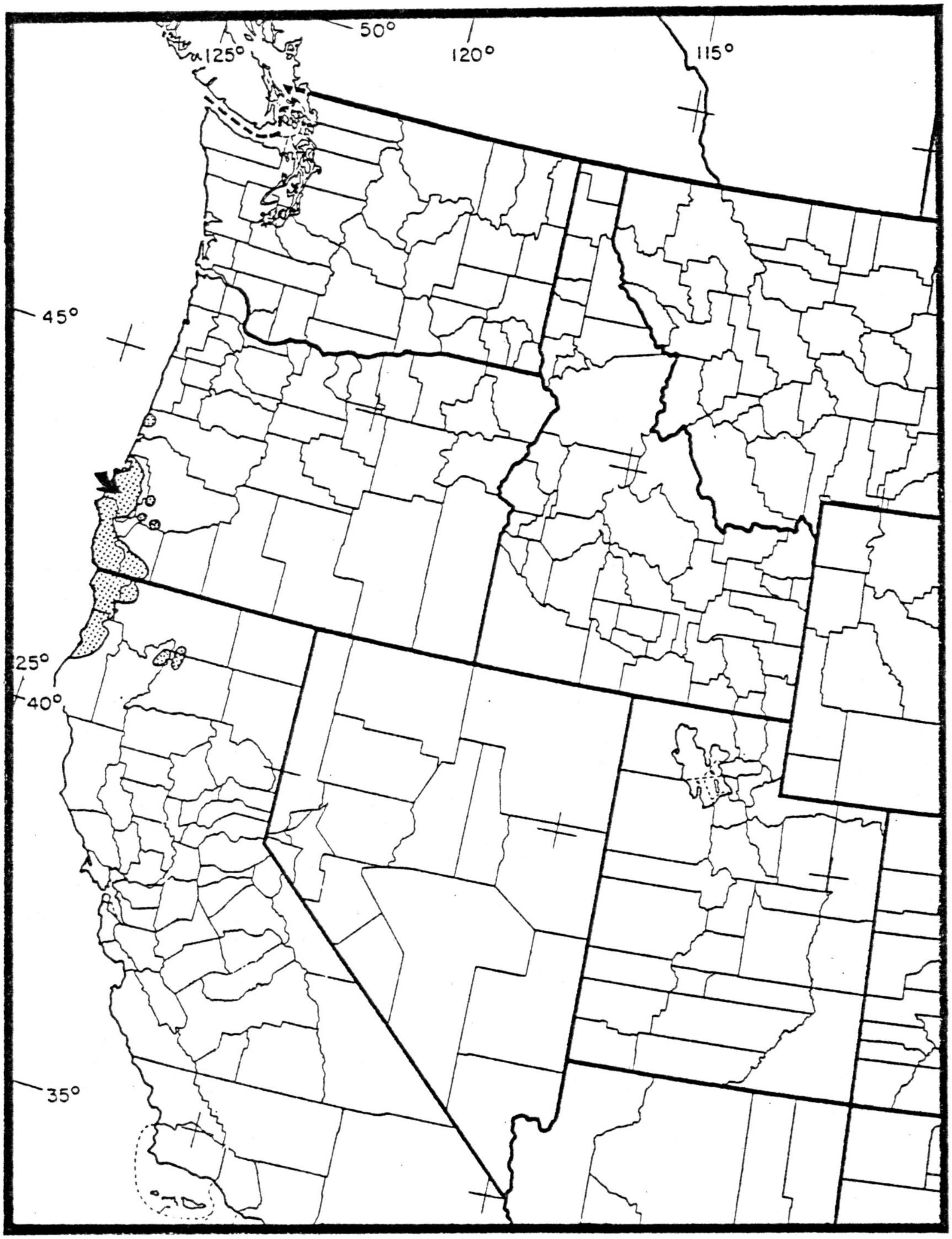

Figure 1. Range of Chamaecyparis lawsoniana; arrow indicates general area of study (from Little, 1971).

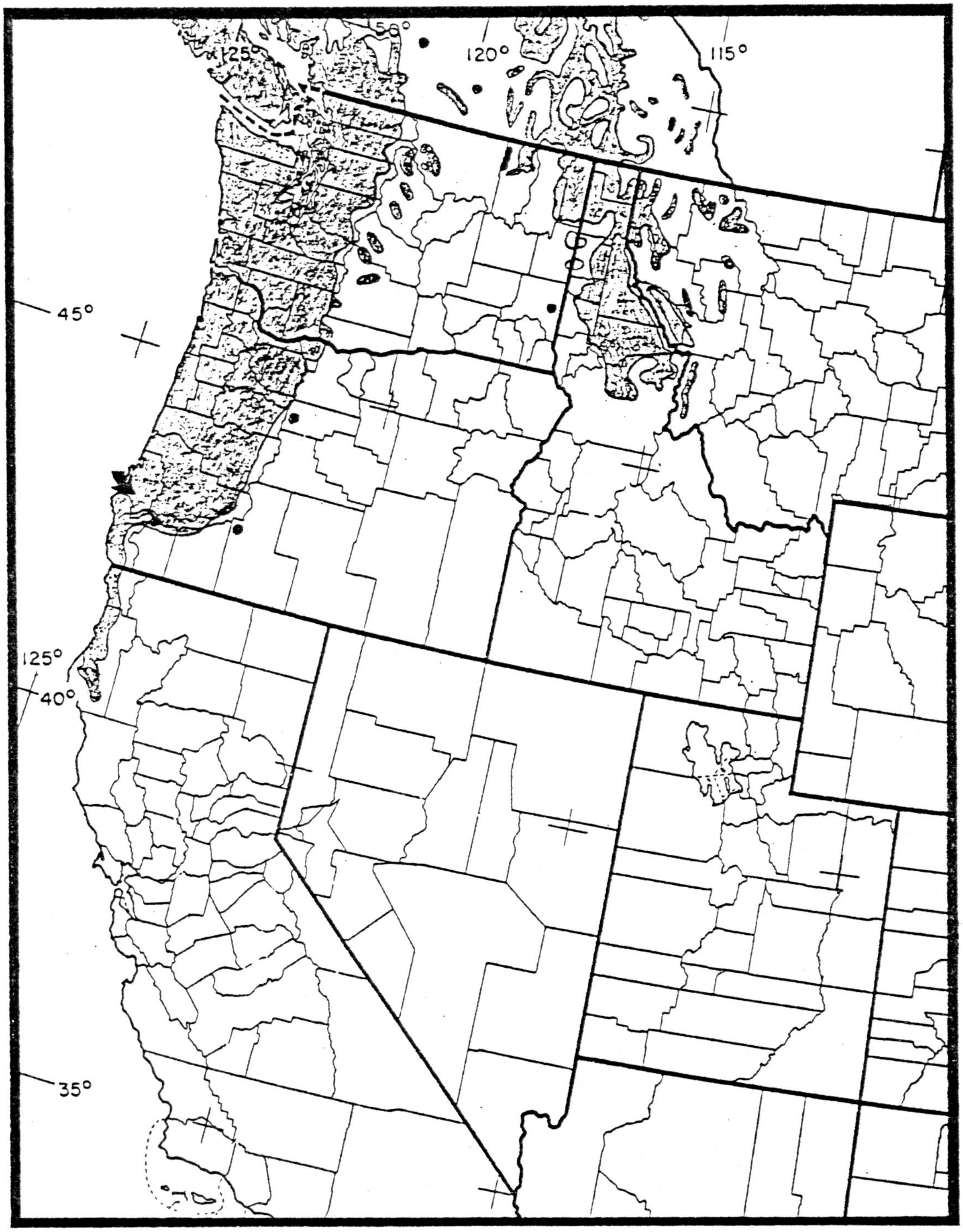

Figure 2. Range of Thuja plicata in the United States; arrow indicates general area of study (from Little, 1971).

Thuja is reported to be confined primarily to regions of abundant precipitation and humidity (Sharpe, 1974). Average rainfall in the coastal region varies from 76 to 330 cm annually, with most falling between November and April. Average annual temperature varies from 7.8 to 11.1°C. Climate in the inland range differs considerably. Mean annual temperature is cooler, 5.6 to 10.0°C, and the 71 to 127 cm precipitation is more evenly distributed throughout the year (Fowells, 1965).

Both trees occur on many parent materials and soils. Chamaecyparis' range is one of the most geologically heterogeneous areas in the western U.S. (Baldwin, 1964; Hawk, 1977). Parent materials include dune sand and sedimentary, granitic, gabbroic, metasedimentary, ultramafic and other basic intrusive rocks (Hawk, 1977; Meyer and Amaranthus, 1979; Whittaker, 1960). Nearly three-quarters of the range, predominately in the south, occurs on soils at least partially derived from ultramafic materials (i.e., peridotite, serpentinite). Tree density as well as volume of Chamaecyparis is greatest on these soils, probably due to reduced competition. However, the tallest and most vigorous trees occur on deep sedimentary soils in the northern part of the range (Hawk, 1977; Zobel and Hawk, 1980).

Given the large distribution of Thuja, similar variability in parent materials is expected. Since the tree commonly grows along streams, or on moist flats and terraces, parent material is often alluvium of mixed origin. On Vancouver Island, Thuja occurs on all parent materials, landforms, and soil textures (Packee, 1976). Within the range of Chamaecyparis, the Soil Resource Inventory for the Siskiyou National Forest lists the occurrence of Thuja on sedimentary, metasedimentary, gabbroic, dioritic, granodioritic, and to some extent serpentinite and peridotite parent materials (Meyer and Amaranthus, 1979). Hawk (1977) reported Thuja in the wettest plots of his Abies concolor-Tsuga heterophylla-Chamaecyparis lawsoniana community on granitic parent materials, some of which included some ultramafic materials. Best growth and development reportedly occurs near the latitudinal center of its distribution in the Puget Sound region, on fertile soils of moist bottom lands (Minore, 1980).

Related to the general diversity of climate and parent materials associated with both species is considerable variation in associated species. Within Chamaecyparis' limited range, it occurs in the Tsuga heterophylla, Abies concolor, Picea sitchensis, and the Mixed Evergreen vegetation zones of Franklin and Dyrness (1973), and several restricted azonal communities, including two on coastal dunes (Hawk, 1977). In Oregon and Washington, Thuja occurs in the Picea sitchensis, Tsuga heterophylla, Abies lasiocarpa, and Abies grandis zones, as well as a number of restricted communities, one on coastal dunes (Franklin and Dyrness, 1973).

The question has arisen as to why Chamaecyparis' natural range is so restricted, given the diversity its environment and associated vegetation exhibit (Franklin and Dyrness, 1973; Zobel and Hawk, 1980). The eastern range limit coincides with a rapid decrease in ratio of precipitation to evaporation, which in southernmost Oregon occurs near the 40-inch (102-cm) isohyet; however, its latitudinal limits are related to no major macroclimatic shift. Distribution to the south seems to end where ultramafic rock is no longer associated with the coastal mountains, major rivers, or high elevations. Various characteristics of ultramafic soils, where sufficient water occurs, are thought to directly or indirectly compensate for above-ground-moisture stress in Chamaecyparis (Zobel and Hawk, 1980). The northern limit is yet to be explained fully, although two hypotheses are proposed. One concerns the phenological development of Chamaecyparis and its interaction with an increasingly short growing season farther north. Chamaecyparis may be able to compete with faster growing species, such as Pseudotsuga menziesii, by having a phenology that takes full advantage of the later part of the growing season where it occurs in the northern part of its range (Zobel, unpublished). This late growth, however, may be fatal with the earlier occurrence of biologically-important frost at the northern boundary. An alternative explanation is suggested by the coincidence between Chamaecyparis' northern limit and the northernmost extent of Eocene-aged sediments originating in mountain ranges to the south, which include ultramafic rock (Baldwin, 1974; Zobel and Hawk, 1980). No evidence indicates consistent discontinuity in soils across the northern boundary, although the possibility has not been studied.

Climatic requirements (i.e., sufficient precipitation, humidity, mean-growing-season temperature) appear to explain the geographical distribution of *Thuja*, at least on a large scale (Packee, 1976; Sharpe, 1974; Sudworth, 1907). Within *Chamaecyparis*' range, occurrence of *Thuja* is reported normally on the wettest, most protected sites (Franklin and Dyrness, 1973; Hawk, 1977). Griffin and Critchfield (1972) reported *Thuja* associated with *Chamaecyparis* in wet coastal sites near the mouth of the Klamath river in California. This is somewhat paradoxical, as *Thuja* sometimes grows on sites too dry for *Tsuga heterophylla* (Franklin and Dyrness, 1973; Packee, 1976). Packee compared *Thuja* to *Pinus contorta*, which competes most efficiently on the wettest as well as drier sites. Yet, *Tsuga* is commonly associated with *Chamaecyparis* where *Thuja* is not. Both trees appear to require abundant soil moisture in the southern end of their ranges, which coincide closely; yet the two seldom are associated locally. It seems likely that factors in addition to moisture requirements may contribute to their limited co-occurrence. The primary purpose of this study was to investigate the possibility of local differences in soil characteristics, primarily those related to nitrogen availability.

Little work has been done with *Chamaecyparis* relevant to the subject of this study. Plocher (1977) investigated soil and plant nutrient relationships of *Chamaecyparis lawsoniana*, as well as the possibility of ecotypic differentiation, by cross-culturing seedlings from four sites on four native soils. Zobel and Hawk (1980) reported some environmental as well as physiological relationships of *Chamaecyparis*, including water relations and foliar nutrient content of trees growing in a range of native soils and forest communities. Leyton (1955) reported the effect of heather mulching on growth and nutrient status of nursery-grown *Chamaecyparis*, and several studies have compared foliar nutrients of nursery-grown *Chamaecyparis* with other species (Crooke *et al*., 1964; Ovington, 1956; Youngberg, 1958; Zobel and Liu, 1979). With the exception of Plocher's work and general studies concerning serpentine soils (Proctor, 1971; Walker, 1954), little is known about the nutrient status of soils under *Chamaecyparis*, particularly in the northern end of the range.

Several studies of *Thuja* bear directly on the subject of this study. Krajina *et al*. (1973) compared growth of *Thuja* in culture with nitrogen supplied as either or both nitrate and ammonium. Garm (1958), working with Krajina, compared the nitrification potential of soil and litter under *Tsuga*-*Pseudotsuga* stands to *Thuja*-*Pseudotsuga* stands, as well as the nitrate storage in the foliage of various associated plants. Krajina (1970) arrived at far-reaching conclusions concerning the nitrogen relations of *Thuja*, *Tsuga* and *Pseudotsuga*, apparently based on these two experiments (Krajina *et al*., 1973; Garm, 1958). Other studies related broad soil patterns to vegetation types, which include *Thuja*, in Idaho (Larsen, 1940) and British Columbia (McLean and Holland, 1958); and Forristal and Gessel (1955) related soil properties to forest cover type and productivity of *Pseudotsuga*-*Thuja* stands in Washington. Soil and humus layers under *Thuja* and *Tsuga* trees were compared by Alban (1969) and Lowe (1972), in Washington and Idaho, and British Columbia respectively. Minore *et al*. have studied a number of soil relationships concerning *Thuja*; these include the relationship of occurrence and growth to water table level and flooding (1968, 1970, 1971), seedling root growth in dense soils (1969), and germination and early growth in organic seed beds (1972). Another source, the Soil Resource Inventory for the Siskiyou National Forest (Meyer and Amaranthus, 1979) provides information related to soils and the occurrence of both *Thuja* and *Chamaecyparis* in the northern portion of *Chamaecyparis*' range. Vegetation, land type, and various site factors are reported; however, nutrient data are lacking, and the large scale limits any detailed comparison. Soils described for regions in which I established plots in this study showed little similarity to the soils which I encountered. Several studies have reported nutrient content of *Thuja* foliage. Walker *et al*. (1955) determined mineral deficiency levels for seedlings grown in culture, and comparisons of foliage content to other trees were made in Pacific Northwest forests (Daubenmire, 1953; Beaton *et al*., 1965; Gessel *et al*., 1951; Tarrant *et al*., 1951), English plantations (Ovington, 1956), and nursery stock (Crooke *et al*., 1964), the latter two including comparison with *Chamaecyparis*.

The objective of this study was to compare the soils in which the two trees grow in southwestern Oregon, and to determine which soil factors relate most to their occurrence and growth. Twelve plots in which *Chamaecyparis* and *Thuja* grow either together or alone (with respect to the other), were characterized in terms of various soil, litter, and groundwater properties in July and September, 1979, and January, 1980. Tree age, height, diameter, basal-area increment and foliage elongation were measured as indices of growth. In addition, foliage nutrient content was compared between sites and species, and related to soils and growth.

This study was conducted for a variety of reasons, the most apparent of which is our lack of knowledge concerning soils under *Chamaecyparis* and *Thuja* in southwest Oregon. What is known concerning the relation of growth to these soils is limited largely to differences in parent material (i.e. serpentine versus sedimentary). More detailed information concerning the physical and nutritional properties of specific soils is needed to adequately understand the requirements of these trees. In addition, both trees are highly valued for their wood, as well as for ornamental use (Bolsinger, 1979; Hawk, 1977). Timber harvest of both is currently exceeding replacement, since neither has been intensively managed, and neither generally occurs in pure stands. In Washington, with about 40% of the U.S. *Thuja* resource, old growth cedar will soon be scarce on lands outside national forests (Bolsinger, 1979). Considerable reduction in *Chamaecyparis*' importance in natural forests is now occurring due to harvest, but more severely due to an exotic and fatal root rot caused by *Phytophthora lateralis* (Roth *et al*., 1972; Zobel and Hawk, 1980). Unfortunately, its elimination as a commercially important tree from much of its present range seems unavoidable. Under these circumstances, comparison of the growing conditions of these trees may be quite important. Minore (1979) states that such a comparison might "provide information about suitable substitutes if *Chamaecyparis lawsoniana*'s ecological niche must be occupied by other species". In addition to indicating if and where *Thuja* is capable of replacing *Chamaecyparis*, study of the soils may shed light on the reasons for *Chamaecyparis*' unexplained northern limit, as well as the restricted distribution of *Thuja* within *Chamaecyparis*' range.

METHODS

Field Methods

Plot Location. During the spring of 1979, field reconnaissance in conjunction with information provided by the U.S. Forest Service, Bureau of Land Management, and Coos County Forestry Department were used to locate suitable sites for field sampling. Two kinds of sites were desired: (1) sites with good presence and growth of *Chamaecyparis* or *Thuja*, well within their own respective distributions, but which appeared to be outside the other's; and (2) sites within the distributional overlap of the species which exhibited local segregation of species that might be partially explained on the basis of soil characteristics. Plots were ultimately placed with emphasis on maximum occurrence of the species concerned, as well as site homogeneity.

Plot Layout and Description. Plots ranged from 110 to 570 m^2, based on the area necessary to include sufficient trees on which to base soil sampling yet maintain homogeneity, and on practical limitations. One group of trees was sampled on an area-less plot basis, where infrequent but consistent occurrence of *Thuja* along a creek made a fixed boundary plot impractical (Plot ASR-1). These trees were sampled for growth and soil environment as in other plots, but statistics based on area could not be calculated. Each plot was mapped, and numbers assigned to each tree.

Shrubs, herbs, and bryophytes were sampled in September, 1979, by 1 m^2 quadrats placed systematically throughout the plot, 30 - 50 per plot. For ASR-1, four quadrats were sampled per tree, placed 1 m from the trunk, and 90 degrees opposed to each other. Percent cover and frequency were estimated by the Daubenmire method (1968). Nomenclature for vascular plants follows Hitchcock and Cronquist (1973), and for bryophytes, follows Lawton (1971).

Representative soil profiles were described for all plots except ASR-1 and POR according to the Soil Survey Manual (1962). Soil at POR consisted of pockets of stream sediments interspersed between boulders, such that no profile was obtainable. In other plots, samples from each horizon were taken to the laboratory for dry color determination and textural analysis.

Understory light, as percent of full local sunlight, was measured in September, 1979, using the ozalid paper method (Friend, 1961). Sensors were placed directly south of each tree sampled for soil, approximately half-way between the trunk and edge of canopy; thus between four and ten measurements were made per plot. Full sunlight was concurrently measured at several open locations near the plots, all of which gave similar results. Sensors were calibrated with a quantum sensor. Insolation at CC and CM plots was not measured.

Thirty-day thermographs were used to measure temperature continuously in the litter and -10 cm in the soil at four plots over four periods between July 6, 1979, and January 6, 1980. Charts were changed and thermographs calibrated on each visit to the sites. Thermographs were placed in plots at Ash Swamp (ASP, ASR-2) and Squaw Lake (SLP, SLR-3) to determine any difference in soil temperature regime where the two species grow together locally. In addition, soil temperature at -10 cm soil depth was measured at the time of each soil sampling. Soil thermometers were inserted adjacent to an opposing pair of the four soil subsamples taken per tree (see Figure 3).

Fine litter mass was estimated in January by removing all litter down to mineral soil in an area equal to 4 dm^2, with three such collections per plot. Sample location was subjectively located to represent an average for the plot. Litter samples were hand-crushed and passed through a 2 mm mesh screen, oven dried for eight hours at 105^oC, and weighed. Thus litter used for the estimate was approximately equal to the F organic horizon.

Growth Estimates. Diameter at breast height (DBH) was measured for all trees; trees greater than 8 cm DBH were aged by an increment core at breast height. An index of growth was derived by measuring radial wood growth for the last ten years. Two cores per tree were used for this measurement, since radial growth was observed to vary considerably between sides of a tree. Ten-year radial growth, DBH, and bark thickness were used to calculate ten-year basal area increment. Tree heights were measured for dominant trees of each species with an Abney level.

In addition to these indicators of growth, foliage elongation was measured between July 6, 1979, and January 4, 1980. Acrylic paint marks were applied near the tips of healthy branches in July, using from 20 to 30 branches per plot. Whenever possible, young saplings were used, but often only larger trees were available. Since growth was found to be highly variable in any plot, the mean of the five highest increments per plot was taken as a relative index of growth. Part of the variability seems to be due to unpredictable apical dominance, primarily seen in *Thuja*, and the elongated active meristem found in both *Thuja* and *Chamaecyparis* branches.

Sample Collection. Soils were collected over a period of two to three days beginning July 6 and September 12, 1979, and January 4, 1980. Sampling was tree-based, with four subsamples per tree removed by soil tube from the top 10 cm of mineral soil. Pattern of subsample location is illustrated in Figure 3. Orientation of sampling was rotated about 25 degrees on each sample date. Subsamples for each tree were composited into plastic bags and kept refrigerated below field temperature until dried in the laboratory. Litter was sampled only in July and January in a manner similar to soil. However, the January samples were combined to make one composite sample per plot. Litter was also cooled in transit.

In June, 1979, 2.5 cm by 1 m-long perforated PVC pipes were inserted into the ground in all plots where a shallow water table was considered likely. In sloping plots two or more pipes were used at different elevations. Pipes were capped to prevent excessive oxygen saturation from air. Before removal of samples in July, September, and

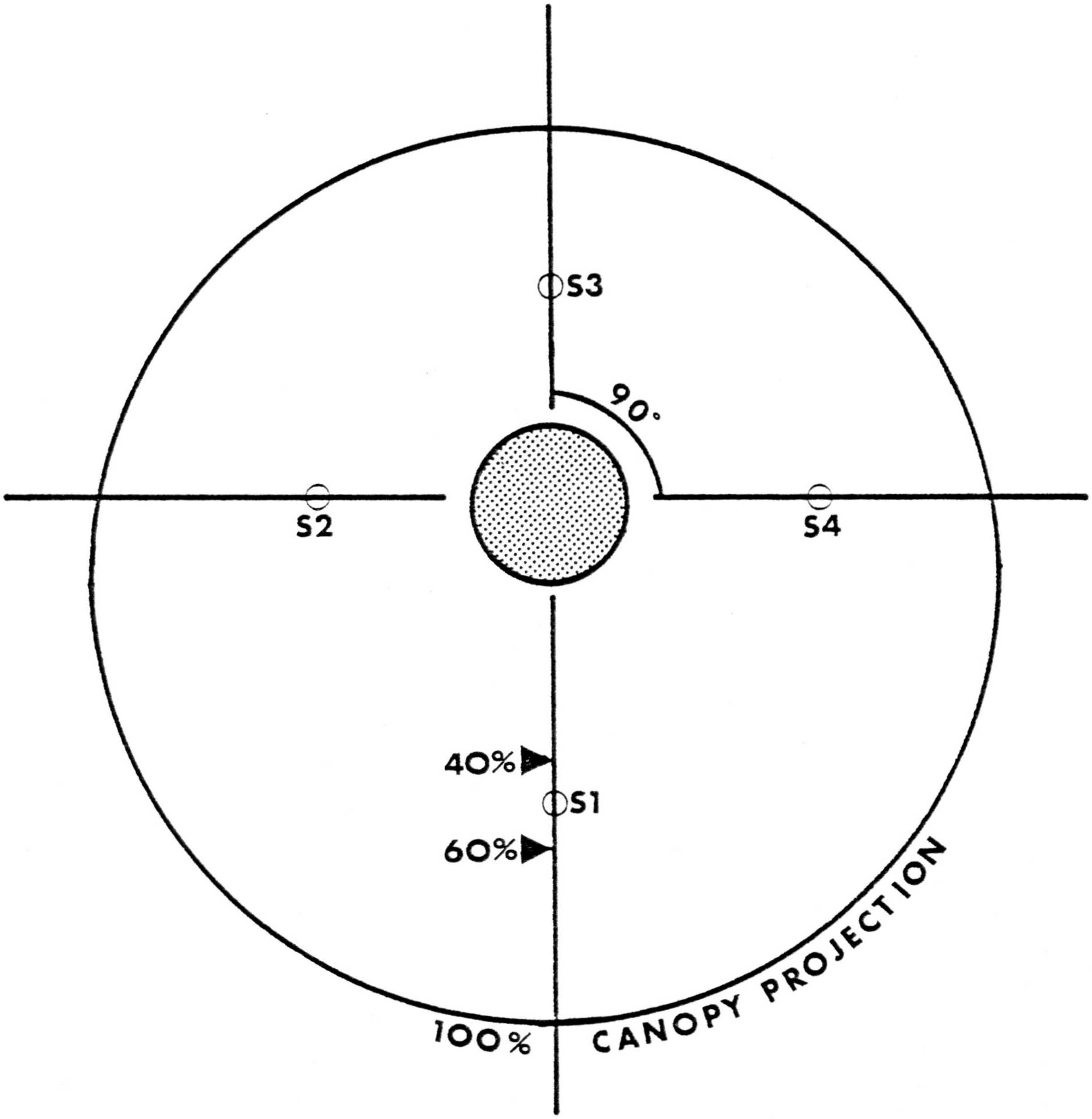

Figure 3. Location of soil and litter subsamples (S1-S4) around each tree sampled; S1-S4 lie between 40 and 60% of the canopy projection from the tree.

January, water depth, oxygen content, pH, and temperature were measured. Oxygen content was measured by a dissolved-oxygen probe lowered into the pipe. Readings were converted to % saturation relative to creek water, considered to be fully saturated. pH was usually measured with a portable glass-electrode pH meter, and temperature with a thermistor. Water was transferred to 125-ml bottles using a suction bulb and plastic hose. Integrity of nitrate and ammonium was fixed by addition of H_2SO_4 (Booth and Thomas, 1973). Samples were cooled until laboratory analysis. Water was sampled and measured similarly in streams and seep areas where they occurred within plots.

Foliage was sampled in September, 1979, from two to seven trees per plot, depending on the availability and accessibility of healthy foliage. The apical 2 dm was collected from at least four branches per tree; whenever possible branches were sampled which extended in four opposing directions. Availability necessitated the sampling of different sized and aged trees, so that sample height in the canopy varied.

Laboratory Methods

Methods of soil, litter, water, and foliage analysis are listed in Table 1.

Soils. Soils were spread to air dry at room temperature, generally within 72 hours of collection. In very wet soils, drying required 72 hours or more. Subsamples were taken prior to drying for determination of field moisture. Air-dry soil was lightly crushed and passed through a 2 mm (No. 10) mesh screen. Portions were separated for analysis of air-dry-moisture content, pH, loss-on-ignition, total N (minus nitrate-N), and extractable nitrate-N and ammonium-N concentrations. Loss-on-ignition is a valid estimate of organic content. For determination of total N concentration, soil was ground in mortar and pestle to pass a No. 50 mesh screen prior to Kjeldahl digestion. Portions were also composited on a plot basis for incubation to

Table 1. Laboratory methods used for analysis of soil, litter, water and foliage.

Soil	
pH	1:2 soil to water mixture; measurement with Beckman glass electrode pH meter (Berg, et al., 1978)
Moisture	Gravimetric determination; oven dried eight hours at 105°C (Dawson, 1977)
Field Capacity (estimate)	Spin centrifuged seven minutes at 2400 rpm (Dawson, 1977)
Organic Matter (estimate)	Loss-on-ignition; two hours at 500°C (Cox, 1972)
Texture	Bouyoucos method (Cox, 1972)
Total Nitrogen	Modified semi-microkjeldahl digestion (Bremner, 1965); measurement with HNU ammonia-sensing electrode (Orion Research Inc., 1978)
Ammonium	Extraction with 2N KCl; measurement with ammonia-sensing electrode (Orion Research Inc., 1978)
Nitrate (+Nitrite)	Extraction with 2N KCl, reduction to ammonia (Orion Research Inc., 1974); measurement with ammonia-sensing electrode (Orion Research Inc., 1978)
Exchangeable Ca, K, Mg	Extraction with ammonium acetate; measurement by atomic absorption (performed by U.S. Forest Service Forestry Sciences Laboratory, Corvallis)
Total Ca, K, Mg	Perchloric acid digestion; measurement by atomic absorption (performed by U.S. Forest Service Forestry Sciences Laboratory, Corvallis)
Exchangeable P	Bray method (performed by Oregon State University Soils Testing Laboratory)
Litter	
pH	1:6 litter to water mixture; measurement with glass electrode pH meter
Moisture	Same as soil
Ammonium	Same as soil
Nitrate	Same as soil

(Continued on next page)

Table 1. Continued.

Water	
pH (in field)	Direct measurement with portable glass electrode pH meter
Ammonium	Direct measurement with ammonia-sensing electrode (Orion Research Inc., 1978)
Nitrate	Reduction to ammonium (Orion Research Inc., 1974); measurement with ammonia-sensing electrode
Foliage	
Moisture	Same as soil
Total Nitrogen	Same as soil
Total Ca, K, Mg	Same as soil
Total P	Molybdate Blue method with Technicon Autoanalyzer (Technicon industrial method 334-74W/B) (performed by Dean Hansen, Soils Science Department, Oregon State University)

determine N mineralization potential, and for determination of the moisture equivalent (an estimate of field capacity). Soils collected in September were composited on a plot basis and submitted elsewhere for analysis of P, Ca, Mg and K. Soils from representative plot profiles were air dried, and analyzed for moisture content and texture.

Litter. Litter was air dried, and all identifiable material removed (i.e. twigs, leaves, cones) prior to analysis. Litter collected in January was hand-crushed and passed through a 2 mm mesh screen; July samples were not screened. Portions were split for measurement of pH, air dry moisture, extractable nitrate-N and ammonium-N concentrations, and for incubation to determine N mineralization potential. Dilution of litter for pH measurement was arbitrarily set at 1:6, litter to water, since this gave sufficient supernatant to submerge the electrode.

Incubation. Aerobic incubation similar to that used by Montes and Christensen (1979) and described by Norman (1955) was used to estimate potential N mineralization rates of the soil and litter. Fifty grams of soil were placed in either 8 oz. styrofoam cups (July) or 8 oz. plastic cups (September and January) and moistened to the moisture equivalent. The soil/water mixture was stirred vigorously to achieve uniform wetness. Treatments consisted of: (1) distilled water, and (2) 10 ppm N (July and September) and 100 ppm N (January) (ppm based on soil oven dry weight), added as ammonium sulphate solution. The cups were sealed with Saran wrap and weighed. Polyethylene is relatively permeable to oxygen but impermeable to water (Bremner, 1965). Water loss was determined periodically. The styrofoam cups used in July permitted excessive evaporation, so that readdition of moisture was necessary midway through the incubation. Three replicates per treatment per plot were incubated in a relatively humid atmosphere and darkness at 28°C. After five weeks, soils were air dried at room temperature and analyzed for nitrate-N and ammonium-N concentration. A similar technique was used for litter with the following changes: 20 g (July) and 30 g (January) litter were used, to which was added a standard 20 ml and 30 ml distilled water respectively. Thus, moisture content was approximately 100% in both incubations. An additional treatment consisting of 100 ug N as ammonium sulphate was included in the July incubation. Controls consisting of 20 ml distilled water only, and 100 ug N (ammonium sulphate) in solution were included in all incubations.

Foliage. Foliage was air dried at room temperature and stripped of its scaly leaves. Some fine branchlets which became brittle on drying were unavoidably included in the samples of both species. Leaves were finely ground and analyzed for moisture content. Individual samples were analyzed for total N (minus nitrate-N). Foliage from trees larger or smaller than 15 cm DBH was composited separately on a plot basis and submitted elsewhere for P, Ca, Mg, and K analysis.

Data Analysis. All analytical results were adjusted to an oven dry weight basis. All figure and table values for soil and litter are the means of four to ten determinations per plot (n listed in Table 2) except where noted. Carbon content for use in deriving C/N ratios was calculated using a regression developed by Ball (1964) for soil ignited at 375°C. The least significant difference (Steel and Torrie, 1960) was used to test significance between plot means, when sample number was sufficient. Student's t-test of significance was used between sample dates within plots. Significance was tested at the 5% level throughout. Multiple linear regression was used to test the significance of various soil and other factors in explaining the variability in basal area increment. Where only one value was available per plot, as for soil Ca, this value was repeated for all observations of tree growth in that plot. Plot means for soil factors based on numerous samples per plot were repeated for all observations of growth, which included trees not specifically sampled for soils. Only variables which significantly (5% level) contributed to the regression in a stepwise format were added to the model, except for tree age, which was added first to all models.

RESULTS

Site Description

Twelve plots were established at six sites in southwestern Oregon (Figure 4; Table 2). Four of the sites were located near the south fork of the Coquille River, well within the range of Chamaecyparis lawsoniana, while sites at Coos County Forest (CC) and Camas Mountain (CM) were near or outside its range boundary. Individual plots are denoted by a two-to-three-letter site code; for sites where I studied both species, the third letter indicates species of primary interest (P = Port-Orford-cedar [Chamaecyparis], R = Redcedar [Thuja]). Numbers follow the letter designation when more than one plot were used for a species at a site.

All sites fall within the Tsuga heterophylla zone (Franklin and Dyrness, 1973; Tables 3 and 4). Those within Chamaecyparis' range are vegetationally similar to either the Tsuga heterophylla-Chamaecyparis lawsoniana/Polystichum munitum-Oxalis oregana community or the Tsuga-Chamaecyparis/Rhododendron macrophyllum-Gaultheria shallon community defined by Hawk (1977). The relatively well drained CC and CM sites are floristically similar to the Tsuga heterophylla/Gaultheria shallon-Polystichum munitum association described by Franklin and Dyrness (1973) for the Oregon Cascades.

Forests sampled ranged from moderate to high density of Thuja and a near absence of Chamaecyparis at CC and CM, to high Chamaecyparis density and absence of Thuja at Coquille River Falls (CRF). Other sites were chosen for their local segregation of the species; individual plots were dominated by Chamaecyparis or Thuja, but often included small amounts of the other.

Long term and 1979 weather station data are included from five stations in southwestern Oregon (U.S. Dept. Commerce; Figure 4; Tables 5 to 7). CC is undoubtedly most affected by marine fog and

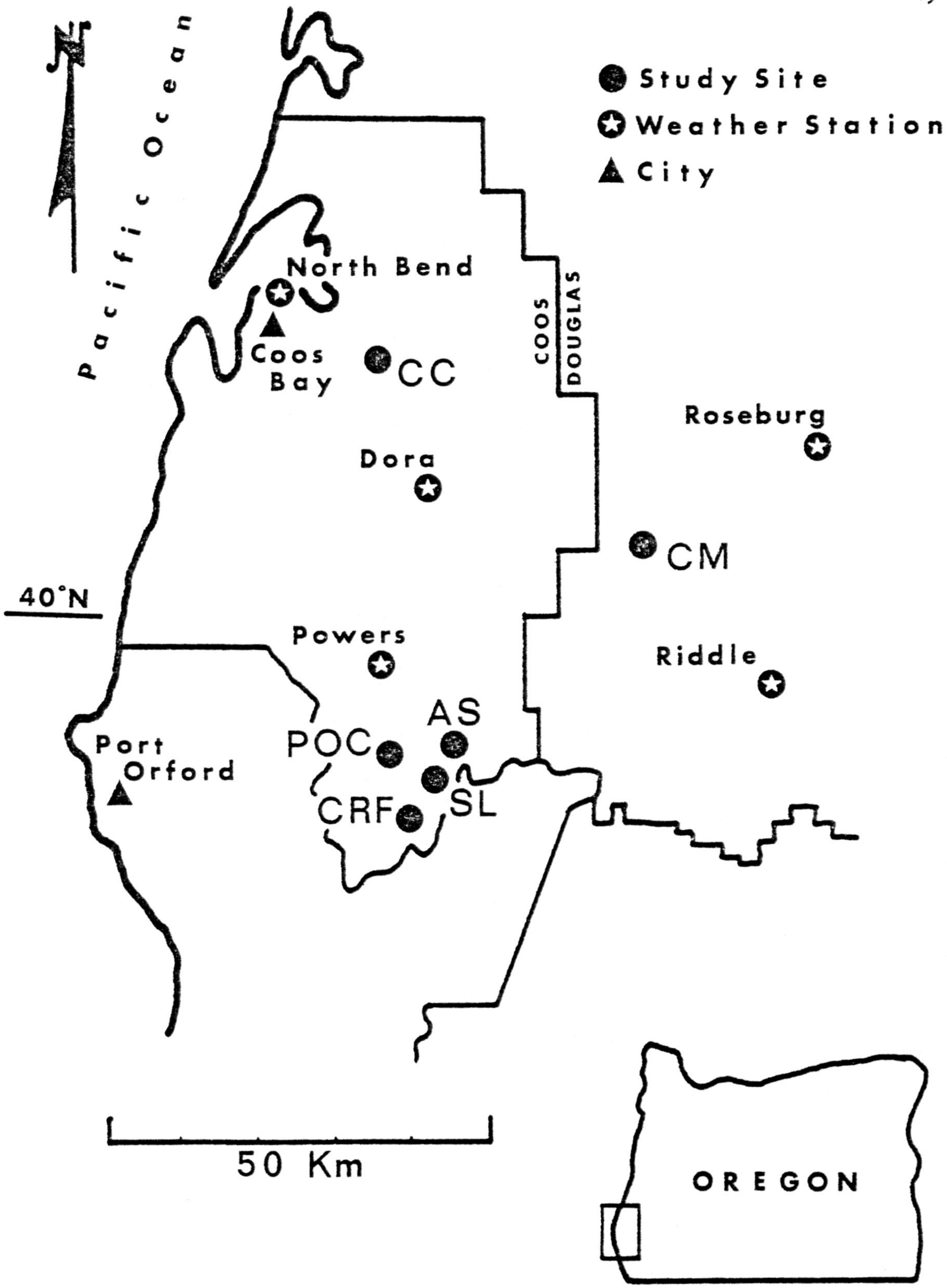

Figure 4. Location of study sites, weather stations and major cities; see Table 2 for key to site abbreviations.

Table 2. Study site characteristics; map symbol refers to Figure 4; species abbreviations Thpl = _Thuja plicata_, Chla = _Chamaecyparis lawsoniana_; n indicates number of soil and litter samples taken; nd = no data.

Site Name	Map Symbol	Plot Designation	Location	Elevation (m)	Aspect	Slope (%)	% Understory Light	Species Sampled	n
Coos County Forest	CCF	CC	SW/4, SW/4, Sec. 24 T26S, R12W	400	S	60	nd	Thpl	10
Camas Mountain	CM	CM	NW/4, SW/4, Sec. 9 T29S, R8W	450	NE	10	nd	Thpl	10
CRFRNA[1]	CRF	CRF	NE/4, NE/4, Sec. 20 T33S, R11W	520	NW	45	0.7	Chla	10
Ash Swamp	AS	ASP	NW/4, SE/4, Sec. 23 T32S, R11W	670	--	0	0.5	Chla	10
	AS	ASR-1	Same as ASP	670	--	0	2.0	Thpl	4
	AS	ASR-2	NE/4, SE/4, Sec. 23 T32S, R11W	670	--	0	0.6	Thpl+Chla	5
Squaw Lake	SL	SLR-1	SE/4, SW/4, Sec. 9 T33S, R11W	640	--	0	1.0	Thpl+Chla	5
	SL	SLR-2	Same as SLR-1	640	SW	5	0.3	Thpl+Chla	5
	SL	SLR-3	Same as SLR-1	640	NW	70	0.3	Thpl	5
	SL	SLP	Same as SLR-1	640	NW	70	0.5	Chla	10
POCRNA[2]	POC	POR	SW/4, SW/4, Sec. 26 T32S, R12W	260	NW	60	1.0	Thpl	6
	POC	POP	NW/4, NW/4, Sec. 35 T32S, R12W	360	N	60	0.8	Chla+Thpl	10

[1] Coquille River Falls Research Natural Area.

[2] Port-Orford-Cedar Research Natural Area.

Table 3. Density and basal area for tree species occurring in 11 of the plots sampled; ASR-1 was sampled on an arealess basis; D - density in stems per hectare; BA - basal area in m^2 per hectare; t - less than $0.5m^2$ per hectare.

Taxon and Size class (cm DBH)	Plot Designation																					
	CC		CM		CRF		ASP		ASR-2		SLR-1		SIR-2		SIR-3		SLP		POR		POP	
	D	BA	D	BA	D	BA	D	BA	D	BA	D	BA	D	BA	D	BA	D	BA	D	BA	D	BA
Chamaecyparis lawsoniana																						
Seedling	-	-	-	-	580	t	120	t	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0-10cm DBH	-	-	-	-	407	1	161	t	164	t	-	-	88	t	-	-	35	t	47	t	234	1
›10cm DBH	-	-	-	-	320	103	1124	35	1066	42	46	65	172	5	-	-	229	22	47	t	292	69
Thuja plicata																						
0-10	1089	t	128	t	-	-	-	-	-	-	92	t	88	1	113	t	35	t	47	1	-	-
›10	445	14	170	16	-	-	-	-	246	10	413	67	708	95	91	11	-	-	190	23	58	3
Tsuga heterophylla																						
Seedling	320	t	400	t	860	t	-	-	-	-	250	t	-	-	-	-	-	-	500	t	200	t
0-10	198	1	128	t	291	1	-	-	-	-	-	-	-	-	45	t	18	t	-	-	-	-
›10	642	23	43	1	320	14	-	-	-	-	92	9	-	-	159	10	70	7	-	-	88	8
Pseudotsuga menziesii																						
Seedling	-	-	-	-	-	-	3400	t	-	-	-	-	-	-	-	-	-	-	1500	t	-	-
0-10	-	-	-	-	-	-	-	-	82	t	-	-	-	-	-	-	-	-	-	-	-	-
›10	150	29	85	69	116	47	201	41	-	-	46	-	-	-	-	-	-	-	47	40	29	9
Abies grandis																						
Seedling	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1750	t	-	-
0-10	-	-	21	t	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
›10	-	-	106	13	-	-	-	-	-	-	-	-	-	-	-	-	-	-	47	18	117	11
Acer macrophyllum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	45	2	18	t	47	4	-	-
Alnus rubra	49	2	-	-	-	-	-	-	574	37	92	22	265	58	45	9	53	13	-	-	29	6
Cornus nuttallii	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	47	1	-	-
Lithocarpus densiflora	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	88	20
Taxus brevifolia	-	-	43	1	-	-	-	-	-	-	-	-	-	-	-	-	18	t	-	-	-	-
Umbellularia californica	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	47	6	29	1
Total (DBH ›0)	2570	69	720	100	1450	166	1490	76	2130	89	780	164	1330	159	500	32	480	42	570	93	960	128

Table 4. Cover and frequency values for species occurring in the twelve plots sampled. C = % cover, F = % frequency as determined by 25-50 1m^2 quadrats per plot, t = less than 0.5% cover.

	Plot Designation											
TAXON	CC C F	CM C F	CRF C F	ASP C F	ASR-1 C F	ASR-2 C F	SLR-1 C F	SLR-2 C F	SLR-3 C F	SLP C F	POR C F	POP C F
Shrubs												
Acer circinatum	-	10 44	-	t 5	9 19	3 4	-	-	-	-	10 33	2 4
Acer macrophyllum	-	-	-	-	-	-	-	-	7 11	t 2	-	-
Berberis nervosa	6 81	t 16	4 17	2 10	-	-	-	-	-	-	4 15	t 12
Cornus nuttallii	-	t 4	-	-	-	-	-	-	-	-	t 2	-
Corylus cornuta	-	-	-	-	-	-	-	-	-	-	30 45	-
Fraxinus latifolia	-	-	-	-	t 12	t 8	-	-	-	-	-	-
Gaultheria shallon	2 16	10 80	t 8	t 7	-	-	-	-	-	-	1 5	-
Holodiscus discolor	-	-	-	-	-	-	-	-	-	-	t 2	-
Lithocarpus densiflora	t 3	-	3 18	-	-	-	-	-	-	-	3 12	2 10
Myrica californica	-	-	-	-	-	-	-	-	t 3	-	t 5	4 6
Rhododendron macrophyllum	-	-	-	6 20	-	-	-	-	-	-	t 4	1 5
Rhamnus purshiana	t 3	-	-	-	-	-	-	-	-	-	-	-
Rhus diversiloba	-	-	-	-	-	-	-	-	-	-	t 5	-
Rosa gymnocarpa	1 6	-	-	t 2	-	-	-	-	-	-	t 2	-
Rubus parviflorus	-	-	-	-	-	t 4	-	-	t 8	t 8	-	-
Rubus spectabilis	t 6	-	-	-	1 19	15 28	4 15	5 13	-	2 10	-	-
Rubus ursinus	-	-	t 2	2 37	t 31	t 8	-	-	-	-	1 28	-
Sambucus racemosa	-	-	-	-	-	-	1 5	-	1 6	3 20	-	-
Umbellularia californica	t 3	-	-	-	-	-	-	-	-	-	-	-
Vaccinium ovatum	1 3	-	2 10	-	-	-	-	-	-	-	-	2 6
Vaccinium parvifolium	3 26	-	t 22	t 2	-	-	-	-	-	-	5 15	t 12
Forbs												
Achlys triphylla	-	t 4	-	t 2	-	-	-	-	-	-	-	-
Adenocaulon bicolor	-	t 4	-	1 22	1 19	-	-	-	-	-	t 2	-
Anemone sp.	-	t 4	-	-	-	-	-	-	-	-	-	-

(Continued on next page)

Table 4. Continued.

	Plot Designation											
TAXON	CC C F	CM C F	CRF C F	ASP C F	ASR-1 C F	ASR-2 C F	SLR-1 C F	SLR-2 C F	SLR-3 C F	SLP C F	POR C F	POP C F
Forbs Cont'd.												
Athyrium felix-femina	-	-	-	-	2 25	3 8	2 12	2 13	10 42	8 38	-	-
Blechnum spicant	-	-	-	-	-	-	-	-	t 8	-	-	-
Circaea alpina	-	-	-	t 2	-	2 76	t 38	-	t 3	t 22	-	-
Corallorhiza mertensiana	t 3	-	-	-	-	-	-	-	-	-	-	-
Disporum smithii	-	t 4	-	1 41	-	-	-	-	-	t 2	-	-
Galium oreganum	-	-	-	-	-	t 32	-	-	-	-	-	-
Galium triflorum	-	t 12	t 2	t 2	t 31	2 52	t 5	-	t 3	-	-	t 4
Goodyera oblongifolia	t 3	t 4	1 54	-	-	-	-	-	-	-	-	-
Hydrophyllum tenuipes	-	-	-	-	t 6	3 64	1 20	3 37	2 25	5 46	-	-
Lysichitum americanum	-	-	-	-	-	-	-	-	-	t 2	-	-
Osmorhiza purpurea	-	-	-	t 25	t 31	t 4	-	-	t 3	-	-	-
Oxalis oregana	-	-	4 56	12 51	14 69	t 8	11 68	t 3	9 50	8 50	6 70	-
Polypodium glycyrrhiza	-	-	-	-	-	t 4	-	-	-	-	-	-
Polypodium scouleri	-	-	-	-	-	-	-	-	-	-	t 5	t 4
Polystichum munitum	13 55	22 80	26 74	t 2	t 12	t 16	30 70	5 30	32 69	36 86	47 92	42 88
Pteridium aquilinum	-	-	2 20	2 20	-	-	-	-	-	-	-	-
Smilacina stellata	-	-	t 12	t 15	5 56	-	-	-	-	t 2	-	-
Stachys mexicana	-	-	-	-	t 12	2 12	-	-	-	-	-	-
Streptopus amplexifolius	-	-	-	-	1 6	-	-	-	-	-	-	-
Tiarella trifoliata	-	t 36	t 10	-	t 6	-	-	-	-	-	-	-
Tolmiea menziesii	-	-	-	-	-	t 8	-	-	t 3	-	-	-
Trientalis latifolia	-	t 20	t 18	t 7	-	-	-	-	-	-	t 2	t 2
Trillium ovatum	t 3	-	-	t 15	-	-	t 5	-	t 11	-	t 2	-
Vancouveria hexandra	-	-	-	t 27	t 12	2 32	-	-	-	-	-	-
Veronica americana	-	-	-	-	2 26	-	-	-	-	-	-	-
Viola sp.	-	1 44	2 54	t 19	3 62	4 76	-	-	-	-	-	-
Whipplea modesta	-	2 56	t 4	-	-	-	-	-	-	-	-	t 4

(Continued on next page)

Table 4. Continued.

TAXON	Plot Designation																							
	CC		CM		CRF		ASP		ASR-1		ASR-2		SLR-1		SLR-2		SLR-3		SLP		POR		POP	
	C	F	C	F	C	F	C	F	C	F	C	F	C	F	C	F	C	F	C	F	C	F	C	F
Graminoids																								
Bromus pacificus	-		-		-		-		5	19	-		-		-		-		-		-		-	
Bromus sp.	-		-		-		t	2	-		-		-		-		-		-		-		-	
Carex laeviculmis	-		-		-		-		1	12	1	28	-		-		-		-		-		-	
Leersia oryzoides	-		-		-		-		-		t	16	-		-		-		-		-		-	
Luzula parviflora	-		t	4	-		t	7	-		-		t	2	-		-		-		-		-	
Bryophytes																								
Brachythecium sp.	-		-		-		-		-		-		-		-		-		-		5	25	t	2
Brachythecium velutinum	-		-		-		-		-		t	4	-		-		3	28	2	16	-		-	
Climacium dendroides	-		19	68	-		t	7	1	19	10	60	2	17	-		-		-		26	78	-	
Dicranum howellii	-		t	8	-		t	2	-		t	16	-		-		-		-		t	5	-	
Eurhynchium oreganum	t	10	11	68	55	98	47	98	22	82	23	96	16	68	9	70	2	14	8	52	12	65	43	98
Hookeria lucens	-		-		-		-		-		-		t	2	-		t	3	t	2	-		-	
Hylocomium splendens	-		-		-		-		-		-		-		-		-		-		t	2	-	
Plagiomnium insigne	-		-		-		t	7	-		6	44	-		-		-		-		-		-	
Porella sp.	-		-		-		-		-		1	16	-		-		-		-		-		-	
Rhizomnium glabrescens	-		2	44	t	4	2	32	8	31	-		t	5	t	3	t	8	2	14	t	2	t	6
Rhytidiadelphus triquetrus	-		2	16	-		t	5	-		3	24	-		-		-		-		-		-	
Other																								
Creek	-		-		-		-		17	--	-		-		4	--	9	--	-		-		-	
Bare ground	73	--	23	--	20	--	34	--	32	--	19	--	32	--	77	--	13	--	36	--	6	--	21	--

precipitation patterns, lying at the northern tip of a ridge about 10 km southeast of Coos Bay. Weather data for North Bend probably best apply here. CM lies at the northeast end of a valley in the Coast Range, and is more cut off from the maritime influence. Its climate is estimated to be transitional between that at Dora, and that at Roseburg and Riddle weather stations, farther inland. Its macroclimate appears to be the driest and most extreme of all sites in terms of temperature fluctuation. Climate at the remaining sites is best compared to that at Powers, though the sites occur from 15 to 25 km south and at higher elevation. This portion of the Coquille drainage receives some marine influence in the form of summer fog and precipitation.

Soil and litter temperatures and other characteristics are described in Tables 8, 9 and 10. Since considerable variation in soils, climate and vegetation existed among plots, and the results are most meaningful on a local basis, sites are further described in detail.

Ash Swamp. Ash Swamp (AS), apparently an old floodplain for the south fork of the Coquille River, has the highest elevation of all sites. Distribution of *Chamaecyparis* and *Thuja* in the swamp shows a clear topographic relationship (Figure 5). *Chamaecyparis* occurs in dense mixed stands with *Pseudotsuga menziesii* on higher ground, as well as at lower elevation where *Pseudotsuga* drops out. *Thuja* is restricted to the banks of Barker Creek, and the lower areas where it is associated with *Chamaecyparis* and *Alnus rubra*. *Thuja* stumps measured 2-3 m DBH in the low areas, evidence of its long-standing presence. No such *Chamaecyparis* stumps were seen.

A plot was established in the higher elevation *Chamaecyparis*-*Pseudotsuga* stand (ASP), and in the lower elevation *Chamaecyparis*-*Thuja*-*Alnus* stand (ASR-2). In addition, individual *Thuja* along Barker Creek were sampled, constituting a third plot (ASR-1). Tree age was between 35 and 60 years in ASP, except for much older *Pseudotsuga*, and evenly aged about 60 years in ASR-2. Little or no regeneration of *Thuja* or *Chamaecyparis* is occurring in the low areas, while

Table 5. Climatic data for southwest Oregon weather stations; refer to Figure 4 for weather station location; normal values based on years 1940 - 1970.

Station	Nearest Site	Lat.(N)	Elev.(m)	Precip.(mm) 1979	Precip.(mm) Normal	Mean Ann.Temp.(C) 1979	Mean Ann.Temp.(C) Normal
North Bend FAA AP	CC	43 25	6	1643	1566	11.8	11.2
Powers	CRF,SL, POC,AS	42 53	230	1431	1592	12.3	11.8
Dora 2W	CM	43 10	90	1557	1293	12.8	nd
Riddle	CM	42 57	680	nd	816	nd	12.2
Roseburg KQEN	CM	43 12	465	903	860	nd	12.2

Table 6. Precipitation data (mm) for southwest Oregon weather stations during 1979.

Month	Weather Station: North Bend FAA AP	Powers	Dora 2W	Riddle	Roseburg KQEN
Jan	100	134	129	81	92
Feb	334	340	337	129	142
Mar	121	79	116	54	62
Apr	132	141	184	106	118
May	114	106	107	38	40
Jun	21	18	29	nd	19
Jul	16	8	12	6	4
Aug	22	29	20	31	21
Sep	71	25	41	17	29
Oct	172	137	130	128	118
Nov	207	172	215	90	134
Dec	333	242	237	150	124

Table 7. Air temperature data for southwest Oregon weather stations, 1979; NB = North Bend FAA AP, PO = Powers, DO = Dora 2W, RI = Riddle, RO = Roseburg KQEN.

	Mean Monthly Max. (C)					Mean Monthly Min. (C)				
Month	NB	PO	DO	RI	RO	NB	PO	DO	RI	RO
Jan	8.7	10.6	10.8	7.4	5.1	0.8	-0.8	0.0	-1.8	-0.6
Feb	10.2	10.7	11.2	10.6	9.9	5.2	3.3	3.7	1.4	3.6
Mar	13.2	16.3	17.2	16.5	16.0	6.4	4.6	5.2	4.1	4.8
Apr	13.9	16.0	16.2	16.8	16.6	6.9	5.3	5.5	5.6	6.3
May	15.7	19.9	20.9	21.2	22.3	8.2	6.6	7.0	6.2	7.7
Jun	17.2	23.8	24.0	nd	25.8	9.1	7.8	7.7	nd	9.9
Jul	19.9	25.9	26.0	29.9	30.3	12.0	10.5	10.7	10.3	13.1
Aug	20.3	25.6	25.3	27.6	27.6	12.6	10.2	10.9	11.4	13.8
Sep	22.2	26.3	27.0	28.0	26.6	12.7	9.9	11.0	9.6	13.0
Oct	18.0	20.9	21.9	21.4	20.3	11.0	8.0	9.0	7.9	10.3
Nov	14.4	14.7	15.2	12.5	11.9	6.1	2.8	3.8	3.3	nd
Dec	13.2	13.7	14.3	10.9	11.2	5.4	2.8	3.1	1.9	3.6

Table 8. Soil temperature (C) at -10 cm at time of soil sampling; values are means of eight to 20 measurements per plot; measurements were taken over a period of two to three days beginning July 6 and September 13, 1979, and January 4, 1980.

Plot Designation	Sample Date			Plot Designation	Sample Date		
	Jul 6	Sep 12	Jan 4		Jul 6	Sep 12	Jan 4
CC	12.1	15.6	6.9	SLR-1	11.0	12.9	7.1
CM	12.8	15.9[1]	nd	SLR-2	10.4	12.4	7.0
CRF	12.3	13.9	7.2	SLR-3	10.2	12.0	6.9
ASP	10.6	11.5	5.3	SLP	10.6	12.5	6.7
ASR-1	11.2	11.6	6.0	POR	13.2	13.9	nd
ASR-2	10.4	11.2	6.8	POP	13.2	14.0	nd

[1] Ground and vegetation disturbed by machinery.

Table 9. Mean daily minimum and maximum temperature for litter and soil at -10 cm for four plots between June 16, 1979 and January 5, 1980.

			Plot Designation			
Sample Period	Location	Mean	ASP	ASR-2	SLP	SLR-3
Jun 16 - Jul 15	Litter	Max	12.2	11.9	12.6	11.9
		Min	9.5	7.7	9.1	9.4
	-10 cm	Max	9.8	10.4	10.8	10.0
		Min	9.0	9.9	10.1	9.7
Jul 16 - Aug 15	Litter	Max	15.7	16.0	14.7	15.4
		Min	12.0	9.8	10.9	12.2
	-10 cm	Max	13.6	12.2	13.8	12.3
		Min	12.5	11.8	12.8	11.9
Sep 4 - Sep 26	Litter	Max	14.2	14.6	15.1	14.9
		Min	11.2	9.5	12.6	12.4
	-10 cm	Max	12.7	11.7	13.7	12.5
		Min	11.8	11.5	13.0	12.2
Jan 3 - Jan 5	Litter	Max	6.3	6.9	7.1	7.2
		Min	5.7	6.3	6.3	6.0
	-10 cm	Max	5.2	6.7	6.0	6.3
		Min	5.1	6.4	5.8	6.1
Absolute Min/Max						
Sep 26 - Jan 3	Litter	Max	14.1	14.9	16.9	15.2
		Min	1.4	-0.2	2.3	2.8
	-10 cm	Max	12.2	11.3	14.5	12.3
		Min	2.2	3.7	3.5	4.6

Table 10. Soil characteristics; fine litter (F layer) = metric tons per hectare; % water at field capacity for 0-10 cm layer soil; parent material types: BAS = basalt, SED = sedimentary, ALL = alluvium; textural abbreviations: vg = very gravelly, L = loam, S = sand, Si = silt, C = clay.

Plot	Fine Litter (T/Ha)	% Water @ Field Capacity	Parent Material	Horizon	Profile Depth(cm)	Sand/Silt/Clay %	Textural Class	Munsell Color (Dry)
CC	3.6	49	BAS	A1	0-10	46/29/25	vg L	5YR 3/4
				A3	10-30	44/30/26	vg L	5YR 3/4
				B	30-42	54/23/23	vg SCL	5YR 4/6
				C	>42	38/26/36	vg CL	5YR 4/6
CM	nd	20	SED	A11	0-14	44/35/21	L	10YR 6/3
				A12	14-23	42/35/23	L	10YR 6/4
				A3	23-43	39/34/27	CL	10YR 7/4
				B2t	43-68	21/20/59	C	2.5YR 5/6
				B3cn	68-78	24/58/48	C	10YR 6/8
				Ccn	>78	24/32/44	C	10YR 7/6
CRF	2.3	30	SED	A1	0-12	54/23/23	SCL	10YR 4/4
				A3cn	12-26	50/24/26	SCL	10YR 5/3
				B1cn	26-40	57/18/25	SCL	10YR 5/4
				B3	40-95	47/25/28	SCL	2.5YR 7/4
				C	>95	60/23/17	SL	2.5YR 8/4
ASP	1.2	29	ALL	A1	0-8	45/20/35	CL	10YR 5/3
				A3	8-45	43/21/36	CL	10YR 5/3
				B	45-75	46/22/32	SCL	10YR 6/4
				C	>75	35/33/32	CL	2.5YR 7/4
ASR-1[1/]	nd	35	ALL	--	0-10	58/20/22	SCL	10YR 5/3

(Continued on next page)

Table 10. Continued.

Plot	Fine Litter (T/Ha)	% Water @ Field Capacity	Parent Material	Horizon	Profile Depth(cm)	Sand/Silt/Clay %	Textural Class	Munsell Color (Dry)
ASR-2	0.5	46	ALL	A1g	0-6	32/37/31	CL	10YR 4/1
				B21tg	6-23	13/48/39	SiCL	10YR 6/2
				B22tg	23-35	11/43/46	SiC	10YR 6/3
				B3g	35-45	18/41/41	SiC	10YR 6/3
				Cg	>45	25/41/34	CL	10YR 7/2
SLR-1	3.0	22	SED	A1	0-12	63/22/11	g SL	10YR 5/4
				B2tcn	12-27	55/25/20	g SCL	10YR 6/4
				C	>27	80/14/6	g LS	10YR 5/6
SLR-2	2.1	19	SED	A	0-12	66/21/13	SL	10YR 4/3
				C	>12	80/10/10	LS	10YR 5/4
SLR-3[2/]	1.6	22	SED			(Upper)		
				A11	0-12	45/24/31	CL	10YR 4/4
				A12	12-45	41/27/32	CL	10YR 5/4
				C	>45	58/21/21	SCL	10YR 6/4
						(Lower)		
				A1	0-12	57/22/21	SCL	10YR 4/4
				B2t	12-30	54/21/25	SCL	10YR 5/6
				B3	30-65	62/23/15	SL	10YR 7/4
				C	>65	64/20/16	SL	10YR 7/3
SLP	2.0	24	SED	A	0-10	66/18/16	SL	10YR 7/6
				C	>10	72/17/11	SL	10YR 6/4

(Continued on next page)

Table 10. Continued.

Plot	Fine Litter (T/Ha)	% Water @ Field Capacity	Parent Material	Horizon	Profile Depth(cm)	Sand/Silt/Clay %	Textural Class	Munsell Color (Dry)
SLP[3] (Adjacent)	nd	nd	SED	A1	0-15	47/19/34	SCL	10YR 4/3
				B21t	15-32	34/23/43	C	10YR 5/4
				B22t	32-60	36/23/41	C	10YR 6/4
				C	>60	41/22/37	g CL	10YR 7/3
POR[4]	nd	15	ALL	--	0-10	72/13/15	SL	10YR 5/1
POP	nd	40	SED	A1	0-15	39/18/43	vg C	10YR 5/6
				B21t	15-45	34/15/51	vg C	10YR 6/8
				B22t	45-90	22/23/55	vg C	7.5YR 6/6
				C	>90	20/25/55	vg C	7.5YR 6/6

[1] Profile not described; similar to ASP.

[2] Profiles sampled both on backslope and footslope corresponding to upper and lower ends of plot.

[3] Profile sampled adjacent to SLP where *Thuja* extends to top of slope.

[4] Profile description not obtainable.

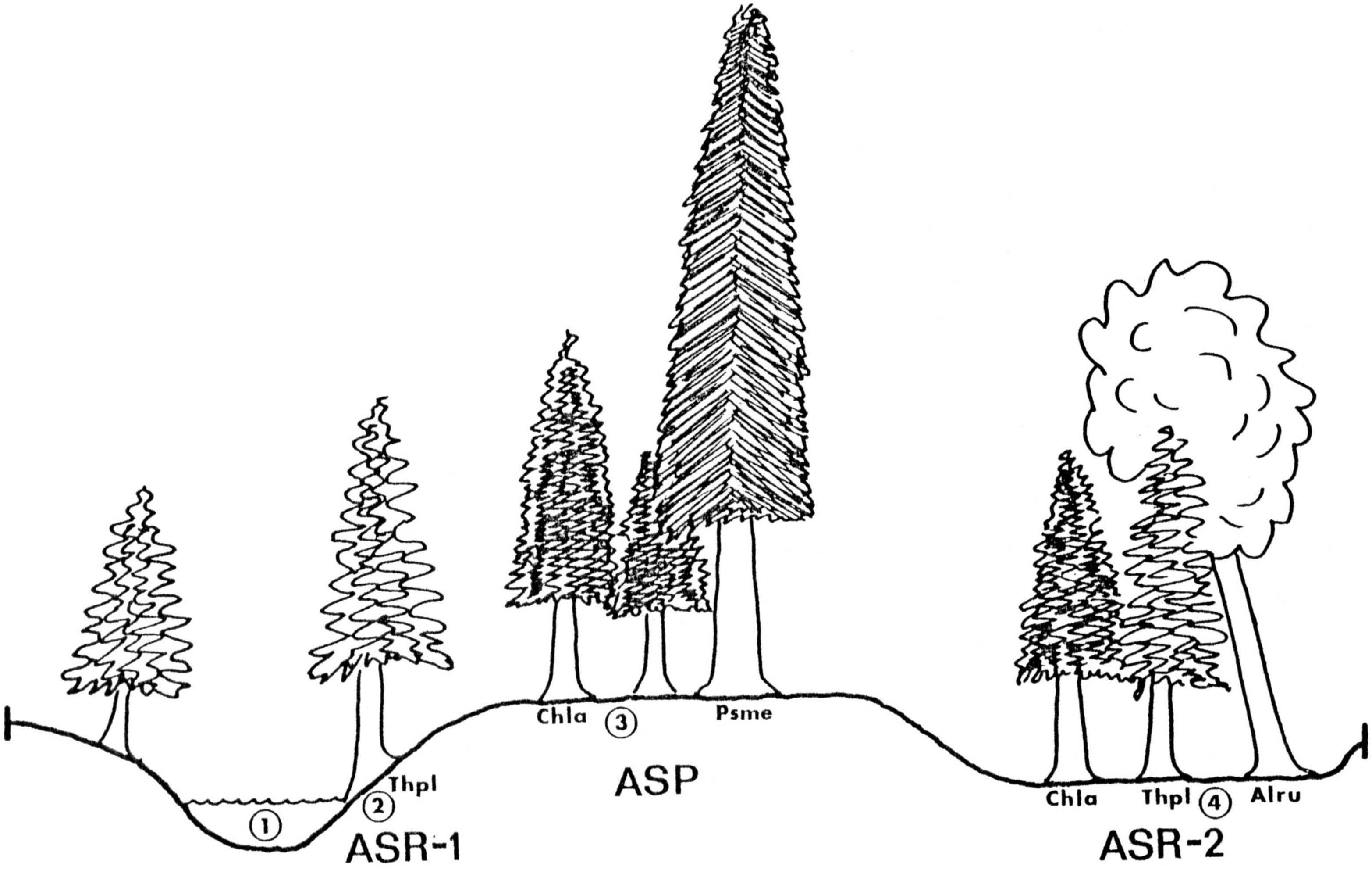

Figure 5. Topographic distribution of trees at Ash Swamp and location of plots (ASP, ASR-1, ASR-2); 1 = Barker Creek, 2-4 indicate location of water sampling pipes; species abbreviations: Thpl = *Thuja plicata*, Chla = *Chamaecyparis lawsoniana*, Psme = *Pseudotsuga menziesii*, Alru = *Alnus rubra*.

Chamaecyparis' reproduction is more common at higher elevations. Thuja sampled along Barker Creek ranged from relatively young to 200+ years old.

Soil moisture data indicate soils are consistently wetter in ASR-1 and ASR-2 than in ASP (Table 11), as expected. Groundwater level was quite variable, particularly in ASR-2 where standing water occurred in January (Table 12). Thermograph records (Table 9) indicated ASR-2 soil was cooler in the summer and warmer in the winter than ASP soil, although the soils at Ash Swamp were the coolest of those studied (Table 8). Parent material in the swamp is Quaternary alluvium (Baldwin, 1974), with surrounding hills consisting of sedimentary rocks of the Tyee and Flournoy formations. Soils are well developed throughout the swamp, tending toward heavier textures in the low areas. Litter mass in ASR-2 was by far the lowest measured (Table 10).

Squaw Lake. The forest near Squaw Lake, at slightly lower elevation than Ash Swamp, also exhibits an interesting segregation of Thuja and Chamaecyparis. All plots were located within ½ km of each other, and were situated on or at the base of a slope which rises several hundred feet above the road (Figure 6). SLP was established in an area of mixed Chamaecyparis, Tsuga and Alnus, surrounding a depression in which year-round seepage occurs. Thuja was sampled in three plots, where it was most important. SLR-1 and SLR-2 were located in small mixed cedar-Alnus groves situated on either side of the road; SLR-1 on a well-drained, raised knoll; and SLR-2 down in a wet depression at the foot of the slope. High basal area for Chamaecyparis in SLR-1 is due to a single large tree aged at 130+ years. SLR-3 was located along a creek about 200 m across slope from SLP, in which conditions were very similar. This plot was one of two locations on the slope where Thuja extended nearly to the ridgetop. Chamaecyparis is conspicuously absent along this creek. In contrast to the SLR plots, surrounding forest is primarily Chamaecyparis, Tsuga and Pseudotsuga. Predominate tree age in all plots is 65 to 85 years, with scattered, much older Pseudotsuga on the slope. Thuja has regenerated (probably

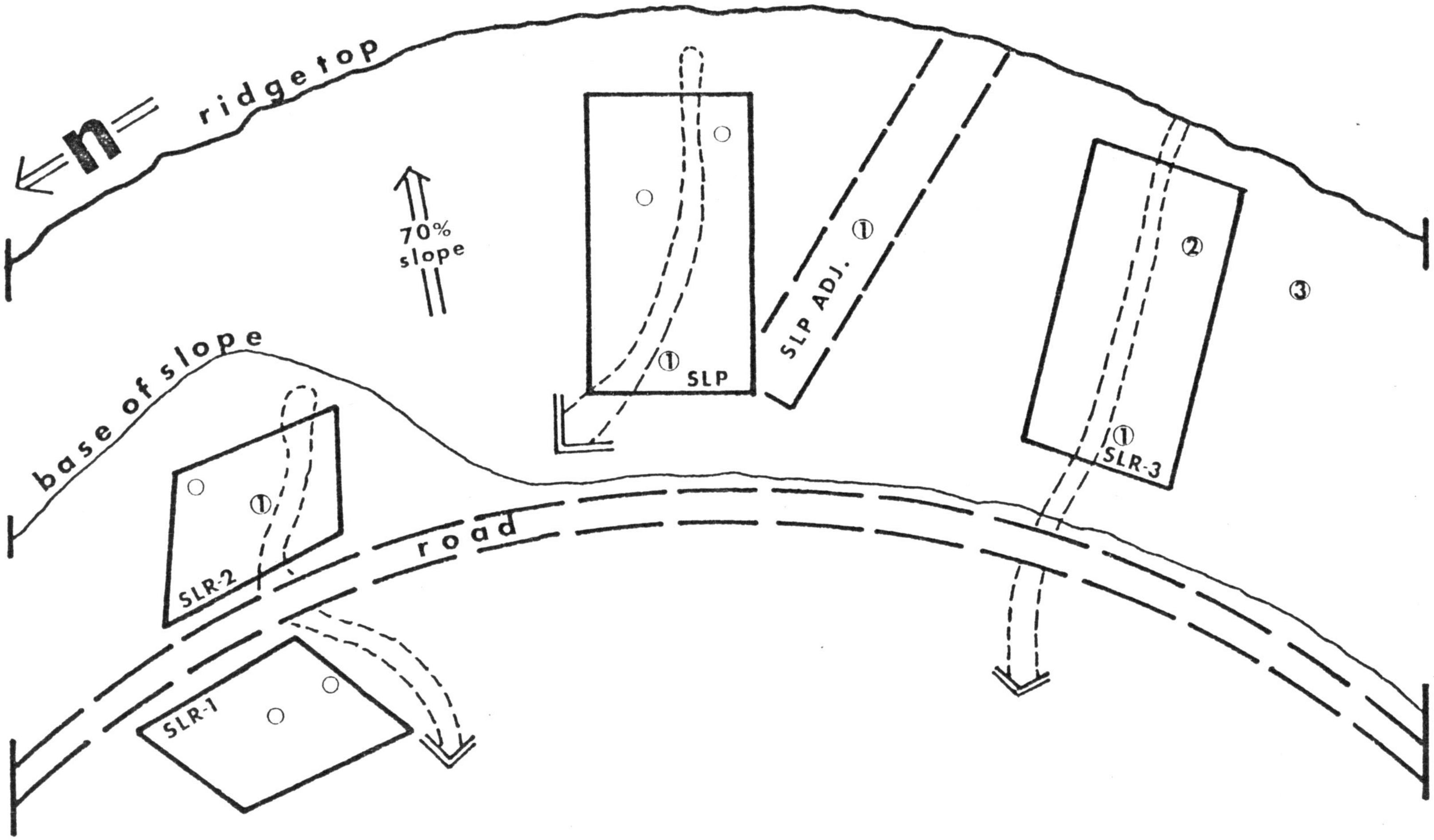

Figure 6. Map of Squaw Lake study site showing location of plots (SLP, SLR-1,2,3); ○ = water pipes, numbers indicate those pipes from which water was sampled (Table 11); dashed arrows = year-round creek or seepage.

by layering) in the seep within SLP, as well as in SLR-3. Young *Chamaecyparis* are common, except in the plots where *Thuja* was sampled.

Soils are generally wettest in SLR-3 and driest in SLR-1. Soil and litter temperatures were similar to those at Ash Swamp, and showed similar annual as well as daily moderation in SLR-3 where *Thuja* occurs, relative to SLP. SLR-2 appeared to behave similar to SLR-3; SLR-1 was consistently the warmest of these soils. Parent material is reported as sediments of the Tyee Formation, composed of micaceous sandstone and siltstone (Baldwin, 1974). Local slumping and erosion seem to be responsible for large differences in soils. Soils are most poorly developed in SLR-2 and SLP, while SLR-1 has a faint Bt horizon. Soil in SLR-3 was most developed and heavily textured, but showed considerable variation within the plot. Systematic sampling of soils adjacent to SLP, in the other area where *Thuja* extends upslope (Figure 6), indicated heavier texture and presence of a Bt horizon were associated with *Thuja* here also. Soil pipes indicated shallow seepage in this area and at the upper end of SLR-3 in January. Litter mass was relatively high in all plots.

Port-Orford-Cedar Research Natural Area. Two plots (POR, POP) were located at the northern end of the Port-Orford-Cedar Research Natural Area. A general description of the area is given by Franklin *et al*. (1972). *Thuja* occurs infrequently along Johnson Creek at the northern border. POR was established in a grove of *Thuja*, 3-6 m above the creek. The trees are rooted in a boulder pile, which is underlain at some depth by a dense gravel bar. This plot included a small amount of *Chamaecyparis*, which (based on foliar nutrient content) appears to be rooted in another soil which intrudes along the edge of the plot. Many of the *Thuja* here appear to have originated by layering. Age of *Thuja* varies between 40 and 90 years, although several *Thuja* seedlings were rooted in rotten logs and the gravel bar. These were nearly the only *Thuja* seedlings seen at any site. POP was located farther upslope in a moderately dense stand of *Chamaecyparis*. *Thuja* occurs very infrequently on the slope. Tree age in the plot was between 40 and

80 years, with a single large *Chamaecyparis* estimated at 150+ years old. *Chamaecyparis* is regenerating well here. Burn marks are present on older *Pseudotsuga*.

POR had the driest soil of all plots, with POP slightly moister. The convex slope around POP is particularly well drained. Soil temperatures in July and September were about the same in both plots, but were warmer than at either Ash Swamp or Squaw Lake. Parent material in POP is Jurassic sediments, consisting of sandstone and siltstone (Baldwin, 1974). Soils are very well weathered but very gravelly. Soil in POR, where present, consists of pockets of sandy alluvial sediments between boulders. Litter in POR formed a mat up to 20 cm thick, which covered the rocks and voids, and in which abundant rooting was noted. Although not measured, litter mass in POP was estimated to be quite low, considerably less than that found at the Squaw Lake plots.

Coquille River Falls Research Natural Area. A single plot (CRF) was sampled in the Coquille River Falls Research Natural Area, representing a site where *Chamaecyparis*' presence and growth are relatively high, and well within its range. A general description of the area is given by Franklin *et al*. (1972). Sites within the natural area have been used recently to study *Chamaecyparis* (Hawk, 1977; Plocher, 1977; Zobel and Hawk, 1980), enabling comparisons with my data. It appeared to me that *Thuja* is absent in the natural area, even in depressions and along drainages. Neither Franklin *et al*. (1972) nor Hawk (1977) record its occurrence here. Age of *Chamaecyparis* in the plot ranges up to 200 years, and *Tsuga* to about 130 years, while *Pseudotsuga* is mostly about 110 years old. *Chamaecyparis* is reproducing well at this site. Burn marks are present on older trees.

Soil here is well drained, although soil moisture was greater than in several *Thuja* plots, including SLR-1. Soil temperature appears to be generally warmer than at Ash Swamp or Squaw Lake, but not as high as at POR or POP. Parent material consists of Eocene sediments of the Tyee Formation, similar to the nearby Squaw Lake site. Soil is moderately developed, and litter mass is similar to that in the

Squaw Lake plots.

Camas Mountain. The plot at Camas Mountain (CM) was located in the Camas Mountain State Park, just east of *Chamaecyparis*' range, on what appeared to be an old stream terrace or bench. A small creek runs adjacent to the plot, but 5-7 m lower in elevation. *Thuja* is unevenly aged to about 125 years, and *Pseudotsuga* evenly aged at about 220 years in the plot. Some young *Thuja* and abundant young *Tsuga* are present.

Soil moisture was quite low in July and September, being lower only in POR. Soil temperatures were the highest of all. Parent material is probably Eocene sediments of the Flournoy Formation, consisting of micaceous sandstone and siltstone (Baldwin, 1974). This was my only sampling of Flournoy sediments, reportedly similar to but slightly older than Tyee sediments. Soil is well developed, with a strong Bt horizon present. Litter mass was not measured, but is estimated to be lower than most of the sites studied.

There are several similarities between CM and CRF which may make comparison of results useful in identifying basic differences between soils under the two species. Both sites are similar in terms of soil moisture and temperature; if anything CM is more extreme than CRF. Parent materials are reportedly similar, and each site has an abundance of either *Chamaecyparis* or *Thuja*, with similar associated vegetation. Both sites exhibit poor growth of these species compared to the other sites studied.

Sampling at this site was discontinued in September due to its unexpected disturbance by heavy machinery. Considerable disruption of the topsoil, litter, and creek occurred. Characteristics of the soil and nutrient availability at this site indicate this potentially may reduce site quality, as is discussed later.

Coos County. The plot in Coos County Forest (CC) occurs near the northern boundary of *Chamaecyparis*' distribution. Although surrounding forests seem to lack any *Chamaecyparis*, the site at CC does exhibit an interesting segregation of Thuja and Chamaecyparis; however, soils under Chamaecyparis were not studied in detail here. The plot was located in a dense stand of Thuja and Tsuga, on a steep south-facing slope. Tree age ranged up to 55 years, corresponding to a date of cutting given by the Coos County Forestry Department. Many young Thuja occur in the forest, and some young Chamaecyparis grow adjacent to the plot.

Soils were relatively moist, in spite of their well-drained nature and southerly aspect. Soil temperature, though moderate in July, was very high in September. This corresponded to a particularly warm spell, and may indicate relative susceptibility of the site to extremes in air temperature. Parent material is Eocene marine basalt of variable lithology (Baldwin, 1974). The site is located at the north end of Blue Ridge, which forms an interfingering of basalt within the surrounding Roseburg Formation sediments. Soil is relatively shallow and very gravelly. Litter mass is the highest of all sites.

The pattern of Chamaecyparis' occurrence warrants description; it appears to relate to soils differences, or past cutting or fire history. About 30 m across the slope from the plot occurred the boundary of a clearcut about five years old. In contrast to its virtual absence within the stand, an abundance of approximately 40-year-old Chamaecyparis lies just outside the clearcut boundary. In addition, Chamaecyparis seedlings are abundant for a short distance into the clearcut; no Thuja seedlings were seen. Soil core samples taken near the seedlings indicate considerably heavier textured and moister soil than in the plot, varying from 35 to 60% clay. However, no lithologic discontinuity could be detected between clearcut and plot.

Results of Analysis

The results of laboratory analysis of soils, litter, and water are presented in Tables 11 to 14 and Figures 7 to 18.

Moisture Availability. ASR-1 and ASR-2 soils were consistently wettest at sampling times, while SLR-1, CM, and POR were driest; no distinction between species was possible on the basis of absolute moisture content (Table 11).

More important in terms of water available to the plant is the relation of field moisture to an estimate of the water-holding capacity of the soil, in this case, field capacity. Assuming the proportion of the field capacity available to the plant is roughly similar for the range of soil textures and organic levels found here, field moisture as a percentage of field capacity should give a better relative estimate of availability of water than absolute moisture alone. However, this gives no indication of the relative amounts of available water present in the soil. Soils sampled where Thuja occurred within Chamaecyparis' range usually exceeded field capacity in July and September (Table 11). Soils in SLR-1 and POR, though relatively dry in July, were somewhat closer to field capacity than POP soil, a more favorable water situation than is indicated by absolute moisture levels. Water appeared to be least available in POP in July and September, followed closely by CC. Percentage moisture of air-dry litter was consistently higher for plots where Thuja occurs than pure Chamaecyparis plots on both sample dates (Table 11).

pH. Soils were all acid, pH ranging from a low 4.5 in POP soil in September to a high 6.3 at SLR-3 in January (Figure 7). Variation among plots generally did not exceed one pH unit on any sampling date. No obvious relation between soil pH and species occurrence was seen on a studywide basis , although there was a local relationship at Ash Swamp, Squaw Lake, and the Port-Orford-Cedar Research Natural Area, where Thuja usually occurred on more basic soils. Generally the same relationships occurred for litter pH, although values were generally lower than in soil (Figure 8). In most cases, local differences in groundwater pH (Table 12) agreed with those in litter and soil. There were definite differences among sampling dates in soil and litter pH. Nearly all soils were significantly more acid in September, and more

Table 11. Field soil moisture (0-10 cm layer) on three sample dates, 1979-1980, and relative water holding capacity of 0-10 cm soil layer and fine litter; ME = moisture equivalent (estimate of field capacity) = mean of two determinations made on separate bulked samples per plot; soil moisture less than ME is indicated as % of ME in parentheses; values for January 4 litter determined on single composite sample per plot.

Factor	Plot Designation											
	CC	CM	CRF	ASP	ASR-1	ASR-2	SLR-1	SLR-2	SLR-3	SLP	POR	POP
Soil												
% H_2O @ ME	49	20	30	29	35	46	22	19	22	24	15	40
% H_2O Jul 6	36(73)	14(70)	23(77)	24(83)	54	56	18(82)	26	40	30	11(73)	24(60)
Sep 12	36(73)	18(90)	28(93)	25(86)	49	64	23	23	32	32	18	27(68)
Jan 4	53	nd	37	37	55	77	33	43	40	39	nd	nd
Litter: % H_2O @ air dry												
Jul 6	10.0	9.8	7.9	9.1	8.1	11.1	10.0	12.0	10.7	9.0	11.4	8.2
Jan 4	7.2	nd	5.8	5.4	5.0	7.0	6.5	6.7	5.9	5.0	nd	nd

Table 12. Stream and ground water characteristics on July 6 and September 12, 1979, and January 4, 1980; pH measurement for July 6 only accurate to nearest half pH unit.

	Water Table Depth (cm)			Approximate % O_2 Saturation			pH			Temp.(C)			Nitrate-N (ppm)			Ammonium-N (ppm)		
Sample	7/6	9/5	1/4	7/6	9/5	1/4	7/6	9/5	1/4	7/6	9/5	1/4	7/6	9/5	1/4	7/6	9/5	1/4
Stream																		
Barker Creek (ASR-1)	-	-	-	98	100	98	8.5	7.6	7.2	10.2	11.2	7.0	0.0	0.1	0.0	0.0	0.0	0.0
Creek (SLR-2)	-	-	-	97	94	92	8.0	7.4	7.6	8.2	8.6	8.1	0.0	0.0	0.2	0.0	0.0	0.1
Creek (SLR-3)	-	-	-	100	96	100	8.5	7.6	7.8	8.3	9.3	8.0	-	0.1	0.1	-	0.0	0.0
Surface seep (SLP)	-	-	-	61	81	85	6.0	7.2	6.7	9.8	10.4	6.7	0.1	0.8	0.9	0.1	1.1	0.0
Water pipe																		
ASR-1	69	54	29	-	67	53	-	6.2	5.8	-	11.0	6.2	-	0.3	0.1	-	0.7	0.1
ASR-2	100+	51[1]	-5	-	66	52	-	6.8	6.5	-	10.8	6.2	-	2.5	0.1[2]	-	0.6	0.1[2]
ASP	100+	100+	85	-	-	-	-	-	6.2	-	-	5.6	-	-	0.2	-	-	0.2
SLR-2	20	20	18	48	39	47	6.5	6.0	6.4	9.0	10.0	8.0	0.0	0.2	0.2	0.0	0.3	0.4
SLR-3 #1	24	31	15	56	62	72	6.0	6.3	7.2	9.4	10.7	8.0	0.2	1.8	0.6	0.0	1.3	0.1
#2	100+	100+	48	-	-	-	-	-	6.5	-	-	-	-	-	0.9	-	-	0.1
#3	100+	100+	70	-	-	-	-	-	6.0	-	-	-	-	-	0.2	-	-	0.3
SLP	55	55	37	49	31	68	6.5	6.6	6.2	9.4	11.2	6.8	0.2	0.6	0.6	0.2	0.2	0.1
SLP (adj)[3]	100+	100+	82	-	-	-	-	-	6.5	-	-	-	-	-	0.2	-	-	0.2

[1] Measured at 73 cm on 9/12.

[2] Data are for surface water; at 50 cm depth = Nitrate-N = 0.0 ppm, Ammonium-N = 0.8 ppm.

[3] Sample taken adjacent to SLP within extension of <u>Thuja</u> to top of slope.

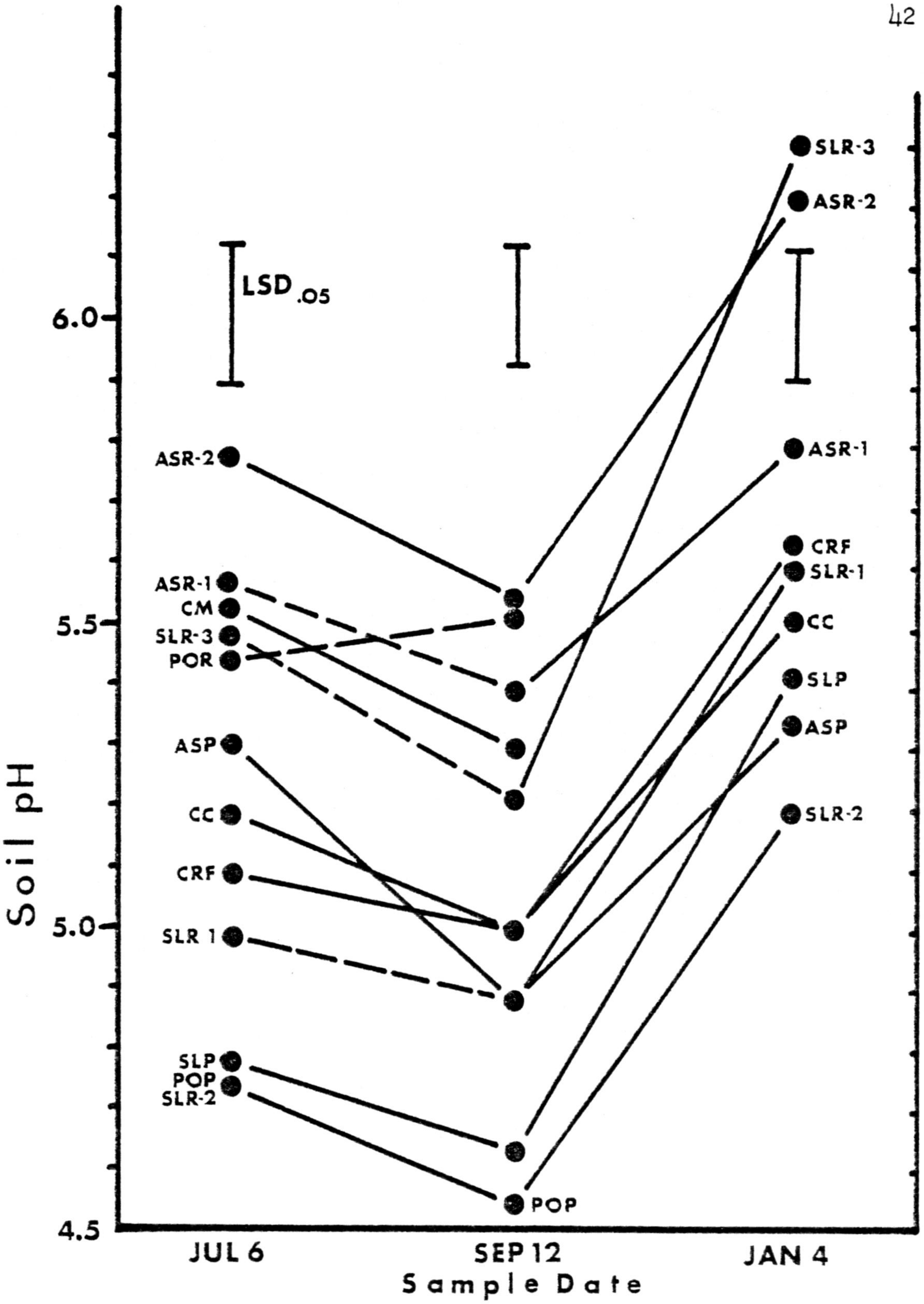

Figure 7. pH of mineral soil on three dates, 1979-1980; solid lines between points indicate significant differences (P = .05); least significant differences (LSD) are shown for each sample date.

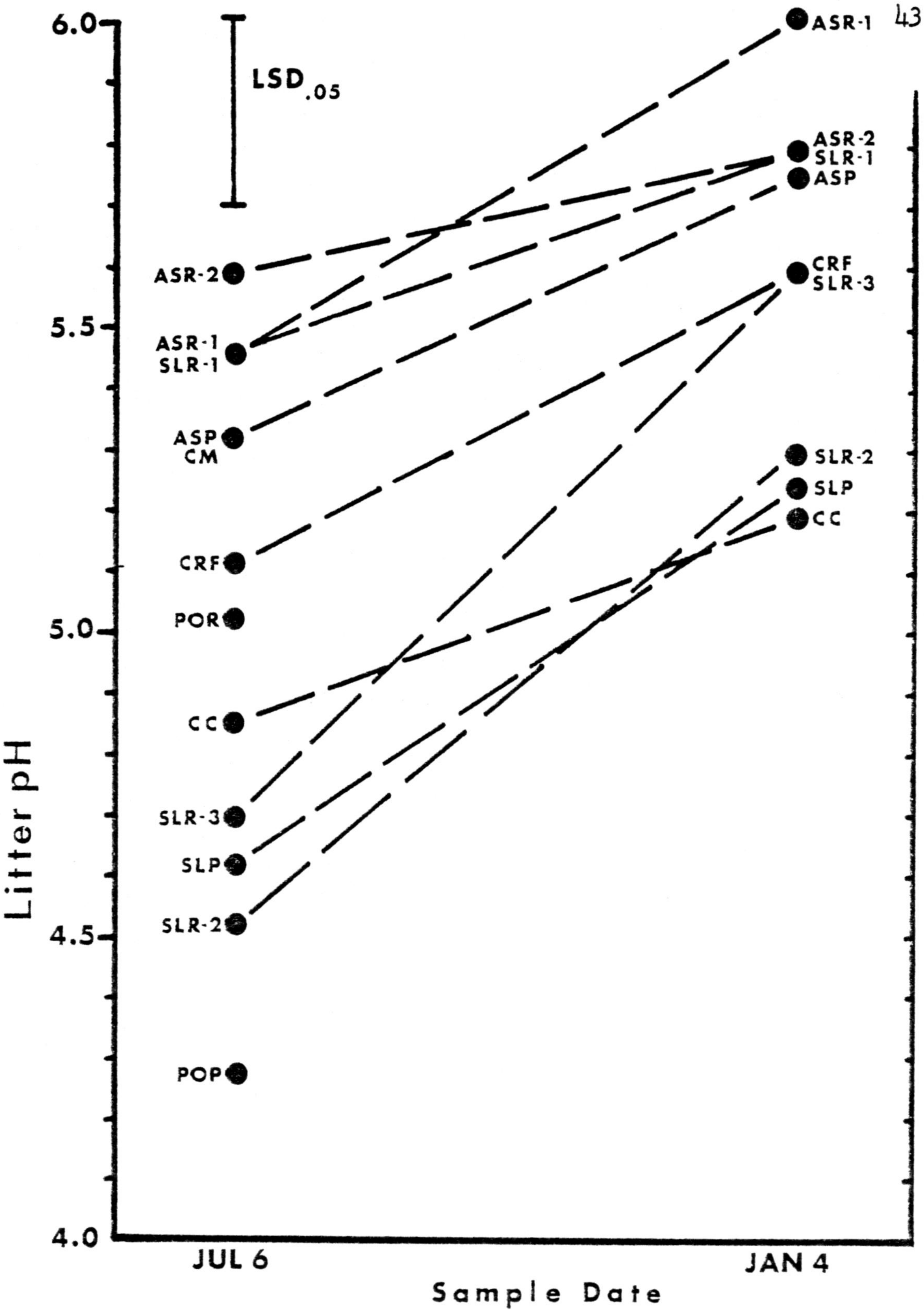

Figure 8. pH of fine litter on two dates, 1979-1980; values for January 4 are based on one composite sample per plot; LSD value is shown for the July measurement.

basic in January than in July. Litter pH showed the same relationship, but seep and groundwater (except in SLR-2 and 3) showed an opposite trend (i.e., more basic in September relative to the other sample dates).

Organic Matter and C/N Ratio. Loss-on-ignition (an estimate of organic content in the soil) ranged from four to 30%, with the sandy loam in POR having the lowest (Table 13). CC had considerably higher values than all other plots, although this appears due to presence of charcoal. Organic content followed the toposequence at Ash Swamp, being higher in the lower, wetter soils. The other sites tended to show slightly higher organic levels under *Chamaecyparis* (i.e., SLP>SLR-1,2,3; POP>POR; CRF>CM). Largely as a result of this, soil C/N ratios were highest in plots dominated by *Chamaecyparis*, with the exception of CC. Organic levels in most soils decreased between July and September, most prominently in the warmer and drier soils. The apparent decline in organic content, as well as an increase in total N levels between July and September, resulted in lower C/N ratios for all soils.

Nitrogen. Total soil N ranged from .08% at CM to .31% at ASR-2 in July (Figure 9). No relation between total N and species occurrence was seen, with *Thuja* occurring on both the lowest and highest nitrogen soils. Somewhat unexpected was the significant seasonal fluctuation in soil N which appeared in some plots. The magnitude of this change is questionable, and is discussed later.

Some correlation was seen between total soil N and ammonium-N levels ($r = .65$ in July). Levels of ammonium-N ranged from one to six ppm in July, generally decreasing on later sample dates (Figure 10). With the exception of POP, plots with little or no *Thuja* (ASP, CRF, SLP) were among the lowest in soil ammonium on all dates. Ammonium was most prominent in groundwater in September, particularly in plots containing *Thuja* (Table 12). Levels were negligible in January groundwater (except in ASR-2) and in streamwater throughout.

Table 13. Loss on ignition and approximate carbon/nitrogen ratios for 0-10 cm soil layer collected July 6 and September 12, 1979; C/N ratios estimated from loss on ignition corrected to carbon content (Ball, 1964) and Kjeldahl nitrogen (not including nitrate).

		Plot Designation											
Factor	Sample Date	CC	CM	CRF	ASP	ASR-1	ASR-2	SLR-1	SLR-2	SLR-3	SLP	POR	POP
% loss on ignition	7/6[1]	29.8	7.0	12.0	10.2	12.4	18.3	7.7	7.6	6.9	8.8	5.6	18.5
	9/12[2]	29.9	5.2*	9.8*	8.8*	12.5	18.3	6.7	6.1	6.1	7.3	3.6*	17.4
C/N	7/6	60	35	42	36	25	26	26	24	28	30	24	35
	9/12	43	25	27	26	22	22	18	20	22	24	11	28

*Significantly different from 7/6 at .05 level.

[1] LSD between plots = 2.8%.

[2] LSD between plots = 2.4%.

Soil nitrate-N and nitrite-N (hereafter both are referred to as nitrate-N) concentrations were substantially lower than for ammonium-N, generally by a factor of six or more (Figure 11). Plots in which Thuja did not occur (CRF, ASP) were consistently lowest in soil nitrate. Groundwater in ASR-2, SLR-3, and SLP contained moderate to high levels of nitrate in September; with the exception of ASR-2, levels remained high in January (Table 12). Within SLR-3, higher nitrate concentrations in groundwater sampled along the creek (Figure 6; Table 12, pipes #1 and 2) than 15 m across slope, near a Chamaecyparis sapling (pipe #3), suggested the higher levels in groundwater might be confined to the immediate area surrounding the creek where Thuja occurs.

Oxygen saturation of the seep and groundwater corresponded well with nitrate concentrations (Table 12). Higher saturation of groundwater at SLP and SLR-3 in January, and lower saturation at ASR-1 and ASR-2 compared to earlier sampling dates, reflected higher and lower nitrate concentrations respectively. Consistently low O_2 saturation of SLR-2 water was consistent with the low nitrate levels found there.

Extractable nitrate and ammonium in the litter were definitely related to distribution of the two species. Litter under Chamaecyparis (ASP, CRF, POP) was consistently low in extractable N, particularly nitrate-N (Figures 12 and 13). Generally, nitrate-N and ammonium-N concentrations in litter exceeded those in soil by a factor of five or more, and litter ammonium-N levels exceeded nitrate-N by a factor of three or more. No consistent change in concentrations occurred between July and January.

Capacity for Mineralization of N. Mineralized N after five weeks' incubation ranged from 8 to 88, 18 to 112, and 14 to 52 ppm in soils collected in July, September and January, respectively, with variation between plots minimized in January (Figure 14). In most cases, mineralization rates were higher in September and lower in January than in July. No clear relationship between soil mineralization rate and species occurred; rates largely reflected total soil N concentrations (r = .90 for July incubation). A significant exception was the

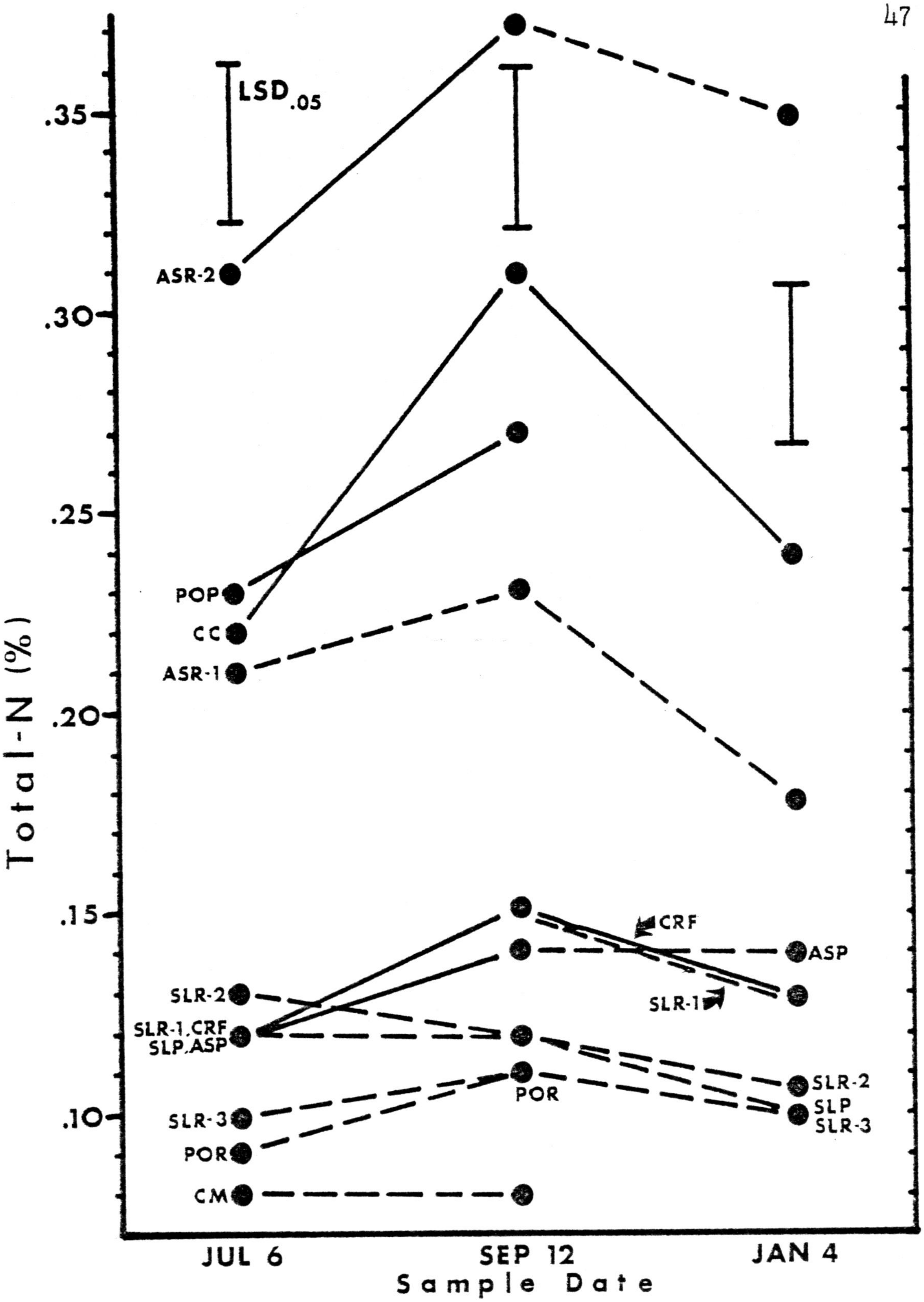

Figure 9. Total N concentrations in mineral soil on three dates, 1979-1980; solid line between points indicates significant differences (P = .05).

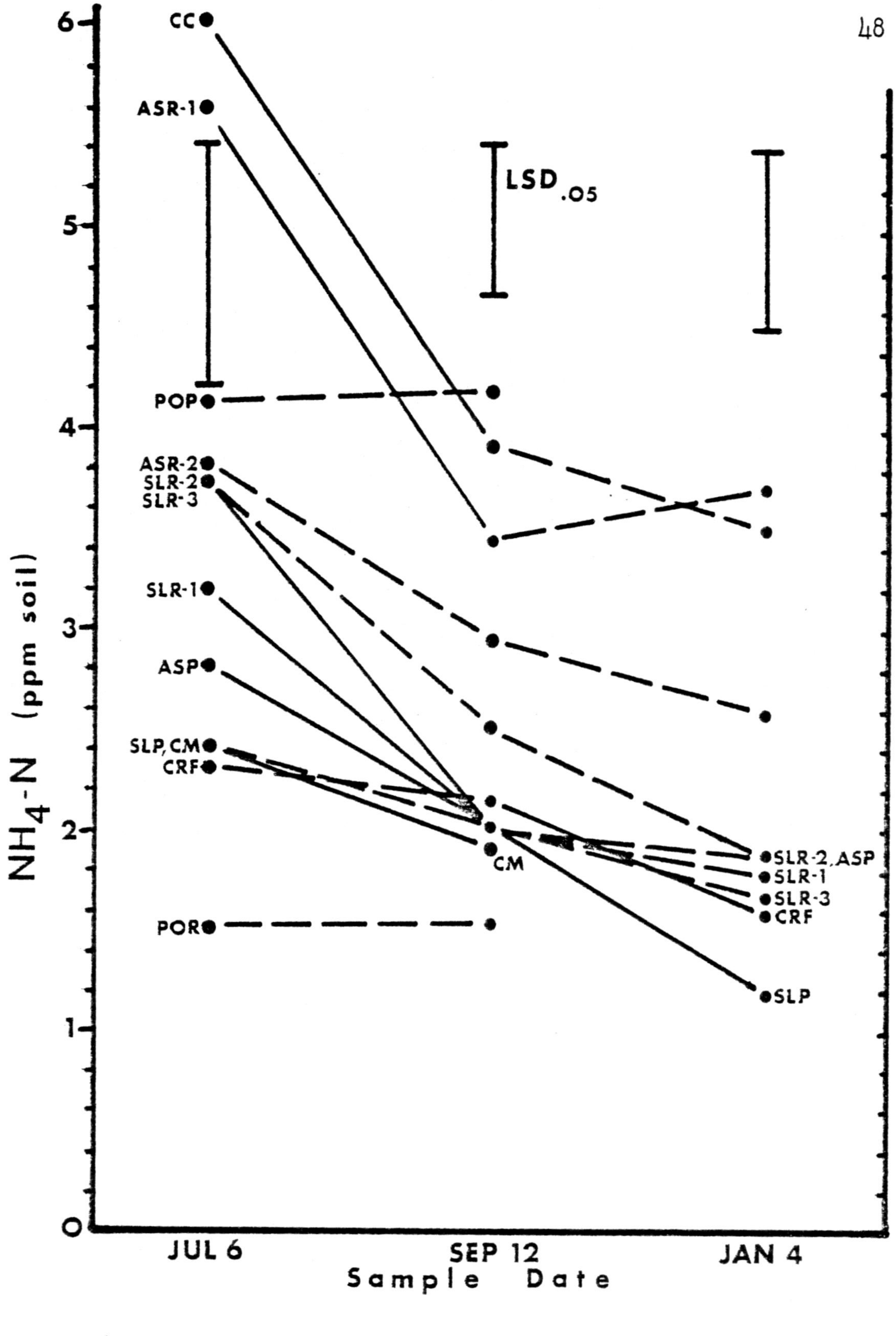

Figure 10. Extractable ammonium-N concentration in mineral soil on three dates, 1979-1980; solid lines between points indicate significant differences (P = .05).

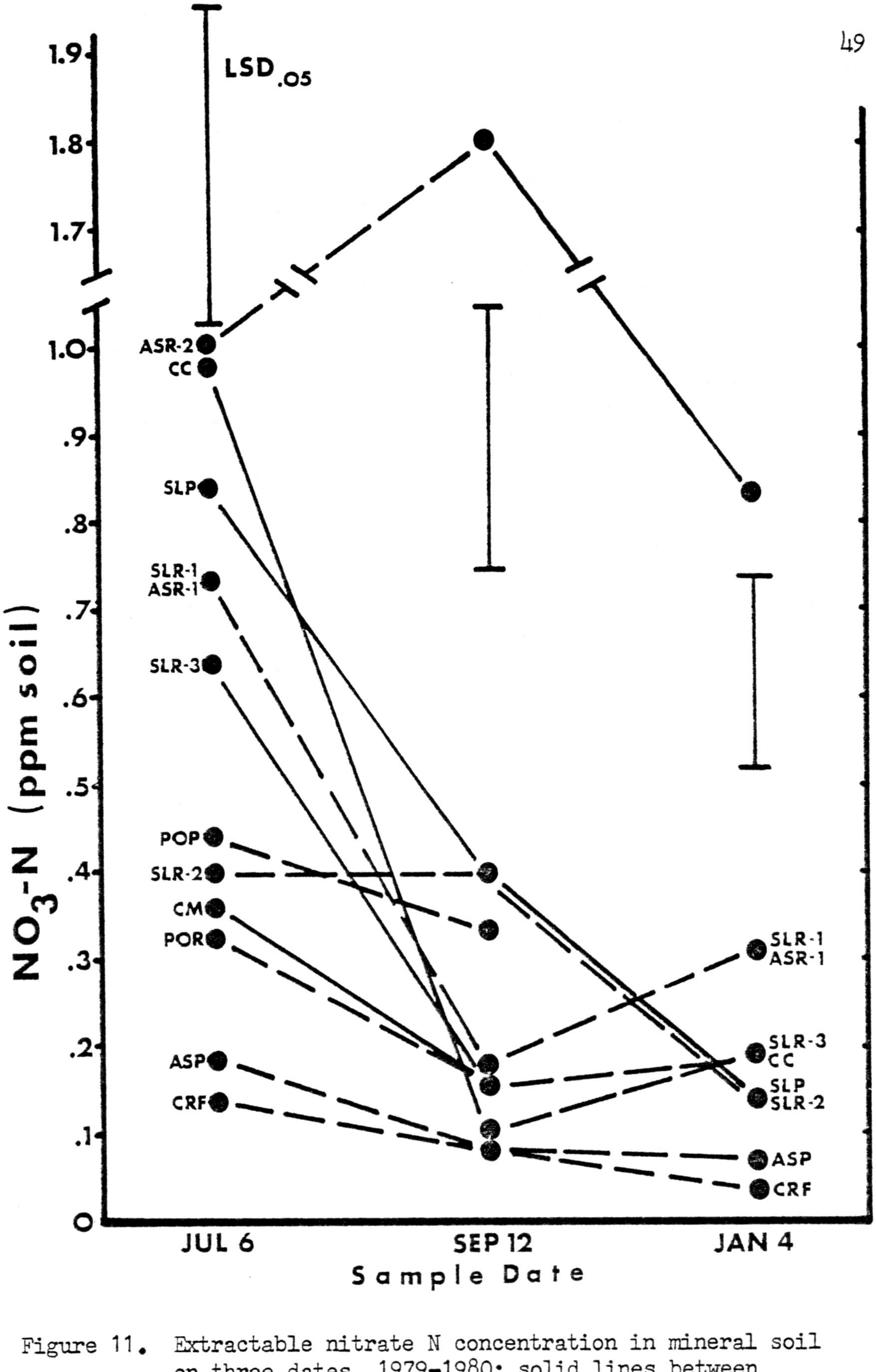

Figure 11. Extractable nitrate N concentration in mineral soil on three dates, 1979-1980; solid lines between points indicate significant differences (P = .05).

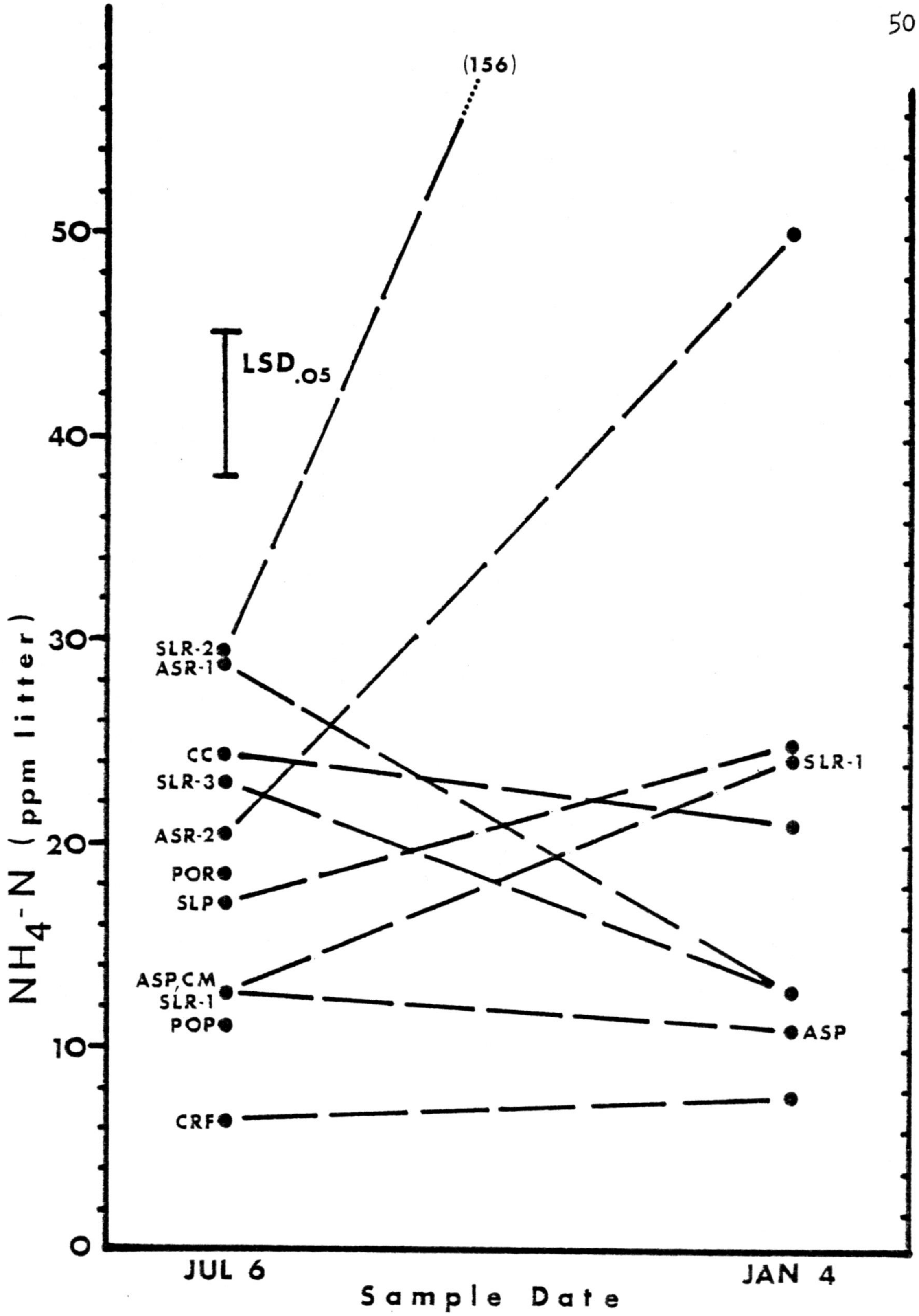

Figure 12. Extractable ammonium-N concentration in fine litter on two dates, 1979-1980; values for January 4 are based on one composite sample per plot.

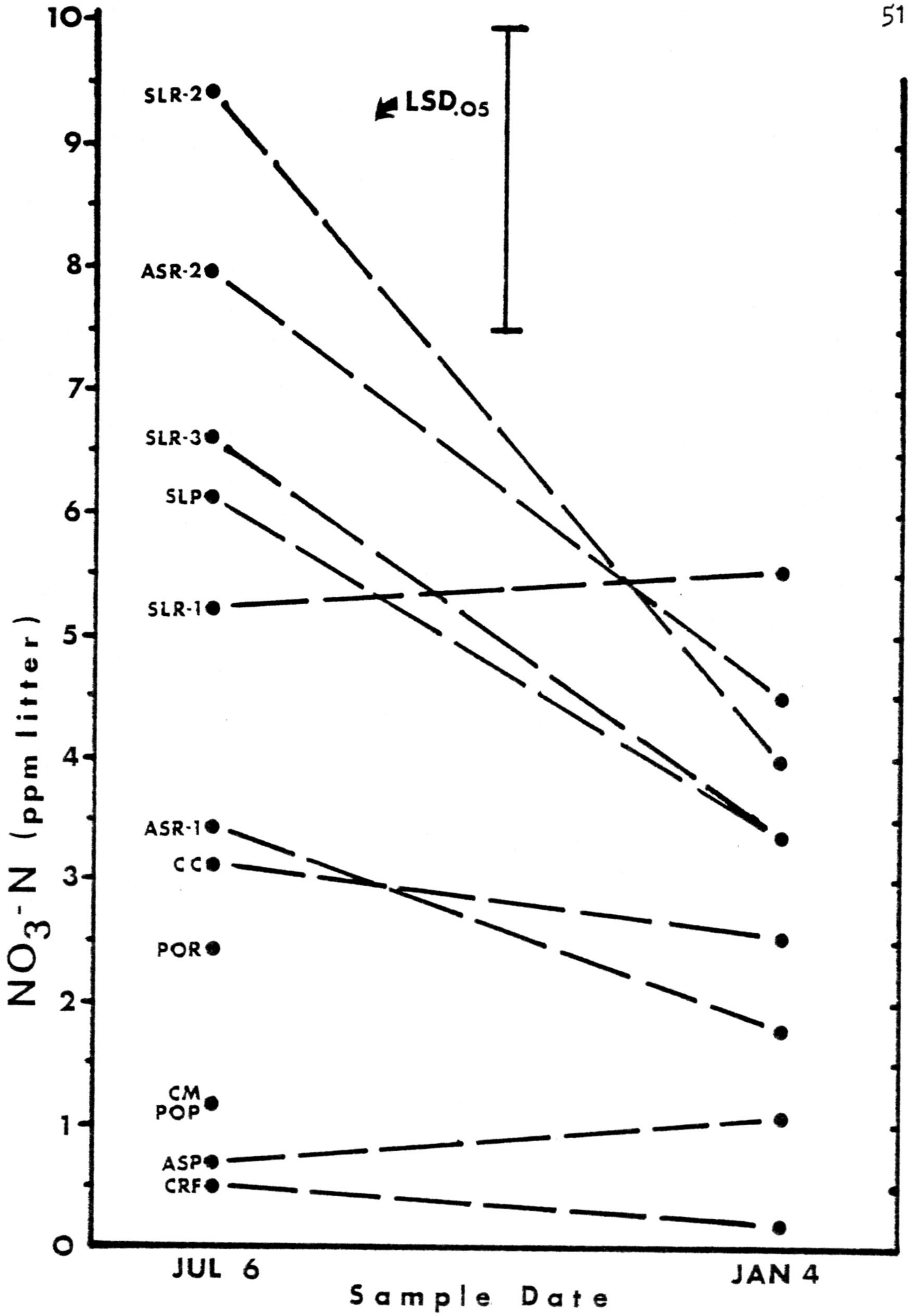

Figure 13. Extractable nitrate-N concentration in fine litter on two dates, 1979-1980; values for January 4 are based on one composite sample per plot.

relatively high mineralization rate in CM soil compared to CRF, opposed to their relationship in total N levels (Figure 14).

Generally the same relationship between plots seen in total mineralized N occurred in both ammonium and nitrate production (Figures 15 and 16). Normally nitrate-N accounted for 15% or less of the total mineralized N. The exception was ASR-2 soil, which contained 65% of its mineralized N as nitrate in the January incubation, when nitrification was slow or lacking in most other soils.

Soils varied considerably in their response to N addition before incubation (Figures 15 and 16). Soils from ASR-2 and the SLR plots showed net uptake of ammonium; with the exception of ASR-2, this was not associated with increased nitrification. Stimulation of nitrification in soils from Ash Swamp and the Port-Orford-Cedar Research National Area was highest in soils under Thuja (i.e. ASR-2<ASR-1<ASP; POR<POP). Response in Squaw Lake soils varied. The most vigorous and consistent stimulation of nitrification occurred in ASR-2, CRF, and CM soils.

Litter incubations differed more among plots and species. Mineralized N after five weeks was large compared to soils, ranging from eight to 980 ppm (Figure 17). With few exceptions, litter under Chamaecyparis (CRF, ASP, SLP, POP) had the lowest mineralization rates. Most rates were low in January compared to July, with the obvious exceptions of SLR-2 and ASR-2. Nitrate-N varied from zero to 60% of the mineralized N, and differed between species much as total mineralized N did (Figure 18). With the exception of SLP (highest for Chamaecyparis) and CM (lowest for Thuja), nitrification rates in litter under Thuja exceeded those under Chamaecyparis in the July incubation. The January incubation produced quite different results, and nitrification was generally reduced. Several plots (ASR-2, ASP, CC, CRF) showed net uptake of nitrate.

Addition of N in the July litter incubation showed the species difference previously mentioned. In most cases nitrification in litter under Thuja was stimulated by added N, and litter under Chamaecyparis was not.

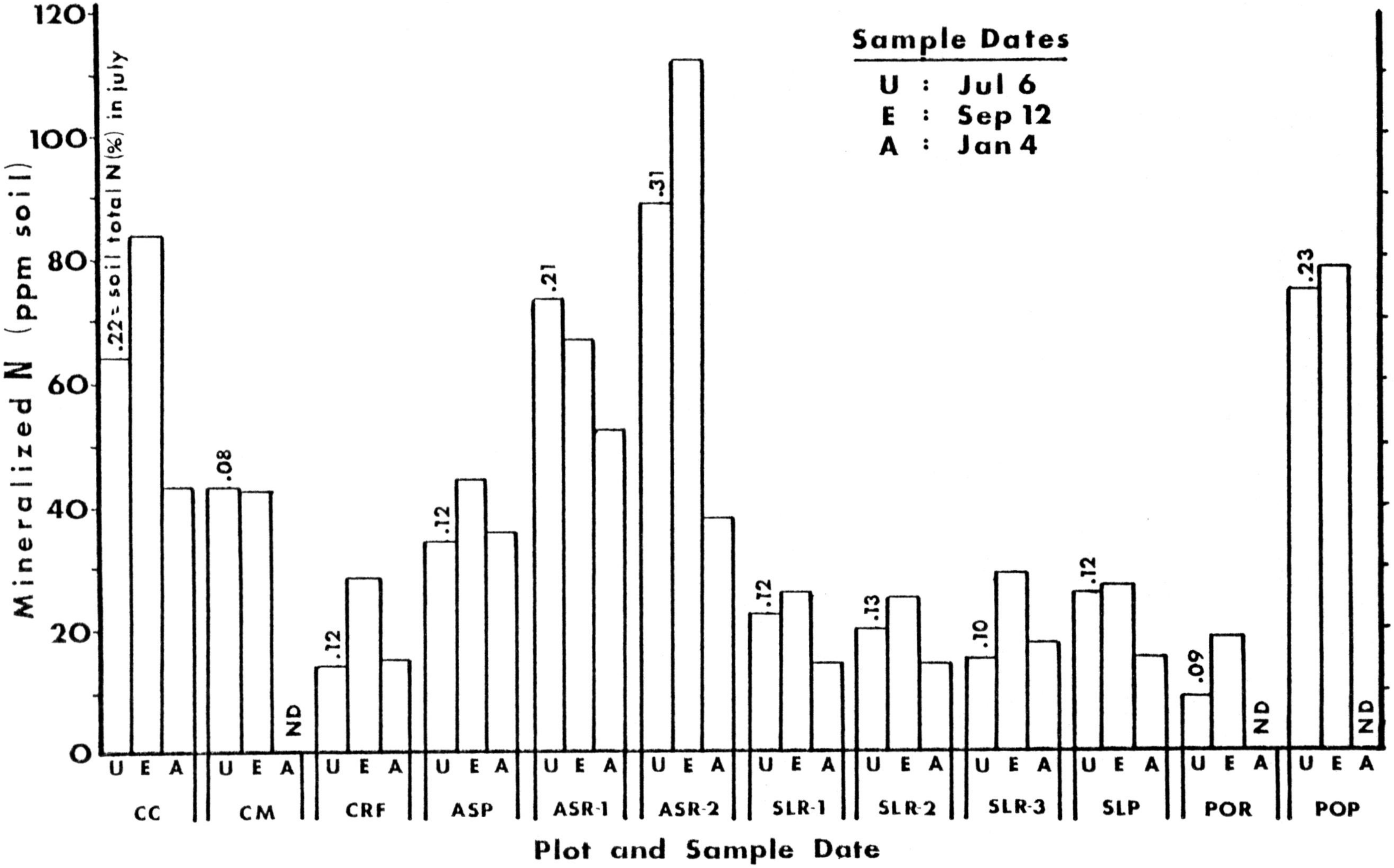

Figure 14. N mineralized in mineral soil incubated for five weeks at 28°C; sample dates: U = July 6, E = September 12, A = January 4.

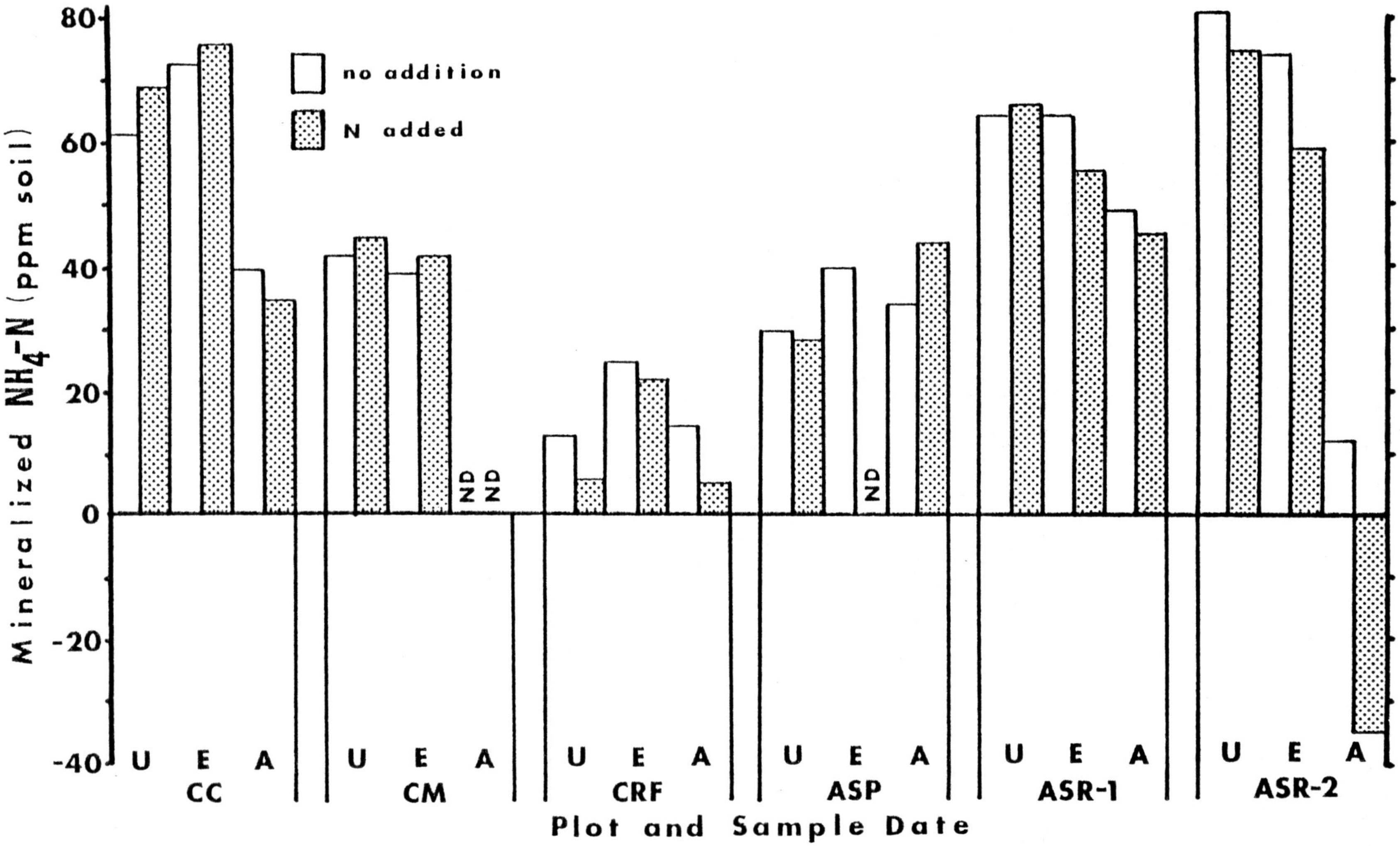

Figure 15 (Part I). Ammonium-N mineralized in mineral soil incubated for five weeks at 28°C; sample dates: U = July 6, E = September 12, A = January 4; N added = 10 ppm July and September, 100 ppm January.

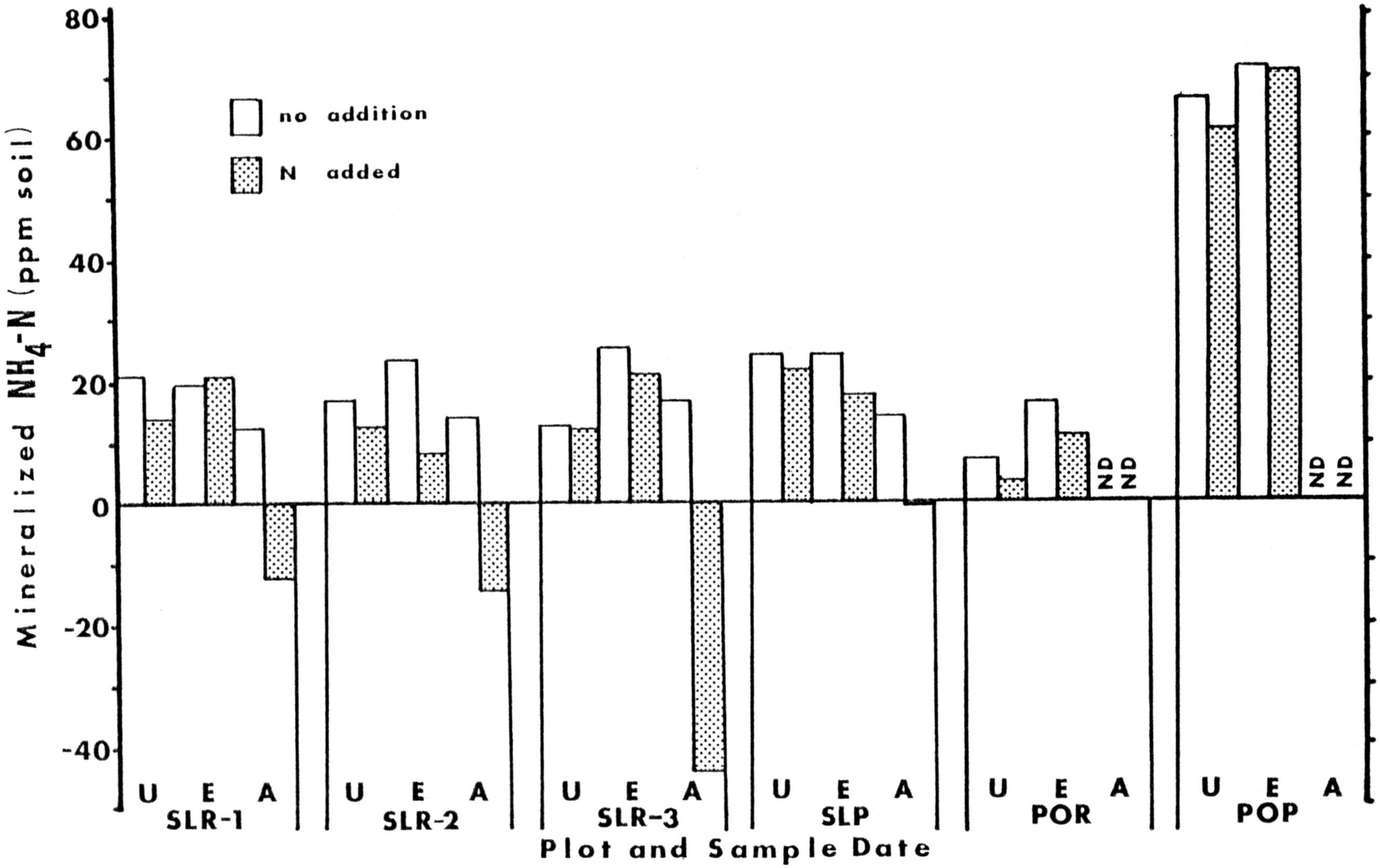

Figure 15 (Part II). See Part I for explanation.

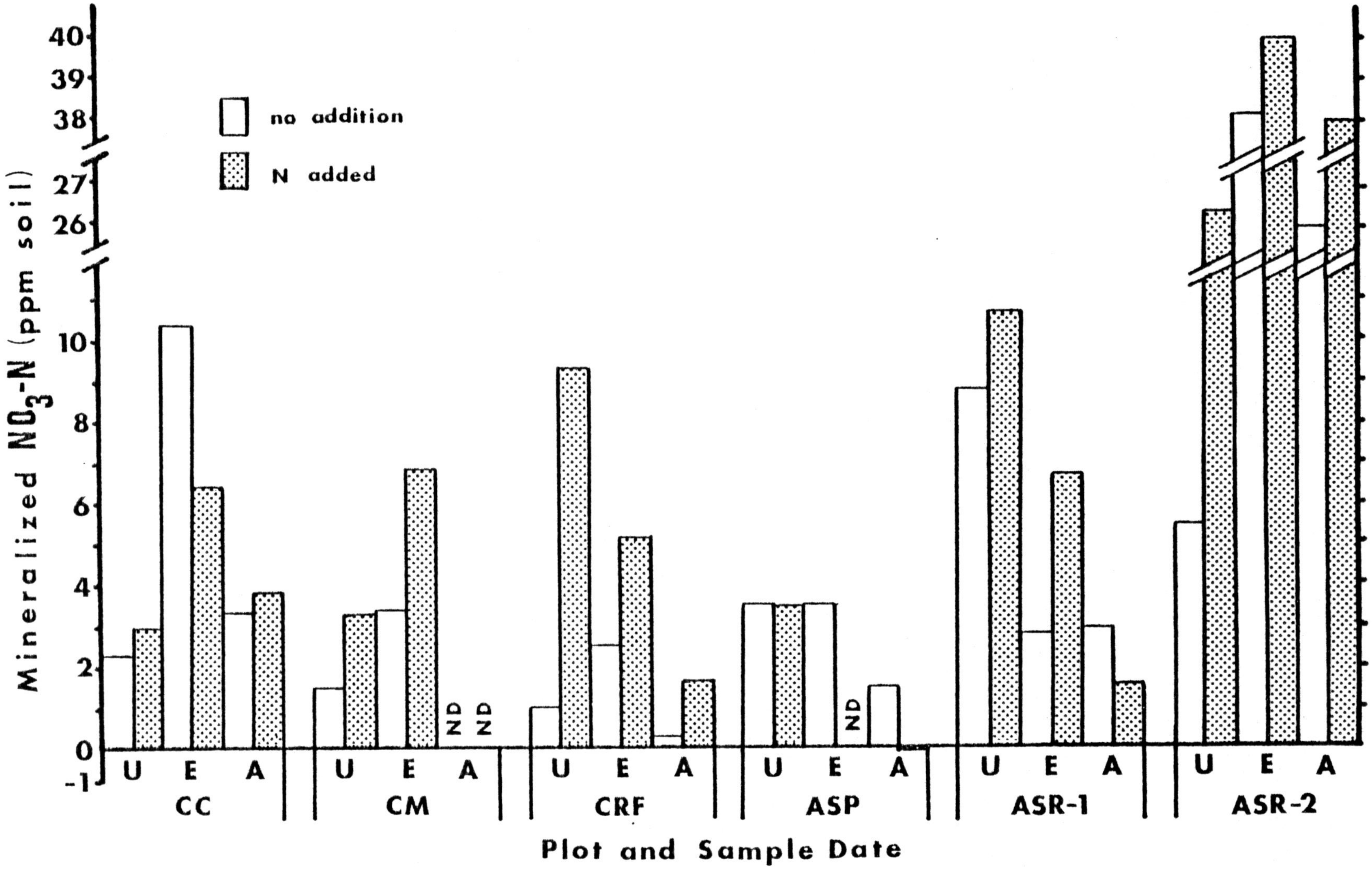

Figure 16 (Part I). Nitrate-N mineralized in mineral soil incubated for five weeks at 28°C; sample dates: U = July 6, E = September 12, A = January 4; N added = 10 ppm July and September, 100 ppm January.

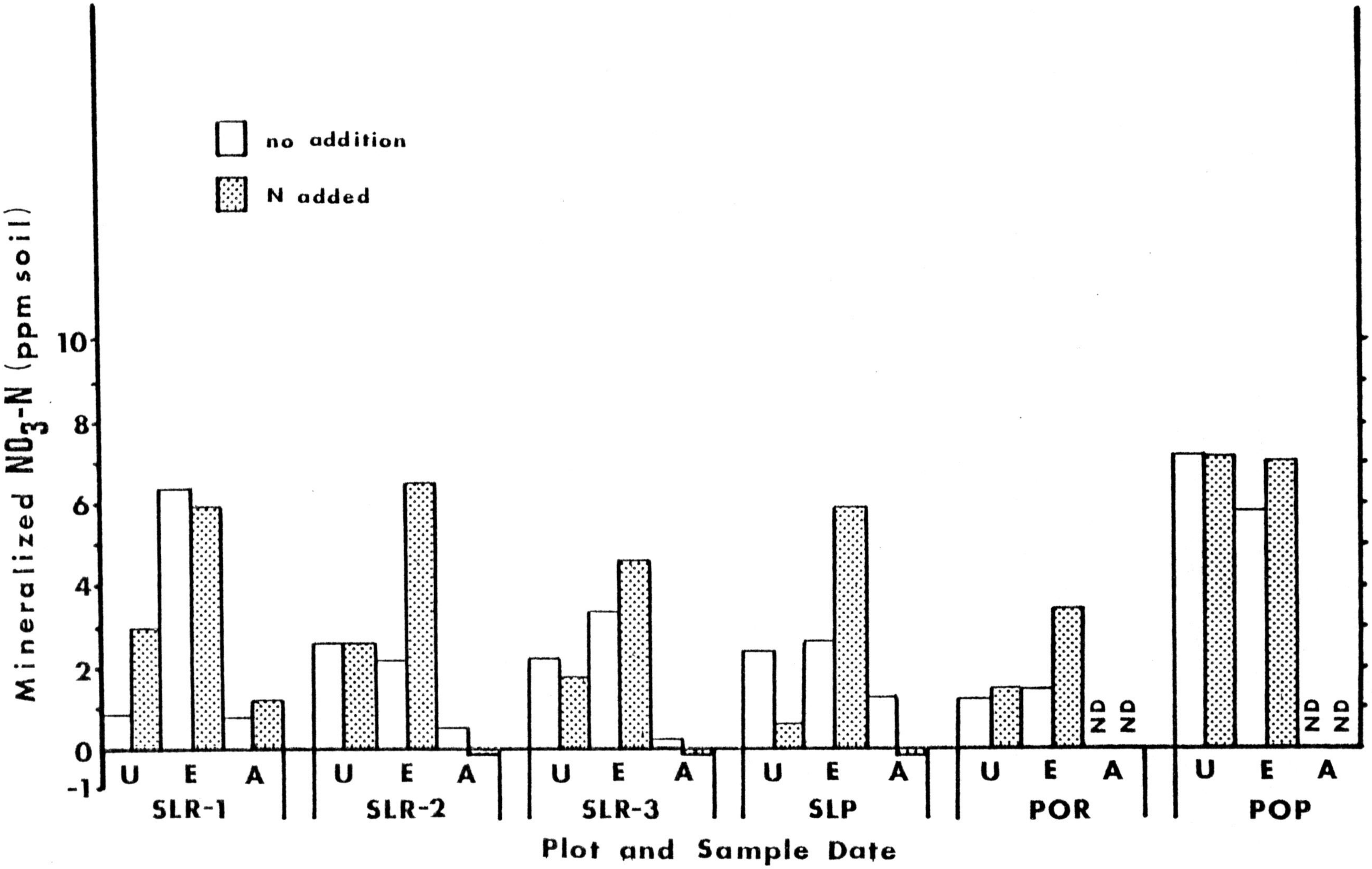

Figure 16 (Part II). See Part I for explanation.

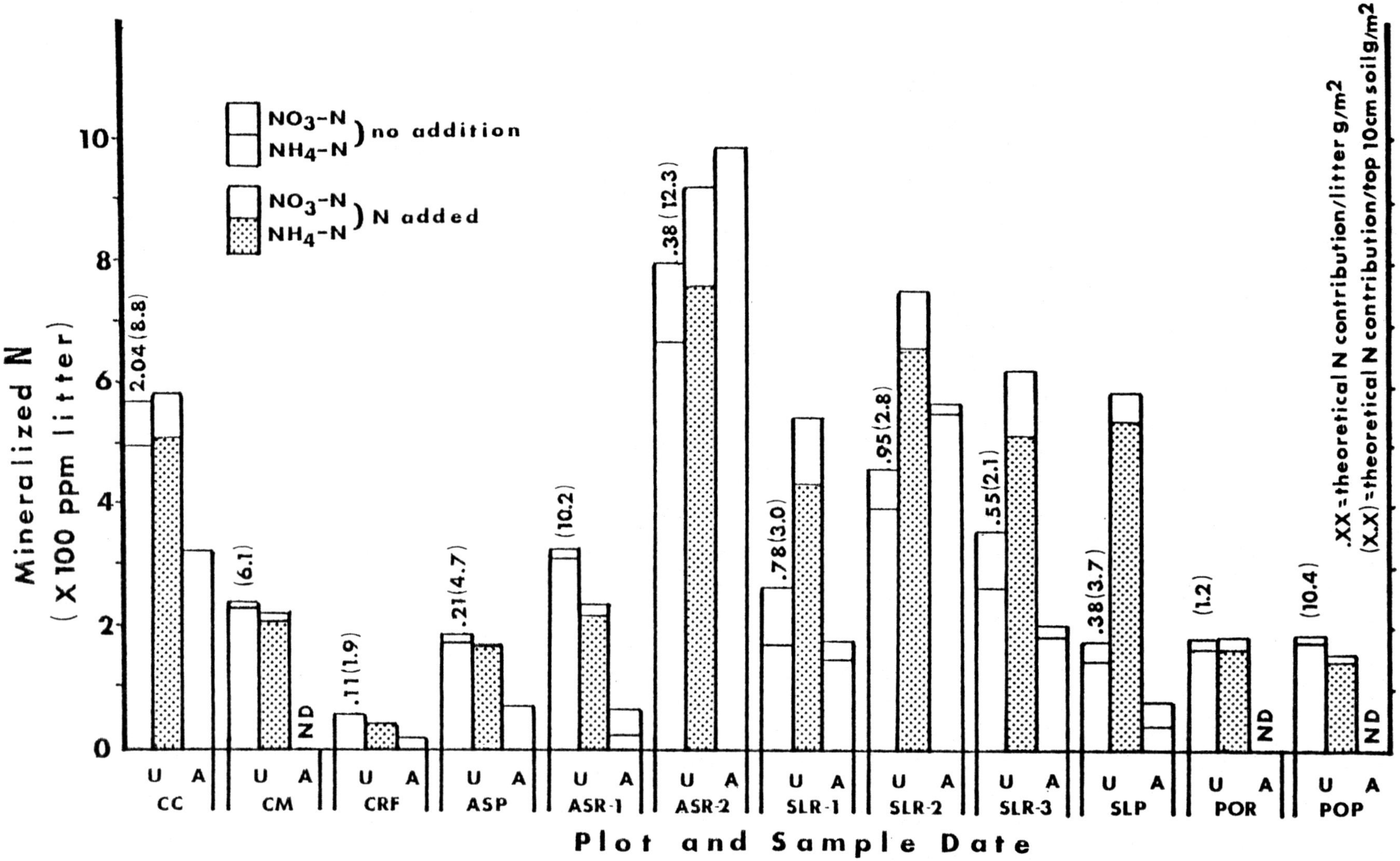

Figure 17. N mineralized in fine litter incubated for five weeks at 28°C; sample dates: U = July 6, A = January 4; N added in July = approximately 7 ppm; theoretical N contributions (based on July 6 litter incubated for five weeks) are reported for those plots in which litter mass was measured; theoretical N contributions by soil (July incubation) based on bulk density of 1.3 g/cc.

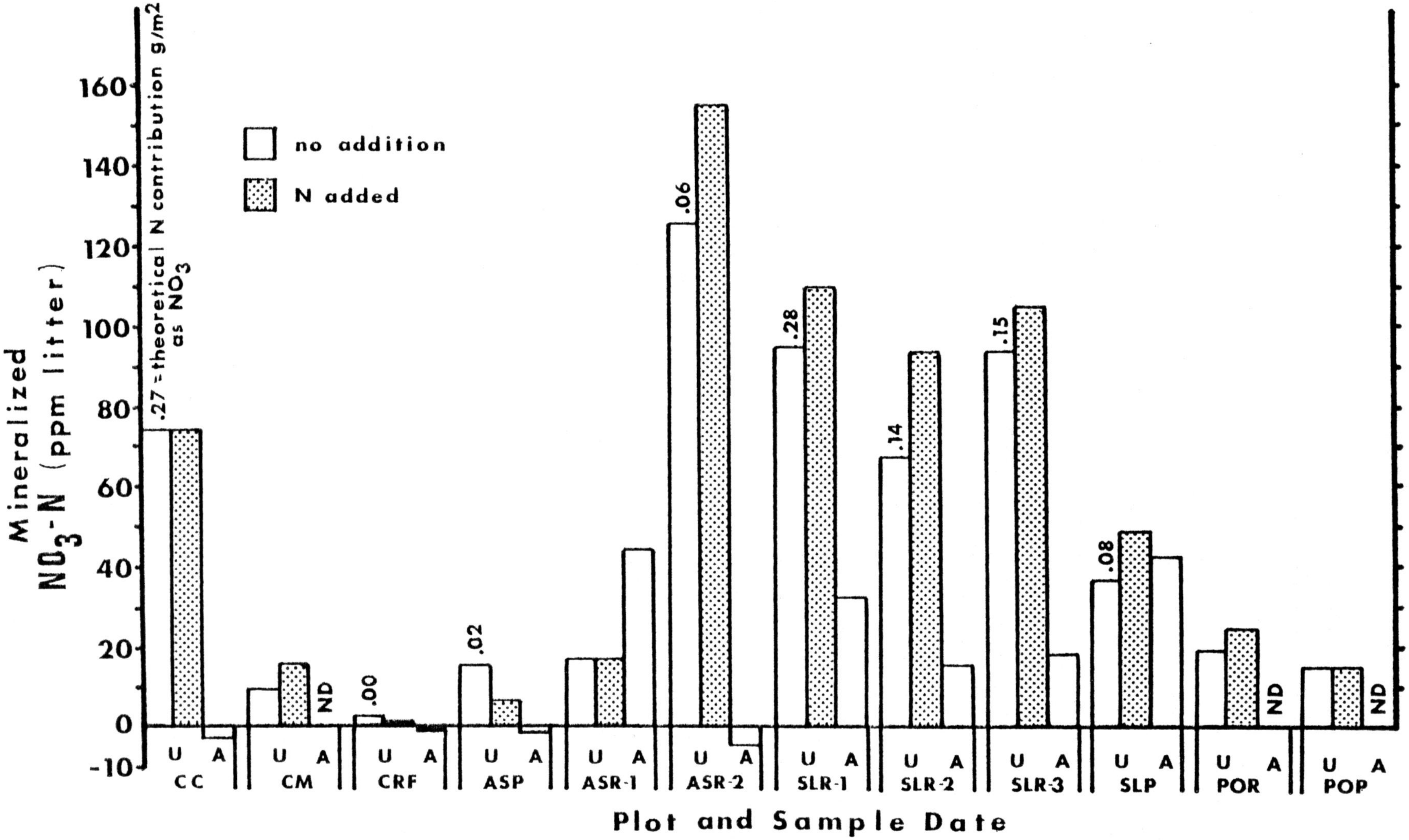

Figure 18. Nitrate-N mineralized in fine litter incubated for five weeks at 28°C; sample dates: U = July 6, A = January 4; N added in July = approximately 7 ppm; theoretical nitrate-N contributions (based on July 6 litter incubated for five weeks) are reported for those plots in which litter mass was measured.

In summary, differences in soil total N among plots were generally reflected in the static levels of ammonium and nitrate in the soil and litter, as well as N mineralization rates. Significant exceptions were the lower ranking of Chamaecyparis plots in terms of ammonium content of litter, nitrate content of soil and litter, and mineralization rates of the litter compared to soil total N concentrations.

Soil P, Ca, K, Mg. Exchangeable soil P and Mg showed no obvious relation to species occurrence; soil Ca and K levels were related to species occurrence on a local basis (Table 14). Exchangeable soil Ca was highest in plots where Thuja is most important locally (i.e., ASR-2 › ASP; SLR-1,2,3›SLP; POR›POP), and was considerably higher at CM than at CRF. In addition, soils in plots where Chamaecyparis was most important (ASP, CRF, SLP, POP) were among the five lowest in total soil Ca. Ca/Mg ratios followed the same relationship, with Thuja being important on soils with higher ratios.

In contrast, plots dominated by Chamaecyparis had slightly greater exchangeable soil K locally (i.e., ASP›ASR-2›ASR-1; SLP›SLR-2, 3; POP›POR), and soils in which Chamaecyparis did not occur (CM, ASR-1, SLR-3 and POR, assuming Chamaecyparis is rooted in soil different from Thuja) were four of the five lowest in exchangeable soil K.

Overall, exchangeable soil concentration of a cation showed little relation to its total concentration (r = .10, -.44, .12 for Ca, K, and Mg, respectively).

Foliar Nutrients. With the exception of foliar K and Ca/Mg ratios, differences between Thuja and Chamaecyparis appeared only on a local basis (Table 15). When all foliage samples are considered, K was significantly higher in Chamaecyparis (P = .01), and Ca/Mg ratios appear to be lower (P = .10). However, the range for both values showed considerable overlap between species. In plots where the two occur together (POP, ASR-2, SLP), or very close (CC), foliar N and K are consistently higher in Chamaecyparis, while Ca is lower. The reverse occurred at POR, indicating the two species are rooted in

Table 14. Soil nutrient concentrations and Ca:Mg ratios determined on composites of n samples from 0-10 cm depth; Ex = exchangeable, Tot = total concentration.

Plot Designation	n	% P	% Ca		% K		% Mg		Ca:Mg
		Ex	Ex	Tot	Ex	Tot	Ex	Tot	Ex
CC	10	.0003	.075	.24	.018	.15	.022	1.28	3.4
CC (Adj)[1/]	3	-	.017		.005		.005		3.4
CM	10	.0007	.082	.31	.007	.18	.005	0.18	15.8
CRF	10	.0016	.039	.20	.013	.18	.008	0.40	4.9
ASP	10	.0008	.101	.24	.013	.30	.013	0.49	7.8
ASR-1	4	.0004	.024	.43	.007	.32	.017	0.76	1.4
ASR-2	5	.0006	.210	.68	.012	.52	.022	0.58	9.5
SLR-1	5	.0017	.224	.90	.016	.25	.022	0.84	10.2
SLR-2	5	.0008	.218	.85	.010	.19	.023	0.82	9.5
SLR-3	5	.0008	.218	.62	.006	.18	.021	0.89	10.4
SLP	10	.0013	.098	.30	.015	.20	.016	0.87	6.1
POR	5	.0017	.036	2.81	.002	1.20	.010	3.26	3.6
POP	10	.0002	.014	.10	.006	.37	.004	0.95	3.5
SLP (Adj)[2/]	1	.0020	.021	.14	.012	.19	.002	0.47	10.5
Plocher[3/] (CRF)	1	.0040	.216		.040		.035		6.2
Plocher[4/] (Range)		.0004 -.0040	.006 -.216		.004 -.040		.002 -.119		.3 -6.2

[1/] Sampled near *Chamaecyparis* seedlings in clearcut, adjacent to CC.

[2/] Sampled adjacent to SLP within extension of *Thuja* to top of slope.

[3/] Data from Plocher (1977) for 0-15 cm layer soil collected near my CRF plot.

[4/] Range of values from Plocher (1977) for soils under *Chamaecyparis* at four sites in southwest Oregon.

Table 15. Foliage nutrient levels and calcium/magnesium ratios for trees less than 15 cm DBH, and greater than 15 cm DBH (marked by asterisk); values are for bulked samples from n trees, except % N which is the mean for n trees sampled.

Species	Plot Designation	n	% N	% P	% Ca	% K	% Mg	Ca:Mg
Thuja plicata	CC	5	1.11	.12	1.66	.52	.23	7.2
	CM	3	1.05	.12	1.66	.56	.13	12.8
		*2	1.20	.13	1.48	.70	.06	24.7
	ASR-1	1	1.60	.24	1.63	.89	.22	7.4
		*2	1.11	.17	1.37	.77	.13	10.6
	ASR-2	1	1.08	.14	1.98	.54	.17	11.6
		*2	1.08	.13	1.49	.67	.12	12.4
	SLR-1	*2	1.22	.16	1.87	.74	.16	11.7
	SLR-3	1	1.28	.13	1.82	.51	.19	9.6
		*1	1.01	.14	1.56	.53	.13	12.0
	SLP	1	1.34	.20	1.18	.81	.14	8.4
	POR	3	1.25	.16	1.20	.95	.15	8.0
	POP	2	.94	.13	1.14	.55	.15	7.6
Chamaecyparis lawsoniana	CC (Adj)[1/]	2	1.31	.12	1.34	.67	.20	6.7
	CRF	4	.90	.11	1.86	.78	.26	7.2
	ASP	2	1.19	.16	1.38	.88	.18	7.7
		*2	1.25	.16	1.46	.95	.19	7.7
	ASR-2	1	1.39	.11	1.15	.81	.11	10.4
		*1	1.40	.15	1.46	1.00	.15	9.7
	SLP	2	1.85	.23	.83	1.20	.16	5.2
		*2	1.50	.16	1.46	.88	.16	9.1
	POR	1	.99	.13	1.52	.88	.13	11.7
	POP	3	1.03	.11	1.07	.78	.13	8.2

[1/] Foliage sampled just outside CC plot; similar conditions.

Table 16. Foliage nutrient levels and calcium/magnesium ratios reported for *Thuja plicata* and *Chamaecyparis lawsoniana*.

Species	Footnote	% N	% P	% Ca	% K	% Mg	Ca:Mg
Thuja plicata	1	.73	.13	1.16	.52	.10	11.6
	2	1.27	.06	1.78	.52	.71	2.5
	3	1.13	.08	1.33	.53	.96	1.4
	4	1.22	.10	1.05	.38	.16	6.6
	5	<1.5	.13	.10-.20	.39-.78	.06-.18	-
Chamaecyparis lawsoniana	4	.92	.06	1.02	.30	.19	5.4
	6	.89	.13	1.20	.59	.21	5.7
	7	.67-1.14	.07-.13	.50-1.20	.59-.68	.11-.24	3.7-5.7
	8	1.07	.20	.60	.69	.20	3.0
	9	.57-1.22	.09-.21	.54-1.24	.53-.84	.11-.30	2.2-11.3
	10	.55-1.39	.12-.24	.51-0.92	.72-.90	-	-
	11	1.70	.34	.59	.59	.17	3.5
	12	.59	.06	-	-	-	-
	13	2.49	.26	-	-	-	-

---

[1] Beaton, *et al.* (1965) in British Columbia; (5) 58-year-old trees.

[2] Gessel, *et al.* (1951) in Washington; (1) 11-year-old healthy tree.

[3] Gessel, *et al.* (1951) in Washington; (3) 100-year-old healthy trees.

[4] Ovington (1956) at Bedgebury, England; composite of (5) 20-year-old trees.

[5] Walker, *et al.* (1955); deficiency levels for seedlings in culture.

[6] Zobel and Hawk (1980) near my CRF plot; (8) 1-3 m saplings.

[7] Zobel and Hawk (1980); range of values for saplings at ten sites within *Chamaecyparis* range.

[8] Plocher (1977) near my CRF plot; single bulked sample from seedlings.

[9] Plocher (1977); range of values for seedlings at four sites within *Chamaecyparis* range.

[10] Youngberg (1958); range of values for whole seedlings in three forest nurseries in Washington and Oregon.

[11] Zobel and Liu (1979); (16) 1½-year-old nursery seedlings in Taiwan.

[12] Leyton (1955); (20) 15-year-old trees from Heathland plantation in England.

[13] Leyton (1955); same as footnote 12 but treated with heather mulch.

different soils there. It appeared that the trees may differ in their relation of foliar Ca levels to tree age. In the four plots where two size classes of Thuja (less than and greater than 15 cm DBH) were sampled, Ca and Mg were consistently lower in foliage of larger trees, yielding higher Ca/Mg ratios. The reverse was seen for Ca in Chamaecyparis' foliage, based on samples from three plots. Of the foliar nutrients measured, N was most correlated with P for both Thuja (r = .78) and Chamaecyparis (r = .89).

Foliar concentrations showed little correlation with soil nutrient levels on a studywide basis, although soil Ca/Mg ratios were reflected well by Thuja foliage (r = .93), but less so by Chamaecyparis (r = .73) in trees less than 15 cm DBH. Nutrients with the best correlation between foliar and soil concentrations for Thuja were Ca (r = .66) and Mg (r = .51), and for Chamaecyparis were P (r = .41) and Mg (r = .37).

Relatively low soil nutrient concentrations, and local differences in soil nutrient availability were reflected in foliar concentrations in many cases. Low levels of soil Ca and P at POP, Mg at CM, and K in soils under Chamaecyparis at CC, agreed with foliar levels of trees growing at those sites. In general, Ca levels in Thuja foliage reflected local changes in its availability (i.e., ASR-2>ASR-1; SLR-1,3>SLP; POR>POP).

Growth. The range in age, size, and occurrence of Thuja and Chamaecyparis within and among plots prevented statistical comparisons or growth estimates among plots.

On a studywide basis, relationships between age, and height and DBH both tend to show the same difference; growth appears more rapid in young Chamaecyparis, but declines in older trees as opposed to Thuja, which continues rapid growth (Figures 19 to 21; Table 17). By 50 years of age, Thuja has reached Chamaecyparis in size, and continues to grow at faster rates. Difference is most noticeable in basal area growth, which in older Thuja is far exceeding that of Chamaecyparis on a studywide basis, and also within individual plots when they occur together (Table 17; Figures 22 and 23). The age when basal area increment in *Thuja* begins to exceed *Chamaecyparis*, estimated by regression equations, is about 25 years. Relation of age to DBH in individual plots support this; *Thuja* exhibits a more logarithmic increase in DBH as opposed to *Chamaecyparis*' more linear increase. Overall, DBH and basal area growth were more clearly related to age in *Thuja* than *Chamaecyparis* (Table 17). This appeared on a local basis as well.

CC appeared to be the best site for growth in basal area of both *Thuja* and *Chamaecyparis*. SLR-3 and SLP also showed excellent growth of *Thuja* and *Chamaecyparis*, respectively. Best growth in height of *Chamaecyparis* occurred at ASP, while its poorest growth in both height and basal area occurred at CRF, followed by SLR-2. *Thuja*'s growth was generally poorest in both respects at CM and ASR-1, and height growth was poor in ASR-2 and POR as well. Differences among other plots cannot be determined.

Overall, foliage elongation between July 2 and September 12 was greatest in *Chamaecyparis*, and exceeded that of *Thuja* on all sites where the two occurred together, except ASR-2 and POR. Elongation after September 12 was negligible in both species, less than .3 mm for any given tree in any plot, although CC and the Squaw Lake plots showed more than others. The relationships between plots were similar to that seen for age/DBH; based on means of the five largest increments (cm) (indicated in parentheses), these are:

Thuja:

SLP < SLR-3 < CC < CM < ASR-1 < ASR-2 < SLR-1 < POR ∼ SLR-2 ∼ POP
(2.44) (2.22) (1.88) (1.74) (1.66) (1.52) (1.22) (.68) (.68) (.70)

Chamaecyparis:

SLP < CC < ASP < CRF < POP < ASR-2 < POR
(3.40) (2.52) (2.3) (1.88) (1.36) (.46) (.32)

The results of regression of various soil and other site variables (Table 18) on 10-year basal area growth are given in Table 19. For *Chamaecyparis*, age did not enter the regression significantly, but was added initially to remove any variation in growth related to age.

Among Pinaceae in the study plots, growth in DBH and height of *Tsuga heterophylla* was usually highest at CC and POP and lowest at CRF (Figure 24). DBH growth of *Abies grandis* appeared slightly greater at POP than CM (Figure 25); comparison of basal area increments (not shown) indicate even larger difference. Growth of *Pseudotsuga menziesii* was best at CC and ASP, and poorest at CRF and CM, but its relatively old age at CM prevents meaningful comparison (Figure 25). Its growth in height appeared stunted at ASP in older trees, compared to the continued sharp increase in DBH.

Table 17. Regression equations relating age to height (HT), DBH, and 10-year basal area increment (BAI) in *Chamaecyparis lawsoniana* and *Thuja plicata*; based on trees less than 100 years old at all sites sampled; predicted value is given for 50 years of age.

Species	Variables	Equation	n	r	@50years
Chamaecyparis	Age/Height	$\mathrm{HT(m)} = 6.89 + .17\mathrm{Age}$	50	.38	15.4 m
Thuja		$\mathrm{HT(m)} = 0.92 + .28\mathrm{Age}$	40	.66	14.9 m
Chamaecyparis	Age/DBH	$\mathrm{lnDBH(cm)} = 2.24 + .013\mathrm{Age}$	76	.36	18 cm
Thuja		$\mathrm{lnDBH(cm)} = 1.53 + .028\mathrm{Age}$	65	.76	19 cm
Chamaecyparis	Age/BAI	$\mathrm{lnBAI(cm^2)} = 2.52 + .021\mathrm{Age}$	76	.27	36 cm^2
Thuja		$\mathrm{lnBAI(cm^2)} = 1.88 + .046\mathrm{Age}$	65	.60	65 cm^2
Chamaecyparis	DBH/BAI	$\mathrm{logBAI(cm^2)} = -1.19 + 2.16\mathrm{logDBH(cm)}$	76	.86	---
Thuja		$\mathrm{logBAI(cm^2)} = -0.69 + 1.94\mathrm{logDBH(cm)}$	65	.94	---

Table 18. Independent variables related to basal area increment by multiple linear regression analysis; factors concerning soil or litter were based on July samples (0-10cm soil), except exchangeable cations and P, which were based on September samples.

Age
Density
Basal area
Soil pH
Soil moisture
Soil field capacity
Soil loss-on-ignition
Soil C/N
Soil total N
Soil NO_3-N
Litter NO_3-N
Soil NH_4-N
Litter NH_4-N
Soil temperature
Exchangeable P
Exchangeable Ca
Exchangeable K
Exchangeable Mg
Soil Ca/Mg
% Clay
NO_3-N mineralization rate-soil
NO_3-N mineralization rate-litter
NH_4-N mineralization rate-soil
NH_4-N mineralization rate-litter
Total N mineralization rate-soil
Total N mineralization rate-litter

Table 19. Variables included in regression of 10-year basal area increment (BAI) on variables listed in Table 18; ** indicating contribution significant at 1% level, * significant at 5% level.

	Order of Entry				
	1	2	3	4	5
<u>Chamaecyparis</u>	Age	**Soil $[NO_3\text{-}N]$	Basal area	Soil temp	--
Regression R^2	.05	.30	.34	.34	--
<u>Thuja</u>	**Age	**Soil [Ca]	*Clay (%)	Loss on ignition	Soil [P]
Regression R^2	.14	.32	.37	.39	.40

Best Model

<u>Chamaecyparis</u> 10-year $\text{BAI}(\text{cm}^2) = -132.4 + 2.2\text{Age} + 260.6\,[NO_3\text{-}N]\,(\text{ppm})$

<u>Thuja</u> 10-year $\text{BAI}(\text{cm}^2) = -482.1 + 3.8\text{Age} + 19.0\,[\text{Ca}]\,(\text{pp}10{,}000) + 9.4\,\text{Clay}(\%)$

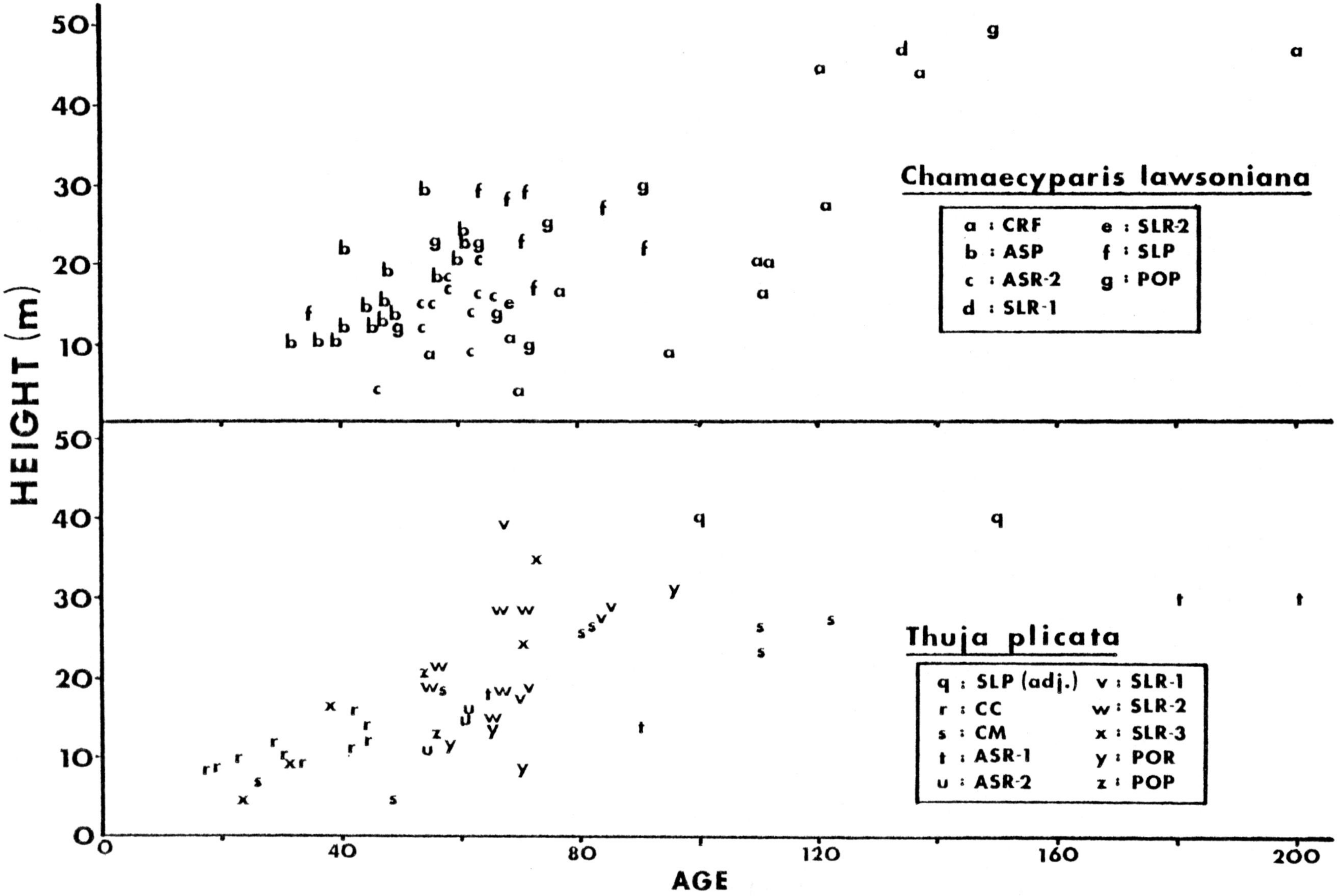

Figure 19. Relationship of height to age for Chamaecyparis lawsoniana and Thuja plicata.

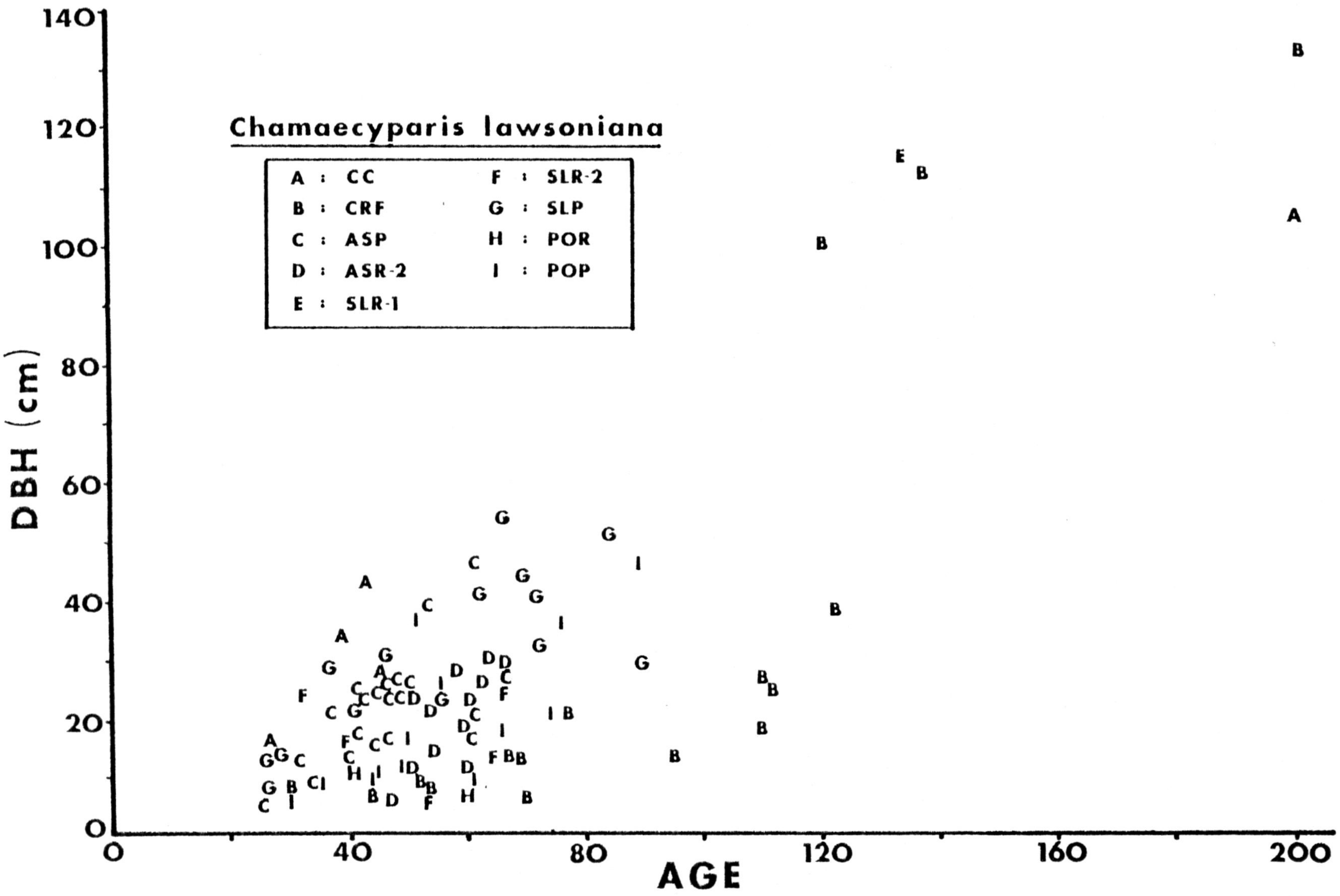

Figure 20. Relationship of DBH to age for *Chamaecyparis lawsoniana*.

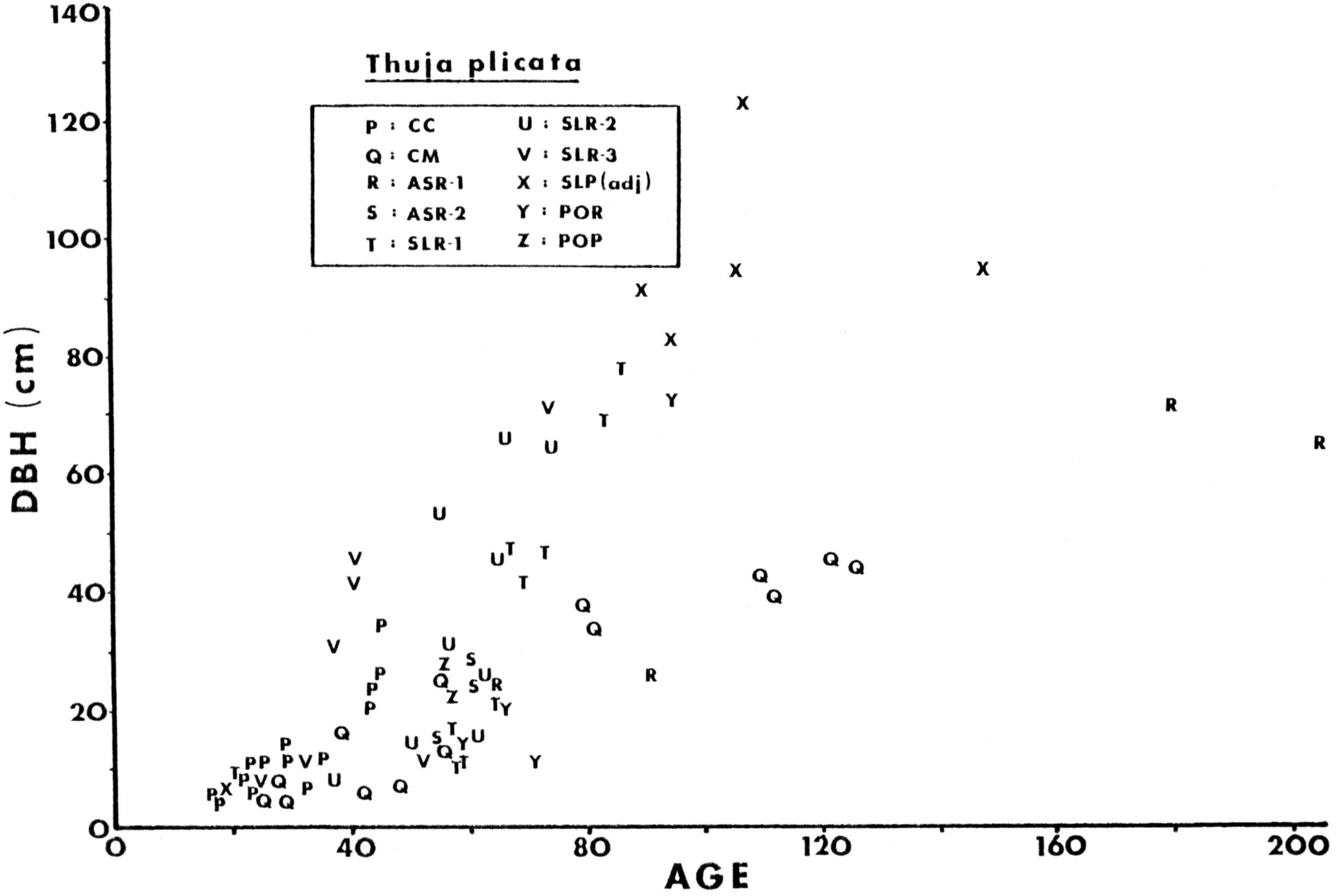

Figure 21. Relationship of DBH to age for Thuja plicata.

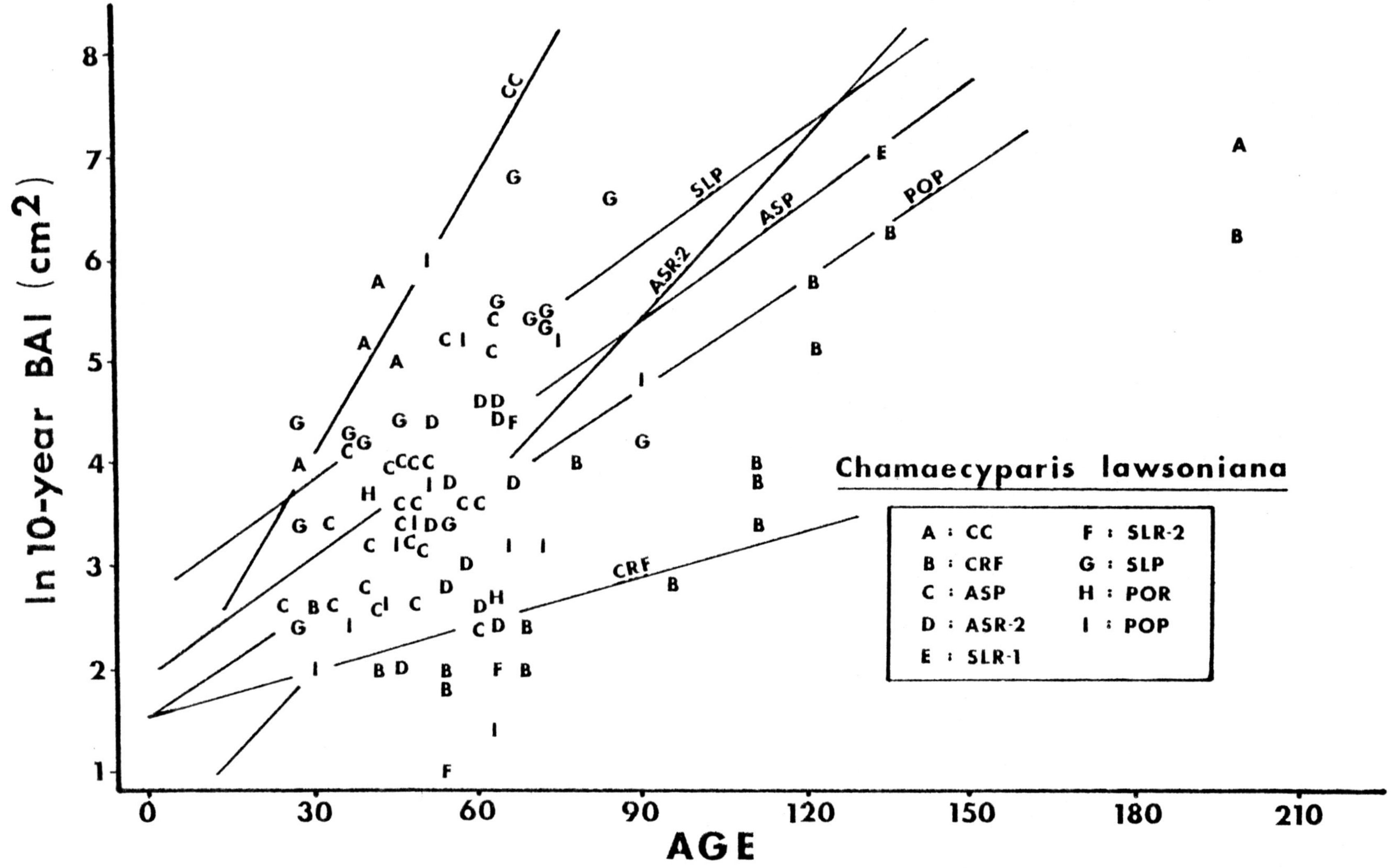

Figure 22. Relationship of natural log of 10-year basal area increment (BAI) to age for Chamaecyparis lawsoniana; regression lines are shown based on trees less than 100 years old in plots where sample number was sufficient; regression r values: .85(CC), .67(SLP), .36(ASR-2), .44(ASP), .44(POP), .45(CRF).

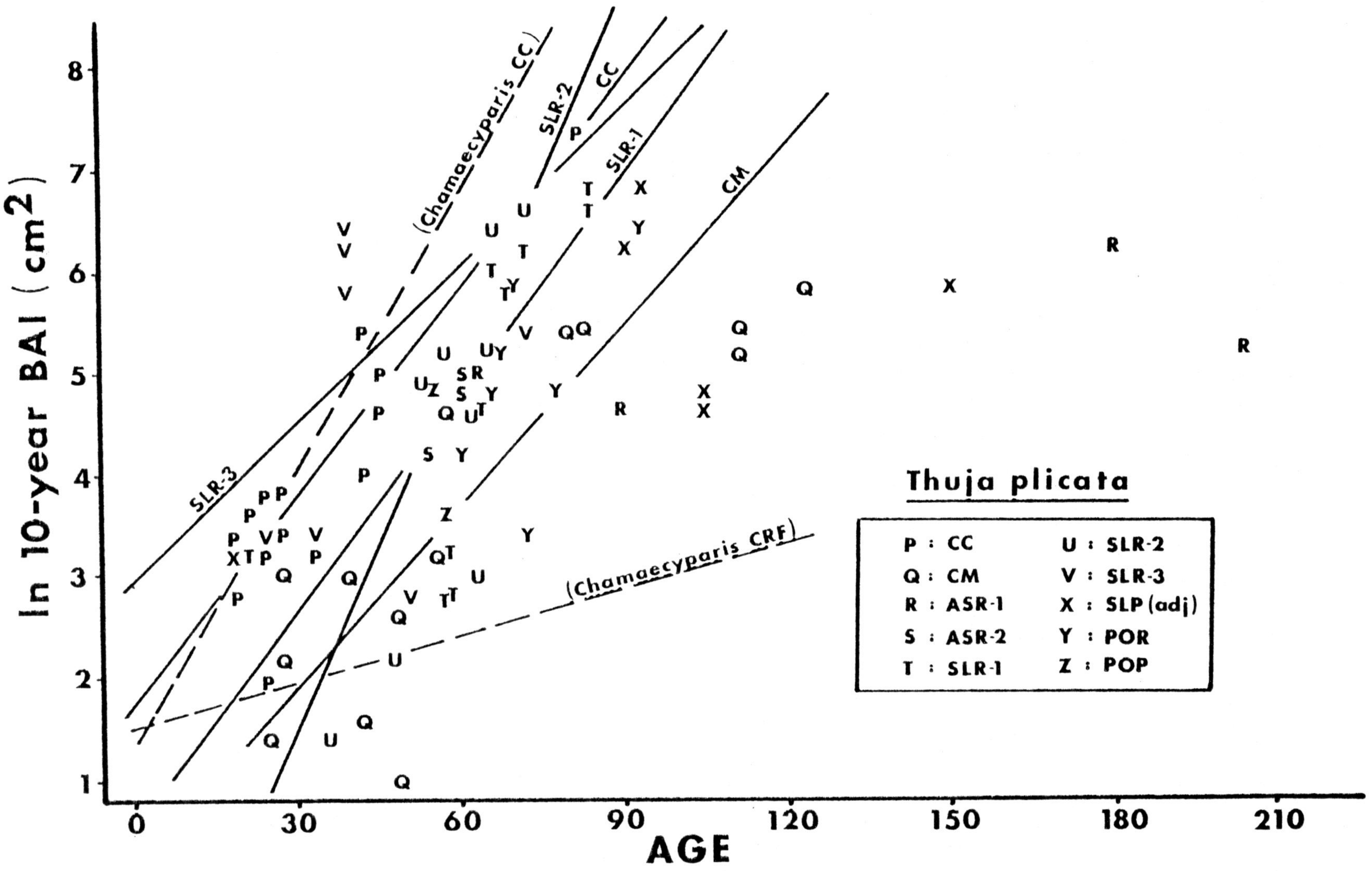

Figure 23. Relationship of natural log of 10-year basal area increment (BAI) to age for Thuja plicata; regression lines are shown based on trees less than 100 years old in plots where sample number was sufficient; regression r values: .82(SLR-2), .73(CC), .47(SLR-3), .74(SLR-1), .77(CM).

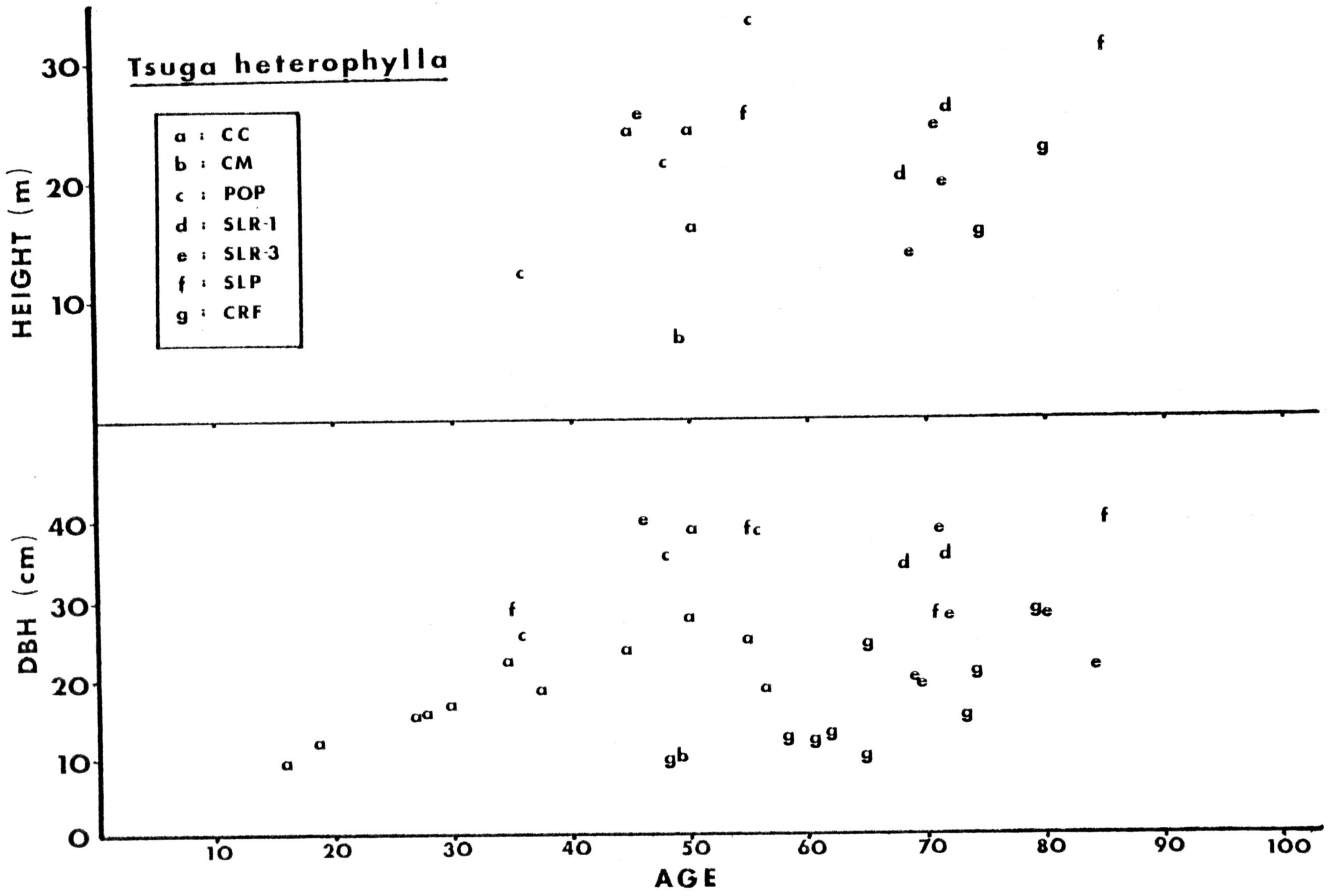

Figure 24. Relationship of height and DBH to age for Tsuga heterophylla.

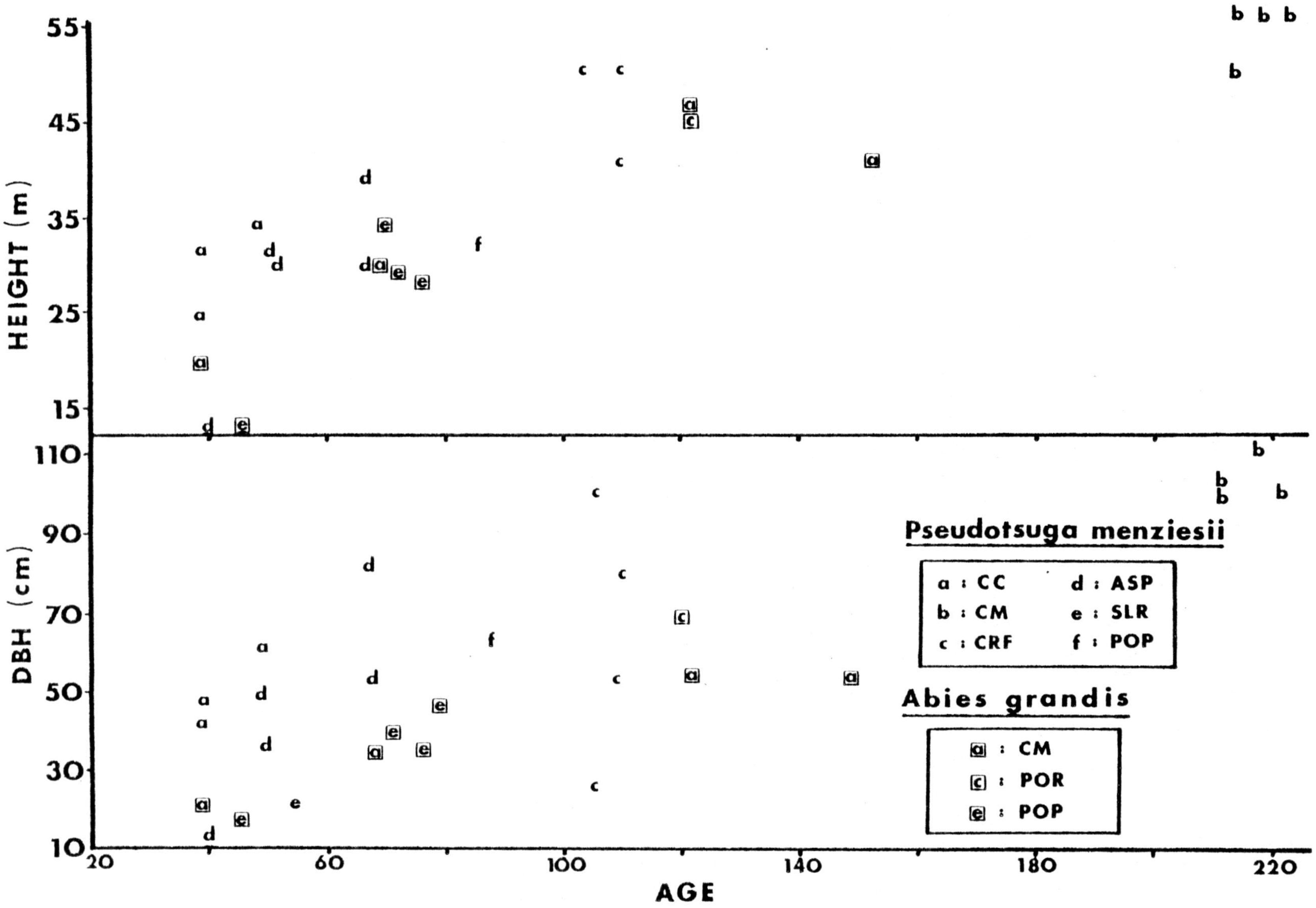

Figure 25. Relationship of height and DBH to age for Abies grandis and Pseudotsuga menziesii.

DISCUSSION

Comments on Methods of Analysis

In a study such as this, it is important to realize that correlation does not mean causality between any of the factors measured. Correlation of species occurrence and soil N or available water does not verify any requirement for such; all may be related to a fourth unmeasured variable. This is clear in light of investigations showing the effect of species on surrounding soils (Alban, 1969; Lodhi, 1977; Zinke, 1962), which imply that existing conditions are not necessarily the same as when the species invaded. However, continuous association with similar environmental conditions, particularly when the conditions correlate with growth, should allow reasonable hypotheses concerning species growth and distribution requirements, providing a basis for more detailed research.

Soil was sampled from the top 10 cm, since the upper horizons have maximum biological activity and N accumulation (Etherington, 1975). Litter was analyzed since it may contain a significant portion of the N stored in some forests (Keeney, 1980). All trees induce a radial systematic change in soil properties, and studies designed to relate soil properties to a particular species must account for the pattern (Lodhi, 1977; Zinke, 1962). In accordance, soil and litter sampling in this study were tree-based, located only under the middle of the crown, to minimize variability.

Three sampling dates cannot accurately describe seasonal fluctuations in the factors measured, and lines between data points in Figures 7-13 in no way imply linear change between dates. In addition, most measurements made in this study may be affected by recent weather (Feller, 1977; Norman, 1955). The short time-span in which samples were taken should make comparisons among plots meaningful. Heavy rain during the September sampling may have raised soil moisture, although this probably had little effect given the high moisture-holding capacity of the forest floor in most stands studied.

An aerobic incubation was used in conjunction with measurement of soil concentrations to assess the relative importance of nitrate and ammonium, and their distribution in soil and litter. Treatment of soil with ammonium-N before incubation was used to determine its potential for nitrification. Incubation for these purposes has been used often in forest systems (Heilman, 1974; Montes and Christensen, 1979; Ohta and Kumada, 1978), and provides a valid index of mineralization capacity (Bremner, 1965; Keeney, 1980). However, since optimum temperature and moisture conditions are used, and interactions with the environment are removed, the mineralization rates measured are potential as opposed to real. This is considered necessary for standard comparison of results, since imitation of natural conditions is impossible (Norman, 1955).

Little relation was seen in this study, as in others (Garm, 1958; Heilman, 1974), between C/N ratio and N mineralization during incubation. Soil at POP and CC, with very high C/N ratios, exhibited vigorous mineralization. Some discrepancy in ratios may be due to overestimation of C by the technique of loss-on-ignition. Charcoal (inactive C) in the samples, loss of CO_3 from calcareous soils, and loss of water from soils with high clay content can give inflated loss-on-ignition estimates of organic matter (Ball, 1964). The latter two problems are probably not significant in most soils I sampled. In addition, loss-on-ignition (500°C) values were converted to C using an equation developed for soils ignited at 375°C (Ball, 1964), so that additional water may have been lost. An alternative explanation of the poor relationship of C/N to mineralization may be that available C/available N ratios (as yet indeterminable) affect microbial activity more directly than the total C/total N ratios determined here (Montes and Christensen, 1979). This may be an important distinction in forests, with highly ligneous litter.

N Availability at the Study Sites

The toposequence at Ash Swamp was related to significant differences in abundance of N in both soil and litter; as well as soil pH, and moisture, Ca, and organic content. Total N and nitrate-N were significantly highest in ASR-2 and lowest in ASP, corresponding to differences in mineralization rates seen in the soil and litter. Ammonium levels were highest in ASR-1 soil, possibly due to lower nitrification activity there than at ASR-2, indicated by incubations. Less nitrification was also indicated by lower nitrate levels in ASR-1 groundwater, and may be related to the low Ca content of ASR-1 soil. Addition of ammonium stimulated nitrification rates in both soil and litter at ASR-1 and ASR-2, in contrast to ASP. Soil and litter at ASP may have intrinsically low nitrification capacity, not related to N availability. The theoretical contribution of N by litter at Ash Swamp is relatively small compared to that of soil (Figure 17). Mineralization rates in ASP litter were extremely low; considerably less litter at ASR-2 potentially contributes more available N than at ASP. Denitrification would be expected to cause a significant loss from ASR-2 during winter flooding (Etherington, 1979), particularly since groundwater appears less oxygenated than earlier in the year (Table 12). This may be reflected by the large decline in soil nitrate and ammonium levels by January, and the absence then of ammonium and nitrate in surface water (Table 12).

Several plants associated with actively nitrifying soils by Krajina (1963) and Garm (1958) grew in ASR-2 or ASR-1, but not in ASP, including *Tiarella trifoliata*, *Tolmiea menziesii*, *Athyrium felix-femina*, and *Galium triflorum*. However, occurrence of *Galium* and *Tiarella* at very low nitrifying sites, such as CRF, indicates little value as indicators in this study.

The plots at Squaw Lake best illustrated the difference between litter under *Thuja* and *Chamaecyparis* on sites with similar soils and associated vegetation. Mineralization rates of *Thuja* litter, particularly nitrification, were considerably greater than *Chamaecyparis*' in all cases, and exceeded most other sites sampled, as well. SLR plots had higher nitrification rates than SLP, but similar nitrate concentrations in soil and litter; this may indicate relatively more uptake of nitrate by Thuja. Difference in the way N is cycled through soils under Thuja and Chamaecyparis is also indicated by the fact that ammonium was taken up by all SLR soils (and by ASR-2 soil) in the January incubation, but not by SLP. Soils or litter in SLP and SLR-3 appeared to continue active nitrification in winter, reflected in nitrate concentrations of groundwater. Underground movement of water here, indicated by its higher oxygenation compared to earlier in the year, may be leaching nitrate from uphill soils. SLR-2 groundwater was continually less oxygenated on all dates, and is probably more subject to continual N losses by denitrification. This may account for consistently lower levels of nitrate in water here than at SLP and SLR-3.

The sites dominated by Thuja and Chamaecyparis in the Port-Orford-Cedar Research Natural Area are quite different with respect to N availability. Total N and mineralization rates were unexpectedly high in POP soil, and were reflected by consistently high soil concentrations of ammonium and nitrate. POR soil had comparatively low N availability. However, POR litter had higher rates of mineralization than POP. Both litter and soil in POR responded consistently to N addition with increased nitrification; POP litter and soil generally did not.

Although CRF has about 30% more total soil N than CM, virtually all measurements of N availability are lower. Static levels of N and mineralization rates of both soil and litter, particularly nitrification, were consistently low in CRF. Litter appears to contribute negligible amounts to the available N pool. Litter N at CM, although limited, is probably significant given the poor N availability in the soil. Soil from both sites responded with vigorous nitrification when ammonium was added, although, as under Chamaecyparis elsewhere, CRF litter did not. Much of the soil N at CRF appears to be unavailable for microbial release, but presence of, or potential for active nitrifying populations in the soil was indicated.

The relatively high total N and availability of N at CC were somewhat unexpected, in light of the other site characteristics measured. Soils are similar to those at POP in most respects (total N, high static levels of nitrate and ammonium, rapid N mineralization), but CC litter showed much more rapid mineralization rates than that under Chamaecyparis at POP. Litter and soil showed little or no stimulation of nitrification on addition of N; in this respect, litter was similar to that under Chamaecyparis.

Relation of N Nutrition to Other Factors

Overall, correlations between availability of soil N (estimated by incubation) and total N concentrations were high (r = .90 [July], .94 [Sept], .64 [Jan])(Figure 14). However, at CRF and CM there was little relationship. Several other factors affect N mineralization rates. Soils with pH 5 or less often show reduced nitrification, which may be related to its requirement for available Ca (Haynes and Goh, 1978; Montes and Christensen, 1979). The C/N ratio of soil also is important, as it affects the competition between heterotrophic and autotrophic bacteria. Normally, when C/N exceeds 20, N released by microbial decomposition is converted into new microbial matter until sufficient C has been respired (Norman, 1955). However, in this study, soil at POP had the lowest pH and Ca content, and a relatively high C/N ratio, but exhibited vigorous nitrification. There was no apparent overall relationship of soil or litter pH, Ca content, or C/N to mineralization rates in incubation.

Others have associated low nitrification in forest soils to inhibitors released by tree litter (Lodhi, 1977; Rice and Pancholy, 1972) and suggest this may be advantageous to the system in terms of conservation of N, as well as energy. In this study, mineralization rates in Chamaecyparis' litter, particularly nitrification, were quite low relative to Thuja. This was not related to the consistent presence of any other species, and may suggest an inhibition of nitrification by

Chamaecyparis. Conservation of N should be advantageous on N-deficient ultramafic soils where *Chamaecyparis* grows over much of its range. Indeed, many plants associated with *Chamaecyparis* on ultramafic soils (*Pinus* spp., ericaceous shrubs) are closely related to plants which have either been shown to prefer ammonium to nitrate as an N source, or which release nitrification inhibitors themselves (Haynes and Goh, 1978; Rice and Pancholy, 1972). This advantage may not be as important to *Thuja*, which normally occurs on higher N soils, as will be shown.

N mineralization rates in litter were high for plots in which *Thuja* occurred, especially when *Alnus rubra* was present. Mineralization rates in soils and litter of mixed *Alnus*-conifer forests (which include *Thuja*) exceed those of pure coniferous forests (Garm, 1958; Bollen and Lu, 1968; Taylor, 1935). However, the differences seen in this study seem more related to presence of *Thuja*, since *Alnus* contributed little to the forest floor in several plots with high nitrification rates.

Seasonal Changes in Soil Chemistry

Soil pH decreased from July to September and then increased in January in most plots. This consistent change among plots indicates a general seasonal trend. Similar fluctuation was reported in soil under several vegetation types (Weaver and Forcella, 1979), and attributed to increased decomposition in the fall, resulting in more CO_2 release. Feller (1977) reported a late summer rise in pH of mineral soil leachate in a *Thuja*-*Tsuga* forest, and speculated that organic acids (leached from above by fall rains) replaced cations on the soil exchange complex. In this study, groundwater generally had its highest NH_4 content and highest pH in September. However, the importance of decomposition as a factor affecting pH is supported by the decline in organic content in most soils; thus both explanations may apply here.

Total soil N appeared to fluctuate seasonally. The increase in

N concentration at ASR-2 between July and September amounted to 780 kg N Ha^{-1} in the top 10 cm of soil, assuming a bulk density of 1.3. This is unlikely under any circumstances. However, no obvious source of variability in the sampling or analytical procedure can account for this. Significant change at this date occurred in only some plots, suggesting measurement technique was not at fault; lack of coincident change in loss-on-ignition seems to eliminate the specific sampling location as a factor.

At least some fluctuation in N levels probably occurred. Ammonification or nitrification capacity increased between July and September in most soils, particularly those which had the largest increase in total N (i.e., ASR-2, CC). The soils with little or no increase in mineralization capacity (CM, ASR-1, SLP) had insignificant increases in total N. Increase in N mineralization is associated with lower C/N ratios (Montes and Christensen, 1979; Norman, 1955), and within this study, correlation of soil total N to N mineralization rates between plots was high, as mentioned above. Soil N mineralization rates in January were relatively low, as was soil N, which declined to July levels. In addition, mineralization rates of litter declined in January, particularly nitrification rates in plots which showed significant increase in soil N in September. It is conceivable that fall rains leached N-rich compounds into the soil, causing a rise in C/N of litter, and increasing the soil N content. Forest floors of sites which support Alnus (such as ASR-2), are particularly rich in N (Tarrant et al., 1951); input from alder and free-living fixation may partially explain the fluctuation in total N.

Other studies have reported N fluctuations exceeding those measured here in Pseudotsuga forest litter (van den Driessche and Webber, 1977) and in organic soil of a Scots pine forest (Usher, 1970). Data from Davy and Taylor (1974) show an increase in N in early fall followed by a decline in two of three grassland soils studied, though no explanation was given.

Although no satisfactory explanation can be given for the magnitude of N fluctuation seen in this study, it is possible that tree-based sampling detected fluctuations not indicative of the soil as a whole. Random sampling of a stand represents conditions overall, but ignores the intimate interaction between trees and the soil.

In most cases soil nitrate and ammonium concentrations were low in September and January, probably due to reduced microbial activity or leaching. However, nitrification appears to occur even in January in Thuja plots at Squaw Lake and Ash Swamp, based on groundwater and soil samples.

A seasonal change in the relationship between mineralization and total N concentrations occurred on a studywide basis, but was most pronounced at Ash Swamp. In July and September, soil N was better correlated to the ammonium-N increase after incubation (r = .89 [July], .76 [Sept.]). In January, the relationship had reversed; N was best correlated to nitrate-N (r = .90), and less to ammonium-N (r = .16) production. The relationship between ammonium-N and nitrate-N mineralization at a site was initially positive, but was negative in January (r = .75 [July], .57 [Sept.], -.18 [Jan.]). It seems that soils with higher total N were better able to maintain or mobilize nitrifying populations in winter, and that ammonium available for nitrification was limited in January (i.e., nitrification rates approached ammonification rates).

Relation of Soils to Other Soils in the Region

Availability of N in southwest Oregon may be low compared to soils farther north. Total soil N in this study ranged from .08 to .37%. Other values reported for southwest Oregon range from .03 to .24%, often for soils under Chamaecyparis (Bullard, 1957; Meyer and Amaranthus, 1979; Plocher, 1977). In contrast, Franklin and Dyrness (1973) report .5% N as representative of the Picea sitchensis zone, in which Thuja commonly occurs near the coast. Bollen and Lu (1968) and Franklin et al. (1968) report a minimum .53% N in soils of the central Oregon coast under pure conifer stands, with much higher levels in soils of mixed broadleaf-conifer stands. Bullard (1957) reports a range of .19 to .64% for coastal Oregon soils.

There are also indications that the portion of *Chamaecyparis'* range sampled in this study may differ from most of its range in terms of nutrient availability. My values for soil Ca are high and Mg values are low compared to those reported for soils under *Chamaecyparis* (Meyer and Amaranthus, 1979). Foliage of *Pseudotsuga* has less N, P, K and Ca, and more Mg where it occurred within *Chamaecyparis'* range, compared to farther north (Zobel and Hawk, 1980). This was attributed to lower availability of those nutrients other than Mg. However, my soil nutrient levels, other than N, show no consistent difference from values for soils under coniferous forests in central coastal Oregon (Bullard, 1957; Franklin *et al.*, 1968) or British Columbia (Feller, 1977). Ultramafic soils in Oregon and California are low in N, Ca, P and Mo, and high in Mg (Walker, 1954), and may have Ca/Mg ratios as low as .09 - .50 (Meyer and Amaranthus, 1979). Mo deficiency may be related to low N in these soils, since N fixation, even in non-ultramafic soils in the Oregon Cascades, appears to be Mo-limited (Warwick Sylvester, personal comm.). *Chamaecyparis* foliage normally reflects properties of the parent material it grows on; trees on ultramafic soils have lower foliar N, K and P, and higher Mg levels than trees on other soils, such as the sedimentary soil at Coquille River Falls RNA. Others have reported relatively high levels of N, P and K in *Chamaecyparis* foliage near my CRF plot, compared to trees on other soils throughout *Chamaecyparis'* range, including ultramafic as well as non-ultramafic soils (Plocher, 1977; Zobel and Hawk, 1980). In contrast, my foliar nutrient values for N, K and Ca at CRF are among the lowest in this study, but are higher than other values reported for *Chamaecyparis'* foliage (Tables 15 and 16).

Soils sampled in this study appear to be transitional between the relatively infertile ultramafic soils in southwestern Oregon and soils farther north; nutrients (including N but excepting Mg) are more available than over much of *Chamaecyparis'* range, but N is low compared to coastal Oregon soils farther north.

Relation of Soil Factors to Local Distribution

Abundant water is a more important requirement for both Chamaecyparis lawsoniana and Thuja plicata than for many northwest conifers. As members of the Cupressaceae, they do not form winter buds; leaves and stem units both are initiated and enlarge in the same growing season, which may partially explain their usual association with a continuous water supply. Water availability is a primary limiting factor for Chamaecyparis lawsoniana (Zobel and Hawk, 1980), restricting its distribution both to the south and the east. It is least topographically limited within the Coquille River drainage, with its marine-influenced climate; this may relate to the occurrence of Thuja here, though it is limited.

In most cases in this study, soils under Thuja were at or near field capacity on all sample dates. Thuja was absent on two soils which were driest in July (ASP, CRF). Litter under Thuja appeared higher in moisture-holding capacity than under Chamaecyparis, as it is compared to Pseudotsuga and Tsuga litter (Minore, 1980). Where moisture may have been limiting, as on the slope at Squaw Lake, Thuja grew only on finer-textured soils with a Bt horizon; this also occurs in forests of the Cascades (C. T. Youngberg, personal comm.). Dominance by Chamaecyparis in the surrounding forest on coarser soils (with similar nutrient availability and other environmental characteristics) indicates it is tolerant of drier soils.

At Ash Swamp and Squaw Lake Thuja was associated with more mild soil temperatures. This probably reflects differences in soil texture and moisture, and not a requirement by Thuja for warmer soils than Chamaecyparis. Moderation of soil temperature by moisture is characteristic of many Chamaecyparis forests (Zobel and Hawk, 1980).

However, Thuja also grows at CM, CC and to a limited extent at POP, which appear to be as dry as ASP and CRF. Associated vegetation in these plots is also similar, and indicates all to be relatively dry sites. Undoubtedly the proximity to the ocean is important at CC, but not at CM. Were it not for Thuja's association with wetter sites within Chamaecyparis' range, CM might be assumed as simply too dry for Chamaecyparis. Others have reported Thuja on very dry soils (Franklin and Dyrness, 1973; Packee, 1976). A reasonable question, then, is whether Thuja's association with wet sites in Chamaecyparis' range is due to its water requirement specifically, or to its requirement for other soil factors often related to moisture, such as available N. My data indicate that availability of N may be of equal importance.

Thuja is often associated with higher soil pH than other conifers (Alban, 1969; Daubenmire, 1953; Forristal and Gessel, 1955; Ovington, 1955), and in this study generally occurred on soils more basic than Chamaecyparis did, on a local basis. Acidity and wetness are associated with organic accumulation, C/N ratio, amount and form of available N and other factors affecting plant nutrition (Etherington, 1975). However, little apparent relationship between pH of litter or soil and any of the soil factors measured was seen on a local basis. Chamaecyparis occurs on soils with a range in pH from 4.2 to 6.3 for soils investigated by Plocher (1977), and 4.8 to 7.1 for a variety of soils in its northern range (Meyer and Amaranthus, 1979), of which the highest values are for ultramafic soils. Therefore, there is no reason to suspect a pH requirement by Chamaecyparis which is any different from Thuja's.

No clear distinction between species occurred in soil organic content; although Chamaecyparis did appear to be associated with higher C/N ratios, differences were small. Organic levels were well correlated to soil water-holding capacity (r = .94), more so than was clay content (r = .58). High organic content may be important for one or both species at well drained sites such as CC or POP. Soils under Thuja with very low organic content were associated with relatively massive litter layers (i.e., POR, SLR-1,2,3); this may indicate importance of the forest floor at these sites for its moisture-holding ability.

Occurrence of Thuja has been associated with relatively high levels of N (Alban, 1969; Forristall and Gessel, 1955; Krajina, 1970;

Larsen, 1940). However, no relation was seen here, with *Thuja* occurring on soils with both the highest and lowest total soil N concentrations. There was a strong relationship between the occurrence of *Thuja* and N-fixing *Alnus rubra* in this study, and those plots which lacked *Alnus* were among the lowest in soil N. Hawk (1977) reported *Thuja* together with *Chamaecyparis* on soils for which parent material was at least partially ultramafic; four of these five plots also included *Alnus*, which could alleviate the usual N shortage in ultramafic soils. Of course, the association of the two may indicate only a common requirement for moist soils, but in an N-deficient region such as *Chamaecyparis*' range, their co-occurrence may take on other significance.

Form and amount of available N are known to have important consequences for growth and distribution of some plants (Stewart *et al.*, 1974). Several conifers prefer ammonium as an N source, including *Pinus radiata*, *P. contorta*, and *Picea glauca* (McFee and Stone, 1968; Bigg and Daniel, 1978). Presence of nitrate reductase in roots has recently been used to indicate ability to assimilate nitrate (Haynes and Goh, 1978); although its presence has not yet been demonstrated in *Thuja* and *Chamaecyparis*, these trees do form mycorrhizal relationships with fungi which possess nitrate reductase (Gerdemann and Trappe, 1974; Ho and Trappe, 1975). Krajina *et al.*, (1973) and Garm, (1958) indicated that *Thuja* and *Pseudotsuga* prefer sites with abundant nitrification. Occurrence of *Tsuga* has been associated with sites which do not exhibit vigorous nitrification (Garm, 1958; Krajina, 1973; Taylor, 1935). The form of N preferred by *Chamaecyparis* is unknown.

In this study, *Thuja* generally occurred on sites with higher N availability, particularly nitrate, either in the soil or the litter. *Thuja* litter at Squaw Lake showed particularly high N mineralization rates, and is probably significant in the development of *Thuja* here, since evidence indicates substantial amounts of N may be absorbed directly from the forest floor (Feller, 1977). *Chamaecyparis* occurred on sites ranging from highest to lowest availability of N, in the latter case where nitrate occurred in negligible amounts; this may indicate less dependance on nitrate as an N source.

Occurrence of *Thuja* at dry sites such as CC, POP and CM, and not at CRF may be related to N availability. Especially at POP, soil moisture, pH and Ca availability are low, not consistent with presence of *Thuja* elsewhere in *Chamaecyparis*' range. The only factor which appears favorable for *Thuja* at POP is the high availability of N. No evidence suggests compensation for drought susceptibility in *Thuja* by N-availability. However, under conditions of drought, root elongation is reduced, thus reducing the amount of available water (Kozlowski, 1968). Since water is required for ion transport into the rhizosphere, absorption in dry soils is limited to nutrients within the range of diffusion. A plentiful supply of available N, such as occurs at POP, would help to offset one effect of drying soil. Foliar nutrient data for both *Thuja* and *Chamaecyparis* at POP indicate ion uptake may be severely limited, perhaps by availability or soil moisture. Foliar N in *Thuja* appears to be near the lower limit of its tolerance, although *Chamaecyparis* occurs with considerably lower foliar-N on ultramafic soils. It may be that high N availability is a critical factor in *Thuja*'s presence at POP (and CC), given the apparent stressful conditions there, as well as other cases where it is reported on dry soils. Poor availability of N at CRF may contribute to absence of *Thuja*.

In August, 1979, considerable disruption of soils at CM occurred due to logging; CM is in Camas Mountain State Park. Since the topsoil and litter at this site were among the lowest studied with respect to available N, removal of these should have somewhat greater effect on N availability for revegetation than on more fertile sites. Based on these results, it is unlikely that *Thuja* will be able to reestablish in the disturbed areas for some time.

Occurrence of *Tsuga* and *Pseudotsuga* did not appear to be related to any factor concerning N availability or nitrification rates.

Importance of *Chamaecyparis* and *Thuja* was also related to differences in soil K, Ca and Ca/Mg ratios. Some serpentine-adapted plants require less Ca than non-serpentine plants (Main, 1974); foliar data from other sources indicate *Chamaecyparis* can tolerate considerably lower foliar Ca levels than *Thuja* (Table 16). In contrast, abundant Ca is important to the nutrition of *Thuja* (Gessel, *et al.*, 1951; Krajina, 1970). *Thuja* has been associated with relatively high Ca/Mg ratios elsewhere (Feller, 1977). Its association with abundant Ca may be related to its apparent preference for soils in which nitrification is vigorous.

The unexpected occurrence of *Chamaecyparis* at CC corresponds with the low soil Ca/Mg ratio here. Nutrient content and texture of soil in the clearcut under *Chamaecyparis* seedlings is nearly identical to that at POP (Table 10 and 15). Conceivably, the marine-basalt found on this ridge is related to the occurrence of *Chamaecyparis*, as opposed to its absence in surrounding Roseburg Formation sediments. On the other hand, the low Ca content of soil in the clearcut (compared to soil sampled in the plot) may be associated with absence of *Thuja* seedlings there.

Other factors may affect the distribution of these trees. *Chamaecyparis* is considerably more tolerant of fire than either *Thuja* or *Tsuga* (Hawk, 1977; Minore, 1980); this may be a factor in the scarcity of *Thuja* at POP, or *Chamaecyparis*' importance at other sites showing evidence of burning. Allelopathic antagonism between *Thuja* and *Chamaecyparis* seems possible, given their aromatic foliage and wood (Erdtman and Norin, 1966). Aromatic compounds associated with *Thuja*'s wood are known to inhibit some plants (Minore, 1980). However, their intimate relationship in some stands indicates this was not a significant factor.

Relation of Soil Factors to Growth

Regression of growth rates on various factors indicated that age, soil Ca concentration and % clay significantly explained 37% of the variability in growth of *Thuja*. Clay may be important in moisture availability, soil CEC, and its interaction with Ca and N retention, factors which were related to *Thuja*'s local distribution. Although not included in the regression, N availability seemed to be a factor in the growth of *Thuja* on these sites. A soil N concentration of .3%, greater than most levels measured here, is known to be a primary limiting factor to growth of *Thuja* in British Columbia forests (Feller, 1977). In this study, growth was best at CC and SLR-3, with relatively abundant nitrate and ammonium, either in the soil or litter, and poorest at CM and POR, where availability of N was low; other factors varied inconsistently. Growth of *Thuja* at ASR-2 should have been good, given the high nutrient availability, but may be stunted by factors related to periodic inundation. Even so, growth is considerably better than *Chamaecyparis*' here (indicated by both basal area and foliage increments) and better than in *Thuja* at nearby ASR-1, corresponding to differences in nutrient availability, particularly nitrate. Reduced growth at SLR-1 and SLR-2 corresponds to reduced soil moisture and excessive competition, respectively, since other factors differ little from SLR-3. The oldest overstory *Thuja* in SLR-2 appear to be growing as well as trees in SLR-3. Its reduced growth in POP, given the high N availability there, is perhaps explained by deficiency of moisture or soil Ca.

Others have associated forests at Coquille River Falls RNA with good growth of *Chamaecyparis* and with a high nutrient availability compared to its range in general (Hawk, 1977; Plocher, 1977; Zobel and Hawk, 1980). However, CRF was my poorest site for growth of *Chamaecyparis*, and among the poorest in nutrient availability, particularly N. Growth of *Chamaecyparis lawsoniana* has been correlated with increased foliar concentrations of K, N, P and Ca (Leyton, 1955; Plocher, 1977). In most cases in this study, foliar K, N and P concentrations increased with increased growth; my lowest foliar concentrations of N and P, and among the lowest in K, occurred in *Chamaecyparis* at CRF, and highest values at SLP. In contrast, foliar Ca and Mg tended to show a negative relationship to growth (i.e., highest in CRF foliage, low or lowest at SLP). K and P concentrations were low at CC, which showed best growth in *Chamaecyparis*; this may be due to foliar sampling of trees a distance away from those measured for growth. It may also be due to increased ability to utilize K for growth in these trees, an adaptation apparently exhibited by populations of Chamaecyparis growing north of Coos Bay (Plocher, 1977).

Of the soil nutrients measured, available soil N (particularly nitrate) appeared to relate most to foliar concentrations as well as to growth in Chamaecyparis, reflected by the growth regression.

Based on the relationship between nitrate availability and growth of both Chamaecyparis and Thuja, and the nitrification potential shown by the N-deficient soils at CRF and CM, it seems reasonable to expect that fertilization with N might result in improved growth of Chamaecyparis and Thuja at these sites, although other factors need to be considered. A similar response in Pseudotsuga forests to N fertilization has been correlated to production of available N during incubation of those soils (Shumway and Atkinson, 1977).

Growth of Tsuga, Pseudotsuga and Abies grandis appeared to follow the same relationship as that of Thuja and Chamaecyparis, being highest in nitrate and ammonium-rich soils at CC and POP, and lowest in the less fertile soils at CRF and CM. Pseudotsuga also shows good growth in DBH at ASP, where nitrate is not very available. However, its growth in height appears stunted here, possibly related to the high water table. In contrast, Chamaecyparis reached its greatest height here. Thus, the contention that Pseudotsuga grows best with the presence of, and Tsuga best with the absence of nitrate or nitrification in soils (Krajina, 1973) was not entirely supported.

Relation of Soil Factors to Overall Distribution

This study suggests that the primary limiting factors for Thuja within Chamaecyparis' range are water and N availability, with possible factor compensation between these. Higher soil Ca and Ca/Mg ratios are also related to occurrence of Thuja. Although both Thuja and Chamaecyparis occupy wetter sites in southwestern Oregon and northern California, Thuja is probably limited to a subset of Chamaecyparis' range, i.e., those sites with sufficient availability of N and Ca. Growth of Thuja on sites where the two species occurred together in this study usually equaled or exceeded Chamaecyparis' in older trees. Also, ranges of foliar nutrient concentrations were generally narrower than in Chamaecyparis, and mostly within the range reported by others (Table 17). This seems to indicate Thuja's site requirements are more specific, but when conditions are suitable for its occurrence, it outgrows Chamaecyparis. At Squaw Lake Thuja forms relatively pure stands, but at POP, where conditions appear marginal for establishment, it remains a minor stand member; even there it appears to grow as well as Chamaecyparis. The situation appears similar to that of Chamaecyparis nootkatensis, which is outgrown by Thuja and other conifers even on good sites (Harris and Farr, 1974). As a result, Thuja seems to be limited more overall by site physical factors rather than by competition from Chamaecyparis.

In contrast, Chamaecyparis' tolerance for varying conditions of soil pH, and water, N and Ca availability seem to rule these out as factors limiting its northern distribution. Higher foliar K, and apparently lower Ca/Mg ratios, which were related to differences in soils, may indicate relatively higher requirements for K and Mg than in Thuja. Although increased Mg availability did not seem to affect its growth, some serpentine-adapted plants require higher external Mg to maintain internal levels (Main, 1974). Absence of Chamaecyparis in the soil adjacent to SLP, and at CM, both low in Mg, suggest Mg may be limiting as levels decrease outside of the range of Chamaecyparis.

No factor measured, besides soil Mg, appeared to differentiate CM from the sites in Chamaecyparis' range. Foliar Mg level in Thuja here is at the bottom of the deficiency range determined by Walker et al. (1955), and below most reported for the species (Table 16). Ca/Mg ratio in both soil and Thuja's foliage is considerably higher than any reported for Chamaecyparis or for soils on which it occurs. CM was the only soil sampled which developed on Flournoy Formation sediments. Chamaecyparis' northeastern boundary seems to follow the occurrence of Flournoy sediments as mapped by Baldwin (1974), and Hawk (1977) makes no mention of *Chamaecyparis* on this geological formation. Although the Flournoy is often combined with the Tyee Formation, there is some question whether the two originated from the same source. Conceivably, there may be a difference in soils (specifically, Mg content) associated with these formations, the investigation of which might yield information pertaining to *Chamaecyparis*' northern limit.

Obviously, any large scale difference in soils associated with difference in geological formation is hypothetical at this time, and the exclusion of *Chamaecyparis* from any particular parent material does not seem likely (Zobel and Hawk, 1980). However, the evidence presented here seems to be consistent with the hypothesis that a residual ultramafic influence in the Eocene sediments covering *Chamaecyparis*' northern range contributes to its occurrence there (Zobel and Hawk, 1980).

The simplest explanation (and one which the data most support) is that as conditions improve for growth farther north, growth of *Chamaecyparis* is less affected than that of *Thuja* or other species; and it is eliminated by competitive exclusion. Thus, its restriction would be indirectly related to soils and their influence on competition. The same situation occurs in the southern part of its range, where properties of ultramafic soils reduce competition by *Pseudotsuga* and other species, probably leading to increased importance of *Chamaecyparis* (Zobel and Hawk, 1980).

It seems that conditions which optimize *Chamaecyparis*' growth (increased availability of nitrate and other nutrients) may indirectly reduce its importance by similarly affecting other species. Both *Chamaecyparis* and *Thuja* appeared to be growing well where they were studied here. Fowells (1965) reported an average *Chamaecyparis* at 100 years is 27 cm DBH, and *Thuja* at 80 years is 23 cm DBH; in this study (on the basis of regression equations for all trees less than 100 years old) average *Chamaecyparis* at 100 years was 34 cm DBH, and *Thuja* at 80 years was 43 cm DBH. Thus, *Chamaecyparis*' fatal flaw seems to be its intrinsically low growth rate compared to other species under most conditions. This may be due to greater apportionment of resources to canopy development rather than stem development compared to other species (Thuja), as seen here. However, Chamaecyparis lawsoniana fills an important niche on soils where some species, including Thuja, apparently cannot survive. Based on this study, it is doubtful that Thuja would ever be a major component of forests on ultramafic soils, or at sites comparable to CRF or ASP, where both moisture and N availability are limited. Thuja is thus unlikely to replace the Chamaecyparis which is lost to disease or forest management practices.

LITERATURE CITED

Alban, D. H. 1969. The influence of western hemlock and western redcedar on soil properties. Soil Sci. Soc. Amer. Proc. 33:453-457.

Baldwin, E. M. 1964. Geology of Oregon, second edition. Univ. of Oregon Coop. Bookstore, Eugene. 165 p.

Baldwin, E. M. 1974. Eocene stratigraphy of southwestern Oregon. Ore. Dep. Geol. Min. Res. Bull. 83. 40 p.

Ball, D. F. 1964. Loss-on-ignition as an estimate of organic matter and organic carbon in noncalcareous soils. J. Soil Sci. 15(1): 84-92.

Beaton, J. D., A. Moss, I. MacRae, J. W. Konkin, W. P. T. McGhee and R. Kosik. 1965. Observations on foliage nutrient content of several coniferous trees in British Columbia. For. Chron. 41:222-236.

Berg, M. G. and E. H. Gardner. 1978. Methods of soil analysis used in the soil testing lab at Oregon State University. Special Report 321, Agric. Exp. Sta., Oregon State Univ., Corvallis.

Bigg, W. L. and T. W. Daniel. 1978. Effects of nitrate, ammonium and pH on the growth of conifer seedlings and their production of nitrate reductase. Plant and Soil 50:371-385.

Bollen, W. B. and K. C. Lu. 1968. Nitrogen transformations in soils beneath red alder and conifers, pp. 141-148. In J. M. Trappe, J. F. Franklin, R. F. Tarrant and G. M. Hansen (ed.). Biology of alder. Pac. Northw. For. Range Exp. Sta., Portland, Oregon.

Bolsinger, C. L. 1979. Western redcedar--a forest resource in transition. USDA For. Serv. Res. Bull. PNW-85, 24 p.

Booth, R. L. and R. F. Thomas. 1973. Selective electrode determination of ammonia in water and wastes. Envir. Sci. Tech. 7:523-526.

Bremner, J. M. 1965. Total nitrogen, Ch. 83 of Methods of soil analysis, Part 2. Agron. Monogr. 9, Amer. Soc. Agron., Madison, Wisconsin. pp. 1149-1176.

Bullard, W. E. (ed.). 1957. An introduction to the forest soils of the Douglas-fir region of the Pacific Northwest. Western Forestry and Conservation Association, Portland, Oregon. 215 p.

Challinor, D. 1968. Alteration of surface soil characteristics by four tree species. Ecology 49(2):286-290.

Cox, G. W. 1972. Lab manual of general ecology, second edition. W. C. Brown Co.

Crooke, W. M., A. H. Knight and J. Keay. 1964. Mineral composition, cation exchange properties and uronic acid content of various tissues of conifers. For. Sci. 10:415-427.

Daubenmire, R. 1953. Nutrient content of leaf litter of trees in the northern Rocky mountains. Ecology 34:786-793.

Daubenmire, R. 1968. Plant communities. A textbook of plant synecology. Harper and Row, New York.

Davy, A. J. and K. Taylor. 1974. Seasonal patterns of nitrogen availability in contrasting soils in the Chiltern Hills. J. Ecol. 62:793-807.

Dawson, M. D. 1977. Mediated instruction in soil science. Oregon State Univ. Bookstores, Inc., Corvallis.

Erdtman, H. and T. Norin. 1966. The chemistry of the order Cupressales. Fortschr. Chem. Organ. Naturstoffe 24:207-287.

Etherington, J. R. 1975. Environment and plant ecology. John Wiley and Sons, New York.

Feller, M. C. 1977. Nutrient movement through western hemlock-western redcedar ecosystems in southwest British Columbia. Ecology 58:1269-1283.

Forristall, F. F. and S. P. Gessel. 1955. Soil properties related to forest cover type and productivity on the Lee forest, Snohomish County, Washington. Soil Sci. Soc. Amer. Proc. 19:384-389.

Fowells, H. A. (Compiler). 1965. Silvics of forest trees of the United States. USDA For. Serv. Agr. Handbook 271, 762 p.

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

Franklin, J. F., C. T. Dyrness, D. G. Moore and R. F. Tarrant. 1968. Chemical soil properties under coastal Oregon stands of alder and conifers, pp. 157-172. In J. M. Trappe, J. F. Franklin, R. F. Tarrant and G. M. Hansen (ed.). Biology of alder. Pac. Northw. For. Range Exp. Sta., Portland, Oregon.

Franklin, J. F., F. C. Hall, C. T. Dyrness and C. Maser. 1972. Federal research natural areas in Oregon and Washington. A guidebook for scientists and educators. USDA For. Serv. Pac. Northw. For. Range Exp. Sta., Portland, Oregon.

Friend, D. T. C. 1961. A simple method of measuring integrated light values in the field. Ecology 42:577-580.

Garm, R. 1958. Some aspects of the nitrogen cycle in soil of the Douglas-fir forest. M. Sc. Thesis, Univ. of British Columbia, 97 p.

Gerdemann, J. W. and J. M. Trappe. 1974. The Endogonaceae in the Pacific Northwest. Mycol. Mem. 5:1-76.

Gessel, S. P., R. B. Walker and P. G. Haddock. 1951. Preliminary report on mineral deficiencies in Douglas-fir and western redcedar. Soil Sci. Soc. Amer. Proc. 15:364-369.

Griffin, J. R. and W. B. Critchfield. 1972. The distribution of forest trees in California. USDA For. Serv. Res. Paper PSW-82, 114 p.

Harris, A. S. and W. A. Farr. 1974. The forest ecosystem of southeast Alaska. 7. Forest ecology and timber management. USDA For. Serv. Gen. Tech. Rep. PNW-25, 109 p.

Haynes, R. J. and K. M. Goh. 1978. Ammonium and nitrate nutrition of plants. Biol. Rev. 53:465-510.

Hawk, G. M. 1977. Comparative study of temperate Chamaecyparis forests. Ph. D. Dissertation, Oregon State Univ., Corvallis, 195 p.

Heilman, P. 1974. Effect of urea fertilization on nitrification in forest soils of the Pacific Northwest. Soil Sci. Soc. Amer. Proc. 38:664-667.

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

Ho, I. and J. M. Trappe. 1975. Nitrate reducing capacity of two vesicular arbuscular mycorrhizal fungi. Mycologia 67:886-888.

Keeney, D. R. 1980. Prediction of soil nitrogen availability in forest ecosystems: a literature review. For. Sci. 26(1):159-171.

Kozlowski, T. T. (ed.). 1968. Water deficits and plant growth, Vol. II. Academic Press, New York.

Krajina, V. J. 1963. Ecology of the forests of the Pacific Northwest. Progress Report. Univ. British Columbia, 97 p.

Krajina, V. J. (ed.). 1970. Ecology of forest trees in British Columbia. In Ecology of western North America, 2(1):1-146.

Krajina, V. J., S. Madoc-Jones and G. Mellor. 1973. Ammonium and nitrate in the economy of some conifers growing in Douglas-fir communities of the Pacific Northwest of America. Soil Biol. Biochem. 5(1):143-147.

Larsen, J. A. 1940. Site factor variations and resources in temporary forest types in northern Idaho. Ecol. Mon. 10:2-53.

Lawton, E. 1971. Moss flora of the Pacific Northwest. Hattori Botanical Laboratory, Japan, 362 p., 195 pl.

Leyton, L. 1955. The influence of heather mulching on the growth and nutrient status of Lawson cypress. Forestry 28:147-151.

Little, E. L. Jr. 1971. Atlas of United States trees. Conifers and important hardwoods. USDA For. Serv. Misc. Pub. 1146, 9 p. (313 maps, folio).

Lodhi, M. A. K. 1977. The influence and comparison of individual forest trees on soil properties and possible inhibition of nitrification due to intact vegetation. Amer. J. Bot. 64(3):260-264.

Lowe, L. E. 1972. Aspects of chemical variability in forest humus layers under a mature western hemlock-western redcedar stand. Can. J. For. Res. 2:487-489.

Main, J. L. 1974. Differential response to magnesium and calcium by native populations of Agropyron spicatum. Amer. J. Bot. 61:931-974.

McFee, W. W. and E. L. Stone. 1968. Ammonium and nitrate as nitrogen sources for Pinus radiata and Picea glauca. Soil Sci. Soc. Amer. Proc. 32:879-884.

McLean, A. and W. D. Holland. 1958. Vegetation zones and their relationship to the soils and climate of the upper Columbia Valley. Can. J. Plant Sci. 38:328-345.

Meyer, L. and M. P. Amaranthus. 1979. Siskiyou National Forest soil resource inventory, review copy. USDA For. Serv. Pac. Northw. Reg.

Minore, D. 1968. Effects of artificial flooding on seedling survival and growth of six northwestern tree species. USDA For. Serv. Res. Note PNW-92, 12 p.

Minore, D. 1970. Seedling growth of eight northwestern tree species over three water tables. USDA For. Serv. Res. Note PNW-115, 8 p.

Minore, D. 1972. Germination and early growth of coastal tree species on organic seed beds. USDA For. Serv. Res. Paper PNW-135, 18 p.

Minore, D. 1979. Comparative autecological characteristics of northwestern tree species--a literature review. USDA For. and Range Exp. Sta. Gen. Tech. Rep. PNW-87, 72 p.

Minore, D. (1980). Western redcedar (Thuja plicata Donn). USDA For. Serv. Publication, PNW Exp. Sta. Corvallis, Oregon. (In preparation).

Minore, D. and C. E. Smith. 1971. Occurrence and growth of four northwestern tree species over shallow water tables. USDA For. Serv. Res. Note PNW-160, 9 p.

Minore, D., C. E. Smith and R. F. Woollard. 1969. Effects of high soil density on seedling root growth of seven northwestern tree species. USDA For. Serv. Res. Note PNW-112, 6 p.

Montes, R. A. and N. L. Christensen. 1979. Nitrification and succession in the Piedmont of North Carolina. For. Sci. 25(2):287-297.

Norman, A. G. (ed.). 1955. Advances in agronomy. Academic Press, New York.

Ohta, S. and K. Kumada. 1978. Studies on the humus forms of forest soils. Soil Sci. Plant Nutr. 24(1):41-54.

Orion Research Inc. 1974. Instruction manual ammonia electrode 95-10. Orion Research Inc., Massachusetts, 23 p.

Orion Research Inc. 1978. Analytical method guide, 9th ed., December. Orion Research Inc., Massachusetts, 49 p.

Ovington, J. D. 1956. The composition of tree leaves. Forestry 29(1):22-28.

Packee, E. C. 1976. An ecological approach toward yield optimization through species allocation. Ph. D. Thesis, Univ. of Minnesota, 740 p. + appendix.

Plocher, M. D. 1977. Growth and nutrient content of *Chamaecyparis lawsoniana* from contrasting soils in Coos County, Oregon. M. S. Thesis, Oregon State Univ., Corvallis, 72 p.

Proctor, J. 1971. The ecology of serpentine: II. Plant response to serpentine soils. J. Ecol. 59:397-410.

Rice, E. L. and S. K. Pancholy. 1972. Inhibition of nitrification by climax ecosystems. Amer. J. Bot. 59(10):1033-1040.

Roth, L. F., H. H. Bynum and E. Nelson. 1972. *Phytophthora* root rot of Port-Orford-cedar. USDA For. Ser. Pest Leafl. No. 131, 7 p.

Sharpe, G. W. 1974. Western redcedar. Univ. of Washington Printing Co., Seattle.

Shumway, J. S. and W. A. Atkinson. 1977. Measuring and predicting growth response in unthinned stands of Douglas-fir by paired tree analysis and soil testing. Washington State Dep. Nat. Resourc., DNR Note 15, 10 p.

Soil Survey Staff, USDA. 1951. Soil survey manual. Wash. D. C., 503 p.

Steel, R. G. D. and J. H. Torrie. 1960. Principles and procedures of statistics. McGraw Hill Co., New York.

Stewart, G. R., J. A. Lee, T. O. Orebamjo and D. C. Havill. 1974. Ecological aspects of nitrogen metabolism, pp. 41-47. *In* R. L. Bieleski, A. R. Ferguson and M. M. Cresswell (ed.). Mechanisms of regulation of plant growth. Bull. 12, Roy. Soc. New Zealand, Wellington.

Sudworth, G. B. 1907. Forest trees of the Pacific slope. USDA For. Ser. Wash. D. C., 441 p.

Tarrant, R. F., L. A. Isaac and R. F. Chandler, Jr. 1951. Observations on litter fall and foliage nutrient content of some Pacific Northwest tree species. J. For. 49:914-915.

Taylor, R. F. 1935. Available nitrogen as a factor influencing the occurrence of Sitka spruce and western hemlock seedlings in the forests of southeastern Alaska. Ecology 16(4):580-601.

U. S. Dept. Commerce, Nat. Ocean. Atmospher. Admin. 1979-1980. Climatological data. Various issues.

Usher, M. B. 1970. Pattern and seasonal variability in the environment of a Scots pine forest soil. J. Ecol. 58:669-679.

van den Driessche, R. and J. E. Webber. 1977. Seasonal variations in a Douglas-fir stand in total and soluble nitrogen in inner bark and root and in total and mineralizable nitrogen in soil. Can. J. For. Res. 7:641-647.

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

Walker, R. B., S. P. Gessel and P. G. Haddock. 1955. Greenhouse studies in mineral requirements of conifers: western redcedar. For. Sci. 1:51-60.

Weaver, T. and F. Forcella. 1979. Seasonal variation in soil nutrients under six Rocky mountain vegetation types. Soil Sci. Soc. Amer. J. 43:589-593.

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

Youngberg, C. T. 1958. The uptake of nutrients by western conifers in forest nurseries. J. For. 56:337-340.

Zinke, P. J. 1962. The pattern of influence of individual forest trees on soil properties. Ecology 43(1):130-133.

Zobel, D. B. (unpub.). Twig elongation patterns of Chamaecyparis lawsoniana.

Zobel, D. B. and G. M. Hawk. 1980. The environment of Chamaecyparis lawsoniana. Amer. Midl. Natur. 103(2):280-297.

Zobel, D. B. and V. T. Liu. 1979. Foliar nutrient concentrations of small Chamaecyparis in Taiwan. Plant and Soil 53:373-384.