DISTRIBUTION AND ABUNDANCE OF TERRESTRIAL AND ARBOREAL LICHENS IN THE OLD-GROWTH CONIFEROUS FORESTS OF THE WESTERN CASCADES OF OREGON, WITH SPECIAL REFERENCE TO NITROGEN-FIXING SPECIES

by

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I. INTRODUCTION

Lichens are a conspicuous component of moist coastal forests west of the crest of the Cascade Mountains from northern California to southern Alaska, a region referred to here as the Pacific Northwest or PNW. Lichens are of interest in this region not only because of their abundance, estimated to be up to one to two metric tons per hectare in mature forests (Edwards et al. 1960; Pike 1971; Pike et al. 1972), but also because several common species fix atmospheric nitrogen (Pike 1973; Pike et al. 1976).

In general, lichens are composed of two organisms--the mycobiont (a fungus) and the phycobiont (an alga)-- which live together in a symbiotic relationship. Some lichens have three symbionts: fungus; green alga; and blue-green alga. Lichens may be referred to as cyanophiles if they contain a blue-green alga or as non-cyanophiles if they contain only a green alga.

If the phycobiont is a blue-green alga of the genus *Nostoc*, then the lichen may be assumed to possess the ability to fix atmospheric nitrogen (Millbank and Kershaw 1970). Several lichen species containing blue-green phycobionts other than *Nostoc* have also been demonstrated to fix nitrogen.

The nitrogen is fixed by the primary phycobiont if the *Nostoc* occurs in a continuous layer throughout the lichen thallus (plant body) or by the secondary phycobiont if the *Nostoc* is concentrated in internal or external cephalodia (nodes).

Since nitrogen is commonly a limiting nutrient in forest communities, management of nitrogen input will be an important tool in forest practices of the future. In addition to, or possibly instead of, applying industrially-fixed nitrogen, it may be desirable to manage the nitrogen input biologically. Cyanophilous lichens appear to play an important role in the nitrogen cycle at the ecosystem level in the Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) region (Pike et al. 1972; Pike 1978).

An understanding of the abundance and distribution of lichens is essential to determine the role of lichens in any given ecosystem, to gain a perspective on their management potential, and to identify their relationship to vascular plant distributions. Several studies of lichen distribution in the PNW have been published: on the scale of individual trees, lichen distributions have been studied on old-growth Douglas fir in the Andrew's Experimental Forest in the western Cascades of Oregon (Pike et al. 1972, 1975, 1977); on the scale of closely adjacent stands, Pike (1971) studied epiphytic lichens in an oak forest in the Willamette Valley of Oregon and Pechanec and Franklin (1968) conducted a study of the epiphytic lichens in stands of red alder (*Alnus rubra* Bong.) at

Cascade Head on the north-central Oregon coast; and on the scale of stands within a broad region are two studies of epiphytic lichens on the Olympic Peninsula in Washington (Brown et al. 1956; Hoffman and Kazmierski 1969) and Szczawinski's (1953) study of lichens living on bark and decaying wood substrates in the Douglas fir forests of Vancouver Island in Canada. None of these studies have made cross-stand comparisons of total lichen abundance, but instead have compared quantities of lichens present on specific portions of host trees (e.g. lower trunk, upper trunk, and branches).

The present distributional study was performed on a scale of forest stands and involves both epiphytic and ground-dwelling lichens. Although age of the stand is clearly an important factor in determining the distribution of lichens, that factor is not considered here and quantitative observations were limited to a set of mature forest stands. This study was undertaken on the H.J. Andrews Experimental Forest near Blue River, Oregon (hereafter referred to as the AEF) as part of a research program attempting to determine the significance of these lichens in the nitrogen cycle of the Douglas fir forests.

The objectives of this study were:

1) to determine what species of cyanophiles occur in AEF
2) to determine the habitat and substrate requirements of these lichens
3) to determine the quantitative distribution of the cyanophiles in the AEF

4) to determine whether lichens are index species to vegetational zones and/or community types
5) to determine which environmental factor(s) are important in the distribution of the lichen flora
6) to determine the biomass and potential for nitrogen fixation by lichens in the AEF

Both cyanophiles and non-cyanophiles were sampled in this study with emphasis on the cyanophiles. The non-cyanophilous species were studied in the hope that they would prove useful as predictors of the distributions of cyanophilous species. The sampling was performed in a variety of communities and habitats found within the AEF.

The cyanophilous and non-cyanophilous lichens include both terrestrial and arboreal species. The biomass of terrestrial lichens can be sampled directly, but the complexities of sampling arboreal species make direct measurements impractical when sampling several stands of trees. Since there is a considerable "rain" of lichen material from the canopy onto the forest floor, the presence of lichens in the canopy can be deduced from an examination of the litter. Furthermore, it is reasonable to assume that even though turnover rates for lichens both in the canopy and in the litter may vary from stand to stand, the abundance of epiphytic litter on the forest floor reflects the abundance of lichens in the canopy. Although epiphytic lichens have different patterns of dispersion over portions of host trees from one stand to another, sampling

of the epiphytic litter gives an integrated picture of biomass and species content of the lichen flora for the whole canopy.

These biomass data for each site were compared and correlated with a wide variety of environmental factors to detect patterns which might help explain the observed lichen distributions. The data gathered in this study were supplemented by environmental data gathered on the AEF by the United States Forest Service and the International Biological Program. This data base provided considerable resources on soils, meteorology, fire history, community types, and the composition of vascular plant flora.

Analysis of the distributional data suggested that the heavy condensation and reduced evaporation in the valley bottoms creates moister conditions for the canopy lichens than at adjacent higher elevations. The relationships of these conditions to lichen distributions were explored by sampling lichens and measuring candensation drip and evaporation along a transect traversing the Lookout Creek Valley in the AEF.

II. DESCRIPTION OF THE STUDY AREA

A. The H.J. Andrews Experimental Forest

The H.J. Andrews Experimental Forest, the site chosen for this study, is located in the central western Cascades near the town of Blue River, Oregon, at 44° 15' North Latitude and 122° 10' West Longitude (Figure 1). It is located approximately sixty-five kilometers east-northeast of Eugene. The AEF is the Oregon Intensive Study Site of the Coniferous Forest Biome, U.S. International Biological Program and also is an Experimental Ecological Reserve.

The AEF is a well-defined watershed bounded by ridges on the east, the south, and the northwest. It encompasses an area thirteen by nine kilometers. The major stream in the watershed is Lookout Creek, of which McRae and Mack Creek are tributaries draining the areas to the north and south of Lookout Creek, respectively (Figure 2).

Located in the older, more eroded western Cascades, the slopes are generally steep with basalt outcrops on the ridges. Elevation ranges from 500 m at the mouth of the watershed to 1600 m at Carpenter Mountain in the northeastern corner of the watershed. The alpine glaciation of the Pleistocene was the main shaping force in the past (Fred Swanson, pers. comm.) The

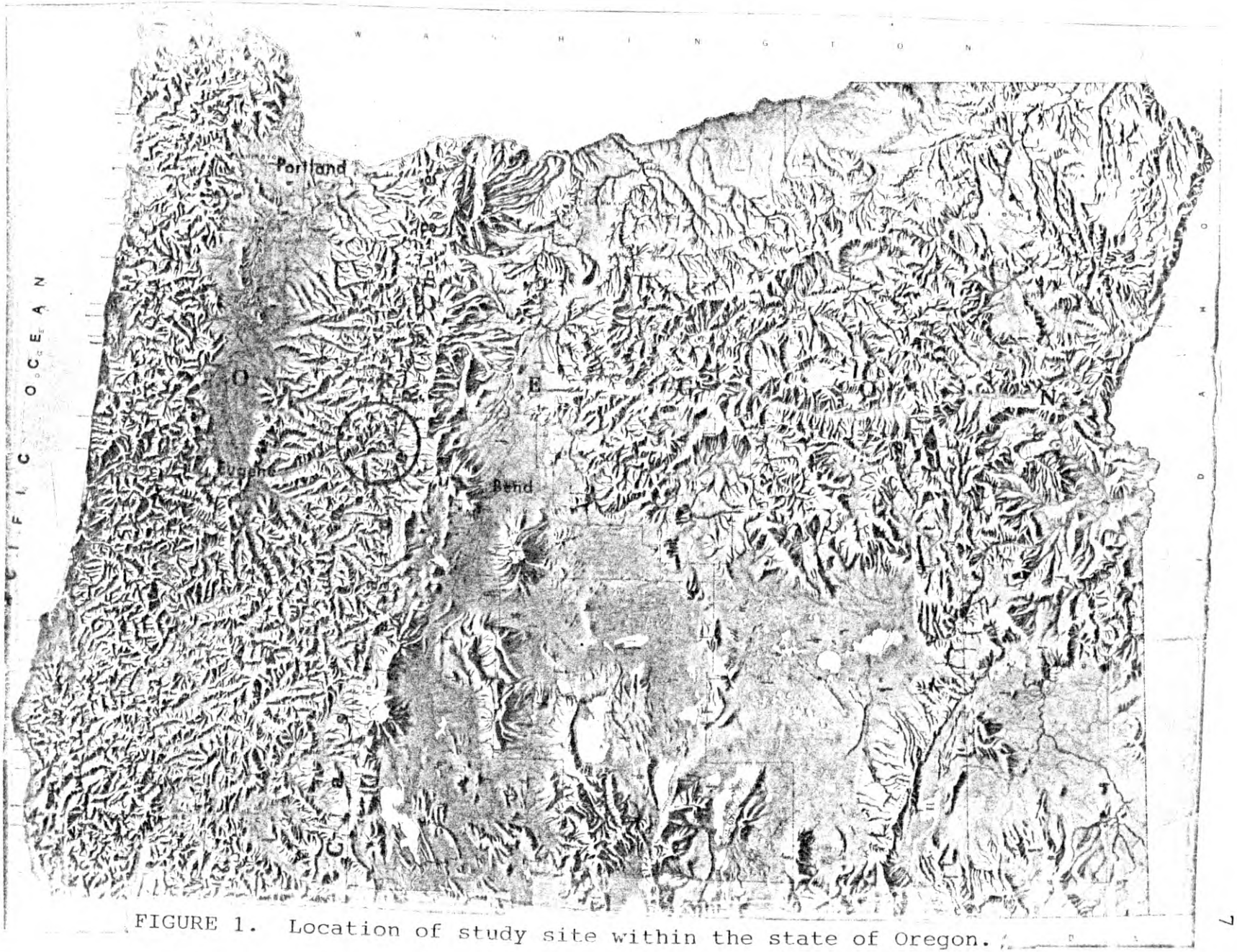


FIGURE 1. Location of study site within the state of Oregon.

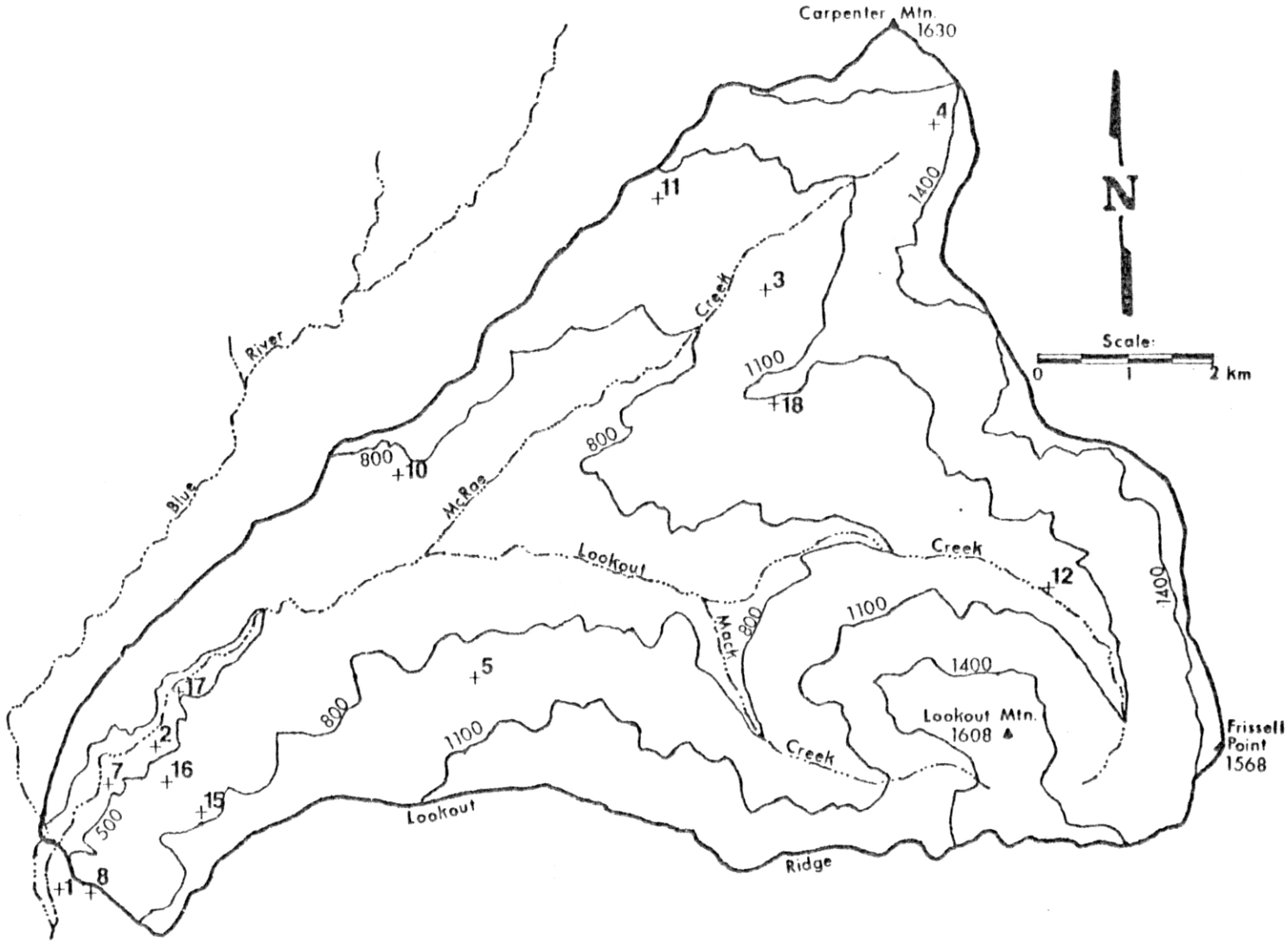


FIGURE 2. H.J. Andrews Experimental Forest. The location of each reference stand is indicated by a (+) and its appropriate reference stand number. Reference stand 13 and 14 are located approximately 7 km to the north-northeast of Carpenter Mountain in the Wildcat Mountain Natural Research Area. Contours are at 300 m intervals.

major present-day erosional processes are those resulting from mass wasting and stream action.

Mapping and description of twelve soil series was done on the AEF (Stephens 1964). These soils have been conveniently grouped into six soil associations (Dyrness et al. 1974).

1) At low elevations along major streams, alluvial soils occupy the terrace positions.
2) At lower elevations on moderate slopes, reddish brown and yellowish brown lateritic soils are found in residuum and colluvium from tuff and breccia bedrock and are generally silt loam to silty clay loam in texture.
3) At low elevations on steep slopes, lithosols and regosols are found with poorly developed profiles and lack B horizons.
4) At higher elevations in landslide areas, soils are generally regosols developed from andesite having weak profile development and textures ranging from loam to sandy loam.
5) At higher elevations on slopes, lithosols derived from andesite or basalt are dark brown or black silt loams.
6) On the high ridges, brown podzolic soils are loam textured and are derived from andesite or basalt.

A maritime climate with mild rainy winters and warm dry summers characterizes the AEF. Figure 3 presents the average annual temperature and precipitation for the AEF Central

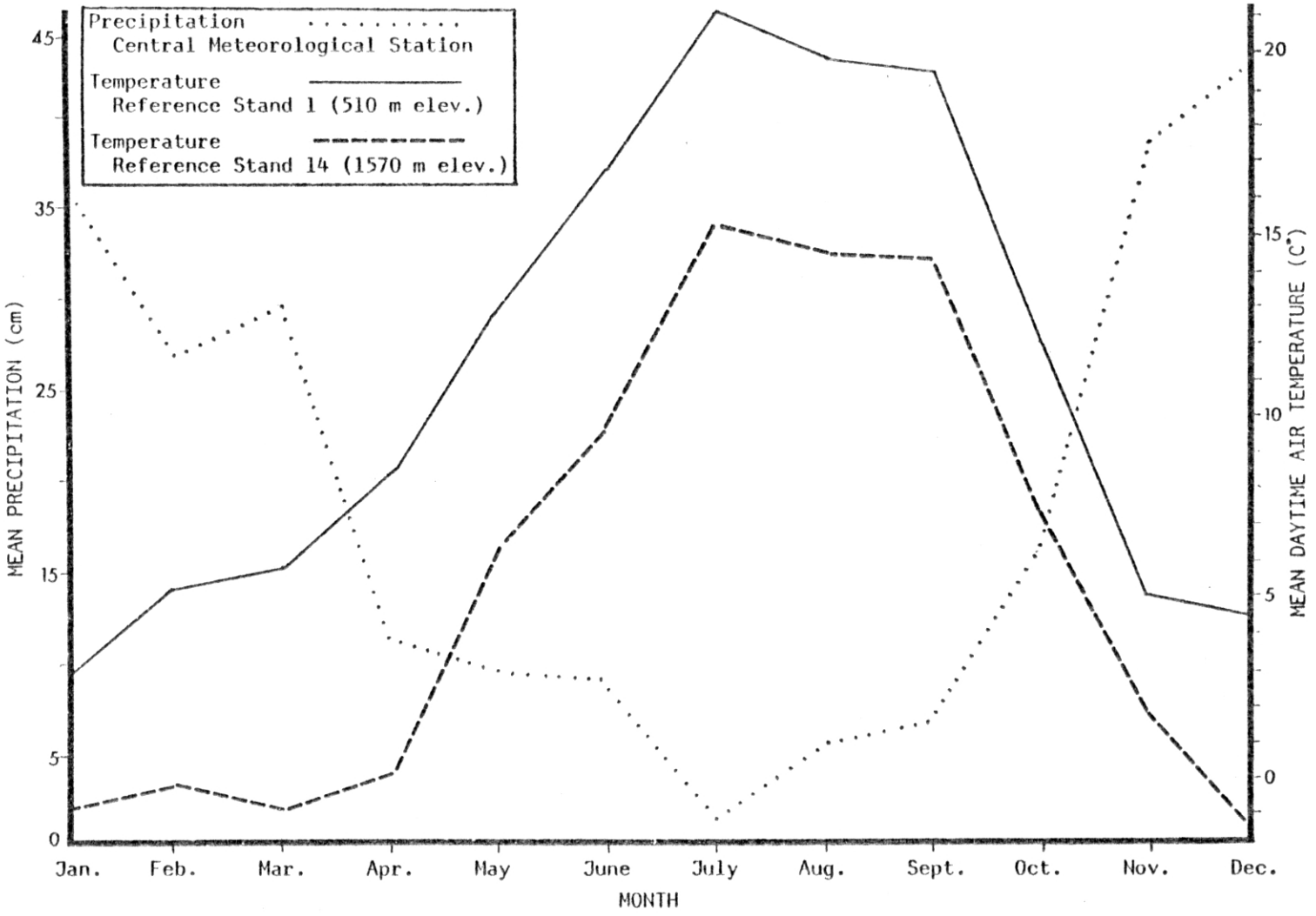


FIGURE 3. Mean monthly precipitation and daytime air temperatures for the H.J. Andrews Experimental Forest, Blue River, Oregon (1973-1977).

Meteorological Station. At the low elevation sites the January mean temperature is approximately 2° C and the July mean is approximately 20° C. At high elevation sites the January mean temperature is approximately -1.5° C with a July mean of approximately 15° C. Extreme temperatures range from -17° C to 38° C. Average annual precipitation at low elevations is about 2300 mm and may exceed 2500 mm on the ridges. At high elevations in the *Abies amabilis* (Dougl.) Forbes zone, snow accumulations average from 1-3 m with amounts of snowfall decreasing at lower elevations (Dyrness et al. 1974).

B. The Reference Stands

As in most forests of the western Cascades, three major vegetation zones are represented in the AEF: the *Tsuga heterophylla* (Raf.) Sarg. zone; a transition zone; and the *Abies amabilis* zone (Dyrness et al. 1974). A series of modal or typical sites have been selected for each plant community type and designated as reference stands (Zobel et al. 1976). These stands have been set aside for research purposes and have been intensively studied since 1971. A wealth of background information has been collected since that date (Table I and Appendix III) thus making these stands ideal sites for the objectives of this study. These reference stands are located on or immediately adjacent to the AEF with the exception of two (#13 and #14), which are located in the Wildcat Mountain Research Natural Area, approximately eight kilometers northwest of the

TABLE I. Characteristics of reference stands in the H.J. Andrews Experimental Forest, Blue River, Oregon. Species names of plants in the community names are given in Table II. (from Zobel et al. 1976)

Zone	Reference Stand no.	Community	Elevation (m)	Aspect	Slope (°)	Percent Cover			
						Tree			
						Mature	Reproducing	Shrub	Herb
Tsuga heterophylla	1	*Pseudotsuga/Holodiscus*	510	SW	35	50	20	46	36
	2	*Tsuga/Rhododendron/Berberis*	520	NW	20	105	10	30	24
	7	*Tsuga/Polystichum-Oxalis*	490	NW	18	110	42	17	41
	8	*Pseudotsuga-Tsuga/Corylus*	500	W	40	81	25	64	27
	10	*Tsuga/Rhododendron/ Gaultheria*	670	SSW	5	89	60	118	7
	11	*Pseudotsuga/Acer/Berberis*	1060	SSE	25	96	35	62	10
	15	*Tsuga/Polystichum*	720	NW	45	108	43	14	18
	16	*Tsuga/Castanopsis*	670	SW	40	107	48	108	7
	17	*Tsuga/Rhododendron/ Berberis*	530	NNW	18	102	47	43	37
Transition	3	*Tsuga-Abies/Linnaea*	950	SW	10	120	88	38	24
	5	*Tsuga-Abies/Rhododendron/ Berberis*	920	N	8	90	27	125	5
	18	*Pseudotsuga/Acer/Whipplea*	1080	SE	30	81	24	92	23
Abies amabilis	4	*Abies/Tiarella*	1440	SW	10	116	50	9	39
	12	*Abies/Vaccinium/Cornus*	1020	W	5	103	31	56	33
	13	*Abies/Clintonia*	1480	S	15	93	20	12	32
	14	*Abies-Tsuga/Xerophyllum*	1570	NW	15	100	27	3	33

AEF (Figure 2).

A prerequisite for the selection of the reference stands was that they be free from direct human disturbances such as those which result from logging or the use of heavy equipment. However, this does not exclude natural catastrophic events that may have occurred in the past, such as mass movement, insect and disease damage, windfall or wildfires. Although information concerning these natural disturbances is not usually available, evidence of wildfire occurences on the AEF have been mapped and studied by Dr. Fred Swanson at Oregon State University.

Based on ground surveys of fire scars and interpretation of aerial photography, Dr. Swanson has been able to map the date and extent of major natural burns in the study area. Findings from his studies show that wildfires have left timber stands of two general age classes, either 130 or 530 years of age (Fred Swanson, pers. comm.). All reference stands fall into the 530 year-old age class, with the exception of reference stand eleven which is in the 130 year-old age class. Figure 4 shows the history of fire disturbance in the AEF, as reconstructed by Swanson. However, my personal observations indicate that reference stands 10 and 18 were also affected by the 1850 fire.

Pseudotsuga menziesii usually dominates in the 530 year-old stands, averaging 120-140 cm dbh and 45-75 m in height, with timber volumes averaging 350-750 m^3 ha^{-1} (Dyrness et al. 1974). Although reference stand 11 is in the *Tsuga heterophylla* zone, it is also dominated by *Pseudotsuga menziesii.*

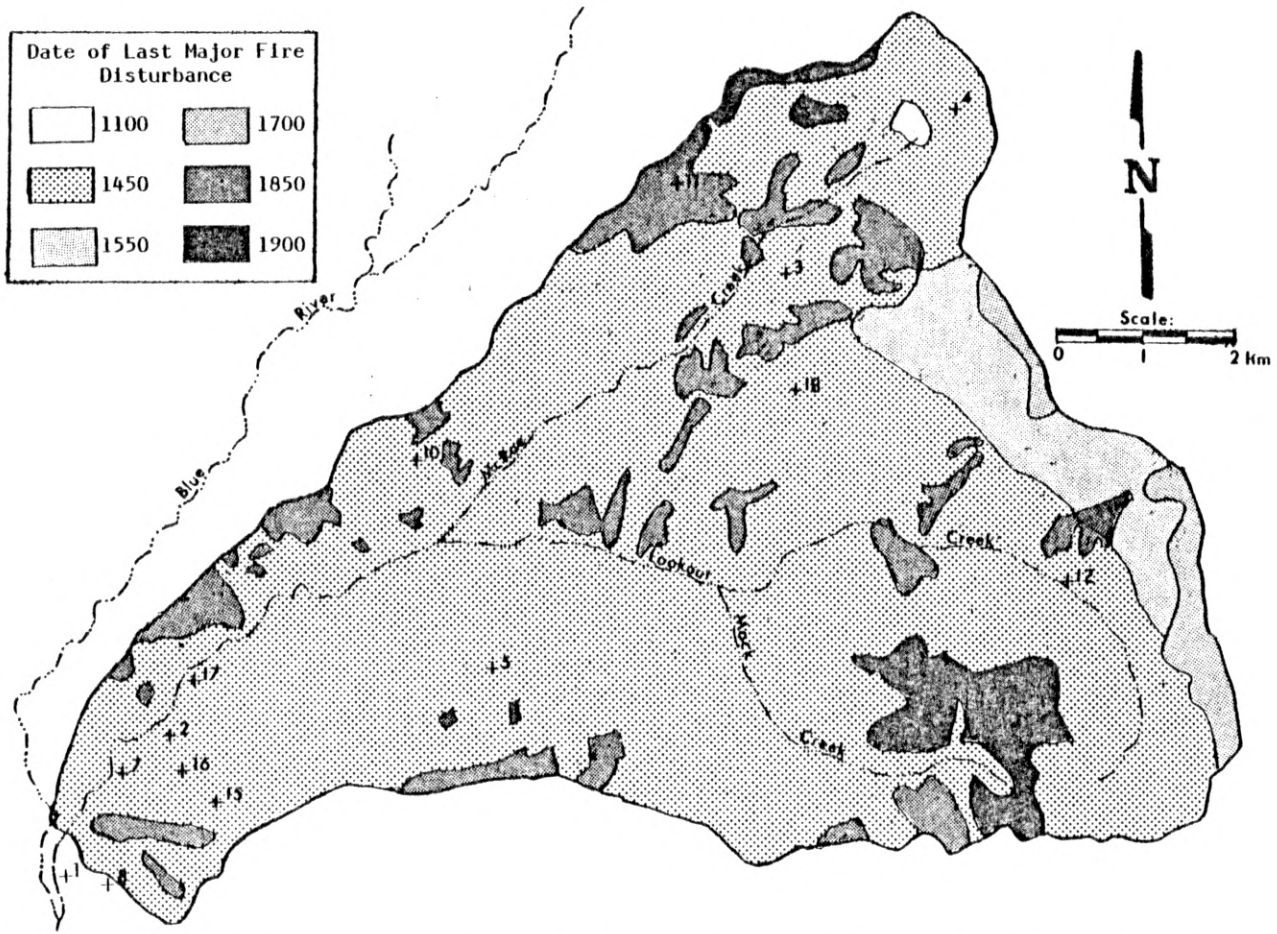


FIGURE 4. History of major fire disturbance in the H.J. Andrews Experimental Forest (from Fred Swanson, unpublished). The location of each Reference Stand is indicated by a (+) and its appropriate reference stand number.

Vegetation integrates the effects of the climate, soils, topography, and disturbances and, therefore, is an extremely important segment of the ecosystem. Dyrness et al. (1974) hypothesized the placement of the reference stands with axes of temperature and moisture (Figure 5).

In the *Tsuga heterophylla* zone, which occupies an approximate elevational range of 500-900 m , *Pseudotsuga menziesii* is climax in the dry sites with *Tsuga heterophylla* being the dominant climax species in that zone. Eight community types are represented by reference stands within this zone: seven climax associations and one seral community. These vegetation classifications were bypothesized to span a moisture gradient which ranges from the *Pseudotsuga menziesii/Holodiscus discolor* (Pursh) Maxim. community type at the dry end to the *Tsuga heterophylla/Polysticum munitum* (Kaulf.) Presl/*Oxalis oregana* Nutt. community type at the moist end of the gradient. The community occurring on the median site is *Tsuga heterophylla/Rhododendron macrophyllum* G. Don /*Berberis nervosa* Pursh.

The transition zone lies roughly between 900 and 1100 m elevation. Community types of this zone are represented by three reference stands: two climax associations and one seral community. All three have been placed in a fairly moist section of the moisture gradient.

The *Abies amabilis* zone occurs approximately between 1100 and 1500 m elevation with *Abies amabilis* dominating the climax stands except at the highest elevation site, where *Tsuga mertensiana* (Bong.) Carr. shares the dominance.

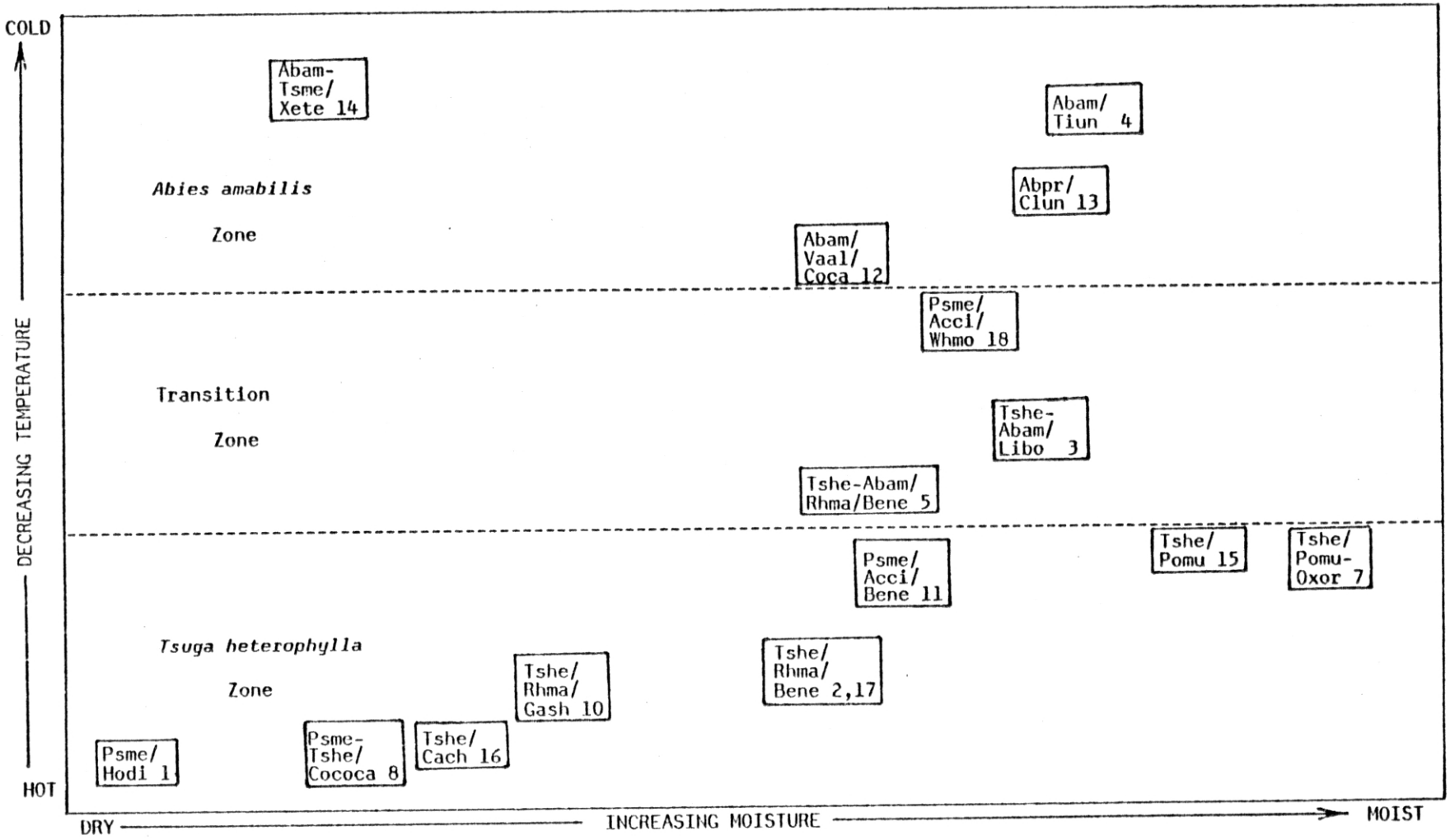


FIGURE 5. Hypothesized relative positions of vascular plant communities in the H.J. Andrews Experimental Forest on axes of temperature and moisture (from Dyrness et al. 1974). Communities enclosed with dashed borders are considered to be seral, the others, climax. The size of the box has no meaning. The numbers correspond to the reference stand. Abbreviations for communities are identified in TABLE II.

TABLE II. Forest communities sampled in this study. Communities determined by Dyrness et al. (1974).

	Community Name	Abbreviation	Reference Stand No.
Tsuga heterophylla zone	*Pseudotsuga menziesii/Holodiscus discolor*	Psme/Hodi	1
	Pseudotsuga menziesii-Tsuga heterophylla/Corylus cornuta	Psme-Tshe/Coco	8
	Tsuga heterophylla/Castanopsis chrysophylla	Tshe/Cach	16
	Tsuga heterophylla/Rhododendron macrophyllum/Gaultheria shallon	Tshe/Rhma/Gash	10
	Tsuga heterophylla/Rhododendron macrophyllum/Berberis nervosa	Tshe/Rhma/Bene	2,17
	Pseudotsuga menziesii/Acer circinatum/ Berberis nervosa	Psme/Acci/Bene	11
	Tsuga heterophylla/Polystichum munitum	Tshe/Pomu	15
	Tsuga heterophylla/Polystichum munitum-Oxalis oregana	Tshe/Pomu-Oxor	7
Transition zone	*Tsuga heterophylla-Abies amabilis/ Rhododendron macrophyllum/Berberis nervosa*	Tshe-Abam/Rhma/ Bene	5
	Tsuga heterophylla-Abies amabilis/ Linnaea borealis	Tshe-Abam/Libo	3
	Pseudotsuga menziesii/Acer circinatum/ Whipplea modesta	Psme/Acci/Whmo	18
Abies amabilis zone	*Abies amabilis-Tsuga mertensiana/ Xerophyllum tenax*	Abam-Tsme/Xete	14
	Abies amabilis/Vaccinium alaskense/ Cornus canadensis	Abam/Vaal/Coca	12
	Abies procera/Clintonia uniflora	Abpr/Clun	13
	Abies amabilis/Tiarella unifoliata	Abam/Tiun	4

Abies procera Rehder is the dominant species in the seral community. Four community types are represented by reference stands in this zone with three of them being considered climax and one seral. The *Abies amabilis-Tsuga mertensiana/Xerophyllum tenax* (Pursh) Nutt. association was hypothesized to occupy the driest site in this zone, while the *Abies amabilis/Tiarella unifoliata* (Hook.) Kurtz. association was thought to occupy the wettest site. The median site here is the *Abies amabilis/Vaccinium alaskaense* Howell/ *Cornus canadensis* L. association. Monitoring of the soil and air temperatures and plant moisture stress on the reference stands has now been carried out and has produced results which in general support these hypothesized relationships (Zobel et al. 1976). The only major difference was that Zobel et al. failed to find the hypothesized gradient in moisture stress in the *Abies amabilis* zone.

III. DISTRIBUTION OF LICHENS IN THE REFERENCE STANDS

A. Methods

The reference stands, 50 meters square, are located within homogeneous areas of specific community types and are designated by stakes placed around the perimeter of each stand at 10 meter intervals. In order to avoid the disturbances that may have occured within the reference stands themselves during the course of past studies, lichens were sampled just outside the perimeter of each reference stand.

Sample data were taken in 28 quadrats (½ x 1 m) in each of the 16 reference stands using a systematic random sampling design. The number and size of the quadrats was determined from reconnaissance surveys with the aim of keeping the standard error of the biomass estimates within 20-25% of the total. The ease and practicality of transporting the sampling paraphernalia and placing quadrats on steep and brushy terrain was also a factor in determining the quadrat size.

From each stake (6 on each side of the reference stand) a distance of ten meters was measured away from the reference stand in a direction perpendicular to the line in which the stakes were located. From that point a random distance and direction were determined from a random numbers table, between 1 and 3 meters (at ½ m intervals) and 0° to 180° (at 45° intervals)

respectively. At that point, a 1 x ½ m polyethylene quadrat was placed on the ground with a predesignated corner over the randomly selected point, keeping the long axes of the quadrat parallel to the randomly determined direction. Also, at each corner stake a distance of 14 meters would be measured in a direction 45° from the line that the stake is in and the same procedure as explained above would be utilized to randomly locate the placement of the quadrat. In all, there were 28 sample plots per reference stand; 6 on each side and 1 at each corner (Figure 6). All of the 16 reference stands were sampled during a seven-week period between October 6, 1976 and November 24, 1976.

Lichens exhibit three main growth forms: 1) crustose (crust-like); 2) foliose (leaf-like); and 3) fruticose (shrub-like). These growth forms are represented both among the epiphytes and among the ground-dwellers. Because of the difficulties encountered in detecting their presence and in classifying them, crustose species were not dealt with unless they were cyanophiles. Only two cyanophilous crustose genera were sampled: *Parmeliella* spp.; and *Pilophoron* spp. For inventory purposes, any cyanophilous lichens observed in the course of sampling was noted even if it was not quantitatively sampled.

The area covered (in square centimeters) by each species of terrestrial lichen and each species of arboreal lichen litter was estimated for each quadrat. Area estimates were also made of the percentage of the quadrat covered by bare soil, rock,

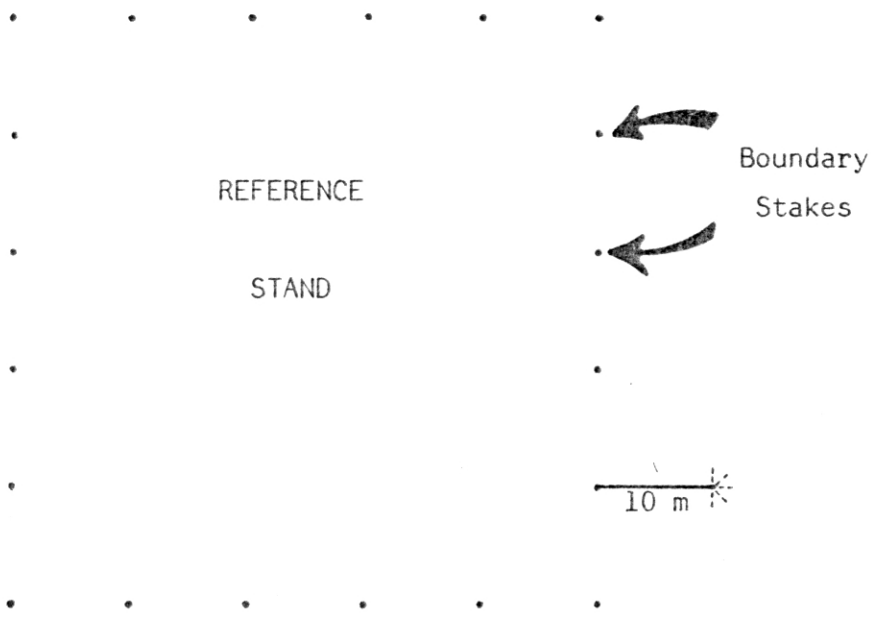


FIGURE 6. Diagram of the sampling procedure used in this study. At a point 10 m from each stake, a random number determined the direction from a straight line in which the quadrat would be placed (straight ahead, 45 to the right, 45 to the left, 90 to the right, or 90 to the left). A second random number determined the distance away from this point that the quadrat was placed (1 m, 1.5 m, 2 m, 2.5 m, or 3 m).

bare wood (> 2 cm diameter), moss, needles, and leaves.

A crude visual estimate of the percent cover of the canopy was made by imagining a 3 meter diameter cylinder extending vertically from the quadrat through the canopy. By standing in the middle of this "cylinder" and looking straight up, the percentage of the area not covered by leaves and allowing light to penetrate was estimated. Canopy cover was then 100 minus the percentage of area not covered. Other environmental data taken at each quadrat included: slope; aspect; the distance to, diameter of and species of the closest tree; and the distance to, height of and species of the closest shrub. The measurements taken on the closest tree and shrub were used to calculate basal area and density. For the purposes of this study, a tree was defined as being greater than 10 cm dbh; and a shrub as any woody plant.

In roughly half the quadrats (selected randomly with $P = 0.5$) all the lichens that were found within the quadrat were collected. These were later cleaned, sorted by species, and weighed. The weight values were then used to convert the area estimates of the non-collected quadrats into a biomass value.

The angle by which each quadrat frame deviated from the horizontal was measured with the aid of a self-leveling protractor mounted on a 1 meter aluminum frame. For purposes of comparison it was necessary to convert all the area estimates of the lichen cover, in each quadrat, to the "horizontal".

This was done by computing a slope correction factor which equals the average of the cosine of the measured slopes for all quadrats at each reference stand. The total area covered by lichens in $m^2\ ha^{-1}$ (X) estimated from the 28 quadrats was then divided by the mean slope correction factor for the reference stand.

$$\text{slope correction factor (F)} = n^{-1} \sum_{i=1}^{28} \cos \theta_i$$

$$\text{corrected area cover} = X\ (F)^{-1}\ ,$$

where θ_i is the slope of the i^{th} quadrat.

Because the weight to area relationships vary greatly from species to species and within species from site to site, area estimates were converted to weight estimates to enable comparisons between species and sites. As was mentioned before, in approximately half of the quadrats, selected randomly, all the lichens found within the quadrat were collected. They were then dried, cleaned and weighed.

Area to weight ratios were calculated for each species in each of the sampled quadrats using the following ratio:

$$\hat{R} = \bar{y}\ (\bar{x})^{-1}\ ,$$

where $\bar{x}$ and $\bar{y}$ are the mean of the areas and weights for the species in the subsampled quadrats. For these data sets this ratio has been found to be essentially unbiased (Pike 1978). The total weight ($\hat{Y}$) of a species for a reference stand is estimated as :

$$\hat{Y} = \hat{R}\ X\ (F)^{-1}\ .$$

The standard error (SE) of the total weight estimate has been approximated as:

$$(SE)\ (Y) = R\ (F)^{-1}\ SE\ (X)\ ,$$

where X is the total of the lichen cover estimated from the 28 quadrats. SE computed by this simple formula is underestimated by 3-5% (Pike 1978).

A simple method was used to estimate total area and density of trees for each reference stand. This "closest individual method" (Cottom and Curtis 1956) requires measuring the distance from each sampling point to the closest tree. Species identification and circumference of the tree were also recorded. Total tree density (D) is calculated as:

$$D_{(\#trees\ ha^{-1})} = \frac{10{,}000_{(m^2\ ha^{-1})}}{4\ \bar{d}^2_{(m)}}\ ,$$

where $\bar{d}$ is the mean of the distances from sampling points to their closest tree. Total basal area (BA) is given as:

$$BA_{T(m^2\ ha^{-1})} = D_{(\#trees\ ha^{-1})}\ x\ \overline{BA}_{(m^2 tree^{-1})},$$

where $\overline{BA}_{(m^2\ tree^{-1})}$ is the mean of the basal areas of all of the trees measured.

An index reflecting the importance of each tree species in each reference stand was computed by summing the basal areas of all trees of that species measured at the reference stand. This tree "area index" weights equally the mean basal area for that species at that site and the relative density of that species at that site.

For an index to the shrub cover, the height (H) and distance (d) to the closest shrub was measured. The mean height was divided by the mean distance squared for a relative index to the shrub cover (SC):

$$SC = \frac{\bar{H}}{\bar{d}^2} \quad .$$

The analysis of the variation in lichen abundance from site to site was attacked in three main phases: 1) regression analysis on lichens versus non-biological factors; 2) regression analysis on lichens versus biological factors; and 3) more intensive regression analysis on the most important lichen species versus the more significant of the non-biological factors.

All the biomass data used in the regression analysis were obtained from measurements made during the course of this study. The biological factors that were measured in this study were: the distance to and the circumference of the closest tree; the total basal area and density per hectare; the distances to the closest shrub and the shrub cover index; the canopy cover estimate; and the area indices for all the tree species. Those lichens which occurred in fewer than three reference stands and had a collective biomass that totaled less than ½ kg ha^{-1} for the sixteen reference stands were eliminated from the regression analysis.

The remainder of the data on biological factors used in the regression analysis were obtained from two additional studies.

The data on the percent cover of the vascular plants and the variable referred to as "Zobel's canopy cover" were taken from Zobel et al. (1976). The data on the total percent cover of moss and the percent cover of *Stokesiella oregana* (Sull.) Robins. were taken from the study of David Sawbridge (unpublished).

In addition to the biological variables, many of the non-biological variables that were used in the regression analysis were measured during the course of this study. These variables include: the average aspect; the average quadrat slope; the vertical distance from the closest stream; and the percent cover of bare soil. The average aspect was calculated from a circular distribution transformation formula (Zar 1974).

Three other studies contributed data on the non-biological variables used in the regression analysis. Brown and Parsons (1977) provided data on such factors as pH of the A1 horizon, base saturation of the A1 horizon, and contents of exchangeable calcium and nitrogen for the soils in each reference stand. Temperature and radiation information were obtained from the IBP data bank; missing data were estimated by regression analysis. The Temperature Growth Index (TGI) and Plant Moisture Stress (PMS) data came from Zobel et al. (1976), except for reference stand 18 the location of which was approximated by Bill Emmingham (pers. comm.). The TGI was computed from a temperature summing formula which weights the soil and air temperatures taken according to their effect on the production of seedling growth. The PMS was taken from pressure chamber

readings on twigs of understory conifers in each reference stand. Also obtained from Zobel et al. (1976) were data on elevation, slope and aspect for each reference stand.

The regression analysis was performed on the IBM 360-50 and, with the use of a statistical package from Western Michigan State University, on the PDP-10 at the University of Oregon Computer Center.

The reference stands were compared on the basis of similarities of their lichen floras. Since biomass of epiphytic litter was estimated to be an order of magnitude lower than the biomass of canopy lichens, total biomass of epiphytic lichens was approximated by multiplying epiphytic litter values by a factor of ten. A matrix of similarity coefficients based on the lichen biomass was created after the actual lichen biomass values were normatized to relative biomass values. This was done by setting the total lichen biomass found at each reference stand equal to 100 and converting each individual species value as a percentage of 100.

$$\text{Relative Biomass of Species A} = \frac{\text{(Biomass of Species A)}}{\text{(Biomass of all Species)}} \times 100.$$

Coefficients of similarity were calculated from the following formula:

$$C = \frac{2w}{a+b} \times 100 \ ,$$

where a and b are the biomass values for all the lichens found in the two standsto be compared and w is the sum of the lesser

value for those species common to the two stands (Kershaw 1973). Since data were normatized, C = w. Thus, if two stands were identical, a, b and w would all be equal and C would equal 100.

Similarity coefficients were then placed in a matrix and seriated. Seriation involves..."the placing of item in a series so that the position of each best reflects the degree of similarity between that item and all other items in the data set" (Johnson 1968). This arrangement results in stands with high similarity being placed next to one another and those with low similarity far from one another, with the final placement arrived at by trial and error.

Then, from these 120 coefficients of similarity, an ordination of the reference stands was done based on their dissimilarity (Mueller-Dombois and Ellenberg 1974). Each coefficient of similarity was subtracted from a maximum similarity value of 100 to obtain the dissimilarity coordinates. The two most dissimilar stands were chosen as the endpoints of an axis 100 units in length. The position of the other stands was determined by rotating two arcs representing the distance of the dissimilarity coordinates from each of the endpoint reference stands respectively and projecting the point of arc intersection perpendicularly onto the axis. A second axis may be constructed using as endpoints two reference stands which are in close proximity to each other on the first axis, but which are separated by a great interstand difference. The remaining stands are positioned following the same procedure as given for the first

axis.

The above analyses, seriation and ordination, deal with similarities between stands based on their lichen floras. The resulting arrangement may provide insight into the nature and strength of important environmental gradients affecting distribution of the lichens.

It is also useful to examine the similarities between lichen species, based on their distributions among the stands. Analysis of association between lichens was conducted by computing Tau (Kendall 1948) for each pair of species. Tau is based on the similarity in the distribution of rank orders of biomass values among reference stands. Rarely encountered species were not included in this analysis. When Tau is computed for any pair of species, only those stands which contain at least one of the two species are included. In other words, sampling zeros are excluded.

B. Results and Discussion

1. Floristic Survey of Nitrogen-fixing Lichens

A total of forty-six species of ground-dwelling and epiphytic cyanophiles were observed in the AEF during this study. Habitat information given for these lichens in Table III and Appendix I represents a synthesis of observations made in this study as well as in other studies (Pike 1972; Pike et al. 1975). The majority of these cyanophilous lichens contain *Nostoc*.

TABLE III. Nitrogen-fixing lichens of the H.J. Andrews Experimental Forest. These lichens have a primary or secondary phycobiont containing either *Nostoc* or some other heterocystous blue-green alga capable of fixing atmospheric nitrogen.

	Substrate				Habitat		
Lichen species	Soil	Rock	Moss	Bark	Aquatic	Terrestrial	Epiphytic
Hydrothyria venosa		x			x		
Koerberia sonomensis		x				x	
Leptochidium albociliatum	x	x	x			x	
Leptogium californicum	x		x			x	
L. lichenoides	x		x			x	
L. palmatum	x		x			x	
L. platynum	x					x	
L. rivale		x			x		
L. sinuatum			x			x	x
L. tenuissimum		x				x	
Lobaria oregana				x			x
L. pulmonaria				x			x
L. scrobiculata				x			x
Massalongia carnosa		x				x	
Nephroma bellum				x			x
N. helveticum				x			x
N. laevigatum				x			x
N. parile			x	x		x	x
N. resupinatum				x			x
N. sp. (yellow, undescribed)				x			x
Parmeliella cyanolepra	x	x				x	
P. microphylla		x				x	
P. saubinetii	x	x	x	x		x	x
Peltigera aphthosa	x		x	x		x	x
P. canina	x					x	
P. collina		x	x	x		x	x
P. leucophlebia	x		x			x	x
P. membranacea	x		x			x	
P. polydactyla			x			x	
P. praetextata	x					x	
P. rufescens	x					x	
P. spuria	x					x	
P. venosa	x	x				x	
Pilophoron acicularis		x				x	
P. clavatus		x				x	
Placopsis gelida		x				x	
Polychidium muscicola			x			x	
Pseudocyphellaria anomala				x			x
P. anthraspis				x			x
P. crocata				x			x
P. rainierensis				x			x
Psoroma hypnorum			x			x	x
Stereocaulon sp.	x					x	
Sticta fuliginosa				x			x
S. limbata				x			x
S. weigelii				x			x

These lichens are all presumed nitrogen fixers since a large number of species with a *Nostoc* phycobiont tested for nitrogen-fixing activity have all yielded positive results (Millbank and Kershaw 1970). The remaining cyanophiles (none of which occurred in the quantitative samples discussed below) contain other heterocystous blue-green algae (mainly *Scytonema*) and are also likely to be nitrogen-fixers (Millbank and Kershaw 1970).

Two of the observed species of cyanophiles occurred in an aquatic habitat on rock substrates. Seven of the total forty-six species of cyanophiles in the AEF are both ground-dwelling and epiphytic. Only one species (*Parmeliella saubinetii* Zahlbr.) is ground-dwelling as well as epiphytic and also lives on all four substrates of soil, rock, moss, and bark. Of the fourteen species that live on moss, half are both terrestrial and epiphytic and half are terrestrial only.

2. Quantitative Survey of Macrolichens

Quantitative observations were made on a total of 47 macrolichen species during sampling in the reference stands of the AEF: 24 cyanophiles; and 23 non-cyanophiles. Of the cyanophiles, eleven were arboreal lichens and thirteen were terrestrial lichens. These 24 cyanophilous lichens represent 50% of the known species of cyanophiles from the AEF (Table III).

All of the non-cyanophiles sampled were arboreal lichens. This is because several terrestrial species of the genus *Cladonia* were present but were excluded from any quantitative analysis

because although *Cladonia* is widespread in the AEF, it was most commonly present as small amounts of sterile squamules. These 23 taxa represent only a fraction of the total flora of non-cyanophiles, largely because crustose species were not sampled. Since during the early stages of this study *Peltigera leucophlebia* (Nyl.) Gyeln. was not accurately distinguished from *P. aphthosa* (L.) Willd., these two distinct species are lumped as *P. aphthosa*. Field observations suggest that *P. aphthosa* and *P. leucophlebia* have similar distributions with *P. aphthosa* in drier microsites.

The standard errors of the biomass of the lichens sampled in this study were within the desired range of 20-25% of the mean for those species that occurred most abundantly. Table IV shows the biomass and the standard errors at each reference stand for two representative species: *Lobaria oregana* (Tuck.) Müll. Arg. for the cyanophiles; and *Alectoria sarmentosa* (Ach.) Ach. for the non-cyanophiles. Standard errors for less abundant species are in general larger and standard errors for totals are smaller.

Of the selected lichen species in Table V, the genus *Peltigera* represents the majority of the terrestrial cyanophile biomass. The biomass values of the lichens in the litter are dominated by *Lobaria oregana* and *Alectoria sarmentosa*. The ratio of arboreal litter biomass to terrestrial biomass is approximately 9:1. The terrestrial cyanophiles are more restricted in their distribution than are the arboreal lichens. The greatest

TABLE IV. Biomass and standard errors for *Lobaria oregana* and *Alectoria sarmentosa* at each reference stand.

Reference Stand	*Lobaria oregana*		*Alectoria sarmentosa*	
	Biomass (kg ha^{-1})	Standard Error (kg ha^{-1})	Biomass (kg ha^{-1})	Standard Error (kg ha^{-1})
1	19.4	± 7.3	4.7	± 2.0
2	39.2	± 7.1	0.1	± 0.1
3	5.5	± 1.3	3.4	± 0.7
4	0	0	11.9	± 2.0
5	4.6	± 1.7	47.1	± 6.6
7	26.2	± 5.6	0.1	± 0.0
8	1.9	± 0.8	1.9	± 0.4
10	23.8	± 6.6	0.3	± 0.0
11	0	0	0.4	± 0.2
12	15.3	± 3.3	4.6	± 0.1
13	0	0	14.3	± 2.5
14	0	0	52.9	± 9.2
15	1.0	± 0.7	1.9	± 0.5
16	1.0	± 0.5	7.1	± 1.1
17	44.5	± 9.5	0.2	± 0.1
18	0	0	12.7	± 2.9

TABLE V. Biomass (kg ha^{-1}) of selected lichens at each reference stand. Reference stands are arranged by elevation. Totals include other species not listed here.

Elevation (m)	Reference Stand	Biomass of Terrestrial Cyanophiles		Biomass of Litter of Arboreal Cyanophiles			Biomass of Litter of Arboreal Non-cyanophiles		
		Peltigera spp.	Total	*Lobaria oregana*	*Pseudocyphellaria* spp.	Total	*Alectoria sarmentosa*	*Hypogymnia* spp.	Total
490	7	8.11	8.12	26.23	1.63	30.43	0.10	1.13	3.46
500	8	3.85	4.09	1.88	0.35	2.61	1.92	2.22	6.84
510	1	41.48	43.04	19.40	0	19.55	4.69	7.52	26.46
520	2	0.94	0.95	39.21	0.19	40.08	0.06	1.54	3.67
530	17	0.04	0.04	44.50	0.71	47.10	0.22	1.21	3.24
670	10	8.80	8.80	23.76	0.81	25.04	0.31	3.85	7.90
670	16	0.58	0.61	1.04	0	1.09	7.12	3.13	15.26
720	15	0	0	1.04	0.34	5.04	1.91	2.99	9.41
920	5	0	0	4.62	0.08	4.71	47.06	5.82	71.42
950	3	0	0	5.46	1.08	9.08	3.48	1.94	9.57
1020	12	0	0	15.28	0.02	15.40	4.55	1.78	18.18
1060	11	0	0	0	0	0	0.38	6.90	13.83
1080	18	0	0	0	0	0	12.75	11.78	40.19
1440	4	0	0	0	0	0	11.86	4.70	34.63
1480	13	0	0	0	0	0	14.30	2.39	23.36
1570	14	0	0	0	0	0	52.95	2.95	80.30

cyanophile biomass occurs at mid to lower elevations but is most abundant at approximately 500 m elevation. In contrast, the arboreal non-cyanophiles are most abundant at the higher elevations.

3. Correlations Between Lichen Biomass and Environmental Variables

Sixty-six environmental variables were examined to determine if there were significant correlations with the patterns of lichen distribution. Since lichens may be preferentially associated with certain tree species, or alternatively, conditions required for lichen survival may closely match those of better studied vascular plants, indices of abundance of several non-lichen species were included in the correlation analysis. Vascular plant species which did not have non-zero indices for at least three sites (Appendix III) were excluded as variables. Of the sixty-one remaining variables, twenty-five were non-biological and thirty-six were biological. The following eight non-biological variables showed no significant correlations ($P \leq .05$) with lichen abundances: the aspect of the entire slope; the slope of the reference stand; the angle of the height of the ridge to the southeast, the south, and the southwest; the percent cover by rock; and the pH of and percent nitrogen in the A1 soil horizon. Twenty-two biological variables showed no significant correlations ($P \leq .05$) with lichen abundances: the average distance from the quadrat to the closest tree; the mean tree basal area; the total tree basal area; tree density; age of the stand; the

mean distance from the quadrat to the closest shrub; the index for the shrub cover (height/distance^2); the percent cover of leaf litter and bare wood litter; the percent canopy coverage; the canopy coverage of *Pseudotsuga menziesii*, *Thuja plicata* Donn., *Abies* spp., *Vaccinium parvifolium*, *Rhododendron macrophylum*, *Taxus brevifolia* Nutt., *Gaultheria shallon* Pursh, and *Polystichum munitum*; and the basal areas of *Tsuga heterophylla*, *Thuja plicata*, *Abies procera*, and *Cornus nutallii*.

Tables VI and VII indicate significant correlations between the twenty-nine environmental variables and the twenty-one lichen species remaining after the exclusion of those lichen species occurring in limited abundance (occurring in fewer than four sites and with a total estimated biomass for all sites of less than 0.5 kg ha^{-1}). Those environmental variables and lichen species showing no significant correlations are omitted from these tables.

The significance of the correlation coefficient was tested by comparing values of r with tabulated probabilities that an r of a given magnitude would occur by chance when the lichen biomass and the environmental variable are in fact not related. The null hypothesis is $r = 0$ and the alternate hypothesis is $r \neq 0$. The probability that a given value of r will be exceeded by chance in a series of comparisons increases as more comparisons are made. Because of the large number of correlation coefficients examined in this analysis, a substantial number of rejec-

TABLE VI. Matrix of relationships between both cyanophiles and non-cyanophiles with biological variables. The sign of the correlation coefficient is indicated by a (+) or a (-) and the significance by asterisks: * $r \geq .497$, $P \leq .05$; ** $r \geq .623$, $P \leq .01$; *** $r \geq .742$, $P \leq .001$. Independant variables are: the % cover of moss (MOSS), *Stokesiella oregana* (STOR), the total moss flora (TMOSS), needle (NEEDLE), *Tsuga heterophylla* (TSHE), *Berberis nervosa* (BENE), *Linnaea borealis* (LIBO), and *Acer circinatum* (ACCI); and the area indices of *Pseudotsuga menziesii* (PSMEA), *Taxus brevifolia* (TABRA), and *Abies amabilis* (ABAMA).

		Biological Variables										
		MOSS	STOR	TMOSS	NEEDLE	TSHE	BENE	LIBO	ACCI	PSMEA	TABRA	ABAMA
CYANOPHILES Terrestrial	*Peltigera aphthosa*	(+)	(-)	(+)	(-)	(-)	(-)	(-)	(+)	(-)	(+)	(-)
	Peltigera membranacea	(+)*	(+)	(+)	(-)**	(-)	(-)	(-)	(+)	(-)	(+)	(-)
	Peltigera polydactyla	(+)*	(+)	(+)	(-)*	(-)	(-)	(-)	(+)	(-)	(+)	(-)
	Peltigera collina	(+)	(-)	(+)	(-)	(-)	(-)	(-)	(+)	(-)	(+)	(-)
	Parmeliella saubinetii	(+)	(-)	(+)	(-)	(-)	(-)	(-)	(+)	(-)	(+)	(-)
CYANOPHILES Arboreal	*Lobaria oregana*	(+)***	(+)***	(+)***	(-)*	(+)*	(-)	(+)**	(-)	(-)	(+)**	(-)
	Lobaria pulmonaria	(+)	(+)	(+)	(-)	(+)	(-)	(-)	(-)	(-)	(+)	(-)
	Pseudocyphellaria anthraspis	(+)	(+)	(+)	(-)	(+)	(-)	(-)	(-)	(-)	(+)	(-)
	Pseudocyphellaria anomala	(+)	(+)	(+)*	(-)	(+)	(-)	(-)	(-)	(-)	(+)	(-)
	Nephroma bellum	(+)*	(+)**	(+)**	(-)	(+)*	(+)	(+)	(-)	(+)	(+)	(-)
NON-CYANOPHILES Arboreal	*Alectoria sarmentosa*	(-)	(-)	(-)	(+)	(-)	(+)	(-)	(+)	(+)	(-)	(+)*
	Usnea sp.	(-)	(-)	(-)	(-)	(-)	(+)	(-)	(+)*	(+)**	(+)	(-)
	Sphaerophorus globosus	(+)	(-)	(+)	(-)	(-)	(+)	(+)	(+)	(+)	(+)	(-)
	Hypogymnia enteromorpha	(-)	(-)	(-)	(+)	(-)	(+)***	(-)	(+)***	(+)	(-)	(-)
	Hypogymnia inactiva	(-)	(-)	(-)	(+)	(-)	(-)	(-)	(-)	(+)	(-)	(+)
	Hypogymnia imshaugii	(-)	(-)	(-)	(+)	(-)	(+)***	(-)	(+)**	(+)	(-)	(-)
	Hypogymnia physodes	(-)	(-)	(-)	(+)	(+)	(-)	(-)	(-)	(-)	(-)	(+)
	Hypogymnia rugosa	(-)	(-)	(-)	(+)*	(-)	(-)	(-)	(-)	(-)	(-)	(+)
	Platismatia glauca	(-)*	(-)*	(-)*	(+)*	(+)	(+)	(-)	(+)	(+)	(-)	(+)
	Platismatia herrei	(-)	(-)	(-)	(+)	(-)	(+)*	(-)	(+)*	(+)	(-)	(+)
	Platismatia stenophylla	(-)	(-)	(-)	(+)	(-)	(-)	(-)	(-)	(-)	(-)	(+)***

TABLE VII. Matrix of relationships between both cyanophiles and non-cyanophiles with non-biological variables. The sign of the correlation coefficient is indicated by a (+) or a (-) and the significance by asterisks: * $r \geq .497$, $P \leq .05$; ** $r \geq .623$, $P \leq .01$; *** $r \geq .742$, $P \leq .001$. Independant variables are: elevation (ELEV); mean quadrat slope (SLOPE); mean quadrat aspect (ASPECT); direction code for aspect (DIR); vertical distance from stream (VDSTR); % cover of bare soil (SOIL); base saturation of A1 horizon (BS); and exchangeable calcium of A1 horizon (EXCA).

			Non-biological Variables							
			ELEV	SLOPE	ASPECT	DIR	VDSTR	SOIL	BS	EXCA
CYANOPHILES	Terrestrial	*Peltigera aphthosa*	(-)	(+)	(-)	(-)	(-)	(+)***	(+)	(+)
		Peltigera membranacea	(-)*	(+)	(-)	(-)	(-)	(+)**	(+)**	(+)*
		Peltigera polydactyla	(-)	(+)	(-)	(-)	(-)	(+)**	(+)*	(+)
		Peltigera collina	(-)	(+)	(-)	(-)	(-)	(+)***	(+)	(+)
		Parmeliella saubinetii	(-)	(+)	(-)	(-)	(-)	(+)***	(+)	(+)
	Arboreal	*Lobaria oregana*	(-)*	(+)	(+)	(-)	(-)**	(+)	(+)	(+)
		Lobaria pulmonaria	(-)	(+)	(+)	(-)	(+)	(+)	(+)	(+)
		Pseudocyphellaria anthraspis	(-)	(+)	(+)	(-)	(-)	(-)	(+)	(+)
		Pseudocyphellaria anomala	(-)	(+)	(+)	(-)	(-)	(-)	(+)*	(+)***
		Nephroma bellum	(-)	(+)	(+)	(-)	(-)	(-)	(-)	(+)
NON-CYANOPHILES	Arboreal	*Alectoria sarmentosa*	(+)*	(-)	(+)	(+)	(+)**	(-)	(-)	(-)
		Usnea sp.	(-)	(+)	(-)	(+)	(+)	(+)	(+)	(+)
		Sphaerophorus globosus	(-)	(+)	(-)	(+)	(-)	(+)*	(+)	(+)
		Hypogymnia enteromorpha	(+)	(-)	(-)*	(+)**	(+)*	(+)	(+)	(+)
		Hypogymnia inactiva	(+)	(+)	(-)	(-)	(+)	(+)	(-)	(-)
		Hypogymnia imshaugii	(+)	(-)	(-)**	(+)***	(+)	(+)	(+)	(-)
		Hypogymnia physodes	(+)	(-)	(-)	(-)	(-)	(-)	(-)	(-)
		Hypogymnia rugosa	(+)*	(-)	(-)	(-)	(-)	(-)	(-)	(-)
		Platismatia glauca	(+)	(-)*	(-)	(+)*	(+)	(-)	(-)	(-)
		Platismatia herrei	(+)	(-)	(-)	(+)***	(+)	(-)	(+)	(-)
		Platismatia stenophylla	(+)**	(-)	(+)	(-)	(+)	(-)	(-)	(-)

TABLE VII. continued. Independant variables are: January mean radiation (JANMR); July mean radiation (JULMR); January maximum radiation (JANXR); July maximum radiation (JULXR); January mean temperature (JANMT); July mean temperature (JULMT); January maximum temperature (JANXT); July maximum temperature (JULXT); temperature growth index (TGI); and plant moisture stress (PMS).

			Non-biological Variables									
			JANMR	JULMR	JANXR	JULXR	JANMT	JULMT	JANXT	JULXT	TGI	PMS
CYANOPHILES	Terrestrial	*Peltigera aphthosa*	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)***
		Peltigera membranacea	(+)	(+)	(+)	(+)	(+)*	(+)	(+)	(+)	(+)*	(+)**
		Peltigera polydactyla	(+)	(-)	(+)	(-)	(+)	(+)	(+)	(+)	(+)	(+)*
		Peltigera collina	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)***
		Parmeliella saubinetii	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)***
	Arboreal	*Lobaria oregana*	(-)	(+)	(-)	(+)	(+)	(+)*	(+)*	(+)*	(+)	(+)
		Lobaria pulmonaria	(-)	(-)	(-)	(-)	(+)	(+)	(+)	(+)	(+)	(-)
		Pseudocyphellaria anthraspis	(-)	(-)	(-)	(-)	(+)	(+)	(+)	(+)	(+)	(-)
		Pseudocyphellaria anomala	(-)	(-)	(-)	(-)	(+)	(+)	(+)	(+)	(+)	(-)
		Nephroma bellum	(-)	(-)	(-)	(-)	(+)	(+)	(+)	(+)	(+)	(-)
NON-CYANOPHILES	Arboreal	*Alectoria sarmentosa*	(-)	(-)*	(-)	(-)*	(-)	(-)*	(-)	(-)**	(-)*	(-)
		Usnea sp.	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)
		Sphaerophorus globosus	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)**
		Hypogymnia enteromorpha	(+)*	(+)	(+)*	(+)	(+)	(-)	(-)	(+)	(+)	(+)*
		Hypogymnia inactiva	(+)	(-)	(+)	(+)	(+)	(-)	(-)	(-)	(-)	(+)
		Hypogymnia imshaugii	(+)*	(+)	(+)*	(+)	(-)	(-)	(-)	(-)	(+)	(+)
		Hypogymnia physodes	(-)	(+)	(-)	(+)	(-)	(-)	(-)	(-)	(-)	(-)
		Hypogymnia rugosa	(+)	(+)	(+)	(+)	(-)	(-)*	(-)**	(-)*	(-)*	(-)
		Platismatia glauca	(+)	(+)	(+)	(+)	(-)	(-)	(-)	(-)	(-)	(-)
		Platismatia herrei	(+)	(+)	(+)	(+)	(-)	(-)	(-)	(-)	(-)	(+)
		Platismatia stenophylla	(-)	(-)**	(-)	(-)**	(-)**	(-)**	(-)*	(-)*	(-)**	(-)

tions of the null hypothesis may be expected even in the event that lichen biomass is in fact not related to any of the environmental variables. For this reason the number of observed correlations significant at 0.05, 0.01, 0.001 levels was compared with the number of correlations expected by chance (Table VIII).

A striking result of the comparison between numbers of expected and observed significant correlations is the small excess of expected over observed (Table VIII). Sixty-four correlations were expected by chance with $0.01 < P \leq 0.05$, and only forty-nine were observed; thus no reliance can be placed on these correlations other than indications of a strong trend. The correlations with $0.001 < P \leq 0.01$ are tentatively regarded as "real" even though of the twenty-four significant correlations observed, 12.8 could be expected by chance. The greatest excess of observed over expected correlations is found in the class with $P \leq 0.001$ (16 observed, 1.3 expected). Thus of a total of 1281 comparisons the total number of correlations significant at $P \leq 0.01$ level exceeded the number expected by chance by only 11.

The small number of significant correlations between lichen abundance and the various environmental variables indicates that many of these variables neither strongly influence lichen distributions directly nor are they highly correlated with other variables which do determine lichen abundance. It is possible that strong relationships with these variables exist, but that they were not detected through this correlation analysis.

TABLE VIII. Number of correlations expected by chance compared with those observed when distributions of cyanophiles and non-cyanophiles are compared with levels of biological and non-biological variables.

Comparisons	Number of significant correlations expected by chance at significance levels of: P≤.05	P≤.01	P≤.001	Number of significant correlations observed at significance levels of: P<.05	P<.01	P<.001
Biological Variables vs. Cyanophiles	18.0	3.6	0.4	8	5	3
Biological Variables vs. Non-cyanophiles	19.8	4.0	0.4	9	2	4
Non-biological Variables vs. Cyanophiles	12.5	2.5	0.3	11	5	7
Non-biological Variables vs. Non-cyanophiles	13.7	2.8	0.3	21	12	2
TOTAL	64.0	12.8	1.3	49	24	16

If abundance of a given species shows a highly non-linear correlation with an environmental variable or if it shows a normal distribution response (bell-shape) with high biomass at some optimum value of the variable and with biomass declining on both sides of the optimum, the two factors may appear correlated by a linear correlation analysis. That significant relations were not hidden by non-linear responses was shown by parallel correlation analyses using non-parametric statistics. Results are not given here since they are similar to those presented in Tables VI and VII. That lichen biomass at least does not commonly exhibit a normal distribution response within the ranges of values for environmental variables explored here was indicated by results of plotting biomass of several lichen species against various environmental variables (results not illustrated).

Inspection of Tables VI and VII for correlations significant at $P \leq 0.01$ and $P \leq 0.001$ levels reveals several consistent patterns. Abundance of several species of terrestrial nitrogen-fixing lichens is highly correlated with the amount of bare soil and with high plant moisture stress. These conditions are found at dry sites with shallow soils. Since the forest floor remains moist for longer periods than the canopy, terrestrial lichens may require relatively dry sites where thalli dry out regularly. Occassional desication appears to be necessary for maintenance of the symbiosis (Ahmadjian 1967).

Peltigera membranacea (Ach.) Nyl. was found to be negatively correlated with needle cover. This lichen is found in moister sites than many other terrestrial lichens; where needle cover is high such a terrestrial species may become buried.

Arboreal nitrogen-fixing lichens in no case show highly significant correlations with any of the above variables. Both *Lobaria oregana* and *Nephroma bellum* (Spreng.) Tuck. show very highly significant correlations with various estimates of moss cover (total cover estimated both in this study, and by Sawbridge and cover of *Stokesiella oregana* as estimated by Sawbridge). Both mosses and these cyanophiles probably require similar (moist) conditions for maximal development. It is also possible that the mosses utilize substances such as ribitol and organic nitrogen compounds which leach from cyanophilous lichens (Cooper and Carroll 1978).

L. oregana biomass also shows a negative correlation with the vertical distance of the site from the closest stream and positive correlation with the cover of *Linnaea borealis* L. and the area index of *Taxus brevifolia* . Correlations with these vascular plant species perhaps reflect similarities in conditions required for their growth. The negative correlation between *L. oregana* and distance from the stream may reflect the optimum mesoclimate for development of *L. oregana* populations; in particular, sites near the stream are moister than sites farther away.

The highly significant correlation between the biomass

of *Pseudocyphellaria anomala* Magn. and exchangeable calcium concentration in the A1 soil horizon has no obvious meaningful explanation. Though some lichens are calciphilous (e.g. some species of the terrestrial genus *Peltigera* Dahl and Krog 1973), arboreal lichens cannot be directly influenced by levels of calcium in the soil. Furthermore, lichens are probably not dependent upon their host trees for calcium since quantities of this element in precipitation are sufficient to meet the needs of lichen population (Pike 1978).

Non-cyanophilous, arboreal lichens show several distinct patterns of correlation with environmental variables. *Alectoria sarmentosa*, *Platismatia stenophylla* (Tuck.) Culb & Culb., and *Hypogymnia "rugosa" = Parmelia physodes* var. *enteromorpha* f. *rugosa* Merr. show strong negative correlations with various temperature indices and positive correlations with variables such as elevation, vertical distance from the stream, and the area index of *Abies amabilis*. Although temperature may play a direct role in influencing the distribution of these lichens, the fact that *Alectoria sarmentosa* occurs in substantial abundance in hot sites (such as reference stand 1) suggests that the influence of temperature may be more complex such as through its effect on moisture.

Hypogymnia enteromorpha (Ach.) Nyl., *Hypogymnia imshaugii* Krog, and *Platismatia herrei* (Imsh.) W.Culb & C.Culb as a group show positive correlations with cover of the shrubs *Berberis nervosa* and *Acer circinatum* Pursh which are species characteristic of moderate

sites in relation to plant moisture stress. They also show positive response to south and west aspects. Development of populations of these lichens appears to be maximal where supplies of soil moisture are readily available to vascular plants, but where the canopy is nonetheless dry. Reference stands where these lichens are best represented appear to be younger than the remaining reference stands, however Swanson's fire history map (Figure 4) does not document this and more accurate data are not currently available.

The biomass of *Sphaerophorus globosus* (Huds.) Vain. is positively correlated with plant moisture stress and *Usnea* spp. biomass with the area index of *Pseudotsuga menziesii*. Whether these correlations provide clues to factors influencing distribution of these species is not clear.

4. Equations for Prediction of Lichen Biomass

Although one objective of this study was to develop relationships useful in predicting biomass of lichens to be found at additional sites, the generally low correlation between lichen biomass and environmental variables discussed in the previous section would appear to make success from this effort unlikely. Several regression analyses were carried out and results from these are discussed briefly below.

Stepwise multiple regression analysis with selected lichen species entered as dependent variables and either a group of

biological factors or non-biological factors as independent variables were performed. (The distinction between biological and non-biological factors is recognized as being somewhat arbitrary.) The significance of the entering variable was tested for each step in the stepwise multiple regression. Only those variables forming a continuous sequence of significant variables were retained in the equation.

Even though a large number of environmental factors were entered as dependent variables, only in a few cases can as much as 80% of the observed site-to-site variability in lichen biomass be explained by regression equations involving either biological or non-biological factors (Tables IX and X). (Note that $r^2 \times 100$ = percent of total variability explained by the regression.) In numerous cases though, 60 to 80% of the variability can be attributed to the regression. In general, variables in the equations are the same as those discussed earlier under correlations.

Subsequent regression analyses involved the same lichen species as dependent variables but either temperature growth index (TGI) and plant moisture stress (PMS) or elevation and vertical distance from the stream as independent variables. Examination of TGI and PMS as variables was prompted by the strong relationship between these variables and the distribution of vascular plants (Zobel et al. 1976). Examination of elevation and vertical distance from the stream as independent variables was persuaded by the ease with which these data can

TABLE IX. Equations resulting from multiple regression analysis for 18 lichen species entered as dependant variables and 13 biological variables entered as independant variables. The order of variables in the equation indicate order of entry in a stepwise regression and asterisks indicate the significance of the step (*, P<.05; **, P<.01; ***, P<.001). Independant variables are: the % cover of moss (MOSS), *Stokesiella oregana* (STOR), the total moss flora (TMOSS), needle (NEEDLE), cumulative canopy cover, *Tsuga heterophylla*, *Berberis nervosa*, *Linnaea borealis* (LIBO), and *Acer circinatum* (ACCI); and the area indices of *Pseudotsuga menziesii* (PSMEA), *Taxus brevifolia* (TABRA), and *Abies amabilis* (ABAMA).

		Species Biomass (kg ha^{-1})	Equation With Biological Variables	Standard Error	r^2
CYANOPHILES	Terrestrial	*Peltigera aphthosa*	= no significant regression		
		Peltigera membranacea	= 6.215 - (0.083)(NEEDLE)**	± 2.113	0.401
		Peltigera polydactyla	= 2.063 - (0.029)(NEEDLE)*	± 0.837	0.337
		Peltigera collina	= no significant regression		
		Parmeliella saubinetii	= no significant regression		
	Arboreal	*Lobaria oregana*	= -0.211 + (0.538)(TMOSS)*** + (0.773)(LIBO)*	± 6.860	0.818
		Lobaria pulmonaria	= no significant regression		
		Lobaria scrobiculata	= 0.004 + (0.004)(STOR)* - (0.315)(TABRA)*	± 0.048	0.619
		Pseudocyphellaria anomala	= 0.014 + (0.008)(TMOSS)*	± 0.240	0.275
		Nephroma bellum	= 0.003 + (0.003)(TMOSS)** - (0.174)(TABRA)*	± 0.029	0.657
NON-CYANOPHILES	Arboreal	*Alectoria sarmentosa*	= no significant regression		
		Sphaerophorus globosus	= no significant regression		
		Hypogymnia enteromorpha	= 1.594 + (0.084)(ACCI)*** - (0.131)(PSMEA)* - (0.018)(MOSS)*	± 0.601	0.811
		Platismatia stenophylla	= 0.014 + (14.708)(ABAMA)***	± 0.647	0.948
		Bryoria sp.	= no significant regression		

TABLE X. Equations resulting from multiple regression analysis for 18 lichen species entered as dependant variables and 16 non-biological variables entered as independant variables. The order of variables in the equation indicate order of entry in a stepwise regression and asterisks indicate the significance of the step (*, P<.05; **, P<.01; ***, P<.001). Independant variables are: elevation (ELEV); mean quadrat slope (SLOPE); mean quadrat aspect (ASPECT); direction code for aspect (DIR); vertical distance from stream (VDSTR); % cover of soil (SOIL); base saturation of Al horizon (BS); exchangeable calcium of Al horizon (EXCA); January mean radiation; July mean radiation; January maximum radiation (JANXR); July maximum radiation (JULXR); January mean temperature; July mean temperature; January maximum temperature; and July maximum temperature.

		Species Biomass (kg ha^{-1})	Equation With Non-biological Variables	Standard Error	r^2
CYANOPHILES	Terrestrial	*Peltigera aphthosa*	= 4.648 + (3.264)(SOIL)*** - (0.355)(SLOPE)*	± 3.017	0.735
		Peltigera membranacea	= -0.938 + (0.793)(SOIL)** + (0.252)(EXCA)**	± 1.456	0.736
		Peltigera polydactyla	= -0.116 + (0.351)(SOIL)**	± 0.703	0.532
		Peltigera collina	= 0.530 - (0.041)(SLOPE)* + (0.373)(SOIL)***	± 0.350	0.728
		Parmeliella saubinetii	= 0.160 + (0.120)(SOIL)*** - (0.012)(SLOPE)*	± 0.111	0.742
	Arboreal	*Lobaria oregana*	= 35.758 - (0.052)(VDSTR)** - (0.018)(ELEV)*	±10.629	0.563
		Lobaria pulmonaria	= no significant regression		
		Lobaria scrobiculata	= no significant regression		
		Pseudocyphellaria anomala	= 0.299 + (0.048)(EXCA)*** - (0.003)(JANXR)**	± 0.111	0.857
		Nephroma bellum	= no significant regression		
NON-CYANOPHILES	Arboreal	*Alectoria sarmentosa*	= 4.496 + (0.027)(VDSTR)** - (0.388)(BS)*	± 9.834	0.691
		Sphaerophorus globosus	= 5.586 + (1.597)(SOIL)* - (0.268)(SLOPE)**	± 1.553	0.666
		Hypogymnia enteromorpha	= 2.431 + (1.645)(DIR)** - (0.010)(ASPECT)*	± 0.795	0.642
		Platismatia stenophylla	= 19.591 + (0.004)(ELEV)** - (0.035)(JULXR)**	± 1.519	0.733
		Bryoria sp.	= -5.946 + (0.009)(ELEV)**	± 3.489	0.495

be obtained and the significant correlations between these variables and abundance of several lichen species.

Elevation and aspect represent another potentially important variable pair, but because of the circular distribution of aspect values only graphical analysis was performed using the most important species from each of the major categories sampled to illustrate these relationships: *Peltigera membranacea* for the terrestrial cyanophiles; *Lobaria oregana* for the arboreal cyanophiles; and *Alectoria sarmentosa* for the arboreal non-cyanophiles.

The circular graphs with axes of elevation and aspect (Figures 7-9) illustrate that the cyanophiles are limited to the lower elevations, and that, conversely, the non-cyanophilous species are found predominately in the higher elevations. Unfortunately, reference stands on east-facing slopes and in the lower elevations on south-facing slopes are not represented in the AEF. Thus, no conclusive statements can be made regarding the independent variable of aspect.

Although PMS and TGI may be powerful variables influencing vascular plant distributions, they are not very powerful in predicting biomass of lichen species (Table XI). There is a significant regression between PMS and abundance of several terrestrial cyanophiles, but not with arboreal cyanophiles or any non-cyanophiles with the exception of *Sphaerophorus globosus*. The regression between TGI and several non-cyanophiles is significant, however TGI is highly correlated with elevation and for all of these taxa, regression with elevation gives a

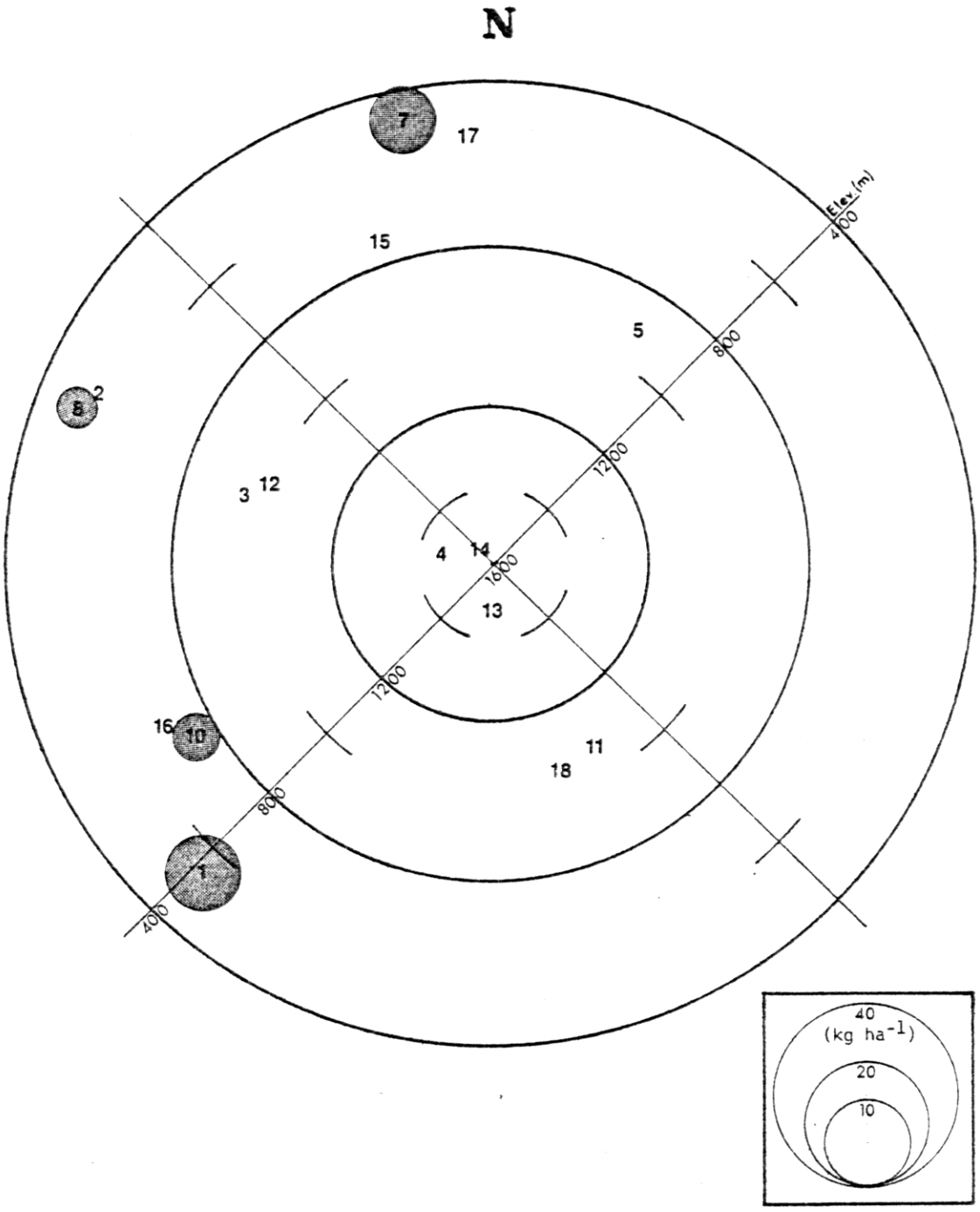


FIGURE 7. Reference stands plotted with axes of elevation and aspect showing biomass (kg ha^{-1}) of *Peltigera membranacea*. The shaded circles, of which the number in the center designates the reference stand, are sized proportionally to the biomass of *Peltigera membranacea* at that reference stand. The two lines divide the circles into four quadrants with elevation increasing from a low of 400 m at the outer circle to a high of 1600 m at the center, topographically representing a single cone-shaped mountain. N indicates the quadrant of North aspect; the other quadrants (in a clockwise direction) face East, South and West respectively.

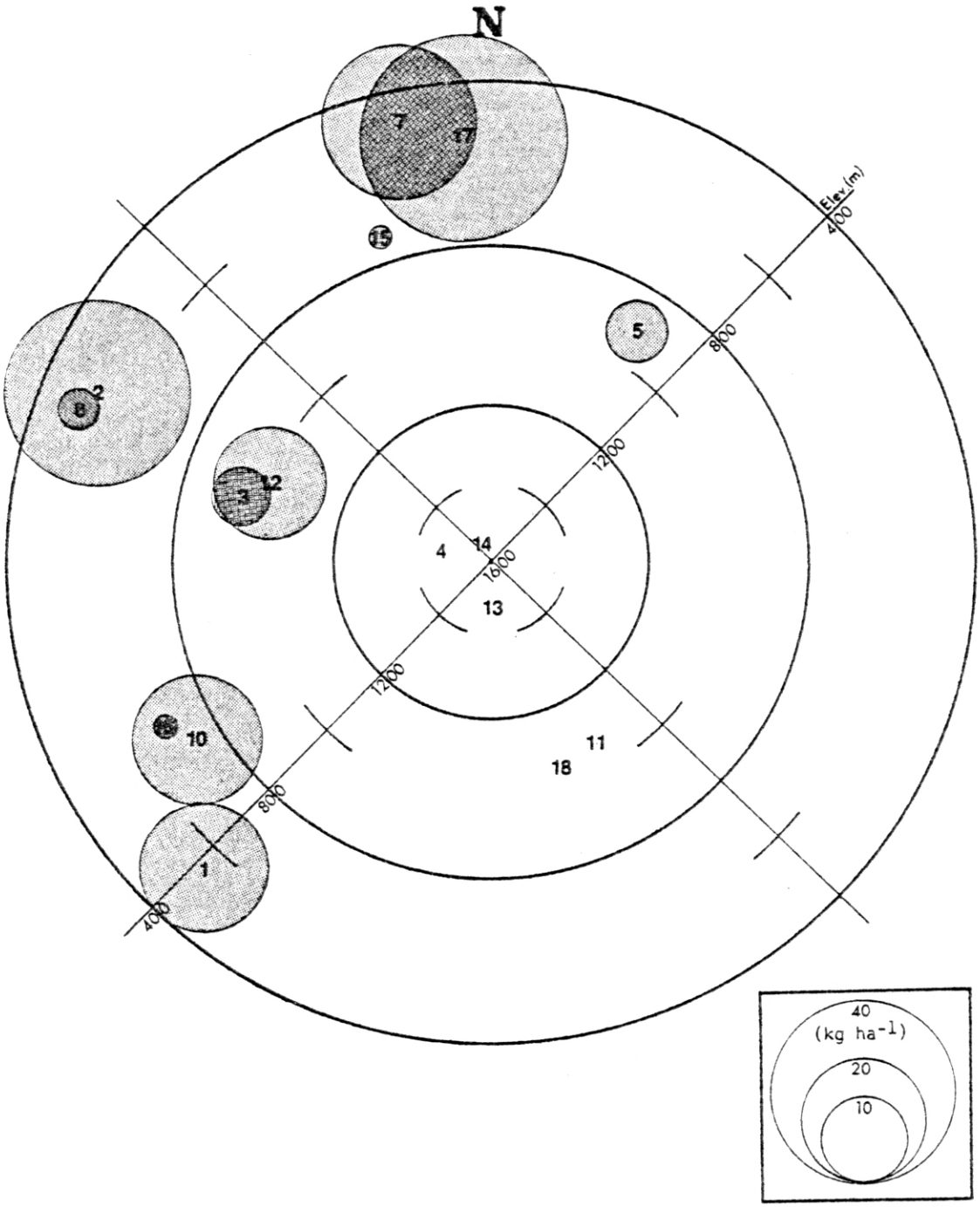


FIGURE 8. Reference stands plotted with axes of elevation and aspect showing biomass (kg ha^{-1}) of *Lobaria oregana*. The shaded circles, of which the number in the center designates the reference stand, are sized proportionally to the biomass of *Lobaria oregana* at that reference stand. The two lines divide the circles into four quadrants with elevation increasing from a low of 400 m at the outer circle to a high of 1600 m at the center, topographically representing a single cone-shaped mountain. N indicates the quadrant of North aspect; the other quadrants (in a clockwise direction) face East, South and West respectively.

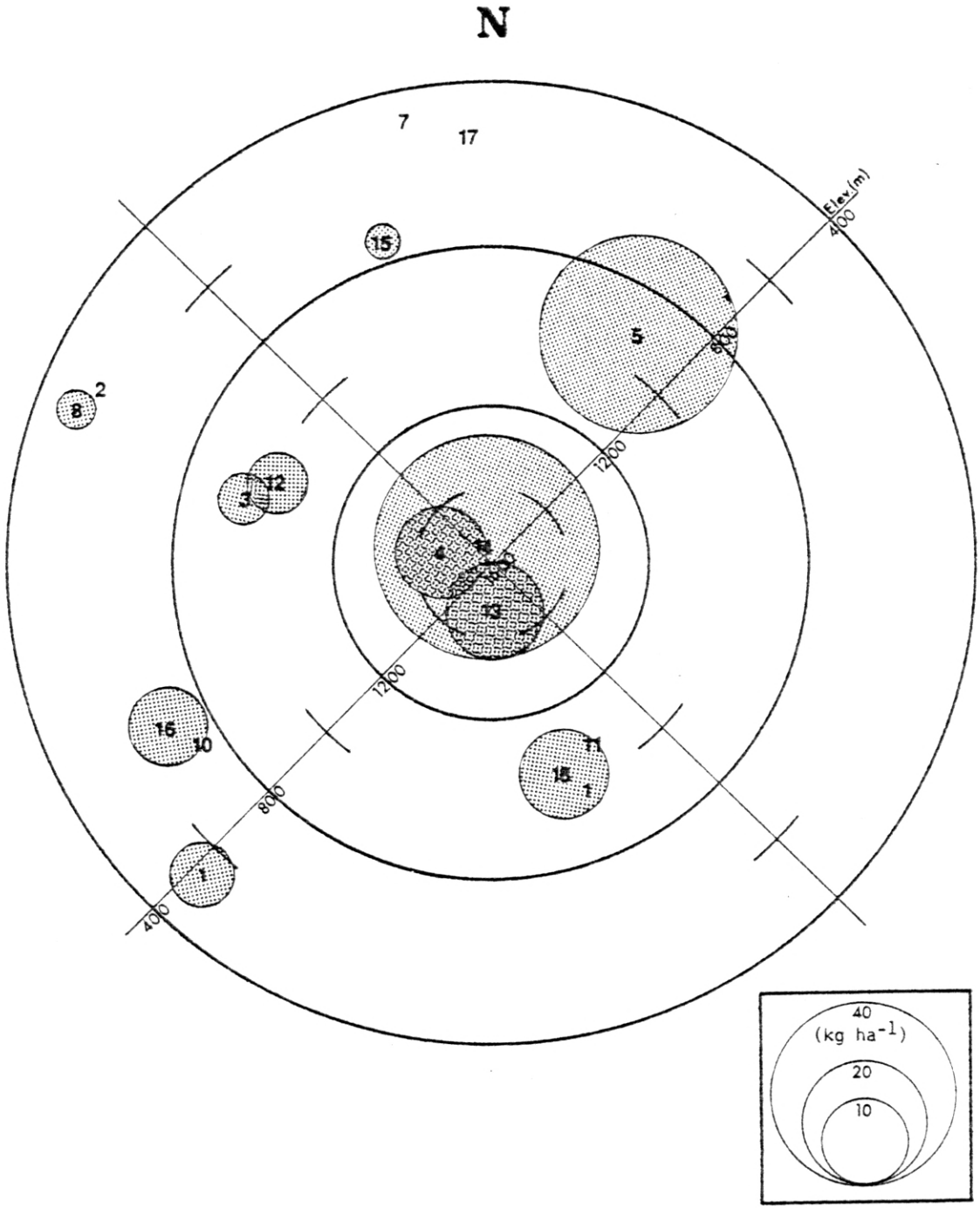


FIGURE 9. Reference stands plotted with axes of elevation and aspect showing biomass (kg ha^{-1}) of *Alectoria sarmentosa*. The shaded circles, of which the number in the center designates the reference stand, are sized proportionally to the biomass of *Alectoria sarmentosa* at that reference stand. The two lines divide the circles into four quadrants with elevation increasing from a low of 400 m at the outer circle to a high of 1600 m at the center, topographically representing a single cone-shaped mountain. N indicates the quadrant of North aspect; the other quadrants (in a clockwise direction) face East, South and West respectively. Although *Alectoria sarmentosa* was sampled at every reference stand, if its biomass was less than 0.5 kg ha^{-1} it is designated by the reference stand number only.

TABLE XI. Equation constants and regression coefficients resulting from regression analysis on 15 lichen species entered as dependant variables with temperature growth index (TGI) and plant moisture stress (PMS) entered as independant variables. Asterisks indicate the significance of the variable (*, P<.05; **, P<.01; ***, P<.001; n.s., not significant).

		Lichen Species	Constant	Coefficient TGI	Coefficient PMS	r^2
CYANOPHILES	Terrestrial	*Peltigera aphthosa*	-1.260	n.s.	0.107**	0.524
		Peltigera membranacea	-0.645	n.s.	0.069*	0.334
		Peltigera polydactyla		n.s.	n.s.	
		Peltigera collina	-0.142	n.s.	0.012**	0.497
		Parmeliella saubinetii	-0.053	n.s.	0.005***	0.674
	Arboreal	*Lobaria oregana*		n.s.	n.s.	
		Lobaria pulmonaria		n.s.	n.s.	
		Pseudocyphellaria anomala		n.s.	n.s.	
		Pseudocyphellaria anthraspis		n.s.	n.s.	
		Nephroma bellum		n.s.	n.s.	
NON-CYANOPHILES	Arboreal	*Alectoria sarmentosa*	70.090	-0.638*	n.s.	0.327
		Sphaerophorus globosus	-5.808	n.s.	o.834**	0.501
		Hypogymnia enteromorpha		n.s.	n.s.	
		Platismatia stenophylla	14.342	-0.162*	n.s.	0.370
		Bryoria sp.	13.525	-0.158**	n.s.	0.453

smaller standard error of the estimate. That arboreal lichen distributions may not bear strong relationship with TGI and PMS is not suprising when one considers the nature of these indices. TGI is based on the frost-free growing season of vascular plants, however, lichen growth is concentrated in the spring and fall and little occurs during the summer. PMS is a measure of summer-time moisture stress of vascular plants and is largely a function of soil moisture which is unavailable to lichens. The stronger relationships between terrestrial lichens and PMS is not surprising since soil factors exert a more direct influence on ground-dwelling lichens. The forest communities are plotted in the environmental field of Zobel et al. with the biomass of the three representative species illustrated in Figures 10-12. *Peltigera membranacea* reaches its greatest abundance in warm, dry forests, *Lobaria oregana* in warm moist forests, and *Alectoria sarmentosa* in cold forest communities.

L. oregana and *A. sarmentosa* exhibit significant multiple regressions with elevation and vertical distance from the stream (Table XII). Graphical analysis clarifies some of these patterns: *P. membranacea* was encountered only below 700 m; within this zone it was absent or rare near the creek and more abundant away from it (Figure 13). *L. oregana* was most abundant at low elevations and near a stream; abundance declined both as a function of increasing elevation and increasing distance from the stream (Figure 14). *A. sarmentosa* shows a pattern opposite to that of *L. oregana* (Figure 15).

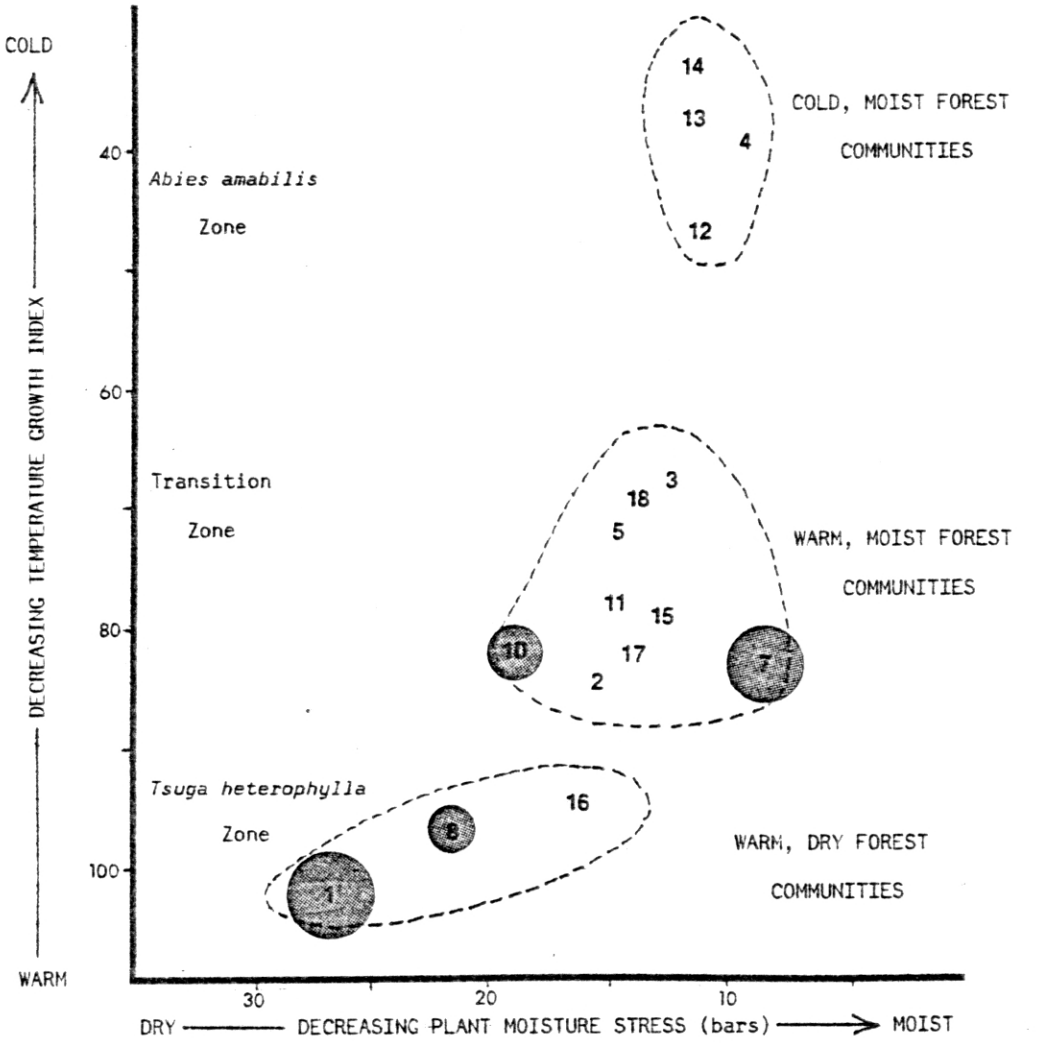
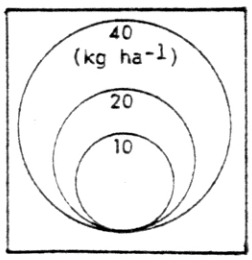
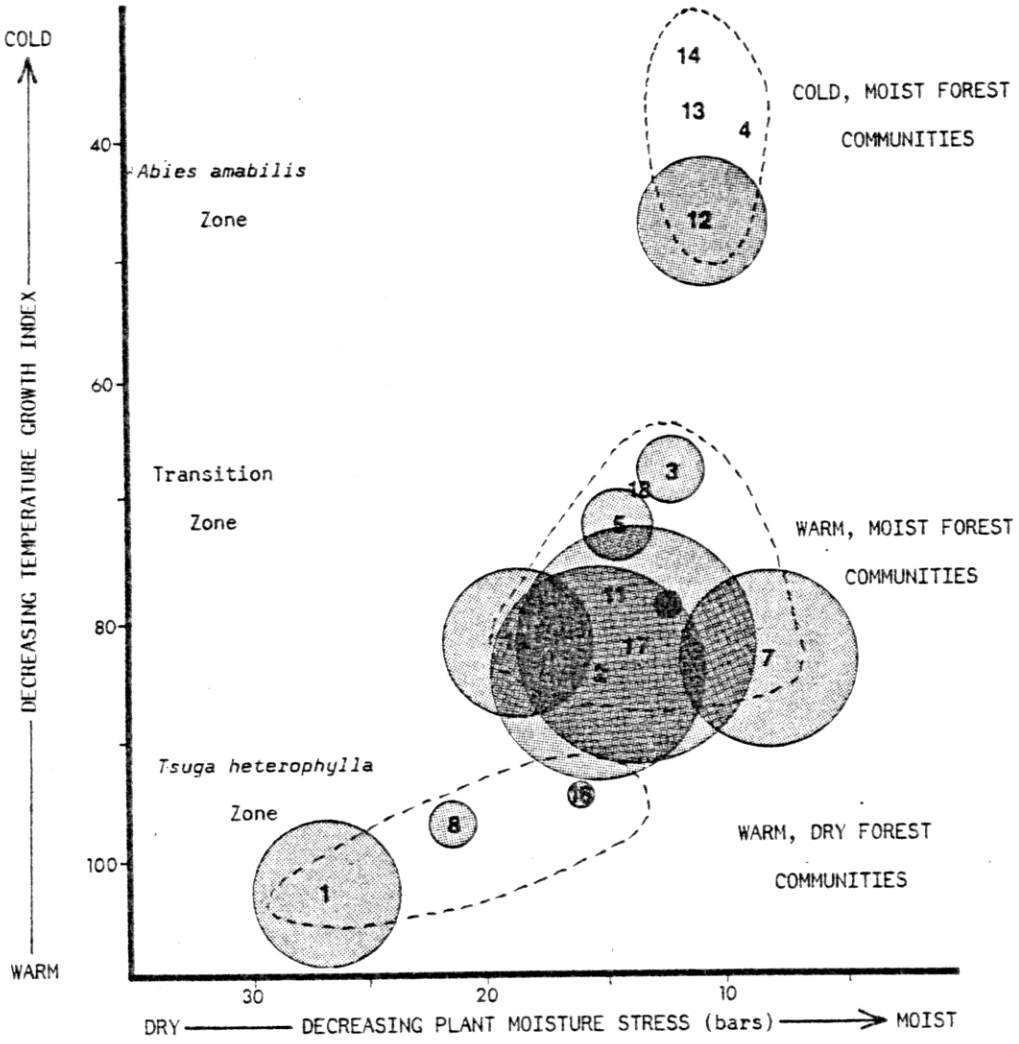


FIGURE 10. Reference stands plotted with axes of temperature growth index (TGI) and plant moisture stress (PMS) showing biomass (kg ha^{-1}) of *Peltigera membranacea*. The shaded circles, of which the number in the center designates the reference stand, are sized proportionally to the biomass of *Peltigera membranacea* at that reference stand. The dashed lines designate groupings of reference stands which seem to have similar TGI and PMS coordinates.





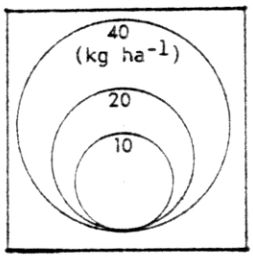
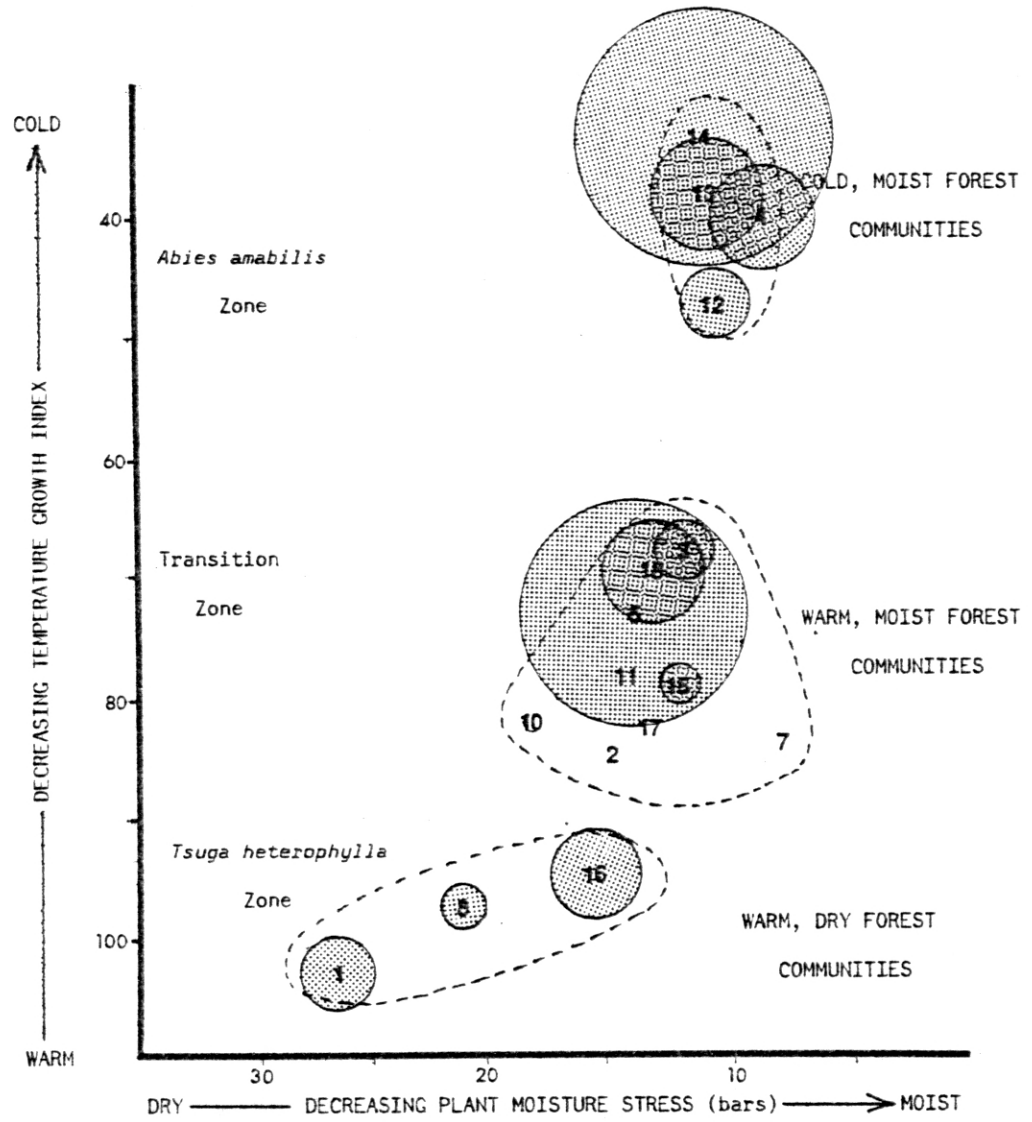


FIGURE 11. Reference stands plotted with axes of temperature growth index (TGI) and plant moisture stress (PMS) showing biomass (kg ha^{-1}) of *Lobaria oregana*. The shaded circles, of which the number in the center designates the reference stand, are sized proportionally to the biomass of *Lobaria oregana* at that reference stand. The dashed lines designate groupings of reference stands which seem to have similar TGI and PMS coordinates.



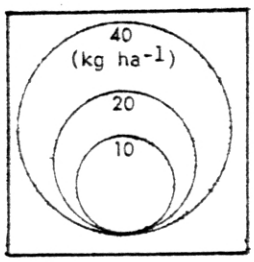


FIGURE 12. Reference stands plotted with axes of temperature growth index (TGI) and plant moisture stress (PMS) showing biomass (kg ha^{-1}) of *Alectoria sarmentosa*. The shaded circles, of which the number in the center designates the reference stand, are sized proportionally to the biomass of *Alectoria sarmentosa* at that reference stand. The dashed lines designate groupings of reference stands which seem to have similar TGI and PMS coordinates. Although *Alectoria sarmentosa* was sampled at every reference stand, if its biomass was less than 0.5 kg ha^{-1} it is designated by reference stand number only.

TABLE XII. Equation constants and regression coefficients resulting from regression analysis on 15 lichen species entered as dependant variables with elevation (ELEV) and vertical distance from the stream (VDSTR) entered as independant variables. Asterisks indicate the significance of the regression (*, P<.05; **, P<.01; ***, P<.001; n.s., not significant).

		Lichen Species	Constant	Coefficient ELEV	Coefficient VDSTR	r^2
CYANOPHILES	Terrestrial	*Peltigera aphthosa*		n.s.	n.s.	
		Peltigera membranacea	1.033	-0.001*	n.s.	0.297
		Peltigera polydactyla		n.s.	n.s.	
		Peltigera collina		n.s.	n.s.	
		Parmeliella saubinetii		n.s.	n.s.	
	Arboreal	*Lobaria oregana*	90.333	-0.045*	-0.126*	0.635
		Lobaria pulmonaria		n.s.	n.s.	
		Pseudocyphellaria anomala		n.s.	n.s.	
		Pseudocyphellaria anthraspis		n.s.	n.s.	
		Nephroma bellum		n.s.	n.s.	
NON-CYANOPHILES	Arboreal	*Alectoria sarmentosa*	-17.122	0.031**	0.084*	0.679
		Sphaerophorus globosus	12.374	-0.008*	n.s.	0.266
		Hypogymnia enteromorpha		n.s.	n.s.	
		Platismatia stenophylla	-6.256	0.010**	n.s.	0.460
		Bryoria sp.	-5.946	0.009**	n.s.	0.495

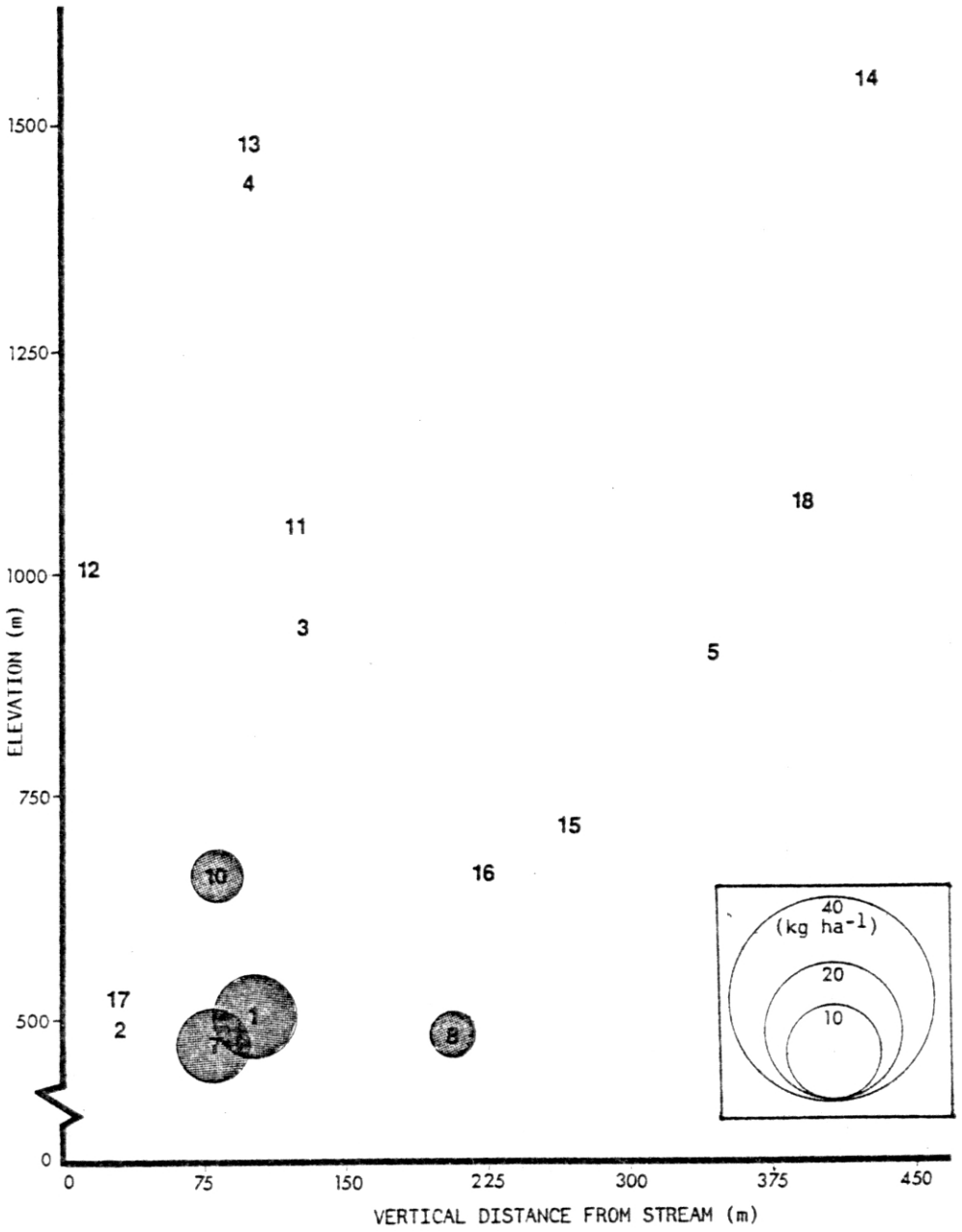


FIGURE 13. Reference stands plotted with axes of elevation and vertical distance from the stream showing biomass (kg ha^{-1}) of *Peltigera membranacea*. The shaded circles, of which the number in the center designates the reference stand, are sized proportionally to the biomass of *Peltigera membranacea* at that reference stand.

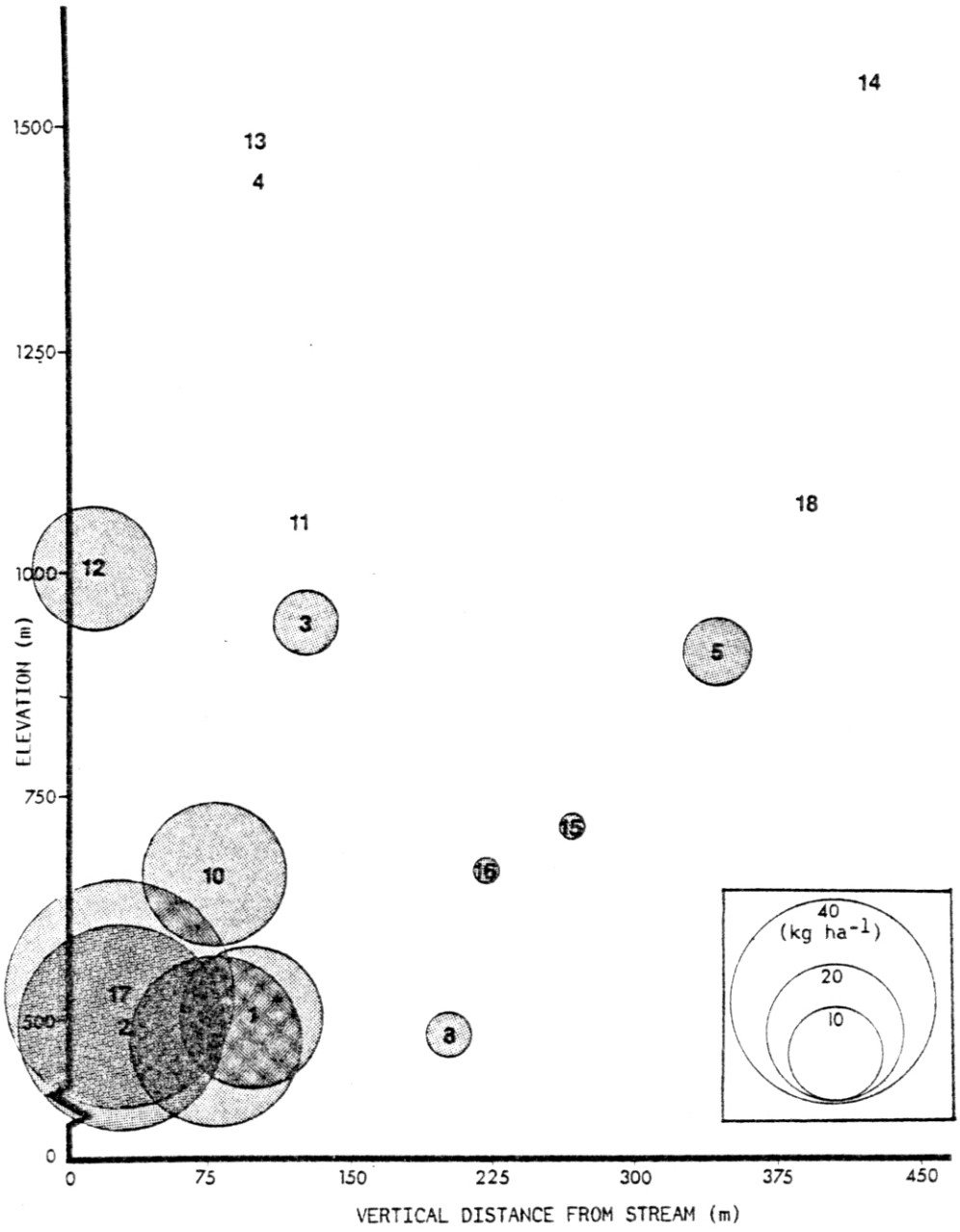


FIGURE 14. Reference stands plotted with axes of elevation and vertical distance from the stream showing biomass (kg ha^{-1}) of *Lobaria oregana*. The shaded circles, of which the number in the center designates the reference stand, are sized proportionally to the biomass of *Lobaria oregana* at that reference stand.

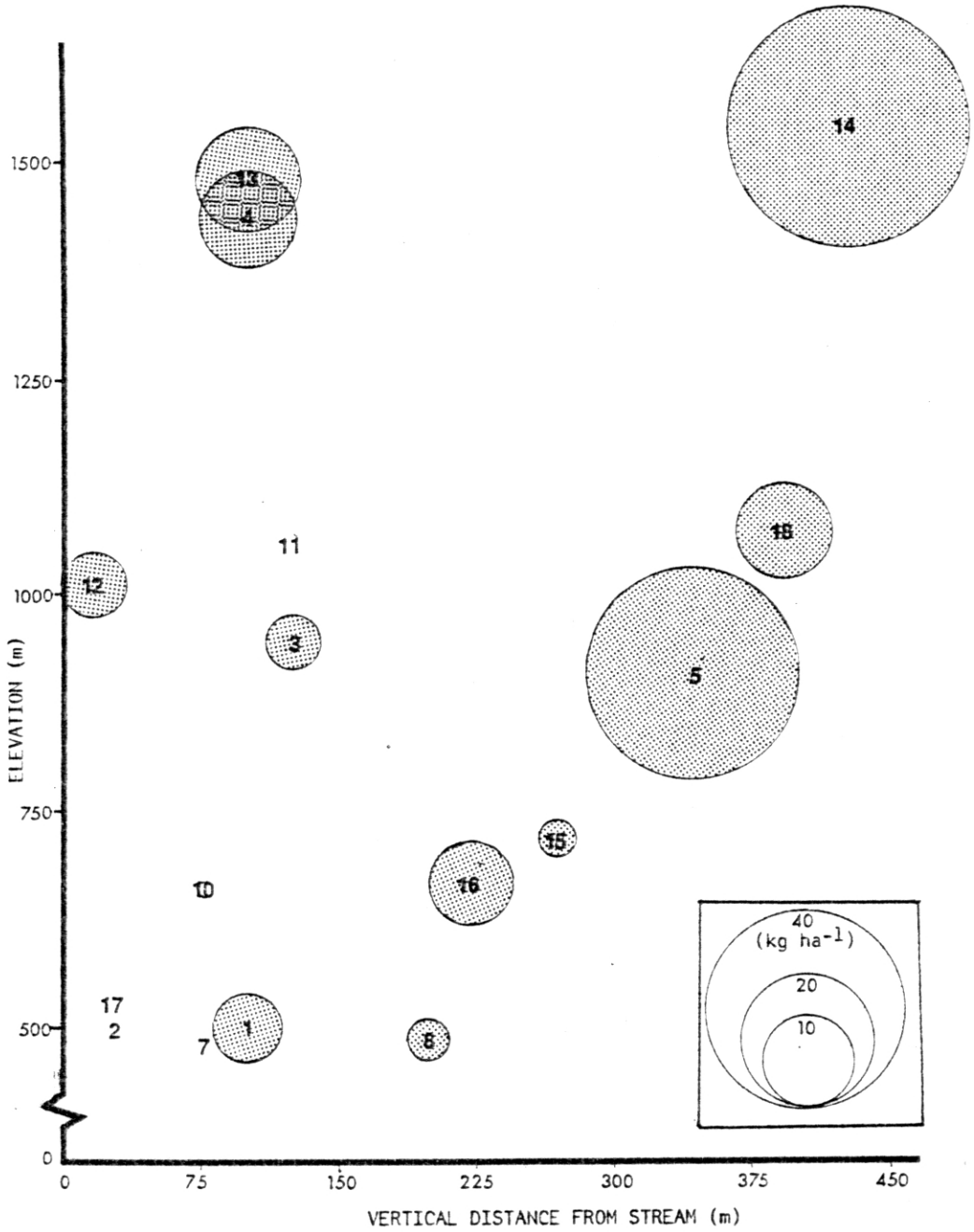


FIGURE 15. Reference stands plotted with axes of elevation and vertical distance from the stream showing biomass (kg ha^{-1}) of *Alectoria sarmentosa*. The shaded circles, of which the number in the center designates the reference stand, are sized proportionally to the biomass of *Alectoria sarmentosa* at that reference stand. Although *Alectoria sarmentosa* was sampled at every reference stand, if its biomass was < 0.5 kg ha^{-1} it is designated by reference stand number only.

Thus, the two most abundant arboreal lichens, at least, appear to be responding to a factor or factors which is correlated with elevation but moderated by the vertical distance of the stand from a major stream.

5. Seriation and Ordination of Reference Stands Based on Lichen Similarity Coefficients

Seriation of reference stands on the basis of their similarity coefficients results in reference stands 14 and 17 being placed far apart in the matrix (Figure 16). In this unidimensional arrangement of the reference stands, high similarity coefficients lie along the diagonal and low similarity scores lie far from it. Need for a second dimension to properly arrange the reference stands can be inferred from such a matrix by noting high values lying far from the diagonal. No such stress is apparent in this matrix and a second dimension appears to be unnecessary. Lack of blocks of stands with mutually high similarity scores separated by regions of low scores suggest that the stands may represent a continuous series along an environmental gradient.

The order of stands resulting from the unidimensional ordination (Figure 17) is nearly identical to that resulting from the seriation (Figure 16). As stated above, the addition of a second axis using as endpoints two reference stands in close proximity to each other on the axis, but which were separated by a great interstand difference (i.e. reference

RS	17	2	1	10	12	1	8	3	15	16	5	18	11	4	13	14
17		95	81	79	51	43	26	34	13	12	12	6	3	3	3	2
2	5		84	81	54	45	29	50	16	14	14	8	5	5	5	4
7	19	16		83	54	48	34	45	27	15	16	10	7	6	6	4
10	21	19	17		63	61	45	45	30	30	21	20	16	10	13	5
12	49	46	46	37		74	58	68	48	43	45	44	28	37	32	20
1	57	55	52	39	26		71	57	49	54	40	40	30	27	34	17
8	74	71	66	55	42	29		63	59	71	52	58	38	38	44	27
3	66	50	55	55	32	43	37		67	47	48	53	35	46	38	24
15	87	84	73	70	52	51	41	33		61	51	52	45	44	40	18
16	88	86	85	70	57	46	29	53	39		74	63	38	54	68	47
5	88	86	84	79	55	60	48	52	49	26		64	33	55	78	65
18	94	92	90	80	56	60	42	47	48	37	36		67	64	56	38
11	97	95	93	84	72	70	62	65	55	62	67	33		56	35	14
4	97	95	94	90	63	73	62	54	56	46	45	36	44		55	49
13	97	95	94	87	68	66	56	62	60	32	22	34	65	45		72
14	98	96	96	95	80	83	73	76	82	53	35	62	86	51	28	

FIGURE 16. Seriated matrix of indicies expressing similarity between lichen floras of reference stands. Similarity coefficients are in the upper-half-right of the matrix and dissimilarity coefficients are in the lower-half-left of the matrix.

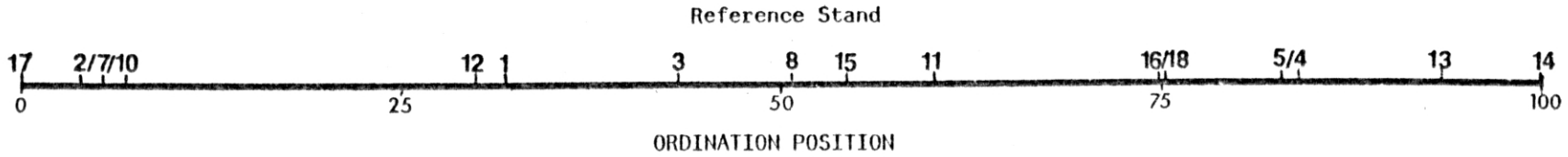


FIGURE 17. Unidimensional ordination of reference stands based on composition of their lichen floras. The position of each reference stand is determined by its dissimilarity with reference stand 17 and 14. Reference stand 17 is arbitrarily placed at 0 and reference stand 14 at 100.

stands 8 and 11), produced a second axis on which positions of stands were highly correlated with those on the first axis ($r = 0.77$, $P<0.001$). Thus, this second axis was considered not to represent a new axis and is not included in the results presented here.

The consistency of the results from ordination and seriation suggest the presence of a single, strong gradient. The position of the reference stands in the seriated matrix is not significantly correlated with PMS, weakly correlated with TGI, highly correlated with elevation, and very strongly correlated with a composite index of elevation and vertical distance from the stream (Table XIII). This high correlation between the lichen flora at a site and simple topographic variables suggests that the lichens are affected by mesoclimatic factors in a manner not reflected by PMS and poorly reflected by TGI.

6. Analysis of Associations Between Lichens

The plexus diagram (Figure 18) illustrates how the cyanophiles as a group have similar patterns for their rank orders of abundance in the reference stands. This association analysis emphasizes the relationships between the lichens themselves rather than the relationships between the lichens and other environmental factors. The strongest positive relationships are shown to be within either the cyanophile group or the non-cyanophile group, but not between groups. There are only two links between groups; both are of the lowest

TABLE XIII. Comparison of order of stands resulting from seriation of similarity scores with order of stands resulting from ordination and with several environmental variables. The test statistic is Spearman's Rank Correlation Coefficient, R. Reference stand 17 is assigned a rank of 1 for both ordination and seriation positions. Significance level of the correlation is given in column P.(n.s.= not significant)

Correlated Variables			R	P
Seriation Order	vs.	Ordination Order	0.946	<0.001
Seriation Order	vs.	Plant Moisture Stress	-0.048	n.s.
Seriation Order	vs.	Temperature Growth Index	-0.615	<0.05
Seriation Order	vs.	Elevation	0.818	<0.001
Seriation Order	vs.	(Elevation ÷ 3)+ dist. from stream	0.937	<0.001

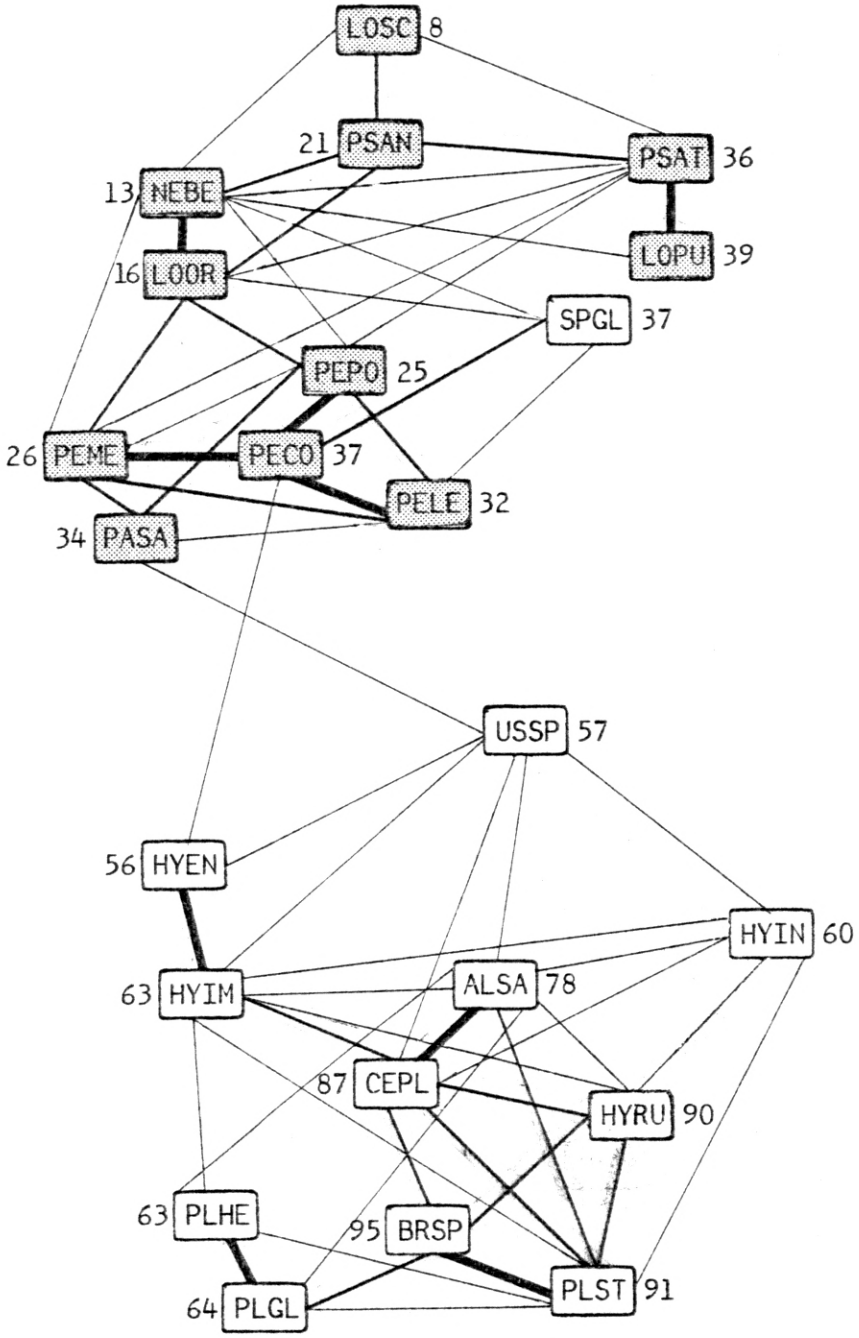


FIGURE 18. Plexus diagram illustrating positive relationships between pairs of lichen species having significantly similar patterns of distribution among reference stands. The test statistic is Kendall's Tau; line widths indicate probability levels at which rank orders of abundance in the reference stands are significantly similar (widest,$P<.001$; medium,$P<.01$; narrowest, $P<.05$). Numbers next to species names indicate centers of distribution of each species along the seriation axis with Reference Stand 17 being placed at 0 and Reference Stand 14 at 100. Shaded boxes indicate those species which are cyanophiles, unshaded boxes indicate non-cyanophiles. Abbreviations for lichen species are identified in Appendix A.

significance level. With the exception of *Sphaerophorus globosus*, the cyanophilous species are almost completely separated from the non-cyanophilous species. Note also that this analysis did not show any strong differences in the distribution patterns of terrestrial and arboreal cyanophiles.

The reason that *S. globosus* (a non-cyanophile) is strongly related to the cyanophiles but not to the non-cyanophiles may be that the cyanophiles and *S. globosus* both can grow only at lower elevation (moister ?) sites. Another possible explanation for the association between *S. globosus* and the cyanophiles may be that it is chemically dependent on nitrogen fixed by *Lobaria oregana*, or other cyanophiles, nitrogen which leaches from those lichens in the canopy. Studies conducted on epiphytes in the canopy indicate that *S. globosus* living in the lower canopy has a higher nitrogen content than *S. globosus* living in the higher canopy (Larry Pike, pers. comm.).

Figure 19 illustrates the negative relationships (also based on the Kendall's Tau statistic) that occur with *L. oregana* (representing the cyanophiles) and those that occur with *Alectoria sarmentosa* (representing the non-cyanophiles)(Figure 20). *L. oregana* showed negative relationships only with non-cyanophiles; *A. sarmentosa* showed negative relationships only with cyanophiles. This reinforces the dichotomy between cyanophiles and non-cyanophiles found in Figure 18, where the lichens are arranged according to positive relationships with each other.

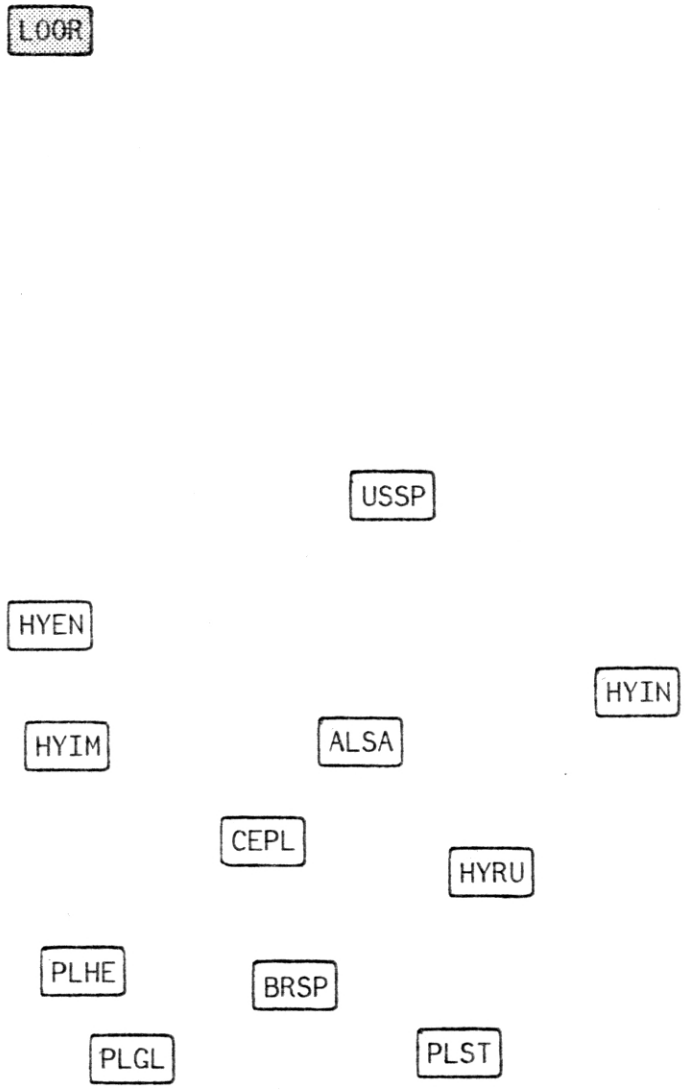


FIGURE 19. Lichen species having negative correlation with *Lobaria oregana* (LOOR) using Kendall's Tau test statistic. Lichen species are positioned from the plexus diagram (FIGURE 18). Unshaded boxes indicate those species having negative correlations with *Lobaria oregana*. Abbreviations for lichen species are identified in Appendix A.

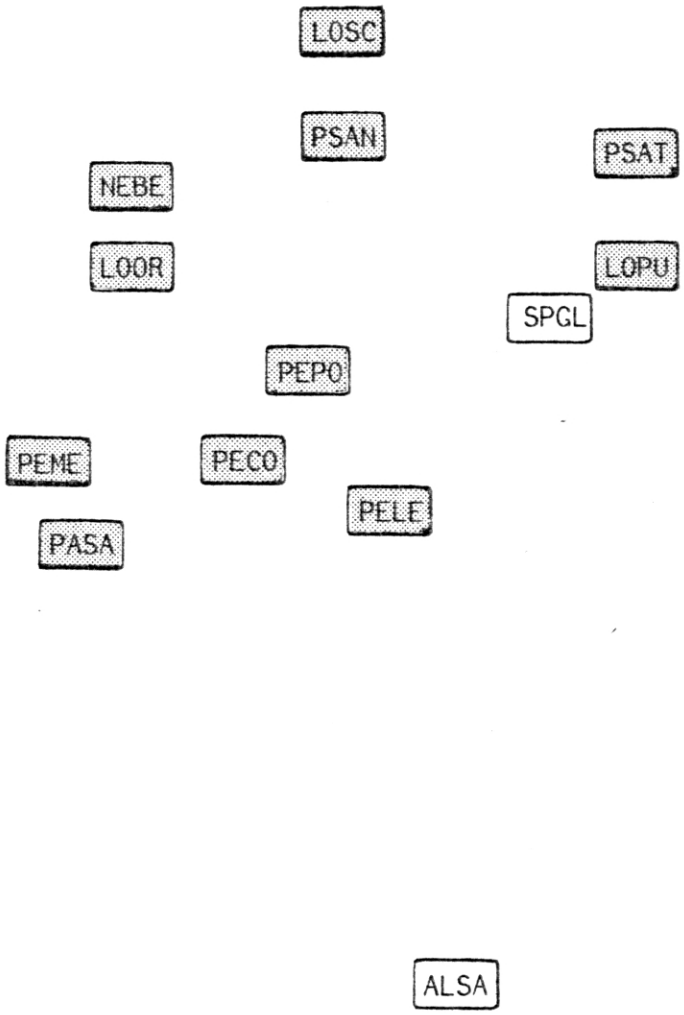


FIGURE 20. Lichen species having negative correlation with *Alectoria sarmentosa* (ALSA) using Kendall's Tau test statistic. Lichen species are positioned from the plexus diagram (FIGURE 18). The shaded boxes with the addition of unshaded box of *Sphaerophorus globosus* (SPGL) indicate those species having negative correlations with *Alectoria sarmentosa*. Abbreviations for lichen species are identified in Appendix A.

At this point, analysis of biomass data implicates elevation and vertical distance from the stream as important correlates determining distribution of lichens. Values of many environmental variables are correlated with elevation making this variable of limited value when trying to identify the specific non-biological environmental factor(s) that ultimately determine the patterns of lichen distribution. Vertical distance from the stream is itself correlated with elevation, as is the vertical distance to the ridge. Lichen biomass values were more highly correlated with vertical distance from the stream than with vertical distance to the ridge above. This implies that there must be some element associated with the stream or the drainage bottom that influences lichen distribution.

IV. EFFECT OF MOISTURE ON LICHEN DISTRIBUTION

A. Lookout Creek Lichen Biomass Transect

An experiment was designed to test the importance of the vertical distance from the stream as a variable determining lichen distributions. A transect was run in the summer of 1977 from the top of a ridge at 1280 m elevation, down its north-facing slope to Lookout Creek at 600 m elevation, and up the opposite south-facing ridge to its top at 1100 m elevation. Six sites were sampled on each side of the creek at vertical intervals of approximately 150 m. Sampling procedures were the same as used previously during the initial sampling of the reference stands in 1976, with two exceptions: the sampling was limited to cyanophiles; and fifty quadrats were sampled per site instead of the twenty-eight quadrats per reference stand in the previous sampling. The hypothesis tested was that the biomass of the cyanophiles would increase as vertical distance from the stream decreased.

Plotting these biomass values graphically illustrates the effect of vertical distance from the stream (Figure 21). The maximum biomass values (25-65 kg ha^{-1}) occurred at those sites located within 150 m vertical distance from the stream. An examination of stream-associated phenomena is necessary to determine why lichens are more abundant closer to the stream.

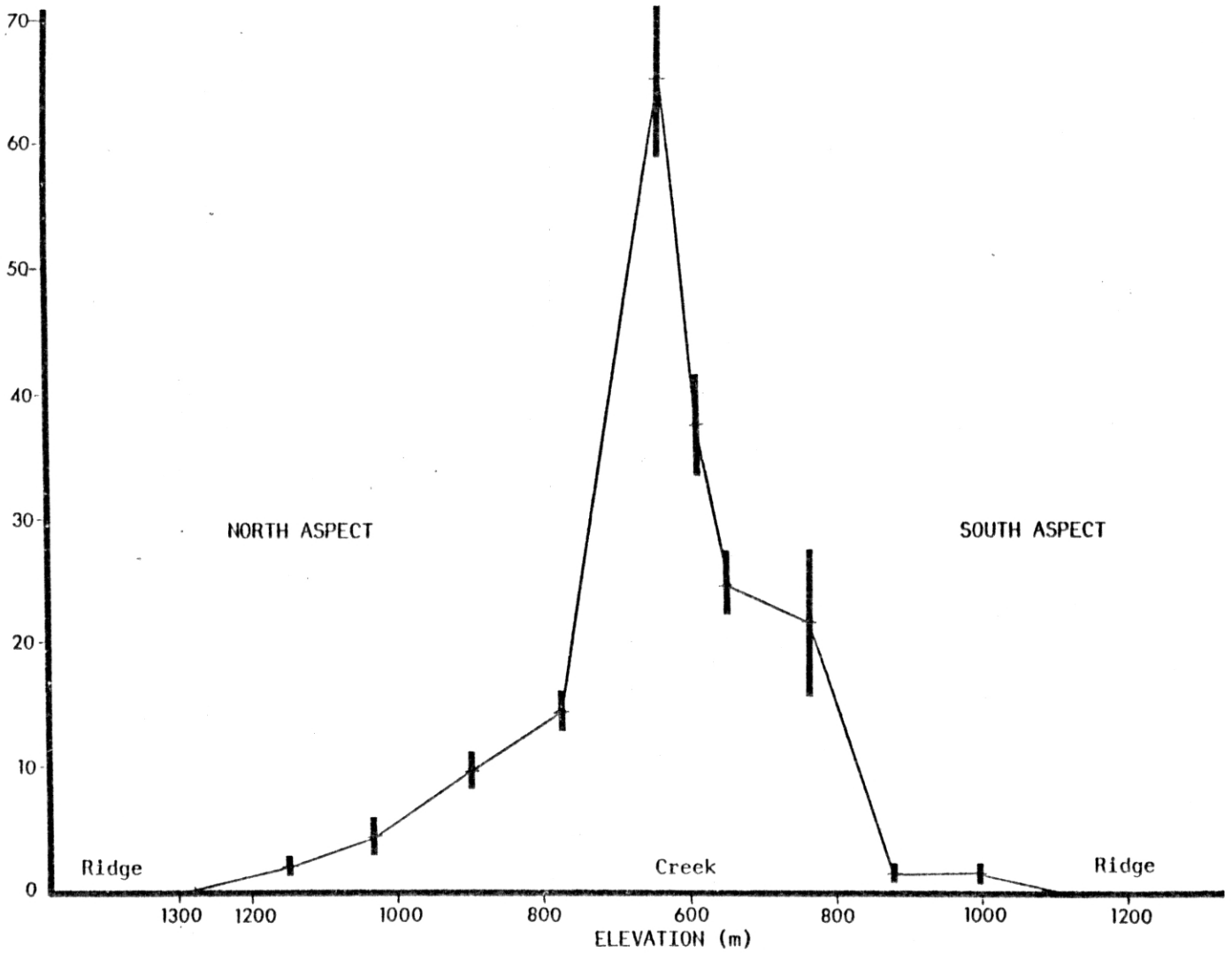


FIGURE 21. Biomass (kg ha^{-1}) of terrestrial and arboreal cyanophiles from Lookout Creek Valley Transect with standard errors.

Some phenomena usually associated with streams in a valley are air drainage, higher humidity and lower evaporation. Thus, it seems possible that moisture or some form of it, and air drainage may influence lichen distribution.

B. Forms of Moisture

An obvious form of moisture to consider is precipitation. Average annual precipitation differences for the past 5 years (1973-1977) between the Central Meteorological Station in the AEF and two other selected weather stations in the western Cascades have been calculated. These two weather stations, Santiam Junction and Detroit Dam, are situated in similar sites at similar elevations (approximately 1000 m) as the Central Meteorological Station. Santiam Junction is 64 km and Detroit Dam is 104 km from the Central Meteorological Station. Their average annual precipitation differs from the Central Meteorological Station's by 5.3 cm and 9.2 cm, respectively (NOAA 1973-1977). Therefore, it seems reasonable to assume that if the rainfall varies so slightly between the AEF and similar sites up to 100 km away, the variability within the AEF, only 11 km across, should be negligible.

Snow, although seasonal, is another form of moisture which should be considered. One to three meters of snow accumulate annually in the high elevation reference stands of the AEF (Dyrness et al. 1974). Since cyanophiles occur most abundantly in the lower elevations, it may simply be that snow is not

an important variable in the distribution of cyanophiles. But a closer look reveals a more complex explanation. Precipitation in the form of snow is unavailable to lichens. If cyanophiles are distributed according to some moisture-related phenomenon, the essentially arid winter habitat created by snow in high elevations may limit their distribution to low elevations. Another, strictly mechanical, variable may also be operating here. The weight of snow buildup on the large, flat thalli of most cyanophiles may cause structural damage.

In addition to rain and snow, moisture may occur in other, less obvious, forms such as humidity and condensation. Atmospheric humidity is an important factor influencing water loss through evaporation and is a source of water supply to the lichen since lichens are capable of drawing considerable quantities of water from atmospheric vapor (Barkman 1958). Condensation may result from ambient fog within the canopy or from the horizontal interception of moisture-laden air masses. Geiger (1959) considers the effect of horizontal interception to be limited to the border of a stand; an edge effect. However, horizontal interception probably plays an important role at the higher elevations where slopes create a continuous edge effect on the forest canopy.

Many times during the course of this study it would be "raining" under the forest canopy on foggy days, yet it would be dry out on the open road. This informal observation gave

rise to the hypothesis that condensation is the form of moisture which may explain the patterns of distribution of cyanophiles. No humidity information was available from previous studies on the AEF with which to correlate the distribution of the lichens. No attempt was made to collect any humidity data in this study due to the difficulties and expenses (in time and sophisticated equipment) in obtaining such data. Thus, an experiment was designed to quantify this "fog drip" phenomena.

C. Lookout Creek Meteorological Transect

A second transect was run across Lookout Creek parallel to the biomass transect with four sample sites on each side of the creek spaced at vertical intervals of approximately 200 m. Meteorological stations were set up at each site. Each was equipped with: 5 condensation drip collectors (15.3 cm diameter coffee cans); 3 evaporimeters (230 ml polyethelene containers with 5 x 5 cm lamp wicks); and a max/min thermometer. The stations were monitored regularly for a sixteen day period, November 1,1977 to November 16, 1977, at which time freezing temperatures and snow put a halt to the experiment.

There was only one day during the time span of this experiment when no precipitation occurred in the form of rain or snow. Thus, the moisture collected for this 48 hour peroid (November 9-11) was the result of canopy drip. The volume of canopy drip collected along this transect directly correlates with the biomass of the cyanophiles sampled in the biomass

transect (Figure 22).

The graph of the evaporimeter weight loss for this same time period, November 9-11, can also be seen in Figure 22. Relatively larger water losses (higher evaporation) occurred at the higher elevations, especially on the south-facing slope, while relatively smaller water losses (lower evaporation) occurred in the lower elevations closer to the creek. The pattern of evaporation is inversely correlated with the biomass values of cyanophiles observed on the biomass transect.

Although the time span of this experiment was short and the equipment was admittedly crude, the instruments were sensitive enough to demonstrate many differences between sites. The values of the graphs are useful only as relative values; it is the general trends that they illustrate which are of importance.

The correlation of evaporation loss and condensation drip to biomass of cyanophilous lichens is consistent with the hypothesis that moisture is a key variable in the distributional patterns of these lichens. Even though these measurements were made during a period in which weather conditions were typical of those for the AEF throughout the period when much of the lichen growth occurs, more data are necessary to conclusively demonstrate this relationship.

The results of the biomass transect and the meteorological observations demonstrate that cyanophiles are abundant close to the stream and that high humidity, low evaporation, and/or condensation may determine this distribution. Perhaps the adaptive

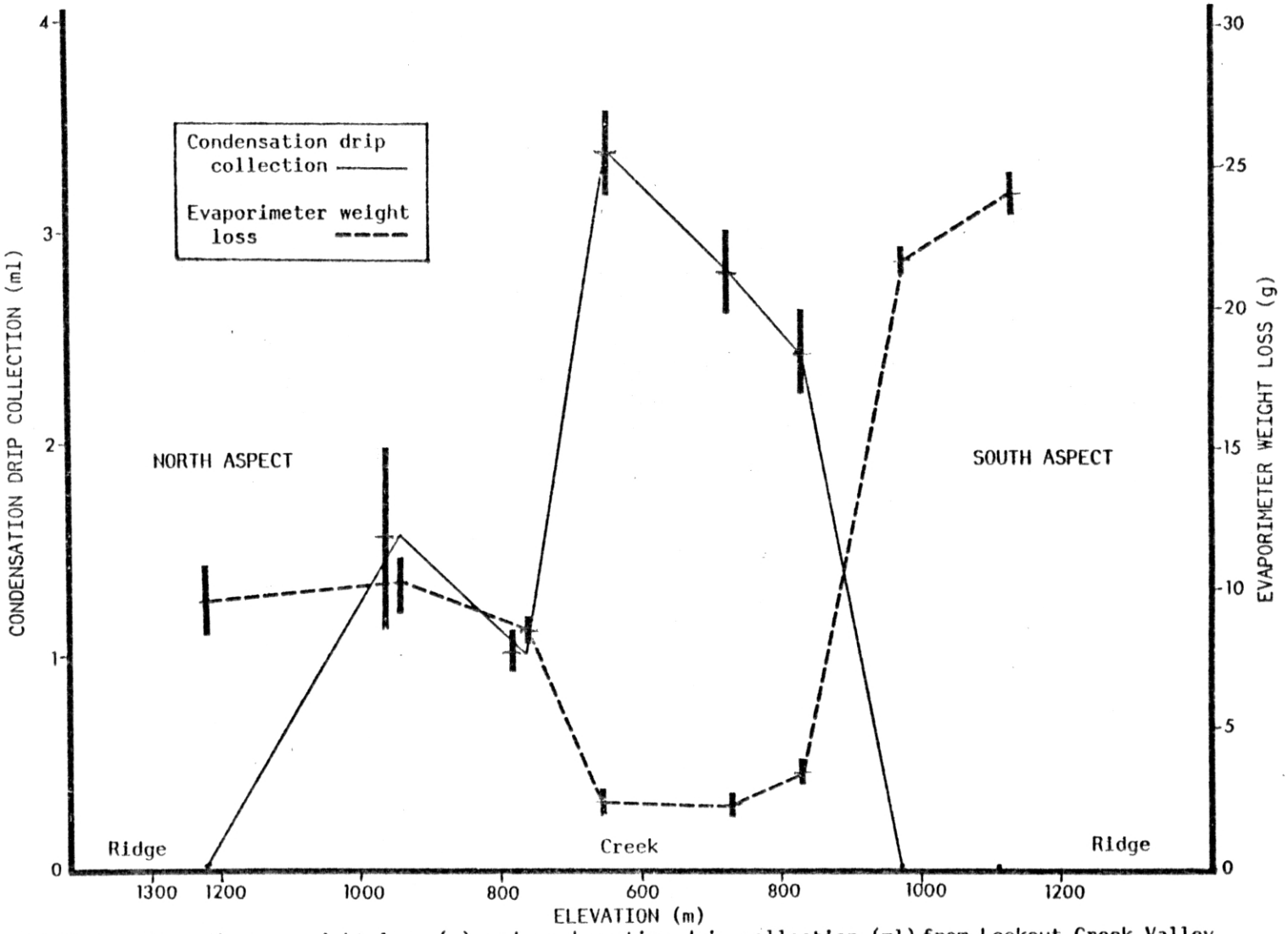


FIGURE 22. Evaporimeter weight loss (g) and condensation drip collection (ml) from Lookout Creek Valley Transect (November 9-11,1977),with standard errors.

strategy of their structure or physiology enables them to thrive in the environment of the valley stream bottoms but inhibits their growth at higher elevations farther from the stream.

Moisture seems to be the main variable in determining the distribution of cyanophiles; perhaps it is also important in determining the distribution of non-cyanophiles. The cyanophile *Lobaria oregana* is positively associated with the vertical distance from the stream (Figure 14). Non-cyanophiles such as *Alectoria sarmentosa* are negatively associated with vertical distance from the stream.

The structural form of the lichen may be the reason that moisture so strongly influences lichen distribution. *L. oregana*, with its thick, dense thallus, seems like it would retain its moisture longer than *A. sarmentosa* which is thinner and less dense with a relatively large amount of surface area. Since water loss and water absorption appear to be entirely physical, not metabolic, processes (Hale 1974; Smith 1962), structural differences may be important in determining distributional patterns of lichens.

D. Water Content Experiment

To further pursue this direction of inquiry, an experiment was devised to determine if the rates of moisture loss for *L. oregana* and *A. sarmentosa* were significantly different. It was hypothesized that the thallus of *A. sarmentosa*, once saturated, would have a higher rate of moisture loss than *L. oregana*, also

saturated. Five thalli of each species (air dry weight of approximately 5 g each) were saturated, then allowed to air dry in a closed room under constant temperature and humidity conditions. The samples were weighed at thirty-minute intervals until they reached their original air dry weight. The rate of water loss was actually lower for *A. sarmentosa* than for *L. oregana*. However, since the water holding capacity of *A. sarmentosa* is much lower than that of *L. oregana*, a given water content was reached more quickly for *A. sarmentosa* than it was for *L. oregana*. For example, *A. sarmentosa* reached a water content of 1 g water per 1 g lichen in half the time it took *L. oregana* to reach this same water content (Figure 23). There is a threshold of water content below which physiological processes of photosynthesis and respiration in the lichen practically cease (Barkman 1958). If this threshold is the same for both *A. sarmentosa* and *L. oregana*, *A. sarmentosa* would reach it much more quickly than would *L. oregana* under identical conditions.

In view of these experimental results, it seems contradictory that *A. sarmentosa* should abound in the drier high elevation stands, while *L. oregana* is restricted to the moist low elevation stands. A look at the literature provides some explanations:

1) A lichen's reaction to temperature extremes is dependent upon the moisture content of its thallus. The heat resistance of dry thalli is very high -- most species have limits upwards of 70° C for air-dried thalli (Hale 1974; Barkman 1958). However, severe

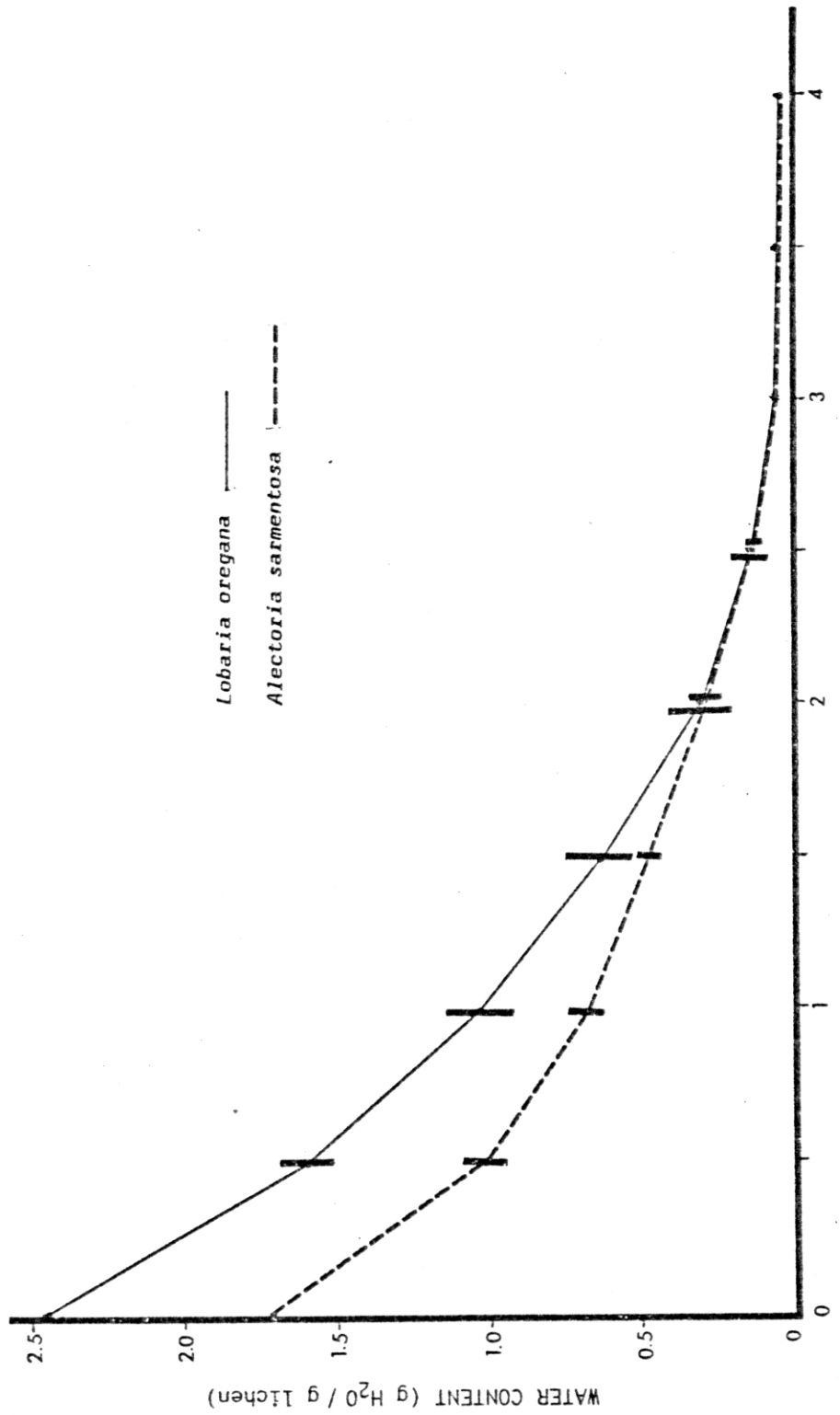


FIGURE 23. Comparison of water loss from thalli of *Lobaria oregana* and *Alectoria sarmentosa*. Initial water content represents saturation for both species. Bars represent 95% confidence intervals.

damage does occur when moist thalli are exposed to heat. *Ramilina maciformis*, a species native to the Negev Desert in Isreal, was able to withstand temperatures of over 70° C when dry, but when hydrated suffered damage at 36° C and was killed at 38° C (Lange 1969).

2) Similarly, dry thalli can withstand freezing temperatures without damage. Most moist thalli can also withstand freezing. After exposure to a temperature of -78° C for 33 hours, the phycobiont (algal component) of *Lobaria pulmonaria* returned to 94% of its original respiration rate (Kappen and Lange 1970). Under the same treatment the phycobiont of *A. sarmentosa* returned to only 3.7% of its original respiration rate. Whether experiments conducted at such temperatures have relavance for more normal temperatures is unclear.

Interpretation of the distributions of *L. oregana* and *A. sarmentosa* in light of these studies suggests that *L. oregana* may be limited to the moist lower elevation near the creek in part because occasional high summertime temperatures at the more exposed higher elevation sites would damage its moist thallus. *A. sarmentosa* would be "resistant" to damage under these conditions because of its ability to reach a lower water content faster than *L. oregana*. Its dry thallus would be resistant to heat, thus enabling *A. sarmentosa* to survive the higher temperatures of the ridges. *A. sarmentosa* is not abundant near the cooler creek bottom because it, unlike *L. oregana*, would suffer freeze damage if its thallus were moist (as it probably

would be near the creek).

When considering the effects of drought on lichens, it is the length rather than the intensity of drought that is important (Hale 1974; Smith 1962; Barkman 1958). However, since the drought resistance of most lichens (two to three months) is far in excess of what would be encountered under natural conditions, it appears that drought is not important in determining the distributions of lichens in a given habitat (Smith 1962).

V. DISCUSSION

A. Use of Litter for Studies of Lichen Distribution

Litter sampling is a novel approach. Relatively precise estimates of the standing crop of litter can be made with comparatively little effort so long as the total standing crop of lichens in the canopy is relatively large (> 500 kg ha^{-1}). Quantities of lichen material in the litter represent a cross-section of the total lichen flora in the canopy but may vary from time to time because of the seasonal nature of litterfall, decomposition, and less predictable events such as wind storms.

Litter samples from any given time represent a population of freshly fallen litter and older litter in various stages of decomposition. Variation in lichen litterfall in a nearby oak forest was found to be related to the rainfall pattern (Pike 1971). Rainfall has also been shown to promote decomposition of lichens on the floor of the oak forest (Pike 1971) and a Douglas fir stand in the AEF (Rossman, unpublished). In the above studies, one-to-two years was required for complete decomposition of lichens. Since rainfall promotes both litterfall and decomposition, these processes tend to cancel one another and variation in the standing crop of litter is likely to be damped.

During the time of initial litter sampling in 1976, a drought was occurring in the Pacific Northwest. No significant wind or rain storms occurred during this period but there may have been residual effects from prior storms. Since storms may differentially affect lichen litterfall from one reference stand to another, they may change the relative distribution of standing crops of litter and thus affect results of correlation and regression analyses. However, since the seriation and ordination analyses utilized biomass values for species normatized within stands, they would not be affected by wind as long as the proportions of the biomass of different species in the litter did not change.

That lichen litter serves as a consistent index to lichen abundance is shown by results from resampling *L. oregana* in four reference stands after winter storms in 1977 using the same sampling procedures as in the initial survey. Only one of these sites (reference stand 15) shows a significant difference in the standing crop of *L. oregana* litter at the two survey times. The relative distribution of *L. oregana* litter among these stands is the same for the two years (Figure 26).

Use of standing crop of lichen litter as an index to standing crop of lichens in the canopy assumes a strong relationship between quantities in the litter and the rates of litterfall. Since decomposition rates may vary from site to site, one may question whether standing crop of litter is likely to be a reliable indicator of the quantity of litter falling per unit

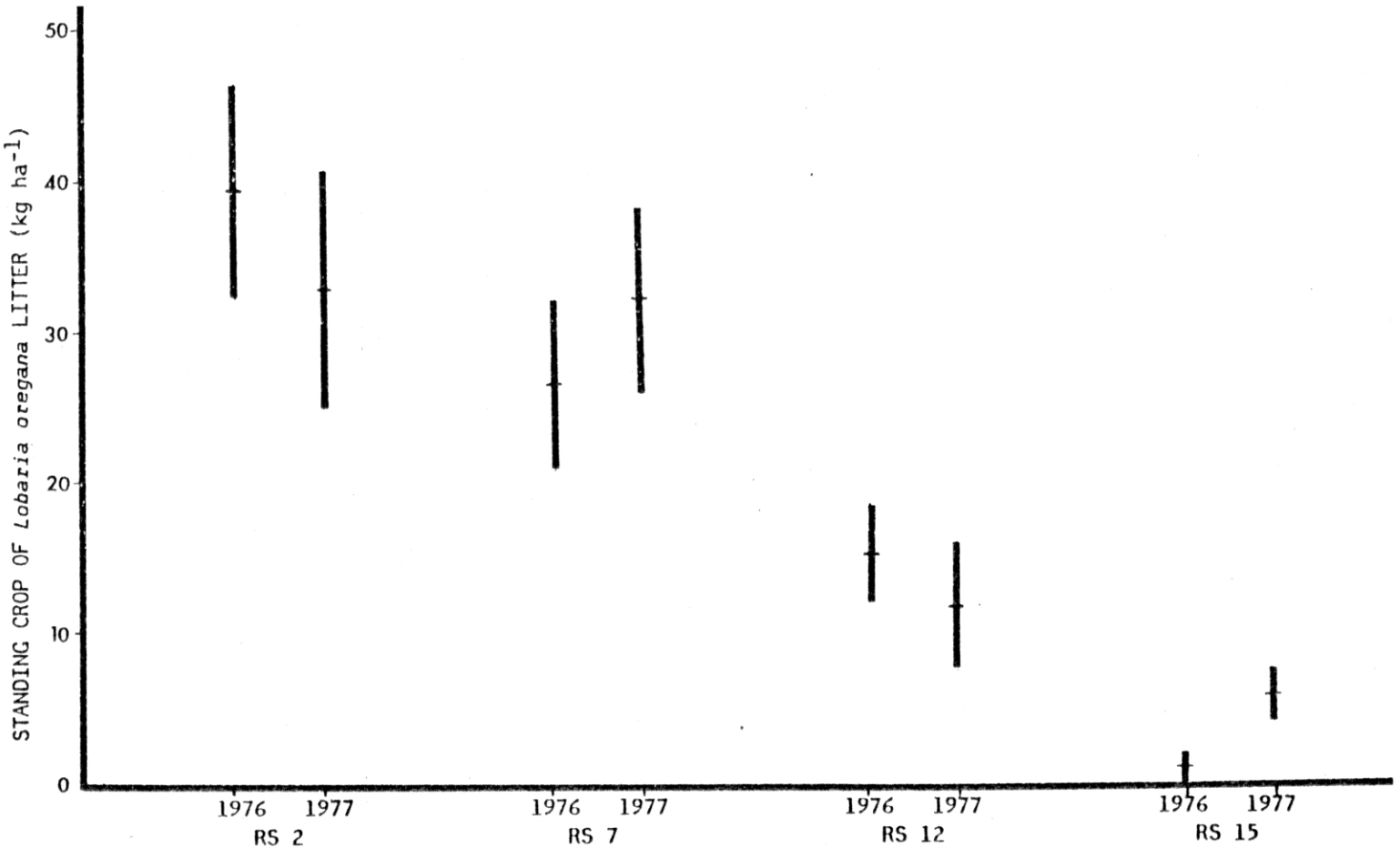


FIGURE 24. Standing crop of *Lobaria oregana* litter at four reference stands sampled both in 1976 and 1977. Vertical bars represent 95% confidence intervals.

time. In an independent study, Fred Rhoades (1978) estimated standing crop of *L. oregana* litter for 29 sites in the AEF in June 1976. He also estimated litterfall during the following year at the same sites. Analysis of logarithmically transformed data (to make variance in litterfall constant for different values of initial standing crop of litter) demonstrates that litterfall and standing crop of litter were significantly correlated ($r = 0.77$, $P < 0.001$).

B. General Factors Influencing Lichen Distributions In the AEF

During the course of this study, it soon became evident that there was not a simple explanation for the patterns of lichen distribution. The numerous, interrelated, variables potentially governing lichen distribution have been discussed by Barkman (1958). Although many of them have been discussed above, they are briefly recapped in the following paragraphs.

Host specificity among lichens of the AEF is apparently rare (Pike 1976). A few lichen species encountered in this study appeared to be more abundant on certain host trees, perhaps because of the chemistry of leachates flowing over the tree surface, i.e. differences in pH, minerals, or various organic compounds. For example, *Lobaria pulmonaria* (L.) Hoffm. was usually found growing on "cedars" -- *Thuja plicata* and *Calocedrus decurrens* (Torr.) Florin. However, since most of the sites studied were dominated by *Pseudotsuga menziesii* and a common

set of associated trees and shrubs, it is extremely unlikely that patterns observed here were due to differences from site to site in the flora of potential host trees. Strong dependencies of epiphytes on particular hosts should have been reflected by many highly significant correlations between abundance of epiphytes and abundance of various trees.

Direct interactions between various species of epiphytes will strengthen correlations in their patterns of distribution. Lichens may be chemically dependent on other lichens for a needed nutrient it obtains through a leaching and absorption process, or may compete for available space on the tree surface. A possible example of the former is *Spaerophorus globosus*, a non-cyanophile significantly positively associated with the various cyanophiles, possibly because *S. globosus* is dependent upon the nitrogen produced by them. *S. globosus* from the lower canopy of a site near reference stand 2, which has abundant *Lobaria oregana*, has a higher nitrogen content than *S. glogosus* from the upper canopy (Larry Pike, pers. comm.). Though competition for space on trees cannot be ruled as a factor affecting patterns of abundance for a given lichen species, this seems unlikely to be a factor of major importance since substantial portions of a tree's surface are not occupied by epiphytes. Furthermore, lichens with widely differing patterns of distribution (i.e. *A. sarmentosa* and *L. oregana*) occur on a wide variety of substrates but with different centers of importance (*A. sarmentosa* on twigs, *L. oregana* on axes, Pike 1976).

Patterns of lichen distribution ultimately appear to be determined by non-biological factors. Correlations can be made between the distribution of lichen species and other biological phenomena, but these in general only hint at the underlying reasons for the distributional patterns. The non-biological factors which influence lichen distribution include light, temperature, wind, and water. The role of light in lichen distribution is minor as evidenced by generally low correlation between lichen abundance and radiation patterns (Table VII) but the incoming radiation or heat energy supplied by sunlight influences whether a site is moist or dry, which in turn is a direct factor in lichen distribution. The effect of temperature extremes on moist thalli is considerable. Otherwise, temperature plays a minor role except in determining availability of water. Although wind may mechanically affect the lichen thallus by dislodging them, the major effect of wind on lichen distribution probably comes from its effect on turnover of ambient air which directly influences evaporation and condensation and, thus, the availability of moisture to lichens. Thus, many factors affect the availability of water. The quantity of precipitation is probably less important in determining lichen distributions than vascular plant distributions because lichens are not dependent on soil moisture. The frequency of rainfall, on the other hand, is relatively more important in determining lichen distributions. Although snow becomes available to vascular plants through their roots, it is unavailable to epiphytes

except for that which is trapped on tree surfaces. The length of time which lichens are in the hydrated state is strongly influenced by humidity and condensation, and seems to be a key factor in explaining lichen distributions.

Humidity is a complex phenomenon in itself. It is independent of precipitation (Barkman 1958), yet highly influenced by topography on a meso-scale and by vegetation on a micro-scale. Meso-scale humidity grades from a maximum at the creek to a minimum on the ridge top and also varies with the aspect of the slope. Micro-scale humidity gradients decrease horizontally from the center of the stand to the edge of the stand, and also vertically from the ground up through the canopy. To further complicate the dynamics of humidity, deviation from these general trends does occur.

The singling out of frequency and duration of a hydrated status as the main determinant of lichen distribution is supported by other authors: "The evaporating power of the air seems to be the condition which most affects the distribution of the lichens" (Plitt and Pessin 1924); "Fog precipitation and its and its climatic conditions favor epiphytic mosses and lichens of the *Pulmonaria* type." (meaning *Lobaria* spp.) (Kaemmer 1975); "...although temperature plays a more or less equal role in determining the distributions... (of both lichens and vascular plants)... the rôle of atmospheric humidity is perhaps of far greater importance in the case of the lichens. This is not surprising as lichens are far more directly dependent on the

atmosphere for their water supply and lack proficient means for controlling their water content" (Brown et al. 1976).

A clearcut pattern in the distribution of lichens revealed through these data is the dichotomy between cyanophiles and non-cyanophiles. The cyanophiles tend to be found at moist low-elevation sites (<1000 m) near the stream while the non-cyanophiles tend to be found at drier high elevation sites (>1000 m) far from the stream. The cyanophiles appear to be dependent on an environment where they are hydrated for long periods of time and where temperatures are not extreme during these wet periods. Non-cyanophiles appear to have adapted to conditions of frequent wetting and drying and in this way escape harmful effects of extreme temperatures in exposed locations.

C. Quantitative Comparison of Lichen-fixed Nitrogen With That of Other Sources

The amount of nitrogen fixed by cyanophiles on the AEF can be approximated on the basis of available information and a few reasonable assumptions. These quantities can then be compared with inputs from other sources. Although portions of the AEF have been recently cut or burned, these calculations are made assuming that the AEF is covered by forests of old-growth Douglas fir and that the composition of the lichen flora of the remainder of the AEF are consistant with that found in the reference stands.

It has been demonstrated that cyanophiles occur primarily below 1000 m elevation and at close distances to streams. Accord-

ingly, the biomass of cyanophiles was calculated for each of the following four zones: Zone 1) below 1000 m elevation and within 150 vertical meters of the stream; Zone 2) below 1000 m elevation and more than 150 vertical meters from the stream; Zone 3) above 1000 m elevation within 150 vertical meters of the stream; and Zone 4) above 1000 m elevation and more than 150 vertical meters from the stream (Figure 25).

The biomass of terrestrial lichens and litter of arboreal lichens for each zone was calculated by averaging the biomasses determined for sites sampled (both reference stands and transect sites) within that zone.

Although biomass of terrestrial lichens has been estimated directly, litter serves only as an index to the abundance of arboreal lichens. Results from previous studies of cyanophilous lichens in stands at approximately 500 m elevation in the AEF (Pike et al. 1972; Pike et al. 1977; and Rhoades 1978) indicate that where *Lobaria oregana* biomass in the canopy is on the order of 600 kg ha^{-1}, standing crop of *L. oregana* litter is on the order of 30 kg ha^{-1}. Thus the average values for epiphytic litter were multiplied by 20 to approximate the amount of arboreal lichens in the canopy. Production by all arboreal cyanophiles is assumed to be equal to that of *L. oregana* or 0.3 g thallus 1 g $thallus^{-1}$ $year^{-1}$ (Rhoades 1978). Relative production by *Peltigera membranacea* is on the order of 1 g 1 g $thallus^{-1}$ $year^{-1}$ (Pike, unpublished data); this value is assumed for all terrestrial cyanophiles. Assuming that a lichen fixes all of the

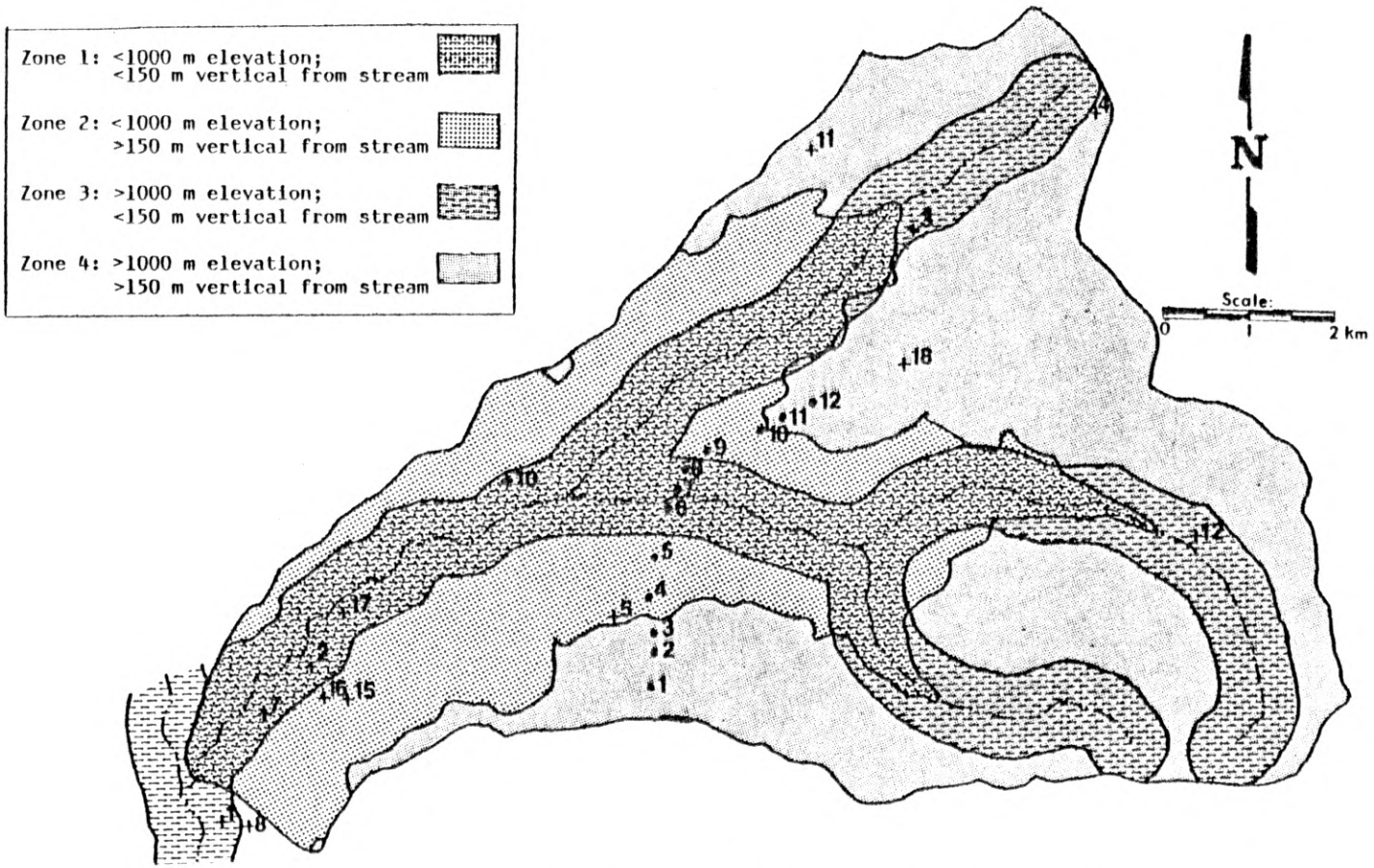


FIGURE 25. Zonal delineation of the H.J. Andrews Experimental Forest according to elevation and vertical distance from the stream. The location of each reference stand is indicated by a (+) and its appropriate reference stand number. The location of each Lookout Creek transect site is designated by a (•) and its appropriate transect site number. The amount of atmospheric nitrogen fixed in each zone, under the assumptions given, is: Zone 1--6731 kg yr^{-1}; Zone 2--1175 kg yr^{-1}; Zone 3--1407 kg yr^{-1}; and Zone 4--200 kg yr^{-1}.

nitrogen necessary for its growth and no more and that the average nitrogen concentrations for arboreal and terrestrial cyanophiles are 2% and 2.75% respectively (Pike 1972) the following formulae may be used to estimate the amount of nitrogen found within each zone:

For Epiphytic Lichens --

Mean Epiphytic Litter Biomass (kg ha^{-1}) X 20 X 0.3(g $g^{-1}yr^{-1}$) X 0.02(g g^{-1}) = Total Nitrogen Fixed $Year^{-1}$;

For Terrestrial Lichens --

Mean Terrestrial Biomass (kg ha^{-1}) X 1.0(g g^{-1} yr^{-1}) X 0.0275 (g g^{-1}) = Total Nitrogen Fixed $Year^{-1}$.

By combining the above formulae, the total nitrogen fixed per hectare per year can be calculated for each zone (Table XIV):

Zone 1 =(35.9 x 20 x 0.3 x .02) + (7.8 x 1.0 x 0.0275) = 4.52 (kg ha^{-1} yr^{-1});

Zone 2 =(6.0 x 20 x 0.3 x .02) + (1.9 x 1.0 x 0.0275) = 0.77 (kg ha^{-1} yr^{-1});

Zone 3 =(12.2 x 20 x 0.3 x .02) + (0) = 1.46 (kg ha^{-1} yr^{-1});

Zone 4 =(0.5 x 20 x 0.3 x .02) + (0.4 x 1.0 x 0.0275) = 0.07 (kg ha^{-1} yr^{-1}).

A polar planimeter was used to determine the area within each zone, and the nitrogen fixation rates (kg ha^{-1} yr^{-1}) were multiplied by the area of the zone to expand estimates of nitrogen fixed annually to zone totals.

TABLE XIV. Estimated biomass (kg ha^{-1}) of terrestrial and arboreal nitrogen-fixing lichens in the H.J. Andrews Experimental Forest by zone. Biomass of arboreal lichens was approximated by multiplying litter estimates by 20. Abbreviations - RS (reference stand), T (transect), VDSTR (vertical distance from stream)

	Site	*Peltigera membranacea*	*Lobaria oregana*	Total Terr. Cyanophiles	Total Arboreal Cyanophiles	TOTAL (Terr. + Arb.)
ZONE 1 1000m elev. & 150m VDSTR	RS 1	8.8	388	43.1	392	435.1
	RS 2	0.9	784	1.0	802	803.0
	RS 7	5.9	524	8.1	608	616.1
	RS 10	3.7	476	8.8	502	510.8
	RS 17	0	890	0.1	942	942.1
	T 6	0.2	838	0.5	1288	1288.5
	T 7	0.5	654	0.7	728	728.7
	T 8	0	416	0.1	486	486.1
	$\bar{X}$	2.5	622	7.8	718	726.3
	$S_{\bar{X}}$	1.2	70	5.2	104	100.8
ZONE 2 1000m elev. & 150m VDSTR	RS 5	0	92	0	94	94.0
	RS 8	2.5	38	4.1	52	56.1
	RS 15	0	20	0	102	102.0
	RS 16	0	20	0.6	22	22.6
	T 4	0	172	0	192	192.0
	T 5	0	223	0.2	284	284.2
	T 9	0.6	162	10.3	198	208.3
	T 10	0.2	14	0.2	16	16.2
	$\bar{X}$	0.4	94	1.9	120	121.9
	$S_{\bar{X}}$	0.3	30	1.3	34	34.1
ZONE 3 1000m elev.& 150m VDSTR	RS 13	0	110	0	182	182.0
	RS 12	0	306	0	308	308.0
	$\bar{X}$	0	208	0	244	244.0
	$S_{\bar{X}}$	0	98	0	64	64.0
ZONE 4 1000m elev. & 150m VDSTR	RS 4	0	0	0	0	0
	RS 11	0	0	0	0	0
	RS 18	0	0	0	0	0
	T 1	0	0	0.1	2	2.1
	T 2	0	26	0	26	26.0
	T 3	1.3	40	2.4	40	42.4
	T 11	0.3	2	0.9	8	8.9
	T 12	0.1	0	0.1	0	0.1
	$\bar{X}$	0.2	8	0.4	10	9.9
	$S_{\bar{X}}$	0.2	6	0.3	6	5.6

Zone 1 = 4.52(kg ha^{-1} yr^{-1}) x 1489.25 ha = 6731.41 kg yr^{-1}.

Zone 2 = 0.77(kg ha^{-1} yr^{-1}) x 1525.51 ha = 1174.64 kg yr^{-1}.

Zone 3 = 1.46(kg ha^{-1} yr^{-1}) x 963.48 ha = 1406.68 kg yr^{-1}.

Zone 4 = 0.07(kg ha^{-1} yr^{-1}) x 2864.54 ha = 200.52 kg yr^{-1}.

Total = 9513.25 kg yr^{-1}.

If computations are made for arboreal and terrestrial lichens, arboreal lichens are estimated to be more than 20 times as important as terrestrial lichens as a source of fixed nitrogen. This conclusion applies only to old-growth forests and preliminary information (Pike, Howe and Topik, unpublished) from the AEF indicates that the converse is true for successional stands. These estimates of lichen-fixed nitrogen are conservative since an additional (small?) quantity of fixed nitrogen is leached from lichens and is not used for growth (Carroll et al. 1977; Pike 1978).

Other natural sources of reduced nitrogen in addition to lichens include precipitation and fixation by symbiosis involving vascular plants and nitrogen-fixing microbes. The number of vascular plant species with nitrogen-fixing symbionts in the AEF (Franklin and Dyrness 1971) is approximately one-half the number of nitrogen-fixing lichens reported here. The bulk of these are legumes which are relatively restricted to recently disturbed sites such as fresh roadcuts and clearcuts. Two nitrogen-fixing vascular plants, red alder (*Alnus rubra*) and snow brush (*Ceanothus velutinus* Dougl.) are widespread and locally abundant, persist for years in a given location, and have

received some attention by researchers.

The nitrogen input from precipitation is equal to approximately 1 kg ha^{-1} yr^{-1} (Gessel et al. 1972). In studies conducted by Tarrant et al. (1969), the nitrogen input from litterfall and enriched throughfall precipitation is equal to approximately 84 kg ha^{-1} yr^{-1} in mixed red alder/conifer stands. However, this cannot be considered equivalent to the quantity of nitrogen fixed since the quantity of litter returned to the forest floor in oak forests of the Willamette Valley is on the order of 70-80 kg ha^{-1} yr^{-1} (Pike 1971), and oak (*Quercus*) is not a nitrogen-fixer. The annual nitrogen-fixation rate in stands of *Ceanothus velutinus* with an average cover of 80% is estimated not to exceed 20 kg nitrogen ha^{-1} (Zavitkovski et al. 1968). Alder and *Ceanothus* may represent significant sources of nitrogen for young forests but not in mature Douglas fir forests where they have been shaded out.

Jones (1970) has raised the possibility of significant fixation of nitrogen by epiphytic bacteria on needle surfaces. However, Jones' observations were made on Douglas fir plantations in England and attempts to detect fixation by these bacteria in the AEF have consistantly yielded negative results (E. Sukoff, unpublished observations). Thus lichens appear to be important sources of fixed nitrogen especially in forests of Zone 1. The quantity of nitrogen fixed annually by lichens in Zone 1 estimated here as 4.5 kg nitrogen ha^{-1} yr^{-1} is midway in the range of 1-10 kg nitrogen ha^{-1} yr^{-1} estimated earlier by Denison (1973)

for *Lobaria oregana*.

Artificial input of nitrogen by the forest industry in the form of urea fertilizer (46% nitrogen) is typically applied at rates of 168-224 kg ha^{-1} $5yr^{-1}$ (Miller et al. 1976; personal communication with S.P. Gessel, 1978; and personal communication with Weyerhaeuser forester Ed Baker, 1978). This is equivalent to approximately 15-20 kg nitrogen ha^{-1} yr^{-1}. The amount of applied nitrogen is effectively decreased by volatilization. This occurs when the urea is converted to ammonia and lost to the atmosphere. These losses have been measured under both field and laboratory conditions. However, discrepancies exist between sources as to the extent of these volatilization losses. Studies by Crane (1972) and Cole et al. (1975) indicate that volatilization losses seldom exceed 10%. Other studies have found that losses up to 46% (Watkins et al. 1972) and 50% (personal communication with R.E. Miller, 1978) can occur. In addition, Miller (1976) indicates that "If stands are refertilized with urea at 4 to 6 year intervals, higher volatilization losses and increased nitrification with perhaps greater likelihood of leaching could occur." Thus, the amount of nitrogen applied through urea fertilization may be reduced by volatilization to an effective rate of 7.5-10 kg ha^{-1} yr^{-1}. The effective fertilization rate and the rate of addition by lichens are perhaps roughly comparable. Lichen-fixed nitrogen is made available to the remainder of the ecosystem more or less continually through processes of litterfall, decomposition, and leaching.

Thus, large losses to the atmosphere are not expected.

These estimates of quantities of nitrogen fixed by lichens are based only on old-growth forests. Lichens do occur in younger forests, however, and whether those lichens (either naturally or under management) can provide fixed nitrogen at a rate comparable to that at which nitrogen in fertilizer is applied by the forest industry is an open question.

VI. SUMMARY

Lichen distribution and abundance were studied in mature forest stands in the H.J. Andrews Experimental Forest (AEF) in the western Cascades of Oregon. Distributions of terrestrial species were obtained from direct estimates of standing crop of lichen biomass, and of epiphytic species were inferred from distributions of the standing crop of epiphytic litter. Standing crops were estimated from quadrats following a systematic random sampling design.

Forty-six cyanophilous lichen species are now known to occur in the AEF. They grow on a variety of substrates -- soil, rock, moss, bark -- nearly equally divided between ground-dwellers and epiphytes.

The biomass of the terrestrial cyanophiles ranged from complete absence to 43 kg ha^{-1}. The standing crop of litter of arboreal cyanophiles ranged from 0 to 47 kg ha^{-1}. The maximum biomass of both terrestrial and arboreal cyanophiles occurred at approximately 500 m elevation, the lower elevational boundary of the AEF. Standing crop of litter of arboreal non-cyanophiles ranged from 3 kg ha^{-1} to 80 kg ha^{-1}, with maximum biomass occurring at elevations greater than 900 m.

Several major patterns seemed evident from correlations between the 21 most abundant lichen species and sixty-one

environmental variables. Of the terrestrial cyanophiles, species of the genus *Peltigera* showed highly significant positive correlation with the cover of bare soil and degree of moisture stress experienced by vascular plants. Of the arboreal cyanophiles, *Lobaria oregana* and *Nephroma bellum* showed highly significant positive correlation with estimates of moss cover. *L. oregana* also showed significant negative correlation with elevation and vertical distance above the major streams. Of the arboreal non-cyanophiles, *Alectoria sarmentosa* and *Platismatia stenophylla* showed consistent negative correlation with all the temperature variables. *A. sarmentosa* also showed significant positive correlation with elevation and vertical distance from the major streams.

Seriation and ordination resulted in two highly-correlated orderings of the reference stands along what is probably a complex gradient representing, in part, water stress to the lichens. Analysis of similarities in patterns of lichen distribution illustrates the relative positions of lichens along this gradient and demonstrates two distinct patterns of association. Cyanophiles tend to occur with other cyanophiles and non-cyanophiles with other non-cyanophiles; the only exception is *Sphaerophorus globosus* a non-cyanophile which has a pattern of distribution significantly similar to that of several cyanophiles alone.

Distribution of lichen biomass in relation to a major stream was analyzed by sampling along a transect across the

Lookout Creek Valley. The bulk of the biomass of cyanophilous lichens was found within 150 vertical meters of the creek. This "creek-bottom" environment was demonstrated to experience relatively high volumes of canopy drip and relatively little evaporation during a brief period of meteorological observations in November, 1977.

An estimate of the significance of cyanophiles in mature forests can be made based on current information on their turnover rates, nitrogen content, and biomass. The cyanophiles may contribute 4.5 kg ha^{-1} yr^{-1} in Zone 1 (below 1000 m elevation and within 150 vertical meters from the stream) but much less in other zones. The quantity of nitrogen fixed by lichens in Zone 1 appears significant when compared to the quantity of nitrogen required for wood accumulation in a mature forest and when compared to the nitrogen input in mature forest stands from sources such as precipitation and nitrogen fixation by other symbiotic organisms and free-living bacteria such as occur in rotting logs.

APPENDIX I. Annotated listing of all the nitrogen-fixing lichen species observed in the H.J. Andrews Experimental Forest during the course of this study. Each listing contains: the name of the lichen; a short description of its habitat and abundance; the vegetational zone in which it occurs; and reference to herbarium specimens. This listing is a synthesis of observations made in this study with previous reconnaissance studies of lichen species in the AEF (Pike 1972; Pike et al. 1975). The zonal classifications are: 1) *Tsuga heterophylla* (TSHE) at elevations less than 1000 m; and 2) *Abies amabilis* (ABAM) at elevations greater than 1000 m. The herbarium specimens cited were examined in either the University of Oregon Herbarium (ORE) or the Oregon State University Herbarium (OSC). All specimens cited were collected in the AEF.

Hydrothyria venosa Russ. Locally abundant, submerged in fast moving streams. Zone: TSHE; probably ABAM. Specimens examined: Denison (OSC 29528); Becking (OSC 33399); Wagner (ORE 55391).

Koerberia sonomensis (Tuck.) Henss. Occasional on rocks in exposed areas at all elevations. Zone: TSHE & ABAM. Specimen examined: Pike (OSC 31479); Howe (ORE 77635).

Leptochidium albociliatum (Desm.) Choisy On moss-covered rocks in dry, open sites. Apparently uncommon in the AEF. Zone: TSHE. Specimens examined: Topik (ORE 77634).

Leptogium californicum Tuck. Occasional on soil or mosses in dry, open areas. Zone: TSHE & ABAM. Specimens examined: Topik (ORE 77633).

L. lichenoides (L.) Zahlbr. Locally abundant on soil or mosses. Often associated with disturbances. Zone: TSHE & ABAM. Specimens examined: Pike (OSC 32545); Topik (ORE 77632); Topik (ORE 79869).

L. palmatum (Huds.) Mont. Abundant on soil and among mosses in disturbed areas, particularly if dry and open. Zone: TSHE. Specimens examined: Denison (OSC 29221); Pike (OSC 31729); Pike (OSC 31306).

L. platynum Herre Infrequently found on soil or mosses both in dry and moist sites. Zone: TSHE. Specimens examined: Topik (ORE 79870).

L. rivale Tuck. Locally abundant, submerged to emergent in fast moving streams. Zone TSHE. Specimens examined: Wagner (ORE 55401); Topik (ORE 79871).

Leptogium sinuatum (Huds.) Mass. Widespread on mosses. Terrestrial in dry, open sites; epiphytic on understory trees and shrubs in moist sites. Zone: TSHE. Specimens examined: Pike (OSC 33269); Topik (ORE 79872).

L. tenuissimum (Dicks) Fr. Common on freshly exposed surfaces of deeply-weathered rocks in dry sites. Zone: TSHE. Specimens examined: Leuthner (OSC 31143); Pike (OSC 31114); Pike (OSC 32570).

Lobaria oregana (Tuck.) Müll. Arg. Abundant in canopy of conifers of moderate to low elevations. Rarely on mossy rocks. Zone: TSHE. Specimens examined: Tracy (OSC 30719); Nielsen (OSC 29231).

L. pulmonaria (L.) Hoffm. Locally abundant in canopy of conifers and understory hardwoods of moderate to low elevations. Often associated with *Calocedrus* and *Thuja*. Zone: TSHE. Specimens examined: Tracy (OSC 33545); Nielsen (OSC 30720).

L. scrobiculata (Scop.) DC. Common on understory hardwoods and in canopy of conifers of moderate to low elevations. Zone: TSHE. Specimens examined: Howe (ORE 79873); Howe (ORE 79874).

Massalongia carnosa (Dicks.) Körb. Frequent on rocks in exposed areas. Zone: ABAM. Specimens examined: Pike (OSC 31474); Howe (ORE 79876); Topik (ORE 79875).

Nephroma bellum (Spreng.) Tuck. Frequent on trees and understory of the moister sites of moderate to low elevation. Zone: TSHE. Specimens examined: Denison (OSC 30574); Tracy (OSC 33574); Nielson (OSC 30715).

N. helveticum Ach. Occasional on understory of the lower elevation moister sites. Zone: TSHE. Specimens examined: Pike (OSC 33536); Tracy (OSC 30716); Vander Schaaf (ORE 52408).

N. laevigatum Ach. Frequent on understory of the lower elevations in moist sites. Zone: TSHE. Specimens examined: Pike (OSC 33535); Pike (OSC 31063); Vander Schaaf (ORE 52351).

N. parile (Ach.) Ach. Occasional on mosses and bark. In the dry, open sites of low to higher elevation it occurs on mossy rocks. In the moist sites of lower elevations it occurs in the canopy. Zone: TSHE & ABAM. Specimens examined: Tracy (OSC 33546); Vander Schaaf (ORE 52426).

N. resupinatum (L.) Ach. Occasional Primarily on understory in both dry and moist habitats. Zone: TSHE. Specimens examined: Pike (OSC 30750); Vander Schaaf (ORE 52412).

Nephroma sp. (yellow undescribed) Common in canopy in the moister sites of moderate to low elevation. Zone: TSHE. Specimens examined: Topik (ORE 79877).

Parmeliella cyanolepra (Tuck.) Herre Locally abundant on soil and rock protected by overhanging rock in dry sites. Zone: TSHE. Specimens examined: Pike (OSC 31113).

P. microphylla Müll. Arg. Occasional on rocks on exposed ridge-tops. Zone: ABAM. Specimens examined: Pike (ORE 79878).

P. saubinetii Zahlbr. Ubiquitous in the TSHE zone. Specimens examined: Pike (OSC 31091); Pike (OSC 31414); Tracy (OSC 31149).

Peltigera aphthosa (L.) Willd. Abundant in dry sites on soil. Occasional in wet sites on trees. Similar in appearance and distribution to *P. leucophlebia*, but grows in slightly drier habitats. Zone: TSHE. Specimens examined: Tracy (OSC 33141); Topik (ORE 52401); Topik (ORE 52400).

P. canina (L.) Willd. Occasional on soil in open somewhat disturbed sites. Zone: TSHE. Specimens examined: Pike (OSC 32526); Topik (ORE 52376); Topik (ORE 52402).

P. collina (Ach.) Ach. Widespread, both terrestrial and epiphytic, on soil and over moss. Zone: TSHE. Specimens examined: Pike (OSC 31288); Topik (ORE 78978); Topik (ORE 79859).

P. leucophlebia (Nyl.) Gyeln. Grows in slightly moister habitats than *P. aphthosa* and is less common as an epiphyte than *P. aphthosa*. Zone: TSHE. Specimens examined: Howe (ORE 52383); Topik (ORE 79860).

P. membranacea (Ach.) Nyl. Locally abundant on soil and terrestrial mosses in successional stands of *Pseudotsuga menziesii*. Less abundant in various disturbances of old forests. Zone: TSHE. Specimens examined: Pike (OSC 31300); Leuthner (OSC 30740); Topik (ORE 52385).

P. polydactyla (Neek.) Hoffm. Occasional on moss and soil. Zone: TSHE. Specimens examined: Howe (ORE 52403); Pike (OSC 31299); Topik (ORE 52415).

P. praetextata (Somm.) Vain. Locally abundant in dry sites. Seems to take the place of *P. membranacea* on soil in disturbed areas. Has both fine coralloid isidia and flattened regeneration squamules. Zone: TSHE. Specimens examined: Howe (ORE52368); Topik (ORE 79861).

P. rufescens (Weis.) Humb. Common on soil in the low elevation dry sites and especially at high elevations in exposed areas. Zone: TSHE & ABAM. Specimens examined: Pike (OSC 32569); Topik (ORE 52404).

Peltigera spuria (Ach.) DC. Frequent on soil in disturbed sites. In moister sites of lower elevations. Zone: TSHE. Specimens examined: Pike (OSC 31324); Pike (OSC 31424); Topik (ORE 52372).

P. venosa (L.) Baumg. Infrequent on soil in the dryer open sites of lower elevations. Zone: TSHE. Specimens examined: Topik (ORE 52399); Topik (ORE 79862).

Pilophoron acicularis (Ach.) Nyl. Frequent yet seldom abundant on rock in both the dry and moist sites of the lower elevations. Zone: TSHE. Specimens examined: Rhoades (OSC 30667); Pike (OSC 31129).

P. clavatus Th. Fr. Occasional on rocks at higher elevations. Only rarely and at elevations of approximately 1000 m do *P. clavatus* and *P. acicularis* cooccur. Zone: ABAM. Specimens examined: Pike (OSC 31486).

Placopsis gelida (L.) Linds. Occasional on rocks in exposed and disturbed sites of lower elevations. Zone: TSHE. Specimens examined: Pike (OSC 31097); Topik (ORE 79863).

Polychidium muscicola (Sw.) S. Gray Infrequent (?) on mosses in exposed sites. Zone: ABAM. Specimens examined: Topik (ORE 79868).

Pseudocyphellaria anomala Magn. Frequent epiphytes in the moister low elevation sites. Zone: TSHE. Specimens examined: Tracy (OSC 30659); Topik (ORE 79867).

P. anthraspis (Ach.) D. Gall. + P. James Frequent epiphytes in the moister low elevation sites. Zone: TSHE. Specimens examined: Tracy (OSC 30660); Tracy (OSC 34515); Pike (OSC 33749).

P. crocata (L.) Vain. Infrequent in moister low elevation sites. Zone: TSHE. Specimens examined: Nielsen (OSC 30661); Topik (ORE 79866).

P. rainierensis Imsh. Occasional locally abundant in the moist sites of the low elevations. Zone: TSHE. Specimens examined: Pike (OSC 33712); Pike (OSC 32527); Pike (OSC 30762).

Psoroma hypnorum (Vahl.) S. Gray Infrequent on epiphytic mosses. In the moist low elevation sites and at higher elevations. Zone: TSHE & ABAM. Specimens examined: Pike (OSC 32521); Topik (ORE 79865).

Stereocaulon sp. (Has poorly developed pseudopodetia) Rarely found in disturbed sites. Zone: TSHE. Specimens examined: Pike (OSC 31472).

Sticta fuliginosa (Dicks.) Ach. Infrequent in moist lower elevation sites. Zone: TSHE. Specimens examined: Topik (ORE 79864).

S. limbata (Sm.) Ach. Infrequent. Zone: TSHE.
Specimens examined: No herbarium specimens found.

S. weigelii (Ach.) Vain. Infrequent. Zone: TSHE.
Specimens examined: Tracy (OSC 30751); Topik (ORE 79858).

APPENDIX II. Biomass (kg ha^{-1}) of all lichens sampled in the H.J. Andrews Experimental Forest during this study. The biomass for each species is given for each reference stand, which are arranged in order of increasing elevation. The following is an alphabetical listing of the names of the lichens and their respective abbreviations.

LICHEN NAME	ABBREVIATION
Alectoria sarmentosa (Ach.) Ach.	ALSA
Bryoria spp.	BRSP
Cetraria canadensis Räs.	CECA
C. chlorophylla (Willd.) Vain.	CECH
C. idahoensis Essl.	CEID
C. merrillii DR.	CEME
C. orbata (Nyl.) Fink	CEOR
C. pallidula Tuck.	CEPA
C. platyphylla Tuck.	CEPL
Hypogymnia enteromorpha (Ach.) Nyl.	HYEN
H. imshaugii Krog	HYIM
H. inactiva (Krog) Ohlsson	HYIN
H. metaphysodes (Asah.) Rass.	HYME
H. physodes (L.) Nyl.	HYPH
H. "rugosa" = Parmelia physodes var. *enteromorpha* f. *rugosa* Merr.	HYRU
H. tubulosa (Schaer.) Hav.	HYTU
Leptogium palmatum (Huds.) Mont.	LEPA
L. sinuatum (Huds.) Mass.	LESI
L. tenuissimum (Dicks) Fr.	LETE
Lobaria oregana (Tuck.) Müll. Arg.	LOOR
L. pulmonaria (L.) Hoffm.	LOPU
L. scrobiculata (Scop.) DC.	LOSC
Nephroma bellum (Spreng.) Tuck.	NEBE
N. helveticum Ach.	NEHE
N. laevigatum Ach.	NELA

APPENDIX II. continued...

LICHEN NAME	ABBREVIATION
Parmelia pseudosulcata Gyeln.	PAPS
Parmeliella saubinetii Zahlbr.	PASA
Parmeliopsis hyperopta (Ach.) Arn.	PAHY
Peltigera aphthosa (L.) Willd.	PEAP
P. collina (Ach.) Ach.	PECO
P. leucophlebia (Nyl.) Gyeln.	PELE
P. membranacea (Ach.) Nyl.	PEME
P. polydactyla (Neck.) Hoffm.	PEPO
P. praetextata (Somm.) Vain.	PEPR
Pilophoron acicularis (Ach.) Nyl.	PIAC
P. clavatus Th. Fr.	PICL
Platismatia glauca (L.) W.Culb & C.Culb	PLGL
P. herrei (Imsh.) W.Culb. & C.Culb	PLHE
P. stenophylla (Tuck.) W.Culb. & C.Culb	PLST
Pseudocyphellaria anomala Magn.	PSAN
P. anthraspis (Ach.) D.Gall + P.James	PSAT
P. crocata (L.) Vain.	PSCR
Sphaerophorus globosus (Huds.) Vain.	SPGL
Sticta fuliginosa (Dicks.) Ach.	STFU
S. weigelii (Ach.) Vain.	STWE
Usnea spp.	USSP

APPENDIX II. continued... Mean Biomass (kg ha^{-1}) for Terrestrial Cyanophiles

Reference Stand	Elevation (m)	Aspect	Slope(°)	PECO	PEAP + PELE	PEME	PEPO	PEPR	LEPA	LESI	LETE	PIAC	PICL	PASA
7	490	NNW	18			5.88	2.23							0.01
8	500	WNW	40		0.56	2.46	0.08			0.02				0.05
1	510	SW	35	0.03	26.55	8.78	3.46	2.48	0.01	0.10	0.01	0.58		0.82
2	520	WNW	20			0.08	0.01							0.01
17	530	N	18		0.04									
10	670	SW	5		3.46	3.75	0.16							
16	670	SW	40	T*	0.42			0.01						0.03
15	720	NNW	45											
5	920	NE	8											
3	950	W	10											
12	1020	WNW	5											
11	1060	SE	25											
18	1080	SE	30											
4	1440	WNW	10											
13	1480	S	15											
14	1570	NW	15											

*T signifies trace amount

APPENDIX II. continued... Mean Biomass (kg ha^{-1}) for Arboreal Cyanophiles

Reference Stand	Elevation (m)	Aspect	Slope (°)	LOOR	LOPU	LOSC	PSCR	PSAN	PSAT	STFU	STWE	NEBE	NEHE	NELA
7	490	NNW	18	26.23	2.54			0.96	0.66			0.04		
8	500	WNW	40	1.88	0.32				0.03			T*		
1	510	SW	35	19.40								0.01		0.01
2	520	WNW	20	39.21	0.18	0.29	0.02	0.03	0.16	0.01	0.01	0.18		T
17	530	N	18	44.50				0.10	0.01			0.02		
10	670	SW	5	23.76		0.01		0.59	0.22	T	T	T	T	
16	670	SW	40	1.04	0.01									
15	720	NNW	45	1.04	3.60	0.01		0.28	0.65			0.01		
5	920	NE	8	4.56				0.01				T		
3	950	W	10	5.46	2.53				1.08					
12	1020	WNW	5	15.28	0.08			0.03				0.07	0.03	
11	1060	SE	25											
18	1080	SE	30											
4	1440	WNW	10											
13	1480	S	15											
14	1570	NW	15											

*T signifies trace amount

APPENDIX II. continued... Mean Biomass (kg ha^{-1}) for Arboreal Non-cyanophiles

Reference Stand	Elevation (m)	Aspect	Slope (°)	ALSA	BRSP	USSP	SPGL	CECA	CECH	CEID	CEME	CEOR	CEPA	CEPL	PAPS
7	490	NNW	18	0.10		0.36	1.01								
8	500	WNW	40	2.09	0.01	1.04	1.08				T*			T	
1	510	SW	35	6.62	0.01	3.14	9.65		0.05					T	T
2	520	WNW	20	0.06	T	0.14	1.51								T
17	530	N	18	0.02	T		1.25								
10	670	SW	5	0.28		0.08	2.72								
16	670	SW	40	7.46	0.03	1.82	1.70				T			T	T
15	720	NNW	45	2.09	0.04	1.27	0.72								
5	920	NE	8	46.69	0.56	3.87	3.96		0.04	0.60				0.05	
3	950	W	10	3.85	0.02	0.01	0.45				T				0.01
12	1020	WNW	5	4.66	0.69	0.06	4.87								T
11	1060	SE	25	0.55	0.07	0.68		T					T		T
18	1080	SE	30	11.95	0.41	1.63	2.10			0.11	T			0.06	T
4	1440	WNW	10	11.13	0.30	0.03			T	T		T	T	0.01	
13	1480	S	15	13.63	2.08	0.51								0.22	
14	1570	NW	15	54.97	14.80	0.30					T			0.05	

*T signifies trace amount

APPENDIX II. continued... Mean Biomass (kg ha^{-1}) for Arboreal Non-cyanophiles

Reference Stand	Elevation (m)	Aspect	Slope (°)	HYEN	HYIN	HYIM	HYME	HYPH	HYRU	HYTU	PLGL	PLHE	PLST	PAHY
7	490	NNW	18	0.55	0.32	0.22		T*			0.95		0.03	
8	500	WNW	40	1.25	0.47	0.41		T			0.41	0.18		
1	510	SW	35	3.11	2.82	2.79		T			1.20	1.06	0.15	
2	520	WNW	20	0.94	0-39	0.21		0.01			0.27	0.14	0.05	
17	530	N	18	0.80	0.12	0.09	0.10	0.01			0.53	0.02		
10	670	SW	5	2.28	0.73	0.92		0.07			0.65	0.18	T	T
16	670	SW	40	1.33	1.83	0.92		0.01		T	1.21	0.24	T	
15	720	NNW	45	1.14	1.50	0.55		0.06			2.28	0.26	0.05	T
5	920	NE	8	2.19	1.00	2.33		0.01	0.01		9.61	2.78	0.23	T
3	950	W	10	1.33	0.31	0.38		0.13			3.60	0.38	T	T
12	1020	WNW	5	1.06	0.59	0.14		0.07			5.32	0.65	0.08	
11	1060	SE	25	2.61	1.09	2.88			0.29		3.72	1.21	0.76	
18	1080	SE	30	5.48	0.67	5.57	T				7.16	3.28	0.67	
4	1440	WNW	10	0.73	3.06	0.69		0.04	0.38		8.76	2.32	6.59	T
13	1480	S	15	1.06	1.26	1.22		0.08	1.05		2.05	0.34	0.23	0.06
14	1570	NW	15	1.78	0.85	0.59		T	0.02			T	9.42	

*T signifies trace amount

APPENDIX III. Quantitative values for all environmental variables measured at each reference stand which are arranged in order of increasing elevation. The following is a listing of all the variables, their units, the source of the data, and explanations if appropriate.

Variable Name	Units	Source of Data	Explanation
Elevation	m	This study	Measured with altimeter which was calibrated by nearby U.S.G.S. benchmarks.
Aspect	degrees	Zobel et al. (1976)	Deviation from S=0; W,E=90; N=180.
Slope	degrees	Zobel et al. (1976)	
Mean Quadrat Slope	degrees	This study	See text. Avg.28quads.
Mean Quadrat Aspect	degrees	This study	Deviation from S=0; W,E=90; N=180. Avg. of 28 quadrats.
Aspect Code		This study	N & E = 1; S & W = 0.
Height of Angle of Ridge to SE,S,& SW.	degrees	This study	Taken off contour map.
Vertical Dist. From Stream.	m	This study	Taken off contour map to nearest major stream
Vertical Dist. From Ridge	m	This study	Taken off contour map to nearest major ridge
% Cover of Bare Soil&Rock	%	This study	
Soil pH of A1 Horizon	pH	Brown & Parsons (IBP Data Bank)	
Base Satuation of A1 Horizon	%	Brown & Parsons (IBP Data Bank)	Calculated from data given in their study
Exchangeable Calcium in A1 Horizon	kg ha^{-1}	Brown & Parsons (IBP Data Bank)	

APPENDIX III. continued...

Variable Name	Units	Source of Data	Explanation
Nitrogen in A1 Horizon	kg ha^{-1}	Brown & Parsons (IBP Data Bank)	
Mean and Maximum, January & July Radiation	ly day^{-1}	Bill Emmingham (IBP Data Bank)	Corrected from Central Meteorological Station for elevation, slope, & aspect.
Mean, Max. & Min., January & July Temperatures	C°	Bill Emmingham (IBP Data Bank)	Corrected from Central Meteorological Station for elevation, slope, & aspect.
Temperature Growth Index		Zobel et al. (1976)	Determined from soil and air temperatures effect on seedling growth during summer
Plant Moisture Stress	bars	Zobel et al. (1976)	Pressure chamber readings on xylem sap of understory conifers during growing season.
Moss Cover	%	This study	
Cover of Total Moss Flora	%	David Sawbridge(1975, unpub.)	
Cover STOR	%	David Sawbridge (1975, unpub.)	*Stokesiella oregana*
Cover of Needle, Leaf, Bare Wood, & Canopy	%	This study	See text
Cumulative Canopy Cover	%	Zobel et al. (1976)	Summation of canopy coverage of each species.

APPENDIX III. continued...

Variable Name	Units	Source of Data	Explanation
Cover PSME	%	Zobel et al.(1976)	*Pseudotsuga menziesii*
Cover TSHE	%	Zobel et al.(1976)	*Tsuga heterophylla*
Cover THPL	%	Zobel et al.(1976)	*Thuja plicata*
Cover ABSP	%	Zobel et al.(1976)	*Abies* spp.
Cover TSME	%	Zobel et al.(1976)	*Tsuga mertensiana*
Cover VAPA	%	Zobel et al.(1976)	*Vaccinium parvifolium*
Cover RHMA	%	Zobel et al.(1976)	*Rhododendron macrophyllum*
Cover TABR	%	Zobel et al.(1976)	*Taxus brevifolia*
Cover BENE	%	Zobel et al.(1976)	*Berberis nervosa*
Cover GASH	%	Zobel et al.(1976)	*Gaultheria shallon*
Cover POMU	%	Zobel et al.(1976)	*Polysticum munitum*
Cover LIBO	%	Zobel et al.(1976)	*Linnaea borealis*
Cover ACCI	%	Zobel et al.(1976)	*Acer circinatum*
Avg. Dist. to Shrub	cm	This study	See text
Index to Shrub Cover		This study	See text
Avg. Dist. to Tree	m	This study	See text
Density	#trees ha^{-1}	This study	
Basal Area	m^2 $tree^{-1}$	This study	
Basal Area	m^2 ha^{-1}	This study	
Area Index PSME	m^2	This study	*Pseudotsuga menziesii*
Area Index TSHE	m^2	This study	*Tsuga heterophulla*
Area Index TSME	m^2	This study	*Tsuga mertensiana*
Area Index TABR	m^2	This study	*Tasus brevifolia*
Area Index THPL	m^2	This study	*Thuja plicata*
Area Index ABAM	m^2	This study	*Abies amabilis*
Area Index ABPR	m^2	This study	*Abies procera*

APPENDIX III. continued...

Variable Name	Units	Source of Data	Explanation
Area Index ABLA	m^2	This study	*Abies lasiocarpa*
Area Index ACCI	m^2	This study	*Acer circinatum*
Area Index CONU	m^2	This study	*Cornus nutallii*
Area Index CACH	m^2	This study	*Castinophsis chrysophylla*
Age of Stand	years	Fred Swanson (unpublished data)	See Figure 4.

APPENDIX III. continued... Quantitative Values for Non-biological Variables

Reference Stand	Elevation (m)	Aspect	Slope (°)	Mean Quadrat Slope (°)	Mean Quadrat Aspect	Aspect Code	Height of Angle of Ridge to SE	Height of Angle of Ridge to S	Height of Angle of Ridge to SW	Vert. Dist. From Stream	Vert. Dist From Ridge	% Cover Bare Soil	% Cover Bare Rock	Soil pH of A1 Horizon	Base Saturation A1 Horizon
7	490	NNW	18	30	170	0	20	13	11	73	512	2.1	0.3	6.0	57.0
8	500	WNW	40	37	111	0	26	5	2	195	171	4.4	0.7	6.2	38.9
1	510	SW	35	35	44	0	25	8	4	98	268	7.4	1.1	6.3	37.3
2	520	WNW	20	25	113	0	24	23	9	24	561	0.2	0.0	6.5	20.4
17	530	N	18	19	177	0	16	20	58	24	598	1.4	0.2	6.6	8.0
10	670	SW	5	12	61	0	13	9	2	73	220	0.0	0.0	6.0	34.1
16	670	SW	40	30	66	0	23	23	17	220	366	2.9	0.2	5.8	34.8
15	720	NNW	45	32	163	0	33	27	18	268	317	1.9	0.8	6.7	21.7
5	920	NE	8	7	150	1	21	23	17	341	488	0.0	0.0	6.5	9.6
3	950	W	10	13	108	0	23	13	5	122	634	0.0	0.0	6.6	6.2
12	1020	WNW	5	12	111	0	16	9	16	15	537	0.1	4.5	5.4	2.5
11	1060	SE	25	19	23	1	5	4	0	122	49	0.0	0.0	6.2	34.0
18	1080	SE	30	19	17	1	5	4	1	390	24	0.0	0.0	6.4	33.3
4	1440	WNW	10	20	113	0	31	16	0	98	98	1.4	4.4	6.4	1.7
13	1480	S	15	19	23	0	12	1	3	98	223	0.0	0.0	6.2	4.9
14	1570	NW	15	21	127	0	19	8	0	439	24	0.4	2.6	6.2	3.1

APPENDIX III. continued... Quantitative Values for Non-biological Variables

Reference Stand	Elevation (m)	Aspect	Slope (°)	Exchangeable Calcium in A1 Horizon	Nitrogen in A1 Horizon	January Mean Radiation	July Mean Radiation	January Maximum Radiation	July Maximum Radiation	January Mean Temperature	July Mean Temperature	January Minimum Temperature	July Maximum Temperature	Temperature Growth Index	Plant Moisture Stress
7	490	NNW	18	18.0	6.0	56.4	477.4	83	604	0.90	19.15	-9.8	33.1	83.9	6.3
8	500	WNW	40	5.6	5.9	(78.3)*	(484.8)	(133)	(613)	(2.03)	(20.16)	(-9.9)	(35.1)	92.7	16.0
1	510	SW	35	5.2	4.9	97.8	504.3	179	649	2.55	20.85	-9.4	36.4	96.3	20.1
2	520	WNW	20	4.0	4.9	68.3	491.7	110	625	0.82	20.52	-10.4	35.5	81.9	9.4
17	530	N	18	3.8	6.0	65.9	501.9	104	641	1.83	19.81	-9.3	34.9	70.9	7.0
10	670	SW	5	13.0	6.0	81.9	537.3	140	689	1.16	19.11	-10.0	34.4	80.8	10.5
16	670	SW	40	8.0	3.9	95.8	520.6	175	(662)	1.21	(19.62)	-10.5	(34.5)	81.7	7.3
15	720	NNW	45	2.2	8.0	(64.9)	(464.2)	(95)	(589)	(1.51)	(18.90)	(-11.2)	(33.4)	77.9	7.8
5	920	NE	8	3.0	4.6	64.3	502.1	101	638	0.50	17.65	-9.9	30.5	68.3	8.3
3	950	W	10	0.4	7.0	73.0	522.8	119	(669)	-0.44	(18.48)	-11.2	(32.8)	69.0	7.2
12	1020	WNW	5	0.3	6.0	73.5	518.3	121	(662)	-0.50	(17.34)	-11.2	(31.0)	56.9	7.1
11	1060	SE	25	2.4	7.0	92.8	537.4	166	(688)	-0.10	17.78	-12.5	32.9	78.3	8.4
18	1080	SE	30	5.6	11.3	(91.2)	(509.1)	(163)	(649)	(0.08)	(17.56)	(-12.5)	(31.9)	70.6	12.1
4	1440	WNW	10	0.1	8.0	(72.2)	488.7	119	622	-0.92	15.47	-13.0	29.6	44.7	6.3
13	1480	S	15	0.8	14.0	73.9	505.9	122	(648)	-2.10	(15.11)	-16.2	(28.7)	43.0	6.4
14	1570	NW	15	0.5	8.7	49.7	418.0	67	525	-1.60	15.11	-15.8	(28.4)	39.4	8.6

*numbers in ( ) designate values determined from regression

APPENDIX III. continued... Quantitative Values for Biological Variables

Reference Stand	Elevation (m)	Aspect	Slope (°)	% Cover Moss	% Cover Total Moss Flora	% Cover STOR	% Cover Needle	% Cover Leaf	% Cover Bare Wood	% Cover Canopy	Cumulative % Cover Canopy	% Cover PSME	% Cover TSHE	% Cover THPL	% Cover ABSP
7	490	NNW	18	51.1	54.8	46.9	30	18	9	68	110	25	55	30	
8	500	WNW	40	35.5	7.5	4.6	32	34	10	61	81	50	5		
1	510	SW	35	42.5	16.9	5.3	28	16	8	55	50	40			
2	520	WNW	20	55.9	53.4	51.3	41	16	6	73	105	50	50		
17	530	N	18	39.6	43.0	38.6	44	21	6	74	102	50	35	5	
10	670	SW	5	26.4	11.8	7.1	61	39	6	68	89	55	15	8	
16	670	SW	40	16.8	14.9	11.0	54	50	7	70	107	55	13		
15	720	NNW	45	18.9	13.3	10.9	52	25	8	69	108	30	35	20	
5	920	NE	8	6.1	0.8	0.8	73	29	7	70	90	55	30		
3	950	W	10	5.6	2.1	0.4	71	41	9	62	120	20	30	45	5
12	1020	WNW	5	21.1	15.0	1.4	55	18	13	54	103	55	40	3	10
11	1060	SE	25	0.2	0.5	0.1	83	15	5	73	96	75	20		2
18	1080	SE	30	2.2	0.9	0.0	84	40	9	71	81	70	10		1
4	1440	WNW	10	0.1	0.8	0.0	80	6	10	63	116	45	20		55
13	1480	S	15	0.3	0.1	0.0	88	8	12	68	93	45			60
14	1570	NW	15	1.2	0.1	0.0	70	21	8	58	100				35

APPENDIX III. continued... Quantitative Values for Biological Variables

Reference Stand	Elevation (m)	Aspect	Slope (°)	% Cover TSME	% Cover VAPA	% Cover RHMA	% Cover TABR	% Cover BENE	% Cover GASH	% Cover POMU	% Cover LIBO	% Cover ACCI	Avg. Dist. to Shrub (cm)	Index to Shrub Cover
7	490	NNW	18		2		1	1	2	7	5	8	0.48	0.15
8	500	WNW	40		1	4	4	7	T*	7	4	28	0.42	0.44
1	510	SW	35		1		5	4		9	4	22	0.39	0.77
2	520	WNW	20		3	4	7	12	2	3	9	7	0.51	0.37
17	530	N	18		1	8	8	1	T	1	26	17	0.39	0.12
10	670	SW	5		1	44	13	9	18	1	2	26	0.19	0.21
16	670	SW	40		T	33	15	6	27	T	3	16	0.36	2.01
15	720	NNW	45		T	T	6	2	4	17	T	4	0.63	0.26
5	920	NE	8		T	60	6	20	2	1	1	33	0.29	0.60
3	950	W	10		4	22	25	8			6	T	0.29	0.19
12	1020	WNW	5		1	2	10	5		T	4	13	0.49	0.58
11	1060	SE	25		1		T	24	11	1	2	12	0.15	0.16
18	1080	SE	30		2		T	29		7	9	57	0.40	0.61
4	1440	WNW	10	1	T			T		T	T	T	1.28	0.10
13	1480	S	15					T				5	1.18	0.26
14	1570	NW	15	65		1							0.51	0.96

*T signifies trace amount

APPENDIX III. continued... Quantitative Values for Biological Variables

Reference Stand	Elevation (m)	Aspect	Slope(°)	Avg. Dist. to Tree(m)	Density (#trees ha^{-1})	Basal Area (m^2 tree^{-1})	Basal Area (m^2 ha^{-1})	Area Index PSME	Area Index TSHE	Area Index TSME	Area Index TABR	Area Index THPL	Area Index ABAM	Area Index ABPR	Area Index ABLA
7	490	NNW	18	3.41	215	0.28	61	5.15	2.44		0.26	0.06			
8	500	WNW	40	3.19	246	0.34	85	9.46	0.04		0.01				
1	510	SW	35	2.88	301	0.20	59	5.37			0.11				
2	520	WNW	20	2.08	578	0.25	142	5.64	1.16		0.09				
17	530	N	18	3.04	271	0.20	55	4.27	0.66		0.56	0.16			
10	670	SW	5	2.40	434	0.94	410	1.88	0.29		0.01	0.42			
16	670	SW	40	2.61	367	0.41	149	10.39	0.36		0.07	0.22			
15	720	NNW	45	2.81	317	0.31	98	5.80	1.93		0.09	0.78			
5	920	NE	8	3.24	238	0.59	140	14.84	1.36		0.21				
3	950	W	10	3.03	272	0.26	72	1.72	1.63		0.09	3.43	0.15	0.38	
12	1020	WNW	5	3.81	172	0.56	96	8.80	6.26		0.02		0.01		0.46
11	1060	SE	25	3.16	250	0.27	68	2.67	0.05						
18	1080	SE	30	3.07	265	0.36	97	9.85	0.01		0.02	0.34			
4	1440	WNW	10	1.97	644	0.21	134	4.38	0.01				0.44	0.94	
13	1480	S	15	2.61	367	0.31	115	6.00					0.02	2.76	
14	1570	NW	15	2.39	438	0.19	83			2.76			0.61	0.73	1.21

APPENDIX III. continued... Quantitative Values for Biological Variables

Reference Stand	Elevation (m)	Aspect	Slope (°)	Area Index ACCI	Area Index CONU	Area Index CACH	Age of Stand
7	490	NNW	18				530
8	500	WNW	40	0.06	0.05		530
1	510	SW	35		0.01		530
2	520	WNW	20				530
17	530	N	18				530
10	670	SW	5		0.01	0.03	530
16	670	SW	40		0.01	0.29	530
15	720	NNW	45	0.03			530
5	920	NE	8				530
3	950	W	10	0.01			530
12	1020	WNW	5				530
11	1060	SE	25				130
18	1080	SE	30				530
4	1440	WNW	10				530
13	1480	S	15				530
14	1570	NW	15				530

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