THE FOREST ASSOCIATIONS OF THE LITTLE LOST MAN CREEK RESEARCH NATURAL AREA, REDWOOD NATIONAL PARK, CA

by

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ABSTRACT

The old-growth redwood (*Sequoia sempervirens*) forest associations of the Little Lost Man Creek Research Natural Area in Redwood National Park, CA, were defined by this study. Eighty stands on a systematic sample grid were inventoried using releve-style sampling procedures of the Zurich-Montpellier (ZM) method of phytosociology. Traditional ZM synthetic procedures and modern multivariate techniques of classification (i.e. two-way indicator species analysis and discriminant analysis) were used to define the associations and to investigate the relationship between the distribution of the associations and topographic and edaphic factors in the natural area. A forest association map derived from the classified sample grid subdivided the vegetation into homogeneous subunits occupying uniform habitats.

Three forest associations were defined: the *Sequoia sempervirens*/*Blechnum spicant* association at lower elevations on relatively moist, concave lower slopes; the *Sequoia sempervirens*/*Arbutus menziesii* association at higher elevations on relatively xeric, convex upper slopes and ridges; and the *Sequoia sempervirens*/*Mahonia nervosa* association at mid-elevations on intermediate, relatively mesic sites.

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INTRODUCTION

This study described the old-growth redwood (*Sequoia sempervirens*) forest associations of the Little Lost Man Creek Research Natural Area in Redwood National Park, California. In 1973, the relatively undisturbed, 972 ha watershed was designated a research natural area by the National Park Service to represent virgin, upland, old-growth redwood forest in the northern part of its range. Little Lost Man Creek was part of a nation-wide system of natural areas on federal lands (U.S. Federal Committee on Ecological Reserves, 1977) that preserved representative ecosystems as baseline areas and provided, through scientific research, information about ecosystem components, processes, and comparisons with manipulated systems (Franklin and Trappe, 1968). This study provided an inventory of vascular plant species and a definition of old-growth redwood forest types in terms of their structure, composition, and distribution along environmental gradients. A forest type map subdivided the vegetation into homogeneous subunits occupying uniform habitats, and thus provided a framework for future studies in the natural area.

Review of Vegetation Studies in the Redwood Forest Region

Several authors listed dominant species associated with Sequoia sempervirens throughout its range (e.g. Clements, 1920; Clark, 1937; Jensen, 1947; Mason, 1947; Munz and Keck, 1968; Franklin and Dyrness, 1973; Ornduff, 1974; Eyre, 1980). These generally included Pseudotsuga menziesii, Lithocarpus densiflora, Rhododendron macrophyllum, Vaccinium ovatum, Gaultheria shallon, Polystichum munitum, and Oxalis oregana. Roy (1966) and Becking (1982) provided more complete redwood floras, but there were few detailed accounts of old-growth redwood vegetation. Kuchler (1977) recognized two redwood forest types on his vegetation map of California. Sequoia sempervirens and Pseudotsuga menziesii were canopy dominants in the redwood forest type mapped from the Oregon border south to Monterey County. Sequoia sempervirens, Lithocarpus densiflora, Arbutus menziesii, and Quercus wislizenii dominated the mixed hardwood and redwood forest type south of Monterey. Parker and Matyas (1979) showed two redwood forest types on their vegetation map of California with a composition and distribution similar to Kuchler's types. Zinke (1977) derived data from the Cooperative Soil-Vegetation Survey maps (Colwell, 1974) and showed dominant overstory species along a moisture gradient determined by latitude and distance from the ocean. Associates of Sequoia sempervirens were shown varying from Tsuga heterophylla and Abies grandis in moist conditions to

Pseudotsuga menziesii, *Lithocarpus densiflora*, and *Arbutus menziesii* in drier situations. In Del Norte and Humboldt Counties, California, Veirs (1982) described a similar sequence of species along a moisture gradient related to elevation and aspect. Waring and Major (1964) used an autecological approach to describing the vegetation of Humboldt Redwoods State Park, California. They recorded the distribution of individual species along environmental gradients of moisture, nutrients, light, and temperature, and then calculated vegetation indices along each gradient for five redwood cover types. The indices for moisture and nutrients showed a gradual progression from relatively moist and fertile scores in pure redwood stands on alluvial flats to relatively dry and infertile scores in mixed stands of *Sequoia sempervirens*, *Pseudotsuga menziesii*, and hardwoods on upper slopes and ridges. Light under the forest canopy gradually increased along this gradient, but temperatures did not vary significantly. Becking (1967) defined two forest alliances in Humboldt Redwoods State Park using the Zurich-Montpellier (ZM) method of phytosociology (Becking, 1957). The "Redwood-Oxalis" alliance (*Sequoia sempervirens*-*Oxalis oregona*) on moist, alluvial flats and lower slopes was dominated by *Sequoia sempervirens*. The shrub layer was generally sparse, but the understory was rich in characteristic herbaceous species, including *Oxalis oregana*, *Blechnum spicant*, *Adiantum pedatum*, and *Athyrium filix-femina*. The "Redwood-Swordfern" alliance (*Sequoia* sempervirens-Polystichum munitum) occurred on upper slopes and ridges where drier conditions supported a mixed stand of Sequoia sempervirens, Pseudotsuga menziesii, Abies grandis, and Lithocarpus densiflora. A dense shrub layer of Rhododendron macrophyllum, Gaultheria shallon, Vaccinium ovatum and Vaccinium parvifolium was characteristic of this alliance. Characteristic members of the sparse herbaceous layer included Viola sempervirens, Mahonia nervosa, and Clintonia andrewsiana. McBride and Jacobs (1978) mapped redwood cover types in Muir Woods National Monument, California which they assigned to the "Redwood-Swordfern" alliance. Dyrness et al., (1973) described old-growth redwood vegetation at the northern extreme of its distribution in southwest Oregon. They presented data from three reconnaissance plots that showed a range of species composition encompassed by Becking's "Redwood-Swordfern" alliance.

Review of Traditional Zurich-Montpellier Methodology and Its Relationship to Modern Multivariate Classification Techniques

The forest types in this study were classified and characterized using both traditional phytosociological methods and modern multivariate classification techniques. The traditional ZM method was generally acknowledged as the most fully-developed and widely-used approach to the classification of vegetation (Whittaker, 1962; Westhoff and

Maarel, 1978). In comparative tests with other methods, the ZM method was consistently favored due to its combination of efficiency and effectiveness (Moore et al., 1970; Frenkle and Harrison, 1974). The standardization of concepts and methods was a major advantage of the ZM approach because it permitted the results of local studies to be integrated into hierarchial classifications of regional vegetation types. Classification studies in the redwood forest (Becking 1957; Muldavin et al., 1981; Lenihan et al., 1982) and related forests in California (Sawyer et al., 1977) and the Pacific Northwest (Becking, 1954; Bailey, 1966; Franklin and Dyrness, 1973) used the ZM or closely related techniques. A major objective in this study was to relate the vegetation of the study area to existing classifications; thus the ZM approach to classification was also used in Little Lost Man Creek.

The ZM method was founded on three basic precepts: 1) the classification of vegetation types was based on total floristic composition, 2) the preference of species for certain vegetation types characterized the types and indicated the environment, and 3) character species served to integrate local vegetation types into formal, hierarchial classification systems for regional vegetation. Such a phytsociological study proceeded in three phases: analytic, synthetic, and syntaxonomic (Becking, 1957; Westhoff and Maarel, 1978; Gauch, 1982). The analytic phase consisted of extensive reconnaissance and data collection. Sample stands were chosen subjectively to represent preliminary interpretations of the vegetation based on reconnaissance, and to satisfy the requirement of stand homogeneity. The dimensions of the sample stands were large enough to exceed minimal area (Mueller-Dombois and Ellenberg, 1974), and variously-shaped to include only homogeneous vegetation. Standard data records, or releves, consisted of notes on vegetation structure, complete lists of vascular and non-vascular plant species, estimates of species cover-abundance and sociability using standard five-point scales (Braun-Blanquet, 1932), indications of species vitality, and notes on the physiographic and edaphic character of the sample site.

The first step in the synthetic phase of the traditional ZM method of vegetation classification involved rearrangement of a floristic data matrix to reveal a major aspect of the matrix structure. The objective of this rearrangement was to concentrate positive matrix entries into blocks along the matrix diagonal so that stands with similar species compositions were grouped together, and species with similar distributions in the stands were grouped together. Matrix rearrangement was an iterative process of selecting species that differentiated groups of stands and stands differentiated by groups of species. The finished product was called the "differentiated" table. The next step in the synthetic phase was the derivation of synthetic characters that floristically defined the vegetation types. Groups of stands with a relatively distinct species composition were outlined on the differentiated table. These stands represented the vegetation types in the determination of species constancy and fidelity. Constancy was a measure of a species' presence within a vegetation type. Fidelity was the degree to which a species was restricted to a given type. Braun-Blanquet (1932) developed a rather complex scheme for fidelity determination based on species presence, abundance, sociability, and vitality. Five fidelity classes and three fidelity catagories were distinguished. Character species (fidelity classes III-V) were those which exhibited a definite preference for a particular vegetation type. Character species were of prime importance in the floristic definition of the vegetation types. Companion species (fidelity class II) were those with about equal preference for all comparable types. Incidental species (fidelity class I) were those with a definite preference for vegetation types other than the type under consideration.

The syntaxonomic stage of a phytosociological study based on traditional ZM methods proceeded only if regional classifications were sufficiently advanced. If so, new types defined by character species were placed in hierarchial classifications of regional units. The fundamental unit of the hierarchy was the association. A number of associations were grouped into alliances defined by alliance character species. Alliances were similarly grouped into orders, and orders into classes.

Despite the proven effectiveness and efficiency of the ZM approach, the methodology was subject to much criticism , especially concerning its inherent subjectivity (Poore 1955a, 1955b). In this study, more objective, multivariate techniques (Gauch, 1982) were substituted for subjective procedures without deviating from basic ZM principles. Perhaps the most criticized step in the traditional approach was the biased selection of sample stands. In response to this criticism, a more objective method was used to locate sample stands in the natural area. Additional criticism concerned procedures in the synthetic phase of the ZM approach. Deriving the differentiated table by iterative rearrangement of the data matrix was a slow, tedious process subject to error, and was partially an art learned by example and practice. The outcome of the rearrangement was somewhat dependent on subjective choices involving initial and problematic groupings. Two-way indicator species analysis (Hill, 1979) was substituted for traditional methods of matrix rearrangement in this study. Two-way indicator species analysis was a polythetic, divisive classification technique that arranged multivariate data in an ordered two-way table by classification of individuals and attributes. In general, polythetic divisive classification techniques were most advantageous because the classification process began with the total data in contrast to agglomerative methods that began with information relating only to pairs of entities. In a test of five common multivariate classification techniques, Gauch and Whittaker (1981) found two-way indicator species analysis among the best analyses due to a combination of effectiveness, robustness, and objectivity. The technique was an improvement over the original method described by Hill et al., (1975) in that species were classified as well as stands. Both classifications were used to structure a two-way table that emphasized the positive diagonal of the data matrix. Matrix rearrangement with this intent resulted in a structured table much like the ZM differentiated table.

Braun-Blanquet's scheme for fidelity determination served as a standard but in practice was rather difficult to apply. The fidelity of a species in a type was defined by reference to its presence in comparable types, and often the determination of comparable types was difficult, especially where regional vegetation classification systems were non-existent, underdeveloped, or uncomparable. Fidelity class determinations also presented some difficulties in that sociability and vitality data were often unavailable. A simplified method proposed by Becking (1957) was used in this study. Becking's method for fidelity determination was based solely on the presence of a species within a type expressed as a percentage of the species' presence throughout its total range. The method was easier to apply and more similar to the basic concept of fidelity because it focused on species presence and eliminated abundance, sociability, and vitality from the determination. Two difficulties remained however.

The first concerned the definition of the species' presence throughout its total range. In this study, a species' total range was defined as its presence throughout the study area as indicated by its presence in the total set of the sample stands. Therefore, the species fidelity classes reported here applied only within the geographical limits of the study area.

The second difficulty was inherent in the fidelity value calculation. The unstated requirement for deriving comparable values was that each vegetation type was represented by an equal number of stands. If the types were represented by unequal numbers of stands, then species in larger groups would have received relatively higher fidelity values. In this study, a systematic sampling scheme and a uneven distribution of forest types in the study area led to the formation of unequal groups of stands in the stand classification derived by two-way indicator species analysis. Discriminant analysis (Tatsuoka, 1970; Williams, 1983), a method of distinguishing among groups by forming linear combinations of discriminating variables, provided an objective criterion for selecting equal subsets of typical stands for the constancy and fidelity calculations. Discriminant analysis was also used to investigate the relationship between the distribution of the forest types and topographic factors in the study area. Environmental data was often included on ZM differentiated tables, but a systematic correlation of vegetation types and environmental parameters was not attempted by the traditional methodology.

This study identified three old-growth redwood forest types in the Little Lost Man Creek watershed: the relatively moist *Sequoia sempervirens*/*Blechnum spicant* association, the mesic *Sequoia sempervirens*/*Mahonia nervosa* association, and the xeric *Sequoia sempervirens*/*Arbutus menziesii* association.

STUDY AREA

Location

The Little Lost Man Creek watershed was located in Redwood National Park in northern Humboldt County, California (Figure 1) at 41 degrees 18 minutes north latitude and 124 degrees 00 minutes west longitude. Primary access to the study area was from Orick, California (Figure 2) located approximately 76 km north of Eureka, California on U.S. Highway 101. The western edge of the study area at Lady Bird Johnson Grove was reached by traveling the Bald Hills Road east of its junction with U.S. 101. An unimproved park service road from the Bald Hills Road at the southern end of the study area provided limited access to the southeastern boundary. The northern end of the study area was reached by traveling north of Orick on U.S. 101, and then taking Geneva Road east to the bridge over Little Lost Man Creek. The northwest and northeast boundaries and interior portions of the study area were accessible only by cross-country travel.

Topography

Little Lost Man Creek was a perennial stream in the greater Redwood Creek drainage basin (California Dept. of Water Resources, 1965). The creek flowed southeast to

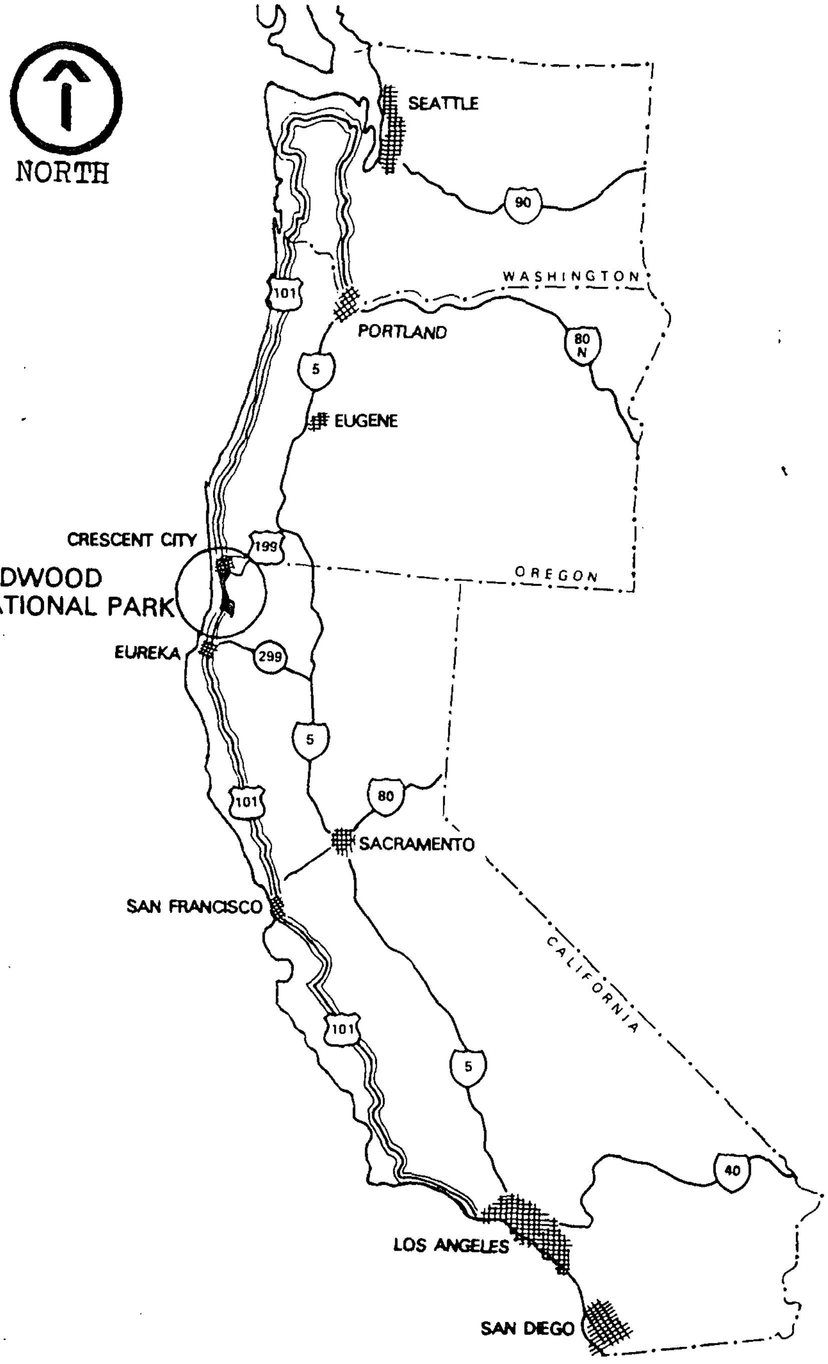


Figure 1. Regional Map Showing the Location of Redwood National Park in California.

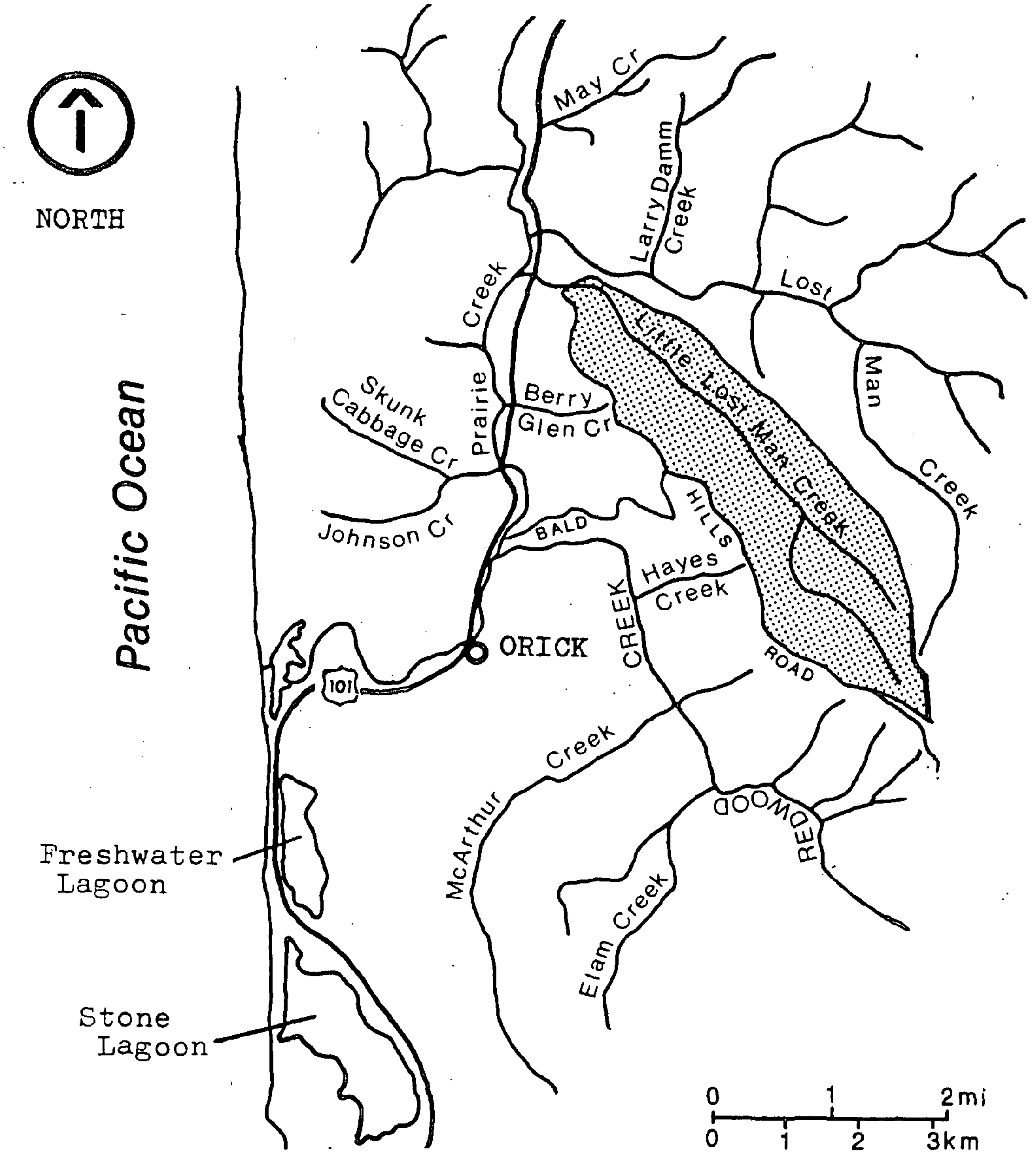


Figure 2. Subregional Map Showing the Location of the Little Lost Man Creek Research Natural Area in Redwood National Park, CA.

northwest for 8.6 km and then joined Prairie Creek. Prairie Creek flowed south from this confluence and emptied into Redwood Creek 3.6 km downstream. The Little Lost Man Creek watershed was a mature landform with a deeply-incised ravine, steep lower slopes, more moderate upper slopes, and a well-defined ridgeline (Figure 3). Numerous intermittent streams dissected the slopes of the watershed, and there was one major perennial tributary in the upper southeast corner of the study area. Elevations ranged from 30.5 m (100 ft) at the mouth of the creek to 731.5 m (2400 ft) in the upper southeast corner of the watershed. Parts of the study area were found on three U.S. Geological Survey topographical quadrangles: the Orick, California sheet (7.5 minute series), and the Orick, California and Tectah Creek, California sheets (15 minute series).

Geology and Soils

The study area was located at the northern end of the Coast Range Province in the central belt of the Franciscan formation (Irwin, 1960). This belt was a complex assemblage of eugeosynclinal rocks deposited in the late part of the Mesozoic from the late Jurassic to the late Cretaceous (Bailey, 1966). The most common rocks in the study area were graywacke sandstones, shales, and conglomerates.

In the Cooperative Soil-Vegetation Survey (DeLapp et al., 1961a, 1961b; DeLapp and Smith, 1977) the majority of

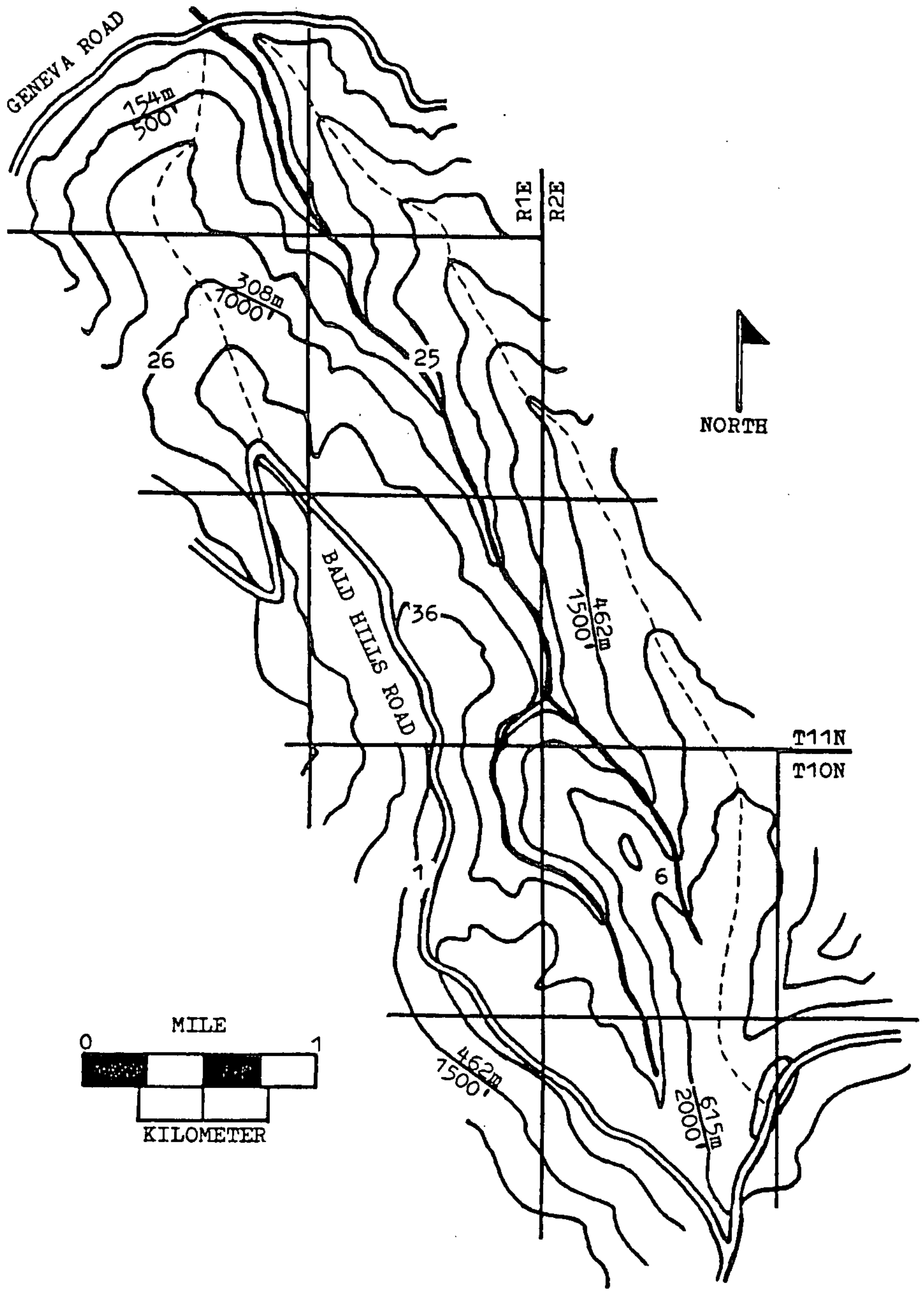


Figure 3. Topographic Map of the Little Lost Man Creek Research Natural Area, Redwood National Park, CA Showing Routes of Access, Section Lines, and Watershed Boundary Indicated by Dotted Line. Sections Lie in T10N, R1E; T11N, R1E; T10N, R2E; T11N, R2E; Humboldt Meridian.

soils in the study area were classified as Melbourne clay loams or Hugo loams. The soil-vegetation maps for the study area (Figure 4) also showed minor inclusions of Mendocino and Usal clay loams, but about 95 percent of the soils were identified as Melbourne, Melbourne-Hugo, or Hugo-Melbourne associations. Typical soil profile descriptions for the Melbourne and Hugo series are provided in Table 1. Soils in the Melbourne series had a moderately rapid to rapid permeability, good drainage, a medium erosion hazard, and high to very high timber productivity (DeLapp and Smith, 1977). Soils in the Hugo series had a moderately rapid to rapid permeability, good to excessive drainage, a moderate to very high erosion hazard, and moderate to very high timber productivity (DeLapp and Smith,1977). In the current soil classification nomenclature, Melbourne clay loams were classified as fine, mixed, mesic ultic haploxeralfs and Hugo loams as fine, loamy, mixed, mesic dystric xerochrepts.

Climate

The study area had a maritime Mediteranean climate with cool, rainy winters and cool, dry, summers. A thirty-year summary (1941-1970) of temperature and preciptation data from the Orick-Prairie Creek weather station (Elford and McDonough, 1974) was compiled (Table 2). This was the station nearest to Little Lost Man Creek which

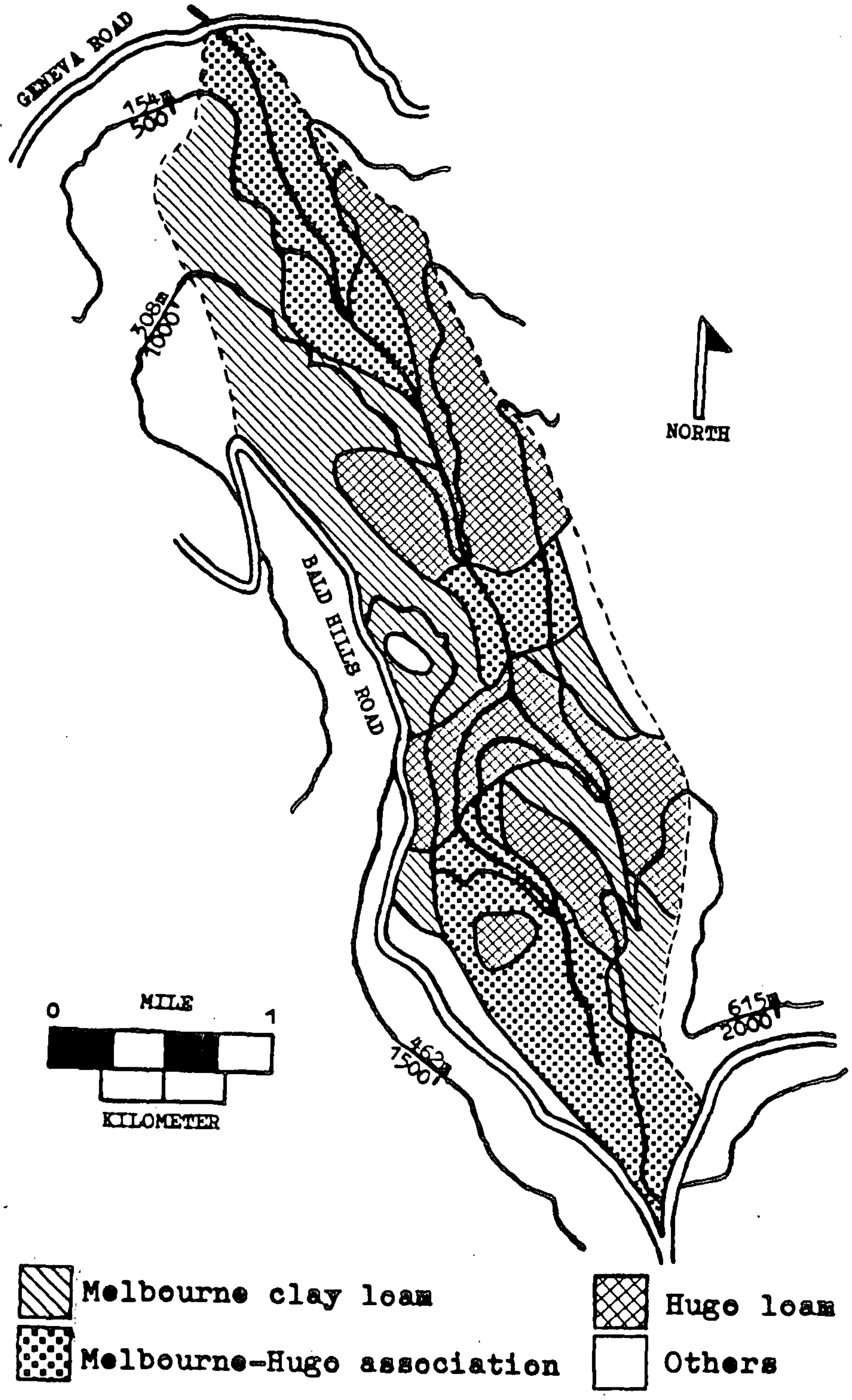


Figure 4. Soils Map with Topographic Contours for the Little Lost Man Creek Research Natural Area, Redwood National Park, CA (after DeLapp et al., 1961a, b).

Table 1. Typical Soil Profile Descriptions for the Melbourne Clay Loam and Hugo Loam Series (DeLapp et al., 1961a; DeLapp and Smith, 1977)

Depth (cm)	Characteristics
Melbourne Clay Loam Series	
0-20	dark brown strongly granular clay loam moderately acid fairly high in organic matter
20-50	strong brown weakly blocky clay loam strongly acid
51-90	strong brown, gley mottled fine blocky heavy clay loam strongly acid few rock fragments
90 +	partially-weathered, fine-grained sandstone
Hugo Loam Series	
0-25	grayish brown granular loam slightly acid few small rock fragments present
25-65	pale brown weakly granular loam strongly acid increasing rock fragments with depth
65 +	shattered, partially-weathered, fine-grained sandstone

Table 2. Thirty-year Summary (1941-1970) of Temperature and Precipitation Data from the Orick-Prairie Creek Weather Station, CA (Elford and McDonough, 1974).

	Month												
	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Annual
Temperature (C)													
Mean	7	8	8	10	12	14	15	16	15	13	9	7	11
Maximum	22	21	25	31	32	37	35	36	35	32	22	19	37
Mean Maximum	11	12	13	15	17	19	21	21	22	18	14	11	16
Minimum	-8	-5	-2	-1	-1	2	4	6	2	2	-3	-3	-8
Mean Minimum	4	4	4	6	7	9	11	11	10	8	6	4	7
Precipitation (mm)													
Mean	302	272	242	119	101	37	9	12	30	158	223	297	1801

also had long-term climatic records. It was located about 4.7 km north of the study area at an elevation of 50 m (165 ft). At higher elevations in the study area, rainfall totals were probably greater. Only trace amounts of snowfall were recorded by the weather station, but light snowfall was common in the study area at higher elevations during the winter months. Heavy, wet fogs produced by onshore movement of moist oceanic air were a common feature of the climate in the summer. The fog often persisted for all but a few hours in the afternoon at lower elevations in the study area. A warm inversion layer formed during the summer months at 457 m (1500 ft) (Freeman, 1971), so fog was probably less common above this altitude.

The data from the Orick-Prairie Creek station were used to construct a water balance diagram (Thornthwaite, 1948) to represent the regional climate of the study area (Figure 5). The climate was characterized by a long wet season with a large water surplus and a short dry season with a slight water deficit. These features were typical of the climate throughout the coastal coniferous forest belt of the Pacific Northwest (Becking, 1954; Franklin and Dyrness, 1973). Climate diagrams constructed by Walter (1967) showed a gradual increase in the duration and intensity of summer drought for coastal locations south from Vancouver, British Columbia to Santa Cruz, California. At the southernmost extent of this coastal belt, in California's redwood region, fog was an important factor moderating aridity in the summer

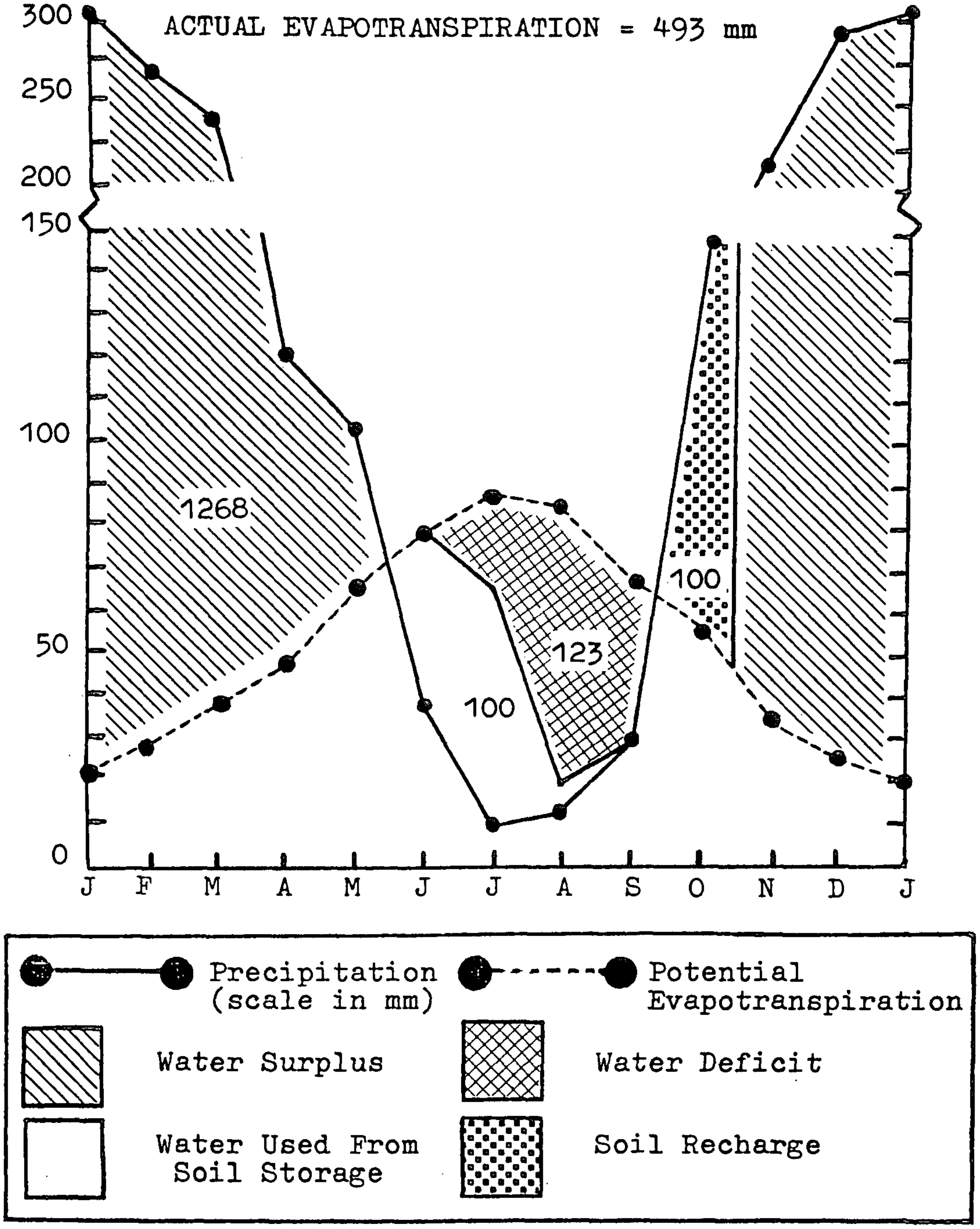


Figure 5. Thornthwaite (1948) Water-Balance Diagram for the Orick-Prairie Creek Weather Station. Temperature and Precipitation Data from Elford and McDonough (1974). Calculations assumed 100 mm of available soil water storage.

months. Fog drip helped offset the summer drought (Azevedo and Morgan, 1974), but reduced evapotranspiration due to higher humidity and reduced insolation was the main effect of fog that moderated summer water deficits in the redwood forest (Byers, 1953).

Vegetation

The vegetation of Little Lost Man Creek was representative of upland redwood forest vegetation at the northern part of its range. The term "upland" was used to distinguish the vegetation from redwood forests on alluvial flats. Forest resource maps prepared for the Department of Interior (1967) showed the stands of the study area as *Sequoia sempervirens* or *Sequoia sempervirens*-*Pseudotsuga menziesii*. The summary of forest classes showed 27 percent of the stands were old-growth in large size classes (i.e. diameters greater than 18.2 cm), 57 percent were old-growth in smaller size classes, and 13 percent were young stands in cutover areas. The species composition of the stands was shown in more detail on soil-vegetation maps for the watershed (DeLapp et al., 1961a, 1961b). On the maps the distribution of the soil-vegetation units indicated a compositional gradient from *Sequoia sempervirens* and *Picea sitchensis* at lower elevations, to *Sequoia sempervirens* and *Pseudotsuga menziesii* at mid-elevations, to *Lithocarpus* *densiflora* and *Arbutus menziesii* in the upper reaches of the watershed.

MATERIALS AND METHODS

Sample points were located by reference to a dot grid placed on a 7.5 minute topographic map of the watershed. Dots on the grid were evenly-spaced at intervals representitive of 300 m. Twenty of the 100 points falling within the boundary of the natural area (Figure 6) fell within in areas disturbed by logging or in non-forested areas (e.g. the narrow riparian zone along the major stem of the creek). These points were eliminated from the sample because the objective of the study was to describe only undisturbed forest vegetation. The ends of lines along the east-west axis of the sample grid were located in the field and the lines were flagged by following an east or west magnetic bearing read from a hand compass. Sample points were located along each line by reference to a pocket altimeter and a topographic map. Given this somewhat approximate method of locating the eighty sample points in the field, each point was identified only as a general area for sampling. The precise location of the sample stand in each area was guided by the criterion of stand homogeneity. The homogeneity of a sample stand was judged by assessing the uniformity of vegetation structure and species dominance (Westhoff and Maarel, 1978).

The area of the 15x25 m (375 m2) sample stands was in accordance with Mueller-Dombois and Ellenberg's (1974)

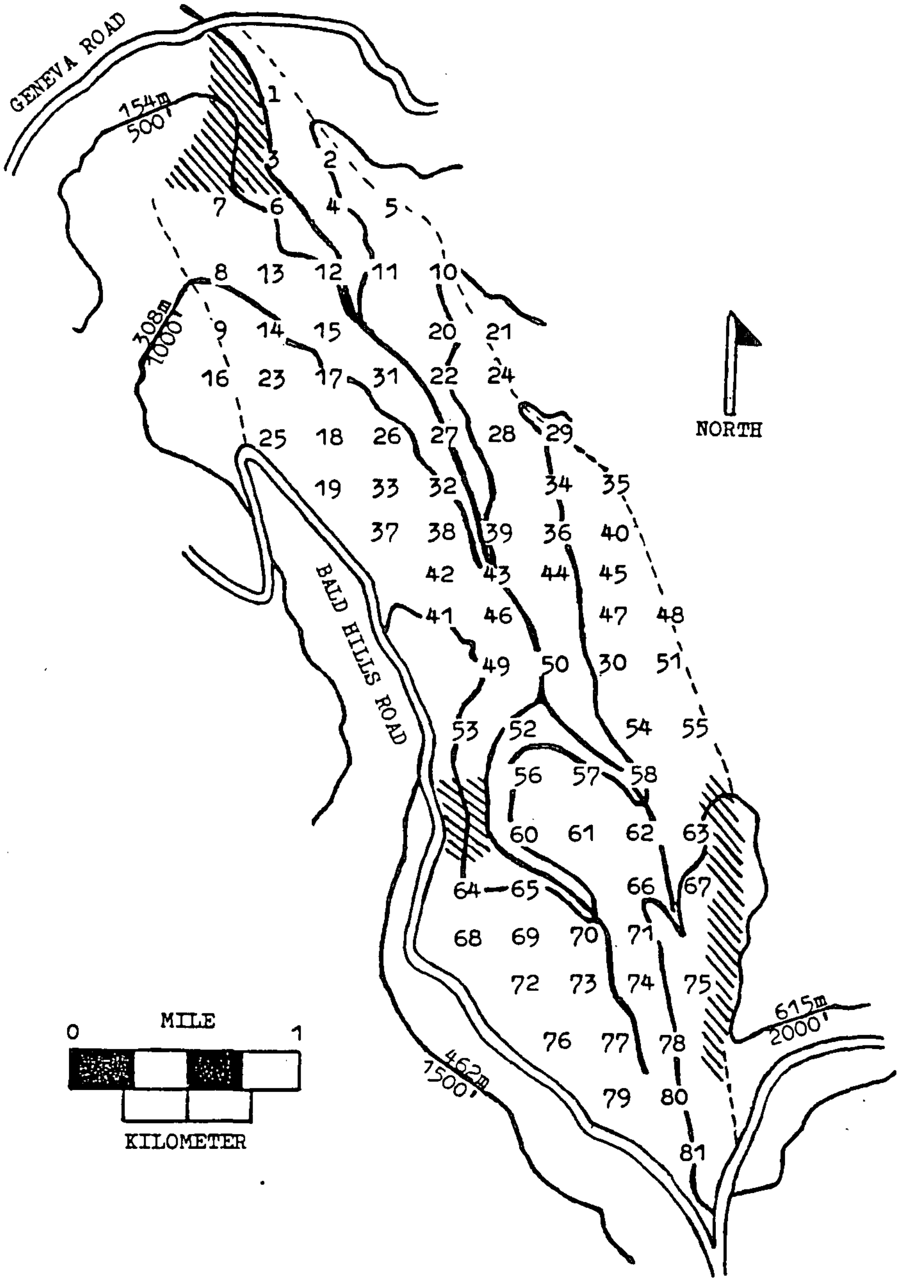


Figure 6. Topographic Map Showing the Systematic Location of Sample Stands and the Stand Numbering System in the Little Lost Man Creek Research Natural Area, Redwood National Park, CA. Dotted Line Indicates Watershed Boundary. Diagonal Shading Indicates Areas Disturbed by Logging.

empirical values for minimal area for sampling in forest vegetation (i.e 300-500 m^2). The stand size exceeded minimal area in all types of vegetation sampled in the study area. Very few species in addition to those in each stand were found outside stand boundaries in each general area for sampling. The rectangular sample stands were positioned so that the longer side was parallel to slope contours. Each stand corner was marked by an aluminum tag nailed to a tree or attached to a large, woody shrub.

Each sample stand was carefully searched and every vascular plant species occurring within stand boundaries was identified (Munz and Keck, 1968) and recorded in Raunkier life-form categories (Mueller-Dombois and Ellenberg, 1974). Non-vascular plants were not recorded because of the difficulty of field identification. The scale used to estimate the cover of each species was the ZM cover/abundance scale (Becking, 1957; Table 3). Also recorded were percentage estimates of the cover of the following life-form/height strata: canopy trees greater than 50 m tall; subcanopy trees greater than 5 m tall; small trees and tall shrubs 2-5 m tall; and the field layer including low shrubs and herbaceous species less than 2 m tall. The basal area of canopy species was estimated in ft^2 per acre by the Bitterlich method (Grosenbaugh, 1952). Two counts were made from the center of the stand using two angle gauges with basal area factors of 50 and 100. The basal area data were later converted to metric units (i.e. m^2 per ha). Several

Table 3. The Zurich-Montpellier Cover-Abundance Scale (Becking, 1957) Used for Estimating Species Cover, the Scale (Maarel, 1979) Used to Transform Cover Data for Analysis, and the Abundance Levels Defined for TWINSPAN

	Percent Cover Range (Midpoint)					
	1-5 (2.5)	1-5 (2.5)	5-25 (15.0)	25-50 (37.5)	50-75 (62.5)	75-100 (87.5)
Cover-Abundance	+	1	2	3	4	5
Transformation	1	2	3	5	7	9
Abundance Level	1	1	2	3	3	3

topographic factors were also measured or described. The aspect was measured in degrees azimuth using a hand compass. The slope was read from a clinometer and recorded in percent. The stand elevation was estimated using a topographic map and a pocket altimeter. The topographic configuration of the stand was described as concave, even, or convex. The soil profile at the center of the sample stand was examined using a hand auger. The profile was described in terms of color, texture, and depth of horizonation. Any additional information that served to characterize the sample stand was added to the notes. The stand was then photograped in black and white from a representative angle.

To improve the efficacy of the data analysis, species with frequencies of less than five percent in the total set of stands were removed from the data set. The cover values for the remaining species were transformed according to a scale by van der Maarel (1979) (Table 3). The reduced, transformed matrix was then entered into a computer program called TWINSPAN (Hill, 1979) and used for two-way indicator species analysis. The first step in the analysis was the construction of a stand ordination for the purpose of revealing the main trend of variation in the sample data. This "primary" ordination was derived by reciprocal averaging. The ordination was then divided at the mean score to form two groups of stands. Preference scores were determined by frequencies on either side of the dichotomized ordination. A preference score of one was assigned to species that exceeded a certain minimum frequency and were at least three times more frequent on one side of the dichotomy as on the other. Rare and less preferential species received scores which were downweighted accordingly, and the scores were signed positive or negative to indicate the species' preference for one side of the dichotomized ordination. To incorporate quantitative data such as cover into the classification procedure, the program constructed "pseudospecies" that represented the species at different levels of abundance. These levels were chosen in accordance with Hill's (1978) recommendation to establish a few classes and not to overweigh the effect of dominance (Table 3). The derivation of a discriminant function called the "refined" ordination was based on the preference scores of the pseudospecies. This function strongly polarized the primary ordination and separated "borderline" stands (i.e stands with scores near the mean ordination score). This process of deriving an ordination, making a dichotomy, and refining the dichotomy was then repeated on each of the two groups of stands formed at the first division level to yield four groups at the second level, eight groups at the third level, and so on until each group had a specified minimum number of stands.

After the stand classification was completed, TWINSPAN then classified the species. The first step was calculating the degree of fidelity of the species for stand groups at each division level of the sample classification hierarchy. Species fidelity values were based on the ratio between the species' mean abundance level in a particular group and its mean abundance level outside the group. The fidelity values became the species' attributes in the species classification process. The same process of deriving a primary ordination, making a dichotomy, and refining the dichotomy at successive division levels was used to classify the species.

The final step in TWINSPAN was the conversion of the species and stand classifications to orderings. The orderings were designed to structure a two-way tabular arrangement of the species and stand groups so that the positive diagonal of the data matrix was emphasized. The ordering criterion was based on a series of group comparisons evaluated by discriminant analysis. The stand classification on the structured TWINSPAN table was interpreted at a division level where the floristic composition of the stand groups was consistant with that of plant assemblages repeatedly observed in the field. Stands in typical groups formed at this level were selected to represent the recurrent assemblages, or forest types, in subsequent steps in the analysis.

Discriminant analysis was used to accomplish three objectives: 1) to provide a criterion for the selection of equal subsets of typical stands for the constancy and fidelity calculations, 2) to classify "transitional" stands (i.e. stands outside the typical groups formed by TWINSPAN), and 3) to relate the distribution of the forest types to topographic variables. The DISCRIMINANT procedure (Klecka, 1975) in the SPSS system of computer programs was used for discriminant analysis in this study. The linear combinations of discriminating variables, or discriminant functions, were derived so that the first function accounted for the greatest amount of group separation, the second accounted for an unique amount of separation given that described by the first, and so on until the number of functions was one less the number of groups or number of discriminating variables, whichever was smaller (Tatsuoka, 1970). It was desirable to limit the number of functions for purposes of interpretation and graphical representation. The importance of each successive discriminant function was assessed by reference to the relative percentage of the eigenvalue (Klecka, 1975). An eigenvalue was a measure of the variance of a function, and the sum of eigenvalues for all possible functions was a measure of the total variance of the discriminanting variables. An eigenvalue expressed as a percentage of the sum of eigenvalues thus provided an index to the relative importance of a function. A discriminant function may have accounted for a large percentage of the total variance and still not have exhibited a high degree of group separation if the variance of the discriminators was not strongly related to group differences, so an index of "discriminatory power" described by Tatsuoka (1970) was used to assess the effectiveness of a derived function. The index was a measure of the percentage variability of a function due to group differentiation.

In discriminant analysis the total sample size should be at least two or three times the number of variables (Tatsuoka, 1970). The full set of species entered into the TWINSPAN analysis was too large to use as a set of discriminanting variables given the number of typical stands representing the forest types. A smaller number of species variables were chosen to serve as discriminators in the discriminant analysis. Selected species had the highest F-ratios in analysis of variance tests for differences among groups of typical stands (Klecka, 1975). A set of functions based on these high F-ratio species was derived to discriminate among the groups of typical stands. The discriminant scores of the stands and the pooled within-groups covariance matrix for the functions were used to derive a classification function for each typical group (Klecka, 1975). All stands were scored on each classification function and the scores were converted to two probabilities of type membership. One was the probability of a stand being as distant from the typical group centroid as the stand under consideration. Stands with the highest "distance" probabilities were selected to form equal subsets of typical stands for constancy and fidelity determinations. Constancy was calculated as the species percentage frequency within a subset of typical stands representing a forest type. Fidelity was calculated as the species presence within a subset of typical stands expressed as a percentage of its presence in the total set of sample stands. The fidelity values were reported in four of the five fidelity classes (Becking, 1957) shown in Table 4. Incidental species (fidelity class I) were not identified in this study. Assigning fidelity value to an erratic species with a definite preference outside of the vegetation type under consideration seemed contradictory.

The second set of probabilities derived from the discriminant classification functions indicated the likelihood of each stand being a member of each type. All stands in the sample set, including those identified as transitionals, were assigned to the type where this "membership" probability was highest. The forest type membership of each stand was then plotted on the sample grid to reveal the spatial distribution of the final classification. Lines were drawn around groups of adjacent stands within the same type to produce a generalized forest type map of the study area (Crawford and Wishart, 1968).

Seven variables served as discriminators in the set of functions derived to describe the relationship between the distribution of the forest types and the topography of the study area. The values of elevation and percentage slope were entered into the analysis as recorded in the field. Topography was coded as an ordinal variable (i.e. one for concave, two for even, and three for convex). The aspect in degrees azimuth was transformed into two directional vectors.

Table 4. Scheme Used to Determine Species Fidelity Classes (Becking, 1957). A Species' Fidelity Value Was Calculated as the Species' Occurrence in One of the Equal Sets of Representitive Stands Expressed as a Percentage of the Species' Occurrence in the Total Set of Stands.

Fidelity Classes	Fidelity Values (%)
Character species	
Fidelity V	90-100
Fidelity IV	75-89
Fidelity III	50-74
Companion species	
Fidelity II	5-49
Incidental species	
Fidelity I	0-4

The cosine of the aspect represented the north-south vector, and the sine represented the east-west vector (Kercher and Goldstein, 1977). The slope position of each sample stand was calculated as the ratio between the stand elevation above the creek and the ridge elevation above the creek. Elevations required by this calculation were taken from the topographic map of the study area. Solar radiation indices based on slope and aspect data were taken from tables presented by Frank and Lee (1966). Discriminant functions based on these variables were derived to discriminate among groups of typical stands. The pooled within-groups correlations between the functions and the topographic variables were examined to identify the variables that best distinguished the forest types. The use of these "structure coefficients" to assess the importance of individual discriminanting variables was recommended by Williams (1983). Topographic variables with large structure coefficients were identified as factors related to the distribution of the forest types.

RESULTS

Eighty-three vascular plant species were encountered in the sample stands (Appendix A). Forty-three species with frequencies of five percent or more (i.e. 52 percent of the total species set) were included in the analysis. Species and stands were arranged in a two-way classification on the structured TWINSPAN table (Appendix B), and the stand classification was interpreted at the second division level where three typical groups and one transitional group were formed. The three typical groups were comprised of sixty-four stands (i.e. 80 percent of the total set of sample stands); these stands were arranged by their TWINSPAN species-orderings and within-group stand-orderings (Table 5).

Twenty-one species (i.e. almost one-third the number of typical stands) had F-ratios with levels of significance greater than 0.0001 in analysis of variance tests for differences among typical groups (Table 6). These twenty-one species with high F-ratios were selected to serve as discriminators in two discriminant functions. These two functions accounted for 86 percent and 14 percent respectively of the total variance of the high F-ratio species. The index of discriminatory power for the set of functions indicated that 99 percent of their variability was due to differentiation among typical stand groups. All stands in the sample grid, including those identified as

Table 5. Species Distributions in TWINSPAN Stand Groups Selected to Represent the *Sequoia sempervirens*/*Blechnum spicant*, *Sequoia sempervirens*/*Mahonia nervosa*, and *Sequoia sempervirens*/*Arbutus menziesii* Forest Types of Little Lost Man Creek, CA. Numbers and Plus Symbols Are ZM Cover-Abundance Values (Becking, 1957). Stand Identification Numbers Are Printed Vertically.

Species	Sequoia/ Blechnum	Sequoia/ Mahonia	Sequoia/ Arbutus
Stand No.	100110000002110 143536875213729	2544332166654221877666554443321 2275651095404744198732868608059	775555477776664875 707543263218619051
Disporum smithii	111 111		
Athyrium filix-femina	12 121 1		
Adiantum pedatum	1 1 1		
Rubus spectabilis	11 1		
Menziesia ferruginea	112 1		
Corylus cornuta	223 2 32		
Rhamnus purshiana	11 1333222133	+ +	
Picea sitchensis	1 1 11		
Blechnum spicant	222223 1 11312	1 +121+	+
Stachys mexicana	21 1	+	
Adenocaulon bicolor	1 11	+	
Vancouveria hexandra	11 1 111	1+1 1	
Oxalis oregana	333333222223223	222 2112122 2221 1 2 1 + 11	
Polystichum munitum	555555543225544	2221211222313311222 11 22 212211	11111 2 1 + +
Vaccinium parvifolium	21 133113142411	211 1 +1 111 11 + 2 11 1 +	12 1 + +
Trillium ovatum	11 +11+1	1 1 12 +	1 1 1 + 11+1
Disporum hookeri	++	1 +11 1 1	1 1
Carex hendersonii		1 1 1	
Actaea rubra		+	
Abies grandis		1 2122 1	
Iris douglasiana		11 1+1 1 11 1 1	
Festuca subulata	+	1111 + 1 1 1 111+1211	
Mahonia nervosa	1+ +1 2	22222222 22 122 21121222222 211	12 2
Galium aparine	+ 1 1 1 +	11 11111111 11111 1 1111111111	1 1
Tsuga heterophylla	1 1 11111	1 1 1132 13 1 1 1 1	11 2 1
Sequoia sempervirens	344454333332423	3232333333223333323333333333333	32223233222222 2222
Trientalis borealis	+ +	1 + 111 +11 1	1 + 1 11 111
Gaultheria shallon	1121321+2	4332435433253342533432433232433	222131123443521352
Vaccinium ovatum	212121233421131	12312232113 135123344334344344	444544523233234315
Lithocarpus densiflora	312 3 21 4232	2245443353313342445334333443424	334544354443545544
Whipplea modesta		21 +111 111 1111+111111 1 1	+ +
Hierochloe occidentalis		2122222211 + 1 11 11112112 211	+
Viola sempervirens	+ + 1 +	2222222112222221222221222121212	211221121 1111+111
Festuca occidentalis		+ +	1 1
Rhododendron macrophyllum	11 3211 1	1 2 232424 2123233143233233	44444333414224 3
Pseudotsuga menziesii	1 11 11 2221 3	122212123 232223322222333333233	222312312222221112
Lathyrus vestitus		+ 1 1 + 111 11 1	
Cardamine integrifolia		1 11 + +111 +11 2	1 11 111
Pleuricospora fimbriolata			+1 1+ 11
Pteridium aquilinum			12111+1 1+
Goodyera oblongifolia		1 1 1 + 2121 1 1 11	211+ 1 1 11 11
Corallorhiza maculata		+	1 + 2 1 1 111
Arbutus menziesii		1+1+	1 11 2 121222

Table 6. Species F-Ratios and Their Significance in Analysis of Variance Tests among Representitive TWINSPAN Stand Groups. Asterisks Indicate Species Selected as Variables for Discriminant Analysis.

Species	F-ratio	Significance	Discriminating Variable
Sequoia sempervirens	18.94	0.0000	*
Pseudotsuga menziesii	11.27	0.0001	
Tsuga heterophylla	0.96	0.3886	
Abies grandis	3.60	0.0334	
Picea sitchensis	8.49	0.0006	
Lithocarpus densiflora	24.21	0.0000	*
Arbutus menziesii	12.08	0.0000	*
Rhododendron macrophyllum	11.95	0.0000	*
Rhamnus purshiana	44.82	0.0000	*
Corylus cornuta	14.02	0.0000	*
Vaccinium ovatum	6.30	0.0033	
Vaccinium parvifolium	17.37	0.0000	*
Menziesia ferruginea	8.08	0.0008	
Rubus spectabilis	5.84	0.0048	
Gaultheria shallon	20.75	0.0000	*
Mahonia nervosa	25.07	0.0000	*
Polystichum munitum	90.37	0.0000	*
Blechnum spicant	25.75	0.0000	*
Actaea rubra	0.53	0.5947	
Adenocaulon bicolor	3.46	0.0377	
Adiantum pedatum	5.84	0.0048	
Athyrium filix-femina	14.58	0.0000	*
Carex hendersonii	1.69	0.1940	
Corallorhiza maculata	12.96	0.0000	*
Disporum hookeri	0.32	0.7272	
Cardamine integrifolia	4.23	0.0191	
Festuca occidentalis	0.85	0.4339	
Festuca subulata	13.18	0.0000	*
Galium aparine	26.06	0.0000	*
Goodyera oblongifolia	6.11	0.0038	
Hierchloe occidentalis	45.60	0.0000	*
Iris douglasiana	7.49	0.0012	
Lathyrus vestitus	7.49	0.0012	
Oxalis oregana	58.62	0.0000	*
Pteridium aquilinum	20.99	0.0000	*
Stachys mexicana	3.69	0.0307	
Trientalis borealis	1.93	0.1541	
Trillium ovatum	2.79	0.0691	
Vancouveria hexandra	5.83	0.0048	
Viola sempervirens	62.17	0.0000	*
Whipplea modesta	25.16	0.0000	*
Disporum smithii	15.57	0.0000	*
Pleuricospora fimbriolata	10.96	0.0001	

transitionals, were assigned to the type where membership probability was the highest (Table 7). The type membership was plotted on the map showing the systematic location of sample stands (Figure 7), and the spatial distribution of this classification was used to generate the forest type map (Figure 8). Fifteen stands with the highest distance probabilities (Table 7) were selected to represent each of the three forest types in the constancy and fidelity calculations. The equal subsets of typical stands were arranged by their TWINSPAN orderings (Table 8).

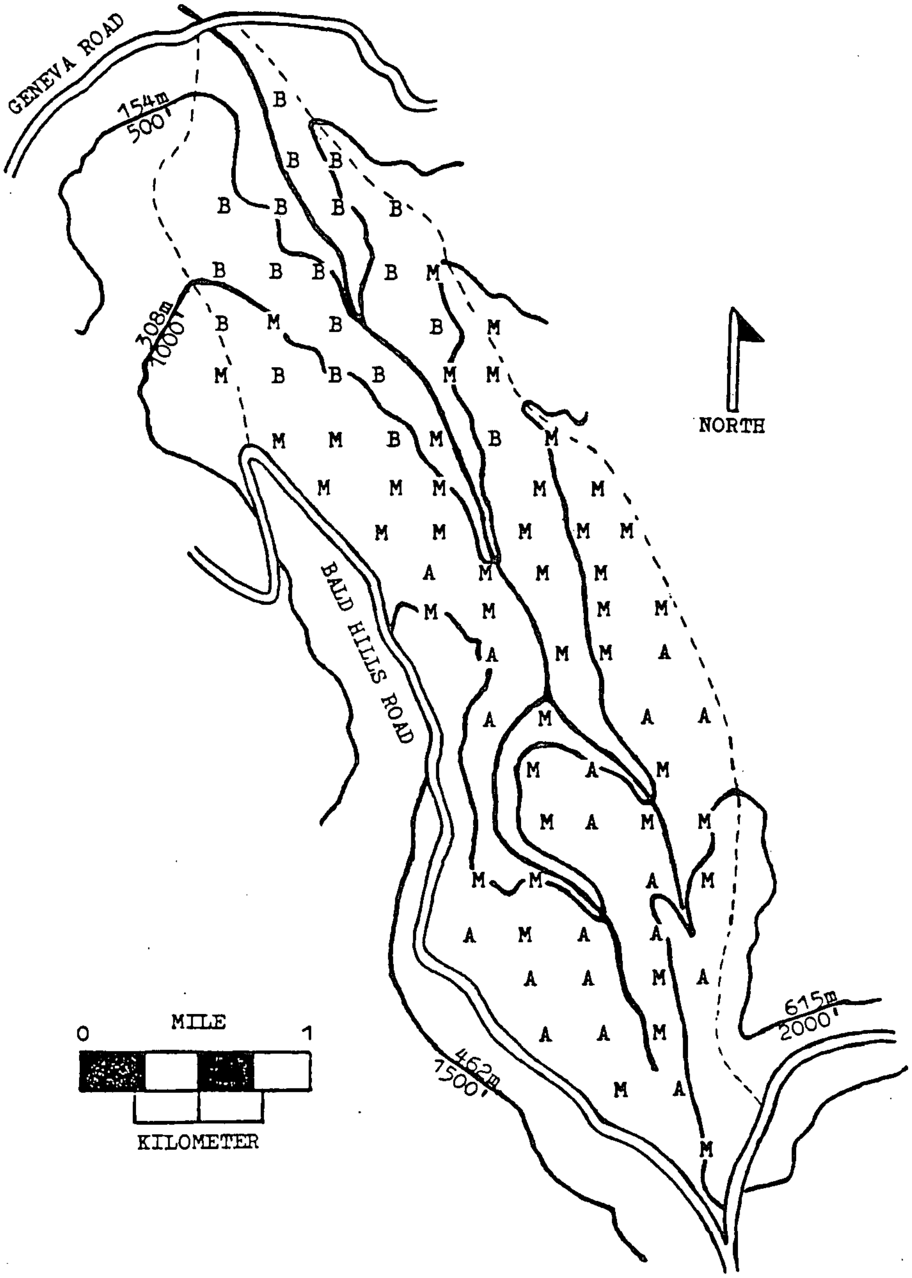
Species modal cover-abundance, constancy (Table 9), and fidelity (Table 10) were calculated for the three forest types. The mean basal area and relative dominance of canopy species (Table 11) were also calculated by forest type. Mean basal area and relative dominance values were based on the subsets of typical stands used to determine fidelity and constancy. The relative dominance of a species was its basal area expressed as a percentage of the total basal area of canopy species in a stand. The forest types were named by appending the binomial of a character species with a modal cover value of two or more to the name Sequoia sempervirens. The three type names derived in this manner were the Sequoia sempervirens/Blechnum spicant (Sequoia/Blechnum) type, the Sequoia sempervirens/Mahonia nervosa (Sequoia/Mahonia) type, and the Sequoia sempervirens/Arbutus menziesii (Sequoia/Arbutus) type.

Table 7. Results of Discriminant Analysis Showing Sample Stands in TWINSPAN Groups and in Groups where Membership Was Predicted by Discriminant Analysis. A Distance Probability Is the Likelihood of Any Stand Being As Distant from the Predicted Group Centroid As the Stand Under Consideration. A Membership Probability Is the Likelihood of a Stand Being a Member of the Predicted Group. Asterisks Indicate Stands Selected to Form Equal Groups of Typical Stands for Constancy and Fidelity Calculations. Group Codes: (1) *Sequoia sempervirens*/ *Blechnum spicant*, (2) *Sequoia sempervirens*/ *Mahonia nervosa*, (3) *Sequoia sempervirens*/ *Arbutus menziesii*, and (4) Transitional Stands.

Stand No.	Selected Stand	TWINSPAN Group	Predicted Group	Probabilities	
				Distance	Membership
1	*	1	1	0.0159	1.0000
2	*	1	1	0.1969	1.0000
3	*	1	1	0.3159	1.0000
4	*	1	1	0.5552	1.0000
5	*	1	1	0.9966	1.0000
6	*	1	1	0.1423	1.0000
7	*	1	1	0.3713	1.0000
8	*	1	1	0.6033	1.0000
9	*	1	1	0.5913	1.0000
10		2	2	0.2737	1.0000
11	*	1	1	0.1410	1.0000
12	*	1	1	0.6975	1.0000
13	*	1	1	0.6202	1.0000
14		2	2	0.2048	0.9996
15	*	1	1	0.4388	1.0000
16		4	2	0.0011	1.0000
17	*	1	1	0.1926	1.0000
18		4	2	0.0000	1.0000
19	*	2	2	0.8946	1.0000
20		4	1	0.0000	1.0000
21		2	2	0.4016	1.0000
22		2	2	0.1338	1.0000
23	*	1	1	0.3108	1.0000
24		2	2	0.1046	1.0000
25	*	2	2	0.8912	1.0000
26		4	1	0.0000	1.0000
27	*	2	2	0.6399	1.0000
28		4	1	0.0069	1.0000
29		4	2	0.0725	1.0000
30	*	2	2	0.4269	1.0000
31		4	1	0.0000	1.0000
32		4	2	0.0000	1.0000
33		4	2	0.0000	1.0000
34		4	2	0.0001	1.0000
35		2	2	0.3335	1.0000
36		2	2	0.1567	1.0000
37		4	2	0.0000	0.9994
38	*	2	2	0.4494	0.9998
39		4	2	0.0001	1.0000
40	*	2	2	0.7001	1.0000

Table 7. Results of Discriminant Analysis Showing Sample Stands in TWINSPAN Groups and in Groups where Membership Was Predicted by Discriminant Analysis. A Distance Probability Is the Likelihood of Any Stand Being As Distant from the Predicted Group Centroid As the Stand Under Consideration. A Membership Probability Is the Likelihood of a Stand Being a Member of the Predicted Group. Asterisks Indicate Stands Selected to Form Equal Groups of Typical Stands for Constancy and Fidelity Calculations. Group Codes: (1) *Sequoia sempervirens*/ *Blechnum spicant*, (2) *Sequoia sempervirens*/ *Mahonia nervosa*, (3) *Sequoia sempervirens*/ *Arbutus menziesii*, and (4) Transitional Stands. (continued)

Stand No.	Selected Stand	TWINSPAN Group	Predicted Group	Probabilities	
				Distance	Membership
41		4	2	0.0014	0.8758
42	*	3	3	0.7754	1.0000
43		4	2	0.0000	1.0000
44	*	2	2	0.9727	1.0000
45		2	2	0.1512	1.0000
46	*	2	2	0.9713	1.0000
47	*	2	2	0.4736	1.0000
48		2	2	0.0514	1.0000
49	*	3	3	0.8969	1.0000
50		2	2	0.3562	0.9999
51	*	3	3	0.7351	1.0000
52	*	2	2	0.6730	1.0000
53	*	3	3	0.6895	1.0000
54	*	3	3	0.4682	1.0000
55	*	3	3	0.9427	1.0000
56		2	2	0.2181	1.0000
57		3	3	0.1455	0.9932
58	*	2	2	0.4375	1.0000
60		4	2	0.0097	1.0000
61	*	3	3	0.5200	1.0000
62		2	2	0.3459	1.0000
63		2	2	0.7438	1.0000
64	*	2	2	0.3653	1.0000
65	*	2	2	0.5417	1.0000
66	*	3	3	0.5882	1.0000
67	*	2	2	0.4292	0.9999
68		3	3	0.1250	1.0000
69		2	2	0.1969	0.9968
70	*	3	3	0.8938	1.0000
71	*	3	3	0.6482	1.0000
72	*	3	3	0.8168	1.0000
73	*	3	3	0.7250	1.0000
74		4	2	0.0053	1.0000
75	*	3	3	0.6722	1.0000
76	*	3	3	0.9077	1.0000
77		3	3	0.2896	0.9993
78	*	2	2	0.7129	1.0000
79		2	2	0.0702	0.9793
80	*	3	3	0.5061	1.0000
81		2	2	0.3792	1.0000



B– *Sequoia sempervirens*/*Blechnum spicant*
M– *Sequoia sempervirens*/*Mahonia nervosa*
A– *Sequoia sempervirens*/*Arbutus menziesii*

Figure 7. Topographic Map Showing the Forest Type Classification of Sample Stands in the Little Lost Man Creek Research Natural Area, Redwood National Park, CA. Dotted Line Indicates Watershed Boundary.

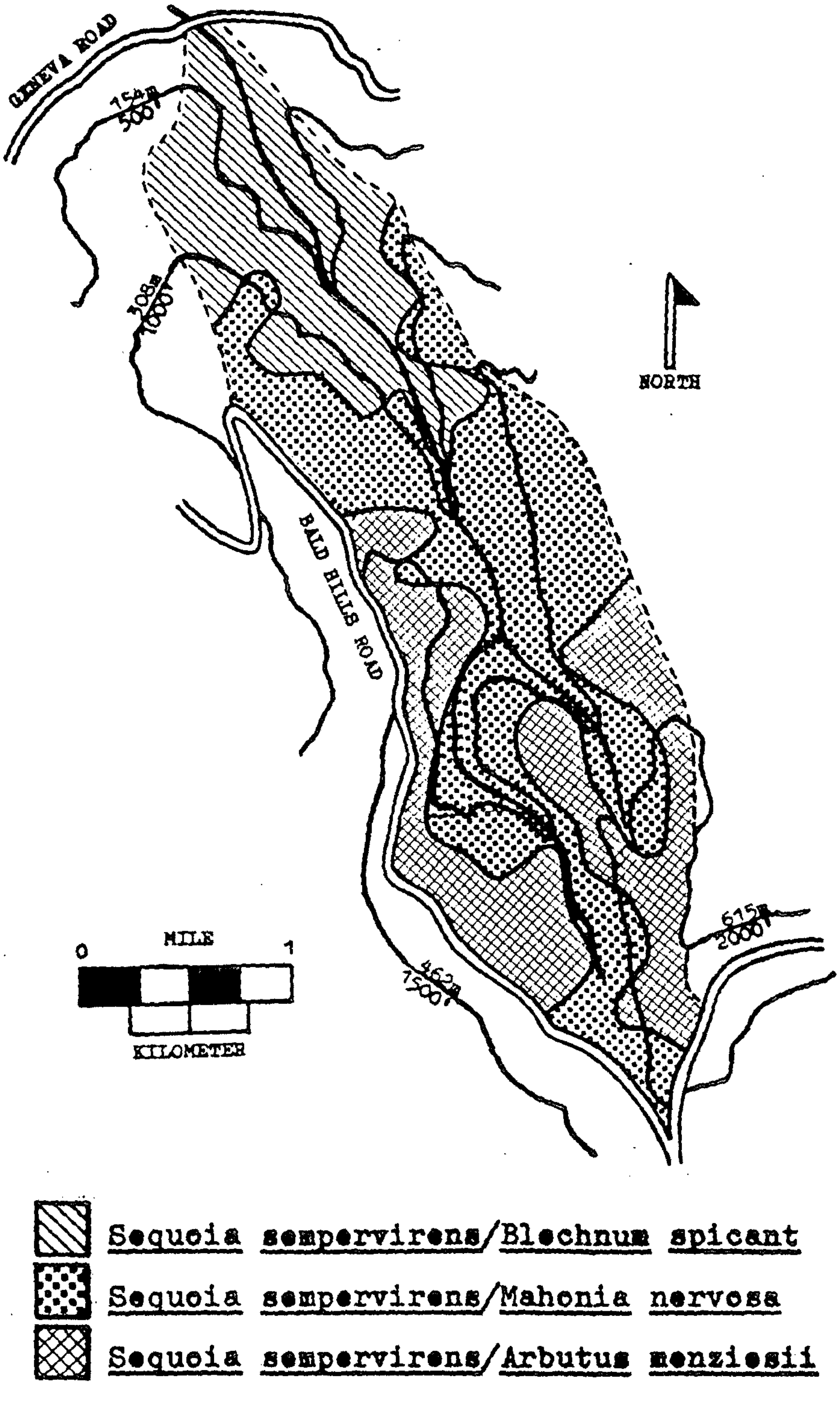


Figure 8. Generalized Forest Type Map of the Little Lost Man Creek Research Natural Area, Redwood National Park, CA. Dotted Line Indicates Watershed Boundary.

Table 8. Species Distributions in Equal Groups of Typical Stands Selected to Represent the *Sequoia sempervirens*/*Blechnum spicant*, *Sequoia sempervirens*/*Mahonia nervosa*, and *Sequoia sempervirens*/*Arbutus menziesii* Forest Types of Little Lost Man Creek, CA. Numbers and Symbols Are ZM Cover-Abundance Values (Becking, 1957). Stand Indentification Numbers Are Printed Vertically.

Stand No.	1	0	0	1	1	0	0	0	0	0	0	2	1	1	0	5	4	6	4	2	7	6	6	5	4	4	3	3	2	1	7	5	5	5	4	7	7	7	7	6	6	4	8	7	5
	1	4	3	5	3	6	8	7	5	2	1	3	7	2	9	2	7	5	4	7	8	7	3	8	6	0	8	0	5	9	0	5	4	3	2	6	3	2	1	6	1	9	0	5	1
Species	Sequoia/ Blechnum															Sequoia/ Mahonia															Sequoia/ Arbutus														
Disporum smithii				1	1	1							1	1	1																														
Athyrium filix-femina	1	2		1	2	1				1																																			
Adiantum pedatum		1		1									1																																
Rubus spectabilis		1	1								1																																		
Menziesia ferruginea				1	1	2		1																																					
Corylus cornuta	2	2	3							2			3	2																															
Rhamnus purshiana			1	1		1	3	3	3	2	2	2	1	3	3																														
Picea sitchensis						1		1		1	1																																		
Blechnum spicant	2	2	2	2	2	3		1		1	1	3	1	2			1	1	+																										
Stachys mexicana			2	1										1																															
Adenocaulon bicolor						1								1	1																														
Vancouveria hexandra	1	1		1								1	1	1		+	1																												
Oxalis oregana	3	3	3	3	3	3	2	2	2	2	2	3	2	2	3	2	2	2	2	2	1			2			+		1	1															
Polystichum munitum	5	5	5	5	5	5	5	4	3	2	2	5	5	4	4	2	2	2	3	3	2	1	1	2	2	1	2	2	1	1	1	1	1			2		1					+		+
Vaccinium parvifolium	2	1		1	3	3	1	1	3	1	4	2	4	1	1	1	1	1					+	2	1	1		1		+		1	2		1				+				+		
Trillium ovatum					1	1			+	1	1	+	1						1									+			1	1						1				1	1	+	1
Disporum hookeri														+	+					+					1			1															1		1
Carex hendersonii																									1																				
Actaea rubra																														+															
Abies grandis																1																													
Iris douglasiana																1	1			1				1		1		1																	
Festuca subulata														+		1	1		1					1	1	2	1	1																	
Mahonia nervosa							1	+				+	1		2	2	2	2	1	2	1	2	1	2	2	2		2	1	1	1					2									
Galium aparine				+		1			1		1			+		1		1	1	1	1		1	1	1	1	1	1	1	1		1				1									
Tsuga heterophylla				1					1		1	1	1	1	1	1		1	2			1		1			1		1		1		2		1										
Sequoia sempervirens	3	4	4	4	5	4	3	3	3	3	3	2	4	2	3	2	3	3	3	3	3	3	3	3	3	3	3	3	3	3	2	2	3	2	3	3	2	2	2	2		2	2	2	2
Trientalis borealis								+					+						+	1										1	1	+						1		1			1	1	1
Gaultheria shallon							1	1	2	1	3	2	1	+	2	3	3	3	3	3	3	4	3	4	2	3	2	4	3	3	2	1	3	1	1	2	3	4	4	5	2	1	3	5	2
Vaccinium ovatum	2	1	2	1	2	1	2	3	3	4	2	1	1	3	1	1	2	1		1	3	3	4	3	3	4	4	3	4	4	4	5	4	4	5	2	3	2	3	2	3	4	3	1	5
Lithocarpus densiflora	3	1	2				3		2	1		4	2	3	2	2	4	3	3	3	5	3	3	3	4	4	3	4	2	4	3	5	4	4	3	5	4	4	4	5	4	5	5	4	4
Whipplea modesta																1		1			1	+	1	1	1			1		1													+		+
Hierochloe occidentalis																1	2	1				1	1	1	1	2		2	1	1															
Viola sempervirens	+								+		1			+		2	2	2	2	2	2	2	2	2	1	2	1	2	1	2	1	2	2	1	1	2	1		1	1	1	+	1	1	1
Festuca occidentalis																												+											1	1					
Rhododendron macrophyllum				1	1		3	2	1	1				1			1	3	2	4	3	2	3	1	2	3	3	2	3	3	4	4	4	3	3	3	3	4	1	2	2	4			3
Pseudotsuga menziesii	1		1	1		1	1		2	2	2	1		3		2	2		2	2	2	2	2	3	3	3	3	2	3	3	2	3	1	2	3	1	2	2	2	2	2	1	1	1	2
Lathyrus vestitus																						+		1	1	1		1																	
Cardamine integrifolia																	1					+	1	1	1	1		2				1							1				1	1	1
Pleuricospora fimbriolata																																							+		1	+		1	1
Pteridium aquilinum																																					1	2	1	1	+	1		1	+	
Goodyera oblongifolia																1			+		2	1							1	1	1	+			1				1	1	1			1	1
Corallorhiza maculata																															1	+				2		1					1	1	1
Arbutus menziesii																					1	+	1									1				1	1		2	1	2	1	2	2	2

Table 9. Summary Synthesis Table Showing Species Constancy /Modal Cover Values in the *Sequoia sempervirens*/ *Blechnum spicant*, *Sequoia sempervirens*/*Mahonia nervosa*, and *Sequoia sempervirens*/*Arbutus menziesii* Associations of Little Lost Man Creek, CA. Constancy Values Are Species Frequencies within Equal Groups of Representitive Stands. Cover Values Are from the ZM Cover-Abundance Scale (Becking, 1957).

Species	Sequoia/ Blechnum	Sequoia/ Mahonia	Sequoia/ Arbutus
Canopy Trees			
Picea sitchensis	0.27/1		
Tsuga heterophylla	0.47/1	0.47/1	0.20/1
Sequoia sempervirens	1.00/3	1.00/3	0.93/2
Pseudotsuga menziesii	0.67/1	0.93/2	1.00/2
Abies grandis		0.07/1	
Subcanopy Trees			
Lithocarpus densiflora	0.67/2	1.00/3	1.00/4
Arbutus menziesii		0.20/1	0.67/2
Small Trees / Tall Shrubs			
Rubus spectabilis	0.20/1		
Menziesia ferruginea	0.27/1		
Corylus cornuta	0.40/2		
Rhamnus purshiana	0.80/3		
Vaccinium parvifolium	0.93/1	0.60/1	0.33/+
Vaccinium ovatum	1.00/1	0.93/4	1.00/4
Rhododendron macrophyllum	0.47/1	0.93/3	0.87/4
Low Shrubs / Herbs			
Disporum smithii	0.40/1		
Athyrium filix-femina	0.40/1		
Adiantum pedatum	0.20/1		
Stachys mexicana	0.20/1		
Adenocaulon bicolor	0.20/1		
Blechnum spicant	0.80/2	0.20/1	
Vancouveria hexandra	0.40/1	0.13/+	
Oxalis oregana	1.00/3	0.67/2	
Polystichum munitum	1.00/5	1.00/2	0.47/1
Trillium ovatum	0.47/1	0.13/+	0.47/1
Disporum hookeri	0.13/+	0.20/1	0.13/1
Gaultheria shallon	0.60/1	1.00/3	1.00/2
Trientalis borealis	0.13/+	0.20/1	0.47/1
Viola sempervirens	0.27/+	1.00/2	0.93/1
Mahonia nervosa	0.33/+	0.92/2	0.13/1
Galium aparine	0.33/1	0.87/1	0.13/1
Festuca subulata	0.07/+	0.53/1	
Carex hendersonii		0.07/1	
Actaea rubra		0.07/+	
Iris douglasiana		0.40/1	
Hierchloe occidentalis		0.73/1	
Lathyrus vestitus		0.33/1	
Whipplea modesta		0.60/1	0.13/+
Festuca occidentalis		0.07/+	0.13/1
Cardamine integrifolia		0.47/1	0.33/1
Goodyera oblongifolia		0.40/1	0.53/1
Corallorhiza maculata			0.47/1
Pleuricospora fimbriolata			0.33/1
Pteridium aquilinum			0.53/1

Table 10. Fidelity Table Showing Species Fidelity Classes for the *Sequoia sempervirens*/*Blechnum spicant*, *Sequoia sempervirens*/*Mahonia nervosa*, and *Sequoia sempervirens*/*Arbutus menziesii* Associations of Little Lost Man Creek, CA. Fidelity Was Calculated as the Species Presence in an Equal Set of Representitive Stands Expressed as a Percentage the Species Presence in the Total Set of Stands. Fidelity Values Are Expressed in Fidelity Classes II-V (Becking, 1957). Character Species Are in Fidelity Classes III-V.

Species	Sequoia/ Blechnum	Sequoia/ Mahonia	Sequoia/ Arbutus
Canopy Trees			
Picea sitchensis	V		
Tsuga heterophylla	II	II	II
Sequoia sempervirens	II	II	II
Pseudotsuga menziesii	II	II	II
Abies grandis		V	
Subcanopy Trees			
Lithocarpus densiflora	II	II	II
Arbutus menziesii		II	IV
Small Trees / Tall Shrubs			
Rubus spectabilis	V		
Menziesia ferruginea	V		
Corylus cornuta	V		
Rhamnus purshiana	V		
Vaccinium parviolium	III	II	II
Vaccinium ovatum	II	II	II
Rhododendron marophyllum	II	II	II
Low Shrubs / Herbs			
Disporum smithii	V		
Athyrium filix-femina	V		
Adiantum pedatum	V		
Stachys mexicana	V		
Adenocaulon bicolor	V		
Blechnum spicant	IV	II	
Vancouveria hexandra	IV	II	
Oxalis oregana	III	II	
Polystichum munitum	II	II	II
Trillium ovatum	II	II	II
Disporum hookeri	II	II	II
Gaultheria shallon	II	II	II
Trientalis borealis	II	II	III
Viola sempervirens	II	II	II
Mahonia nervosa	II	III	II
Galium aparine	II	III	II
Festuca subulata	II	IV	
Carex hendersonii		V	
Actaea rubra		V	
Iris douglasiana		V	
Hierchloe occidentalis		V	
Lathyrus vestitus		V	
Whipplea modesta		IV	II
Festuca occidentalis		II	III
Cardamine integrifolia		III	II
Goodyera oblongifolia		II	III
Corallorhiza maculata			V
Pleuricospora fimbriolata			V
Pteridium aquilinum			V

Table 11. Mean Basal Area (BA) (M^2/Ha) and Relative Dominance (RD) (Percent) of Canopy Species in the *Sequoia sempervirens*/*Blechum spicant*, *Sequoia sempervirens*/*Mahonia nervosa*, and *Sequoia sempervirens*/*Arbutus menziesii* Associations in Little Lost Man Creek, CA. Relative Dominance is the Species' Basal Area Expressed as a Percentage of the Total Basal Area.

	Sequoia/ Blechnum		Sequoia/ Mahonia		Sequoia/ Arbutus	
Canopy Species	BA	RD	BA	RD	BA	RD
Picea sitchensis	2	1				
Tsuga heterophylla	4	3	7	5	2	3
Sequoia sempervirens	126	82	84	59	39	54
Pseudotsuga menziesii	22	14	52	35	31	43
Abies grandis			2	1		
Total Basal Area	154		145		72	

The first discriminant function based on topographic variables accounted for 98 percent of the total variance. The second function accounted for just two percent of the total variance and was therefore considered insignificant. The index of discriminatory power indicated 86 percent of the variability of the first function was due to differentiation among typical stand groups. The structure coefficients for the first function (Table 12) showed elevation, topographic configuration, and slope position were the topographic variables that best distinguished the forest types. A plot of the typical stands in the discriminant space formed by the scores on the first two functions (Figure 9) showed the forest types were well-separated along the axis representing the first function (the axis representing the insignificant second function was included for graphical purposes only).

The mapped distribution of the forest types showed a relatively weak correspondence with the distribution of the soil series as mapped by the Soil-Vegetation Survey (DeLapp et al., 1961a, 1961b). Comparisons of soil profile descriptions from the groups of typical stands revealed a somewhat stronger correlation between forest types and soil series. Soils on the concave lower slopes at the northern end of the study area where the Sequoia/Blechnum type was best developed were generally dark brown to brown clay loams with gleyed subsurface horizons. These were the most Melbourne-like soils in the study area. Soils on convex upper slopes and ridgetops at the southern end of the study

Table 12. Structure Coefficents for First Discriminant Function Derived for Discriminant Analysis Relating Distribution of Forest Types to Topographic Factors in Little Lost Man Creek, CA. Large Coefficients Indicate Factors Most Related to Forest Type Distribution.

Variable	Coefficient
Stand Elevation	0.61730
Topograpic Configuration	0.21580
Slope Position	0.11148
Radiation Index	0.10696
North-South	-0.08558
East-West	0.06079
Slope	-0.06028

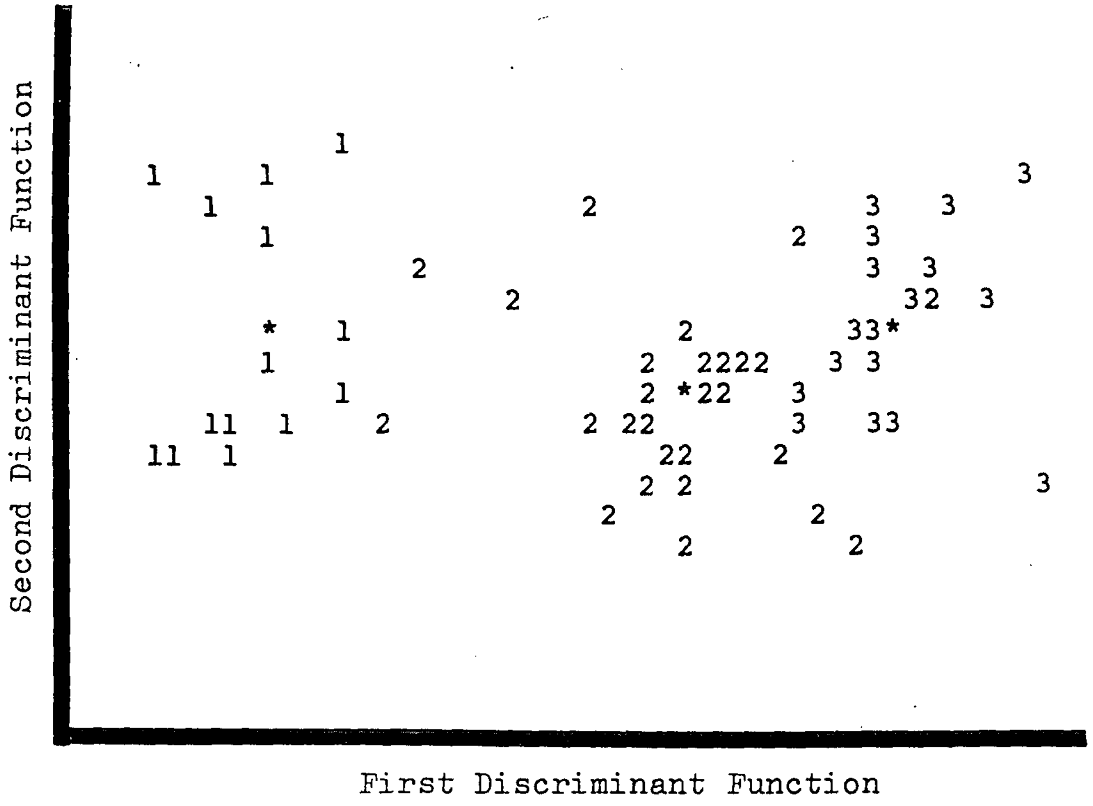


Figure 9. Distribution of Sample Stands on the Axis Representing the First Function Derived by Discriminant Analysis to Relate the Distribution of the Forest Associations to Topographic Factors in the Little Lost Man Creek Research Natural Area, Redwood National Park, CA. The Axis for the Second Non-Significant Function Was Included for Graphical Purposes Only. Asterisks Indicate Group Centroids. Group Codes: (1) Sequoia sempervirens/Blechnum spicant association, (2) Sequoia sempervirens/Mahonia nervosa association, (3) Sequoia sempervirens/Arbutus association.

area where the Sequoia/Arbutus type was best developed were generally grayish brown to pale brown gravelly loams and clay loams. These were the most Hugo-like soils in the study area. The soils occupied by the Sequoia/Mahonia type were generally intermediate in character between the Melbourne and Hugo extremes. The edaphic, topographic, and floristic character of the three forest types are summarized and contrasted in Table 13.

Table 13. Synoptic Table for the *Sequoia sempervirens*/*Blechnum spicant*, *Sequoia sempervirens*/*Mahonia nervosa*, and *Sequoia sempervirens*/*Arbutus menziesii* Associations of Little Lost Man Creek, CA Showing Mean Cover of Each Life-form Stratum, Dominant Species with Modal Cover of 5-25 Percent or Greater, Character Species in Fidelity Classes III-V, and Typical Topographic and Edaphic Conditions in Each Association.

	Sequoia / Blechnum	Sequoia / Mahonia	Sequoia / Arbutus
Canopy Trees			
Mean Cover (percent)	70	60	40
Dominant Species	Sequoia sempervirens	Sequoia sempervirens Pseudotsuga menziesii	Pseudotsuga menziesii Sequoia sempervirens
Character Species	Picea sitchensis	Abies grandis	
Subcanopy Trees			
Mean Cover (percent)	35	50	75
Dominant Species		Lithocarpus densiflora	Lithocarpus densiflora
Character Species			Arbutus menziesii
Small Trees and Tall Shrubs			
Mean Cover (percent)	30	60	70
Dominant Species	Rhamnus purshiana	Vaccinium ovatum Rhododendron macrophyllum	Vaccinium ovatum Rhododendron macrophyllum
Character Species	Rhamnus purshiana Corylus cornuta Menziesia ferruginea Vaccinium parvifolium Rubus spectabilis		
Low Shrubs and Herbs			
Mean Cover (percent)	90	50	30
Dominant Species	Polystichum munitum Oxalis oregana Blechnum spicant	Gaultheria shallon Viola sempervirens Mahonia nervosa Polystichum munitum	Gaultheria shallon
Character Species	Blechnum spicant Oxalis oregana Athyrium filix-femina Adiantum pedatum Stachys mexicana Disporum smithii Adenocaulon bicolor Vancouveria hexandra	Mahonia nervosa Hierchloe occidentalis Lathyrus vestitus Whipplea modesta Galium triflorum Festuca subulata Iris douglasiana Cardamine integrifolia	Pteridium aquilinum Pleuricospora fimbriolata Corallorhiza maculata Goodyera oblongifolia Festuca occidentalis Trientalis borealis
Elevation Range (meters)	60-310	240-555	430-620
Topographic Position	moist sites, esp. concave lower slopes	mesic sites, esp. even middle slopes	xeric sites, esp. convex upper slopes and ridgetops
Soil Series	Melbourne	Melbourne-Hugo	Hugo-Melbourne
Soil Texture	clay loam	gravelly clay loam	gravelly loam to clay loam
Surface/Subsurface Color	dark brown / brown with gley mottling	brown / brown to strong brown	grayish brown / strong brown to pale brown

DISCUSSION

Ecological Relationships

Elevation, slope position, and topographic configuration were the topographic variables that best discriminated among the forest associations of the study area. The Sequoia/Blechnum association was found at lower elevations and primarily on lower slopes where the topographic configuration was generally concave. The Sequoia/Arbutus association was found at higher elevations and primarily on upper slopes and ridgetops where the topographic configuration was generally convex. The Sequoia/Mahonia association was found at intermediate positions in the study area (i.e. convex upper slopes and ridgetops at lower elevations and concave lower slopes at higher elevations). The distribution of the forest associations along this topographic gradient formed a "toposequence" (Barbour et al., 1980). Toposequences formed in regional vegetation types were commonly interpreted as expressions of variation in microclimate and soil moisture availability (e.g. Becking, 1967; Franklin and Dyrness, 1973; Zinke, 1977; Sawyer et al., 1977; Veirs, 1982).

Concave lower slopes tend to be cooler because they accumulate cold air and thus radiate heat more rapidly at night, while convex upper slopes and ridgetops tend to be warmer because they drain off cold air and thus radiate heat less rapidly at night (Spurr and Barnes, 1980). Soil moisture availability is generally greater on concave lower slopes because evapotranspiration rates are lower in cool microclimates and because both water and soil material is transported downslope towards these sites, while there is generally less soil moisture availability on convex upper slopes and ridgetops because evapotranspiration rates are higher in warm microclimates and because water and soil material is transported downhill away from these sites (Buol et al., 1980). In the study area, extremes in microclimate and soil moisture availability from one end of the toposequence to the other (i.e. from relatively cool, moist sites on concave lower slopes to relatively warm, xeric sites on convex upper slopes and ridgetops) were probably accentuated by the higher incidence of summer fog at lower elevations in the study area (Freeman, 1971). Fog cover reduces both insolation and evapotranspiration, and thus concave lower slopes at lower elevations where the incidence of fog was highest were probably the most cool and moist sites in the study area. Convex upper slopes and ridgetops at higher elevations where the incidence of fog was lowest were probably the most warm and xeric sites in the study area.

The Sequoia/Blechnum association (Figure 10) attained its best development on lower slopes at lower elevations at the moist end of the toposequence. Here the fog was probably

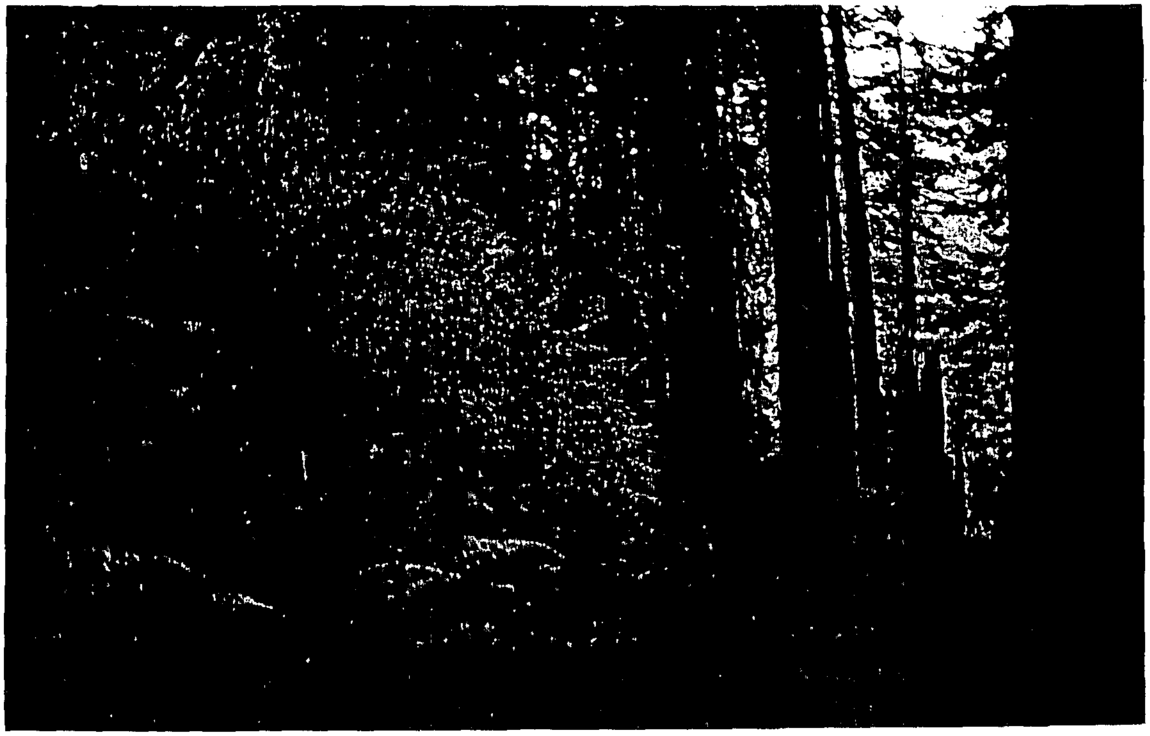


Figure 10. Photograph of Stand No. 3 Representing the *Sequoia sempervirens*/*Blechnum spicant* Association of Little Lost Man Creek, CA.

frequent during the otherwise dry summer months (Freeman, 1971), and consequently, the relative humidity was probably higher, especially in cool, sheltered sites. The fine-textured colluvial soils on concave topography also probably contributed to a relatively high moisture regime. These Melbourne-like soils were morphologically those with the highest moisture-holding capacity in the study area, and the gley-mottled subsurface horizons were indicative of downslope movement of groundwater towards the lower slope sites (Buol et al., 1980).

Sequoia sempervirens dominance in the canopy of the Sequoia/Blechnum association was probably related to a favorable moisture regime and the effects of disturbance factors. Fire and mass-wasting of slopes were two major agents of disturbance in similar forest-types throughout the region (Becking, 1967; Franklin and Dyrness, 1973; Zinke, 1977; Sawyer et al., 1977; Veirs, 1982; Lennox, 1982). Earthflows and slumps were the most common mass-wasting events on moist lower slopes near the study area (Coleman, 1973). In stands near the study area, Sequoia sempervirens attained dominance on moist mineral soils exposed after landsliding either directly through seedling dominance (Lennox, 1982) or indirectly through an Alnus rubra seral stage (Becking, 1967). In either case, Sequoia sempervirens probably gained dominance by virtue of its longevity and immense stature on sites with a favorable moisture status. Assuming a cool microclimate, relatively high humidity, and moist soils, and given the lack of a dense woody understory in the Sequoia/Blechnum association, it is likely that the frequency of fire was relatively low and surface fires were most common on the lower slopes at lower elevations in the study area (Barbour et al., 1980). *Sequoia sempervirens* maintained its dominance under a light fire regime in old-growth redwood stands near the study area (Veirs, 1982). In the presence of infrequent surface fires on moist lower slopes, the longevity, stature, and fire-resistant characteristics of *Sequoia sempervirens* (Stone et al., 1972) probably favored the species over its shade-tolerant but less fire-resistant associates. The shade-intolerant *Pseudotsuga menziesii* (Fowells, 1965) was found in different size-classes widely scattered throughout lower slope stands in the study area. This mode of occurrence suggested establishment in association with small gaps in the canopy formed by windthrow or fire. Species comprising the subcanopy and small tree/large shrub layers in the Sequoia/Blechnum association probably needed more phytosynthetic energy to maintain their woody structure (Whittaker, 1970), so these strata were not well-developed except in association with gaps in the dense canopy. *Polystichum munitum* and other fern species in the dense low shrub/herb layer were indicative of low light and high moisture in old-growth redwood forests (Waring and Major, 1964).

The Sequoia/Arbutus association (Figure 11) was best developed on upper slopes and ridgetops at higher elevations

Figure 11. Photograph of Stand No. 66 Representing the *Sequoia sempervirens*/*Arbutus menziesii* association of Little Lost Man Creek, CA.

at the xeric end of the toposequence. At elevations above the 457 m (1500 ft) inversion layer, the incidence of summer fog was probably low (Freeman, 1971). Consequently, the relative humidity was probably lower, especially in warm, exposed positions. The coarse-textured residual soils on convex topography also probably contributed to a xeric moisture regime. The Hugo-like soils occupied by the Sequoia/Arbutus association were morphologically those with the lowest moisture-holding capacity in the study area (Buol et al., 1980).

The co-dominance of *Sequoia sempervirens* and *Pseudotsuga menziesii* and the dense subcanopy of sclerophyllous hardwoods in the Sequoia/Arbutus association was probably related to a relatively xeric moisture regime and the effects of fire. Assuming a warm microclimate, relatively high humidity, and relatively dry soils, and given the greater exposure to lightning strikes near ridgetops and the dense woody understory of the Sequoia/Arbutus association, it is likely that the frequency of fire was relatively high and destructive crown fires were more common on upper slopes and ridgetops in the study area (Barbour et al., 1980). *Sequoia sempervirens* maintained co-dominance with *Pseudotsuga menziesii*, *Lithocarpus densiflora*, and *Arbutus menziesii* under a relatively frequent and intense fire regime in old-growth redwood stands on upper slopes and ridgetops near the study area (Becking, 1967; Veirs, 1982). Here *Sequoia sempervirens* and hardwoods probably sprouted from lignotubers and thus survived destructive crown fires which opened up the canopy and exposed dry mineral soils and thus favored establishement of Pseudotsuga menziesii seedlings. The light intensity under the canopy and subcanopy of the Sequoia/Arbutus association in the study area was evidently sufficient to support the dense, woody structure of the small tree/large shrub layer, but the dense shade, dry soils, and thick accumulations of Lithocarpus densiflora litter below this stratum probably inhibited the growth and germination of many species other than mycotrophic ones (Furman and Trappe, 1971; Franklin et al., 1981). The sparse low shrub/herb layer in the Sequoia/Arbutus association was characterized by several species which parasitize mycorrhizal fungi for nutrients, including Goodyera oblongifolia, Pleuricospora fimbriolata, and Corallorhiza maculata.

Sites occupied by the Sequoia/Mahonia association (Figure 12) formed the mesic portion of the toposequence between the moist and xeric extremes. This forest association seemed to occur throughout the watershed wherever a combination of topographic and edaphic factors formed a relatively mesic moisture regime. At lower elevations where fogs were probably more frequent, the Sequoia/Mahonia association occupied exposed, convex positions on ridgetops and upper slopes where soils were often shallow and gravelly. At higher elevations where fogs were probably less frequent, the mesic association occupied cool, sheltered sites adjacent

Figure 12. Photograph of Stand No. 38 Representing the *Sequoia sempervirens*/*Mahonia nervosa* association of Little Lost Man Creek, CA.

to the creek, especially in concave positions where soils were deeper and finer-textured.

In the Sequoia/Mahonia association, *Pseudotsuga menziesii* was nearly co-dominant with *Sequoia sempervirens* as in the xeric association, but the total basal area and crown cover of canopy species were as great as those in the moist association. The subcanopy of *Lithocarpus densiflora* was better developed in the Sequoia/Mahonia association compared to the moist association, but the subcanopy had a lower mean cover than in the xeric association and lacked *Arbutus menziesii*. The structure and composition of stands in the Sequoia/Mahonia association seemed to indicate an intermediate moisture and fire regime relative to those described for the moist and xeric types. The canopy structure probably created intermediate light levels in the understory of the Sequoia/Mahonia association relative to those in the moist and xeric types. The light penetration was evidently sufficient to support a well-developed small tree/large shrub layer similar in composition to that in the xeric association but lower in cover. The low shrub/herb stratum in the Sequoia/Mahonia association was the most diverse in the study area. Dominant species in this layer included species common in the moist forest association (i.e. *Polystichum munitum* and *Oxalis oregana*) as well as those common in the xeric association (i.e. *Gaultheria shallon* and *Viola sempervirens*). The co-dominance of typically moist and xeric species and the presence of several characteristic species in the low shrub/herb stratum seemed to indicate the mesic status of the Sequoia/Mahonia association. Character species such as Hierchloe occidentalis, Iris douglasiana, and Whipplea modesta were indicative of both intermediate light and mesic moisture conditions in old-growth redwood forests (Waring and Major, 1964).

Relationships to Regional Vegetation Types

The forest type classification scheme for Little Lost Man Creek was closely related to Becking's (1967) redwood alliance classification. The forest types of the study area were identified as associations within Becking's forest alliances based on shared floristic characteristics. The Sequoia/Blechnum association was placed in the "Redwood-Oxalis" alliance based on the shared characteristics of the strong dominance of Sequoia sempervirens in the overstory; the sparse small tree/large shrub layer characterized by Rhamnus purshiana, Vaccinium parvifolium, and Rubus spectabilis; the dense low shrub/herb layer dominated by Polystichum munitum and Oxalis oregana and characterized by Blechnum spicant, Athyrium filix-femina, Adiantum pedatum, Stachys mexicana, and Disporum smithii. Both the Sequoia/Mahonia and Sequoia/Arbutus associations in the study area were placed in the "Redwood-Swordfern" alliance based on shared characteristics of the co-dominance of Sequoia sempervirens, Pseudotsuga menziesii, and

Lithocarpus densiflora and the characteristic presence of Arbutus menziesii in a two-layered overstory; the dense small tree/large shrub layer comprised of Rhododendron macrophyllum and Vaccinium ovatum; the low shrub/herb layer co-dominated by Polystichum munitum and Gaultheria shallon and characterized by Mahonia nervosa, Viola sempervirens, Actaea arguta, Hierchloe occidentalis, Lathyrus vestitus, Festuca occidentalis, Corallorhiza maculata, and Goodyera oblongifolia. The hierarchial classification of the associations within Becking's alliances was supported by the results of the TWINSPAN analysis. The two groups of stands formed at the first division level (Appendix B) represented the classification at the alliance level. Pseudospecies with high preference scores on the "Redwood-Oxalis" side of the dichotomized ordination included Polystichum munitum, Oxalis oregana, Rhamnus purshiana, and Blechnum spicant. Pseudotsuga menziesii and Viola sempervirens scored high on the "Redwood-Swordfern" side.

The floristic composition of the forest associations in Little Lost Man Creek also indicated their relationship to redwood border forest types. Kuchler (1977) on his vegetation map of California showed the "Picea-Abies" forest type (Picea sitchensis-Abies grandis) forming a narrow strip between the ocean and the western edge of the redwood forest. Species characteristic of the Sequoia/Blechnum association including Picea sitchensis, Vaccinium parvifolium, Menzieisia ferruginea, Polystichum munitum, and Oxalis oregana were common components of coastal "Picea-Abies" forests (Franklin and Dyrness, 1973).

"Tsuga-Pseudotsuga" forests (_Tsuga heterophylla-Pseudotsuga menziesii_) formed a border with redwood forest at the northern edge of Sequoia's range in southwest Oregon, about 98 km north of the study area. Franklin and Dyrness (1973) described _Sequoia sempervirens_ forests as variants of the "Tsuga-Pseudotsuga" forests of western Washington and Oregon. "Tsuga-Pseudotsuga" forest types described by Becking (1954), Bailey (1966), and Franklin and Dyrness (1973) showed a close floristic relationship to the moist Sequoia/Blechnum and mesic Sequoia/Mahonia associations in the study area. Moist "Tsuga-Pseudotsuga" forest types were characterized by the dominance of _Polystichum munitum_, _Oxalis oregana_ and the presence of species such as _Blechnum spicant_, _Athyrium filix-femina_, _Adiantum pedatum_, _Disporum smithii_, and _Vancouveria hexandra_. Mesic types were characterized by the dominance of _Rhododendron macrophyllum_, _Vaccinium ovatum_, _Gaultheria shallon_, _Mahonia nervosa_, and _Viola sempervirens_.

Kuchler's (1977) map showed mixed evergreen forest forming the eastern border forest in the region of the study area. The mixed evergreen forest types of California were described by Sawyer et al., (1977). Their "Psuedotsuga-hardwood" forest type (_Pseudotsuga menziesii_) showed a floristic relationship to the xeric Sequoia/Arbutus association in the study area. Both types had a two-level canopy co-dominated by _Pseudotsuga menziesii_ and _Lithocarpus_ *densiflora* and characterized by the presence of *Arbutus menziesii*. The understories in both types were dominated by *Rhododendron macrophyllum*, *Vaccinium ovatum*, and *Gaultheria shallon*. *Pteridium aquilinum* and *Goodyera oblongifolia* were shared characteristic herbaceous species. Barrows (1984) noted the presence of several mycotrophic species in the understory of old-growth "Pseudotsuga-hardwood" forests, including species of *Allotropa*, *Pityopus*, and *Pyrola* also found in the Sequoia/Arbutus association in the study area.

There was no definite southern redwood border forest in the region of the study area. Kuchler (1977) mapped "Sequoia-Pseudotsuga" (*Sequoia sempervirens*-*Pseudotsuga menziesii*) as a near-continuous unit extending south from the Oregon border to Monterey county. Descriptions of redwood vegetation in southern Humboldt county (Becking, 1967), Mendocino county (Zinke, 1977), Marin county (Howell, 1970, McBride and Jacobs, 1978), Santa Cruz county (Cooney-Lazaneo and Lyons, 1981), and Monterey county (Becking, 1971) indicated a compositional gradient from conifer to hardwood dominance on a transect extending south from the study area. Moving south through the redwood forest belt, *Lithocarpus densiflora* and *Arbutus menziesii* were increasingly important stand components. The composition and structure of modal (i.e. mesic) redwood forests from Mendocino county south to Santa Cruz county were much like those in the xeric Sequoia/Arbutus association, except for the presence of *Umbellularia californica* and *Quercus* species in the southern stands. In Monterey county at the southern edge of *Sequoia sempervirens*' range, the species occurred as isolated groves within mixed hardwood forests dominated by *Lithocarpus densiflora*, *Arbutus menziesii*, *Quercus* sps., and *Pinus coulteri*. Here *Pseudotsuga menziesii* and characteristic understory components of the northern redwood forest and related forest types were very scarcely represented (Becking, 1971).

Together the old-growth forest associations of Little Lost Man Creek and the related seral types of the lower Redwood Creek basin (Muldavin et al., 1981; Lenihan et al., 1982; Appendix C) helped define regional redwood habitat-types. Both Stone et al., (1972) and Daubenmire (1975) recommended definition of redwood habitat-types for the purposes of vegetation management in Redwood National Park. Here National Park Service policy (Leopold et al., 1963) mandated restoring about 5,700 ha of cutover parkland to a more pristine appearance (i.e. as they appeared before the advent of white man). A forest habitat-type includes all land areas potentially capable of producing the same old-growth forest community (Daubenmire, 1952). A habitat-type map based on the floristic relationships between old-growth forest associations and seral vegetation types would therefore represent the distribution of the old-growth associations under pristine conditions in the lower Redwood Creek basin. Management treatments of seral vegetation would probably produce similar within-type results, and these results could be evaluated by reference to the standard composition and structure of corresponding old-growth forest associations in the Little Lost Man Research Natural Area.