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OLD-GROWTH FOREST ASSOCIATIONS IN THE NORTHERN RANGE OF COASTAL REDWOOD

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ABSTRACT

Old-growth *Sequoia sempervirens* (D. Don) Endl. (redwood) forests occurring in northwestern California and southwestern Oregon were classified and described using data from 206 systematically placed plots. Data were collected from Jedediah Smith Redwoods State Park, Del Norte Coast Redwoods State Park, northern Redwood National Park, and the southwestern portion of the Siskiyou National Forest. Plot data were analyzed using TWINSPAN and polar ordination. Six associations within the redwood series were classified: *Sequoia sempervirens/Polystichum munitum* (Kaulf) C. Presl (SESE/POMU), *Sequoia sempervirens-Pseudotsuga menziesii* (Mirbel) Franco/*Rhododendron macrophyllum* D. Don (SESE-PSME/RHMA), *Sequoia sempervirens-Tsuga heterophylla* (Raf.) Sarg./*Vaccinium ovatum* Pursh (SESE-TSHE/VAOV), *Sequoia sempervirens-Tsuga heterophylla/Polystichum munitum* (SESE-TSHE/POMU), *Sequoia sempervirens-Tsuga heterophylla/Rubus spectabilis* Pursh (SESE-TSHE/RUSP), and *Sequoia sempervirens-Alnus rubra* Bong./*Rubus spectabilis* (SESE-ALRU/RUSP).

Discriminant analysis was used to assess the relationships between abiotic site variables and classified floristic associations. Elevation and coastal proximity explained 81.1 percent of the variation among associations. Aspect and topographic position explained 14.2 percent of the remaining variation. Moisture was the primary environmental variable controlling the distribution of classified forest associations.

Sequoia sempervirens (D. Don) Endl. (redwood) forests are endemic to coastal margins and mesic inland sites from central California to southern Oregon. Along this broad latitudinal gradient, *S. sempervirens* is limited to a narrow belt 10 to 50 kilometers wide (Roy 1966; Fox 1989). The extreme northern range of *S. sempervirens* has not been adequately classified and described. Vast tracts of old-growth forest in Jedediah Smith Redwoods State Park, Del Norte Coast Redwoods State Park, and northern sections of Redwood National Park have been virtually ignored in the *S. sempervirens* literature. The difficult access, steep terrain, and huge volume of coarse woody debris characterizing interior portions of these parks may explain the dearth of botanical information in the region. As a result of this relative isolation, these parks contain some of the most primeval and undisturbed old-growth (Helms 1998) redwood vegetation in existence. Southwestern Siskiyou National Forest contains a patchy network of old-growth representing the northernmost natural *S. sempervirens* stands. Since they exist at the terminus of the redwood range, these stands are ecologically significant. They may give insight into processes affecting other parts of the range, including gradients in soil moisture and temperature that affect species composition and stand dynamics.

METHODS

Study Area. The northern range of redwood, as defined in this study, includes Jedediah Smith Redwoods State Park, Del Norte Coast Redwoods State Park, and northern Redwood National Park, all located in northern California, and portions of Siskiyou National Forest located in southwestern Oregon. It extends from 41°47'N to 42°10'N, and 124°4'W to 124°12'W. The study area is topographically diverse—elevations range from sea level to over 490 m. Rocks of the Franciscan Formation, a subduction complex consisting of accreted fragments of oceanic crust and forearc sediments, underlay most of the region (Aalto and Harper 1989). Soils were mapped as predominantly Melbourne and Empire series by the California State Cooperative Soil-Vegetation Survey (Smith et al. 1977; Delapp et al. 1978).

Crescent City, CA is the closest weather station to the study area. Precipitation data (1948–2000) indicated that maximum precipitation fell during December and January, averaging 27.7 cm and 29.6 cm, respectively. The least amount fell during July and August, averaging 1.0 cm and 2.0 cm, respectively. Annual average precipitation was 168.1 cm. The highest mean temperatures occurred in Crescent City during August and September, at 14.9°C and 14.6°C, respectively. The lowest mean temperatures occurred in December and January, at 8.8°C

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TABLE 1. COVER ABUNDANCE SCALE AND MIDPOINTS USED IN OCULAR ESTIMATES.

Cover class	Range of cover (%)	Class midpoints (%)
8	75–100	87.5
7	50–75	62.5
6	25–50	37.5
5	5–25	15
4	1–5	3
3	0.1–1	0.6
2	0.01–0.1	0.06
1	0.001–0.01	0.006

and 8.7°C, respectively (Western U.S. Climate Historical Summaries 2000).

Study area vegetation conforms to the Society of American Foresters redwood forest cover type (Eyre 1980). East and north of the study area, the Douglas-fir forest cover type dominates.

Sampling. For Jedediah Smith Redwoods State Park, Del Norte Coast Redwoods State Park, and Redwood National Park, old-growth forest was identified on 1:12,000 color infrared aerial photographs. Two hundred plots were stratified based on three elevation classes (0–105 m, 106–215 m, and >215 m), and placed onto USGS topographic quadrangles in a systematic grid 485 meters apart.

For Siskiyou National Forest, four old-growth polygons were identified on maps obtained from the USDA Forest Service GIS database, and transferred to 1:24,000 USGS topographic quadrangles. Five plots were placed in each polygon via a systematic sampling grid, with plot spacing proportional to polygon area.

Riparian zones within Jedediah Smith Redwoods State Park were sampled separately to best characterize this unique and diverse vegetation. Fifteen sample plots were systematically placed approximately 1500 m apart (total stream length/15) along Cedar Creek, Mill Creek, Clarks Creek, and several other unnamed perennial drainages within park boundaries.

Of 235 plots slated for sampling, 206 were eventually field checked. The remaining plots were not sampled because of difficult or dangerous access, or the plot was not in an old-growth forest. The 206 circular 0.05 ha (500 m²) plots were thoroughly searched and all vascular plant species identified and recorded with an ocular cover estimate using a modified Braun-Blanquet cover abundance scale (Table 1; Mueller-Dombois and Ellenberg 1974). Tree species were tallied based on stem density in three height classes: 0–3 m, 3–10 m, and >10 m. Basal area, taken from plot center, was estimated using a “cruise angle” sighting device for canopy (dominant, co-dominant, and intermediate crown classes) species. Elevation was determined with a pocket altimeter and topographic map. Slope angle was recorded in percent using a clinometer. Aspect

was assessed with a hand compass. Distance from the ocean was estimated using a topographic map. Topographic position was recorded for each plot.

Data Analysis. Two-Way Indicator Species Analysis (TWINSPAN) (Hill 1979) was used to simultaneously classify species and samples. Only species occurring in greater than 5 percent of plots were used in the analysis (Gauch 1982). Plots were analyzed in TWINSPAN with species cover cut levels of 0.6, 3.0, 15.0, 37.5, 62.5, and 87.5 percent. The 15.0 and 37.5 cut levels were weighted to emphasize dominance (Stuart et al. 1996). TWINSPAN groupings were analyzed using a polar (Bray-Curtis) ordination, to further analyze and refine the TWINSPAN output. Species richness was determined by randomly selecting 5 plots from each association and calculating the mean number of species per plot (Stuart et al. 1996). In addition, stem density per hectare in three height classes and canopy species basal area were averaged for each association.

Discriminant analysis was performed using NCSS 2000 (Hintze 1998) to relate floristic associations with abiotic site characteristics. Elevation, slope angle, coastal proximity, and a Moisture Equivalency Index (MEI) were used as abiotic variables in the discriminant analysis. The MEI was adapted from Sawyer and Thornburgh (1974) and Matthews (1986). It incorporates topographic position and aspect, two variables important to soil moisture. A lower index number (1–15) assumes greater soil moisture available to plants.

RESULTS AND DISCUSSION

TWINSPAN and polar ordination analysis produced six groups that were interpreted as associations (Fig. 1). Groups were consistent with vegetation units observed in the field. All associations were in the *Sequoia sempervirens* series, with *Pseudotsuga menziesii* (Mirbel) Franco, *Tsuga heterophylla* (Raf.) Sarg., and *Alnus rubra* Bong. sub-series. The first TWINSPAN division separated groups based on understories dominated by either *Vaccinium ovatum* Pursh or *Polystichum munitum* (Kaulf) C. Presl. Within these broad groupings, subsequent TWINSPAN division levels reflected groupings based on other indicator understory species such as *Lithocarpus densiflorus* (Hook. & Arn.) Rehder, *Rhododendron macrophyllum* D. Don, and *Rubus spectabilis* Pursh. The following association descriptions are presented from relatively dry types to wet types. A more detailed treatment of the associations can be found in Mahony (1999).

The Sequoia sempervirens-Pseudotsuga menziesii/Rhododendron macrophyllum Association.

Total vegetation cover averaged 85 percent, and total overstory cover averaged 68 percent. Overstories were dominated by *Sequoia sempervirens* and *Pseudotsuga menziesii*, with mean cover values

Level

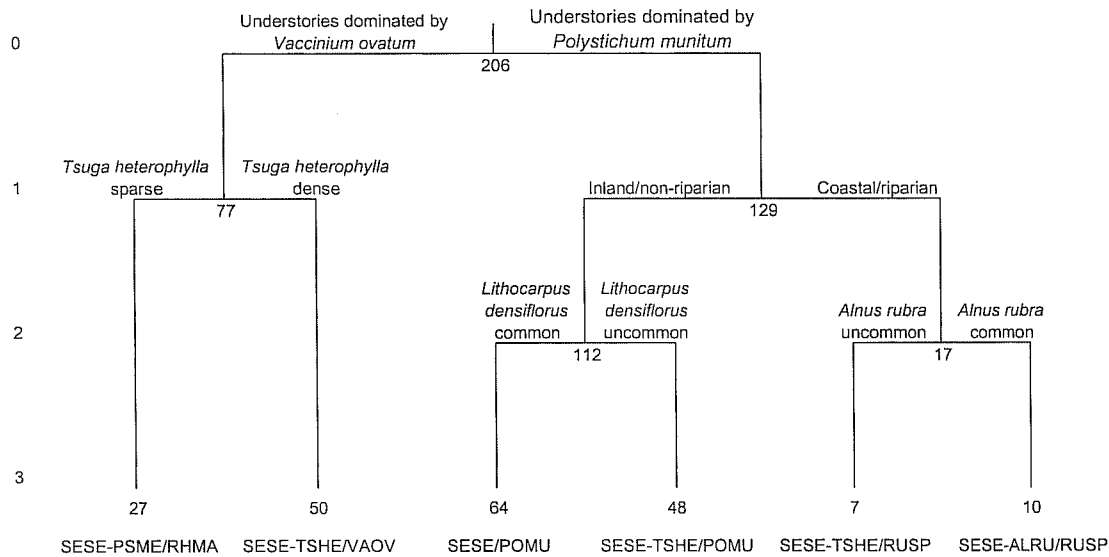


FIG. 1. Dendrogram of TWINSpan classification. Numbers beneath lines represent the number of plots prior to division. Numbers above association acronyms are the number of plots in each classified association. Association acronyms are: SESE-PSME/RHMA = *Sequoia sempervirens*-*Pseudotsuga menziesii*/*Rhododendron macrophyllum*, SESE-TSHE/VAOV = *Sequoia sempervirens*-*Tsuga heterophylla*/*Vaccinium ovatum*, SESE/POMU = *Sequoia sempervirens*/*Polystichum munitum*, SESE-TSHE/POMU = *Sequoia sempervirens*-*Tsuga heterophylla*/*Polystichum munitum*, SESE-TSHE/RUSP = *Sequoia sempervirens*-*Tsuga heterophylla*/*Rubus spectabilis*, SESE-ALRU/RUSP = *Sequoia sempervirens*-*Alnus rubra*/*Rubus spectabilis*.

of 43 and 31 percent, respectively, and mean constancies of 96 and 100 percent, respectively (Table 2). *Tsuga heterophylla* was occasionally present but contributed minimal cover. *Lithocarpus densiflorus* dominated the sub-canopy. Basal area averaged 123 m²/ha (Table 3).

The shrub layer was extremely dense. *Vaccinium ovatum* and *Rhododendron macrophyllum* dominated, with mean cover values of 47 and 35 percent, respectively, and mean constancies of 100 percent each. *Berberis nervosa* Pursh, *Gaultheria shallon* Pursh, *Rhamnus purshiana* DC., and *Vaccinium parvifolium* Smith each had greater than 30 percent constancy but less than 3 percent cover.

The herb layer was virtually absent. *Polystichum munitum* was the most dominant species in this layer with 7 percent cover and 93 percent constancy. *Disporum hooker* (Torrey) Nicholson, *Galium triflorum* Michaux, *Oxalis oregana* Nutt., *Trillium ovatum* Pursh, and *Viola sempervirens* E. Greene were common but contributed negligible cover.

The *Sequoia sempervirens*-*Pseudotsuga menziesii*/*Rhododendron macrophyllum* association was generally found on upper slopes and ridges in Siskiyou National Forest and Del Norte Coast Redwoods State Park. Elevations ranged from 58–470 m, averaging 312 m. Distance from the ocean averaged 8.5 km. Slopes averaged 43 percent, and Moisture Equivalency Index (MEI) scores averaged

9.8. Species richness averaged 13.6 species (Table 4).

Vegetation dynamics. *Lithocarpus densiflorus* and *Sequoia sempervirens* dominated reproduction. Veirs (1979) suggested *S. sempervirens* and *L. densiflorus* were components of the "climax" vegetation and would remain in the stand regardless of disturbance such as fire. The presence of *S. sempervirens* in all height classes represents an uneven age structure for redwood. *Pseudotsuga menziesii* is a seral species that will disappear from stands without major disturbance (Daubenmire 1975; Veirs 1979; Eyre 1980). Low *P. menziesii* stem densities for the 0–3 m and 3–10 m height classes, and high density of trees >10 m, suggested that a cohort resulted from disturbance, and additional disturbance will be necessary for continued presence of *P. menziesii* in this association.

Relationships to previous classifications. The *Sequoia sempervirens*-*Pseudotsuga menziesii*/*Rhododendron macrophyllum* association closely resembled the midslope stands encountered by Dyrness et al. (1972) in Wheeler Creek Research Natural Area, and Tanoak-coast redwood association stands described by Atzet and Wheeler (1984) for southwestern Oregon. Other similar types include the *Sequoia sempervirens*-*Pseudotsuga menziesii*/*Vaccinium ovatum* association described by Matthews

TABLE 2. AVERAGE COVER AND CONSTANCY FOR SPECIES USED IN TWINSPAN ANALYSIS. Species reported are those with >50 percent constancy. See Figure 1 for plant association acronyms. Cov = average cover (%). Con = constancy (%).

	SESE- PSME/ RHMA		SESE-TSHE/ VAOV		SESE/POMU		SESE-TSHE/ POMU		SESE-TSHE/ RUSP		SESE- ALRU/RUSP	
	Cov	Con	Cov	Con	Cov	Con	Cov	Con	Cov	Con	Cov	Con
<i>Maianthemum dilatatum</i>							<1	52				
<i>Menziesia ferruginea</i>							3	69				
<i>Pseudotsuga menziesii</i>	31	100	17	78								
<i>Rhododendron macrophyllum</i>	35	100	13	76								
<i>Viola sempervirens</i>	<1	74	<1	90	<1	61						
<i>Disporum hookeri</i>			<1	54	<1	66						
<i>Lithocarpus densiflorus</i>	45	100	21	94	16	95			8	57		
<i>Vaccinium ovatum</i>	47	100	51	98	16	97	14	98	5	57	2	70
<i>Tsuga heterophylla</i>			41	100	24	75	39	88	21	86		
<i>Trillium ovatum</i>	<1	93	<1	98	<1	98	<1	69	<1	86		
<i>Vaccinium parvifolium</i>	1	70	2	70	3	73	5	94	3	86		
<i>Blechnum spicant</i>			3	72	4	73	11	96	10	100	<1	50
<i>Polystichum munitum</i>	7	93	12	100	55	100	67	100	30	100	24	100
<i>Sequoia sempervirens</i>	43	96	37	100	60	100	53	98	22	86	36	80
<i>Oxalis oregana</i>	<1	52	<1	78	13	98	9	100	16	100		
<i>Disporum smithii</i>							<1	67	<1	100		
<i>Rhamnus purshiana</i>							<1	60	1	57		
<i>Gaultheria shallon</i>	2	78	2	74	5	80	1	75	6	71	10	80
<i>Galium triflorum</i>			<1	54	<1	61			<1	57	<1	60
<i>Vancouveria hexandra</i>					<1	55			<1	57	<1	10
<i>Dryopteris expansa</i>							2	75	1	86	2	50
<i>Rubus spectabilis</i>							5	63	25	100	22	100
<i>Acer circinatum</i>									19	71		
<i>Acer macrophyllum</i>									10	57		
<i>Adiantum aleuticum</i>									<1	71		
<i>Corylus cornuta</i>									14	57		
<i>Ribes bracteosum</i>									1	57		
<i>Asarum caudatum</i>									<1	71	<1	70
<i>Athyrium filix-femina</i>							<1	58	2	100	2	60
<i>Tolmiea menziesii</i>									<1	71	2	60
<i>Alnus rubra</i>											38	100
<i>Claytonia sibirica</i>											<1	80
<i>Marah oreganus</i>											5	80
<i>Polypodium scolopendri</i>											<1	50
<i>Rubus parviflorus</i>											3	90
<i>Sambucus racemosa</i>											3	70
<i>Stachys ajugoides</i>											<1	90

(1986) and the *Sequoia sempervirens*/*Arbutus menziesii* Pursh association described by Lenihan (1986). This association might be considered an extension of the *Pseudotsuga*-hardwood forests described by Sawyer et al. (1977).

The Sequoia sempervirens-Tsuga heterophylla/Vaccinium ovatum Association.

Total vegetation cover averaged 88 percent, and total overstory cover averaged 74 percent. *Sequoia sempervirens*, *Tsuga heterophylla*, and *Pseudotsu-*

TABLE 3. MEAN BASAL AREA (M²/HA) FOR CANOPY SPECIES BY ASSOCIATION.

	SESE- PSME/RHMA	SESE- TSHE/VAOV	SESE/POMU	SESE- TSHE/POMU	SESE- TSHE/RUSP	SESE- ALRU/RUSP
<i>Sequoia sempervirens</i>	86.0	114.0	165.0	170.0	73.0	87.0
<i>Pseudotsuga menziesii</i>	37.0	21.0	10.0	2.0	2.0	7.0
<i>Tsuga heterophylla</i>	0.4	23.0	15.0	23.0	11.0	0.0
<i>Picea sitchensis</i>	0.0	0.0	0.0	4.0	6.0	10.0
<i>Abies grandis</i>	0.0	3.0	1.0	0.2	0.0	3.0
Total basal area	123.4	161.0	191.0	199.2	92.0	107.0

TABLE 4. ENVIRONMENTAL CHARACTERISTICS, TREE DENSITY IN THREE HEIGHT CLASSES, AND SPECIES RICHNESS FOR EACH FOREST ASSOCIATION.

	SESE- PSME/RHMA	SESE- TSHE/VAOV	SESE/POMU	SESE- TSHE/POMU	SESE- TSHE/RUSP	SESE- ALRU/RUSP
Elevation (m)	312.0	161.0	143.0	114.0	67.0	136.0
Distance (km)	8.5	7.4	6.4	5.5	6.8	3.6
Slope (%)	42.9	36.2	36.2	34.9	38.0	49.7
MEI (1-15)	9.8	9.0	7.5	7.0	1.3	6.7
Stems/ha:						
0-3 m	71.8	87.6	114.0	54.0	68.6	74.0
3-10 m	127.6	76.8	86.6	66.2	51.6	168.0
>10 m	180.8	206.0	172.4	165.8	72.0	170.0
Sp. Richness	13.6	16.6	19.0	15.6	26.8	19.4

ga menziesii dominated the canopy, with mean covers of 37, 41, and 17 percent, respectively, and mean constancies of 100, 100, and 78 percent, respectively (Table 2). *Abies grandis* (Douglas) Lindley appeared occasionally in the canopy. *Lithocarpus densiflorus* was common in the subcanopy. Basal area averaged 161.0 m²/ha (Table 3).

The shrub layer was dense. *Vaccinium ovatum* dominated, averaging 51 percent cover and 98 percent constancy. *Rhododendron macrophyllum* had 13 percent cover and 76 percent constancy. *Berberis nervosa*, *Gaultheria shallon* and *Vaccinium parvifolium* each had greater than 40 percent constancy but less than 2 percent cover. *Corylus cornuta* Marsh. and *Rhamnus purshiana* occurred sporadically.

The sparse herb layer was dominated by *Polystichum munitum*, averaging 12 percent cover and 100 percent constancy.

The *Sequoia sempervirens*-*Tsuga heterophylla*/*Vaccinium ovatum* association was usually found on inland upper slopes and ridges in Jedediah Smith Redwoods State Park. Elevations ranged from 40-460 m, averaging 161 m. Distance inland averaged 7.4 km. Slopes averaged 36 percent, and MEI scores averaged 9. Species richness averaged 16.6 species (Table 4).

Vegetation dynamics. *Tsuga heterophylla* and *Lithocarpus densiflorus* dominated reproduction. *Tsuga heterophylla* seedlings were particularly abundant on downed logs. Combs (1984) noted a similar pattern of *T. heterophylla* regeneration in the Little Lost Man Creek Research Natural Area in Redwood National Park. He suggested that few seedlings would reach maturity because of vulnerability to fire and disease. Daubenmire (1975) noted extensive *T. heterophylla* in all size classes in Jedediah Smith Redwoods State Park, but believed the species would decline without disturbance. Veirs (1979) suggested that light ground fires, unaffected the canopy, will favor *T. heterophylla* regeneration. The high density of *T. heterophylla* and the complete absence of *P. menziesii* seedlings suggested a light fire regime, sufficient for *S. semper-*

virens and *T. heterophylla* regeneration, but not for regeneration of *P. menziesii*.

Relationships to previous classifications. The *Sequoia sempervirens*-*Tsuga heterophylla*/*Vaccinium ovatum* association was unique compared to other redwood types described in the literature due to the importance of *Tsuga heterophylla*. While other redwood classifications have noted the presence of *T. heterophylla* (Dyrness et al. 1972; Atzet and Wheeler 1984; Lenihan 1986), none have shown such dominance by this mesic conifer. The *Sequoia sempervirens*/*Berberis nervosa* association described by Lenihan (1986), and the *Tsuga* phase of the *Pseudotsuga*-hardwood forests described by Sawyer et al. (1977) were similar in composition to this association.

The *Sequoia sempervirens*/*Polystichum munitum* Association.

Total vegetation cover averaged 90 percent. Total overstory cover averaged 76 percent. *Sequoia sempervirens* dominated the canopy with 60 percent cover and 100 percent constancy (Table 2). *Tsuga heterophylla* was common, and *Pseudotsuga menziesii* appeared occasionally in the canopy. *Abies grandis*, *Cupressus lawsoniana* A. Murray and *Umbellularia californica* (Hook. & Arn.) Nutt. occurred sporadically, contributing minimal cover. *Lithocarpus densiflorus* was ubiquitous in the subcanopy. Basal area averaged 191.0 m²/ha (Table 3).

Vaccinium ovatum dominated the relatively sparse shrub layer, averaging 16 percent cover and 97 percent constancy. *Gaultheria shallon*, *Rhododendron macrophyllum*, and *Vaccinium parvifolium* each had greater than 40 percent constancy but less than 5 percent cover. *Acer circinatum* Pursh, *Berberis nervosa*, *Corylus cornuta*, and *Rubus spectabilis* occurred sporadically, contributing minimal cover.

Herbaceous cover and species diversity was moderately high. *Polystichum munitum* dominated, averaging 55 percent cover and 100 percent constancy. *Oxalis oregana* was extremely common.

The *Sequoia sempervirens*/*Polystichum munitum*

association was found throughout the study area, generally on lower and middle slopes at moderate distances from the ocean. Elevations ranged from 21–369 m, averaging 143 m. Distance from the ocean averaged 6.4 km. Slopes averaged 36 percent, and MEI scores averaged 7.5. Species richness averaged 19 species (Table 4).

Vegetation Dynamics. *Lithocarpus densiflorus* and *Sequoia sempervirens* dominated reproduction. The moderate levels of *Abies grandis*, *Tsuga heterophylla*, and *L. densiflorus* reproduction may be indicative of the light fire regime in intermediate to mesic sites referred to by Veirs (1979). However, he noted that these species exhibited an all aged pattern and can reproduce regardless of fire.

Relationships to previous classifications. The *Sequoia sempervirens/Polystichum munitum* association contained elements of the *Sequoia sempervirens/Blechnum spicant* (L.) Smith association described by Lenihan (1986), though Lenihan's association appeared wetter. The dominance of *Sequoia sempervirens*, the sparse shrub layer, and the well-developed herb layer related this association to Becking's (1967) Redwood-oxalis alliance.

The *Sequoia sempervirens-Tsuga heterophylla/Polystichum munitum* Association.

Total vegetation cover averaged 92 percent, and total overstory cover averaged 75 percent. *Sequoia sempervirens* and *Tsuga heterophylla* dominated the canopy, with mean covers of 53 and 39 percent, respectively, and mean constancies of 98 and 88 percent, respectively (Table 2). *Abies grandis*, *Lithocarpus densiflorus*, *Picea sitchensis* (Borg.) Carrière and *Pseudotsuga menziesii* occurred sporadically, contributing minimal cover. *Thuja plicata* D. Don appeared occasionally in mesic sites. Basal area averaged 199.2 m²/ha (Table 3).

The shrub layer was generally not well developed. *Vaccinium ovatum* was the most abundant shrub, averaging 14 percent cover and 98 percent constancy. *Menziesia ferruginea* Smith, *Rubus spectabilis*, *Vaccinium parvifolium*, *Gaultheria shallon*, and *Rhamnus purshiana* each had greater than 60 percent constancy but less than 6 percent cover.

The herbaceous layer was dense. *Polystichum munitum* dominated, averaging 67 percent cover and 100 percent constancy. *Blechnum spicant* and *Oxalis oregana* were common.

The *Sequoia sempervirens-Tsuga heterophylla/Polystichum munitum* association was generally found at lower slopes and elevations, especially in southwestern areas of Jedediah Smith Redwoods State Park exposed to maritime influence. Elevations ranged from 40–274 m, averaging 114 m. Distance inland averaged 5.5 km. Slopes averaged 35 percent, and MEI scores averaged 7. Species richness averaged 15.6 species (Table 4).

Vegetation Dynamics. *Tsuga heterophylla* and *Sequoia sempervirens* dominated reproduction. *Se-*

quoia sempervirens had fewer stems in the lower height classes relative to *T. heterophylla*, but the longevity and resilience of *S. sempervirens* makes abundant individuals in the reproduction layers unnecessary to ensure continued dominance.

Relationships to previous classifications. The *Sequoia sempervirens-Tsuga heterophylla/Polystichum munitum* association, like *Sequoia sempervirens-Tsuga heterophylla/Vaccinium ovatum*, appeared unlike any previously described redwood types. It was similar in many respects to the mesic *Tsuga/Polystichum* association described by Franklin and Dyrness (1973) for Oregon Coast Range forests in the *Tsuga heterophylla* Zone. Additionally, it contained elements of the *Tsuga-picea/Oplopanax horridum/Athyrium filix-femina* association of *Picea sitchensis* Zone forests described by Franklin and Dyrness (1973). It related tangentially to Lenihan's (1986) *Sequoia sempervirens/Blechnum spicant* association.

The *Sequoia sempervirens-Tsuga heterophylla/Rubus spectabilis* Association.

Total vegetation cover averaged 94 percent, and total overstory cover averaged 55 percent. *Sequoia sempervirens* and *Tsuga heterophylla* were canopy dominants, averaging 22 and 21 percent cover, respectively. Both species had 86 percent constancy (Table 2). *Picea sitchensis* and *Thuja plicata* were occasional to common in mesic sites. *Pseudotsuga menziesii* occurred sporadically. *Acer macrophyllum* was common, especially near stream channels. *Lithocarpus densiflorus* was common in the subcanopy. *Alnus rubra* and *Sambucus racemosa* L. appeared occasionally. Basal area averaged 92.0 m²/ha (Table 3).

Rubus spectabilis dominated the dense shrub layer, averaging 25 percent cover and 100 percent constancy. *Acer circinatum* and *Corylus cornuta* were abundant in this layer having 71 percent and 57 percent constancy and 19 percent and 14 percent cover, respectively. Other common shrubs having greater than 40 percent constancy but less than 6 percent cover included *Gaultheria shallon*, *Menziesia ferruginea*, *Rhamnus purshiana*, *Ribes bracteosum* Douglas, *Rubus parviflorus*, *Vaccinium ovatum*, and *V. parvifolium*.

The herbaceous layer was dense and floristically diverse. *Polystichum munitum* dominated with 31 percent cover and 100 percent constancy. *Oxalis oregana* and *Blechnum spicant* were abundant.

The *Sequoia sempervirens-Tsuga heterophylla/Rubus spectabilis* association was restricted to interior perennial drainages in Jedediah Smith Redwoods State Park. Elevations ranged from 37–122 m, averaging 67 m. Distance from the ocean averaged 6.8 km. Slopes averaged 38 percent, and MEI scores averaged 1.3. Species richness averaged 26.8 species (Table 4).

Vegetation Dynamics. *Tsuga heterophylla* and *Lithocarpus densiflorus* dominated reproduction.

TABLE 5. STANDARD CANONICAL COEFFICIENTS USED IN DISCRIMINANT ANALYSIS.

Variable	Variate 1	Variate 2	Variate 3	Variate 4
Elevation	-0.874009	0.717388	0.045912	-0.376631
Slope	0.189664	0.275203	0.477507	0.858742
Distance	-0.828487	-0.300679	-0.599034	0.465420
MEI	-0.376680	-1.100974	0.339726	0.143424

Riparian conditions produced the wettest and most floristically diverse association encountered in the study area. Conifer basal area was greatly reduced compared to other associations. *Sequoia sempervirens* attained its lowest basal area, but still dominated conifer basal area. The streamside environment allowed mesic woody species such as *Acer macrophyllum*, *A. circinatum*, *Corylus cornuta*, and *Rubus spectabilis* to thrive.

Relationships to previous classifications. The *Sequoia sempervirens-Tsuga heterophylla/Rubus spectabilis* association appeared much wetter than any redwood association previously described. It shared many of the same riparian components, such as high cover of herbaceous and hardwood species, described by Dyrness et al. (1972) for lower slopes in the Wheeler Creek Research Natural Area in southwestern Oregon, and appeared similar in many respects to the *Tsuga heterophylla/Acer circinatum/Polystichum munitum-Oxalis oregana* association described by Franklin and Dyrness (1973) for alluvial terrace vegetation in the *Tsuga heterophylla* Zone of Oregon. The absence of *Sequoia sempervirens* in *Tsuga heterophylla* Zone forests makes comparison difficult, however.

The Sequoia sempervirens-Alnus rubra/Rubus spectabilis Association.

Total vegetation cover averaged 93 percent, and total overstory cover averaged 71 percent. *Sequoia sempervirens* dominated the canopy, averaging 36 percent cover and 80 percent constancy (Table 2). *Picea sitchensis* was common in coastal sites. *Pseudotsuga menziesii* and *Abies grandis* occurred sporadically. *Alnus rubra* dominated the subcanopy. *Acer macrophyllum*, *Lithocarpus densiflorus*, *Rhamnus purshiana*, *Sambucus racemosa*, and *Umbellularia californica* appeared occasionally in the subcanopy. Basal area averaged 107.0 m²/ha (Table 3).

Rubus spectabilis dominated the moderately dense shrub layer, averaging 22 percent cover and 100 percent constancy. *Gaultheria shallon* had 10 percent cover and 80 percent constancy. Other common shrubs included *Acer circinatum*, *Corylus cornuta*, *Rubus parviflorus*, *R. ursinus* Cham & Schldl., and *Vaccinium ovatum* with constancies greater than 20 percent but with less than 8 percent cover.

The herbaceous layer was diverse. *Polystichum munitum* dominated, averaging 24 percent cover and 100 percent constancy. *Oxalis oregana* oc-

curred sporadically, but was generally abundant when it did occur.

The *Sequoia sempervirens-Alnus rubra/Rubus spectabilis* association was generally found along the Smith River, or on coastal bluffs in Del Norte Coast Redwoods State Park. Elevations ranged from 18–299 m, averaging 136 m. Distance from the ocean averaged 3.6 km. Slopes averaged 50 percent, and MEI scores averaged 6.7. Species richness averaged 19.4 species (Table 4).

Vegetation dynamics. *Sequoia sempervirens* dominated reproduction. *Picea sitchensis* was very common on coastal bluffs, and *Pseudotsuga menziesii* was common along the Smith River. *Alnus rubra* achieved high cover in the subcanopy. The mesic, high light environments of the Smith River floodplain and exposed coastal bluffs provided favorable conditions for this shade intolerant hardwood (Hibbs et al. 1994; Harlow et al. 1996). Additionally, natural disturbance from Smith River flooding likely enhanced the competitive ability of *A. rubra*, which is more tolerant of flooding and poor drainage than its associates (Hibbs et al. 1994). Tolerance of salt spray and resistance to windthrow allowed *A. rubra* to thrive along the coastal bluffs of Del Norte Coast Redwoods State Park. Periodic disturbances likely benefited the seral *Pseudotsuga menziesii*. *Alnus rubra* showed high stem densities in the 3–10 and >10 m height classes, but minimal density in the 0–3 m class, indicating many stands may be recovering from disturbance.

Relationships to previous classifications. The *Sequoia sempervirens-Alnus rubra/Rubus spectabilis* association was similar to coastal sections of the Wildcat Hills transect described by Zinke (1977), as well as the red alder series described in Sawyer and Keeler-Wolf (1995). It should be noted that a pure *Picea sitchensis* forest type may exist immediately adjacent to the coast in Del Norte Coast Redwoods, but was not sampled.

Discriminant Analysis. Discriminant analysis revealed that elevation, coastal proximity, and topographic position/aspect (MEI) were statistically significant ($P < 0.01$) in discriminating among floristic associations. Elevation and coastal proximity had the greatest influence on the first discriminant function (Table 5). This function explained 81.1 percent of the variation between groups. MEI had the greatest influence on the second discriminant function,

which explained 14.2 percent of group variation. Together, the first two discriminant functions, influenced by elevation, distance to the ocean, and MEI, explained 95.3 percent of group variation. The physiographic factors influencing floristic associations, in decreasing order of importance, were elevation, coastal proximity, and aspect/topographic position (MEI).

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