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OLD-GROWTH CHARACTERISTICS ON A COAST REDWOOD (*SEQUOIA
SEMPERVIRENS* (D. DON) ENDL.) PYGMY FOREST ECOTONE

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ABSTRACT

Old-growth *Sequoia sempervirens* (D. Don) Endl. (Cupressaceae) forests are commonly assumed to be populated by massive trees, but those growing on nutrient poor soils can be stunted and display unusual growth-forms. We characterized soils, stand structure, growth form, and crown complexity using a combination of random and targeted stratified sampling across an old-growth redwood/pygmy forest ecotone. ANOVA indicated significant variation in stand structure metrics and soil characteristics [pH, cation exchange capacity (CEC), and nutrient availability] among strata, with tree height, basal area, and the relative dominance of redwood-associated species declining under the influence of pygmy forest soils; while shrub cover and the dominance of pygmy associated species increased. Pearson's coefficients indicated positive correlations between tree height and diameter with CEC, P, K, Ca, and Na. Stepwise linear regression suggested that P, K, and CEC were the strongest predictors of tree height and diameter. Growth form and crown structure of *S. sempervirens* also varied considerably across the ecotone, with stunted multi-stemmed individuals and clusters of small diameter trees observed where pygmy soil conditions were most extreme, and larger, but still stunted ancient redwoods with complex crown structures, resident epiphytes, and large fire hollows, existing on the edge of the pygmy forest. The ancient redwoods sampled within the old-growth/pygmy ecotone were remarkably small in stature, yet contained many of the same structural characteristics associated with the largest and oldest *S. sempervirens*.

Key Words: Cation exchange capacity, crown structure, epiphyte, phosphorus, podsols, potassium.

The coast redwood forest of northern California is dominated by *Sequoia sempervirens* (D. Don) Endl. (Cupressaceae), a species that can live for more than 2500 years, and grows to heights exceeding 100 meters on productive soils (Sillett and Van Pelt 2000b). The term “old-growth” is traditionally defined by an absence of substantial logging history (Peterken 1996; Frelich and Reich 2003), but certain characteristics have become associated with these relatively undisturbed stands. First, certain structural characteristics, including fire hollows, complex crown structures, and epiphytic communities, are generally limited to ancient trees (Helms 2004; Spies and Duncan 2009). These features are important ecologically, as they reflect a life history punctuated by stochastic disturbance, and provide habitat for a variety of wildlife species (Sillett and Van Pelt 2000a, Spickler et al. 2006; Sillett and Van Pelt 2007). Second, large tree size and low stand density have also been commonly associated with old-growth, but this pattern may be due more to site productivity than to management history (Gerhart 2006). While large trees are often found on productive sites, old-growth stands that persist on marginal sites can exhibit relatively high stand densities and relatively small tree sizes (Berrill et al. 2017). And while trees on marginal sites tend to be small in stature, the level of stress and disturbance that they experience may allow them to develop structural complexity comparable to trees on productive sites (Wardle 1993).

Crown Complexity in Old-Growth Forests

The development of complex structural features in the forest canopy appears to be a function of age and disturbance history, rather than tree size (Wardle 1993; Ishii et al. 2004). Young *S. sempervirens* trees exhibit strong apical dominance with an orthotropic and monopodial main trunk, characterized by straight vertical growth and branching originating from a single axis (Harris and Harris 2001; Sillett and Van Pelt 2007). Apical dominance declines with age, and with the help of stochastic events such as wind, lightning, and mechanical damage, crown structure is reshaped. Codominant trunks are common in older specimens of *S. sempervirens*, and in some cases can result in reiterated trees high in the canopy (Sillett and Van Pelt 2000a; Shigo 2008). Large lateral branches are also formed, which provide habitat features in the form of deep crotches and platforms, and vegetative sprouting from the tree bole allows for the creation of epicormic branches and root growth into arboreal soils. As a result, the canopies of *S. sempervirens* are more complex than any other coniferous species (Sillett and Van Pelt 2000b).

The ecological value of this complexity is measured in the diversity of species that it supports. Epiphytic plants inhabit arboreal soils created from leaf litter, redwood bark, and dead roots, on lateral structures high in the tree's crown, and commonly

include species such as *Vaccinium ovatum* Pursh (huckleberry) and *Polypodium scolieri* Hook. and Grev. (leather fern) (Sawyer et al. 2000). These epiphytic communities, in turn, provide habitat for wildlife species such as *Aneides vagrans* (Wake & Jackman 1998) (wandering salamander), a species that spends its entire life cycle in the forest canopy (Zielinski and Gellman 1999; Enloe et al. 2006; Spickler et al. 2006; Sillett and Van Pelt 2007). Mossy lateral branches provide nesting habitat for endangered avian species including *Brachyramphus marmoratus* (Gmelin and JF 1789) (marbled murrelet) and *Strix occidentalis caurina* (Merriam 1898) (northern spotted owl) (LaHaye and Gutiérrez 1999; Sillett and Van Pelt 2000a; Baker et al. 2006). Large persistent fire caves, both at the base of trees, and in the canopy, provide habitat for *Sitta pygmaea* Vigors 1839 (pygmy nuthatches), *Tyto alba* (Scopoli 1769) (barn owls), nesting *Tachycineta thalassina* (Swainson 1827) (violet-green swallows), in addition to a variety of species of spiders and bats (Zielinski and Gellman 1999; Willet 2001). The result is a complex community that is dependent on features that develop on ancient trees (Nadkarni 1994). In total, old-growth redwood forests provide habitat for 42 vertebrate species listed by state and federal agencies as endangered, threatened, or a species of special concern; and four invertebrate species listed as endangered or threatened (Cooperrider et al. 2000).

The Pygmy Forest Community

In Mendocino County, patches of hydrophobic podsols exist on ancient uplifted marine terraces within the coast redwood forest (Waring and Major 1964; Zinke 1988; Sawyer et al. 2000). These highly acidic nutrient poor soils support the pygmy forest vegetation formation, populated by a suite of endemic species and scattered patches of stunted *S. sempervirens* (Westman 1975; Westman and Whittaker 1975; Northup et al. 1995). The ecotone between pygmy and redwood forest soils has been described as abrupt, with only few species tolerating the harsh pygmy forest conditions (Zinke 1988; Aitken and Libby 1994; Northup et al. 1998). Nevertheless, solitary redwood trees have been found occupying these infertile soils (Jenny 1973; Westman and Whittaker 1975; Sawyer et al. 2000).

Pygmy podsols are dominated by two endemic dwarf tree species; *Pinus contorta* ssp. *bolanderi* (Parl.) Critchf. (bolander pine) and *Hesperocyparis pygmaea* (Lemmon) Bartel (pygmy cypress). *Pinus muricata* D.Don (bishop pine) is common in a stunted form, and is accompanied by a number of Ericaceous shrubs including *Arctostaphylos nummularia* A.Gray ssp. *mendocinoensis* (P.V.Wells) V.T.Parker, M.C.Vasey and J.E.Keeley (pygmy manzanita), *Rhododendron macrophyllum* D.Don (coast rhododendron), *Rhododendron columbianum* (Piper) Harmaja (western Labrador tea), and *Gaul-*

theria shallon Pursh (salal) (Jenny 1973; Westman 1975; Westman and Whittaker 1975; Northup et al. 1995). Jenny (1973) originally observed these species dominating the pygmy forest landscape, however, on rare occasions, a stunted “yellow-leaved struggling redwood tree” was found tolerating the nutrient-deficient soils.

Pygmy forest conditions developed on coastal terraces as a result of tectonic movements, wave activity, and fluctuation in sea levels during the Pleistocene period (Aitken and Libby 1994). The terraces increase in age with distance from the coast, with the oldest terraces, where pygmy forests, estimated at between 300,000 years of age (Merriitts et al. 1991). The first terrace, closest to the ocean, is dominated by grassland with rich prairie mollisols (Jenny 1973). The second terrace is host to prolific stands of coast redwood (Aitken and Libby 1994). The third, fourth, and fifth terrace, where pygmy forests grow, are dominated by highly acidic podsols that have been weathered for millennia (Merriitts et al. 1991). These soils are characterized by low pH, little organic matter, and hydrophobic tendencies. The A horizon in pygmy forests tends to be poorly developed and is often underlain by a distinctive ash-grey layer and an iron-stained clay layer known as “hardpan” which is found approximately 30 cm below the soil surface, and can severely limit root growth (Johnston 1994). The clay hardpan is extraordinarily impermeable; during winter rains prolonged flooding occurs and water drains slowly to lower terraces (Aitken and Libby 1994). In addition, pygmy soils are severely limited in available nutrients, such as phosphorus (P), potassium (K), and manganese (Mg), due to leaching over centuries in the presence of charged clay particles (Jenny 1973; Fox 1976; Walker and Syres 1976; Yu et al. 1999). Recent research suggests that P limitation may play a particularly important role in the formation of the pygmy community (Izquierdo et al. 2013). Pygmy forest soils do not provide productive growing conditions for *S. sempervirens*, and yet individuals of the species are able to survive within the community.

The concept of old-growth is commonly associated with productive forests and large trees. However, ancient stunted coast redwood trees have been observed in the proximity of the pygmy soil formation (Jenny 1973, Westman and Whittaker 1975). While forest composition, growth form, and crown structure of *S. sempervirens* have been studied extensively in productive stands, they have not been studied thoroughly in marginal sites, such as the pygmy forest ecotone. Our objectives were to characterize these features across a pygmy/old-growth redwood transition in order to expand the scope of understanding of what old-growth is by including a broader range of site conditions than past studies; and to determine if complex late-seral structural features exist on *S. sempervirens* growing in these marginal sites.

METHODS

Study site. Data were collected in the Russell Unit of Mendocino Headlands State Park approximately 1 km east of the Pacific Ocean, south of the town of Mendocino in Northern California, during the summer of 2012 (June–September). The area's average annual precipitation is approximately 99 cm, with an average temperature of 12.5° C (Northup et al. 1995). Though sections of the property were selectively logged in the late 19th and early 20th centuries, much of the site is dominated by old-growth, and mixed old-growth/second-growth stands. On the northwest portion of the property, old-growth gives way to pygmy forest, creating an ideal site to study this ecotone.

Study design and data collection. The transition between pygmy and old-growth redwood was divided into five strata (adapted from Westman and Whitaker 1975), including: 1) Extreme Pygmy (EP), dominated by endemic Ericaceous shrubs and conifers including *Arctostaphylos nummularia* ssp. *mendocinoensis*, *Pinus contorta* ssp. *bolanderi*, and *Hesperocyparis pygmaea*; 2) Short Pygmy (SP), an area with less stunted vegetation, but still dominated by pygmy forest associates; 3) Tall Pygmy (TP), an area dominated by pygmy forest associates, but with less dominance of pygmy endemics; 4) Transitional (T), with small single stem redwoods occurring as co-dominants *P. contorta* ssp. *bolanderi* and *H. pygmaea*; 5) Pygmy Redwoods (PR) dominated by stunted ancient redwoods, with rare occurrence of pygmy forest endemics.

We used a random sampling strategy to compare vegetation and soil between strata, and opportunistic sampling to characterize individuals of the target species (*S. sempervirens*) found within each stratum. A total of 50 (7 m diameter) sample plots were randomly located and stratified evenly across strata. Vegetation metrics recorded on each plot included: canopy cover (measured with a spherical densitometer); average crown height and maximum tree height (measured with a tape-measure); diameter at breast height (dbh) (or basal diameter for trees < 1.37 m height) of tree stems by species; number of stems; percent cover and height of shrub species; and percent cover herbaceous species.

Fourteen opportunistic samples were used to gather data on the growth form and structure of individual *S. sempervirens*, with the following metrics recorded: tree height, number of stems emerging from the root structure, diameter of largest stem, and presence of old-growth structural characteristics (large lateral branches, reiterated trunks, epiphytes, and fire hollows), and an estimate of crown complexity using the branch hierarchy method for trees with substantial crown structure (Van Pelt and Sillett 2008). Trees that were less than 3 m in height were accessed using an extension ladder. For trees larger than 3 m in height, the crown was accessed using International Society of Arboriculture climbing

techniques. Prior to accessing the crown of a tree, assessments were made to ensure that disturbance to wildlife were minimized. Arboreal soil depth and volume was measured with a marked probe that was inserted into the surface of the substrate; with each measure averaged from three samples (Sillett and Van Pelt 2007). Epiphytic plants were identified to species.

To characterize soils, a soil sample of 450 ml was collected from each plot. The sample was taken 10 cm below true ground. The following soil properties were analyzed: percent of organic matter, phosphorus (Weak Bray and Sodium Bicarbonate-P), parts per million (ppm) of extractable cations (potassium, magnesium, calcium, sodium), hydrogen, sulfate-S (ppm), pH, cation exchange capacity (meq/100g), and percent cation saturation (computed). The soil analysis sample report with reference guide explanations from A & L Plains Labs, Inc. describe the weak Bray test, P1, as the most accurate for soils with low pH, and an ideal level of P is between 20ppm and 30ppm. Water-holding capacity was measured using a FieldScout TDR 200 (Spectrum Technologies, Inc., Painfield, Illinois). This device measures water-holding capacity by calculating the traveling time of an electromagnetic waveguide, which is dependent on the porosity and permeability of the soil. A marked 1 m probe was used to measure duff layer depth. In addition, four samples were taken from the A horizon with a soil auger on each randomly selected plot to estimate pH.

Statistical analysis. In order to detect changes across the ecotone, all possible ANOVAs comparing vegetation metrics and soil characteristics among the five strata were conducted, with Tukey HSD used for post-hoc mean separation. Pearson's Correlation Coefficient (r) was conducted as a preliminary test to measure independence between variables and shared variation. A correlation was considered strong if $r \geq 0.50$, or ≤ -0.50 . The correlation was considered significant if $p < 0.05$. If the relationship was strong and significant, it was followed by a multiple stepwise linear regression analysis to obtain a predictive model. Two stepwise linear regression analyses were employed, one for "tree height" of redwoods and one for "stem diameter" of redwoods across all strata to build multivariate predictive models using each of 14 soil metrics as independent variables; and tree height and stem diameter as response variables. Additional simple linear regression analyses were used to identify the relationship between pH and biotic variables. Exploration of the growth form and crown structure of individual *S. sempervirens* specimens was primarily descriptive, with quantitative and qualitative comparisons made between samples. Features analyzed included branching patterns using the hierarchical system developed by Van Pelt and Sillett (2008), where the maximum number of features (main trunk, limbs, reiterated trunk, and branch) on a single limb

TABLE 1. MEAN VALUES OF VEGETATION AND SOIL CHARACTERISTICS MEASURED ACROSS A PYGMY/REDWOOD ECOTONE ON FIVE STRATA: EXTREME PYGMY (EP), SHORT PYGMY (SP), TALL PYGMY (TP), TRANSITIONAL (T), AND PYGMY REDWOOD (PR). Basal area was calculated from diameter (d) using $BA = \pi (\frac{1}{2}d)^2$. Within each row, strata sharing the same lower case letters did not exhibit significant differences based on single factor ANOVA analysis ($\alpha = 0.05$). Mean values for each metric below are reported with \pm SE.

	EP	SP	TP	T	PR
Canopy height (m)	2.09 ^a	5.64 ^b	11.95 ^c	21.50 ^d	39.61 ^e
Canopy cover (%)	37.12 ^a	49.25 ^b	59.22 ^b	83.91 ^c	91.73 ^d
Shrub cover (%)	70.8 ^a	89.3 ^b	78.1 ^b	60.4 ^c	34.1 ^d
Herb cover (%)	1.8 ^a	1.3 ^a	3 ^a	0.4 ^a	2.35 ^a
Understory richness	6 ^a	10 ^b	10 ^b	10 ^b	15 ^c
Basal area (m ² /ha)	1429 ^a	1866 ^a	668 ^b	1094 ^a	3713 ^c
Basal area of <i>S. sempervirens</i> (m ² /ha)	<0.01 ^a	<0.01 ^a	<0.01 ^a	1019 ^b	3351 ^c
Basal area of <i>H. pygmaea</i> (m ² /ha)	1368 ^a	1752 ^a	611 ^b	33 ^c	0 ^c
pH	4.00 ^a	4.81 ^b	4.95 ^b	5.00 ^b	5.58 ^c
% Organic matter	3.52 ^a	2.90 ^a	3.96 ^a	6.63 ^b	10.13 ^b
% Water holding capacity	35.33 ^a	35.67 ^a	26.24 ^b	13.50 ^c	26.56 ^b
Cation exchange capacity (mEq/100g)	2.62 ^a	2.57 ^a	3.20 ^a	6.96 ^b	8.53 ^c
% cation saturation (K)	2.00 ^a	2.42 ^a	2.93 ^a	4.19 ^b	4.22 ^b
% cation saturation (Mg)	7.91 ^a	8.43 ^a	9.67 ^b	10.82 ^c	11.43 ^c
% cation saturation (Ca)	10.05 ^a	7.91 ^a	22.76 ^b	23.45 ^b	20.53 ^b
% cation saturation (Na)	3.12 ^a	2.83 ^a	4.67 ^b	4.67 ^b	4.90 ^b
P (weak bray) ppm	2.73 ^a	1.76 ^a	2.84 ^a	5.52 ^b	5.55 ^b

emerging from a redwood was calculated. Other features compared included the presence and absence of fire hollows, the number of stems emerging from a single root bole, and the presence of above ground versus below ground root structures. All statistical analysis was conducted using SPSS software (IBM Corp. Version 19.0. Armonk, NY)

RESULTS

Soil characteristics, vegetation, and the size and growth-form of *Sequoia sempervirens*, varied significantly across the pygmy/redwood ecotone. Analysis of variance indicated that mean soil properties were significantly different among strata (Table 1). Nutrient availability was generally below what is considered ideal for normal soils, and pH ranged from 4.0 to 5.8, with the most acidic soils found in the “extreme pygmy” stratum. Potassium, calcium, and phosphorus exhibited the lowest measures where pygmy vegetation was most pervasive. A similar pattern was observed for organic matter and CEC. Water holding capacity did not exhibit significant variation in relationship to the ecotone strata.

Vegetation composition and structure also exhibited significant variation among strata (Table 1). Canopy height and canopy cover were relatively low on the most extreme pygmy soils, while shrub cover was relatively high. Herbaceous cover was uniformly low across the ecotone except for the “pygmy redwood” stratum, where it was significantly higher. *Hesperocyparis pygmaea* and *Pinus contorta* ssp. *bolanderi* had the highest relative dominance on first three strata, and *S. sempervirens* and *Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii* on the last three strata (Fig. 1). The presence of *P. menziesii* in the tall pygmy (TP) stratum and *H. pygmaea* in the

transitional (T) stratum suggests a somewhat porous boundary between the two communities. Variation was also found in understory species across the ecotone. Both herbaceous cover and richness of understory species were significantly higher in “pygmy redwood” compared to all other strata. There were, however, a number of species that were limited to pygmy soils including two California Native Plant Society listed species, *Arctostaphylos nummularia* ssp. *mendocinoensis* and *Lilium maritimum* Kellogg (coast lily) (Table 2).

Pearson’s correlations indicated that basal area of *S. sempervirens* on targeted plots had a significant positive association with phosphorous ($r = 0.517$, $P = 0.02$), potassium ($r = 0.761$, $P < 0.001$), calcium ($r = 0.619$, $P = 0.005$), CEC ($r = 0.726$, $P < 0.001$), and sodium ($r = 0.523$, $P = 0.049$). In addition, significant associations were found between tree height and phosphorous ($r = 0.553$, $P = 0.013$), potassium ($r = 0.677$, $P = 0.002$), calcium ($r = 0.598$, $P = 0.007$), and CEC ($r = 0.666$, $P = 0.002$).

Multivariate analysis, using stepwise regression, resulted in a strong predictive model ($P < 0.001$; $R^2 = 0.724$) for stem diameter, with CEC ($P < 0.001$) and P ($P = 0.002$) as the strongest predictors (diameter = $-0.290 + 0.135 \text{ CEC} + 0.113 \text{ P ppm}$). A model was also developed for tree height ($p = 0.002$; $R^2 = 0.578$), with K ($P < 0.001$) and P ($P = 0.004$) as predictors (height = $15.452 + 0.262 \text{ K ppm} + 0.493 \text{ P ppm}$). Models for other vegetation metrics did not yield significant results. While pH did not emerge as a strong predictive variable, simple linear regression indicated that several biotic metrics were positively correlated with soil pH (Table 3); including canopy cover, canopy height, herbaceous cover, understory richness, total basal area, and the basal area of *S. sempervirens*. Soil pH was negatively

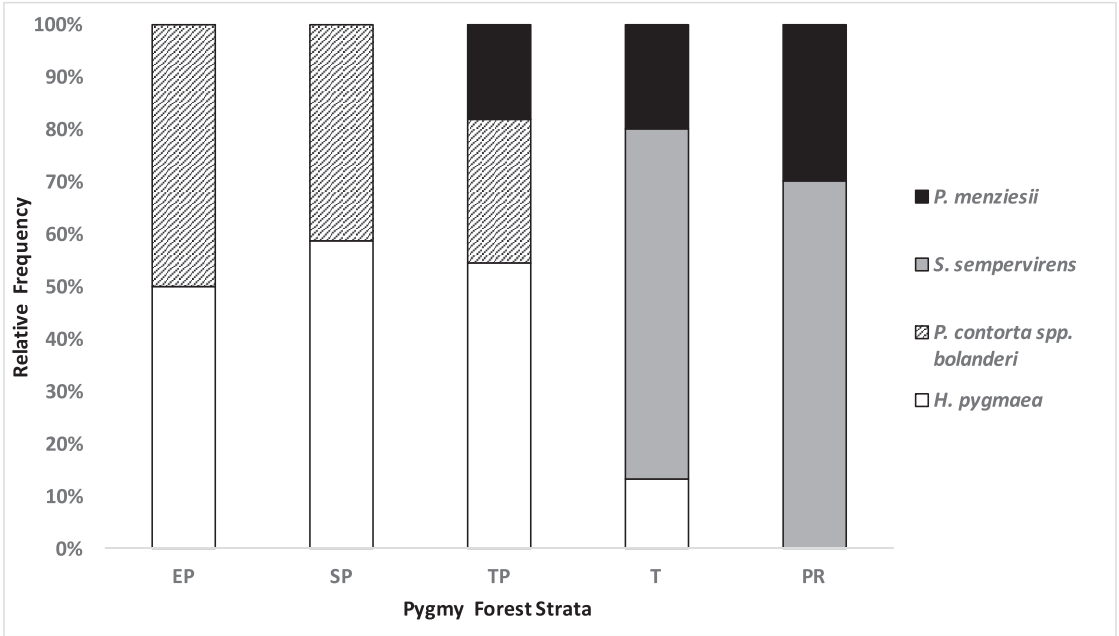


FIG. 1. Relative frequency of the four most commonly occurring tree species across a pygmy redwood forest ecotone on five strata: extreme pygmy (EP), short pygmy (SP), tall pygmy (TP), transitional (T), and pygmy redwood (PR).

correlated with shrub cover and basal area of *H. pygmaea*.

Growth Form and Structure

Qualitative analysis of the growth-form of *S. sempervirens* across the pygmy/redwood ecotone

indicated notable variation among strata (Table 4). Redwood trees were stunted, multi-stemmed, and shrub-like close to the center of the pygmy formation, but exhibited more upright forms closer to the ecotone. A total of 312 epiphytic plants were observed growing on *S. sempervirens* in the “tall pygmy,” “transitional,” and “pygmy redwood”

TABLE 2. MEAN PERCENT COVER OF UNDERSTORY SHRUBS AND HERBACEOUS SPECIES OCCURRING ON A PYGMY/REDWOOD FOREST ECOTONE ACROSS FIVE STRATA: EXTREME PYGMY (EP), SHORT PYGMY (SP), TALL PYGMY (TP), TRANSITIONAL (T), AND PYGMY REDWOOD (PR).

Species	Family	EP	SP	TP	T	PR
<i>Pteridium aquilinum</i> (L.) Kuhn	Dennstaedtiaceae	5.4	3.4	1.8	0.9	1.5
<i>Polystichum munitum</i> (Kaulf.) C. Presl	Dryopteridaceae	0	0	0	0	0.3
<i>Arctostaphylos columbiana</i> Piper	Ericaceae	0	0	0.3	0	0
<i>Arctostaphylos nummularia</i> ssp. <i>mendocinoensis</i>	Ericaceae	0	0.2	0.2	0	0
<i>Chimaphila menziesii</i> (D. Don) Sprengel	Ericaceae	0	0	0	0.1	0
<i>Gaultheria shallon</i>	Ericaceae	8.9	8.9	9.4	7.5	9.5
<i>Rhododendron columbianum</i>	Ericaceae	24.5	46	4.5	0	0
<i>Rhododendron macrophyllum</i>	Ericaceae	3.5	4.2	29.5	13.1	4.6
<i>Vaccinium ovatum</i>	Ericaceae	23.7	25.3	27	32.5	5.6
<i>Vaccinium parvifolium</i> Sm.	Ericaceae	0	0.1	1.7	1.1	1.2
<i>Chrysopsis chrysophylla</i> (Hook.) Hjelmq.	Fagaceae	0	0	1.6	0	0
<i>Clintonia andrewsiana</i> Torr.	Liliaceae	0	0	0	0	0.5
<i>Lilium maritimum</i>	Liliaceae	0	0.1	0	0	0
<i>Trillium ovatum</i>	Melanthiaceae	0	0	0	0.1	0.7
<i>Claytonia sibirica</i> L.	Montiaceae	0	0.1	0	0	0.1
<i>Morella californica</i> (Cham.) Wilbur	Myricaceae	5.6	3.8	4.2	6.2	8.7
<i>Lysimachia latifolia</i> (Hook.) Cholewa	Myrsinaceae	0	0	0	0	0.1
<i>Calypso bulbosa</i>	Orchidaceae	0	0	0	0.1	0.25
<i>Goodyera oblongifolia</i>	Orchidaceae	0	0	0	0.1	0.2
<i>Polypodium scolieri</i>	Polypodiaceae	0	0	0	0	0.5
<i>Viola sempervirens</i> E. Greene	Violaceae	0	0	0	0	0.1

TABLE 3. LINEAR REGRESSION BETWEEN SOIL pH AND EIGHT RESPONSE VARIABLES ACROSS A PYGMY/OLD GROWTH REDWOOD ECOTONE. Basal area was calculated from diameter (d) using $BA = \pi (\frac{1}{2}d)^2$.

	Coefficient	R ²	P-value
Canopy height (m)	+ 0.015	0.29	< 0.001
Canopy cover (%)	+ 0.011	0.25	< 0.001
Shrub cover (%)	− 0.008	0.23	0.003
Herb cover (%)	+ 0.052	0.34	< 0.001
Understory richness	+ 0.023	0.27	< 0.001
Basal area (m ² /ha)	+ 0.027	0.33	< 0.001
Basal area of <i>S. sempervirens</i> (m ² /ha)	+ 0.035	0.41	< 0.001
Basal area of <i>H. pygmaea</i>	− 0.020	0.35	< 0.001

strata including *Gaultheria shallon*, *Polypodium scolieri* , and *Vaccinium ovatum*. Fire hollows and complex canopy features of substantial size (> 12 cm diameter) were found exclusively in the “transitional” and “pygmy redwood” strata.

Variation among individual *S. sempervirens* with respect to growth form was observed within strata as well. In the “extreme pygmy” one highly clustered individual with small yellowed leaves (EP-1) and 338 stems (0.01–1.83 m in height; maximum of 2 cm basal diameter) occupied space of 4.86 m² and originated from an above ground root bole (Fig. 2). Two other individuals (EP-2 and EP-3) were less tightly clustered, with fewer stems (16 and 37 respectively). The stems for EP-2 and 3 were taller (maximum 2.49 m) and greater in basal diameter (maximum 7 cm) than those observed for EP-1. In addition, the individual stems of EP-1 all originated from under-ground root systems, rather than an above ground root bole, and included co-dominance and miniature lateral branching structures.

Trees within the “short pygmy” stratum were highly variable in terms of size and structure. SP-1 consisted of a single tree with two clonal stems originating at the base, and a total height of 9.2 m and a dbh of 16.26 cm. SP-2 included a single root bole with eleven stems originating at the burl, with the tallest stem measured at 5.2 m with a dbh of 22.1 cm. SP-3 included 124 stems within an area of 20.6 m². The largest stem had a maximum dbh of 34 cm, and had a total height of 8.8 m.

The “tall pygmy stratum” was characterized by islands of redwoods growing within a sea of pygmy dominants. TP-1 included ninety-one stems and



FIG. 2. A stunted shrub-like specimen of *S. sempervirens* with clustered 338 stems located in the extreme pygmy (EP) stratum of the pygmy/redwood ecotone.

occupied approximately 32.09 m². The maximum height measured was 10.85 m, with a dbh of 34 cm. A single epiphytic *G. shallon* was observed growing out of the trunk of a tree, 38 cm above ground. TP-2 included ninety-nine stems within an area of approximately 18.18 m². The tallest stem measured 5.89 m in height and had a dbh of 10 cm. TP-3 included 82 stems within an area of 18.7 m². The tallest tree measured 12.1 m and had a dbh of 37.85 cm. This individual had a broken top and two reiterations above 3 m. Fire marks were present at the base of the tree, and there were five *P. scouleri* established on the decaying top.

The “transitional stratum” included three samples. Two of these samples included trees with measurable complex crown features. T-1 was characterized by three intertwined clonal stems with heights observed at 20.45 m, 28.35 m, and 38.15 m; and dbh of 133 cm, 176 cm, and 240 cm. Two of the stems had fire hollows with a volume of 0.56 m³ and 1.21 m³ respectively. The maximum crown complexity observed in this stratum was five, resulting from 40.13 cm diameter lateral branch growing off of the largest (T1) stem, with hierarchical order BRRLT (where B = branch; R = reiterated trunk; L = limb; and T = main trunk). Twenty-five *P. scouleri* were observed growing as epiphytes on the largest and smallest stems. T-2 included eight stems within an area of 54.06 m². The structure of the trees in this plot had an umbrella like appearance. Where the tops had not

TABLE 4. OLD-GROWTH CHARACTERISTICS OBSERVED ON A PYGMY/REDWOOD ECOTONE ACROSS FIVE STRATA; EXTREME PYGMY (EP), SHORT PYGMY (SP), TALL PYGMY (TP), TRANSITIONAL (T), AND PYGMY REDWOOD (PR). Dashes indicate listed data type was not observed.

	EP	SP	TP	T	PR
Maximum crown complexity order	-	-	-	5	8
Maximum fire hollow volume	-	-	-	1.21 m ³	10 m ³
Number of epiphytes observed	-	-	6	44	264
Epiphyte species observed	-	-	<i>G. shallon</i> <i>P. scouleri</i>	<i>P. scouleri</i>	<i>P. scouleri</i> <i>V. ovatum</i>



FIG. 3. A single stem *S. sempervirens*, 7.4 m in height, with complex crown features located in the transitional stratum (T) of the pygmy/redwood ecotone. Photo courtesy of Dylan Crutchfield, Department of Environmental Studies, San Jose State University.

been broken off, but the growth was somewhat decurrent. The largest stem had a height of 17.50 m and a dbh of 105 cm. Fifteen *P. scouleri* individuals were observed on two of the stems with 14 individuals recorded on the largest stem. A single fire hollow was also observed on this tree with a volume of 0.48 m³. T-3, measured 7.4 m in height, and had a dbh of 58 cm (Fig. 3). A maximum crown complexity index of three was observed for T-3 on a 24.89 cm lateral branch with a hierarchical order of (BRT).

The “pygmy redwood” stratum included four samples, all of which exhibited old-growth characteristics including fire hollows, complex crown structure, and colonization by epiphytic plants. The first tree sampled (PR-1) grew as part of an eight stem clonal grouping, and was 26.1 m tall with a dbh of 230 cm. Extensive fire damage to the main stem resulted in a large fire hollow at the base, with a volume of approximately 8 m³ and an internal height of 6.33 m. PR-1 had a total of 41 structural characteristics, with basal diameter of 66 cm or greater at the trunk, and one major reiteration with a diameter of 40.6 cm. PR-1 had a maximum crown

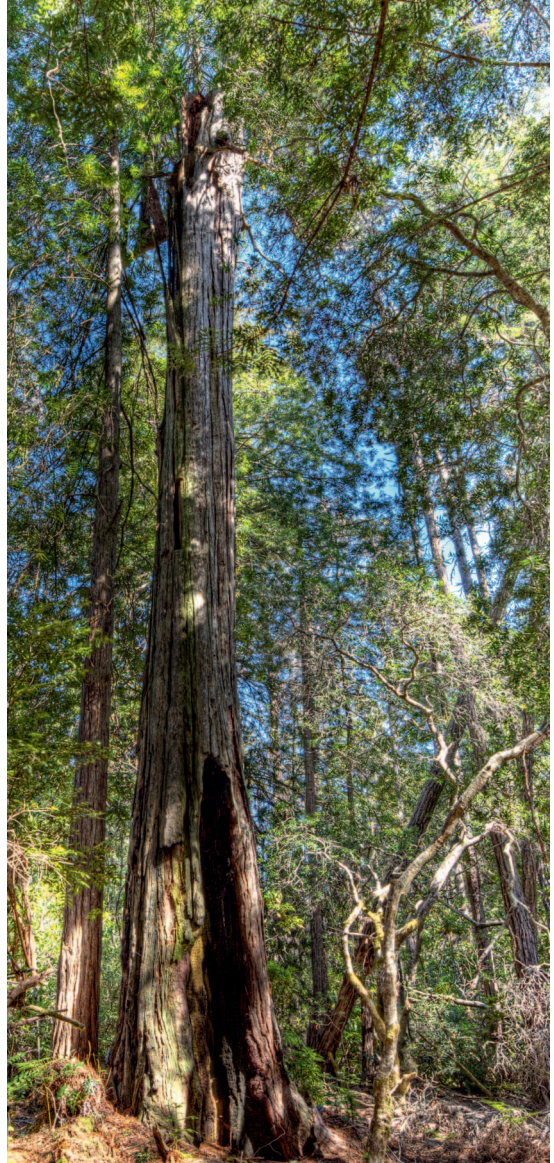


FIG. 4. A stunted ancient redwood (PR-3) found in the pygmy redwood strata with a height of 27.43 m. A continuous fire hollow ran from top to bottom, and was a nesting site for *Tyto alba* (barn owls). Photo courtesy of Dylan Crutchfield, Department of Environmental Studies, San Jose State University.

complexity order of eight on the 40.6 cm diameter reiteration with a hierarchy of (BRLRLRLT). A total of 262 epiphytic *P. scouleri* and 12 *V. ovatum* were observed growing on decaying limbs and crotches. The largest fern mat had an area of 98 cm², with 0.09 m³ arboreal soil. PR-2 was a single stem 33.46 m high with a dbh of 1.42 m. This tree had a bifurcated top with two reiterations originating 3 m below where a decayed former apical stem was observed. PR-2 had a maximum crown complexity

order of six on a 25.16 cm diameter lateral branch with a hierarchy of (BRLRLT). Two epiphytic *P. scouleri* were found on a live limb. PR-3 (Fig. 4), had a total height of 27.43 m and dbh of 157 cm. The maximum crown complexity order for PR-3 was seven on a 78.11 lateral branch with a hierarchy of (BRLRRLT). The main stem had been significantly damaged by fire so that the trunk was almost entirely hollow. A fire cave originated at the bottom and extended to a height 12.8 m, with an estimated volume of 10 m³. This hollow was a nesting site for barn owls (*Tyto alba*), based on personal observation of the owl leaving the hollow, as well as a proliferation of owl pellets around the base of the tree. The owl tree included one main reiteration 14.62 m from the ground, and 52 epiphytic *P. scouleri*. PR-4 consisted of two clones originating at the same basal point. The largest clone had a height of 35.1 m and a dbh of 1.59 m. A fire hollow measured 0.31 m³, with an internal height of 2.73 m. Several large reiterations were observed (two larger than 80 cm in diameter, and six between 18–34 cm). PR-4 had a maximum crown complexity order of seven on a 34.04 cm diameter reiteration with a hierarchy of (BRLRLRLT).

DISCUSSION

The stunted *S. sempervirens* trees found on the edge of the pygmy soil formation exhibited complex crown features, fire caves, and epiphytic plant associations, supporting the theory that forests need not produce large trees in order to provide the habitat features associated with old-growth (Wardle 1993). Stress response and disturbance history is likely the primary factor determining structural complexity, rather than tree size or stand density.

Characterization of soils across the ecotone supported previous research, and indicated that particular soil conditions were associated with vegetation structure and composition (Jenny 1973; Westman and Whittaker 1975; Brady 1990; Yu et al. 1999). As expected, pH and the availability of nutrients (P, K, Ca, and Na) were positively correlated with tree size and a variety of other floristic parameters (Table 1, Fig. 1), in agreement with the conclusions of previous investigations (Northup et al. 1998; Yu et al. 1999). In addition, multivariate analysis supported the theory that phosphorus limitation plays a crucial role in predicting the structure and composition of pygmy vegetation (Izquierdo et al. 2013).

A variety of floristic patterns emerged across the pygmy/redwood ecotone as well. The dominance of the pygmy endemic tree species (*Hesperocyparis pygmaea* and *Pinus contorta* ssp. *bolanderi*) was greatest in the “extreme pygmy” stratum, as was the cover of pygmy associated Ericaceous shrubs *Arctostaphylos nummularia* ssp. *mendocinoensis* and *Rhododendron columbianum*. Ericaceous generalists (*Rhododendron macrophyllum* and *Vaccinium ovatum*)

exhibited no preference for either habitat type, and a number of redwood associated herbaceous species (Mahony and Stuart 2000) were observed exclusively in the redwood-dominated strata (*Calypso bulbosa* (L.) Oakes, *Clintonia andrewsiana* Torrey, *Goodyera oblongifolia* Raf., *Polypodium scouleri*, and *Trillium ovatum* Pursh). The sensitivity of redwood-associated understory species to pygmy soil conditions is likely a result of intolerance to lack of shade from overstory canopy and poor nutrient availability resulting from low soil pH (Northup et al. 1998), with the possibility of mycorrhizal relationships being affected as well (Wurzbarger and Bledsoe 2001).

Three essential growth-forms of *S. sempervirens* were observed: a multi-stemmed shrub-like form; a vertical, highly stunted sub-canopy form; and a tall vertical co-dominant form with complex canopy structure. *Sequoia sempervirens* was able to manifest these multiple growth-forms as a result of prolific basal and epicormic sprouting (Ishii et al. 2002; Douhovnikoff et al. 2004; Van Pelt et al. 2016). Sprouting in *S. sempervirens* is a stress response, and where the stresses are unremitting, sprouting is continuous. The multi-stemmed shrub-like form of *S. sempervirens* is essentially a mass of basal sprouts emerging from a single half buried lignotuber. Each sprout strives to assert itself, but water and nutrient availability are limited to the point where no sprout can develop apical dominance. On more productive sites where the type and magnitude of stressors are stochastic in nature, epicormic sprouting plays its part in the development of crown complexity. Mechanical damage resulting from an adjacent tree-fall or lightning strike, or physiological damage from a freeze or prolonged drought, can trigger a sprouting response in the canopy, resulting in the production of trunk reiterations and unusual branching patterns.

There is a tendency to think of old-growth *S. sempervirens* forests as uniformly impressive in terms of stature, but as these results indicate, redwoods are highly variable in terms of growth form. Old-growth, as defined by management history (Peterken 1996), can also include ancient dwarfed trees growing on soils with low nutrient availability. These stunted redwoods, that grow at the edge of the species' ecological tolerance, may provide insight into the future of *S. sempervirens*. With changes in climate predicted over the coming decades, a growing proportion of the range may be relegated to poor site conditions (Johnstone and Dawson 2010).

The most noteworthy finding of this study was the extent of old-growth forest features observed on trees within the influence of pygmy soils. Complex crown structures and extensive fire hollows were discovered on stunted trees growing on marginal soils within the “transitional” and “pygmy redwood” strata, and epiphytic relationships existed even deeper into the pygmy forest formation with *P. scouleri* thriving on the decaying to top of a small redwood in the “tall pygmy” strata. These results support findings from other forest types as well, suggesting that the growth

form of trees was the result of repeated disturbances rather than size or age (Fahey et al. 2015; Wardle 1993).

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