

# 'Pygmy' Old-Growth Redwood Characteristics on an Edaphic Ecotone in Mendocino County, California

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## Abstract

The 'pygmy forest' is a specialized community that is adapted to highly acidic, hydrophobic, nutrient deprived soils, and exists in pockets within the coast redwood forest in Mendocino County. While coast redwood is known as an exceptionally tall tree, stunted trees exhibit unusual growth-forms on pygmy soils. We used a stratified random sampling procedure to characterize forest composition, structure, and growth-form, across the pygmy/redwood ecotone. Results indicate that tree height, canopy cover, basal area, herbaceous cover, shrub height and cover, and the dominance of pygmy forest endemics decreased across strata, and were negatively correlated to soil pH. In addition, the structure of individual redwoods varied significantly across the ecotone, exhibiting three main growth-forms: 1) Stunted multi-stemmed (>100 stems) individuals >2 m in height; 2) Small diameter multi-stemmed (two to six stems) individuals with an average height of 12 m growing as subcanopy under pygmy cypress and bolander pine; 3) Pygmy old-growth redwoods with a maximum height of 41 m growing as a co-dominant and exhibiting complex canopy structure. The results of this study indicate that while the growth-form of individual redwoods is significantly affected by pygmy soil conditions, stunted trees on the edge of the pygmy formation exhibit structural characteristics and canopy complexity similar to full stature redwoods.

*Key words:* Coast redwood, hydrophobic podisols, pygmy forest, *Sequoia sempervirens*

## Introduction

Coast redwood (*Sequoia sempervirens*) is the tallest tree species in the world reaching heights exceeding 112 m (Preston 2007). Where site conditions are less than optimal, however, growth can be stunted (Noss 2000). In the most extreme cases, *S. sempervirens* exhibits a shrub-like growth-form with an abundance of clonal stems connected to a single root mass, with no single stem exerting apical dominance. In less extreme cases *S. sempervirens* will develop a growth-form similar to the giants for which the species is known, but on a smaller scale. The most dramatic transition from giant redwoods to stunted redwood shrubs occurs on the ecotone between the 'pygmy forest' formation and the coast redwood forest in Mendocino County, California.

The pygmy forest is found on a series of five coastal terraces that increase with age as they progress inland from the coast (Fox 1976, Yu et al. 1999); the oldest with soils of approximately one million years (Westman and Whittaker 1975). Variation in vegetation between terraces is related to soil conditions. The first terrace has well

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drained soils rich in organic matter and nutrients (Aitken and Libby 1994) supporting shore pine (*Pinus contorta* subsp. *contorta*), bishop pine (*Pinus muricata*), and sitka spruce (*Picea sitchensis*) (Sholars 1982). Coast redwood mixes with western hemlock (*Tsuga heterophylla*) and Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*) on the second terrace, where podzolized soils begin to develop. The third, fourth, and fifth terraces where pygmy forest are found contain highly acidic, extremely podzolized, soils with a hydrophobic hardpan (Aitken and Libby 1994). Consequently, pygmy forest species, dominated by two endemic species, bolander pine (*Pinus contorta* subsp. *bolanderi*) and pygmy cypress (*Hesperocyparis pygmaea*), are well adapted to both high water table conditions (Sholars 1982, Wurzbürger and Bledsoe 2001) and summer drought (Westman and Whittaker 1975).

Complex lateral branching patterns, reiterated trunks, arboreal soils, and epiphytic plants have been well documented on full stature redwoods, which commonly occur on productive alluvial soils (Sillett and Van Pelt 2000). These features have been shown to provide habitat for threatened species such as the marbled murrelet (*Brachyramphus marmoratus*) and northern spotted owl (*Strix occidentalis caurina*) (Sawyer et al. 2000), and for less well known species such as the wandering salamander (*Aneides vagrans*) (Spickler et al. 2006). The occurrence of these features has not been adequately studied on less productive sites, such as those occurring adjacent to the pygmy forest formation. The objective of our research was to characterize the structure and composition of vegetation across the pygmy/redwood ecotone with particular emphasis on the growth-form of *S. sempervirens*.

## Methods

This study was conducted on the Russell Unit of the Mendocino Headlands State Park, a 50 ha property composed of mixed primary old-growth and mature second-growth redwood, with patches of riparian and pygmy forest habitat. Stratified random sampling was used to locate 10 (7 m diameter) sample plots within each stratum.

Six stratum radiating out from the center of the pygmy formation were defined loosely on Westman (1975) and included: ‘extreme pygmy’ dominated by stunted pygmy cypress and bolander pine; ‘short pygmy’ with similar species composition but less stunted trees; ‘tall pygmy’ dominated by tall Ericaceous shrubs and large specimens of bolander pine and pygmy cypress; ‘transitional’ dominated by tall pygmy cypress mixed with bishop pine and sub-canopy coast redwood; ‘pygmy redwood’ characterized by stunted old-growth redwoods growing as co-dominants, or sub-canopy species, with bishop pine; and ‘extreme redwood’ dominated by tall old-growth redwoods with western hemlock, grand fir (*Abies grandis*), and Douglas-fir associates.

Data recorded on each plot included biotic factors including diameter (dbh) of trees by species, canopy cover, average canopy height, percent cover and height of shrub species, percent cover herbaceous species; and abiotic factors including pH of the A horizon, depth to the hardpan, and distance to the center of the pygmy formation. In addition, the growth-form of individual *S. sempervirens* specimens sampled on each plot were described with the following characteristics: height, number of stems emerging from root bole, diameter of largest stem, and presence of

old-growth canopy characteristics (large lateral branches, reiterated trunks, epiphytes, and fire hollows).

The relationship between stand characteristics and soil pH were analyzed using linear regression. Variation of response variables between strata was analyzed using ANOVA with Benferroni post-hoc analysis.

## Results

The size and growth-form of trees, composition of vegetation, and soil pH varied significantly across the pygmy/redwood ecotone. Soil pH ranged from 4.0 to 6.6, and was found to be the best abiotic predictor of stand characteristics. 'Depth to hardpan' and 'distance to the pygmy center' were found to be poor predictors.

A positive linear relationship was found between canopy height and pH, suggesting a negative correlation between canopy height and pygmy soil conditions. ANOVA analysis confirmed this relationship with significant differences in canopy height between strata with the highest canopy found in the 'extreme redwood' stratum, and the lowest found in the 'extreme pygmy' stratum (*table 1*).

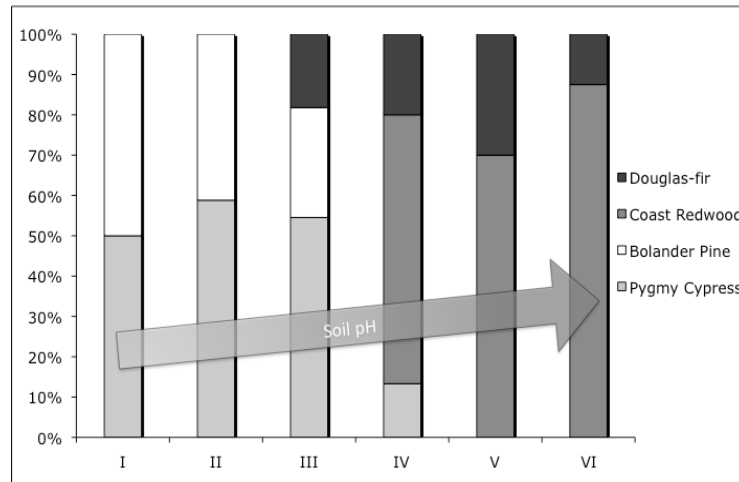
**Table 1**—*Relationship between soil pH and six dependant variables measured across a pygmy/redwood ecotone on six strata; (I) extreme pygmy, (II) short pygmy, (III) tall pygmy, (IV) transitional, (V) pygmy redwood, and (VI) extreme redwood. Reported R<sup>2</sup> and p-value result from linear regression analysis with soil pH. Strata sharing the same lower case letters did not exhibit significant differences based on ANOVA.*

	I	II	III	IV	V	VI	R <sup>2</sup>	P-value
Median soil pH	4.8 <sup>a</sup>	4.95 <sup>b</sup>	4.95 <sup>b</sup>	5 <sup>b</sup>	5.25 <sup>c</sup>	5.95 <sup>c</sup>	-	-
Canopy Height (m)	2.09 <sup>a</sup>	5.64 <sup>b</sup>	11.95 <sup>c</sup>	21.5 <sup>d</sup>	39.6 <sup>e</sup>	58.3 <sup>f</sup>	0.29	>0.001
Canopy Cover (%)	37.1 <sup>a</sup>	49.2 <sup>b</sup>	59.2 <sup>b</sup>	83.9 <sup>c</sup>	91.7 <sup>d</sup>	97.7 <sup>d</sup>	0.25	>0.001
Shrub Cover (%)	70.8 <sup>a</sup>	89.3 <sup>b</sup>	78.1 <sup>b</sup>	60.4 <sup>c</sup>	34.1 <sup>d</sup>	46.3 <sup>d</sup>	0.23	0.003
Herb Cover (%)	1.8 <sup>a</sup>	1.3 <sup>a</sup>	3 <sup>a</sup>	0.4 <sup>a</sup>	2.35 <sup>a</sup>	16.4 <sup>b</sup>	0.34	>0.001
Understory richness	6 <sup>a</sup>	10 <sup>b</sup>	10 <sup>b</sup>	10 <sup>b</sup>	15 <sup>c</sup>	24 <sup>d</sup>	0.27	>0.001
Basal Area (m <sup>2</sup> /ha)	142.9 <sup>a</sup>	186.6 <sup>a</sup>	66.8 <sup>b</sup>	109.4 <sup>a</sup>	371.3 <sup>c</sup>	479.8 <sup>c</sup>	0.33	>0.001
Basal Area of Redwood	0 <sup>a</sup>	0 <sup>a</sup>	0 <sup>a</sup>	101.9 <sup>b</sup>	335.1 <sup>c</sup>	371.3 <sup>c</sup>	0.41	>0.001
Basal Area of Pygmy Cypress	136.8 <sup>a</sup>	175.2 <sup>a</sup>	61.1 <sup>b</sup>	3.3 <sup>c</sup>	0 <sup>c</sup>	0 <sup>c</sup>	0.35	>0.001

Percent tree canopy cover, shrub cover, and herbaceous cover, also exhibited linear relationships with soil pH as well as significant differences between strata. Tree canopy cover was relatively low on pygmy soils, while shrub cover was

relatively high. Herbaceous cover was uniformly low across the ecotone except for the ‘extreme redwood’ stratum, which was significantly higher.

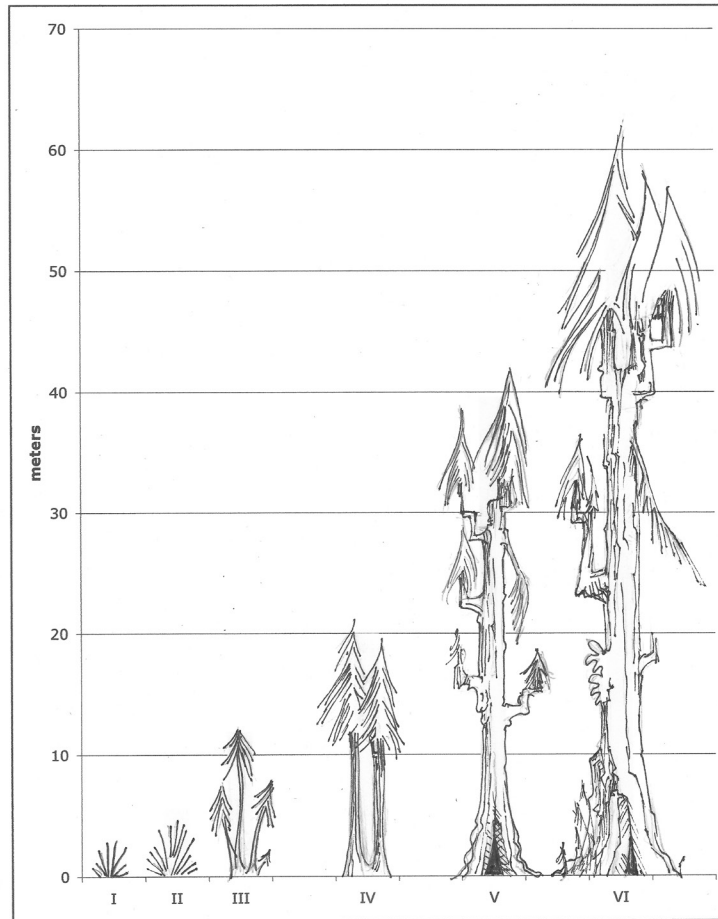
Total basal area, and the basal area of coast redwood, exhibited positive linear relationships with soil pH, while the basal area of pygmy cypress exhibited a negative linear relationship (*table 1*). Pygmy cypress and bolander pine had the highest relative frequency on first three strata, and coast redwood and Douglas-fir on the last three strata (*fig. 1*). The presence of Douglas-fir in the ‘tall pygmy’ stratum and pygmy cypress in the ‘transitional’ stratum suggests a somewhat porous, boundary between the two communities.



**Figure 1**—Relative frequency (n=60) of the four most commonly occurring tree species across six strata: (I) extreme pygmy, (II) short pygmy, (III) tall pygmy, (IV) transitional, (V) pygmy redwood, and (VI) extreme redwood, on a pygmy ecotone.

The maximum height, and growth-form, of coast redwood trees also varied significantly across the pygmy/redwood soil gradient (*fig. 2*). In the ‘extreme pygmy’ and ‘short pygmy’ strata the growth-form coast redwood was limited to rare multi-stemmed (>100 stems/plant) shrub-like forms. Still infrequent, but less stunted forms, were found in the ‘tall pygmy’ and ‘transitional’ strata. Individuals within these two strata tended to be vertical in form with fewer stems (two to six) and generally grew in a conical form with little lateral branching in the crown.

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**Figure 2**—Canopy height of *S. sempervirens* across six strata (n=60); (I) extreme pygmy, (II) short pygmy, (III) tall pygmy, (IV) transitional, (V) pygmy redwood, and (VI) extreme redwood, on a pygmy forest ecotone in Mendocino, California (SE=0.26; 0.76; 1.54; 4.31; 5.26; 7.34).

Individual redwood trees in the 'pygmy redwood' and 'extreme redwood' strata grew in a vertical upright form, and exhibited complex canopy features including lateral branching patterns and multiple trunk reiterations. Well-developed fire hollows were common on older trees in both strata (fig. 4), and epiphytic vascular plants such as leather fern (*Polypodium scolieri*) huckleberry (*Vaccinium ovatum*), and billberry (*Vaccinium parvifolium*) were observed growing in the canopy. In many ways the growth-form of old-growth trees was comparable between the 'pygmy redwood' and 'extreme redwood' strata, except in regard to scale. The maximum tree diameter measured in the 'extreme redwood' was 750 cm compared to 244 cm in the 'pygmy redwood' and the maximum heights were 66 m and 41 m respectively.



**Figure 4**—The ‘Owl Tree’ found in the ‘Pygmy Redwood’ strata with insert illustrating complex branching pattern at the top of tree. A continuous fire hollow ran from top to bottom, and was a nesting site for barn owls (*Tyto alba*). Photo courtesy of Dylan Crutchfield, Department of Environmental Studies, San Jose State University.

Similarities between the ‘pygmy redwood’ and ‘extreme redwood’ strata were less pronounced in regard to understory species. Both herbaceous cover and richness of understory species were significantly higher in ‘extreme redwood’ compared to all other strata (*table 1*). There were, however, a number of species that were limited to pygmy soils including two California Native Plant Society listed species, pygmy manzanita (*Arctostaphylos mendocinoensis*) and the coast lily (*Lilium maritimum*) (*table 2*).

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**Table 2**—Mean percent cover per plot of understory shrubs and herbaceous species occurring on a pygmy forest ecotone across six strata, (I) extreme pygmy, (II) short pygmy, (III) tall pygmy, (IV) transitional, (V) pygmy redwood, and (VI) extreme redwood. Association designations indicate species that were limited to specific habitat types.

Association		I	II	III	IV	V	VI
Pygmy	<i>Arctostaphylos columbiana</i>	0	0	0.3	0	0	0
Pygmy	<i>Arctostaphylos mendocinoensis</i> <sup>a</sup>	0	0.2	0.2	0	0	0
Redwood*	<i>Blechnum spicant</i>	0	0	0	0	0	2.4
Redwood*	<i>Boschniakia strobilacea</i>	0	0	0	0	0	0.1
Redwood	<i>Calypso bulbosa</i>	0	0	0	0.1	0.25	0.5
Redwood*	<i>Cardamine californica</i>	0	0	0	0	0	2.1
Redwood	<i>Chimaphila menziesii</i>	0	0	0	0.1	0	0
Pygmy	<i>Chrysopsis chrysophylla</i>	0	0	1.6	0	0	0
	<i>Claytonia sibirica</i>	0	0.1	0	0	0.1	0.15
Redwood	<i>Clintonia andrewsiana</i>	0	0	0	0	0.5	1.5
Redwood*	<i>Corallorhiza mertensiana</i>	0	0	0	0	0	0.3
Redwood*	<i>Disporum hookeri</i>	0	0	0	0	0	0.2
Redwood*	<i>Epipactis gigantea</i>	0	0	0	0	0	0.1
Redwood*	<i>Equisetum telmateia</i> subsp. <i>braunii</i>	0	0	0	0	0	0.2
	<i>Gaultheria shallon</i>	8.9	8.9	9.4	7.5	9.5	23.2
Redwood	<i>Goodyera oblongifolia</i>	0	0	0	0.1	0.2	0.1
Pygmy	<i>Ledum glandulosum</i>	24.5	46	4.5	0	0	0
Pygmy	<i>Lilium maritimum</i> <sup>b</sup>	0	0.1	0	0	0	0
	<i>Myrica californica</i>	5.6	3.8	4.2	6.2	8.7	0
Redwood*	<i>Oxalis oregana</i>	0	0	0	0	0	6.2
Redwood	<i>Polypodium scolopendri</i>	0	0	0	0	0.5	0
Redwood	<i>Polystichum munitum</i>	0	0	0	0	0.3	9.8
	<i>Pteridium aquilinum</i> var. <i>pubescens</i>	5.4	3.4	1.8	0.9	1.5	0.5
Redwood*	<i>Rhamnus californica</i>	0	0	0	0	0	0.1
	<i>Rhododendron macrophyllum</i>	3.5	4.2	29.5	13.1	4.6	7.3
Redwood*	<i>Smilacina racemosa</i>	0	0	0	0	0	0.1
Redwood*	<i>Stachys bullata</i>	0	0	0	0	0	0.1
Redwood*	<i>Tiarella trifoliata</i> var. <i>unifoliata</i>	0	0	0	0	0	0.5
Redwood	<i>Trientalis latifolia</i>	0	0	0	0	0.1	0
Redwood	<i>Trillium ovatum</i>	0	0	0	0.1	0.7	1.4
	<i>Vaccinium ovatum</i>	23.7	25.3	27	32.5	5.6	1.8
Redwood	<i>Vaccinium parvifolium</i>	0	0.1	1.7	1.1	1.2	3
	<i>Viola sempervirens</i>	0	0	0	0	0.1	1.25

<sup>a</sup>CNPS special status 1B.2

<sup>b</sup>CNPS special status 1B.1

\*Species only observed in 'extreme redwood' strata

## Discussion

Westman and Whittaker (1975) described the pygmy forest region of northern California as the area containing the “smallest and the largest forests in the world.” This dramatic contrast between the pygmy and coast redwood communities is based on an edaphic gradient of soil pH, moisture, and nutrient availability. While massive redwoods growing on productive soils have been the subject of intense study, the tenacious specimens of *S. sempervirens* persisting on the edge of their ecological tolerance have been neglected in the literature.

While our study involved an analysis of six strata, each with unique characteristics, we observed essentially three growth-forms of *S. sempervirens*: a multi-stemmed shrub-like form; a vertical, highly stunted sub-canopy form; and a tall vertical co-dominant form with complex canopy structure. *S. Sempervirens* is able to manifest multiple growth-forms as a result of prolific basal and epicormic sprouting. Sprouting in coast redwood is a stress response, and where the stresses are unremitting the sprouting is continuous. The multi-stemmed shrub-like form of *S. sempervirens* found in the ‘extreme pygmy’ is essentially a mass of basal sprouts emerging from a single half buried lignotuber.

In addition to variation in the growth-form of *S. sempervirens*, stand structure and composition of the stand as a whole varied across the pygmy/redwood ecotone. As expected the dominance of pygmy cypress and bolander pine and the cover of Ericaceous shrubs (*Arctostaphylos mendocinoensis*, *Gaultheria shallon*, *Ledum glandulosum*, *Rhododendron macrophyllum*, *Vaccinium ovatum*) were at their maximum, and canopy cover and canopy height were at their minimum, within the pygmy formation. What was not predicted in the literature was the porosity of the boundary between the two communities with Douglas-fir observed within the ‘tall pygmy’ strata and pygmy cypress found growing in transitional stands. The influence of pygmy soil conditions on adjacent redwood stands was also surprising. In stands that would not be considered ‘pygmy’ by any of the traditional pygmy forest definitions, stand characteristics varied significantly from ‘extreme redwood’ stands and trended toward pygmy conditions. For example, lower cover of herbaceous species in the ‘pygmy redwood’ as compared to ‘extreme redwood’ suggests a sensitivity of understory species to pygmy soil conditions, possibly as a result of poor nutrient availability resulting from low soil pH (Northup et al. 1998).

There is a tendency to think of coast redwood forests as uniformly impressive in terms of stature. In fact, redwoods are highly variable, and where redwoods grow at the edge of their ecological tolerance it is their resilience, and morphological flexibility, that is truly impressive.

## Acknowledgments

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