Reference Conditions for Old-Growth Redwood Restoration on Alluvial Flats

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Abstract

We quantified structural attributes in three alluvial flat old-growth coast redwood stands. Tree size parameters and occurrences of distinctive features (e.g., burls, goose pens) were similar between stands. Occurrence of distinctive features was greater among larger trees. Tree size-frequency distributions conformed to a reverse-J diameter distribution. The range of tree sizes was similar between study sites. Redwood density ranged from 118 to 148 trees ha^{-1} and upper canopy tree density ranged from 45 to 74 trees ha^{-1}. Crown ratio was similar across study sites with an overall mean of 64.3 percent, except that crown ratio of the largest trees was lower at the site with the highest growing space occupancy. The percentage of plot area in canopy gaps ranged from 17 to 25 percent. Seedling regeneration was no more frequent beneath canopy gaps. These and other results describe structure in old-growth redwood forests and can serve as reference conditions for old forest restoration on alluvial flats.

Key words: canopy gaps, regeneration, *Sequoia sempervirens*, stand structure

Introduction

Old-growth redwood (*Sequoia sempervirens*) forests are structurally diverse, having been shaped over centuries by a wide range of forces (Lorimer et al.2009). Trees with diameters of 2 to 4 m and heights of 60 to 100 m are common. The desire to restore some of these features in managed forests has prompted application of various silvicultural practices, yet to date, little attention has been directed at developing a detailed description of structural parameters and distinctive features found in old-growth redwood forests that describe the historic condition and could serve as reference conditions for restoration.

Quantification of old-growth forest structure supports restoration efforts by providing reference conditions that could serve as targets for management activities (Harrod et al. 1999, SERISPWG 2004). The objective of this study was to identify structural parameters and distinctive features that were characteristic of alluvial flat old-growth redwood stands and may thus serve as targets for restoration of old forest structures. We hypothesized that: (1) multivariate analysis would not successfully discriminate between study sites on the basis of tree size and crown parameters; (2) seedling regeneration was no more frequent directly beneath canopy gaps than beneath tree crowns; and (3) the occurrence of distinctive features (e.g., epicormic sprouting) on live trees differed between sites, and was greater among larger trees. To test these hypotheses, calculate canopy gap areas and canopy volume, and summarize total live stem biomass, coarse woody debris, and regeneration data, we made detailed measurements of various tree size and crown size parameters, mapped tree locations, and recorded instances of distinctive features on individual redwood trees.

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Methods

Three study sites were selected—from the few larger remaining old growth groves on alluvial flats in northern California—to each represent different conditions and locations. Two of the study sites, named Children's and Rockefeller, were located at Humboldt Redwoods State Park in the southern part of Humboldt County (N 40°18.5', W 123°54.4'). The study site at Children's Forest in HRSP was located along the south fork of the Eel River adjacent to Myers Flat. Children's differed from the other two study sites in that a wildfire occurred there 1.5 years prior to study installation. The Rockefeller site in HRSP was approximately 14 km NW of the Children's site and located along the small perennial Bull Creek. Mean annual temperature for the HRSP area is 12.6 °C and mean annual precipitation is 123 cm. The third study site, named Armstrong, was located alongside a seasonally dry creek at Armstrong Redwoods State Preserve (ARSP) in the Russian River region of Sonoma County (N 38°53', W 123°0.6'). Mean annual temperature for ARSP is 13.9 °C and mean annual precipitation totals 104 cm.

Plants common to these redwood-dominated sites included redwood sorrel (*Oxalis oregano*) and western sword fern (*Polystichum munitum*). Hardwoods such as tanoak (*Notholithocarpus densiflorus*), bigleaf maple (*Acer macrophyllum*), and California bay (*Umbellularia californica*) were found in small numbers in openings or near streams.

At each site, a 1 ha sample plot (100 m x 100 m) was established with the objective of quantifying the horizontal and vertical structure. All trees ≥ 15 cm diameter at 1.37 m breast height (dbh) were mapped using a survey laser mounted on a tripod. Species, dbh, and location (e.g., azimuth and horizontal distance to the middle of each tree from reference points) were recorded. To assure mapping was accurate, the angle and distance from plot center to each reference point was recorded and cross-checked with tree locations taken from both plot center and the respective reference point. Additionally, all trees ≥ 15 cm dbh were measured for total height, live crown base height, and crown radius. Live crown base height was defined as the height of the lowest major branch that formed part of the main canopy. The number of crown radius measurements varied with complexity of crown shape. A minimum of four crown radius measurements were taken, each in a cardinal direction, for small trees with circular crowns. A maximum of eight measurements were taken for large trees with irregular crowns. Crown class, crown shape, and crown fullness estimates were recorded for each tree. The three-dimensional shape of individual tree crowns was most often described as a parabola; however, some were described as a cone, cylinder, or diamond. Crown fullness was an ocular estimation of the percentage of the live crown occupied by branches and foliage (e.g., 50, 66, 75 percent). Because older trees often have discontinuous crowns, incorporating the "fullness" variable into the crown volume equation provided a more accurate estimate of actual space occupied by live tree crowns.

For each redwood tree, we noted presence or absence of the following distinctive features: burls, epicormic sprouting, goose pens, and reiterations. A goose pen was defined as a large fire-created basal hollow greater than 30 or 60 cm tall for trees less than or greater than 1 m dbh, respectively. A reiteration was defined as an erect sprout or branch found on an existing tree but supporting its own network of horizontally oriented branches. Three 100 m north-south transects were established in each 1 ha plot with the objective of quantifying regeneration, understory vegetation, and groundcover. Height, location, species, and regeneration source (i.e., sprout versus seedling) were recorded for all trees < 15 cm dbh in a continuous 4 m wide belt centered on each transect line. Percent ground cover values were obtained by dividing the entire length of each transect line into one centimeter sections and recording species of shrubs, herbaceous vegetation, bareground, and litter covering ground directly below the transect line. Down logs ≥ 30 cm diameter and ≥ 2 m length were mapped and measured to determine the volume, mass, and percent cover of large down wood at Children's and Rockefeller. Diameter at the midpoint of each length of down log, log length, and location were recorded. Only the portions of logs falling inside the plot were measured. Down logs at Armstrong were not measured due to a history of removal of down wood from the site. Standing dead trees (snags) ≥ 15 cm dbh were mapped and measured for dbh at the three study sites.

Data for live trees with dbh ≥ 15 cm were summarized to give per-hectare stem density, basal area, and stem volume, stand density index (Reineke 1933), and maximum tree height for each species at the three study sites. Stem volume (V) was calculated using a simple conic shape: $V=\pi(0.5\ dbh)^2h/3$ where *dbh* = dbh in m and *h* = total tree height in m. Stand density index (SDI) was calculated as a summation of individual tree values because the dbh data were not normally distributed: $SDI=\sum(0.04dbh_i)^a$ where dbh_i = dbh in cm of the i^{th} tree in the plot, and a = 1.605 (Long and Daniel 1990, Shaw 2000). Trees were grouped into 30 cm dbh size classes to give size-frequency distributions for each site. Individual tree size parameters of dbh, height, crown radius, crown volume, and crown ratio (ratio of crown length to total tree height) were analyzed using canonical discriminant analysis. The objective was to identify individual parameters or groups of parameters that differed least between sites, assuming these 'commonalities' would be more useful targets for restoration than parameters that differed between sites. Prior to analysis, a logarithmic transformation of dbh was applied to achieve normality of the residual variances.

After arc-sine transformation, average crown ratio was calculated for redwood trees in each 30 cm dbh size class. Average crown ratios for each size class were subjected to an ANOVA to test for significant differences (α = 0.05) between study sites. The length of clear bole was defined as the portion of the tree stem not occupied by the canopy (equivalent to live crown base height). Clear bole length was summarized by 30 cm dbh size classes to further describe the vertical structure of standing trees at each site. Crown volume for each tree was calculated using crown length, radius, shape, and fullness. Summing crown volume data for all trees in the 1-ha plots allowed for a site-by-site comparison of total canopy volume. To determine the vertical distribution of crowns and crown volume at each site, individual tree crown volume was separated into layers at 10-m height intervals and summed for each 10 m layer.

ArcGIS ArcMap (ESRI) was used to delineate and calculate plot area not covered by the downward projection of tree crowns. Crown canopy maps of each site were created using stem locations and crown radius measurements. Spatial coordinates of crown extent were created for each crown radius measurement and then connected for each tree to create polygons representing tree crown extent. Polygon boundaries were smoothed using a t-spline. To obtain an accurate estimate of gap area within the 1 ha plots, portions of the crown of trees surrounding the plot that extended inside plot boundaries were included in the crown canopy maps. This necessitated mapping and measurement of crown radii for trees with crowns encroaching on the plot area. Crown canopy maps were used to examine the relationship between canopy gaps and regeneration.

Location coordinate data for regeneration in each 4-m wide belt transect were imported into the crown canopy maps for each site. Each record of regeneration (all trees <15 cm dbh) was coded as occurring directly beneath a canopy gap or beneath an opening in the canopy. Binomial proportions tests were used to test for differences in occurrence of regeneration beneath tree crowns versus regeneration under canopy gaps, by species type (i.e., redwood or hardwood) and source of regeneration (i.e., sprout or seedling). Count data for regeneration under canopy gaps or tree crowns were each divided by the proportions of transect area either under canopy gaps or beneath tree crowns, respectively, making count data comparable when different proportions of transect area were located directly beneath the canopy and under canopy gaps.

Logistic models were developed to predict probability of occurrence of burls, epicormic sprouting, goose pens, and reiterations on individual redwood trees as a function of tree-size parameters. Dummy variables for study site were also included to test for significant differences in presence-absence of these distinctive features between the three study sites. Model goodness-of-fit in terms of -2 Log Likelihood was compared between models to identify the tree size parameter (i.e., dbh, height, live crown base height, crown length, crown radius) most strongly associated with probability of occurrence of distinctive features on redwood trees. Data were analyzed using SAS statistical analysis software (SAS Institute 2004).

Results

Redwood density ranged from 118 to 148 trees ha^{-1} and density of all live stems ranged from 118 to 183 trees ha^{-1} for the three study sites (*table 1*). The two sites at Humboldt Redwoods State Park (Children's and Rockefeller) were almost completely comprised of redwood. In contrast, the site at Armstrong Redwood State Park (Armstrong) contained a mix of hardwoods. Hardwood crowns had not attained upper canopy status. The distribution of stems by 30 cm dbh class indicated that Armstrong's higher stem density was mostly in the small size classes and because of the hardwood presence. The frequency distribution of redwood tree diameters was a reverse-J shape at the three study sites. The two northern sites (Children's and Rockefeller) contained larger diameter trees while a narrower distribution of diameters at Armstrong was observed (*fig. 1*). Mean dbh was similar at Armstrong and Children's (1.10 and 1.08 m, respectively). Mean dbh at Rockefeller was 1.45 m.

Table 1—*Species composition and stem density per hectare by crown class for all live trees ≥ 15 cm dbh in the 1-ha plot at the three alluvial flat old-growth redwood study sites.*

Site	Species	Dominant	Codom.	Intermediate	Suppressed	Total
Armstrong	*S. sempervirens*	47	27	27	47	148
	A. macrophyllum	--	--	4	2	6
	N. densiflorus	--	--	5	2	7
	U. californica	--	--	19	3	22
	Total	56	27	46	54	183
Children's	*S. sempervirens*	13	33	45	37	128
	U. californica	--	--	2	1	3
	Total	14	33	46	38	131
Rockefeller	*S. sempervirens*	29	16	44	29	118

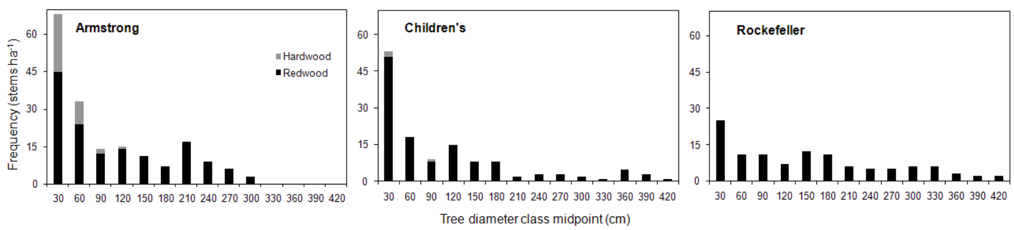

Figure 1—Diameter distribution of live trees ≥ 15 cm dbh for 1-ha plots at the three alluvial flat old-growth redwood study sites.

Structural attributes of redwood basal area, canopy volume, and total standing stem volume tended to be similar at Children's and Armstrong study sites, and highest at Rockefeller (*table 2*). Among these structural attributes, total standing stem volume differed most between study sites. Basal area and total standing stem volume at Rockefeller were at least 30 and 37 percent greater, respectively, than at Children's and Armstrong. Similarly, redwood SDI was greater at Rockefeller than at Children's and Armstrong (metric SDI: 2529, 1884, 2057, respectively). Maximum height was similar at the two northern sites and taller compared to Armstrong. Total canopy volume for the three sites was similar in overall value but was distributed differently along the vertical profile (*table 2*, *fig. 2*). Peak canopy volume values differed between the three study sites; Armstrong peaked at a lower height (40 m) than the two northern sites, Children's peaked at 50 m, and Rockefeller had the most crown volume at 60 m above ground.

Table 2—*Basal area (BA), canopy volume, total standing stem volume, and height of the tallest tree (Max. Ht.) for live trees ≥ 15 cm dbh in the 1-ha plot at the three alluvial flat old-growth redwood study sites.*

Site	Species	BA (m^2 ha^{-1})	Canopy volume (m^3 ha^{-1})	Stem volume (m^3 ha^{-1})	Max. Ht. (m)
Armstrong	*S. sempervirens*	228.3	168,281	5,542	95
	A. macrophyllum	0.3	838	1.7	24
	N. densiflorus	0.3	588	1.3	18
	U. californica	4.8	15,363	60.2	49
	Total	233.7	185,070	5,605	--
Children's	*S. sempervirens*	225.1	171,806	6,732	105
	U. californica	0.8	1,186	15.9	59
	Total	225.9	172,992	6,748	--
Rockefeller	*S. sempervirens*	307.8	174,588	9,272	107

Canonical discriminant analysis revealed significant structural differences between the three sites. Armstrong and Children's sites were found to be the most different ($P < 0.0001$) while the two northern sites, Children's and Rockefeller, were found to be the least different ($P = 0.007$). The analysis discriminated between the sites predominantly on the basis of dbh and height, suggesting that height to diameter ratio was the most important structural difference between sites. The analysis also revealed different tree diameter – crown volume relations between sites. However, modest allocation rates (42 to 57 percent) indicated that the sites could not be separated easily by tree size parameters.

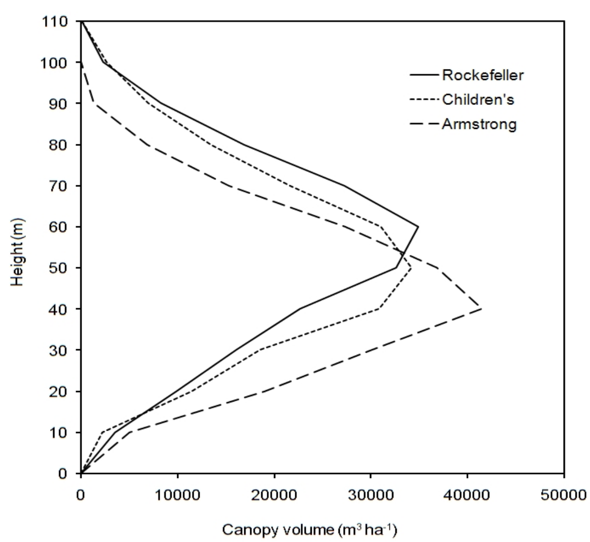

Figure 2— Canopy volume distribution by 10-m height interval along vertical profile for each alluvial flat old-growth redwood study site, based on tree crown volume estimates for redwood stems ≥ 15 cm dbh.

Long crowns were a common feature at the three study sites (*table 3*). The overall mean crown ratio for the three study sites was 64.6 percent. An F-test failed to detect significant differences in mean crown ratio for each 30-cm dbh size class between the three study sites ($P = 0.14$). However, differences in crown ratio between sites were detected in an F-test of tree crown ratio data for large trees (i.e., trees > 1.5 m dbh; $P = 0.001$). Further analysis of data for large trees detected no significant difference in crown ratio between Children's and Armstrong sites ($P = 0.92$), whereas crown ratios at these two sites differed significantly from the Rockefeller site ($P \leq 0.005$) where the larger trees had longer clear boles and shorter crowns (*table 3*).

Table 3—*Average crown ratio (CR) and length of clear bole (CB) by 30 cm dbh size class for all redwood trees ≥ 15 cm dbh at the three alluvial flat old-growth redwood study sites.*

Dbh class	Armstrong			Children's			Rockefeller		
midpoint (cm)	n	CR	CB (m)	n	CR	CB (m)	n	CR	CB (m)
30	45	.61	6	51	.62	8	31	.68	6
60	24	.71	9	18	.70	13	11	.76	9
90	12	.69	16	8	.69	21	11	.69	17
120	14	.65	22	15	.66	24	7	.67	23
150	11	.64	24	8	.66	27	12	.69	22
180	7	.74	21	8	.61	34	11	.58	34
210	15	.67	23	2	.74	22	6	.64	32
240	11	.55	35	3	.68	30	5	.50	44
270	6	.61	32	3	.64	34	5	.59	40
300	3	.65	30	2	.65	35	6	.58	41
330	0	--	--	1	.47	47	6	.50	47
360	0	--	--	5	.61	39	3	.50	47
390	0	--	--	3	.73	27	2	.62	38
420	0	--	--	1	.84	15	2	.54	46
Mean	--	.65	--	--	.65	--	--	.64	--

The sum of canopy gap areas as a percentage of total plot area was similar at the three sites, ranging from 17 to 25 percent. Gap shape and size were variable (*fig. 3*). For gaps contained within plot boundaries there was an approximate reverse-J distribution in gap sizes. Rockefeller had one large gap (>1272 m^2) which extended beyond the plot boundary and accounted for 50 percent of the total gap area within the plot.

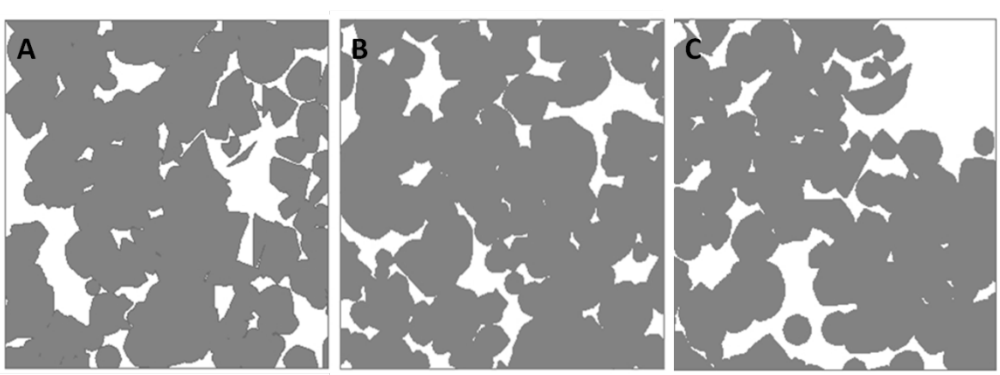

Figure 3—Canopy map of tree crown projections in 1-ha plots at (a) Armstrong; (b) Children's; and (c) Rockefeller alluvial flat old-growth redwood study sites.

Regeneration density and species composition differed between study sites (*table 4*). Hardwood trees < 15 cm dbh were found at Armstrong and Rockefeller. Armstrong contained a mix of hardwoods including tanoak, California bay, and red alder (*Alnus rubra*). In contrast, Rockefeller contained only one hardwood species, tanoak. Redwood sprouts and seedlings were present at all three sites. Binomial proportions tests did not detect differences between the occurrence of redwood sprouts or seedlings occurring in canopy gaps and redwood regeneration beneath the canopy ($P \geq 0.31$), nor between hardwood sprouts or individuals occurring in gaps or beneath the canopy ($P \geq 0.12$). Most redwood regeneration found along transects was in the form of basal sprouts associated with an existing root system.

Table 4—*Regeneration density per hectare for all trees < 15 cm dbh in three 400 m^2 belt transects at each alluvial flat old-growth redwood study site.*

Site	Species	Sprouts	Seedlings	Total
Armstrong	*Sequoia sempervirens*	1125	48	1173
	Hardwoods	404	538	942
Children's	*Sequoia sempervirens*	1538	25	1563
Rockefeller	*Sequoia sempervirens*	158	150	308
	Hardwoods	483	517	1000

The main constituents of the forest floor were similar among sites, with redwood sorrel, sword fern, and litter most prevalent. However, the proportions of these elements differed between sites. Rockefeller contained almost an even mix of litter, redwood sorrel, and sword fern (35, 21, and 32 percent, respectively). Children's groundcover was almost a complete blanket of redwood sorrel (76 percent), probably as a result of the fire. Armstrong's ground cover was dominated by litter (54 percent) followed by redwood sorrel (30 percent), and sword fern (6 percent). Consistent with the higher tree species diversity found at Armstrong, the understory was also most diverse and included fragrant bedstraw (*Galium triflorum*), trail marker (*Adenocaulon bicolor*), fairybell (*Disporum hookeri*), and wood rose (*Rosa gymnocarpa*).

Epicormic sprouting was the most common distinctive feature at each site. Burls, epicormic sprouting, goose pens, and reiterations were more common among larger redwood trees (*fig. 4*). Most redwood trees had one type of distinctive feature and very few trees had all of these features. The natural logarithm of tree dbh was a stronger predictor of the probability of occurrence of distinctive features than either tree height, live crown base height, crown length, or crown radius. The probability of occurrence of epicormic sprouting was greater at Children's and lower at Armstrong when compared with incidence of epicormic sprouting for any given tree size at Rockefeller. Logistic model coefficients indicated that redwood trees at Children's were less likely to have a goose pen than trees of equivalent dbh at either Armstrong or Rockefeller (*table 5*).

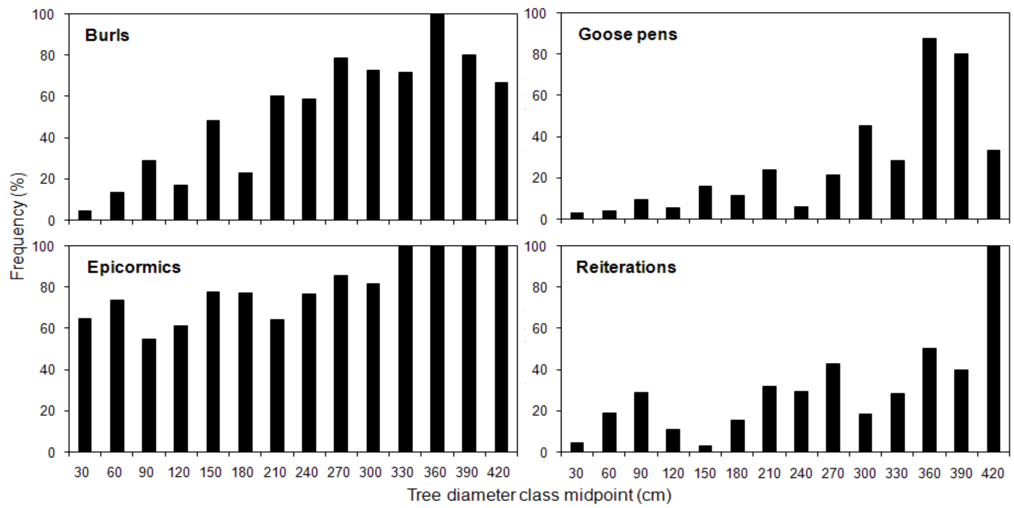

Figure 4—Percentage frequency distribution of redwood trees having a distinctive feature by 30 cm dbh class, based on pooled data from the three alluvial flat old-growth redwood study sites.

Table 5—*Coefficients and fit statistics for logistic model of the presence of burls, epicormic sprouts, goose pens, and reiterations as a function of the natural logarithm of dbh for alluvial flat old-growth redwood trees ≥15 cm dbh (n=394). Dummy variables for study sites were included when differences detected between sites (α=0.05).*

Distinctive Feature	Parameter	Coefficient	s.e.[a]	Wald's χ^2	Pr > χ^2
Burls	Intercept	1.0617	0.15	52.70	<0.0001
(Model -2LL = 346.5)	*Ln* dbh	-1.7086	0.20	76.08	<0.0001
Epicormic sprouts	Intercept	-1.0899	0.13	70.94	<0.0001
(Model -2LL = 438.9)	*Ln* dbh	-0.3871	0.13	9.43	0.0021
	Armstrong	-0.7871	0.16	25.48	<0.0001
	Children's	0.7660	0.19	16.47	<0.0001
	Rockefeller	0.0000	--	--	--
Goose pens	Intercept	2.4330	0.23	107.86	<0.0001
(Model -2LL = 225.8)	*Ln* dbh	-1.7091	0.28	36.91	<0.0001
	Armstrong	0.2623	0.25	1.12	0.2894
	Children's	-0.8022	0.24	11.31	0.0008
	Rockefeller	0.0000	--	--	--
Reiterations	Intercept	1.6237	0.15	123.64	<0.0001
(Model -2LL = 327.1)	*Ln* dbh	-0.8489	0.17	24.51	<0.0001

-2LL = -2 Log Likelihood, measure of goodness of fit.
[a] s.e. = standard error for coefficient.

The number of large fallen logs was similar at Children's and Rockefeller study sites. Logs at Rockefeller were slightly longer and larger in diameter which resulted in almost twice the amount of volume and area covered by logs at Rockefeller (*table 6*). There appeared to be no trend in the direction of tree fall and most of the logs were found to be scattered widely across each site. One exception occurred at Rockefeller. The eastern side of the plot contained a large gap which was created by three large fallen trees that fell in the easterly direction.

Table 6—*Coarse woody debris characteristics for Children's and Rockefeller alluvial flat old-growth redwood study sites. Minimum dimensions of logs sampled were 2 m length and 30 cm midpoint diameter. Standard error for mean log diameter shown in parentheses.*

Site	Density (logs ha^{-1})	Mean diameter (m)	Volume (m^3 ha^{-1})	Cover [a] (%)	Mass [b] (tons ha^{-1})
Children's	14	1.09 (0.12)	570	3.7	114
Rockefeller	19	1.25 (0.17)	1072	6.8	214

[a] Cover represents percent ground area covered by downward projection of logs.
[b] Mass estimated as volume by an averaged wood density from Bingham and Sawyer (1988).

Standing dead trees (snags) ≥ 15 cm dbh appeared to be exclusively redwood at the three sites. The two snags within the plot at Armstrong were 1.5 and 1.6 m dbh. The two snags at Rockefeller were 0.7 and 3.5 m dbh. The eight snags at Children's included four small dead-standing redwood trees (dbh < 40 cm) that appeared to have sustained severe fire damage and died recently. The other four snags at Children's ranged from 0.9 to 2.2 m dbh.

Discussion

Our work provides an important description of structural characteristics in alluvial flat old-growth redwood forests. Density, diameter distribution, crown ratio, and total canopy gap area were most similar among study sites. As such, they may serve as key reference conditions for future restoration treatments (*table 7*).

Table 7—*Reference conditions for alluvial flat old-growth redwood forests.*

Condition	Description
Stand density[a]	Redwood 118-148 trees ha^{-1}
Upper canopy tree density[b]	45-74 trees ha^{-1}; mean dbh 2.1 m; range 0.55-4.27 m dbh
Crown ratio	Trees > 1.5 m dbh: 0.56-0.64; trees ≤ 1.5 m dbh: 0.65
Canopy gap area	17-25% total area in gaps
Coarse woody debris[c]	Density 14-19 logs ha^{-1}; mean midpoint diameter 1.2 m; mean length 26.6 m; cover 3.7-6.8%; mass 114-214 tons ha^{-1}
Snags	2-4 dead standing trees ha^{-1}; range 0.9-3.5 m dbh
Spatial pattern	Random pattern for redwood > 1.5m dbh (Dagley 2008)

[a] Trees ≥ 15 cm dbh.
[b] Dominant and codominant trees.
[c] Logs ≥ 30 cm midpoint diameter and 2 m length.

Similarities between our data and published density data suggest both overall redwood density and upper canopy density can be useful reference points in old forest restoration efforts. Van Pelt and Franklin (2000) reported a main canopy density of 46 trees ha^{-1}. Sugihara (1992) reported an overall redwood density of 182 trees ha^{-1} for trees > 10 cm dbh and a density of 67 trees ha^{-1} for redwood trees > 1.5 m dbh. A redwood density of 107 trees ha^{-1} for trees > 10 cm dbh was reported for a stand located in Prairie Creek Redwoods State Park (Sawyer and others 2000). Fujimori (1977) reported 66 trees ha^{-1} for trees > 1 m dbh.

Stand density index (SDI) is a measure of growing space occupancy, and is useful for quantifying relative density across a wide variety of stand conditions (Long and Daniel 1990). Reineke (1933) reported that the maximum SDI for redwood is approximately 2500 (equivalent to an SDI of 1000 in English units) based on data from even-aged second growth stands. The SDI was highest at Rockefeller, and slightly exceeded the maximum reported by Reineke (1933). This could explain the lower crown ratios among larger trees (*table 3*) and lower regeneration density (*table 4*) at Rockefeller.

Old-growth redwood tree crowns occupy an immense amount of space. Van Pelt and Franklin (2000) reported a canopy volume of 230,100 m^3 ha^{-1} with the maximum occurring at a height of 50 m for a stand on the alluvial flats in Humboldt Redwoods State Park. This value exceeded our estimates (172,992 to 185,070 m^3 ha^{-1}; *table 2*) but was based on a conic representation of tree crown volume. We generated more realistic estimates by describing the shape and fullness of individual tree crowns. Crown shape impacts volume estimation and placement of crown volume in the vertical profile (*fig. 2*). For example, the volume of a parabola is 50 percent greater than that of a cone. When compared with crown volume estimates obtained using a cone shape, canopy volume estimates from this study were 10 m higher in the vertical profile when shape was taken into account. The shape was most often described as a parabola and the average crown fullness was 60 percent.

Total canopy gap area ranged from 17 to 25 percent between sites. These values closely resembled reported values from other old-growth stands ranging from 18 to 20 percent (Busing and Fujimori 2002, Sugihara 1992, Van Pelt and Franklin 2000). Gap size and shape were variable, suggesting that treefall events involved individual trees or groups of trees.

A preference to establish under canopy gaps was not detected among redwood regeneration. Hunter (1995) found the influence of canopy gaps to only account for 4.6 percent of the variation in understory light levels in a mixed evergreen forest (containing redwood) in Northern California. He proposed that several factors limit the effects of canopy gaps on the understory: temperate latitude placing the sun at lower angles, a dry summer season restricting growth when light is at its highest angle in the sky, a tall canopy, and small gap diameters. Van Pelt and Franklin (2000) found no relationship between understory tree location and canopy gaps.

Exposure to wind and windstorm events likely affects stem form. Results from the multivariate discrimant analysis revealed differences in tree height-diameter relations between study sites. Our use of a simple conic shape to estimate stem volume is repeatable, but highlights need for reliable predictive volume and taper equations. Existing equations predict merchantable volume above a tall stump to large top diameters, not total stem volume. Differences in stem taper and incidences of top breakage and reiteration will complicate the task of modeling stem volume and whole-tree biomass: a priority for future research.

Our characterization of coarse woody debris highlighted differences between sites (*table 6*). These differences may in part be due to stand history. Over time, down logs may have been removed for use or aesthetics. Yet, the lowest published estimates remain two to five times greater than those reported for most other temperate or tropical forests (Franklin and Waring 1980). Our estimates of 114 and 214 metric tons ha^{-1} for Children's and Rockefeller, respectively, fall within the range of values reported for alluvial flats (Busing and Fujimori 2005, Sugihara 1992).

The study sites at Armstrong, Children's, and Rockefeller were selected to represent alluvial flat old-growth redwood forests with different site characteristics and/or recent disturbance histories. Our data and analyses revealed that each stand had unique attributes, but also shared features with the other study sites, suggesting that these commonalities could represent general reference conditions or "targets" for future restoration efforts (*table 7*). For example, managers seeking to accelerate development of old-growth characteristics in a young stand might begin by identifying approximately 50 to 80 overstory trees ha^{-1} in a random spatial arrangement, and releasing these trees from competition. Retaining more trees would allow for artificial creation of 2 to 4 snags ha^{-1} in the absence of natural mortality. Concurrently identifying one or more open areas to serve as large canopy gaps between overstory tree crowns might preclude future conflict between overstory tree density and canopy gap area requirements. Less regard, at least initially, might be paid to structural parameters or distinctive characteristics that differed between the three reference sites or that correlated with tree size. When combined with descriptions of the spatial pattern of tree locations within stands (Dagley 2008), this work represents a detailed quantitative description of the three dimensional structure and complexity found in old-growth redwood forests on alluvial flats.

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