

Coast Redwood Live Crown and Sapwood Dynamics

John-Pascal Berrill,¹ Jesse L. Jeffress,¹ and Jessica M. Engle¹

Abstract

Understanding crown rise and sapwood taper will help meet management objectives such as producing long branch-free boles for clear wood and old-growth restoration, or producing sawlogs with a high proportion of heartwood. Coast redwood (*Sequoia sempervirens*) tree crown ratio data were collected 20 years after partial harvesting in a 65-year-old second growth stand. Crown ratio correlated with stand density and relative tree height, and differed between stand interior and edge locations. The sum of tree crown lengths in each plot gave crown length/ac which exhibited an asymptotic relationship with stand density (i.e., crown length/ac peaks at higher densities). Maximum crown length/ac can be used to constrain simulations of crown rise by limiting the increase in crown length following thinning. Sapwood cross-sectional area was sampled at breast height and at the base of the live crown (BLC) of redwood trees growing in northern, central, and southern portions of redwood's natural range. Variability in sapwood area taper prevented detection of significant differences between regions, but on average sapwood tapered most rapidly among northern trees and least among southern trees. We present a robust sapwood taper model derived from the power function that has the desirable property of predicting zero taper for trees with BLC at breast height. Models predicting sapwood area at breast height from DBH allow prediction of sapwood from forest inventory data. Results indicated that dominant and codominant trees in the northern region had more sapwood than trees of similar size growing in the hotter, drier southern region.

Key words: crown ratio, crown rise, heartwood, leaf area, live crown ratio, sapwood taper, *Sequoia sempervirens*

Introduction

Contemporary management objectives for young coast redwood stands include old-growth restoration and clear wood and heartwood production. Distinguishing characteristics of old-growth forests include long branch-free boles. These can be re-created by artificial pruning, or by manipulating stand density to control crown rise. Crown height and size affect tree growth which largely comprises sapwood and heartwood development. Understanding the impacts of stand density on crown rise and its relationship with tree size, sapwood, and heartwood content permits us to design density management regimes for aesthetic and wood quality objectives. For example, it may be worthwhile to sacrifice tree diameter development to induce crown rise and produce valuable knot-free heartwood with narrower growth rings.

Crown rise in monospecific plantations of loblolly pine (*Pinus taeda*) and Sitka spruce (*Picea sitchensis*) has been predicted successfully using estimates of average tree height and either tree count per unit area or average inter-tree distance (Valentine

¹Assistant Professor and undergraduate students, respectively, Department of Forestry and Wildland Resources, Humboldt State University, 1 Harpst St, Arcata, CA 95521. (pberrill@humboldt.edu).

et al. 1994). The same variables correlated with crown length in old-growth spruce-fir forests in British Columbia (Antos et al. 2010). Tree size and stand density measures, and topographic site factors were useful predictors of crown ratio throughout the forests of Austria, where crown ratio differed between species and was most affected by competition (Hasenauer and Monserud 1996). Norway spruce (*Picea abies*) crown ratio and crown length varied between age groups and were affected by thinning (Kantola and Mäkelä 2004).

Estimates of tree crown leaf area for individual trees and forest stands are useful predictors of tree growth and forest productivity in terms of tree growth efficiency (defined as the ratio of stem wood production to total leaf area), net primary productivity, and carbon sequestration. Growth efficiency can be used as a reference for a stand's susceptibility to disease or insect attack or for other trends in forest health (Maguire and Batista 1996). The relationship between redwood tree growth, growth efficiency, and tree leaf area is affected by stand structure and the tree crown's position within the stand (Berrill and O'Hara 2007a). Therefore redwood stand density and structure can be manipulated to affect leaf area, stand growth, and tree size at harvest (Berrill and O'Hara 2007b, 2009). The pipe model theory (Shinozaki and others 1964) proposes that a given amount of foliage is supported by a proportional cross-sectional area of 'pipes', i.e., a close functional relationship exists between sapwood area (SA) and leaf area (LA). Sapwood area at the base of the live crown (SA_{BLC}) is more strongly correlated with leaf area than sapwood area at breast height (SA_{BH}) (Waring et al. 1982). A taper model predicting SA_{BLC} from measured SA_{BH} will improve leaf area estimates (Waring et al. 1982). The existing sapwood taper model for redwood was constructed using data for second-growth trees of varying size in different canopy positions within stands in the central portion of redwood's natural range (Stancioiu and O'Hara 2005).

We examined crown ratio data for redwood trees in the central portion of redwood's natural range and sapwood area among redwood trees in the southern, central, and northern parts of the range. Our objectives were to:

- (i) Develop models that predict redwood crown ratio in managed and unmanaged stands.
- (ii) Construct an equation that predicts SA_{BLC} for the southern, central, and northern regions, and test for regional differences in sapwood taper.
- (iii) Model SA_{BH} as a function of diameter at breast height (DBH) to enable prediction of SA_{BH} and SA_{BLC} from traditional forest inventory data.

Methods

Crown ratio data were collected in 234 permanent sample plots within the 260 ac Railroad Gulch Harvest Demonstration Area on Jackson Demonstration State Forest (JDSF), near Ft. Bragg in Mendocino County, north coastal California. After clearcutting in 1920, a mixture of redwood, Douglas-fir (*Pseudotsuga menziesii*) and tanoak (*Notholithocarpus densiflorus*) regenerated naturally, supplemented by planting of redwood seedlings. In 1982, tenth-acre plots were established on a grid pattern across the 260 ac demonstration area. Then, the area was divided into 14 blocks: individual tree selection was applied in four 20 ac treatment blocks, group selection applied in four 20 ac blocks, and a combination of both regeneration

methods was applied in four 20 ac blocks. Two smaller blocks were reserved as ‘no treatment’ control areas. The plots have been measured three times at 10 year intervals. Tree measurements included DBH, total height, and height to BLC.

Sapwood data from the southern portion of redwood’s range were collected at five sites between Santa Clara County and Napa County. These were relatively hot and dry redwood sites, being located near the inland limits of redwood’s range (*fig. 1*). Sapwood data for the central region were obtained from a previous study on JDSF (Stancioiu and O’Hara 2005). Two study sites were chosen for sampling in the northern region: Arcata Community Forest and Freshwater Forest, near Humboldt Bay in Humboldt County. The northern sites are shrouded in fog for much of the growing season, and have an average mid-summer daytime high temperature of only 64 °F. Summer fog generally dissipates during the daytime at the central sites in Mendocino County, and average summer high temperatures exceed the value of 67 °F reported for the weather station at the coast. At all study sites, most rainfall occurs between November and March. Mean annual precipitation is approximately 40 in at the northern and central sites and at the inland Napa County site (Las Posadas State Forest). However, we categorized the Napa site as ‘southern’ because it receives less fog and its summer temperatures are much higher (86 °F in July), much like the other southern sites (76 to 88 °F). Annual precipitation averaged approximately 21 in at Gilroy near sampling sites at Bodfish Canyon and Mt Madonna in Santa Clara County and 26 in at Roberts and Redwood Regional Parks in Alameda and Contra Costa Counties, respectively (<http://www.weather.com>).



Figure 1—Natural range of coast redwood and study site locations for northern, central, and southern regions.

Dominant and co-dominant redwood trees approximately 80 to 130 years old and about 110 ft tall were selected for sapwood measurement in the northern and southern regions: 19 trees from the two northern sites and 18 trees from the five southern sites. Trees were climbed using a flip line and spurs. Total height and height to BLC were measured, where the lowest living vigorous branch defined BLC (whereby excluding epicormic branches found lower on the stem). Diameter at BLC and DBH were measured with a steel tape. Two increment cores were taken at both breast height and BLC. Bark thickness measurements were taken at the site of each increment core. The point of transition from translucent live sapwood to dry sapwood adjacent to the red-colored heartwood was marked on each core. Live sapwood radial bandwidths including the vascular cambium were measured using calipers. Data for 10 trees in the central region were obtained from a destructive sample of cross-sectional discs cut from felled trees (Stancioiu and O'Hara 2005).

Analysis of crown ratio involved separating tree size and crown data from the most recent measurement at Railroad Gulch into damage classes: top damaged, forked, and undamaged (no top damage or forking). Differences in crown ratio between damage classes justified exclusion of damaged trees. Tree data were also separated into two crown class groups: dominant and codominant trees, and intermediate and suppressed trees, and summarized for each group. Differences in crown ratio between groups justified separate analysis of crown class groups. Too few dominant tree data were available to model data for individual crown classes. Data for height to BLC, crown length, crown ratio, and height – diameter ratio were regressed against redwood stand density index (SDI). Estimates of redwood SDI were obtained using an SDI-adjustment procedure where a new plot area was calculated for the redwood component growing in mixture within a sample plot. The ratio of redwood component SDI to plot SDI gave an estimate of the proportion of total growing space occupied by redwood within each plot. This ratio was applied to the plot area, giving an estimate of area occupied by redwood. This 'SDI-adjusted' redwood plot area was used to calculate stand-level estimates of average tree size, basal area, and SDI for redwood. Generalized linear mixed models were constructed to account for nesting of trees within plots within harvest treatment blocks. The models were fitted to crown ratio data for individual redwood trees from each crown class group using PROC GLIMMIX in SAS statistical analysis software (SAS Institute 2004). The effects of topographic and species composition variables on crown ratio were tested. A dummy variable for stand edge versus interior locations, and relative height – the height of a tree relative to the crown class group average – were also tested as explanatory variables. Tree height and crown data from previous measurements at Railroad Gulch were not amenable to crown ratio modeling, but pre-harvest species composition and stand density estimates were included in the crown ratio analysis. Random effects in the mixed models were plot and treatment block. Crown length was summed in each plot, giving total redwood crown length/ac. Crown length/ac estimates were binned in increments of stand density (for example SDI 50 to 150, 150 to 250, and so forth), and an approximation of their upper limit (99th percentile) regressed against SDI using PROC REG in SAS. This relationship was assumed to represent an approximate upper limit to average tree crown length for redwood in managed and unmanaged stands, for use constraining crown rise simulations within realistic limits.

Preparing data for sapwood analysis involved calculating heartwood diameter by subtracting the average live sapwood bandwidth from the total diameter inside bark

(DIB). Both DIB and heartwood diameter were converted to area. Sapwood cross-sectional area (SA) for breast height and BLC were determined by subtracting heartwood area from basal area inside bark. Sapwood taper equations were fitted to sapwood data from each region using the non-linear regression analysis procedure PROC NLIN in SAS. The taper models predict SA_{BLC} as a function of SA_{BH} and breast height crown ratio (BHCR, defined as crown length/ (total height – 4.5ft)) for each region, and for all regions combined. Equations that predict SA_{BH} as a function of tree basal area were also fitted to sapwood and tree size data from each region using the linear regression analysis procedure PROC REG in SAS.

Results

Crown rise

Of the 2,894 second-growth redwood trees within 234 plots at Railroad Gulch, 69 percent did not show signs of forking or top damage, and 41 percent were classified as either dominant or codominant. Forty-four percent of intermediate and suppressed trees were forked or exhibited top damage. Among dominants and codominants, forked trees had the highest average crown ratios. Trees with top damage had lower crown ratios than other trees in the intermediate and suppressed crown class group (table 1). Therefore, trees with forks or top damage were excluded from analyses of crown ratio. Redwood tree and crown size varied according to position within the canopy (table 2). On average, edge trees were larger, more tapered, and had longer crowns than trees growing inside the stand (fig. 2). Average crown ratio among dominant and codominant trees in each plot decreased with increasing crowding (SDI). Dominant and codominant trees in plots with higher redwood SDI had higher crown base heights and less taper, but maintained similar live crown lengths to redwood trees growing in less crowded conditions (fig. 3).

Table 1—Damage summary: count and crown ratio of second-growth redwood trees classified as either dominant or codominant (D+C), or intermediate or suppressed (I+S), with and without forking or top damage, at Railroad Gulch, JDSF.

	Number of trees			Crown ratio		
	D+C	I+S	All trees	D+C	I+S	All trees
Forked trees	40	52	92	0.48	0.35	0.41
Trees with top damage	129	732	861	0.42	0.30	0.32
Forked and top damage	156	754	910	0.44	0.30	0.33
No forking or top damage	1040	944	1984	0.43	0.36	0.39
All trees (incl. damaged)	1196	1698	2894	0.43	0.33	0.37

Table 2—Tree size and crown summary data for second-growth redwood trees without forking or top damage at Railroad Gulch, JDSF. Standard deviations listed in parentheses beside means for each crown class.

Crown class	n	DBH (in)	HT (ft)	H:D ratio ^a	BLC (ft) ^b	Crown ratio
Dominant	28	33.6 (9.2)	131.1 (18.1)	49.2 (09.9)	64.3 (14.3)	0.50 (0.11)
Codominant	1012	23.5 (5.9)	117.1 (20.6)	61.9 (11.9)	66.6 (16.0)	0.43 (0.11)
Intermediate	445	14.0 (4.8)	77.1 (23.1)	68.3 (16.0)	46.0 (17.5)	0.40 (0.15)
Suppressed	499	7.0 (4.2)	38.5 (17.7)	73.4 (23.5)	26.0 (12.3)	0.31 (0.15)

^aH:D ratio = ratio of total height (ft) to diameter at breast height (ft).

^bBLC = height to base of live crown.

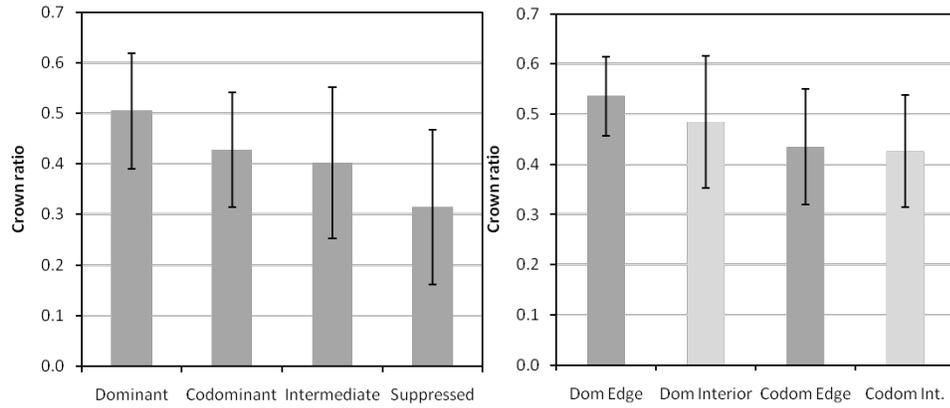


Figure 2—Average crown ratio for each crown class (left), and for dominant and codominant second-growth redwood trees growing on stand edges and inside the stand (right) at Railroad Gulch, JDSF. Error bars depict standard deviation for each group mean.

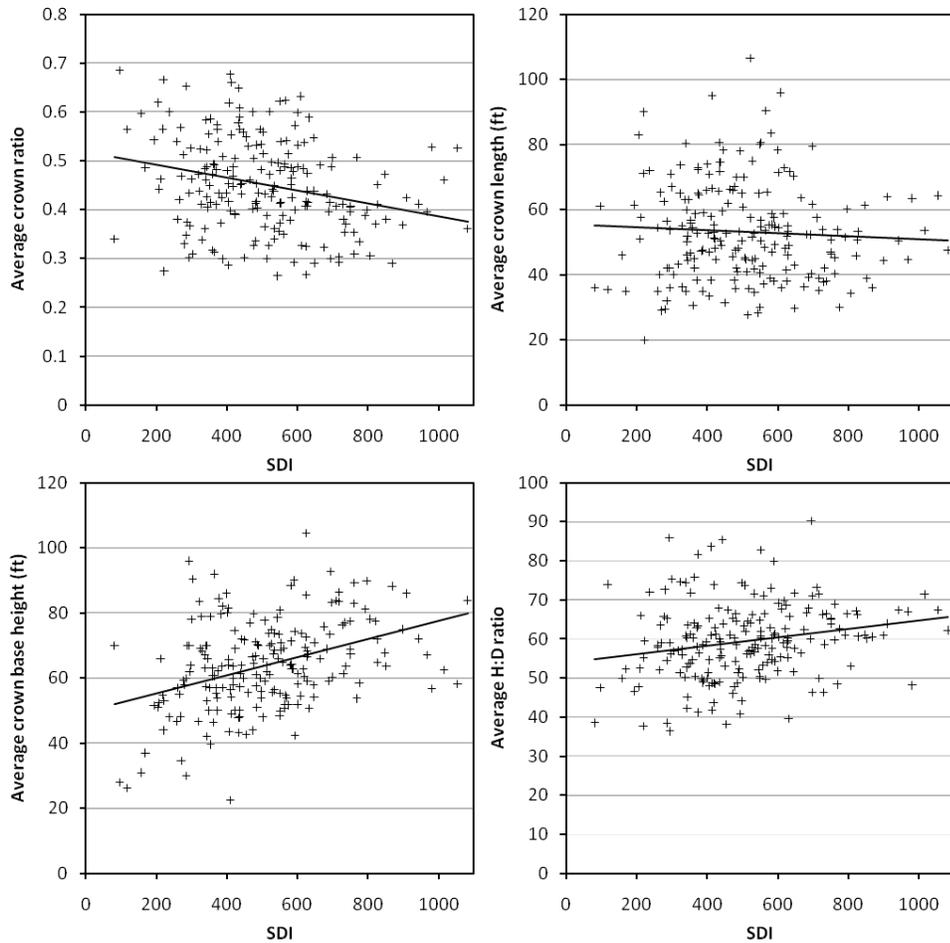


Figure 3—Average crown and stem taper data for dominant and codominant second-growth redwood trees and redwood stand density index (SDI) in 203 plots at Railroad Gulch, JDSF.

Species composition, aspect, and site index did not significantly affect redwood tree crown ratio. Dominant and codominant redwood crown ratios were slightly lower in plots with more Douglas-fir basal area, and slightly higher in plots with aspects tending towards northeast and in plots with higher site index, but these effects were not significant ($Pr > t$ 0.49, 0.13, 0.46, respectively). Redwood crown ratio was unaffected by pre-harvest and current percent hardwood basal area and percent slope. Crown ratio was higher with greater relative height (height relative to average height of trees in each crown class group), and lower with increasing redwood SDI (fig. 4). The best crown ratio models in terms of AIC (goodness-of-fit criterion favoring models with fewer variables) included only tree location (edge or interior) and SDI (table 3). Model predictions indicated that tree location was a more important determinant of crown ratio among intermediate and suppressed trees than among dominants and codominants. The effects of relative height were important among trees in both crown class groups.

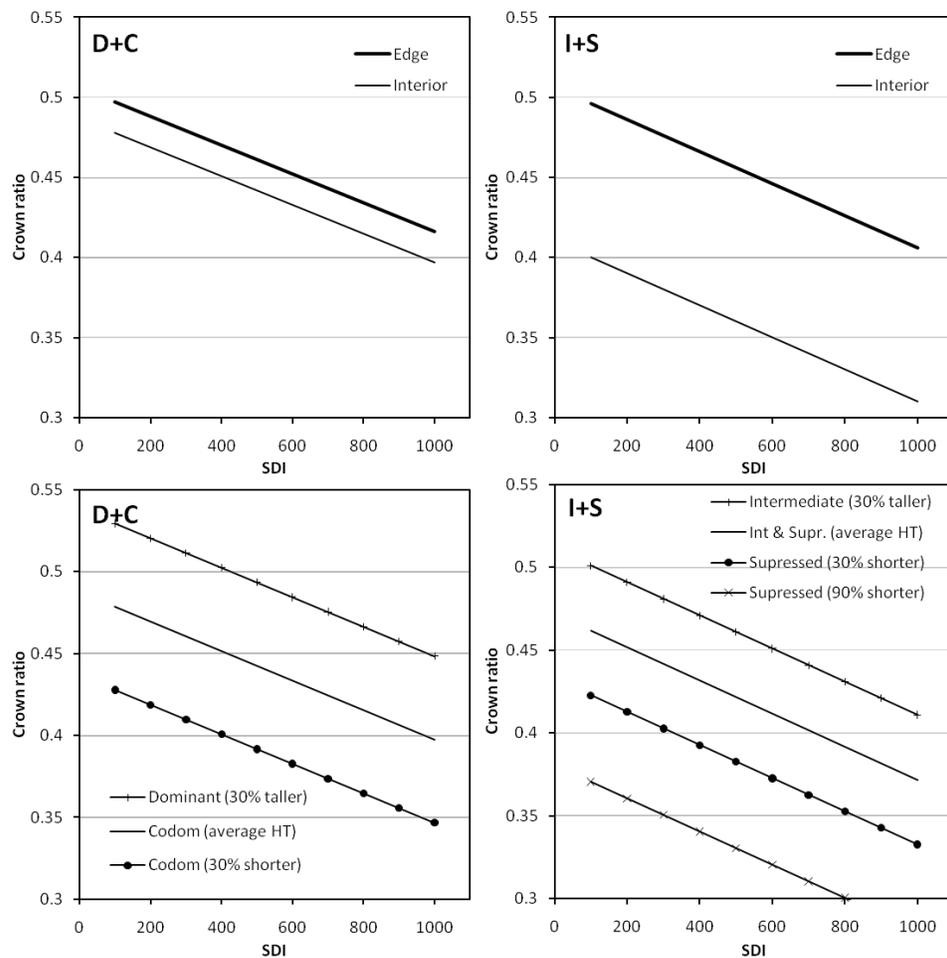


Figure 4—Generalized linear mixed model predictions of redwood crown ratio among dominant and codominant (D+C) trees and intermediate and suppressed trees (I+S) in stand edge and interior locations (above), and for interior trees with different relative heights (below), at Railroad Gulch, JDSF.

The approximate upper limit of the per-acre sum of redwood tree crown lengths in each plot attained 13,000 ft/ac at SDI 1000. The relationship was best described by a second-order polynomial equation (fig. 5).

Table 3—Generalized linear mixed effects models of redwood crown ratio as a function of tree location (stand edge, interior) and stand density index (SDI), with/without relative height (above/below), for dominant and codominant (D+C) and intermediate and suppressed (I+S) crown class groups at Railroad Gulch. Dummy variable for edge location is added to intercept; interior location is latent variable (intercept only).

Data	Model fit	Parameter	Coefficient	s.e.	d.f.	t	Pr> t
D+C (n=1028)	$\chi^2 = 10.19$ AIC=-1709	Intercept (β_0)	0.31800	0.03426	13	9.28	<.0001
		Edge (d_1)	0.01820	0.00926	987	1.96	0.0497
		Relative height (β_1)	0.16960	0.02980	987	5.69	<.0001
		SDI (β_2)	-0.00009	0.00002	987	-4.47	<.0001
I+S (n=900)	$\chi^2 = 15.15$ AIC=-1011	Intercept (β_0)	0.34130	0.02655	13	12.86	<.0001
		Edge (d_1)	0.08437	0.01452	859	5.81	<.0001
		Relative height (β_1)	0.13050	0.01857	859	7.03	<.0001
		SDI (β_2)	-0.00010	0.00003	859	-3.35	0.0008
D+C (n=1028)	$\chi^2 = 10.52$ AIC=-1682	Intercept (β_0)	0.48700	0.01721	13	28.29	<.0001
		Edge (d_1)	0.01917	0.00940	988	2.04	0.0417
		SDI (β_1)	-0.00009	0.00002	988	-4.38	<.0001
I+S (n=900)	$\chi^2 = 16.02$ AIC=-969	Intercept (β_0)	0.41040	0.02498	13	16.43	<.0001
		Edge (d_1)	0.09567	0.01482	860	6.46	<.0001
		SDI (β_1)	-0.00010	0.00003	860	-3.59	0.0004

Relative height = tree height/average height for crown class group.

χ^2 = generalized chi-square for model.

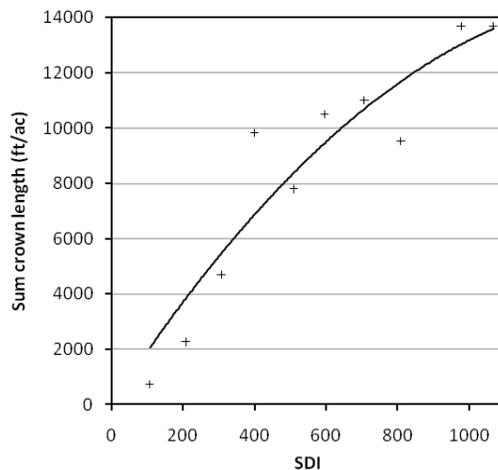


Figure 5—Relationship between 99th percentile of crown length/ac in plots grouped by SDI and the average SDI for each group, where crown length/ac = $19.832 \text{ SDI} - 0.0067 \text{ SDI}^2$.

Sapwood taper

Northern and southern sample trees were larger than trees from the central region where a wide range of tree sizes were sampled across all crown classes (table 4). Different taper model coefficients for region-specific models indicated that, on average, northern trees exhibited greater sapwood taper between breast height and

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BLC (table 5, fig. 6). However, variability in sapwood taper within regions prevented detection of significant differences in taper between the different regions, justifying a combined model for the entire redwood range. When re-arranged to predict SA_{BLC} as a function of SA_{BH} , the non-linear power model gave a mean prediction error of 4.4 $in^2 SA_{BLC}$ for $n = 47$ trees from northern, central, and southern regions.

Table 4—Summary data for redwood sapwood sample trees by region.

Region	Statistics	DBH (in)	Height (ft)	BHCR ^a	SA_{BH} (in ²)	SA_{BLC} (in ²)
Northern (n=19)	Mean	31.1	115.8	0.73	179.5	122.7
	s.d.	7.5	24.6	0.11	69.4	47.8
	Max.	51.4	158.8	0.93	304.6	204.2
	Min.	19.4	75.1	0.49	84.0	54.7
Central (n=10)	Mean	13.6	78.1	0.68	59.3	41.2
	s.d.	10.3	42.6	0.13	73.3	52.9
	Max.	36.5	148.3	0.84	248.3	179.5
	Min.	3.7	27.9	0.50	8.3	6.9
Southern (n=18)	Mean	29.1	111.8	0.56	113.4	69.3
	s.d.	6.9	21.6	0.12	45.4	34.1
	Max.	43.4	163.0	0.76	215.4	137.0
	Min.	18.5	71.5	0.37	52.7	27.2

^aBHCR = breast height crown ratio; crown length/(total height - 4.5 ft).

Table 5—Summary statistics for sapwood taper model $SA_{BLC} = SA_{BH} * (1-(1-BHCR)^a)$.

Location	Coefficient	s.e.	Appr. 95% confidence limits	
			Lower	Upper
Southern	1.1549	0.1123	0.9180	1.3917
Central	1.0776	0.0771	0.9031	1.2521
Northern	0.9020	0.0737	0.7471	1.0569
Combined	1.0362	0.0565	0.9224	1.1499

Regional coefficients for linear models fitted to tree basal area and SA_{BH} data were separated by greater than two standard errors (north: $\beta_1 = 0.20611$ s.e. = 0.015; south: $\beta_1 = 0.15058$ s.e. = 0.012), indicating that, on average, northern trees contained relatively more sapwood than southern trees for a given DBH. The models for northern and southern trees were compared against the model presented by Berrill and O'Hara (2007a) for 891 redwood trees >4 in DBH growing in all canopy positions within even-aged and multiaged stands on JDSF. Predicted sapwood at breast height for dominant and codominant sample trees from the northern and southern regions exceeded the published $SA_{BH} - BA$ model predictions (fig. 6).

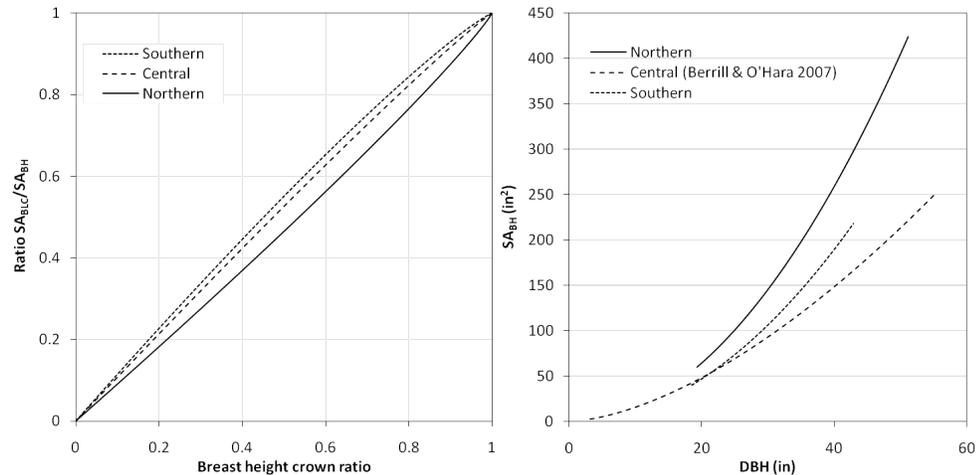


Figure 6—Sapwood taper models for northern, central, and southern regions $SA_{BLC}/SA_{BH} = 1-(1-BHCR)^a$ (left), and $SA_{BH} - DBH$ relations for northern and southern regions $SA_{BH}=0.155 a \pi (1.27 DBH)^2$ and existing model for the central region (Berrill and O'Hara 2007a) (right).

Discussion

Greater incidence of top damage sustained by relatively short redwood trees at Railroad Gulch reminds us that care must be taken to protect residual trees and advanced regeneration during partial harvesting. Damage rates reported in *table 1* include damage from natural causes and harvesting, and could be used to estimate number of replacement trees required in younger cohorts under multiaged management. Retaining more replacement trees in younger cohorts leaves less growing space for other trees within multiaged stand structures (Berrill and O'Hara 2009).

The crown ratio models apply to redwood trees in the oldest cohort of uncut and partially cut second-growth stands around age 85 years at Railroad Gulch. Plots with lower SDI had total crown lengths/ac below the curve for maximum crown length (*fig. 5*) suggesting that maximum crown length had not been attained 20 years after partial harvesting. Therefore the crown ratio model slope coefficients for SDI may be too low, and should be revised after future re-measurements. The models can be applied to simulate crown rise in managed stands using a bi-conditional approach where crowns do not rise until sometime after partial harvesting when crown length/ac approaches the upper limit (*fig. 5*), after which time crown ratio can be predicted from SDI (*table 3*). The relationships between stand density and tree taper, crown length and height, and crown ratio among dominant and codominant trees (*fig. 3*) may be explained by 'plasticity' in redwood physiology. Trees in crowded plots may have responded with increased allocation of energy to height growth, at the expense of diameter growth, resulting in reduced taper. While tempting to infer that redwood trees can maintain a long live crown under crowded conditions, it is more likely that winners and losers had emerged; that loss of crown length resulting from crowding (*fig. 4*) eventually led less competitive trees to relinquish their dominance within the canopy.

Redwoods regulate water use poorly (Burgess and Dawson 2004). We found that, on average, southern trees in hotter, drier climates had less SA_{BH} for a given tree size but a lower rate of sapwood taper above breast height (*fig. 6*). These differences may reflect on adaptation to conserve water resources in drier climates by restricting sap flow. If the current trend of decreasing fog (Johnstone and Dawson 2010) continues, central and northern redwood trees may respond to increased evaporative demand by altering sapwood dimensions and crown morphology. Our sapwood taper sampling controlled for tree size and crown class between northern and southern regions, focusing on large dominant and codominant redwood. Faster growth in the north meant that sample trees were younger than trees of equivalent size in the south. Apparent differences in sapwood taper between regions (*fig. 6*) could be age-related. A large sample would be needed to examine effects of tree age, size, and position within the stand.

We present a non-linear power model of sapwood taper that provides a more realistic depiction of sapwood taper than the existing model, $SA_{BLC} = 0.7460SA_{BH} - 3.8293(H_{BLC} - 1.37)$ (Stancioiu and O'Hara 2005). The published model predicts negative values for SA_{BLC} for trees with small SA_{BH} , while our model makes realistic predictions for trees of all SA_{BH} and BHCR. Predicting SA_{BLC} as a function of BHCR in the non-linear model has the desirable property that when BHCR = 1, the BLC is at breast height and, therefore, $SA_{BLC} = SA_{BH}$, making negative predictions for SA_{BLC} impossible. We also developed models to facilitate implementation of the taper model by predicting SA_{BH} from DBH (*fig. 6*), but these only apply to large dominant and codominant trees (*table 4*), whereas the model presented by Berrill and O'Hara (2007a) applies to a wider range of tree sizes and growing conditions. When applied in combination, crown ratio and sapwood models can be used to predict SA_{BLC} from traditional forest inventory data. First, SA_{BH} can be predicted from DBH. Then, the sapwood taper model can be applied to the estimate of SA_{BH} , and BHCR calculated from tree height and BLC data or crown ratio model predictions, giving predicted SA_{BLC} , which in turn allows for prediction of tree leaf area and stand LAI.

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