

Article

Bark Thickness in Coast Redwood (*Sequoia sempervirens* (D.Don) Endl.) Varies According to Tree- and Crown Size, Stand Structure, Latitude and Genotype

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Abstract: *Research Highlights:* Bark thickness (BT) in coastal redwood (*Sequoia sempervirens* (D.Don) Endl.) varies in accordance with tree size, crown ratio, position within the canopy, height along the tree stem, genetic identity and latitude. However, current BT predictive equations do not account for such variability, leading to inaccurate BT estimations. We present improved BT models to increase the accuracy of BT estimates for coastal redwood in northern California. *Background and Objectives:* BT is an important metric that has many practical applications in forest management. However, BT varies substantially across species and environments, as well as across individuals and populations. Our objectives were to investigate BT along various gradients of change, with factors accounting for genetics, tapering of BT along the tree bole, differences in BT according to tree crown position within the stand, and the latitude. *Materials and Methods:* We collected BT data throughout most of redwood's natural range along a north–south latitudinal gradient. Subsets of these data were used to examine the influence of particular variables on BT while holding the other variables constant. *Results:* Regionally, the bark was thicker among more xeric southern redwoods and thinner among more mesic northern redwoods. We found that the BT of codominant, intermediate and suppressed trees was around 8%, 14%, and 18% thicker, respectively, than bark of the same size dominant tree. Redwood trees growing in the partial shade of an overstory had thicker bark than trees growing in even-aged stands and incorporating genetic identity yielded major improvements in the BT model estimates, suggesting that BT is under genetic control. Bark thickness decreased with increasing height along the tree stem, with notable differences in the BT above and below breast height. *Conclusions:* We recommend utilizing the best available BT equations (over standard 'bark factors') in forest science, modeling and management applications. We also recommend the adoption of our drilling method for BT measurement on larger trees due to the potential for error associated with traditional bark gauge measurements.

Keywords: bark factor; bark ratio; bark model; tree allometry; uneven-aged silviculture

1. Introduction

Understanding how the thickness of tree bark varies within and among trees has practical application in forest science and management. Bark thickness (BT) informs fire science research topics such as modeling post-fire tree mortality because trees with thicker bark are generally more resistant [1]. Dendrochronology researchers studying tree rings can use BT equations to reconstruct historical BT

for every year the tree was alive [2]. Forest scientists and managers are interested in quantifying tree stem wood volume inside bark from measurements taken outside the bark, without destructive sampling [3–5]. Forest managers contemplating commercial thinning in young stands need estimates of the inside-bark diameter of logs to ensure that cut trees will yield logs meeting merchantability specifications for minimum small-end diameter [6]. In these instances, to derive inside-bark dimensions of wood in trees, we can subtract predictions from BT equations from outside-bark data or model estimates [7,8].

There is also interest in identifying factors influencing BT and how these might be altered by forest management activities. It could be advantageous to enhance BT in fire-prone areas, or reduce BT if this resulted in a concomitant increase in wood production. Tree bark is considered a ‘defense feature’ that encases living tissues and shields them from external biotic and abiotic forces [9]. A tree’s allocation of resources to growth versus defense features such as bark will vary among species [10,11]. The strong correlation between tree size and BT signals potential to increase BT by thinning to enhance the tree diameter growth. However, there is some evidence that slower growing trees have a thicker bark relative to their diameter, suggesting that BT is also dependent on tree age [12]. Site quality and soil fertility may influence BT directly, or indirectly by affecting the tree growth rates [13]. Similarly, BT may be controlled indirectly by stand density which influences the tree growth and form and can be altered by forest management [14]. Substantial within-stand variability in tree BT-diameter relationships [9] suggests that additional factors such as genetics are affecting or controlling BT. If BT is under genetic control, there is potential for selection and tree breeding to enhance or reduce BT. If trees from certain regions have thicker or thinner bark gradients [5], we might make selections from these populations in an attempt to produce planting stock with desirable BT. Trees in other parts of California have shown a latitude gradient in BT [9], but this has not been studied in the coast redwood (*Sequoia sempervirens* (D.Don) Endl.) forests of north coastal California.

Redwood is a shade-tolerant species with morphological plasticity that enables it to respond to disturbances and quickly reoccupy growing space [15,16]. Shade tolerance enables suppressed redwood trees to persist in low light, but grow slowly [17]. It is not known whether these suppressed trees have increasing BT with advancing age despite slow diameter growth [18]. Conversely, dominant redwood trees have large crowns intercepting much direct sunlight and exhibit high volume growth efficiency [19], but may have low BT relative to their diameter. Moreover, it is also unknown how redwood BT changes along the length of a tree bole. This information would enable individual logs or standing trees to be more accurately scaled and valued, increasing economic efficiency [20]. While there are published studies correlating BT to tree diameter [21–24], there is comparatively little research which also includes assessments of other candidate factors such as genetics, the tapering of BT along the tree bole, different BT according to tree crown position within the stand and trends in BT according to latitude along the long, narrow north–south range of redwood in northern California.

The objective of our study was to quantify BT along various gradients of change. We hypothesized that redwood BT varied principally according to tree size and height above ground, but also varied according to genetics, crown size, crown position, stand structure and latitude. Specifically, we expected BT to be: (i) less variable within than among distinct genotypes represented by multiple sprouts sharing a root system; (ii) greater at southern latitudes, either due to slower growth on these more xeric sites or as an adaptation to more frequent fire; (iii) greater among older trees in multiaged stands (two or more age classes), where trees underwent some degree of height suppression during their time in the understory, relative to even-aged stands where young trees grow rapidly in full sun with less time to develop thick bark; (iv) greater for older trees of any given size in multiaged stands; and (v) declining exponentially with increasing height above ground.

2. Materials and Methods

We collected BT data throughout most of redwood’s natural range, from Humboldt County in the north, Mendocino County in the center of redwood’s range, down to multiple counties at the

southern end of the range (Figure 1, Table 1). Subsets of these data were used to examine the influence of particular variables on BT while other influential variables were held constant. We held age constant to test for genetic effects in terms of differences in the BT among sprout clumps in the same stand. Crown class was also held constant to test for regional differences among stands in the north, central, and southern parts of redwood's natural range. We studied stand structure and age effects in data from one region, and the tapering of bark along the stem in a single forest. For the purposes of this study, we use the term tree bark in reference to various tissues including the inner living phloem and dead outer tissue [25]. We use the term BT to refer to the radial linear thickness measurement of all materials outside the xylem, i.e., the combination of cellular structures from inside the cambium layer to the outside of the exterior bark.

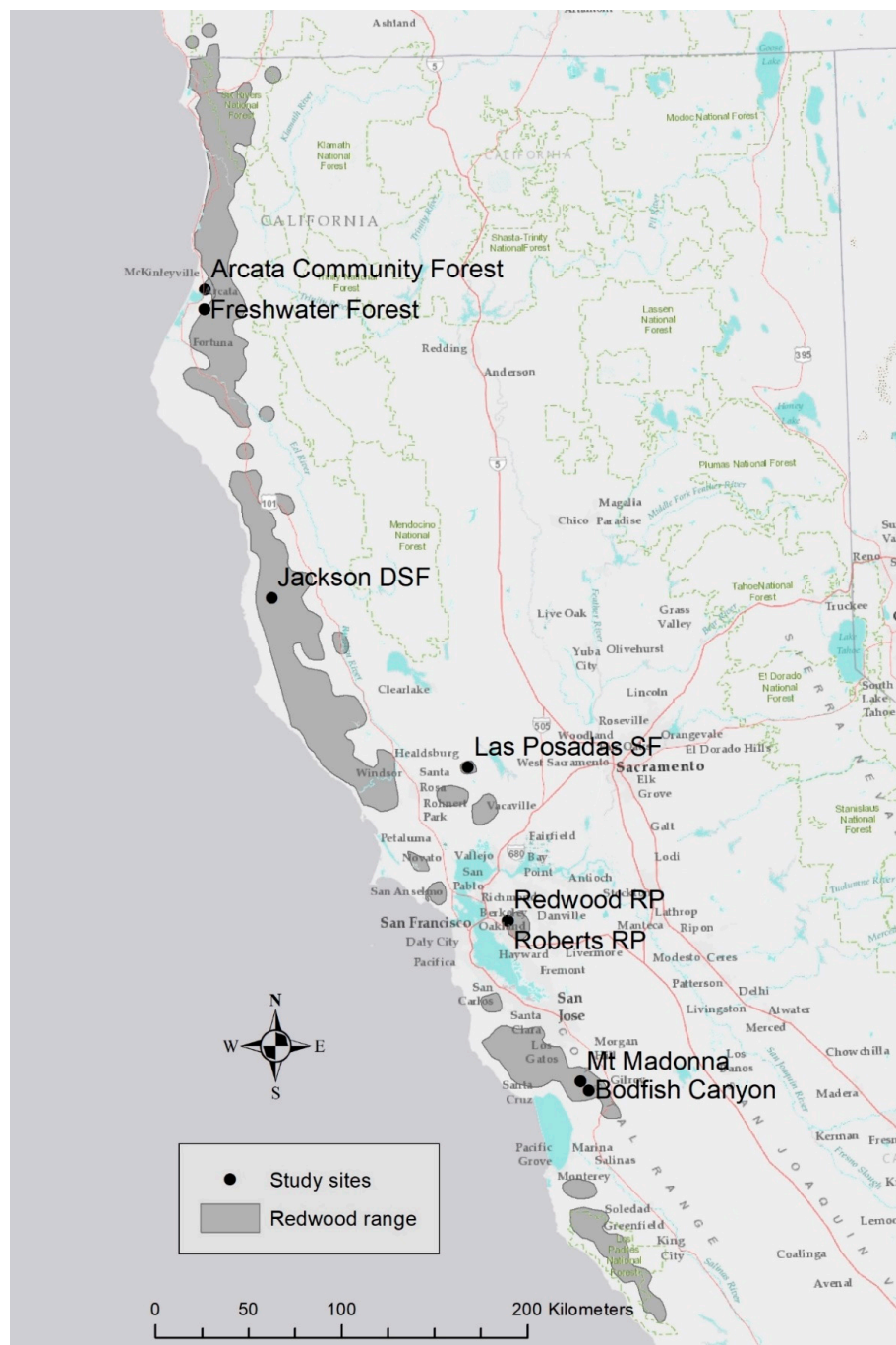


Figure 1. Study sites and approximate range of redwood in northern California and southern Oregon.

Table 1. Redwood bark thickness study site location information.

Site	County	Latitude	Longitude	Elevation (m)
Arcata Community Forest	Humboldt	40.872169	−124.070013	100
Freshwater Forest	Humboldt	40.776107	−124.072185	27
Jackson Demonstration State F.	Mendocino	39.380276	−123.631004	229
Las Posadas State Forest	Napa	38.559367	−122.410412	404
Roberts Regional Park	Alameda	37.813329	−122.175263	444
Redwood Regional Park	Alameda	37.814919	−122.171610	447
Mt. Madonna	Santa Clara	37.030449	−121.740942	618
Bodfish Canyon	Santa Clara	36.984844	−121.692426	399

2.1. Data for Analysis of Clonal Effects

Jackson Demonstration State Forest (JDSF) is a 20,000 ha redwood-dominated forest managed for research and demonstration objectives using a variety of silvicultural prescriptions. A history of forest management activity has created an assortment of stand structures and age classes available for observational studies. Centrally located in Mendocino County, JDSF has a climate that is intermediate between more mesic northern redwood forests to the north, and more xeric conditions further south and inland. The Mediterranean climate is characterized by warm dry summers, and wet cool winters. Coastal fog regularly extends inland from the Pacific Coast and has a cooling effect throughout the growing season.

In three stands on JDSF, a well stocked area dominated by redwood was selected for measurement. A large rectangular 0.2 ha sample block was established. All trees greater than 10 cm in diameter at 1.37 m breast height (DBH) were mapped and measured for DBH, total height and height to the live crown base—defined as stem height above which the tree crown was generally continuous on one or more sides. We assigned each tree a crown class: dominant, codominant, intermediate, and suppressed. Pith-to-bark cores collected from dominant trees gave approximate breast height age of the sample stands. BT was measured twice on each tree; for individual stems, uphill and sidehill BT were measured 90 degrees apart, and for redwood stems in clumps—due to the elliptical cross-section with greater growth away from clump center—BT was measured 90 degrees apart on one side, tending towards the center and then again towards the outside of the clump. We used a standard 50 mm bark gauge on the smaller trees. On the larger trees we used a portable drill and hole saw to remove a cylindrical piece of the bark and expose the cambium. Then, we measured BT between the cambium and the metal tape used to measure the DBH encircling the stem at breast height. This gave the thickness of bark consistent with the method of DBH measurement.

2.2. Data for Analysis of Regional Differences

BT data from the southern portion of redwood's range were collected at five sites between Santa Clara County and Napa County [26]. These were relatively hot and dry redwood sites, being located near the inland limits of redwood's range. 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 18 °C. Summer fog generally dissipates during the daytime at the central sites in Mendocino County and the average summer high temperatures exceed the value of 19 °C reported for the weather station at the coast. At all the study sites, most rainfall occurs between November and March. The mean annual precipitation is approximately 1000 mm 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 (30 °C in July), much like the other southern sites (24–31 °C). Annual precipitation averaged approximately 530 mm at Gilroy, near the sampling sites at Bodfish Canyon and Mt Madonna

in Santa Clara County and 660 mm at Roberts and Redwood Regional Parks in Alameda and Contra Costa Counties, respectively (<http://www.weather.com>).

Dominant and co-dominant redwood trees approximately 80 to 130 years old and about 110 ft tall were selected for BT measurement in the northern and southern regions: 40 trees from the two northern sites and 25 trees from the five southern sites. BT data for 195 dominant and codominant redwood trees representing the central region were extracted from the following dataset for JDSF.

2.3. Data for Analysis of Stand Structure and Age Effects

Throughout the Jackson Demonstration State Forest we established 52 fixed radius plots of various sizes from 0.01 to 0.5 ha: most were 0.02 ha or 0.04 ha. Each plot sampled a forested area absent of recent disturbance or edge effects, but differing in size, structure, and composition. In 23 of these plots, every tree >5 cm diameter at breast height (DBH) was measured for DBH, height, and live crown base height. In the remaining plots, every tree >10 cm DBH was measured. Trees were assigned a canopy layer (stratum) designation of (A) the crown emergent above main canopy, (B) the crown within the main canopy, and the crown within one or more understory layers (C, D), and assigned one of four crown classes within each stratum. BT was measured once on the smaller trees and measured twice and then averaged for each tree >20 cm DBH. A subset of trees (660 out of the 969 measured trees) were cored for breast-height age. Plots with one age class (cohort) of trees were designated as even-aged. Plots with two or more cohorts were designated as multiaged.

2.4. Data for Analysis of Bark Taper along Stem

Within the Arcata Community Forest (ACF) in Humboldt County, 31 redwood focal trees were selected at distances >100 m apart along a “wandering” transect designed to capture a range of the tree sizes and stand densities. BT and diameter measurements were taken at intervals from the base of the stem to the base of the live canopy. Trees were climbed using the flip-line and spur method and the diameter was repeatedly measured along the stem. At the same height of each diameter measurement, the BT was measured twice 90 degrees apart using a standard 50 mm bark gauge. The BT was measured from the wood surface to the contour of the diameter tape wrapped around the tree [27]. Measurements were separated vertically by roughly 0.30 m at heights below 2 m and roughly 3 m above 2 m in height with the final measurement taken upon reaching the live crown base. More frequent diameter and BT measurements were taken below 2 m to account for the greater tapering of BT near the tree base.

To evaluate the influence of stand density on BT, each focal tree that we climbed was designated as the center of a variable-radius plot. DBH was measured for each plot tree, and used to calculate stand density index (SDI) [28] using the angle-summation method [29]. The basal area factor (BAF) was selected based on a desire to have five to nine trees within the plot. Plots with relatively low density were established using a 4.59 m² ha⁻¹ BAF prism, moderate density plots with a 9.18 m² ha⁻¹ BAF prism, and high density plots were established with a 13.77 m² ha⁻¹ BAF prism.

2.5. Analysis

We analyzed the nested data for genetic effect on the BT using the generalized linear mixed-effects regression with PROC GLIMMIX in SAS [27]. The fixed effects were tree DBH, crown ratio (CR), and the categorical variable: crown class. We incorporated a random effect for the class variable: CloneID, a unique identifier for each clump of redwood sprout-origin stems. For the analysis of north–south latitudinal gradient in BT, we used generalized linear regression (PROC GLM) analysis with categorical variables for the region (north, central, south) and the continuous variables DBH and CR. Similarly, for the analysis of the stand structure effects, we used GLM with a categorical binary variable for even-aged or multiaged stand structure, and continuous variables for DBH and CR. The analysis of tree age and canopy position was also done using GLM with the categorical variable canopy strata (emergent, main canopy, understory) and continuous variables: DBH, CR, and breast-height age. For

each of these analyses, the response variable was transformed to reduce skewness in the distribution of the BT data. We used Akaike's Information Criterion AIC for model selection, where decreases greater than 2 points were considered significant improvements [30].

Lastly, we developed a BT taper equation predicting the BT for any height along the tree bole. For analysis, the measurement height data were converted to a proportion of the total tree height (HT) above breast height (BH), such that:

$$\text{Measurement HT relative to BH} = \frac{\text{Measurement HT} - 1.37}{\text{Tree HT} - 1.37} \quad (1)$$

BT was also converted to a proportion of breast height BT. Our BT data exhibited negative exponential tapering with increasing height above ground, so we subtracted our measurement height relative to the breast height from one to invert the data in order to fit a nonlinear power model. After preliminary analysis it was decided that two separate nonlinear equations (one for above BH and one for below BH) would better represent redwood BT tapering which appeared to taper more rapidly below breast height; Maguire and Hann [8] also used separate equations to model the tapering of BT above and below breast height. We excluded the data for one outlier tree with unusual bark taper characteristics. Data were analyzed using PROC NLIN in SAS [31].

3. Results

3.1. Bark Thickness in Even-Aged Stands—Effects of Tree Size, Taper, Crown Ratio, and Genetics

Holding the stand age constant at 85 years in two stands and 100 years in the third even-aged stand allowed us to isolate the effects of tree variables and quantify variation in the breast-height BT among the genotypes (i.e., $n = 74$ individual sprout clumps comprising 2–12 trees). Each sample stand had a different mean and maximum tree size, but a similar basal area comprised of more or less trees (Table 2). Size-differentiation was pronounced, with many trees in the suppressed crown class (Table 3).

Table 2. Summary data for 0.2 ha plot in three even-aged stands at age 85–100 years in the Jackson Demonstration State Forest.

	Stand 1	Stand 2	Stand 3
Position on slope	Ridge	Gully	Upslope
Age	85	100	85
Area (ha)	0.2	0.2	0.2
Number of trees sampled	263	78	230
Density (stems/ha)	1315	390	1150
Average DBH (mm)	332	610	398
Maximum DBH (mm)	926	1394	1127
Maximum height (m)	44.6	63.8	50.1
Basal area (m ² ha ^{−1})	144.7	142.0	179.0
Stemwood volume (m ³ ha ^{−1})	1286	2126	1961

Several models of the BT in even-aged stands had equivalent AIC. The most parsimonious model included DBH and crown class. Testing CloneID as a fixed effect gave a major improvement in AIC, indicating that the BT differed among the sprout clumps and was under genetic control (Table 4). In this model, solutions for fixed effects indicated that the BT varied within a 6.4 mm range (−1.0–5.4 mm) among sprout clumps.

When CloneID was treated as a random effect, an important amount of variation in BT was detected among sprout clumps (Table 5). There was relatively more random (residual) variation in the BT than among the genotypes, and more variation among sprout-clump genotypes (CloneID) than among the three sample stands (Plot) (Table 5). The best BT model indicated that the bark was thickest among the suppressed trees and thinnest among the dominant trees, after controlling for the tree size and age effects in the GLM analysis. Comparing the modeled BT among redwood trees with 450–650 mm DBH (i.e., where the data for all the crown classes were available), the bark of codominant, intermediate, and suppressed trees was around 8%, 14%, and 18% thicker, respectively, than the bark of the same size dominant tree (Figure 2).

Table 3. Summary data for redwood trees in each crown class in three even-aged stands at age 85–100 years in Jackson Demonstration State Forest.

Variable	Crown Class	<i>n</i>	Mean	s.d.	Min.	Max.
Bark thickness (mm)	All trees	571	35.59	22.06	1.00	119.50
	Dominant	67	60.05	18.87	34.50	111.50
	Codominant	100	54.34	17.90	24.50	119.50
	Intermediate	78	46.40	12.32	24.50	75.50
	Suppressed	326	22.23	14.47	1.00	72.00
DBH (mm)	All trees	571	396.69	224.55	100.00	1394.00
	Dominant	67	700.90	196.33	453.00	1394.00
	Codominant	100	609.56	185.89	305.00	1165.00
	Intermediate	78	461.92	99.55	310.00	784.00
	Suppressed	326	253.26	114.26	100.00	660.00
Crown ratio	All trees	571	0.31	0.10	0.01	0.69
	Dominant	67	0.38	0.08	0.19	0.60
	Codominant	100	0.37	0.08	0.20	0.64
	Intermediate	78	0.31	0.08	0.15	0.53
	Suppressed	326	0.28	0.10	0.01	0.69
Height:diameter ratio	All trees	571	0.83	0.19	0.32	1.45
	Dominant	67	0.66	0.11	0.35	0.87
	Codominant	100	0.70	0.11	0.49	1.05
	Intermediate	78	0.79	0.11	0.44	1.05
	Suppressed	326	0.91	0.19	0.32	1.45

Table 4. Comparing candidate even-aged redwood bark thickness (BT) models. Generalized linear mixed-effects models for square-root transformed BT (mm) as a function of candidate fixed effects: DBH, height:diameter ratio (HD), crown ratio (CR), crown class (CC), and a unique sprout clump identifier (CloneID) included in every model as either a fixed or a random effect. Models fitted to redwood tree data (*n* = 571) for three even-aged stands at age 85 years in Jackson Demonstration State Forest.

Candidate Models	AIC	ΔAIC
$BT^{0.5} = \beta_0 + \beta_1 LnDBH + \beta_2 CClass + \beta_3 CloneID$	980.04	-
$BT^{0.5} = \beta_0 + \beta_1 LnDBH + \beta_2 CR + \beta_3 LnDBH \times CR + \beta_4 CC$	1121.42	141.38
$BT^{0.5} = \beta_0 + \beta_1 LnDBH + \beta_2 CClass$	1121.69	141.65
$BT^{0.5} = \beta_0 + \beta_1 LnDBH + \beta_2 CR + \beta_3 CClass$	1121.73	141.69
$BT^{0.5} = \beta_0 + \beta_1 LnDBH + \beta_2 HD + \beta_3 CClass$	1121.97	141.93
$BT^{0.5} = \beta_0 + \beta_1 LnDBH + \beta_2 HD + \beta_3 LnDBH \times HD + \beta_4 CC$	1123.00	142.96
$BT^{0.5} = \beta_0 + \beta_1 LnDBH + \beta_2 CR + \beta_3 LnDBH \times CR$	1146.24	166.20
$BT^{0.5} = \beta_0 + \beta_1 LnDBH + \beta_2 HD + \beta_3 LnDBH \times HD$	1146.44	166.40
$BT^{0.5} = \beta_0 + \beta_1 LnDBH$	1149.83	169.79

Table 5. Even-aged redwood bark thickness (BT) model. Linear mixed-effects model for square-root transformed BT (mm) in each crown class as a function of DBH (mm) at age 85 years in three even-aged stands in Jackson Demonstration State Forest.

Effect	Variable	Estimate	s.e.	DF	t Value	Pr > t
Fixed	Intercept	−15.6668	0.5105	2	−30.69	0.0011
	LnDBH	3.6526	0.0806	490	45.30	<0.0001
	Dominant	−0.6847	0.1170	490	−5.85	<0.0001
	Codominant	−0.3876	0.1007	490	−3.85	0.0001
	Intermediate	−0.1497	0.0938	490	−1.60	0.1110
	Suppressed	0	–	–	–	–
Random	Plot	0.1471	0.1520			
	CloneID	0.2327	0.0589			
	Residual	0.3442	0.0219			

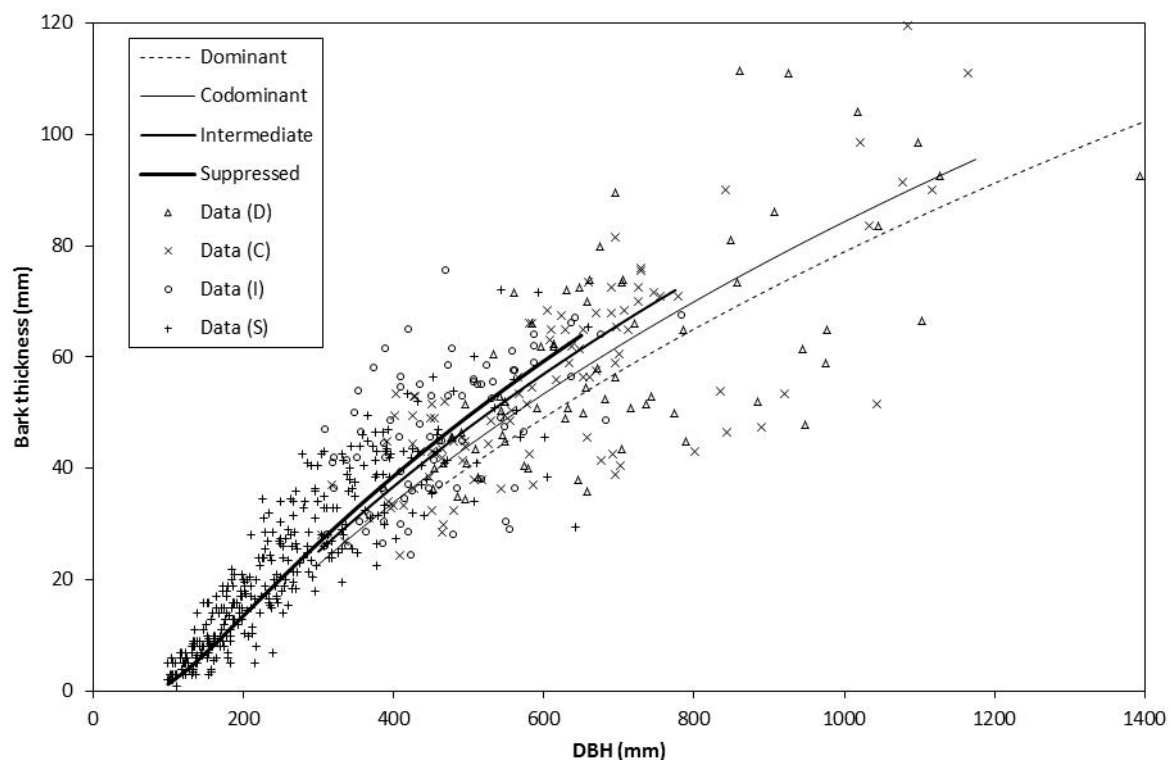


Figure 2. Redwood bark thickness data and linear mixed-effects model predictions for each crown class at age 85 years in three even-aged stands in Jackson Demonstration State Forest.

3.2. Bark Thickness of Dominants and Codominants along North–South Gradient

In light of the differences among the crown classes, we analyzed a subset of data for only the dominant and codominant redwood trees of similar size and age in the northern, central, and southern portions of redwood's natural range. We excluded the data for trees below 470 mm DBH, the size of the smallest tree measured in the southern region which had the fewest data (Table 6). The improvement of 24 AIC points indicated that the BT differed among the regions. The bark was significantly thicker at breast height among the southern redwoods and thinner among northern redwoods (Table 7).

3.3. Bark Thickness in Even-Aged and Multiaged Stands—Effects of Stand Structure

Redwood trees sampled for BT in even-aged stands had shorter crowns than trees of comparable size in multiaged stands (Table 8). Distinguishing between the even-aged and multiaged stands using a dummy variable and incorporating the crown ratio into BT models gave a significant improvement

in the model fit (Table 9). The best model indicated that redwood trees growing in the partial shade of an overstory had thicker bark than trees growing in even-aged stands, after accounting for the effects of tree size (positive) and crown ratio (negative) on BT (Table 10).

Table 6. Summary data for redwood trees in the northern, central, and southern parts of redwood's natural range.

Variable	Region	<i>n</i>	Mean	s.d.	Min.	Max.
DBH (mm)	North	40	791.65	211.43	487.70	1342.00
	Central	195	684.03	187.81	471.00	1562.10
	South	25	745.24	167.58	471.00	1103.00
Crown ratio	North	40	0.66	0.11	0.46	0.91
	Central	195	0.52	0.16	0.15	1.00
	South	25	0.58	0.14	0.36	0.89
Bark thickness (mm)	North	40	57.36	20.13	31.80	117.50
	Central	195	57.39	17.31	22.00	117.00
	South	25	80.58	28.79	31.50	164.00

Table 7. Bark thickness (BT) model for dominant and codominant redwoods in the northern, central, and southern parts of redwood's natural range (regional model) and for all the data combined (range-wide model). Generalized linear model for the natural log (*Ln*)-transformed BT (mm) as a function of DBH (mm).

Model	Variable	Estimate	s.e.	DF	<i>t</i> Value	Pr > <i>t</i>	AIC
Regional	Intercept	−0.1846	0.418	0	−0.44	<0.0001	31.71
	<i>Ln</i> DBH	0.6855	0.063	256	10.88	<0.0001	
	North	−0.3704	0.064	256	−5.83	<0.0001	
	Central	−0.2608	0.053	256	−4.90	<0.0001	
	South	0	-	-	-	-	
Range wide	Intercept	−0.4013	0.4261	0	−0.94	<0.0001	56.19
	<i>Ln</i> DBH	0.6800	0.06524	258	10.42	<0.0001	

Table 8. Summary data for the redwood trees in even-aged stands versus understory trees in multiaged stands. Data for trees < 400 mm DBH (*n* = 279) collected in 32 plots sampling even-aged and multiaged stands in Jackson Demonstration State Forest.

Variable	Stand Structure	<i>n</i>	Mean	s.d.	Min.	Max.
DBH (mm)	Even-aged	41	170.43	79.59	73.66	398.78
	Multiaged	238	153.86	74.82	50.00	370.00
Crown ratio	Even-aged	41	0.54	0.17	0.19	0.85
	Multiaged	238	0.72	0.18	0.25	0.99
Bark thickness (mm)	Even-aged	41	11.76	9.04	2.00	36.50
	Multiaged	238	12.28	9.67	1.00	58.00

Table 9. Comparing candidate redwood bark thickness (BT) models. Generalized linear models for natural log (*Ln*)-transformed BT (mm) as a function of the candidate predictor variables: DBH, crown ratio (CR), and a dummy variable for redwood trees in even-aged stands versus understory trees in multiaged stands in Jackson Demonstration State Forest.

Candidate Models	AIC	ΔAIC
$LnBT = \beta_0 + \beta_1 LnDBH + \beta_2 CR + \beta_3 \text{Even-aged}$	376.13	-
$LnBT = \beta_0 + \beta_1 LnDBH + \beta_2 \text{Even-aged}$	381.52	5.39
$LnBT = \beta_0 + \beta_1 LnDBH + \beta_2 CR$	383.15	7.02
$LnBT = \beta_0 + \beta_1 LnDBH$	384.16	8.03

Table 10. Bark thickness (BT) model for redwood trees in even-aged stands and understory trees in multiaged stands. Generalized linear model for natural log (Ln)-transformed BT (mm) as a function of DBH (mm) and crown ratio.

Variable	Estimate	s.e.	DF	t Value	Pr > t
Intercept	−4.9977	0.2988	0	−16.73	<0.0001
Ln DBH	1.5192	0.0583	275	26.08	<0.0001
Crown ratio	−0.4170	0.1536	275	−2.72	0.0070
Even-aged	−0.2669	0.0831	275	−3.21	0.0015
Multiaged	0	−	−	−	−

3.4. Effect of Tree Age and Canopy Layer on Bark Thickness in Multiaged Stands

To avoid the confounding effect of stand structure, we extracted a subset of data for sample trees of known age that were exclusively located in multiaged stands. These trees covered a broad range of ages, sizes and crown ratios (Table 11). Accounting for the position of each tree crown within the stand by assigning it to a canopy layer (i.e., canopy stratum) did not improve the BT models (Table 12). Breast-height age was a more useful predictor of the BT than the canopy stratum. Older trees of a given size and crown ratio were found to have thicker bark, however the age effect was not pronounced and a simpler model without age had the same AIC (Table 13). The best model included DBH and CR and represented a significant improvement over the simplest model predicting BT as a function of DBH alone.

Table 11. Summary data for redwood trees separated into three canopy layers (strata) in even-aged and multiaged stands. Data for trees with breast-height age data ($n = 565$) collected in 48 plots sampling even-aged and multiaged stands in Jackson Demonstration State Forest.

Variable	Canopy Stratum	n	Mean	s.d.	Min.	Max.
DBH (mm)	Emergent	38	973.92	240.78	625.00	1562.10
	Main canopy	336	442.80	206.70	58.42	1130.30
	Understory	191	154.85	72.75	51.00	357.00
Crown ratio	Emergent	38	0.54	0.11	0.37	0.80
	Main canopy	336	0.51	0.18	0.14	1.00
	Understory	191	0.70	0.19	0.21	0.99
Tree age (years)	Emergent	38	98.08	12.45	60.00	131.00
	Main canopy	336	61.51	23.98	13.00	130.00
	Understory	191	28.83	17.42	6.00	100.00
Bark thickness (mm)	Emergent	38	67.89	15.85	36.00	117.00
	Main canopy	336	40.22	19.19	3.00	109.00
	Understory	191	12.36	9.90	1.00	58.00

Table 12. Comparing candidate multiaged redwood bark thickness (BT) models. Generalized linear models for square root-transformed BT (mm) as a function of the candidate predictor variables: DBH, crown ratio (CR), breast-height age (years) and the categorical variables for redwood trees in the different canopy strata and in even-aged stands versus multiaged stands in Jackson Demonstration State Forest.

Candidate Models	AIC	Δ AIC
$BT^{0.5} = \beta_0 + \beta_1 LnDBH + \beta_2 CR + \beta_3 Age^{0.5}$	1337.60	−
$BT^{0.5} = \beta_0 + \beta_1 LnDBH + \beta_2 CR$	1337.90	0.30
$BT^{0.5} = \beta_0 + \beta_1 LnDBH + \beta_2 CR + \beta_3 Age^{0.5} + \beta_4 Stratum$	1338.85	1.25
$BT^{0.5} = \beta_0 + \beta_1 LnDBH + \beta_2 CR + \beta_3 Stratum$	1340.26	2.66
$BT^{0.5} = \beta_0 + \beta_1 LnDBH$	1361.80	24.20

Table 13. Bark thickness (BT) models for redwood trees in multiaged stands. Generalized linear model for the square root-transformed BT (mm) as a function of DBH (mm) and crown ratio, with and without breast-height age (years).

Model	Variable	Estimate	s.e.	DF	t Value	Pr > t	AIC
Age effect	Intercept	−8.6640	0.3059	0	−28.32	<0.0001	1337.60
	LnDBH	2.4423	0.0713	561	34.26	<0.0001	
	CR	−0.6628	0.1919	561	−3.45	0.0006	
	Age ^{0.5}	0.0675	0.0285	561	2.36	0.0184	
Without age	Intercept	−8.8130	0.3005	0	−29.32	<0.0001	1337.90
	LnDBH	2.5726	0.0454	562	56.68	<0.0001	
	CR	−0.8729	0.1707	562	−5.11	<0.0001	

3.5. Bark Tapering along the Stem

Dominant and codominant trees sampled for bark tapering covered a range of tree sizes (Table 14). The resultant dataset for the modeling of BT tapering comprised a total of 129 measurements of BT at different heights below breast height and 208 measurements above breast height.

Table 14. Summary data for DBH and the breast-height bark thickness (BT) of redwood trees sampled for bark tapering (BT at various heights) at Arcata Community Forest, Humboldt County, California.

Variable	n	Mean	s.d.	Min.	Max.
DBH (mm)	31	703.79	288.27	182.90	1342.00
Bark thickness (mm)	31	48.86	24.15	10.20	110.50

Our sample of 31 trees from the ACF revealed relatively consistent decreases in BT with increasing height along the tree stem. However, there were notable differences in the BT above and below the breast height, which led to the formulation of two separate models to predict BT tapering for each respective segment (above and below breast height).

Lower variability in BT above breast height led to more precise predictions of BT (6.76 mm root mean square error (RMSE)) when the non-linear model of BT as a proportion of the breast-height BT (BT_{BH}) was rearranged to predict the actual BT (mm) for each sample measurement height (H_{BT}) above the breast height, such that:

$$\text{Proportion of } BT_{BH} = (1 - H_{BT} / (HT - 1.37))^{1.977} \quad (2)$$

Greater variability in the BT below breast height led to less precise nonlinear power model predictions (7.49 mm RMSE) for the BT (mm) below breast height where:

$$\text{Proportion of } BT_{BH} = (10.686 * ((1 - H_{BT} / (HT - 1.37)) - 1)^{1.151}) + 1 \quad (3)$$

Bark thickness (BT) tapering above and below breast height (BH) varies according to the total tree height. The rate of tapering below breast height ranks from least to most rapid for three redwood trees of different heights: 50 m, 35 m, and 20 m total height (Figure 3). Model predictions of BT tapering show how BT quickly becomes thinner above breast height, and thickens below breast height. For example, halfway up a 50 m tree, the nonlinear model predicts that the BT is only 26.8% of breast-height BT. Similarly, halfway up a 35 m tree, BT is 27.5% of the breast height BT, and halfway up a 20 m tree, BT is 29.2% of the breast height BT. Within the tree crown, towards the tree top, BT tapers less (Figure 3).

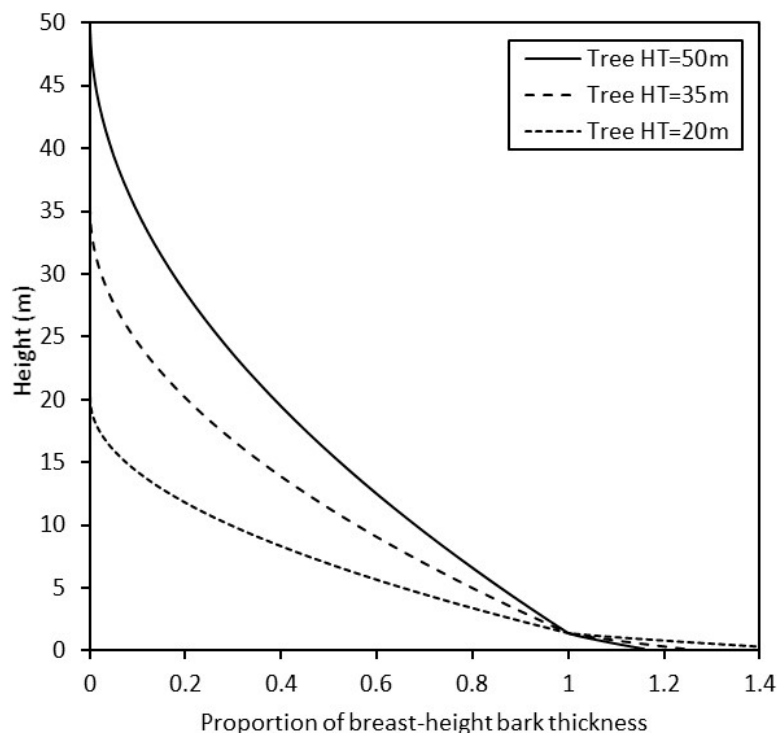


Figure 3. Modeled bark thickness (BT) tapering above and below the breast height (1.37 m) for three redwood trees of different heights: 50 m, 35 m, and 20 m total height.

4. Discussion

Redwood BT was most strongly associated with DBH, but was also found to be negatively correlated with the CR. Like CR, crown class was negatively correlated with BT, meaning that among trees of a given DBH, dominant trees had the least BT and suppressed trees had the most BT. After including these influential tree variables in the BT regressions, other factors explaining additional variation in BT included genotype, stand structure (BT ranked even-aged < multiaged), and geographic region (BT ranked north < central < southern regions). The regional variation in BT has also been detected among Sierra Nevada conifers throughout California [12] but not white spruce (*Picea glauca*) across Alaska [32].

The influence of stand structure on the BT manifested itself as greater BT for redwoods grown in multiaged versus even-aged stands. This difference was detected even after accounting for the influence of DBH and CR. We expected trees in multiaged stands to be older than trees of the same size in even-aged stands, and have different stem and crown allometry and branching characteristics [11,33–35]. For example, crowns of the shade-tolerant Pacific silver fir (*Abies amabilis*) had longer crowns when grown in shade, and presumably different branching patterns and allometry [35]. Stem allometry and tapering of bark along the stem may also vary between redwoods grown in multiaged versus even-aged stands, requiring more investigation. Marshall et al. [4] found that the Douglas-fir BT varied among stands, and recommended applying localized coefficients to account for this source of variation in BT. In addition, it is unknown how the patterns of BT tapering along the stem may also vary regionally. Pemberton [36] reported on the tapering of BT in terms of bark factor at BH (av. 15.6%, range 14–16%) and the half height (av. 10.7% of stem diameter at half height, range 9.7–11.1%) for redwood in Del Norte and Humboldt Counties.

Other factors may also influence the BT in redwood and other species. The thick bark on redwood that imparts resistance to fire is often partially consumed in non-lethal ground fires (Figure 4). Hence, the BT near the ground on large trees may be less than further up the stem. Similarly, anthropogenic burning may have favored trees with thicker BT as reported in *Pinus radiata* [37]. Bark thickness in redwood has also been reported to shrink and swell with variations in moisture content [38].



Figure 4. Bark of old redwood trees partially consumed by wildfire.

In multiaged stands, older trees of a given size and crown ratio were found to have slightly thicker bark, but the age effect was not pronounced. A simpler BT model without age included DBH and CR, and itself represented a major improvement in predictive power over the simplest model predicting the BT in multiaged stands as a function of DBH alone. This finding has practical significance. First, it appears that a generalized BT model applies to all trees in multiaged stands which means it will make consistent predictions when implemented within individual tree growth and yield modeling frameworks predicting change in the DBH and CR over time. Secondly, the importance of CR and DBH for the prediction of BT suggests that constant ‘bark factors’ (sometimes referred to as bark ratios) [36,39] will be inadequate for many applications. In particular, trees at either extreme of DBH or CR will have the BT under/overpredicted by a constant bark factor. For example, Pemberton [36] reported a constant bark factor of 15.6 for second-growth redwood in Humboldt and Del Norte Counties, meaning that 15.6% of a tree’s DBH comprised bark (both sides). Dividing this factor by two (7.8%) makes it comparable to our data and models for one-sided average radial BT. Compared against our BT predictions for dominant and codominant trees in Humboldt County, the constant bark factor gives a 52% underprediction of BT for a small redwood (15 cm DBH), a 2% overprediction for a 60 cm DBH redwood, and a 24% overprediction for a 135 cm DBH redwood tree. Therefore, we recommend replacing bark factors with the best available BT equations in forest science, modeling and management applications. We also recommend the adoption of our drilling method for BT measurement on larger trees due to the potential for error associated with bark gauge measurements [40].

Redwood stems within a sprout clump had a similar BT, and the BT varied widely among the clumps in the same stands. The strong genetic variance component for redwood BT suggests that BT should be assessed in tree improvement field trials along with other important traits such as tree size, form, health, epicormic branching and wood properties [41,42]. Redwood planting stock with thinner bark tendencies could be deployed in areas where wildfire risk is low (e.g., closer to the Pacific coast) with the objective of sequestering and storing more carbon into long lived wood products and producing less bark residues [43]. Alternatively, redwood planting stock with high BT could be deployed to more xeric and fire-prone inland areas [44], and for use in redwood range expansion

projects where redwood is being planted outside its natural range in more stressful environments and may benefit from added protection from the elements [45,46].

5. Conclusions

In summary, redwood BT varied along gradients, at the tree level, in accordance with stand structure, as well as regionally. Factors other than DBH explained important amounts of variance and should be considered when modeling the BT instead of relying on simple bark factors that overpredict BT for larger, older trees such as those grown on longer rotations or to later ages under multiaged silviculture.

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