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Second-Log Branching in Multiaged Redwood and Douglas-Fir: Influence of Stand, Site, and Silviculture

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Abstract: We studied branching in *Sequoia sempervirens* (Lamb. ex D. Don) Endl. (coast redwood) and *Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii* (coast Douglas-fir) because of their commercial value to coastal northern California. We focused on branching in the second log, which constitutes an important part of a tree's wood volume and potential value. We quantified branch size and branch growth of overstory trees in multiaged stands in Mendocino County, California, in response to topographic, silvicultural, and stand- and tree-related variables. Higher stand density—a measure of competition averaged across the sample plot—did not correlate with size of the largest second-log branch measured but was associated with a smaller average diameter of the largest branches measured on all sides of the study tree. The largest branch measured was smaller when in closer proximity to branches of its immediate neighbor tree. Redwood had larger branches than Douglas-fir but their size was more sensitive to an ecological gradient of soil-moisture deficit. Branches responded differently to individual tree selection harvest of conifers versus herbicide control of hardwoods. Residual conifer branches in harvested plots responded almost immediately with increased growth, but this release was short-lived. Branches in herbicide-treated plots exhibited a delayed release, giving more consistent branch growth throughout two five-year measurement periods after treatment.

Keywords: BIX; branch growth response; branch size; *Pseudotsuga menziesii*; *Sequoia sempervirens*; silvicultural treatment response; tree branch model; uneven-aged management

1. Introduction

Controlling tree branching is a challenge for forest managers concerned about knots in timber products [1–3] or fuel ladders in fire-prone regions [4,5]. Larger branches have probably lived longer than smaller branches, and persist longer on the tree stem before decaying, breaking, and falling to the ground. The stem takes longer to occlude after larger branches are removed or fall. Trees with large lower branches are more likely to allow fire to climb into the tree crown, which can result in active crown fires within forests in fire-prone regions [6]. Trees with large branches yield sawn timber with large knots, which can impact performance and lower the value of their lumber [7–9].

Factors affecting branch size and development include genetics, stand structure, and the environment. Branching is under genetic control, but the extent of interactions between genetics and environmental factors is not well understood. For instance, the number of branches, branch length, and branch diameter varied significantly between *Populus* clones that performed differently when planting densities were varied. The clones that grew fastest in dense plantings were those that had the largest sum of branch length [10]. Crown structure variables were under genetic control in loblolly pine (*Pinus taeda L.*) and slash pine (*P. elliottii* Engelm.) plantations, affording selection for desired traits including branch diameter [11]. In a Douglas-fir progeny test, trees that had small branches at age 12 also had relatively small branches at age 24, and the same was true for large-branched trees [12]. In these studies of tree branching, genotypes were known and compared under experimental conditions such as maintaining uniform spacing between trees to minimize the influence of confounding factors on tree growth and branching. Alternative approaches are needed to study branching in naturally-regenerated multiaged stands with varying tree sizes and spacing. One such approach involves treating genetic variations as random error while sampling branches across gradients of stand density, stand structure, or environmental variables.

Most information on stand density and branch size relationships comes from even-aged stands. For example, mean and maximum branch diameter had a strong negative correlation with number of stems per acre in Douglas-fir [13]. Young Norway spruce (*Picea abies* (L.) *Karst.*) branch diameter increased with decreasing stand density [14]. Time from branch initiation to occlusion was shorter in high density stands corresponding to reduced branch size for silver birch (*Betula pendula* Roth) [15]. Branch diameters in precommercially thinned redwood and Douglas-fir were 35% larger than in unthinned stands, with branches larger in redwood than Douglas-fir [16]. Multiaged stand structures are more complex than relatively simple even-aged stands and plantation monocultures. Under multiaged management, each cohort and in some cases, individual trees, develop in different environments. Growing space is unevenly distributed among trees, and understory trees may alter their branching in response to shade from older (taller) cohorts. For instance, in the shade tolerant species Pacific silver fir (*Abies amabilis* (Douglas ex Loudon) Douglas ex Forbes), overstory trees had greater crown rise rates than trees in the understory where branches continued to survive at light levels where overstory tree branches had died. Eastern white pine (*Pinus strobus* L.), an intermediate tolerant species, had lower crown ratio in the understory than in the overstory [17]. Partial harvests create openings in the canopy allowing a new cohort to establish, but at the same time, these openings may affect residual tree characteristics including branching [14]. These findings suggest that a tree crown's position within the canopy and stand should be considered when studying branching, and that we can expect variation between species.

Tree branching is affected by factors other than stand structure and density. For example, the climate and the environment influenced the branching of Monterey pine (*Pinus radiata* D. Don) plantations. Branch diameter exhibited a strong correlation with high winds [18]. Site fertility and fertilization affected Scots pine (*Pinus sylvestris* L.) branch characteristics, with branch size generally increased with increasing fertility [19]. In Norway spruce, however, site fertility and fertilization were not significant predictors of branching, and branch properties did not vary with nutrient availability [20]. We are not aware of any research comparing branching between two tree species—with narrow and wide ecological amplitude—growing along a major environmental gradient.

Coast redwood and coast Douglas-fir form mixed stands along the coastal range of northern California. Redwood has a small natural range thought to be restricted by limited tolerance for drought and cold. Douglas-fir has wider ecological amplitude and a much larger natural range. A history of repeated partial cutting to extract these valuable conifers had favored tanoak (*Notholithocarpus densiflorus* (Hook. & Arn.) P.S. Manos, C.H. Cannon, & S.H. Oh), a prolific shade-tolerant hardwood that regenerates via seedlings and stump sprouts. Recently, forest managers throughout the region have worked to restore conifer dominance, reducing tanoak densities by cutting or chemical treatment, and replanting conifers after partial harvesting. Unknown is the influence of these treatments on conifer branching along an east-west soil moisture gradient. Summer rain is rare in northern California. A wide belt of fog aligned with the coast moderates temperature and can provide soil moisture in the form of "fog drip" falling from fog-wetted tree crowns. The fog belt's influence is most pronounced near the coast, but the fog can extend several kilometers inland overnight before retreating to the coast the next day. Therefore, sites further inland experience fog less frequently, are warmer, and have greater soil moisture deficit [21]. The impact of this gradient in soil moisture deficit on tree branching is unknown.

Our goal was to quantify branch size and branch growth of redwood and Douglas-fir trees and relate these branching characteristics to plot-level conditions and silvicultural treatments. Our objectives were to: (1) model branch size as it related to stand density and neighbor tree competition and the influence of an east-to-west ecological gradient; and (2) model the influence of two different methods of release from competition on branch growth. We focused on branching within the second log (i.e., log immediately above the butt log, located approximately 5 m above ground). It was chosen because pruning of the second log is generally cost prohibitive due to its height above ground, yet it represents a significant portion of the total stemwood volume and therefore gain/loss in value from branching-related lumber grade demotion (e.g., from excessive knot size; [22]). We hypothesized that branch diameter would be negatively correlated with stand density for both species [13–15,23], branch diameter would be more sensitive to the east-west ecological gradient in redwood than Douglas-fir, branches can respond to removal of neighbor-tree competition, and branch growth response would differ between the shade-tolerant redwood and mid-tolerant Douglas-fir.

2. Materials and Methods

2.1. Study Area

We studied branching in plots traversing the coastal range between the coastal town of Mendocino (39°18′36″ N, 123°47′24″ W) and the inland town of Ukiah (39°09′27″ N, 123°12′59″ W) in Mendocino County, California. The study area extended between Highway 128 (near Pacific coast) and Highway 101 (inland) on Mendocino Redwood Company's Navarro tract (Figure 1). Redwood, Douglas-fir, and tanoak were the most prevalent species within the study area. Less common associates present in the area sampled were Pacific madrone (*Arbutus menziesii* Pursh), coast live oak (*Quercus agrifolia* Née), giant chinkapin (*Castanopsis chrysophylla* (Douglas ex Hook.) Hjelmqvist), grand fir (*Abies grandis* (Douglas ex D. Don) Lindl.), Monterey pine (*Pinus radiata*), western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), red alder (*Alnus rubra* Bong.), and (exotic, naturalized) Tasmanian blue gum trees (*Eucalyptus globulus* Labill.).

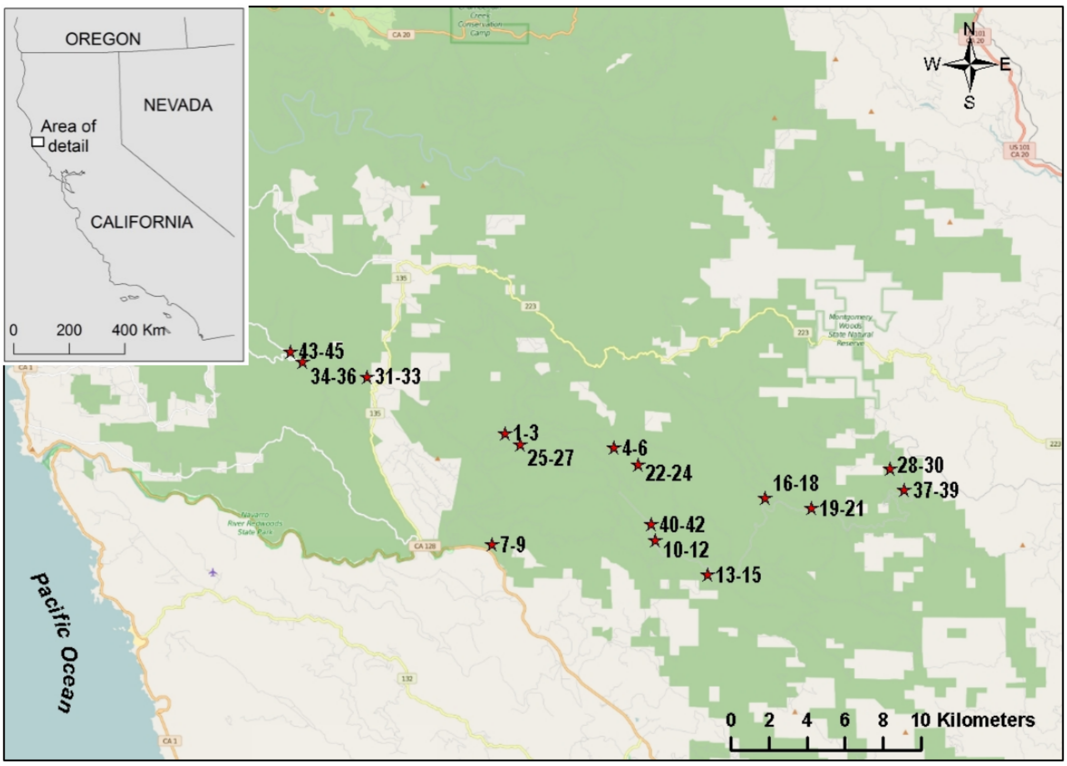

Figure 1. Distribution of sample plots across Mendocino Redwood Company timberlands in Mendocino County, California. Each point represents a group of three plots (one for each treatment type).

2.2. Data Collection

In summer 2012, we used "triplet" groups of three fixed-area plots to sample two different silvicultural treatments and a no-treatment control. The treatments had been implemented between 1998 and 2003. We installed two plots within a treated area and a third plot just outside in an untreated location. The two plots within the treated area represented one of two types of treatment: (i) herbicide treatment of tanoak with no harvest; and (ii) herbicide treatment of tanoak with partial conifer harvest. Fifteen replicates of the three plots were sampled along a 26.7 km east-west gradient across the study area (Figure 1). Each plot was a circular area of 0.04 ha with radius of 11.28 m. We used ArcMAP 10.1 (ESRI, Redlands, CA, USA) to derive site-level variables describing topography in each plot: percent slope, aspect, elevation, and flow accumulation (the upslope area contributing water to a given point).

We mapped trees greater than 15.24 cm diameter-at-breast height (dbh) by recording distance and azimuth from the center of the plot. For each tree we measured dbh, total tree height, and height to the base of the live crown (isolated live branches below the main living crown were disregarded). Bark-to-pith increment cores gave breast height age of overstory trees. Within herbicide and harvest treatment plots, diameters of stumps over 15.24 cm at the base were measured and their location mapped in the same manner as the living trees in order to calculate approximate pre-harvest stand density. Measurements of the diameter at ground level of living redwood, Douglas-fir, and tanoak trees within control plots were regressed against dbh to produce a model to reconstruct stand structure and density at the time of treatment from the harvested and herbicide-treated stump measurements. A three-strata canopy model, including dominant-emergent (A), upper-continuous (B), and understory (C) layers [24], was used to classify trees into distinct canopy layers. Classes of dominant, co-dominant, intermediate, and suppressed crowns were assigned according to the tree's height and position in comparison to its neighbors, describing tree crown position within each canopy stratum.

We measured branch attributes on a subset of trees in each plot. Two trees closest to the center of the plot were selected to meet the following criteria: one redwood and one Douglas-fir from the A or B strata and classified as being in the dominant or codominant crown class. On the selected trees, the largest branch in each radial quadrant of the bottom half of the second log (4.88–7.32 m above ground) was sampled. The branch length (BL), azimuth, and overlap from neighboring trees were measured while the branch was on the tree. Azimuth was cosine transformed from 0–360 degrees to range from 0–20 points, with a maximum of 20 points at azimuth 45 degrees (northeast facing branch) to a minimum of zero points at 225 degrees (southwest facing branch) and with 10 points representing both 135 and 315 degrees azimuth. Distance to the nearest neighbor tree along the branch azimuth path was measured, and the branches were removed with a pole saw. The base diameter of each branch was measured at the widest and narrowest points. Branch diameter growth response to silvicultural treatment was expressed as a ratio of post-/pre-treatment radial increment by measuring five annual ring widths for three five-year periods: (i) five years immediately before treatment; (ii) immediately after herbicide/harvest treatment (post-treatment years 1–5); and (iii) a second increment period following the first post-treatment increment period after treatment (post-treatment years 6–10). A total of 77 trees were sampled: 41 redwoods and 36 Douglas-fir.

2.3. Analysis

We used regression analysis to study relationships between response variables and multiple candidate explanatory variables. Response variables described either branch size attributes or branch growth. Explanatory variables were categorized as site-level and stand-level (common to each plot), tree-level, and branch-level variables (Table 1). We used three model selection methods to determine the best combination of variables in a particular regression model: stepwise Akaike's information criterion (step AIC), adjusted R^2, and Mallows CP. The resultant models were then compared in terms of the sum of the absolute value of the residual error and AIC and AICc values. The best model was checked for errors and outliers using residual plots, normal Q-Q plot to test for normality, and Cook's distance to check for high leverage outliers. In addition, Box-Cox graphs were used to test if transformation on the predictor variable was needed, and the Durbin-Watson test was used to identify autocorrelations among selected explanatory variables [25–28]. We used R version 2.15.0 (R Core Team 2013, Vienna, Austria) to perform these analyses and create graphs of actual data and predicted values.

Table 1. Candidate variables for maximum branch (MaxB) size, BIX, and inventory models of branch diameter and branch growth for redwood and Douglas-fir in the overstory of multiaged stands in Mendocino County, California.

Variable	Description	Scale	Type
Tpha	Number of trees per hectare	P	Continuous
SDI	Stand density index (metric; [29])	P	Continuous
BA	Basal area ($m^2 \cdot ha^{-1}$)	P	Continuous
BAL	Basal area of trees larger ($m^2 \cdot ha^{-1}$)	P	Continuous
eBAI	Redwood BAI Index (BAI above/below average) **	P	Percentage
Slope	Slope of plot	P	Percentage
Aspect	Cardinal direction of the downhill plot slope	P	Range (0–20)
Coast.d	Distance of plot from Pacific coastline (km)	P	Continuous
Flow acum.	Flow accumulation	P	Continuous
Trtmt *	Herbicide (H) or harvest (X) treatment	P	Categorical
Period *	0 = first and 1 = second 5-year period post-treatment	P	Categorical
Species	Species of tree sampled	T	Categorical
Dbh	Diameter at breast height (cm)	T	Continuous
Dbh.p	Tree dbh divided by plot mean dbh	T	Percentage
HT	Total height of tree (m)	T	Continuous
HT.p	Tree height divided by plot mean height	T	Percentage
HDR	Height to diameter ratio	T	Percentage
N.dist	Distance to the most influential neighbor (m)	B	Continuous
Condition	Living or dead condition of branch (MaxB only)	B	Categorical
B.Azi	Azimuth of the branch (MaxB only)	B	Range (0–20)

* Variable only included in branch growth models. ** Productivity index of redwood component BAI in plot [30]. Variables categorized as site-level and stand-level (P; common to each plot), tree-level (T), and branch-level (B) scale.

We studied branch size using two response variables. This led to the development of two types of branch models. The first type, known as BIX, modeled the average size of large branches surrounding the second log, specifically the average diameter of the largest branch from each of four radial quadrants [31]. The second model type predicted the maximum branch diameter (MaxB) in the second log, which was the largest branch sampled among the four quadrants. For both of these model types, all candidate predictor variables were tested for inclusion in the best-fitting linear regression model, hereafter referred to as the "AICc-derived model". In addition, we created "informative models" to reveal additional correlations between branching and candidate variables. These models would inform our understanding of branching patterns. Models were also created for use with a variety of basic forest inventory data. The first so-called "inventory model" depended only on BA, which is commonly collected using a prism or relascope. The second model included dbh that would be collected from simple fixed-area plots or point sample data including a tally of trees in each dbh class. The third inventory model included variables that depended on tree height data. Height data are the least-commonly collected in forest inventories, but we expected tree height, taper, or HT.p (i.e., height in relationship to the mean stand height) variables to improve model fit. Variables tested for inclusion in the inventory models predicting MaxB and BIX are listed in Table 1. BIX and MaxB model variables differed in that the means of the branches and corresponding neighbor tree distances were used in BIX models whereas the MaxB model included the actual variables recorded for the particular quadrant where the largest branch was measured. The MaxB and BIX models were only fit to data collected in the control plots because these data were not impacted by the confounding effects of silvicultural treatments applied 10–15 years earlier.

The response of branches to the herbicide and harvest treatments required modeling the ratio of increased growth (the difference in post-harvest annual growth over pre-harvest growth) as the response variable. This model selected from the variables shown in Table 1 and two additional variables: (i) time since treatment (period)—a dummy variable accounting for differences in branch growth between the first and second five-year period after harvest; and (ii) pre-harvest growth rate (PH5A)—the average annual branch diameter growth rate in millimeters from five years immediately preceding harvest. We examined climate data and noted inter-annual variations between years of measured branch growth (i.e., five years before and 10 years after treatment). However, we did not include climate variables in our analysis of branch growth by 5-year time period because we had no control over treatment dates that also varied (1998–2003). The branch growth model was only fit to data collected in the harvested and herbicide-treated plots since there was no treatment applied in control plots.

3. Results and Discussion

3.1. Models for BIX—Average Diameter of Four Largest Branches

Our sample plots were located between 18 and 745 m above sea level, within the natural range of redwood. The average breast-height age of overstory trees was 49 years in control plots, 45 years in herbicide plots, and 47 years in plots treated with herbicide and partial harvest. Trees sampled for branching ranged from 22 to 110 cm dbh for redwood and 18 to 100 cm dbh for Douglas-fir (Supplemental File, Tables S1 and S2). Basal area ranged from 21 to 91 $m^2 \cdot ha^{-1}$ in the control plots and from 7 to 83 $m^2 \cdot ha^{-1}$ in the herbicide only and herbicide and harvest plots (Supplemental File, Tables S3 and S4). Tree size was an important predictor of branch size. All BIX models included dbh and dbh^2 terms indicative of a quadratic rise-peak-fall behavior where branch and tree size increased together up to ~60 cm dbh, above which larger trees had progressively smaller branches in the second log (Figure 2A, Table 2). It is probable that these large trees had initially grown within a considerably denser stand structure than we see today. These dense stands would have promoted more rapid crown rise resulting in smaller branch and knot formation within the second log. We do not expect our current stand-level values for measured variables to accurately represent the conditions when the branches on these larger diameter trees formed. Our assumption that larger trees in this study were older was tenable because we only sampled overstory trees in the dominant and codominant crown classes. After accounting for the tree-size effect in the BIX models, stands with higher density at the time of measurement had smaller branches on the second log (Figure 2B). Branch diameter's negative correlation with increasing stand density has been well documented [13].

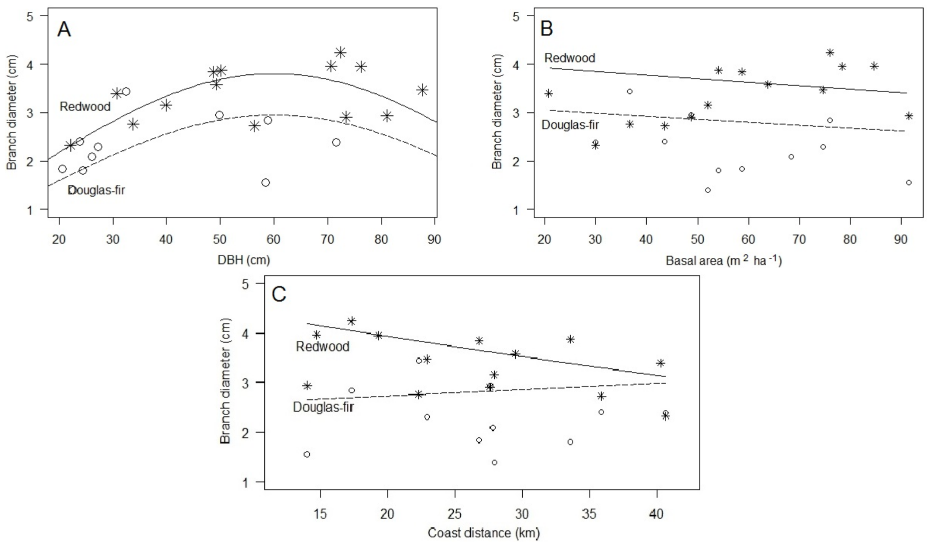

Figure 2. BIX relationship to (**A**) dbh and (**B**) stand density in terms of basal area, and (**C**) the influence of the ecological gradient (distance from the coast), and actual data from the control plots for redwood (*) and Douglas-fir (o) BIX in Mendocino County, California.

Table 2. BIX branch model coefficients (s.e. as percent of coefficient in parentheses) for Mendocino County, California.

Model	Dbh Inventory		Dbh & Height Inventory		Informative Model		AICc-Derived	
Selection method	AIC		AIC		AIC		AICc	
Intercept	1.12200	(14%)	1.18900	(13%)	1.14000	(25%)	1.73100	(16%)
dbh (cm)	0.00988	(59%)	0.01747	(39%)	0.02008	(37%)	0.00591	(89%)
dbh^2	−0.00008	(65%)	−0.00014	(45%)	−0.00017	(41%)	−0.00008	(59%)
Species *	0.12730	(41%)	0.11850	(40%)	0.33700	(48%)	0.06009	(84%)
BAL ($m^2 \cdot ha^{-1}$)	−0.00127	(123%)	-	-	-	-	-	-
BA ($m^2 \cdot ha^{-1}$)	-	-	−0.00046	(252%)	−0.00106	(176%)	-	-
HT.p	-	-	−0.20990	(61%)	−0.22360	(59%)	-	-
HDR	-	-	-	-	-	-	−0.62850	(37%)
Coast.d (km)	-	-	-	-	0.00214	(257%)	-	-
Species × Coast.d	-	-	-	-	−0.00779	(72%)	-	-
AICc	−34.886		−33.643		−27.389		−41.835	
AIC	−39.553		−40.231		−39.389		−46.501	
Adjusted R^2	0.5206		0.5466		0.5534		0.6369	

* Species dummy variable: redwood = 1; Douglas-fir = 0. BIX = average diameter of the largest branch in four quadrants of the second log (cm). Response = $BIX^{0.33}$.

The best informative BIX model included an interaction between species and distance to coast. The coefficient for "coast distance" was positive, but the interaction between species and coast distance indicated that redwood branch diameters were progressively smaller with increasing distance from the coast. Redwood had greater second-log BIX values than Douglas-fir, but the model predicted that Douglas-fir branch diameters were slightly larger further inland (Figure 2C).

The inventory models for dbh-data-only and dbh-and-height data included the same variables except that BAL was replaced by BA and relative height (HT.p) in the latter (Table 2). Consistent with the best-fitting "informative model" for BIX, the inventory models also indicated that redwood had a larger average branch size than Douglas-fir. Distance to coast was deliberately excluded from the inventory models, so they predict larger branch size for redwood than Douglas-fir throughout the sampled range. A model containing only BA and species was rejected because the predictions were not significantly different from the mean branch size. The AICc-derived BIX model had the lowest AICc values and was the most likely of the four BIX models (Table 2). We found that stem taper (HDR) was correlated with other variables representing stand density, so only one of these variables was included in any model. Regression fit statistics for each BIX model are provided in Supplemental File, Tables S5–S8.

3.2. Models for MaxB—Diameter of the Largest Branch

Models predicting diameter of the single largest branch on the second log (MaxB) were similar to the BIX models. The dbh-data-only and dbh-and-height inventory models included the same variables as the BIX models (Table 3). The informative model for MaxB was unique in that diameter of the largest individual branches could be regressed against data for the specific quadrant of the largest branch. The MaxB informative model selection process identified differences in branch size according to the branch's "condition" (i.e., branch was alive/dead). Live branches had larger diameter than dead branches for redwood and Douglas-fir (Figure 3). As with our BIX models, the quadratic relationship with tree size (dbh + dbh^2) improved model fit. Distance from the coast and its interaction with species were also included in the informative model, indicating that Douglas-fir MaxB was slightly larger further inland while redwood MaxB was larger near the coast (Figure 3). The AICc-derived MaxB model had the lowest AICc values and was the most likely of the four models. The AICc model selection procedure excluded our stand density variables. The two inventory models did include stand density, but its effect was minor. The stands we sampled had relatively low stand densities (Supplemental File, Table S3), and model coefficients for stand density were small (i.e., not very influential) and uncertain (Table 3; Supplemental File, Tables S9–S12). This suggested that MaxB was primarily affected by local competition from neighboring trees adjacent to the largest branch as opposed to overall stand density. Though we expected both BIX and MaxB to decrease with stand density, the natural irregularity of tree spacing, size and crowns created small gaps that individual branches exploited and became the largest. Stand density does not account for these micro gaps, explaining why there was little response from MaxB.

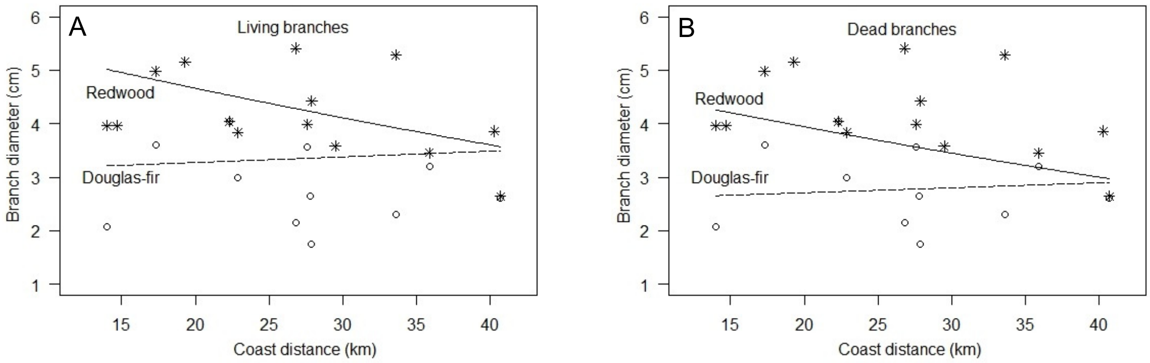

Figure 3. Influence of ecological gradient 'distance from the coast' on MaxB within the second log for living (**A**) and dead (**B**) redwood and Douglas-fir branches, and actual data for redwood (*) and Douglas-fir (o) in Mendocino County, California.

Table 3. MaxB model coefficients (s.e. as percent of coefficient in parentheses) for Mendocino County, California.

Model	Dbh Inventory		Dbh & Height Inventory		Informative Model		AICc-Derived	
Selection method	AIC		AIC		AIC		AICc	
Intercept	1.16000	(14%)	1.20200	(14%)	1.13107	(27%)	1.09300	(12%)
dbh (cm)	0.01277	(49%)	0.01946	(39%)	0.02516	(33%)	0.01364	(44%)
dbh^2	−0.00011	(52%)	−0.00016	(42%)	−0.00021	(35%)	−0.00012	(49%)
Species *	0.14680	(38%)	0.14270	(36%)	0.35479	(48%)	0.16820	(28%)
BAL ($m^2 \cdot ha^{-1}$)	−0.00115	(146%)	-	-	-	-	-	-
BA ($m^2 \cdot ha^{-1}$)	-	-	−0.00009	(1479%)	−0.00029	(741%)	-	-
Condition **	-	-	-	-	−0.09094	(69%)	-	-
HT.p	-	-	−0.18530	(76%)	−0.20894	(67%)	-	-
Coast.d (km)	-	-	-	-	0.00158	(371%)	-	-
Species × Coast.d	-	-	-	-	−0.00844	(69%)	-	-
AICc	−31.047		−28.741		−21.026		−33.978	
AIC	−35.713		−35.329		−36.741		−37.136	
Adjusted R^2	0.5173		0.5237		0.5795		0.5295	

* Species dummy variable: redwood = 1; Douglas-fir = 0. ** Condition: sample branch dead = 1; live = 0. MaxB = diameter of largest branch within second log (cm). Response = $MaxB^{0.33}$.

While BIX was easier to model and is important for understanding a tree's general branch development, MaxB is important when determining log and lumber grades [14,32,33]. Branch diameter models were fit to the data from control plots. These plots were located in areas that did not appear to have been harvested or otherwise disturbed at the time when the adjacent "harvest" and "herbicide" treatment plots were most recently treated. Branch diameters were best predicted with the more parsimonious AICc-derived models for both BIX and MaxB because models with the lowest AICc value were closest to "reality" [27]. Though the informative models were not the best models, they still provided insight into branch diameter response to tree, stand, and environmental variables.

3.3. Branch Growth Models

Branch growth response (BGR) ranged from −0.94 to 14.81 for harvested plot branches averaging 3.2 cm diameter, and −0.93 to 1.61 for herbicide plot branches averaging 2.6 cm diameter.

Post-treatment increase in branch growth was short-lived, often not lasting more than five years. However, in some cases, BGR was extremely high. For example, there were branches growing at around ten times the pre-treatment rates in the harvested plots (Supplemental File, Table S2). The average branch growth for a harvested plot was around 2.5 times the pre-harvest rate. The average living branch diameter was approximately 3 cm for Douglas-fir, and the pre-harvest branch growth was approximately 0.63 mm· $year^{-1}$. Under this scenario the branch diameter would increase to ~4.6 cm over five years. A sound knot over 5 cm or a loose knot of 3.18 cm reduces Douglas-fir 2 × 4 lumber from a construction/standard grade to a utility or stud grade. Stud and utility grades are worth about 25% less than construction/standard grades [22].

The best-fitting model of branch growth response (BGR) included the variable SDI removed (SDIm.r) (Table 4; Supplemental File, Table S13). This was expected to approximate response to the amount of occupied growing space liberated by removal (harvest) or treatment (herbicide) of neighbor trees within each plot. The interaction between plot type (i.e., treatment type) and SDIm.r indicated that BGR differed between the harvest treatment physically removing trees and herbicide treatment that left tanoak standing (dead). The interaction between period and plot type indicated that branch growth response—in terms of ratio of post- to pre-treatment growth rate—was greater in the first post-treatment period (0–5 years) than growth in the second period. The herbicide treatment plots had less decrease in branch growth in the second period than the sharper decrease in branch growth during the second period (5–10 years) in harvested plots (Table 4).

Table 4. Branch growth response (BGR) model for Mendocino County, California.

BGR Model Variables	Coefficient	s.e.
Intercept	−0.34262	(735%)
Plot.type *	−2.84374	(56%)
Period	−0.36712	(162%)
sqrt(dbh)	0.61700	(49%)
SDIm.r	0.00129	(262%)
Species **	−1.23171	(44%)
SDI (metric)	−0.00152	(73%)
PH5A (mm)	−3.29443	(25%)
Plot.type * × period	−1.65798	(48%)
Plot.type * × SDIm.r	0.00720	(55%)

* Treatment dummy variable: herbicide = 1; harvest + herbicide = 0. ** Species: redwood = 1; Douglas-fir = 0. BGR = ratio of average growth for the first and second five-year periods to pre-treatment radial growth increment: ((post-treatment − pre-treatment)/pre-treatment). s.e. as percent of coefficient in parentheses. AICc = 498.36, AIC = 495.72, Adjusted R^2 = 0.42.

Plotting modeled estimates of BGR across the range of sampled tree sizes, stand density, and SDI removed depicted the magnitude of their influence on redwood and Douglas-fir BGR after each treatment. Douglas-fir branches responded with a greater increase in the rate of branch diameter growth after treatment than redwood. Stand density negatively influenced BGR for both species. Trees with larger dbh had more BGR in Douglas-fir and redwood. Redwood trees in harvested plots had positive response for the entire range of sampled tree sizes in the first period, but only trees with dbh larger than ~56 cm had positive BGR in the second period. Douglas-fir in harvested plots had positive BGR in the second period among trees with dbh down to ~30 cm. The BGR in herbicide plots was positively influenced by increasing dbh as well, but redwood was predicted to only have positive BGR above ~48 cm dbh. The second period response in herbicide plots was positive for redwood trees over ~56 cm dbh, which was the same in the harvested plots. Douglas-fir in herbicide treatment plots was predicted to have positive BGR for trees over ~23 cm dbh in the first period and for trees over ~32 cm dbh in the second period. Branches growing well before treatment (herbicide or harvest) did not respond as much as branches exhibiting slow pre-harvest growth (PH5A; Table 4).

The positive relationship of dbh and branch growth differed from the branch diameter models because the BGR model only applies to living branches. A large tree with a long crown (i.e., high crown ratio) reflects high tree vigor and abundant resource availability [34]. Vigorous trees have more carbohydrate available for growing branches within the second log. Redwood trees in harvested plots had positive response for the entire range of sampled dbh in the first period, but BGR had dropped off in the second period (Figure 4). Douglas-fir had positive BGR in the second period among the larger trees. Though the BGR was larger for Douglas-fir, the rate of change with dbh was the same for both species. We held SDIm.r at the mean for each plot type to show the expected growth in each treatment type for each species. The harvested treatment had about twice the mean SDIm.r as the herbicide treated plots, explaining why predicted BGR was lower following herbicide only treatment (Figure 4).

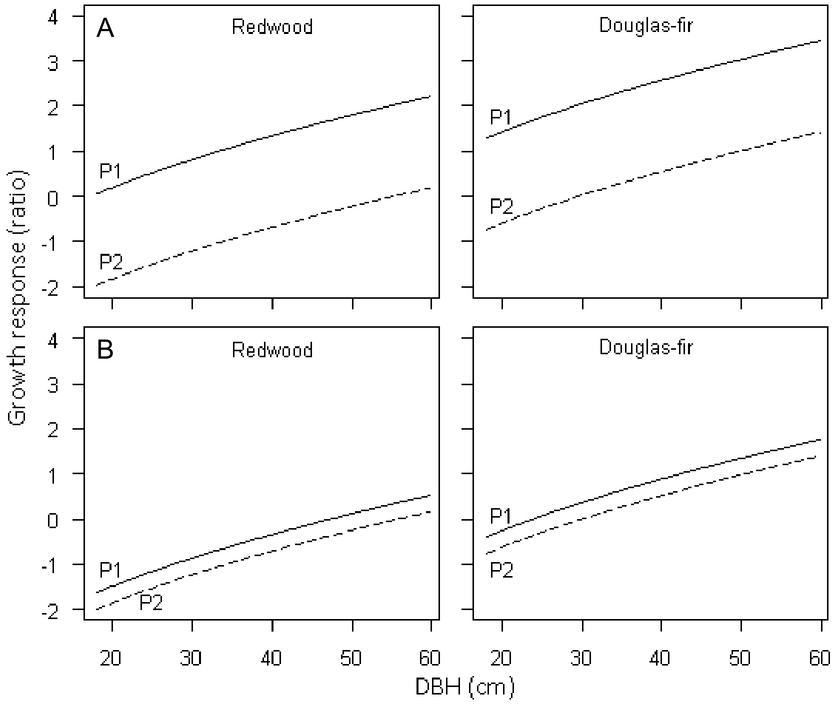

Figure 4. Redwood and Douglas-fir branch growth response (BGR) to increasing dbh for harvest + herbicide (**A**), and herbicide (**B**) plot types in the first 5-year period (P1) and second 5-year period (P2) after treatment in Mendocino County, California. The model variable SDI removed was fixed at the means for each plot type to show relationship between BGR and dbh.

Stand density negatively influenced branch growth in both treatments. Stands with the lowest observed stand densities after treatment had branches that were predicted to release at almost twice the rate of branch response for conifers at the highest observed post-treatment stand densities. On average, redwoods in harvested stands had positive BGR across all sampled densities in the first period (Figure 5). By the second period, redwood branch growth rate declined to less than pre-harvest rates. Douglas-fir BGR was greater than redwood BGR in both periods. Even in the second period, Douglas-fir BGR was positive at densities below 1200 metric SDI. This is approximately 80% of maximum SDI (1500) for Douglas-fir [29]. Redwood in herbicide plots had negative BGR in the first and second period for all observed stand densities when holding dbh at the mean. The average-sized redwood in herbicide treated plots may not have released much because tanoak crowns were competing more with small and mid-sized trees. By the time these tanoak canopies had disintegrated, the larger conifer crowns had probably grown into gaps higher in the canopy (above the tanoak) and were shading and hindering the release of second-log branches below.

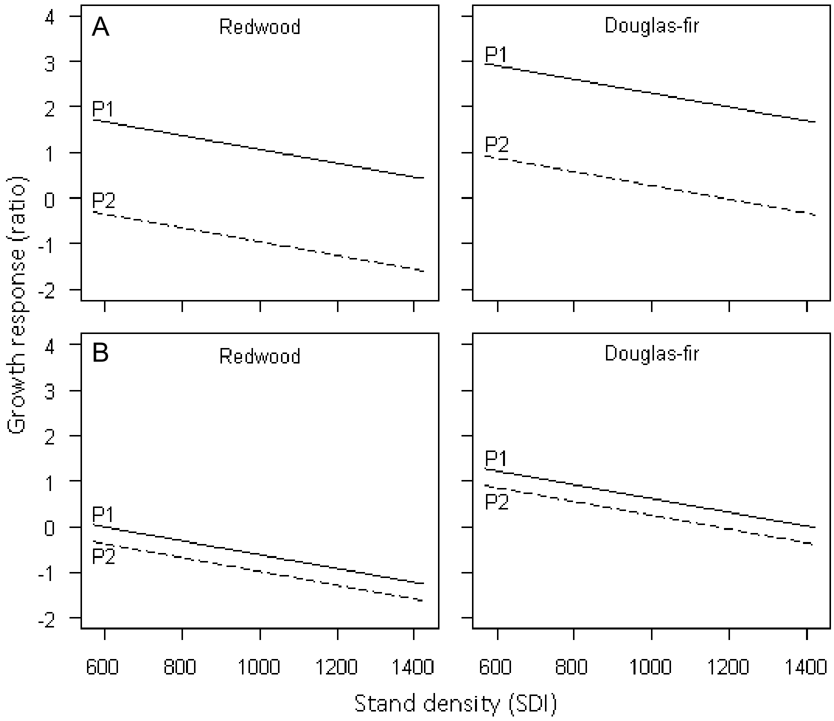

Figure 5. Redwood and Douglas-fir branch growth response to increasing post-treatment SDI for harvest + herbicide (**A**), and herbicide (**B**) plot types in the first 5-year period (P1) and second 5-year period (P2) after treatment in Mendocino County, California. Model variable SDI removed was fixed at the means for each plot type to show relationship between BGR and metric SDI.

Response of branches in the second log to treatment intensity (SDIm.r; the amount of stand density removed or treated within each stand) varied among species and treatment type (Figure 6). In the first 5-year post-treatment period, redwood did not have positive BGR to SDIm.r until ~400 SDI was removed from the stand in both the harvested and herbicide plots. In the second period, redwood only had positive BGR after greater than ~625 SDI was removed or treated in the stand. Douglas-fir BGR for the herbicide treatment plots was positive at all levels of SDIm.r in the first and second periods. Douglas-fir in harvested plot types had positive BGR above ~275 SDIm.r in the first period. In the second period, harvested plot BGR was negative until at least ~500 SDIm.r. Although the harvested plot type had less branch growth at lower SDIm.r than the herbicide plots, SDIm.r from harvested stands averaged ~580 whereas the herbicide treatment averaged ~270 SDIm.r. At these levels, BGR in the harvested plots was above BGR in the herbicide treatment plots in the first period and equal or greater in the second period. Branches in the herbicide plots exhibited a more gradual decline in BGR over the two periods.

The BGR model predicted the largest increase in branch growth in response to SDI removal in plots where conifers had been harvested in addition to herbicide treatment of tanoak. Tanoak treated with herbicide were killed but remained standing in the plot. Tanoak can retain dead leaves for several years after their death [35]. In the herbicide-treated stands, these dead tanoak tree crowns could have reduced the amount of light reaching the lower canopy and second-log branches on conifers. BGR in the herbicide-treated stands without harvest may have been delayed until the tanoak crowns collapsed around the end of the first post-treatment period. The release should have carried into the beginning of the second five-year period, but the effect may have been limited as each conifer's own upper branches grew and shaded their own second-log branches. The reduction of BGR with increased shade is consistent with the hierarchal order of branch development for loblolly pine, where branch diameter growth was least important [36].

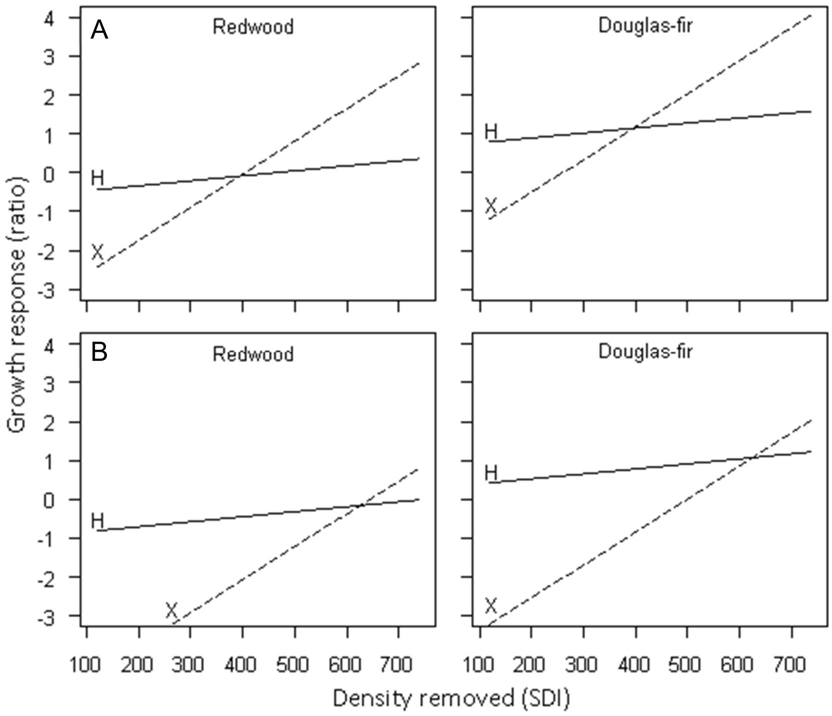

Figure 6. Redwood and Douglas-fir branch growth response to SDI removed in herbicide (H) and harvest + herbicide (X) plot types in the first 5-year period (**A**) and second 5-year period (**B**) after treatment in Mendocino County, California.

Douglas-fir responded to the harvest and herbicide treatments more than redwood throughout the range we sampled. Redwood consistently had larger branches than Douglas-fir over the range of sampled dbh, stand density, and distance from the coast (although the difference diminished with increasing distance from the ocean). Conversely, in the more mesic Del Norte County, Douglas-fir had larger branches than redwood but redwood had greater BGR in precommercial thinned stands than Douglas-fir [16]. These differences may not be conflicting because the stands, treatments, and sampling methods differed. We were sampling multiaged stands and modeling percent release, as opposed to branch size in younger even-aged stands. The conifers in our mixed multiaged stands behaved similarly to uneven-aged Pacific silver fir and eastern white pine [17]. Like the branches of shade-tolerant Pacific silver fir that developed in partial shade, our redwood branches developing in partial shade may have survived longer and grown more slowly than would be expected in high light [37]. For our Douglas-fir to behave like eastern white pine, also of intermediate shade tolerance, and undergo accelerated crown rise in partial shade (i.e., lower branches becoming shaded, ceasing growth, and dying sooner) is consistent with our finding that Douglas-fir branches were smaller than redwood branches in multiaged stands.

While log size affects sawmill efficiency, knot size is important in determining performance and value of structural lumber, the primary use for Douglas-fir lumber [38]. Loose knots originating from persistent dead branches may not impact structural lumber grade, provided that they are not large. Conversely, larger knots may be acceptable or even desirable for some "appearance" or "exterior" applications, provided that they are intergrown (i.e., not loose) and do not impact the integrity and stability of the wood in service. Redwood is valued for appearance and exterior applications. Keeping redwood branches alive to produce lumber with intergrown knots may become more important and valuable to forest owners than simply maximizing total stemwood volume yields. Maximizing value in mixed stands of Douglas-fir and redwood will likely involve manipulating spatial pattern and species composition to create localized variations in shade and competition [39]. For example, tanoak might be retained near young redwood to restrict branch growth and promote crown rise and production of knot-free clearwood after small lower branches have fallen. Tanoak could be removed at the next stand entry timed to release second-log branches from competition. As Douglas-fir reach the overstory and grow taller than tanoak over time, they may benefit from shade cast by tall conifer neighbors to control branch size [40]. Retention of overstory conifers might be balanced to provide partial shade controlling Douglas-fir branch development in the upper logs while allowing enough light to pass through the canopy and keep lower branches alive in redwood.

4. Conclusions

We studied branch size and branch growth in mixed multiaged redwood and Douglas-fir stands. We modeled branch size in terms of BIX and MaxB. Topographic variables such as aspect, slope, and flow accumulation did not improve model predictions of branch size. Most influential were tree species, tree size, and for redwood, distance from the coast. Stand density impacted BIX but not MaxB. To provide flexibility, we created progressively simpler models for predicting branch size that included variables derived from forest inventory data. Although predictions of second-log branch diameters were less precise using the simpler models, they still provide useful estimates. Forest managers seeking to minimize BGR have options. According to our regression analysis, less BGR occurs after treatment in higher density stands and following lower reductions in SDI. In our sample, larger overstory trees—many of which also had larger branches—had greater BGR. Douglas-fir had greater BGR than redwood, which is a concern if excessive knot size causes the structural lumber milled from second logs to be downgraded. Given that BGR appears to be short-lived in multiaged stands, more frequent light entries might be needed to keep redwood's lower branches alive while maintaining stand density at levels needed to control branching and knot size in Douglas-fir structural lumber.

Supplementary Materials: The following are available online at www.mdpi.com/1999-4907/7/7/147/s1, Figure S1: Depiction of Control plot number 8606 the large circle represents the 0.04 ha plot area. The small circles are the trees within the plot depicting their actual dbh and the lines are the sample tree branches the branch length and diameter is accurately depicted at Mendocino County, California, Figure S2: Depiction of Harvest plot number 8611 MRC California. The large circle represents the 0.04 ha plot area. The small circles are the trees within the plot depicting their actual dbh and the lines are the sample tree branches the branch length and diameter is accurately depicted at Mendocino County, California, Figure S3: Depiction of Herbicide plot number 8610 MRC California. The large circle represents the 0.04 ha plot area. The small circles are the trees within the plot depicting their actual dbh and the lines are the sample tree branches the branch length and diameter is accurately depicted at Mendocino County, California, Table S1: Summary table of target tree and branch level variables for control plots Mendocino County, Table S2: Summary table of target tree and branch level variables for Herbicide and Harvest treatment plots Mendocino County, California, Table S3: Stand level summary of variables for control plot type Mendocino County, California. Flow accumulation = 1 k ten meter cells contributing water to plot, Table S4: Stand level summary of variables for Herbicide and Harvest treatment plot types Mendocino County, California. Flow accumulation = 1 k ten meter cells contributing water to plot, Table S5: BIX Informative Model (AIC) for redwood (SESE) and Douglas-fir (PSME; latent dummy variable) Mendocino County, California, Table S6: BIX Dbh & Height Inventory Model (AIC) Mendocino County, California, Table S7: BIX Dbh Inventory Model (AIC) Mendocino County, California, Table S8: AICc-derived Model for BIX including Dbh and Height at Mendocino County, California, Table S9: MaxB Informative Model (AIC) Mendocino County, California, Table S10: MaxB Dbh & Height Inventory Model (AIC) Mendocino County, California, Table S11: MRC MaxB Dbh Inventory Model (AIC) Mendocino County, California, Table S12: AICc-derived model for MaxB at Mendocino County, California, Table S13: MRC percent growth response Model (AIC) Mendocino County, California.

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Conflicts of Interest: The authors declare no conflict of interest.

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