APPLIED RESEARCH

For. Sci. 61(4):780–789
http://dx.doi.org/10.5849/forsci.14-178

silviculture

Twelve-Year Response of Coast Redwood to Precommercial Thinning Treatments

Kevin L. O'Hara, Lakshmi Narayan, and Kathleen G. Cahill

Six precommercial thinning treatments and two types of control treatments were established in 9- to 11-year-old, even-aged coast redwood (*Sequoia sempervirens* (D Don) Endl.) forests in coastal California to study the impact of thinning on stand and individual tree level volume growth. Species composition was 74% redwood and 23% coast Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco). Treatments were replicated across seven stands and monitored for 12 years. Data analysis included both analysis of variance (ANOVA) to compare treatment means and mixed-effects modeling to examine broader trends and important variables affecting increment. The ANOVA used target treatment densities as the predictor variable, whereas the mixed models used actual posttreatment densities. Results showed great variation within treatments, largely because high variability in spatial patterns of regeneration resulted in difficulty achieving target initial treatment densities. Ingrowth from sprouting redwood and, to a lesser extent, broadleaved trees and seedlings of other conifers also contributed to large variation in density levels. Results indicate tree increment generally decreased with increasing density and stand increment increased with density. Total stand increment, including both initial trees and ingrowth, was highest at the 4 × 4-ft spacing and lower in control treatments and thinning treatments that left lower densities. Both analysis procedures provide useful information to guide evaluation of thinning studies and complementary results to guide management regimes.

Keywords: density management, *Sequoia sempervirens*, vegetative reproduction, even-aged, growth and yield

Precommercial thinning is a common treatment in many even-aged stands to reduce stocking and concentrate growth on a smaller number of select trees. These "early" treatments correspond to the period after regeneration establishment, and before trees have reached a commercial size. The reduction in density is important for increasing growth rates of residual trees and enhancing productivity into the stand's commercial stages. Early thinning can achieve other objectives related to stand structure such as favoring certain species, favoring well-formed trees, or promoting old forest stand features. In stands with primarily seedling-origin trees or high forests, precommercial thinning can result in a well-spaced stand of desirable trees (Reukema 1975). However, in stands with primarily coppice or sprout regeneration, thinning may stimulate a sprouting response that negates the intended reduction in density. Evaluations of thinning response should consider the growth of residual trees, the potential for a rapid and significant amount of sprout reproduction, and the effect on stand structure.

Coast redwood (*Sequoia sempervirens* (D Don) Endl.) is an evergreen conifer species growing in cool temperate coastal regions of California and southwest Oregon. It is noted for its large size and longevity. Redwood is shade tolerant, fast growing, and adapted to a variety of disturbances, including fire and flooding (Lorimer et al. 2009, Ramage et al. 2010). It is among the most productive conifers with periodic increment measured over 1,080 ft^3/ac/yr (75 m^3/ha/yr) (Jones and O'Hara 2012). Redwood is unique in that it reproduces vegetatively through vigorous sprout production, an apparent fire-adaptive strategy (Lorimer et al. 2009, Ramage et al. 2010). Sprouts originate from lignotubers (Del Tredici 1998) and dormant buds and therefore may emerge from cut stumps, standing trees, down logs, or roots. Redwood also regenerates by seed.

Redwood is successfully managed with even-aged or multiaged systems by private industrial, public, and small private landowners (Thornburgh 2000). In even-aged stands, usually following clearcutting, sprout regeneration develops quickly as vigorous

Manuscript received September 23, 2014; accepted January 14, 2015; published online March 5, 2015.

Affiliations: *Kevin L. O'Hara (kohara@berkeley.edu), University of California-Berkeley, Berkeley, CA. Lakshmi Narayan (shmi.narayan@gmail.com), University of California-Berkeley. Kathleen G. Cahill (kategardcahill@gmail.com), University of California-Berkeley; current address: Mendocino Redwood Company, Ukiah, CA.*

Acknowledgments: *The authors are grateful for all the assistance provided by Amy Barg, William Baxter, Marc Jameson, Fred Postler, Brandon Rodgers, Lynn Webb, and Fay Yee during this study. Jackson Demonstration State Forest, California Department of Forestry and Fire Protection also provided support to set up and monitor this study, as well as funding to support this analysis. This work was partially supported by the USDA National Institute of Food and Agriculture (NIFA).*

sprout clumps. Individual redwood stumps can produce over 100 sprouts per stump (Neal 1967), resulting in highly aggregated spatial patterns of regenerating trees. It is therefore common to interplant redwood or coast Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco) in spaces between sprout clumps to provide more uniform spatial patterns of stocking (Jameson and Robards 2007). Thinning of sprout clumps is effective at increasing size of residual sprouts in full sunlight but with little apparent effect in partial shade (Boe 1974, Cole 1983). In poor light environments, sprout clumps may completely die (O'Hara and Berrill 2010).

A typical young, even-aged redwood stand often includes dense sprout clumps and other saplings. Precommercial thinning is often considered for these stands because it reduces overall density and produces a more uniform spatial pattern by thinning individual sprout clumps. However, precommercial thinning of a sprouting species, such as redwood, can stimulate a sprouting response from residual trees and cut stumps where excessive ingrowth negates the reduction in density from the thinning. Additionally, early thinning in some parts of the redwood range can encourage bear damage that is often concentrated on the largest and most vigorous trees (Giusti 1990, O'Hara et al. 2010).

Previous studies with early spacing in young redwood stands include those focused on even-aged stand development for timber or similar objectives (e.g., Lindquist 2004, 2007) and studies focused on restoration thinning or directing stand development toward old forest structures (e.g., Keyes et al. 2008, O'Hara et al. 2010, 2012, Teraoka and Keyes 2011, Berrill et al. 2013). Both types of studies have occurred in even-aged redwood stands and used, or simulated, similar types of thinning methods. Although the objectives are different, the resultant effects on early stand development are comparable. Long-term results from these studies are limited. Lindquist's (2004, 2007) long-term Caspar Creek study on Jackson Demonstration State Forest documented thinning in 19-year-old redwood stands over 17 years at densities ranging from 100 to 300 trees/ac and in untreated controls. Results showed positive effects of thinning on average tree size but no effect on stand cubic volume increment. Because young redwood stands grow rapidly, thinning at age 19 may be considered late for a precommercial thinning when rotations may be only 50 years. For example, pretreatment average diameter was already 8 in. for trees over 4.5 in. at dbh at the initiation of Lindquist's study. In a restoration thinning using variable-density thinning (Carey 2003, O'Hara et al. 2012) in 12- to 15-year- old redwood–Douglas-fir stands, tree growth was also enhanced by thinning 4 years after treatment, but bear damage was concentrated in thinned treatments (O'Hara et al. 2010). No other study has presented early thinning results in redwood.

In this study, we document results 12 years after precommercial thinning in 8- to 11-year-old redwood stands on Jackson Demonstration State Forest. The objectives were to document the effects of early precommercial thinning on growth, ingrowth, and mortality in predominantly redwood stands originating after clearcutting.

Methods

Study Design

The study area was located within the Jackson Demonstration State Forest, a 48,500-ac forest in Mendocino County, California. The climate is Mediterranean, characterized by a pattern of high rainfall in winter and cool, dry summers with coastal fog. Precipitation in the Caspar Creek watershed averages approximately 51 in./yr. Coast redwood was the dominant species with significant amounts of coast Douglas-fir. In 2012, at end of the study, redwood dominated with 74% of trees (63% sprouts and 11% planted), coast Douglas-fir 23%, and grand fir (*Abies grandis* (Dougl. ex D. Don) Lindl.) 3%. Other species present included tanoak (*Notholithocarpus densiflorus* (Hook. & Arn.) Manos et al.), western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), and Scouler's willow (*Salix scouleriana* Barratt ex Hook.). Competing vegetation included blueblossom (*Ceanothus thyrsiflorus* Eschsch.), evergreen huckleberry (*Vacinium ovatum* Pursh), and a variety of grasses. Prior to the harvests in the 1980–1990s, these stands were first harvested in the early 1900s.

The north fork of Caspar Creek (39°22.3′ N, 123°43.2′ W) is part of a larger, long-term watershed study examining effects of forest management on hydrologic processes (Reid and Lisle 2010). The study area is located approximately 6 miles from the Pacific coast. From 1989–1991, "second-growth" stands in the north fork drainage were harvested in a series of clearcuts (Figure 1). After harvest, approximately half of these clearcut units were broadcast burned, and hardwoods were treated with Triclopyr (3,5,6-trichloropyridinyloxyacetic acid) (Table 1). All units were interplanted, between redwood sprout clumps, with plug-1 redwood and Douglas-fir seedlings totaling approximately 150 trees/ac.

In 2000, a study area was selected within each of seven clearcuts using aerial photos. These study areas were chosen because they were large enough to include a treatment block and had sufficient stocking to support a thinning study. These study areas were located away from stand edges and any residual (uncut) trees. A "block midline" was cut through the thick shrub and tree regeneration layer in the clearcut units. On either side of this midline, square spacing treatment areas were established (Figure 2). Treatment areas (including controls) were randomly assigned locations along the midline. Treatment areas varied in size to accommodate a single circular measurement plot along with a buffer. When possible, due to existing stand density and unit sizes, treatments included spacings approximating 4, 8, 12, 16, 20, and 24 ft (Table 1). Actual spacings ranged higher and lower than the targets due to the highly variable spatial patterns of regeneration (Table 2). For example, all of the 4-ft spacings were well below the target density of 2,723 trees/ac. Control treatment plots, with and without vegetation control (manual cutting of shrubs), were also installed. Trees in treatment areas were marked—in order of priority—to achieve the target spacing, to favor dominant trees, and to prioritize species/regeneration types to favor redwood sprouts, then redwood seedlings, Douglas-fir seedlings, and other species.

A circular measurement plot was installed within each treatment area prior to implementation of thinning treatments. Plot sizes varied from 0.2 to 1.1 ac in size and were designed to include approximately 25 trees at the target spacing (Table 2). Buffer areas outside plots, but within treatment areas, were equivalent to two trees (e.g., for 4-ft spacing, buffers were 8 ft; for 24-ft spacings, buffers were 48 ft). Only trees or sprouts greater than 4.5 ft were included as measurement trees. Within each plot, each marked (retention) tree was tagged, painted, and measured for height, height to crown base, dbh, and origin (sprout or seedling).

Thinning treatments were implemented prior to the 2001 growing season. In the summers of 2007 and 2012, all plots were visited for maintenance and remeasurement. Remeasurement protocols were similar to those in plot establishment. Notable differences were the establishment of subplots to sample ingrowth in the wider spacings. These subplots were randomly chosen quarters within the established circular plots in the 20- and 24-ft spacings. During the

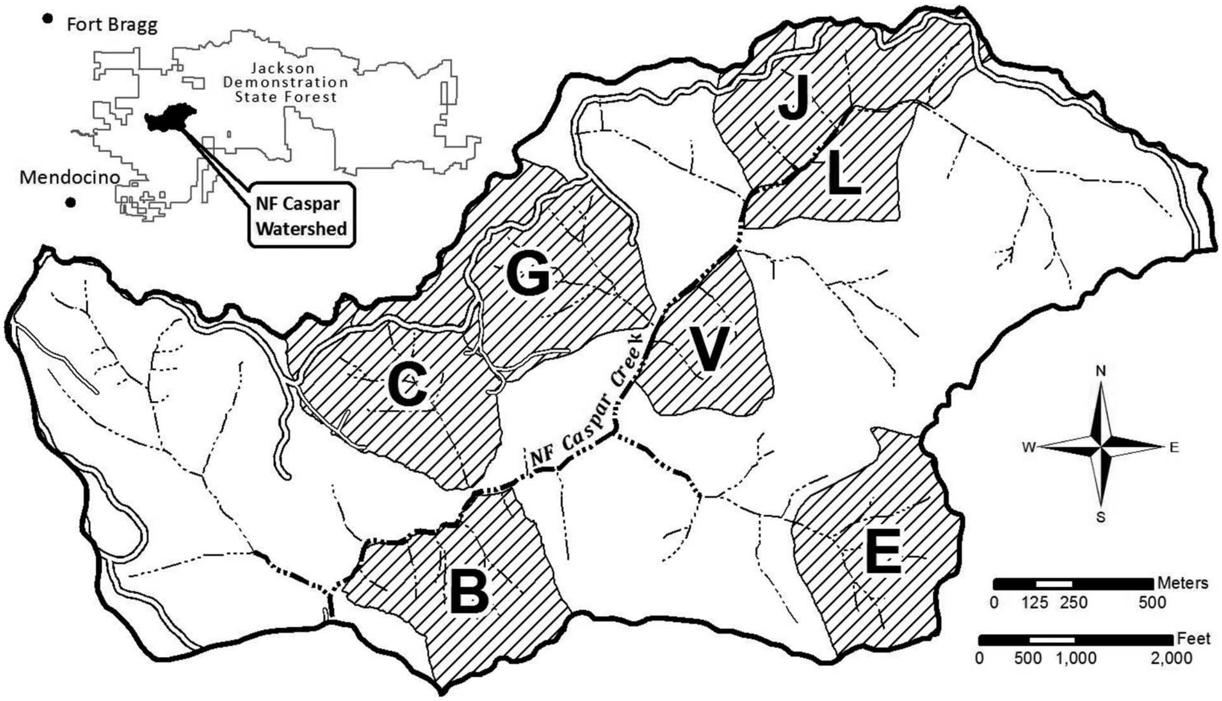

Figure 1. Map of the north fork of Caspar Creek showing units included in precommercial thinning study.

Table 1. Clearcut unit management history and spacing treatments included.

Unit	Year harvested	Postharvest treatments	Aspect	Spacings included (ft)
B	1991	None	NW	4, 8, 12, 16, 20, 24, C
C	1991	None	SE	4, 8, 12, 16, 20, 24, Cv
E	1990	Burn, herbicide	NE	4, 8, 12, 16, 20, 24, C, Cv
G	1991	Burn, herbicide	SE	4, 8, 12, 16, 20, 24, Cv
J	1990	Burn, herbicide	S	4, 8, 12, 16, 20, 24, C, Cv
L	1990	Burn, herbicide	N	4, 8, 12, 16, 20, 24, Cv, Cv
V	1990	None	NW	8, 12, C

Spacings were included if space permitted and if appropriate pretreatment spacing provided sufficient trees. C refers to control plots without vegetation control and Cv to control plots with vegetation control. NW = northwest, SE = southeast, NE = northeast, S = south, N = north.

intense period of competition following sprouting, redwood stump sprouts often lose dominance by adopting a more branchlike angle (i.e., lower angle relative to the horizon) from the stem. These sprouts were included as trees (initial or ingrowth) only when their angle to the horizon was greater than 45°.

Several plots were dropped from the analysis due to plot boundary errors. These included the control plots in units C, G, and L; the control/vegetation plots in units B, E, and V; and the 4-ft spacing treatment in unit V. Both units C and L had two control plots each: Both were dropped in unit C and one was dropped in unit L. Additionally, 20 trees were dropped from individual tree analyses because of negative volume increment over the 12-year analysis period.

Analysis

Our analysis consisted of two major parts: Comparison of treatment means for individual tree growth, ingrowth, and stand-level growth using ANOVA and, when significant, Tukey multiple comparison tests to determine which means were significantly different, and mixed-effects models to assess the effect of stand density and other variables on tree and stand volume increment, as well as ingrowth. ANOVA provides a simple comparison of means of the dependent variable; mixed-effects modeling allows the simultaneous inclusion of many predictor variables to determine which variables have the greatest effect on the dependent variable. Whereas the ANOVA models used the intended treatment spacings (e.g., 4 × 4, 20 × 20, etc.) as categorical variables in all analyses, the mixed-effects models used the actual postthinning spacings (trees/ac) as a continuous variable. This provided two complementary analyses to assess the effects of early thinning on tree and stand increment.

Over 1,000 trees were tagged and measured in the 2000 measurement of this precommercial thinning study. Additional trees were added with the development of ingrowth during the 12 years following thinning. As a result of large sample sizes and difficult field conditions, some trees were missed during measurements. Trees with missing measurements were excluded for individual tree analyses. For stand-level (unit area) analyses, missing height values were estimated with height-diameter regressions for redwood sprouts, planted redwoods, and Douglas-fir (O'Hara et al. 2014) because existing height-diameter relationships (e.g., Eng 2012) were for larger trees. Regression models included the effects of unit and thinning treatment on tree height and height–diameter relationship to accurately predict missing tree heights. There were no missing height measurements for other species. Using these models, missing heights were estimated for 20 trees in the initial 2000 measurement, 6 trees in 2007, and 2 trees in 2012. There were no trees missing only dbh measures. For trees with both height and dbh missing in a measurement, tree volume increment was estimated using plot-level averages for each measurement period. Volume increment was estimated for 33 trees in 2000, 15 in 2007, and none in 2012.

In individual tree analyses, cubic volume increment of individual trees from 2000–2012 was the dependent variable. Likewise, cubic volume increment from 2000–2012, expressed on a per acre basis, was the dependent variable for stand-level analyses. All tree cubic

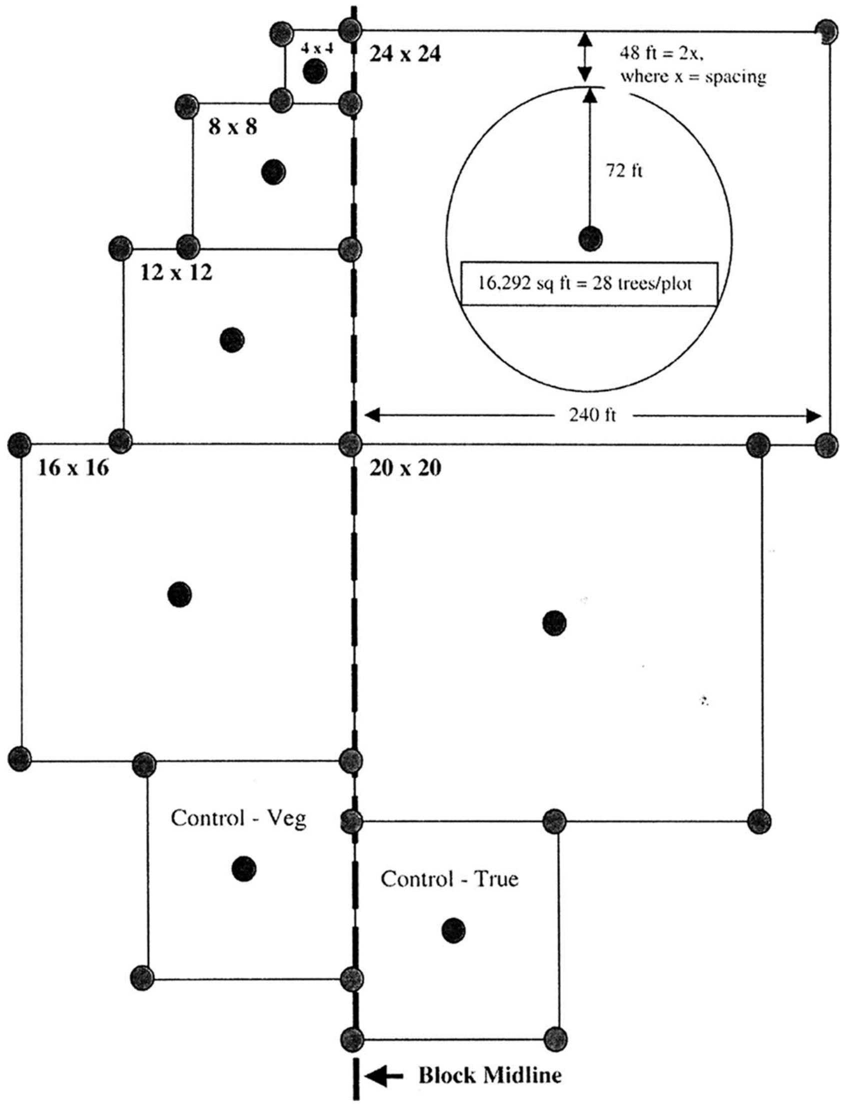

Figure 2. Example treatment and plot layout. Treatment blocks (squares) were established along midline. Circular research plots were inside treatment blocks with a buffer.

Table 2. Target and posttreatment densities in spacing treatments.

Spacing treatment (ft)	Plot sizes (ac)	Target density (trees/ac)	Mean density (trees/ac) (SD)	Range (trees/ac)	Mean basal area (ft^2/ac) (SD)
C	0.02	-	853 (120)	758–1,029	30.8 (16.9)
CV	0.02	-	885 (600)	108–1,625	35.2 (44.2)
4	0.01	2,723	856 (201)	642–1,113	76.6 (23.1)
8	0.04	681	471 (84)	337–602	23.4 (11.5)
12	0.09	303	283 (43)	203–332	20.4 (7.7)
16	0.16	170	164 (22)	132–193	11.0 (2.9)
20	0.26	109	107 (4)	100–112	8.8 (1.5)
24	0.37	76	77 (7)	67–86	7.2 (2.6)

C and CV refer to control treatments without vegetation control (C) and with vegetation control (CV). SD refers to the standard deviation.

volumes were estimated from an equation from Wensel and Krumland (1983) that assumed a 1-ft stump and 5-in. top (inner bark). Because of the large variation in initial spacing within a target spacing treatment due to heavy spatial variation between units and plots (e.g., Table 2), the initial number of trees expanded out to an acre-basis was used instead of the target spacing in all mixed-effects models. Because half of the units received a postharvest burning and herbicide treatment, this treatment could not be included in models that included "unit" as a random effect. Instead, the effect of the postharvest burning was tested separately using simple *t*-tests. Substantial ingrowth was apparent from the first measurement in 2007. To separate the effects of ingrowth from residual (i.e., "initial trees") tree growth in stand-level analyses, we calculated volumes separately for these two groups.

For our mixed-effects modeling, we followed the model-selection procedures outlined in Zuur et al. (2009). For each model, we chose a random effects structure by using Akaike's information criterion (AIC) and likelihood ratio tests to compare models with increasingly complicated random effects structures. If two models had similar AIC values and model fit, the simpler of the two models was chosen (Burnham and Anderson 2002). We used a similar approach to select variance structures, when necessary. To select fixed effects to include in our models, we used backwards stepwise regression. For individual tree analyses, many numeric variables had distributions that were extremely right-skewed. We used power transformations on initial tree volume growth and 2001 volume and a base ten log transformation on volume growth of ingrowth trees and

Table 3. Mean tree sizes for initial trees by treatment.

Spacing treatment (ft)	Mean dbh increment (cm) (SD)	Mean height increment (ft) (SD)	Mean tree volume increment (ft^3) (SD)
C	2.4 (1.6)	19.0 (11.8)	1.9 (2.3)
CV	2.6 (1.8)	19.1 (12.1)	2.3 (3.3)
4	3.6 (1.9)	20.0 (9.3)	3.9 (4.5)
8	4.8 (2.2)	26.4 (9.9)	5.1 (5.1)
12	5.8 (2.2)	27.1 (10.1)	7.3 (6.7)
16	6.2 (2.6)	23.8 (10.7)	7.1 (6.3)
20	7.2 (2.8)	23.2 (9.9)	8.6 (7.5)
24	7.1 (2.6)	23.0 (9.0)	9.2 (7.8)

Treatment	C	CV	4	8	12	16	20	24
C	-							
CV		-						
4	DV	DV	-					
8	DHV	DHV	DH	-				
12	DHV	DHV	DHV	DV	-			
16	DHV	DHV	DV	D		-		
20	DHV	DHV	DV	DV	DH	D	-	
24	DHV	DHV	DV	DV	DH	V		-

Matrix shows means that were significantly different (Tukey test, $\alpha = 0.05$) for dbh (D), height (H), and tree volume (V). The upper part of table shows means and the lower part shows the matrix of significance for tree sizes by spacing.

Table 4. Individual tree sizes and numbers of ingrowth trees by treatment in 2012.

Spacing treatment (ft)	Numbers of trees/ac (SD)	Mean dbh (cm) (SD)	Mean height (ft) (SD)	Mean volume (ft^3) (SD)
C	297.9 (295.0)	1.4 (1.1)	18.7 (11.0)	0.2 (0.3)
CV	108.3 (132.7)	1.7 (1.5)	18.2 (10.9)	0.3 (0.6)
4	107.0 (96.6)	3.0 (2.5)	23.4 (13.4)	0.8 (1.3)
8	106.6 (83.2)	3.3 (2.0)	28.5 (12.0)	1.0 (1.2)
12	160.5 (85.1)	4.2 (1.5)	32.3 (8.6)	1.2 (1.7)
16	306.9 (84.8)	4.3 (0.9)	32.3 (6.5)	1.0 (0.6)
20	325.5 (144.9)	4.8 (1.4)	32.3 (8.0)	1.4 (1.3)
24	415.9 (147.6)	4.7 (1.4)	33.5 (7.9)	1.4 (1.3)

Treatment	C	CV	4	8	12	16	20	24
C	-							
CV		-						
4	DV	D	-					
8	DHV	DHV		-				
12	DHV	DHV	DHV	D	-			
16	DHV	DHV	DHV	DV		-		
20	DHV	DHV	DHV	DV	D	D	-	
24	DHV	DHV	DHV	DHV	D	DV		-

Matrix shows means that were significantly different (Tukey test, $\alpha = 0.05$) for dbh (D), height (H), and tree volume (V). The upper part of table shows means and the lower part shows the matrix of significance for tree sizes by spacing.

initial trees per acre. Initial tree dbh was square-root transformed. Residuals from all models were plotted against fitted values and covariates to look for deviations from normality.

Results

Individual Tree Results

Twelve years after precommercial thinning, mean dbh, mean height, and mean volume of initial trees were all greatest in the widest spacing treatments. However, because of the large amount of within-treatment variation, not all differences were statistically significant ($\alpha = 0.05$). The control with vegetation control produced trees with larger mean dbh, height, and volume compared to the control without vegetation control, but none of these differences were significant (Table 3). Trees in both control groups were significantly smaller than all treatments 8 ft or greater. Ingrowth trees were larger and more numerous at wider spacings (Table 4). In the 24-ft spacing, mean dbh was approximately 3 times the dbh in the controls, and mean tree volume was nearly 6 times the volume in the controls.

The mixed-effects model for individual tree growth included the initial trees/acre, species, 2001 volume, interactions between trees/ac and species, and 2001 volume and species (Table 5). Initial trees/ac had a negative effect on tree growth, and initial tree volume had a positive effect on tree growth, indicating that trees grew more rapidly at lower densities and that larger trees grew more than smaller trees in absolute terms. This positive effect of initial tree size was strongest for redwood sprouts and Douglas-fir. The initial volume of grand fir and planted redwoods had a less of an effect on their growth. However, redwood sprouts tended to have the greater initial volume (1.056 ± 0.999 ft^3) than other tree types (planted redwood: 0.139 ± 0.317 ft^3, Douglas-fir: 0.0673 ± 0.0827 ft^3, grand fir: 0.0132 ± 0.0211 ft^3), which makes it difficult to disentangle the effect of initial volume versus tree type on tree growth.

Table 5. Mixed models used for individual tree and stand-level analyses. The baseline species for comparison is redwood sprouts.

Individual tree models			
	Fixed effects		Random effects
Model	Variable	Coefficient (*P* value)	Variable
Initial trees	Intercept	0.3399 (0.1778)	Unit
	InitTPA	−0.2354 (<0.0001)	Unit × InitTPA
	Spp:rp	0.2782 (0.1799)	Unit × Spp
	Spp:df	1.1120 (<0.0001)	
	Spp:gf	1.5215 (0.0082)	
	2001Volume	2.9804 (<0.0001)	
	InitTPA × Spp:rp	0.0924 (0.0004)	
	InitTPA × Spp:df	−0.0152 (0.4579)	
	InitTPA × Spp:gf	−0.0217 (0.7418)	
	2001Volume × Spp:rp	−1.0029 (<0.0001)	
	2001Volume × Spp:df	−0.1900 (0.2562)	
	2001Volume × Spp:gf	−1.5251 (0.0014)	
Ingrowth	Intercept	0.9571 (<0.0001)	Unit
	InitTPA	0.0168 (0.8086)	Unit × InitTPA
	Spp:rp	1.1156 (<0.0001)	
	Spp:df	1.1851 (<0.0001)	
	Spp:gf	1.7820 (<0.0001)	
	InitTPA × Spp:rp	−0.6273 (<0.0001)	
	InitTPA × Spp:df	−0.5180 (<0.0001)	
	InitTPA × Spp:gf	−0.7831 (<0.0001)	
Stand-level models			
	Fixed effects		Random effects
Model	Variable	Coefficient (*P* value)	Variable
Initial trees	InitTPA	2.0779 (<0.0001)	Unit
Ingrowth	InitTPA	−0.2589 (<0.0001)	None

Variable names: InitTPA = initial trees/ac; Spp:rp = planted redwood; Spp:df = Douglas-fir; Spp:gf = grand fir; 2001volume = tree volume in 2001; Unit = clearcut unit; Spp = species. The upper part of table shows means and the lower part shows the matrix of significance for tree sizes by spacing.

Stand-Level Results

Mortality was low during the 12-year study and relatively constant across the lower density thinning treatments but higher in the controls and higher density treatments (Figure 3). Basal area ranged from approximately 7 to 77 ft^2/ac after treatment (Table 2) and was highest in the 4-ft spacing. Stand-level volume growth was greatest in the 4-ft spacing treatment and lower in controls and all wider spacings (Table 6). However, the only significant differences for either initial trees or ingrowth were between the narrowest and widest spacings. Standard deviations were high for all treatments and, in the case of the control with vegetation control, exceeded the mean. Stand totals for ingrowth volume were lowest in the control treatments and increased with increasing spacing treatments (Table 6).

Cumulative volume increment (including ingrowth) by spacing treatment was greatest in the 4-ft spacing and was less in the controls and in wider spacing treatments. Cumulative volume increment in the 4-ft spacing was nearly three times that of the 24-ft spacing. T-tests indicated no significant differences in stand volume increment between burned and unburned units for either the initial trees ($P > 0.904$) or ingrowth trees ($P > 0.597$).

The mixed model for stand volume increment included the number of initial trees as the only fixed variable (Table 5). For the ingrowth mixed-effects model, the number of initial trees was also the only fixed variable included, but for the ingrowth model this coefficient was negative. These results indicate greater initial tree volume increment when density is high but greater opportunity for ingrowth when density is low. Ingrowth trees contributed a large proportion of volume in wider spacings: In the 24-ft treatment, ingrowth volume was approximately 41% of the total 12-year increment compared to less than 4% in the 4-ft treatment (Table 6; Figure 4).

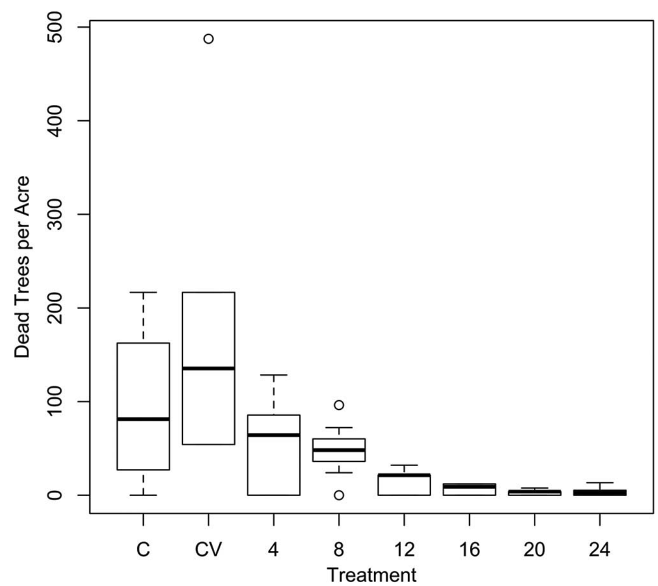

Figure 3. Mortality from 2001–2012 by treatment. The dark line shows the median, and boxes show the interquartile range. Whiskers show the range, excluding outliers, which are shown by open circles.

Table 6. Volume increment by initial trees and ingrowth per acre over the 12-year study.

Spacing treatment (ft)	n	Volume increment (ft^3/ac)		
		Initial trees (SD)	Ingrowth (SD)	Total
C	4	1,638.2 (917.1)	39.4 (73.7)	1,677.6
CV	6	2,065.1 (2196.4)	56.3 (83.8)	2,121.4
4	6	3,186.6 (1097.6)	111.3 (156.2)	3,297.9
8	7	2,186.2 (1030.7)	107.3 (91.1)	2,293.4
12	7	1,942.8 (840.3)	193.2 (135.6)	2,136.0
16	6	1,125.0 (391.1)	317.5 (89.6)	1,442.5
20	6	882.1 (412.1)	369.5 (208.2)	1,251.6
24	6	666.3 (314.6)	467.0 (244.6)	1,133.3

Treatment	C	CV	4	8	12	16	20	24
C	-							
CV		-						
4			-					
8				-				
12					-			
16			S			-		
20	I	I	S				-	
24	I	I	SI	I	I			

Matrix shows means that were significantly different (Tukey test, $\alpha = 0.05$) where S represents the initial trees and I represents ingrowth.

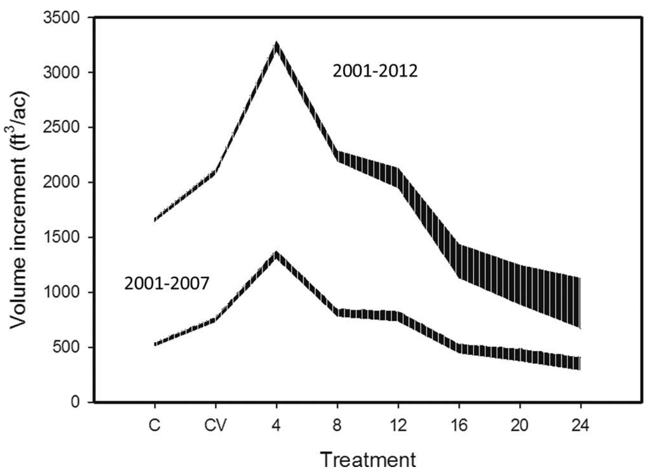

Figure 4. Cumulative mean volume increment and ingrowth from 2001 through 2007 and 2001 through 2012 by treatment. Shaded area in each relationship is the proportion of volume increment that was from ingrowth.

Discussion

Coast redwood develops highly aggregated spatial patterns, particularly in young stands. Following clearcut harvest, cut stumps may produce over 100 sprouts (Neal 1967) forming confined, but highly competitive, microenvironments dispersed among larger spaces where seedling regeneration may, or may not, become established. Several generations of cut stumps may further accentuate the aggregated nature by producing expanded clumps of clonal sprouts (Douhovnikoff et al. 2004). Over all plots in our study, redwood sprouts comprised 63% of all trees and redwood seedlings another 11%. Other sprouting species, such as tanoak, Pacific madrone (*Arbutus menziesii* Pursh), and several shrubs may also form sprouts clumps along with redwood. Seedling regeneration or planted seedlings of redwood, coast Douglas-fir, grand fir, and other conifers may reproduce in the spaces between clumps. The resultant early stand structure is characterized by extreme variability in tree sizes, growth rates, and spatial patterns of tree locations. Silvicultural studies in young redwood stands are therefore hampered by requiring either extremely large plot sizes, many plots, or having to accept high levels of variation. This study attempted to overcome these difficulties by installing a wide range of treatments in seven different stands.

Individual tree growth increment for residual trees following the original thinning was greater at wider spacings (Table 3) as is commonly reported in other thinning studies, including thinning studies in redwood (Oliver et al. 1994, Lindquist 2004, O'Hara et al. 2010). This is an expected outcome when available growing space is increased for individual trees (Long 1985). In this study, tree increment increased with wider spacings throughout the range of spacings sampled, and differences were often significant with each increase in spacing. This was an unexpected result given that actual spacings varied considerably from target spacings for some treatments (Table 3). For accelerating tree increment, these results suggest that early precommercial thinning is effective regardless of whether the ultimate objective relates to timber production or developing old forest stand structures.

ANOVA results from the present study indicate few significant differences in stand-level increment between early thinning treatments after 12 years (Table 6). This was consistent with Lindquist's (2004) precommercial thinning work in slightly older redwood stands in a nearby redwood stand at Jackson Demonstration State Forest. His work included early spacing treatments ranging from 100 to 300 trees per acre and a control. However, in our study, absolute differences were substantial across the range of treatments with the 4-ft treatment producing a periodic increment of 3,297.9 ft^3 or 274.8ft^3/yr over the 12-year study compared to 139.8 ft^3/yr in the control and 94.4 ft^3/yr in the 24-ft treatment. The lack of statistical significance is due to the inability to meet initial target densities (Table 2), the effect of ingrowth, and the general high level of variability in these stands (Tables 2–6).

Oliver et al. (1994) reported results from commercial thinning in 40- to 50-year-old redwood and found some significant differences in increment between three treatments and a control. Although their results were not conclusive, they did suggest an optimal density between 50 and 75% of basal area of untreated stands. In a redwood plantation thinning study, control treatments had greater periodic

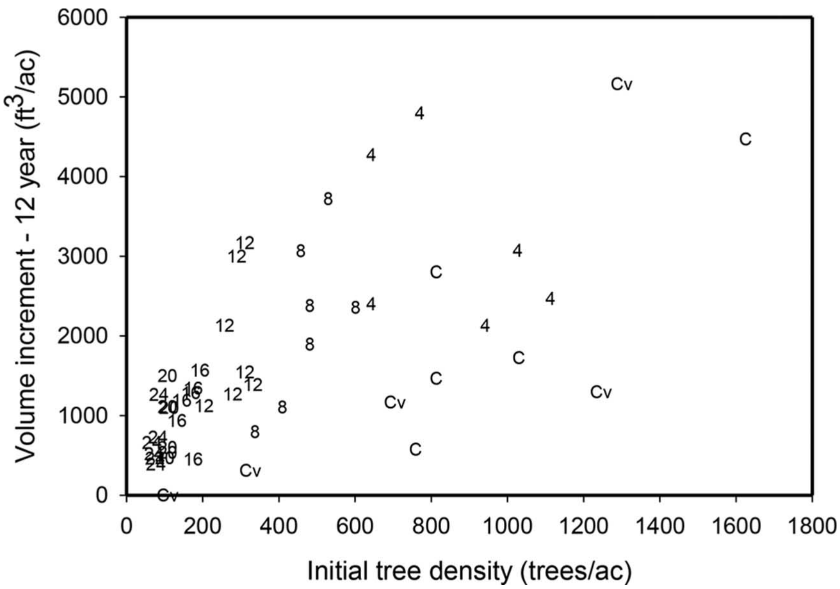

Figure 5. Volume increment by actual spacing (initial tree density) showing treatment variation. Numbers denote spacing treatments, C = control, and Cv = control with vegetation control.

and mean annual increment than four thinning treatments (Jones and O'Hara 2012). Thinning studies focused on restoration have generally not reported stand-level increment (e.g., O'Hara et al. 2010, Teraoka and Keyes 2011). Precommercial thinning studies with other species have also found poor relationships between stocking and either basal area or volume increment. For example, Schneider et al. (2013) found no differences in increment related to stocking over 28 years in balsam fir (*Abies balsamea* (L.) Mill.) in Quebec.

These results indicate greater increment at the 4-ft spacing. However, there is too much variation in both spacing and increment at any target spacing (Table 2) to support theories about maximum production at an intermediate density. For example, the actual mean density in the 4-ft treatment was closer to the target density of the 8-ft spacing. The scatter of treatment means by actual posttreatment trees/ac (Figure 5) shows that variation in actual trees/ac is considerable. Although the lower density treatments are clustered in lower actual densities, the 4-ft spacing has a considerable range in initial density. These results are not sufficient to support an increment–density relationship other than a model of increasing increment throughout the range of increasing density (Long 1985, Curtis et al. 1997). Land managers considering precommercial thinning treatments can be confident in improved individual tree increment following thinning and less confident about effects on stand-level increment. However, following this study beyond the 12 years reported in this analysis may reveal more significant trends in stand-level increment.

Ingrowth in thinned young redwood stands may be an impediment to thinning treatments whether the objective is timber or restoration to old forest structures. Following thinning, cut redwood stems produce stump sprouts, basal sprouts, and root sprouts. Stump sprout clumps that are thinned may resprout, thereby replacing the cut sprouts. This situation is unique because of the prolific sprouting capacity of cut redwood stems. The mean volume/ac of ingrowth in the 24-ft treatment was nearly 12 times the ingrowth of the control and represented 40% of the total production in the 24-ft treatment (Table 6). The high levels of ingrowth in this study suggest there may be some advantages to thinning later when stands have reached a point where canopy shade and within-clump shade can suppress sprouting. Redwood sprouts are sensitive to their light regimes. Probability of survival drops dramatically for redwood sprouts at less than 10% above canopy light, and growth rates are suppressed in light regimes less than 40% above canopy light (O'Hara et al. 2007, O'Hara and Berrill 2010). There may also be hormonal controls on sprouting when sprout clumps include older individuals. Lindquist (2004) also reported substantial ingrowth but did not conclude that it was problematic. He noted the desirable effect of crown closure on suppression of shrubs and smaller conifer regeneration.

Precommercial thinning treatments in stands of primarily sprouting species, such as coast redwood, require a different set of decisions than similar stands of nonsprouting species. The results from this study indicate that these early treatments may be too early, thereby stimulating the development of large numbers of sprouts and possibly negating the value of the thinning treatment. In the development of a redwood stump sprout clump, O'Hara and Berrill (2010) described the carbon balance as initially being negative (production less than consumption) but also having surplus reserves at the time of cutting, with declining reserves in the years following cutting. New carbohydrates are produced by the sprouts, but these are initially less than the respiration demands of the full root system. Only with time and rebuilding sufficient photosynthetic area will the stump regain a positive carbon balance. This negative carbon balance probably results, in combination with plant growth substances, in stimuli to produce more sprouts until a carbon balance is achieved. Wiant and Powers (1967) described the point when carbohydrate production equaled a tree's requirements as a "physiological equilibrium." They speculated that after this point, sprouting would decline and self-thinning of sprouts would begin. A delayed thinning treatment may be less likely to produce a profusion of sprouts than an earlier thinning.

Light and heat also stimulate sprout production. A poor light regime will result in less sprouting and will reduce growth of sprouts (O'Hara et al. 2007, O'Hara and Berrill 2010). Delaying thinning until greater canopy development has occurred or until individual sprout clumps are more developed will likely inhibit sprout production.

Once thinned, the residual sprouts grow more quickly than unthinned sprouts (Boe 1974, Cole 1983). This achieves the goal of developing fewer, larger trees. It also avoids the common characteristic of redwood stems from a single clump fusing together as they develop. This leads to stem deformities and makes felling stems more difficult. In the northern part of the range of coast redwood, girdling stems by black bears (*Ursus americanus*) is an impediment to silvicultural activities such as thinning (Giusti 1990). Bear girdling damages or kills stems and stimulates a sprouting response. Bears are also more likely to damage trees in thinned stands and typically damage the most vigorous trees (O'Hara et al. 2010).

Other considerations in developing early thinning regimes are the slash generated and the alternative of using multiple thinning treatments rather than a single heavy treatment. After a severe restoration thinning, O'Hara et al. (2010) reported mean slash depths over 3 ft, but these declined by a third in 4 years. Thinning regimes can also be altered to include more than one early thinning or to schedule an early commercial thinning. Berrill et al. (2013) recommended multiple thinnings to achieve restoration objectives. Lighter thinnings may also inhibit sprout development or reduce susceptibility of stands to bear damage. As with any silvicultural treatment, there are tradeoffs related to timing, intensity, and number of early thinnings. This study is the first to document the ingrowth response to early thinning in coast redwood.

Both analysis methods have advantages and disadvantages. ANOVA is not as well suited as mixed models for analyzing growth responses in studies with large amounts of spatial variability or size variability. The categorization of highly variable densities into single spacing classes that were not necessarily representative of actual spacings is also problematic. Due to the low number of redwood stems in treatment areas, the study was only able to come close to target densities in the 16-, 20-, and 24-ft spacings. Analyzing these data with trees/ac as a continuous variable provides a powerful tool for integrating this variation into response relationships. However, mixed-model results are inherently more complex and difficult to interpret.

Conclusions

Precommercial thinning in young, even-aged redwood stands resulted in large amounts of ingrowth and highly variable rates of volume increment. Ingrowth in tree numbers and volume increment were greatest at lower densities. Results for stand increment were highly variable because the heterogeneous structures of young redwood stands that regenerate from a mixture of dense clumps of sprouts and more scattered seedlings. Nevertheless, stand increment was greatest at higher densities. As expected, lower densities produced greater tree sizes with mean tree size over 7 in. dbh at stand ages of 21–23 years at the 20- and 24-ft spacing treatments. ANOVA and mixed-effect modeling are complementary analytical procedures for assessing responses to thinning treatments since the former compares treatment means and the latter compares the relative effects of different variables in affecting stand increment.

These results indicate precommercial thinning is effective for increasing average tree size and concentrating volume increment on a smaller number of trees. Total stand increment, including both initial trees and ingrowth, was highest at the 4-ft spacing and lower in control treatments and in thinning treatments that left lower densities. Individual tree size was greatest at the widest spacings. High levels of ingrowth suggest that thinning at ages 9–11 years may be too early because much of the advantage of concentrating growth on fewer trees is negated by large amounts of ingrowth. Later thinning may provide more suppression of sprouting, but 12 years may be insufficient to assess the effect of competition on these ingrowth trees.

Literature Cited

BERRILL, J., C.B. BEAL, D.H. LAFEVER, AND C.M. DAGLEY. 2013. Modeling young stand development towards the old-growth reference condition in evergreen mixed-conifer stands at Headwaters Forest Reserve, California. *Forests* 4(2):455–470.

BOE, K.N. 1974. *Thinning promotes growth of sprouts on old-growth redwood stumps.* USDA For. Serv., Res. Note PSW-290, Berkeley, CA. 5 p.

BURNHAM, K.P., AND D.R. ANDERSON. 2002. *Model selection and multimodel inference,* 2nd ed. Springer-Verlag, New York. 488 p.

CAREY, A.B. 2003. Biocomplexity and restoration of biodiversity in temperate coniferous forest: Inducing spatial heterogeneity with variable-density thinning. *Forestry* 76(2):127–136.

COLE, D.W. 1983. Redwood sprout growth 3 decades after thinning. *J. For.* 81(3):148–150:157.

CURTIS, R.O., D.D. MARSHALL, AND J.F. BELL. 1997. LOGS: A pioneering example of silvicultural research in coast Douglas-fir. *J. For.* 95(7):19–25.

DEL TREDICI, P. 1998. Lignotubers in *Sequoia sempervirens:* Development and ecological significance. *Madrono.* 45(3):255–260.

DOUHOVNIKOFF, V., A. CHENG, AND R. DODD. 2004. Incidences size and spatial structure of clones in second-growth stands of coast redwood *Sequoia sempervirens* (*Cupressaceae*). *Am. J. Bot.* 91(7):1140–1146.

ENG, H. 2012. Tree height estimation in redwood/Douglas-fir stands in Mendocino County. P. 649–656 in *Proceedings of the coast redwood forests in a changing California: A symposium for scientists and managers,* Standiford, R.B., T.J. Weller, D.D. Piirto, and J.D. Stuart (eds.). USDA For. Serv., Gen. Tech. Rep. PSW-GTR-238, Pacific Southwest Research Station, Albany, CA.

GIUSTI, G.A. 1990. Black bear feeding on second growth redwoods: A critical assessment. P. 214–217 in *Proceedings of the 14th vertebrate pest conference,* Davis, L.R., and R.E. Marsh (eds.). University of California—Davis, CA.

JAMESON, M.J., AND T.A. ROBARDS. 2007. Coast redwood regeneration survival and growth in Mendocino County, California. *West. J. Appl. For.* 22(3):171–175.

JONES, D.A., AND K.L. O'HARA. 2012. Carbon density in managed coast redwood stands: Implications for forest carbon estimation. *Forestry* 85(1):99–110.

KEYES, C.R., P.J. MATZKA, K.C. WRIGHT, R. GLEBOCKI, AND H.S. HAN. 2008. Early precommercial thinning of redwood sprout clumps: Evaluation of four techniques. *Int. J. For. Eng.* 19(2):28–36.

LINDQUIST, J.L. 2004. *Precommercial stocking control of coast redwood: A seventeen-year status report (1981–1998).* Calif. For. Rep. No. 2, Sacramento, CA. 24 p.

LINDQUIST, J. 2007. Precommercial stocking control of coast redwood at Caspar Creek, Jackson Demonstration State Forest. P. 295–304 in *Proceedings of the redwood region For. Sci. symposium: What does the future hold?* Standiford, R.B., G.A. Giusti, Y. Valachovic, W.J. Zielinski, and M.J. Furniss (eds.). USDA For. Serv., Gen. Tech. Rep. PSW-GTR-194, Pacific Southwest Research Station, Albany, CA.

LONG, J.N. 1985. A practical approach to density management. *For. Chron.* 61(1):23–27.

LORIMER, C.G., D.J. PORTER, M.A. MADEJ, J.D. STUART, S.D. VEIRS JR., S.P. NORMAN, K.L. O'HARA, AND W.J. LIBBY. 2009. Presettlement and modern disturbance regimes in coast redwood forests: Implications for the conservation of old-growth stands. *For. Ecol. Manage.* 258(7): 1038–1054.

NEAL, R.L. JR. 1967. *Sprouting of old-growth redwood stumps—First year after logging.* USDA For. Serv., Pac. Southwest For. and Range Expt. Station, Res. Note PSW-137, Berkeley, CA. 8 p.

O'HARA, K.L., AND J. BERRILL. 2010. Dynamics of coast redwood sprout clump development in variable light environments. *J. For. Res.* 15(2): 131–139.

O'HARA, K.L., L.P. LEONARD, AND C.R. KEYES. 2012. Variable-density thinning and a marking paradox: Comparing prescription protocols to attain stand variability in coast redwood. *West. J. Appl. For.* 27(3): 143–149.

O'HARA, K.L., L. NARAYAN, AND K.G. CAHILL. 2014. Precommercial thinning in coast redwood: Twelve-year results for stand increment and ingrowth. Unpublished report to Jackson Demonstration State Forest, California Department of Forestry and Fire Protection, Fort Bragg, CA. 28 p.

O'HARA, K.L., J.C.B. NESMITH, L. LEONARD, AND D.J. PORTER. 2010. Restoration of old forest features in coast redwood forests using early-stage variable-density thinning. *Restor. Ecol.* 18:125–135.

O'HARA, K.L., P.T. STANCIOIU, AND M.A. SPENCER. 2007. Understory stump sprout development under variable canopy density and leaf area in coast redwood. *For. Ecol. Manage.* 244(1–3):76–85.

OLIVER, W.W., J.L. LINDQUIST, AND R.O. STROTHMANN. 1994. Young-growth redwood stands respond well to various thinning intensities. *West. J. Appl. For.* 9(4):106–112.

RAMAGE, B.S., K.L. O'HARA, AND B.T. CALDWELL. 2010. The role of fire in the competitive dynamics of coast redwood forests. *Ecosphere* 1(6): art. 20.

REID, L.M., AND T.E. LISLE. 2010. The Caspar Creek watershed studies: Long-term research in a temperate, rain-dominated forest. *Int. Assoc. Theor. Appl. Limnol. Proc.* 30(part 9):1326–1328.

REUKEMA, D.L. 1975. *Guidelines for precommercial thinning of Douglas-Fir.* USDA For. Serv., Pac. Northwest Res. Sta. Gen. Tech. Rep. PNW-30, Portland, OR. 10 p.

SCHNEIDER, R., J. BEGIN, A. DANET, AND R. DOUCET. 2013. Effect of selective precommercial thinning on balsam fir stand yield and structure. *For. Chron.* 89(6):759–768.

TERAOKA, J.R., AND C.R. KEYES. 2011. Low thinning as a forest restoration tool at Redwood National Park. *West. J. Appl. For.* 26(2):91–93.

THORNBURGH, D.A. 2000. Managing redwoods. P. 22–262 in *The redwood forest: History, ecology, and conservation of the coast redwoods,* Noss, R.F. (ed.). Island Press, Washington, DC.

WENSEL, L.C., AND B.E. KRUMLAND. 1983. *Volume and taper relationships for redwood, Douglas-fir, and other conifers on California's north coast.* Div. of Agri. Sciences, Univ. of Calif., Berkeley, Bull. 1907, Berkeley, CA. 39 p.

WIANT, H.V. JR., AND R.F. POWERS. 1967. Sprouting of old-growth redwood. P. 88–90 in *Proc. Soc. Am. For., 1966.* Society of American Foresters, Washington, DC. 232 p.

ZURR, A.F., E.N. IENO, N.J. WALKER, A.A. SAVELIEV, AND G.M. SMITH. 2009. *Mixed effects models and extensions in ecology with R.* Springer, New York. 574 p.