STRUCTURE AND COMPOSITION OF OLD-GROWTH AND UNMANAGED SECOND-GROWTH RIPARIAN FORESTS AT REDWOOD NATIONAL PARK, USA

by

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SIGNATURE PAGE

ABSTRACT

Structure and Composition of Old-growth and Unmanaged Second-growth Riparian Forests at Redwood National Park, USA

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Restoration of riparian forests that have been harvested in the past has become an important issue for managers of redwood (*Sequoia sempervirens* [D. Don] Endl.) forest reserves. Old-growth riparian forests can be used as a reference to direct restoration efforts, but in the redwood region they have lacked detailed study. Riparian forests in adjacent watersheds at Redwood National Park were studied to understand the structure and compositional differences between old-growth and unmanaged second-growth forests. In the old-growth, redwood was the dominant species in the overstory in terms of basal area, height, stem density, and importance values. Second-growth was dominated by red alder (*Alnus rubra* Bong.), Douglas-fir (*Pseudotsuga menziesii* [Mirbel] Franco), and redwood. *Polystichum munitum* (Kaulf.) C. Presl, *Blechnum spicant* (L.) Sm., and *Athyrium filix-femina* (L.) Roth dominated the understory in both old-growth and second-growth riparian forests. Understory species were similar in both forests, although *Oxalis oregana* Nutt. and *Trillium ovatum* Pursh had greater importance values in the old-growth whereas *Vaccinium parvifolium* Sm., *Dryopteris* sp and sedges *Carex* spp. had greater importance values in the second-growth. A growth model was used to project 50 years of growth in the second-growth riparian forest for three different scenarios: the current stand without any manipulation; the current stand without red alder (to evaluate the role of red alder on riparian forest development); and the current stand following a thinning prescription designed to reduce basal area of the stand by 25% targeting removal of dominant and co-dominant Douglas-fir. Growth projections of scenarios with red alder resulted in declines in red alder importance after 50 years. All growth projections resulted in redwood increasing importance to a dominant or co-dominant role in the stand with Douglas-fir. However, Douglas-fir maintained a higher position in the canopy than redwood across all scenarios with much higher densities than in the old-growth. Results suggest that if the desired future condition of the second-growth riparian forest is redwood-dominated (comparable to that found in old-growth), intervention will be necessary to reduce the dominance of Douglas-fir, especially dominant, upper canopy Douglas-fir, while maintaining redwood both in the upper and lower canopy.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

The silvicultural restoration of upland second-growth forests to accelerate old-growth forest conditions has emerged as a top priority for managers of redwood (*Sequoia sempervirens* [D. Don] Endl.) forest reserves in northern coastal California (e.g. Redwood National and State Parks 2004, Keyes 2005, Porter et al. 2007, Lorimer et al. 2009). Upland second-growth stands in this region that have emerged following the clearcut logging of old-growth forests are often characterized by high tree densities, presence of non-native tree species, and suppressed stand growth and development (Redwood National and State Parks 2004, Teraoka 2004, Chittick 2005, Plummer 2008). Lacking treatment, the region's second-growth forests are expected to remain in this condition for decades without providing the same aesthetic and ecological values that old-growth forests provide (Redwood National and State Parks 2004, Teraoka 2004, Chittick 2005, O'Hara et al. in press). Of equal importance as a restoration issue are the region's riparian forests that connect upland forests with adjacent aquatic ecosystems. Riparian forest structure and composition have strong bearing on stream habitat quality (e.g. Keller et al. 1995, Lisle and Napolitano 1998, Benda et al. 2002, Andrus 2008), yet both have been substantially altered by past forest management practices (Urner and Madej 1998, Andrus 2008, Russell 2009, Villarin et al. 2009).

Riparian forests contain some of the most ecologically diverse and structurally complex vegetation of the Pacific Coast region (Naiman et al. 1998). Old-growth riparian forests are characterized as having great horizontal and vertical structural complexity, including large and small living trees, old standing dead trees, massive fallen logs, a relatively open canopy with many layers of foliage, and a diverse understory of shrubs and herbs (Alaback 1982, Spies and Franklin 1991, Busing and Fujimori 2002, Franklin and Van Pelt 2004, Zenner 2004, Sillett and Van Pelt 2007, Dagley 2008, Lorimer et al. 2009). On forestlands managed for timber, current state forest regulations and federal policies regulate harvesting activities in riparian forests. Historically, however, riparian forests were often the first areas logged because of the occurrence of large trees and the ease of transporting logs downstream (Magnuson et al. 1996).

Timber harvest in Pacific Northwest riparian zones has typically altered vegetation community composition, with early successional tree species such as red alder (*Alnus rubra* Bong.) replacing conifers as the dominant riparian vegetation over large areas (Urner and Madej 1998, Andrus 2008, Russell 2009, Villarin et al. 2009) There is concern that second-growth riparian forests inadequately replace old-growth riparian stands in the provision of important aquatic ecosystem services to streams and rivers, such as canopy shade, nutrients from arboreal detritus, structure and habitat from large woody debris, and stream bank stabilization (Vannote et al. 1980, Gregory et al. 1991, Keller et al. 1995, Hibbs and Bower 2001, Frazey and Wilzbach 2007, Andrus 2008). Concern for water quality and fish habitat has focused attention in recent years on the condition and management of riparian forests, especially around headwater stream reaches. Headwater streams are strongly influenced by adjacent riparian vegetation of the surrounding forests through shading and inputs of nutrients and organic matter

(Vannote et al. 1980, Bilby and Bisson 1992, Andrus 2008). Headwater streams represent over 80% of the cumulative channel length of northern California coastal watersheds and 89% of streams within Redwood National Park (Redwood National and State Parks 2010).

Land use history, vegetation change and restoration potential are especially prominent concerns at Redwood National Park, which is home to a variety of old-growth and second-growth riparian forests. Past timber harvest heavily impacted more than one-third of the lands now within the Redwood National Park (Redwood National and State Parks 2004) and has influenced many kilometers of riparian forest, including those of the 720 km^2 Redwood Creek watershed and the 52 km^2 Lost Man Creek watershed. The current structure and composition of disturbed, second-growth riparian forests is poorly understood in the redwood region (Arguello, L. 2005. Personal communication. Redwood National Park, South Operations Center, Orick, California 95555). No prior study has comprehensively documented the deviation in stand attributes between old-growth and second-growth riparian redwood forests. Such an understanding is vital to determining whether restoration efforts are necessary and to establish reference conditions and objectives for future practices.

The objectives of this study were to characterize and contrast the structure and composition of old-growth and unmanaged second-growth riparian forests along Little Lost Man and Lost Man Creeks in Redwood National Park. The study was designed to gather baseline data to calculate stand metrics and indicators for old-growth riparian forests in Little Lost Man Creek and second-growth riparian forests in Lost Man Creek in order to evaluate whether an active forest restoration strategy is necessary, and to provide insight for such restoration planning. To determine trajectories of species composition, three contrasting scenarios were developed that encompassed different restoration approaches: the current stand without any manipulation; the current stand without red alder (to evaluate the role of red alder on riparian forest development); and the current stand following a thinning prescription. The growth of the stand was modeled for each scenario over fifty years to evaluate how the structure and composition of the stand would change with different restoration approaches. Information generated by this study will be useful to resource managers at Redwood National Park, as well as managers of other private and public second-growth riparian redwood forests that occur throughout northern California.

STUDY SITES

The study area included two adjacent watersheds in Redwood National Park on the north coast of California (Figure 1). Study sites were located along first and second-order sections of Lost Man and Little Lost Man Creeks near Orick, California (+41° 17' 15.72", -124° 4' 5.19"; Figure 2). All sites were within 10 km of the Pacific coast. The two watersheds are geographically similar (i.e. overall slope, aspect, soils, underlying geology, and distance to the coast). Thus this watershed pairing isolated harvesting history (logging) as the factor primarily responsible for differences in riparian forest conditions. Few watersheds in the redwood region are pristine today, but the Little Lost Man Creek watershed is almost entirely (~89%) composed of undisturbed old-growth redwood forest (Redwood National and State Parks 2010). In contrast, 76% of the Lost Man Creek watershed was clear-cut between 1954 and 1962 and left to regenerate naturally. The area was acquired by the National Park Service in 1978. Some restoration efforts have recently begun in the upland forest, but the riparian areas have remained unmanaged.

The climate of the area is coastal Mediterranean, characterized by average annual rainfall of 1,706 mm (Western Regional Climate Center 2010); 90% of which occurs between October and April. The dry summer months are characterized by the occurrence of coastal fog that can extend inland up to 24 km from the coast. Temperatures generally range from 6 to 16° C (Western Regional Climate Center 2010).

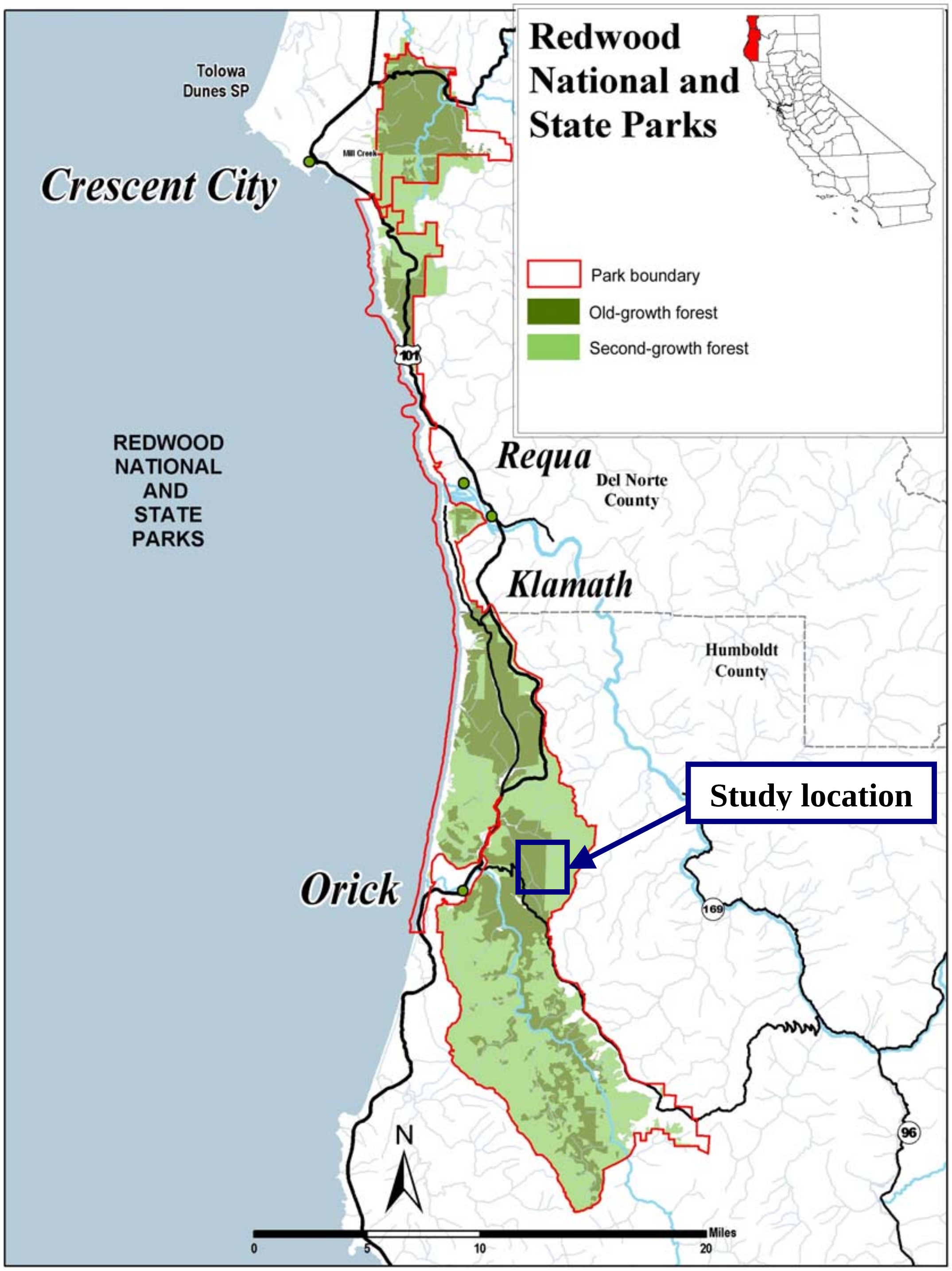

Figure 1. Location of study area within Redwood National Park in northern California (map courtesy of Redwood National Park).

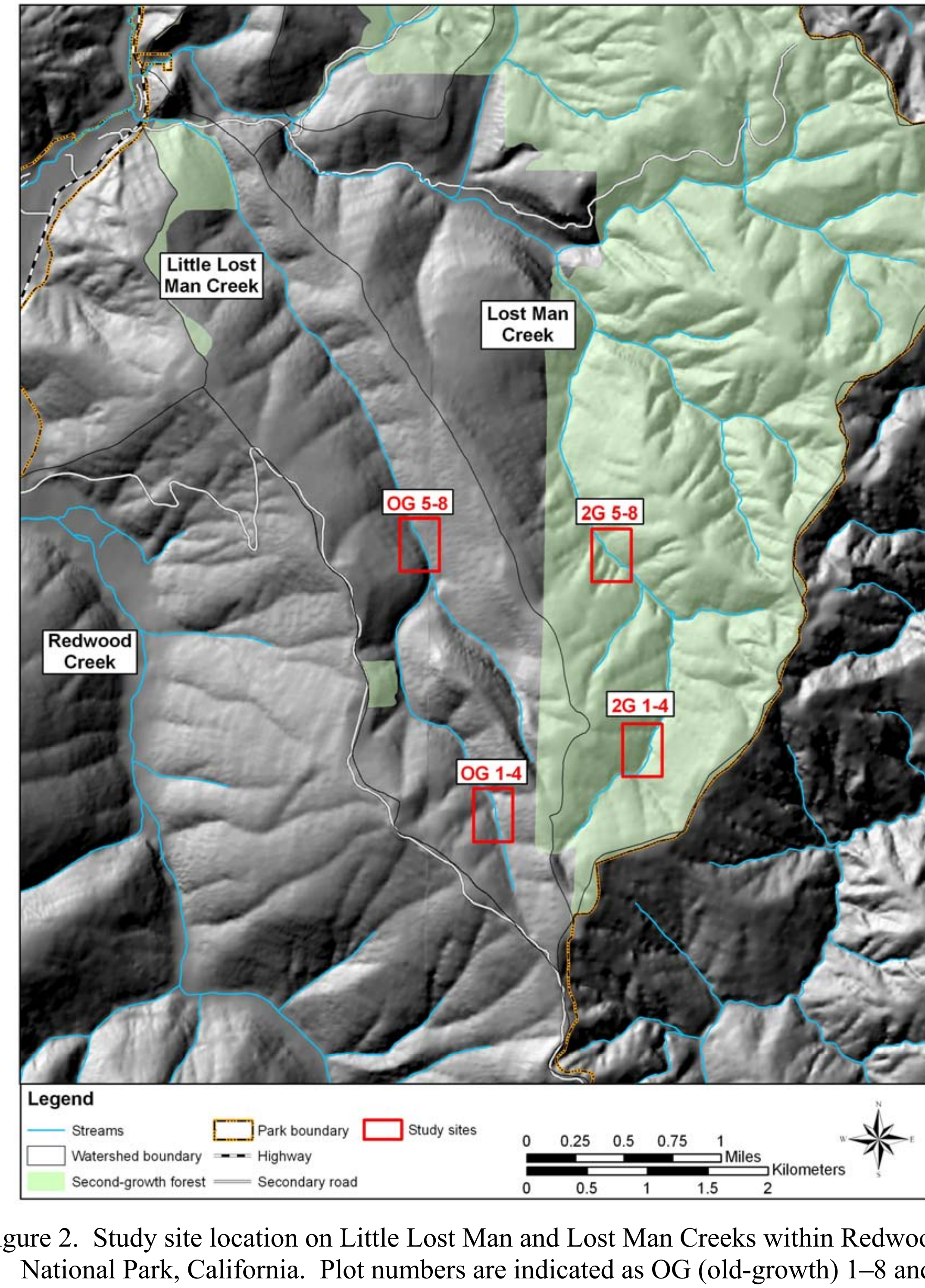

Figure 2. Study site location on Little Lost Man and Lost Man Creeks within Redwood National Park, California. Plot numbers are indicated as OG (old-growth) 1–8 and 2G (second-growth) 1–8.

The region is characterized by steep, highly erodible landscapes; in the study area soils are underlain by rocks of the Franciscan formation (United States Department of Agriculture 2008). Franciscan rocks consist of mudstone, sandstone and schist; they are often sheared and are susceptible to mass movement (Nolan et al. 1987, United States Department of Agriculture 2008). Soil types in the study area consist of Sasquatch-Sisterrocks-Ladybird, Coppercreek-Slidecreek-Lackscreek, and Atwell-Coppercreek complexes along Little Lost Man Creek and Coppercreek-Slidecreek-Lackscreek and Sisterrocks-Ladybird-Footstep complexes along Lost Man Creek (United States Department of Agriculture 2008). These soils are all well-drained and the upper soil horizons are made up of loam, silt loam, and gravelly loam with parent material of colluvium, residuum, and earthflow deposits derived from sandstone and mudstone (United States Department of Agriculture 2008).

METHODS

Data Collection and Analysis

To compare the structure and composition of old-growth and second-growth riparian forests, sixteen 20 m × 10 m plots were installed; eight in the old-growth forest of Little Lost Man Creek and eight in the second-growth forest of Lost Man Creek (Figure 2). Plots were selected on the following basis: inclusion of a flat valley floor or terrace immediately adjacent to the creek that was at least 5 m wide with an adjacent hillslope; a minimum of 50 m from the previous site; and absence of any major logging road (second-growth; skid roads and trails were acceptable). To minimize variation in aspect and landform characteristics, all plots were located on the east side of creeks. Plots were initially located in second-growth with the use of topographic maps, aerial photographs and field reconnaissance so as to avoid logging roads within the plot boundary. Plots with matching stream order and elevation were then selected in the old-growth using aerial photographs, topographic maps, and field reconnaissance.

Sampling occurred from July to October 2005. Tree data were collected in the 200 m^2 rectangular plots immediately adjacent the stream's mean high water level. In each plot, species, diameter at 1.37 m (diameter at breast height; DBH), height, and height to live crown base were measured for all live trees greater than 10 cm DBH. Plant nomenclature followed the Jepson Manual (Hickman 1993). Occasional residual old-growth trees in the second-growth were noted as such. Height:Diameter (H:D) ratio and percentage live crown were calculated for each tree. Basal area, stem density (trees ha^{-1}), and frequency were calculated for each species from plot data. Basal area, stem density, and frequency were converted into relative values by dividing by the total value for the stand, summed, and divided by 3 (or 2 when only 2 of the 3 measurements were available) to calculate an importance value (IV) for each species (Mueller-Dombois and Ellenberg 1974). IV can be used to maximize the differences between stands with similar species compositions that may not be apparent using a single measure (Curtis and McIntosh 1951, Bell 1974, Goebel and Hix 1996, Barker et al. 2002). All snags greater than 10 cm DBH were measured for diameter, height, and decay category (United States Department of Agriculture 2004); species was identified when possible. Canopy cover was estimated three times in each plot using a concave spherical densiometer (model B; Barbour et al. 1999). Old-growth and second-growth metrics were compared using two-sample t-tests and Mann-Whitney U Tests (for non-parametric data; Zar 1999) and the medians of multiple groups of species were compared using Kruskal-Wallis Multiple Comparison Z-value tests (Zar 1999) in NCSS (Hintze 2004). Non-parametric tests were used because of the relatively small sample size and because the two populations (old-growth and second-growth) could not be considered normal. The significance level for all statistical tests was $\alpha = 0.05$.

Understory and tree regeneration data were collected with a row of three 10 m^2 circular sub-plots spaced evenly within each plot. The number of saplings (height > 1.4 m; DBH < 10 cm), seedlings (height > 10 cm and < 1.4 m) and small seedlings (height < 10 cm) were tallied for each species within the sub-plot. For each species of shrub and herb present, cover was visually estimated to the nearest percent.

Each species was estimated independently; therefore, the total could exceed 100%. Relative frequency and cover were calculated, summed and divided by 2 to calculate an IV for each species. Average height of shrubs was visually estimated to the nearest 15 cm. Shannon diversity (H′) and evenness (J′) based on H′ were calculated for the understory in the old-growth and second-growth to compare species diversity and relative diversity (Brower et al. 1990). The Jaccard Coefficient of Community was calculated for the understory in both forest types to compare the similarity of the two communities (Mueller-Dombois and Ellenberg 1974). The Jaccard Coefficient of Community is an index of community similarity ranging from 0% (no species in common) to 100% (all species in common).

Forest Growth Simulation

Second-growth forest development over fifty years was projected using the Cooperative Redwood Yield Project's Timber Output Simulator (CRYPTOS) version 7.8 (Wensel et al. 1994). Three scenarios were projected: the current stand without any manipulation (Current Stand); the current stand without red alder (to evaluate the role of red alder on riparian forest development; Alder Absent); and the current stand following a thinning prescription (South Fork Lost Man Creek Thinning). The thinning prescription was based on the preferred treatment prescription (Alternative 2) from the South Fork Lost Man Creek Second Growth Forest Restoration Draft Environmental Assessment (Redwood National Park 2008). The thinning prescription reduced the basal area of the stand by 25%, targeting removal of dominant and co-dominant Douglas-fir (*Pseudotsuga menziesii* [Mirbel] Franco) trees to maximize canopy openings. Only trees 20.3–50.8 cm DBH were eligible for removal and the largest 10% of trees were not cut.

For the growth simulation, grand fir (*Abies grandis* [Dougl. ex D. Don] Lindl.), western hemlock (*Tsuga heterophylla* [Raf.] Sarg.), and western red cedar (*Thuja plicata* Donn ex D. Don) were grouped into one category called “other conifers” to be compatible with CRYPTOS. The model does not calculate growth for these species individually, but groups them together. Site index was calculated for each species or species group for use in the CRYPTOS model runs using the average height of the trees in the tallest quartile (Table 1). If there were fewer than two individuals of any species in the tallest quartile, the average height of the tallest two trees in the stand were used. Descriptive statistics, including basal area and stem density, were modeled for all three scenarios at year 0 and after 50 years of growth. Basal area and stem density were converted into relative values and summed to calculate an IV (Mueller-Dombois and Ellenberg 1974) for each species group. Similar statistics were calculated for the old-growth riparian forest for comparison with the second-growth scenarios and growth projections.

Table 1. Site index values used in the CRYPTOS model growth projections. Site index was calculated using the average height of the trees in the tallest quartile. If there were fewer than two individuals of any species in the tallest quartile, the average height of the tallest two trees in the stand were used.

Species	Site index
Redwood	120
Douglas-fir	113
Other conifers	110
Tanoak	36
Red alder	113
Other hardwoods	N/A
Residual redwood	120
Other residuals	N/A

[a] Site index for residual redwood was assumed to be the same as the second-growth redwood.

RESULTS

Overstory Structure and Composition

Metrics of overstory stand structure differed significantly between the old-growth and the second-growth riparian forests. Stem density was significantly lower in old-growth riparian stands than in second-growth riparian stands, 250 trees ha^{-1} and 575 trees ha^{-1}, respectively ($P<0.04$; Table 2). However, basal area in old-growth riparian forest was more than 6 times as high as the second-growth, 396.1 m^2 ha^{-1} and 61.6 m^2 ha^{-1}, respectively ($P < 0.003$; Table 2).

Redwood represented the clear majority of the total basal area in the old-growth, but less than half of the stem density (Table 2, Figure 3). Redwood was clearly the dominant tree in the old-growth forest with the highest IV (75.4%) of the species observed (Table 2). Redwood comprised 45% of the relative stem density and 94% of the relative basal area (Table 2) in old-growth stands. In the second-growth riparian stands, red alder had the highest IV (46.2%), followed by Douglas-fir (39.4%) and redwood (33%; Table 2). Mean canopy cover was significantly greater in second-growth than in old-growth ($P < 0.004$), but the magnitude of this difference was marginal. Second-growth averaged 96% (SD 1.84) and the old-growth 92% (SD 3.02).

There was a narrow range of quadratic mean diameters for species in the second-growth stands (excluding residual redwood) and the mean basal area for each species had small standard deviations (Table 3). In the second-growth stands, redwood,

Table 2. Trees found in the old-growth and second-growth riparian forests in Redwood National Park, California. Standard deviation is indicated parentheses for stem density and basal area; rank is indicated in parentheses for importance value.

	Frequency (# plots)		Relative frequency[a] (%)		Stem density (trees ha^{-1})		Relative density[b] (%)		Basal area (m^2 ha^{-1})		Relative BA[c] (%)		Importance value[d] (%)	
Tree species[a]	Old-growth	Second-growth	Old-growth	Second-growth	Old-growth	Second-growth	Old-growth	Second-growth	Old-growth	Second-growth	Old-growth	Second-growth	Old-growth	Second-growth
Douglas-fir *Pseudotsuga menziesii*	1	6	12.5	75.0	12.5 (4.4)	143.8 (19.6)	5.0	25.0	8.1 (2.9)	11.1 (1.5)	2.0	18.1	6.5 (4)	39.4 (2)
Grand fir *Abies grandis*	-	1	-	12.5	-	12.5 (4.4)	-	2.2	-	2.2 (0.8)	-	3.6	--	6.1 (7)
Red alder *Alnus rubra*	-	7	-	87.5	-	181.3 (19.2)	-	31.5	-	12.0 (1.3)	-	19.5	-	46.2 (1)
Redwood *Sequoia sempervirens*	7	5	87.5	62.5	112.5 (14.1)	156.3 (25.5)	45.0	27.2	371.0 (35.8)	7.2 (1.6)	93.7	11.7	75.4 (1)	33.8 (3)
Tanoak *Lithocarpus densiflorus*	4	2	50.0	25.0	50 (7.5)	12.5 (2.9)	20.0	2.2	0.9 (0.1)	0.2 (0.0)	0.2	0.3	23.4 (3)	9.2 (6)
Western hemlock *Tsuga heterophylla*	7	2	87.5	25.0	75 (8.2)	43.8 (11.3)	30.0	7.6	16.1 (2.4)	4.0 (0.9)	4.1	6.5	40.5 (2)	13.0 (5)
Western red cedar *Thuja plicata*	-	1	-	12.5	-	12.5 (4.4)	-	2.2	-	0.8 (0.3)	-	1.3	-	5.3 (8)
Redwood (residual) *Sequoia sempervirens*	N/A	2	N/A	25.0	N/A	12.5 (2.9)	N/A	2.2	N/A	24.0 (6.7)	N/A	39.0	N/A	22.1 (4)
Totals	N/A	N/A	N/A	N/A	250 (43.3)	575.0 (74.8)	100.0	100.0	396.1 (130.0)	61.6 (8.0)	100.0	100.0	-	-

[a] Relative frequency is the number of plots that the species was found in divided by the total number of plots (N=8).
[b] Relative density is the stem density of each species divided by the total stem density of all species.
[c] Relative basal area is the basal area of each species divided by the basal area of all species.
[d] Importance value is the sum of relative frequency, relative density, and relative basal area divided by 3. Importance value rank is the rank of the species in the stand from highest importance value (most important) to lowest (least important).

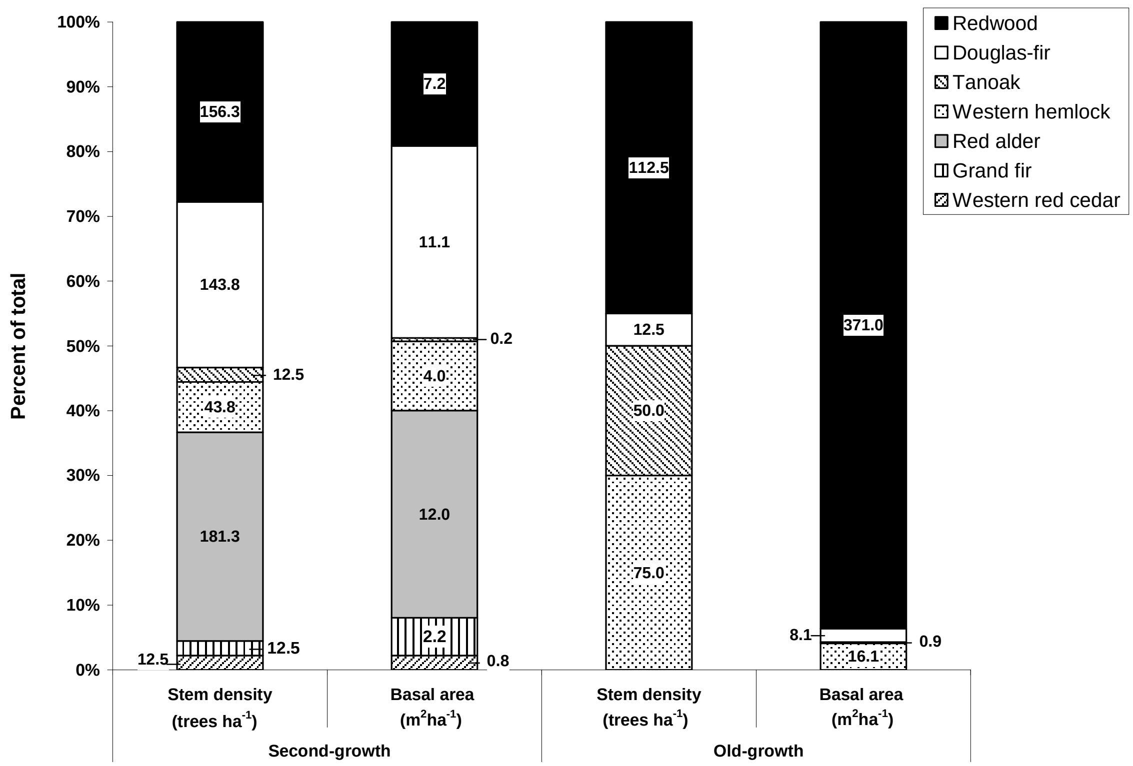

Figure 3. Percent of total basal area and stem density by species for old-growth and second-growth riparian forests at Redwood National Park, California. Numbers on bars indicate the actual basal area or stem density. Residual redwood trees are not included for the second-growth.

Table 3. Average height, quadratic mean diameter, percentage live crown, and height:diameter (H:D) ratio for all trees in the old-growth and second-growth riparian forests in Redwood National Park, California. Standard deviation is indicated in parentheses where applicable, range is indicated in parentheses for quadratic mean diameter.

Tree species[a]	N		Height (m)		Quadratic mean diameter (cm)		Percentage live crown (%)		H:D	
	Old-growth	Second-growth	Old-growth	Second-growth	Old-growth	Second-growth	Old-growth	Second-growth	Old-growth	Second-growth
Douglas-fir *Pseudotsuga menziesii*	2	23	42.83 (7.14)	30.06 (5.16)	90.7 (90.7 - 90.7)	31.4 (29.7 - 34.4)	0.21 (0.01)	0.43 (0.17)	49.82 (8.23)	100.93 (15.79)
Grand fir *Abies grandis*	-	2	-	36.15 (0.3)	-	47.2 (47.2 - 47.2)	-	0.45 (0.03)	-	76.91 (5.93)
Red alder *Alnus rubra*	-	29	-	24.81 (7.71)	-	29.1 (19.5 - 51.1)	-	0.41 (0.15)	-	95.62 (28.23)
Redwood *Sequoia sempervirens*	18	25	46.04 (30.39)	14.35 (7.46)	204.9 (97.3-454.1)	24.2 (15.2 - 31.0)	0.54 (0.18)	0.52 (0.17)	48.92 (23.49)	69.14 (21.8)
Tanoak *Lithocarpus densiflorus*	8	2	8.23 (2.58)	10.98 (1.75)	15.1 (13.7 - 15.8)	14.3 (11.6 - 16.5)	0.57 (0.08)	0.72 (0.16)	54.4 (13.31)	79.01 (7.0)
Western hemlock *Tsuga heterophylla*	12	7	25.11 (16.23)	23.81 (7.45)	52.4 (14.3-120.0)	34.2 (30.1 - 42.8)	0.6 (0.17)	0.78 (0.16)	63.28 (11.35)	84.83 (22.89)
Western red cedar *Thuja plicata*	-	2	-	22.18 (3.48)	-	29.0 (29.0 - 29.0)	-	0.44 (0.2)	-	22.95 (34.23)
Redwood (residual) *Sequoia sempervirens*	N/A	2	N/A -	48.75 (11.25)	N/A-	156.4 (101.5-196.6)	N/A-	0.68 (0.04)	N/A-	34.52 (8.01)
All trees	40	92	32.04 (26.59)	23.61 (10)	142 (86.4-321.8)	36.9[b] (28.7 - 77.1)	0.54 (0.17)	0.49 (0.19)	54.37 (18.7)	86.72 (26.55)

[b] If residual redwoods are not included, the average quadratic mean diameter for the second-growth is 28.9 cm (range 22.2 cm - 32.4 cm).

Douglas-fir and red alder comprised equal proportions of the total stem density (Kruskal-Wallis multiple-comparison Z-value test all z-values < 1.96). Other species present (tanoak [*Lithocarpus densiflorus* (Hook. & Arn.) Rehder], western hemlock, grand fir, western red cedar and residual old-growth redwood) comprised only a small proportion (16.3% combined) of the total stem density.

Stand quadratic mean diameter was almost 4 times higher in the old-growth forest (Table 3). Redwood also had the largest quadratic mean diameter (204.9 cm; range 97.3–454.1 cm) of any species present and was, by far, the tallest tree species in the old-growth, making up the majority of the trees present in the upper canopy (Table 3, Figure 4). In stark contrast with the old-growth, every tree species except tanoak had a larger quadratic mean diameter than redwood in the second-growth (Table 3). While there was not a clear distinction of which species in the second-growth was tallest, red alder and Douglas-fir occupied higher positions in the canopy than redwood (Figure 4).

The size and canopy position of species in the old-growth and second-growth stands were also quite different. Species in old-growth stands were each in different size categories (Figure 3, Tables 2 and 3) and each species occupied specific places in the canopy. Douglas-fir was only found in the mid- to upper canopy whereas tanoak and western hemlock were present as subordinate trees in the mid- to lower canopy (Figures 4 and 5). Redwood was present in many of the diameter and height classes, but it was the only species found in diameter classes greater than 130 cm and height classes greater

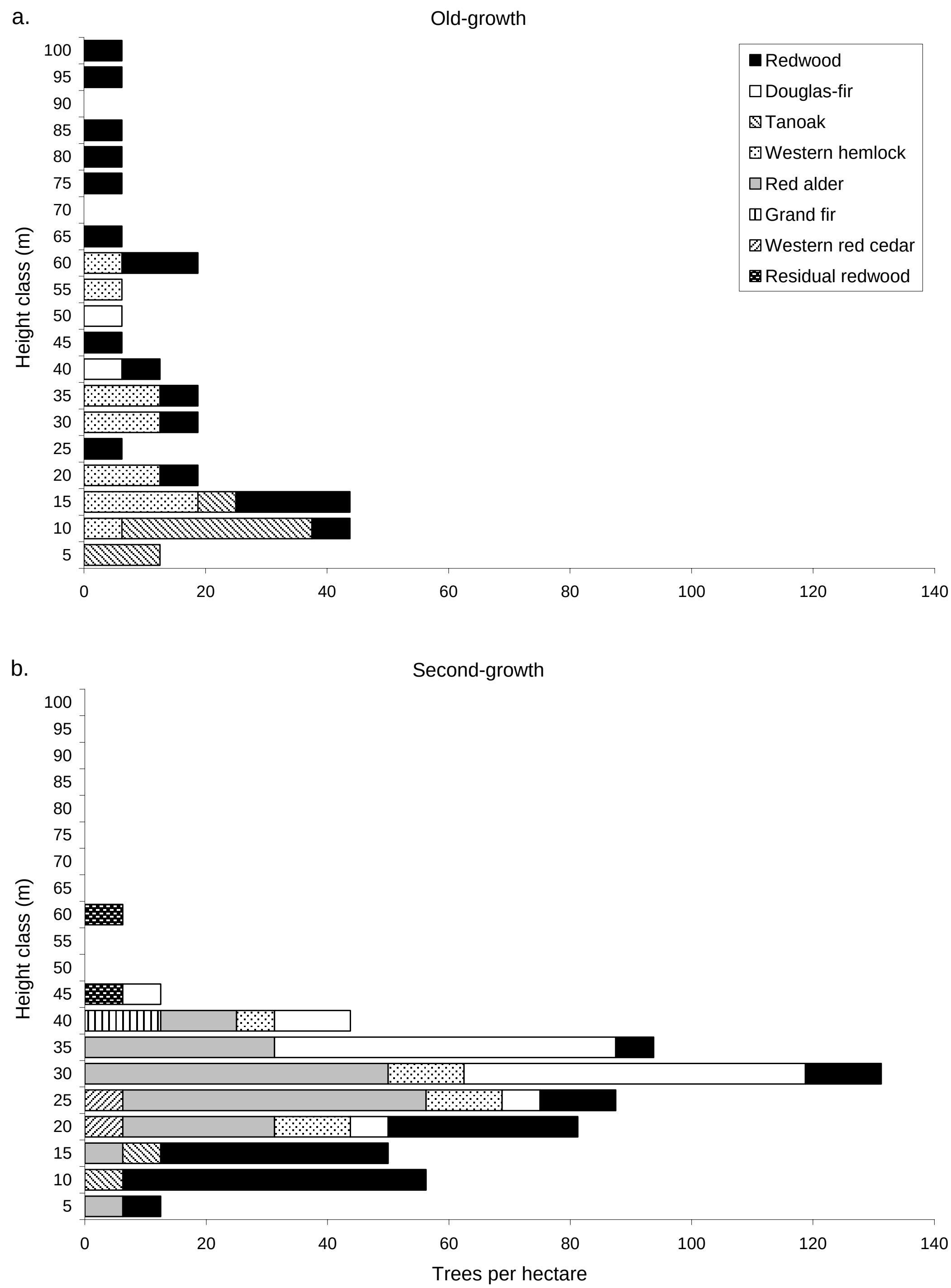

Figure 4. Height distribution in meters for (a) old-growth and (b) second-growth riparian forests in Redwood National Park, California.

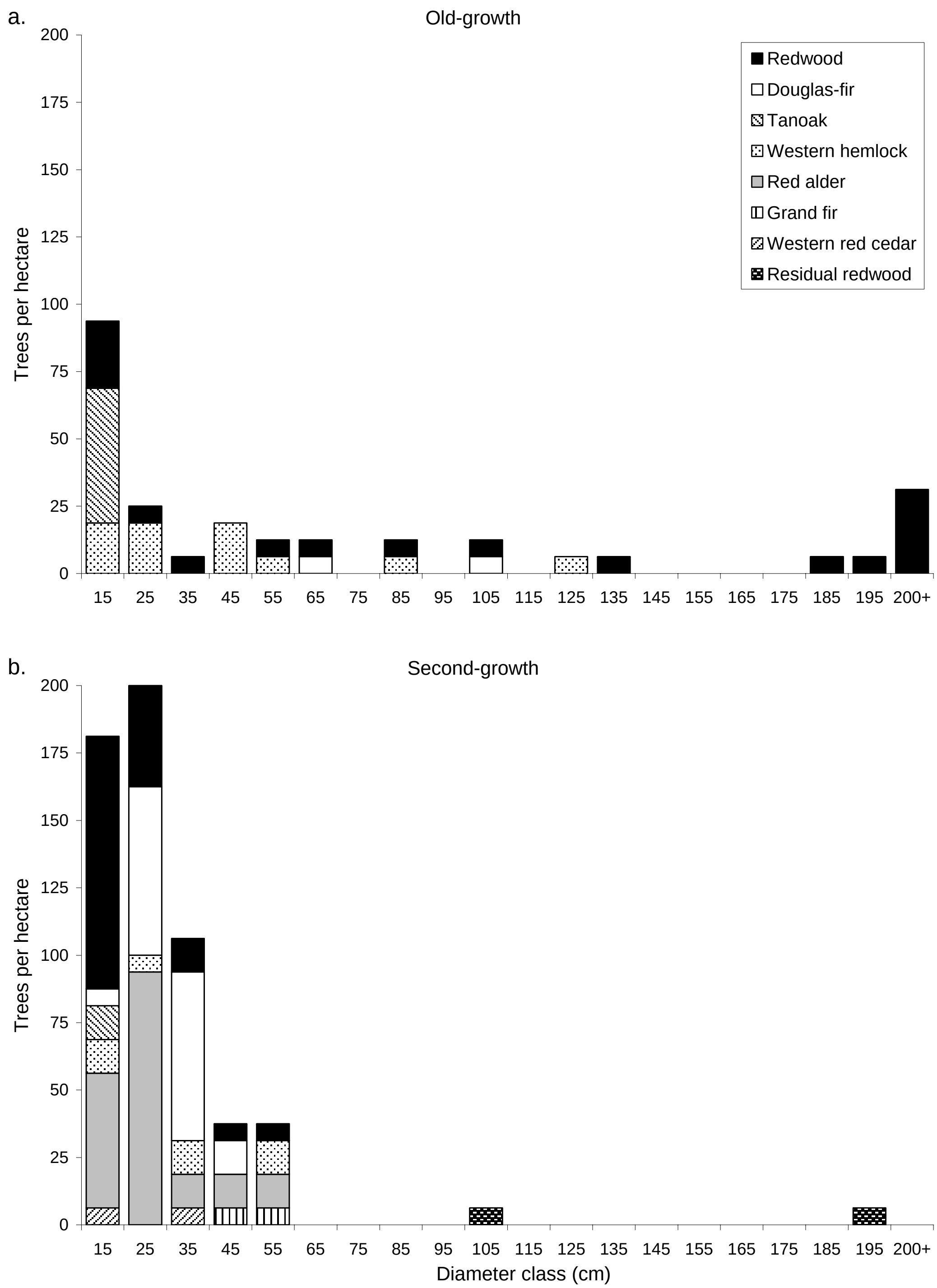

Figure 5. Diameter distributions in centimeters for (a) old-growth and (b) second-growth riparian forests at Redwood National Park, California.

than 65 m (Figures 4 and 5). Old-growth stands were made up of numerous small-diameter (10–15 cm) understory trees, several very large diameter (>185 cm) upper canopy trees and a relatively even mix in the remainder of the diameter and canopy classes (Figures 4, 5). In the old-growth stands, redwood had the greatest frequency in the 10-19 cm (25 trees ha^{-1}) and greater than 200 cm classes (31.3 trees ha^{-1}).

Second-growth, in contrast, was comprised mostly of small to medium diameter trees (10–35 cm DBH) with some larger diameter trees (45–55 cm DBH; excluding residual redwood; Figure 5). In the second-growth riparian stands, red alder, redwood and Douglas-fir together comprised 83.7% of all trees with diameters ranging from 10 to 59 cm. The majority of Douglas-fir (87%, 125 trees ha^{-1}) was in the intermediate diameter classes (29–39 cm) whereas the majority of redwood (84%, 131.3 trees ha^{-1}) was in the smallest diameter classes (10–29 cm).

The second-growth riparian stands were also confined to a more narrow range of heights than the old-growth sampled here (excluding residual old-growth trees; Figure 4). Some species (Douglas-fir, western red cedar, and western hemlock) were only present in the upper canopy (20–45 m height classes), but redwood and red alder were found in nearly all of the height classes and presented no distinction between an upper and lower canopy (Figure 4).

Average percentage live crown in the old-growth riparian forest ranged from 21% in Douglas-fir up to 60% in western red cedar (Table 3). In the second-growth stands, average percentage live crown ranged from 41% in red alder to 78% in western red cedar.

There was no statistical difference identified between percentage live crown in the old-growth and second-growth ($P > 0.23$). When divided into quartiles based on height (Table 3), percentage live crown in the old-growth ranged from 46.9 to 58.7% with the greatest percentage live crown in quartiles 2 and 4 (58.7 and 58.4%, respectively; Figure 6). In the second-growth stands, percentage live crown ranged from 44.7 to 51.5% with the greatest percentage live crown in quartiles 2 and 4 (51.5 and 49.7% respectively; Figure 6).

In the old-growth forests sampled, the lowest H:D ratios were found in the tallest trees, whereas the lowest H:D ratios were found in quartile 1 in the second-growth (Figure 6, Table 3). With the exception of quartile 1, the majority of trees in the second-growth had H:D ratios exceeding 80:1, whereas almost all of the old-growth trees had H:D below this threshold (Figure 6). Redwood had the lowest average H:D ratio in the old-growth whereas western red cedar had the lowest average H:D ratio in the second-growth followed by redwood (Table 2).

Snags in second-growth stands were more numerous ($P < 0.001$), shorter ($P < 0.002$), and less decayed (58% of snags in the second-growth were in decay classes 1 and 2 compared to 33% in the old-growth) than in old-growth stands. In the second-growth, there were 206.3 snags ha^{-1}, comprised mostly of Douglas-fir (42%) and red alder (36%). The remaining snags were redwood, western hemlock and tanoak. The average diameter for second-growth snags was only 20.5 cm (SD 10.5), whereas their average height was

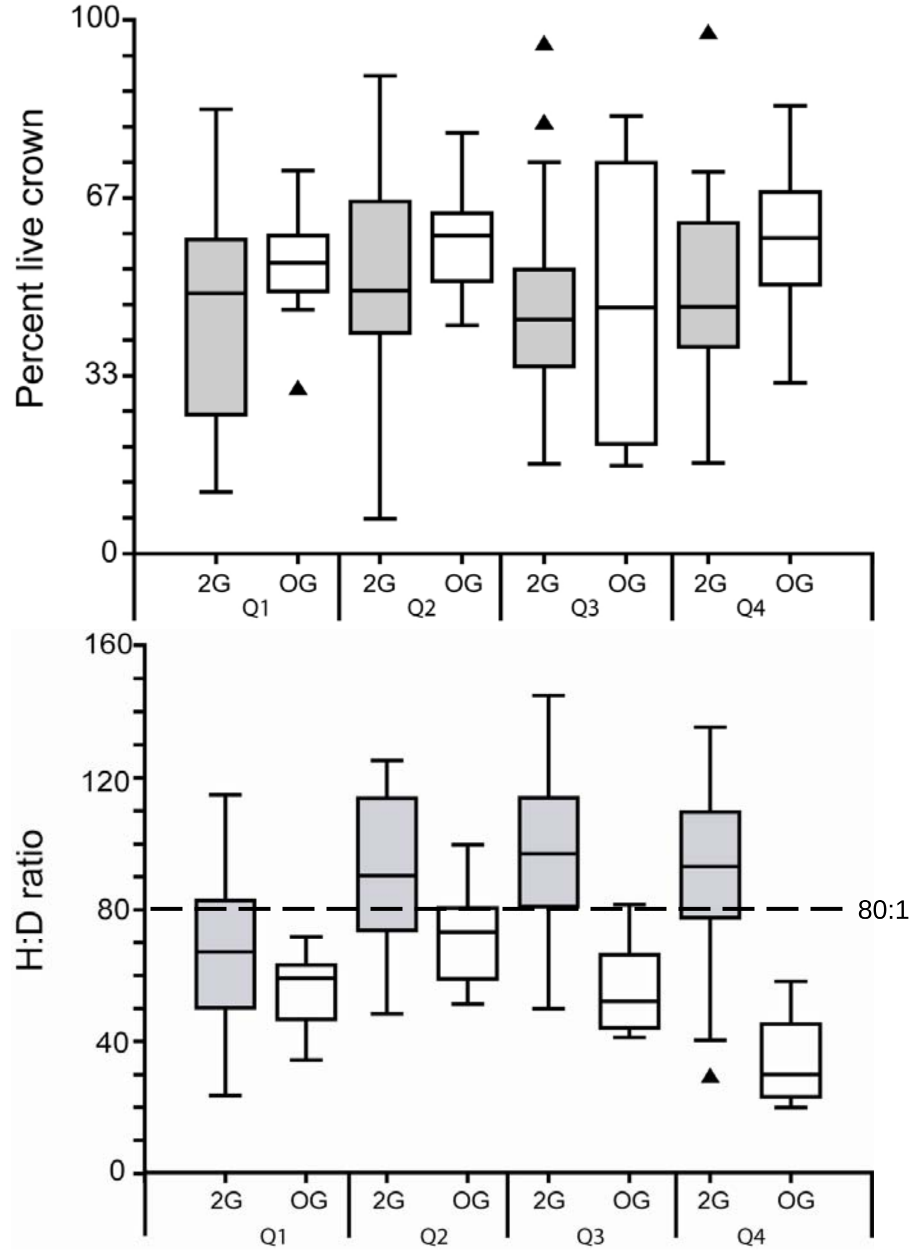

Figure 6. Percentage live crown (top) and height to diameter ratio (H:D; bottom) by quartile (determined by tree height) for old-growth (OG) and second-growth (2G) riparian forests in Redwood National Park, California. For H:D ratios, horizontal line (80:1) denotes the commonly-reported threshold below which trees exhibit resistance to wind damage.

12.9 m (SD 7.7). In the old-growth stands, there were only 18.8 snags ha^{-1} comprised of only two species: western hemlock and redwood (67% and 33%, respectively). The average diameter was 42.7 cm (SD 29.4) and average height was 8.0 m (SD 6.8).

Understory Vegetation

Understory plant species composition did not differ substantially between old-growth and second-growth riparian stands (Table 4). The Jaccard Coefficient of Community showed that old-growth and second-growth had 54% of species in common between the two communities, with 19 species observed in the old-growth stands (14 herbs and 5 shrubs) and 21 species in the second-growth stands (16 herbs and 5 shrubs; Table 5). Species unique to the old-growth were *Atriplex rosea* L., *Disporum hookeri* (Torr.) G. Nicholson, *Goodyera oblongifolia* Raf., *Rhododendron macrophyllum* D. Don ex G. Don, and *Rhododendron occidentale* (Torr. & Gray ex Torr.) A. Gray. Species unique to the second-growth were *Ranunculus uncinatus* D. Don, *Ribes* sp., *Rubus spectabilis* Pursh, *Rubus ursinus* Cham. & Schldl., *Dryopteris* sp., *Equisetum* sp., and *Asplenium* sp.. Shannon diversity (H′) and evenness based on H′ (J′) did not differ between old-growth and second-growth for all understory species combined ($P > 0.05$; Table 5); however, H′ and J′ for shrubs were significantly greater in the old-growth ($P < 0.03$; Table 5)) whereas H′ and J′ for herbs was significantly greater in the second-growth ($P < 0.03$; Table 5).

Table 4. Understory plant frequency, cover and importance value in old-growth and second-growth riparian forests in Redwood National Park, California. Importance value rank for the 10 highest importance values is indicated in parentheses.

Plant name[a]	Relative frequency[a]		Relative cover[b]		Importance value[c]	
	Old-growth	Second-growth	Old-growth	Second-growth	Old growth	Second-growth
Adiantum sp.	4%	4%	0.1%	0.4%	2.2%	2.3%
Asplenium sp.	0%	4%	0.0%	0.0%	0.0%	2.1%
Athyrium filix-femina	17%	21%	0.4%	1.8%	8.6% (7)	11.3% (7)
Atriplex rosea	13%	0%	0.2%	0.0%	6.4% (9)	0.0%
Blechnum spicant	67%	67%	15.4%	10.6%	41.0% (3)	38.7% (2)
Carex sp.	4%	25%	0.1%	5.0%	2.2%	15.0% (6)
Disporum hookeri	8%	0%	0.2%	0.0%	4.3%	0.0%
Dryopteris sp.	0%	29%	0.0%	1.1%	0.0%	15.1% (5)
Equisetum sp.	0%	21%	0.0%	0.5%	0.0%	10.7% (9)
Galium sp.	17%	21%	0.3%	0.5%	8.5% (8)	10.7% (10)
Gaultheria shallon	58%	50%	11.4%	8.6%	34.9% (4)	29.3% (3)
Goodyera oblongifolia	8%	0%	0.1%	0.0%	4.2%	0.0%
Mahonia nervosa	8%	8%	0.6%	0.4%	4.5%	4.4%
Oxalis oregana	96%	21%	16.4%	1.1%	56.1% (2)	11.0% (8)
Polystichum munitum	92%	96%	50.7%	52.6%	71.2% (1)	74.2% (1)
Ranunculus uncinatus	0%	8%	0.0%	0.6%	0.0%	4.4%
Rhododendron macrophyllum	4%	0%	0.3%	0.0%	2.3%	0.0%
Rhododendron occidentale	8%	0%	1.4%	0.0%	4.8% (10)	0.0%
Ribes sp.	0%	4%	0.0%	0.1%	0.0%	2.1%
Rubus spectabilis	0%	8%	0.0%	3.6%	0.0%	6.0%
Rubus ursinus	0%	8%	0.0%	0.2%	0.0%	4.3%
Trientalis borealis	4%	4%	0.0%	0.1%	2.1%	2.1%
Trillium ovatum	46%	8%	0.9%	0.1%	23.4% (5)	4.2%
Vaccinium ovatum	4%	4%	0.2%	0.2%	2.2%	2.2%
Vaccinium parvifolium	21%	38%	1.1%	12.0%	11.0% (6)	24.7% (4)
Viola sempervirens	4%	13%	0.1%	0.4%	2.1%	6.5%

[a] Relative frequency is the number of plots that the plant was found in divided by the total number of understory plots (N=24).
[b] Relative cover is the percentage cover of each plant divided by the total percentage cover of all plants.
[c] Importance value is the sum of relative frequency and cover divided by 2.

Table 5. Total number of species (s), average percentage cover of individuals (N), Shannon diversity (H´), evenness using H´ (J´) average total percentage cover for plants found in the understory in the old-growth and second-growth riparian forests in Redwood National Park, California. Standard deviation is in parentheses.

		s	N	H´	J´	Percentage cover
Herbs	Old-growth	14	14.91 (9.62)	0.41 (0.14)	0.32 (0.11)	9.1 (7.7)
	Second-growth	16	16.38 (18.58)	0.29 (0.19)	0.23 (0.15)	52.3 (26.0)
Shrubs	Old-growth	5	7.29 (14.60)	0.11 (0.17)	0.14 (0.21)	39.0 (20.1)
	Second-growth	5	7.34 (8.96)	0.23 (0.13)	0.29 (0.16)	13.3 (13.5)
All understory	Old-growth	19	14.32 (9.60)	0.45 (0.17)	0.33 (0.13)	62.0 (22.7)
	Second-growth	21	11.34 (7.24)	0.45 (0.16)	0.32 (0.12)	52.9 (27.3)

No statistical difference was detected between total understory cover in old-growth and second-growth stands ($P = 0.48$). Shrub cover, however, was significantly greater in old-growth than second-growth ($P < 0.02$; Table 5). Herbaceous cover was significantly greater in second-growth ($P < 0.002$; Table 5). *Polystichum munitum* (Kaulf.) C. Presl had the highest relative cover of all plants found in the understory for both old-growth and second-growth stands, 52.3% and 71.2%, respectively. It also had the highest IV (Table 4). *Oxalis oregana* Nutt. had significantly higher percentage cover in old-growth stands than in second-growth stands (10.1% and 0.6%, respectively; $P < 0.001$) as well as the second highest IV in the old-growth stands (56%). It only had an IV of 11.0% in the second-growth (IV rank 8). Shrubs were taller on average in old-growth stands (0.88 m; SD 0.49) than in second-growth (0.56 m; SD 0.27), although the differences were not significant ($P = 0.14$).

The seedling stratum differed tremendously between old-growth and second-growth riparian forests sampled. Seedling composition in old-growth stands was dominated by western hemlock and tanoak (47% and 41% of stems, respectively). Redwood accounted for the remaining 12% of the tree regeneration (167 stems ha^{-1}). In second-growth stands, redwood made up 85% of seedlings (1,708 stems ha^{-1}). Tanoak and red alder made up the remaining 15% of tree regeneration with 208 and 83 stems, respectively. Though the mean stem density of seedlings contrasted in the old-growth and second-growth, there was substantial variation between sites and no significant difference was identified for any species except western hemlock (667 stems ha^{-1} in the old-growth, zero stems ha^{-1} in the second-growth; $P < 0.04$).

Future Stand Conditions

Growth projections in CRYPTOS illustrated the potential effects of restoration treatments on future stand characteristics in the second-growth redwood stands (Tables 6, 7). Growth projections indicated that there was little variation among the three scenarios after 50 years of growth in stem density, basal area, quadratic mean diameter, percentage live crown, or H:D ratio (Tables 6, 7) whether considering the stand as a whole or just the three dominant species (red alder, Douglas-fir, and redwood). According to growth projections, the largest increase in total stand basal area after 50 years will occur in the Alder Absent scenario. This scenario also showed the largest increase in basal area and quadratic mean diameter for redwood (Tables 6, 7). The model projections indicate that red alder will not maintain its position in the canopy in either the Current Stand or the South Fork Lost Man Creek Thinning scenarios after 50 years and its IV will decrease from the most important species in the stand to the fourth most important (Table 6). The South Fork Lost Man Creek Thinning scenario is the only scenario where the growth projection indicates that redwood will become the dominant species in terms of IV (Table 6). After the 50 year simulation, Douglas-fir was projected to be the dominant species (highest IV) in the other two scenarios. The growth projections indicate that Douglas-fir

Table 6. Basal area (m^2 ha^{-1}), stem density (trees ha^{-1}) (relative basal area, and relative density are indicated in parentheses), Importance value, and importance value rank for second-growth riparian forests at Redwood National Park, California at year 0 and after 50 years of CRYPTOS-modeled growth for the Current Stand and under two scenarios: Alder Absent and the South Fork Lost Man Creek Thinning and for old-growth riparian forests at year 0.

	Species	Current Stand			Alder Absent			South Fork Lost Man Creek Thinning			Old-growth
		Year 0	Year 50	% change	Year 0	Year 50	% change	Year 0	Year 50	% change	
Basal area (m^2/ha) (relative basal area[b] %)	Redwood	7.2 (11.7%)	18.5 (19.7%)	157.1	7.1 (14.8%)	22.0 (24.3%)	207.8	7.1 (12.3%)	20.1 (22.3%)	180.9	371.0 (93.7%)
	Douglas-fir	11.1 (18.1%)	26.5 (28.2%)	138.0	11.1 (22.9%)	28.3 (31.2%)	154.8	7.9 (13.6%)	20.1 (22.4%)	156.3	8.1 (2%)
	Other conifers[a]	7.0 (11.4%)	15.4 (16.4%)	119.7	6.3 (13.1%)	16.3 (18.0%)	157.2	7.0 (12.1%)	16.5 (18.3%)	135.1	16.1 (4.1%)
	Tanoak	0.2 (0.3%)	0.5 (0.5%)	143.0	0.1 (0.1%)	0.3 (0.3%)	520.0	0.2 (0.3%)	0.5 (0.6%)	160.7	0.9 (0.2%)
	Red alder	12.0 (19.5%)	9.3 (9.9%)	-23.0	-	-	-	12.0 (20.7%)	8.9 (9.9%)	-25.8	-
	Residual redwood	24.0 (39%)	23.8 (25.3%)	-1.0	23.8 (49.1%)	23.8 (26.2%)	0.0	23.8 (41.0%)	23.8 (26.4%)	0	-
	All species	61.6	93.9	52.5	48.4	90.7	87.3	58.0	89.9	55.1	49.8
Stem density (trees ha^{-1}) (relative density[c] %)	Redwood	156.3 (27.2%)	127.5 (31.5%)	-18.4	155.7 (41.0%)	127.8 (40.0%)	-17.9	155.7 (29.1%)	128.3 (34.4%)	-17.6	112.5 (45%)
	Douglas-fir	143.8 (25%)	113.9 (28.1%)	-20.7	143.3 (37.7%)	113.9 (35.7%)	-20.5	105.9 (19.8%)	84.0 (22.5%)	-20.6	12.5 (5%)
	Other conifers[a]	68.8 (12%)	59.1 (14.6%)	-14.1	65.4 (17.2%)	59.3 (18.6%)	-9.3	68.5 (12.8%)	59.3 (15.9%)	-13.4	75.0 (30%)
	Tanoak	12.5 (2.2%)	9.9 (2.4%)	-20.9	3.1 (0.8%)	5.9 (1.9%)	90.5	12.5 (2.3%)	9.9 (2.7%)	-20.6	50.0 (20%)
	Red alder	181.3 (31.5%)	82.1 (20.3%)	-54.7	-	-	-	180.6 (33.7%)	79.1 (21.2%)	-56.2	-
	Residual redwood	12.5 (2.2%)	12.4 (3.1%)	-1.1	12.4 (3.3%)	12.4 (3.9%)	0.0	12.4 (2.3%)	12.4 (3.3%)	0.0	-
	All species	575.0	404.8	-29.6	379.8	319.3	-15.9	535.5	373.0	-30.4	17.0
Importance Value[d] (Rank[e])	Redwood	19.4 (4)	25.6 (2)	-	27.9 (2)	32.1 (2)	-	20.7 (3)	28.4 (1)	-	69.3 (1)
	Douglas-fir	21.5 (2)	28.2 (1)	-	30.3 (1)	33.4 (1)	-	16.7 (4)	22.5 (2)	-	3.5 (4)
	Other conifers[a]	11.7 (5)	15.5 (3)	-	15.2 (4)	18.3 (3)	-	12.4 (5)	17.1 (3)	-	17.0 (2)
	Tanoak	1.2 (6)	1.5 (6)	-	0.5 (5)	1.1 (5)	-	1.3 (6)	1.6 (6)	-	10.1 (3)
	Red alder	25.5 (1)	15.1 (4)	-	-	-	-	27.2 (1)	15.5 (4)	-	-
	Residual redwood	20.6 (3)	14.2 (5)	-	26.2 (3)	15.0 (4)	-	21.7 (2)	14.9 (5)	-	-

[a] Other conifers includes grand fir, western red cedar, and western hemlock.
[b] Relative basal area is the basal area of each species divided by the basal area of all species.
[c] Relative density is the stem density of each species divided by the total stem density of all species.
[d] Importance value is the sum of relative density, and relative basal area divided by 2.
[e] Importance value rank is the rank of the species in the stand from highest (most important) to lowest (least important).

Table 7. Quadratic mean diameter (cm), height to diameter ratio, and percentage live crown for second-growth riparian forests at Redwood National Park, California at year 0 and after 50 years of CRYPTOS-modeled growth for the Current Stand and under two scenarios: Alder Absent and the South Fork Lost Man Creek Thinning and for old-growth riparian forests at year 0.

		Current Stand			Alder Absent			South Fork Lost Man Creek Thinning			Old-growth
	Species	Year 0	Year 50	% change	Year 0	Year 50	% change	Year 0	Year 50	% change	
Quadratic mean diameter (cm)	Redwood	24.2	43.0	77.5	24.2	46.8	93.7	24.2	44.6	84.7	204.9
	Douglas-fir	31.4	54.4	73.3	31.4	56.2	79.0	30.7	55.2	79.7	90.7
	Other conifers[a]	36.1	57.7	59.9	35.1	59.2	68.4	36.1	59.5	64.8	52.4
	Tanoak	14.3	25	75.3	14.3	25.8	80.4	14.3	25.9	81.2	15.1
	Red alder	29.1	37.9	30.4	-	-	-	29.1	37.8	30.2	-
	Residual redwood	156.4	156.5	0.1	156.5	156.5	0.0	156.5	156.5	0.0	-
	All species	36.9	54.4	47.2	40.3	60.1	49.3	37.1	55.4	49.2	142.0
Height to diameter ratio	Redwood	69.1	83.3	20.4	69.1	83.0	20.0	69.1	83.5	20.8	48.9
	Douglas-fir	100.9	90.2	-10.6	100.9	87.6	-13.2	99.0	88.7	-10.4	49.8
	Other conifers[a]	84.4	90.7	7.5	85.3	88.6	3.9	84.6	89.1	5.3	63.3
	Tanoak	79.0	114.4	44.7	78.7	119.1	51.4	78.7	115.5	46.8	54.4
	Red alder	95.6	79.3	-17.1	-	-	-	95.8	79.4	-17.1	-
	Residual redwood	34.5	34.5	0.0	34.5	34.5	0.0	34.5	34.5	0.0	-
	All species	86.7	85.2	-1.7	84.0	86.1	2.4	86.3	84.5	-2.1	23.6
Percentage live crown	Redwood	52%	25%	-52.5	52%	27%	-47.5	52%	26%	-49.5	54%
	Douglas-fir	43%	32%	-24.5	43%	33%	-21.8	43%	34%	-20.4	21%
	Other conifers[a]	66%	40%	-39.0	64%	41%	-36.2	66%	41%	-37.1	60%
	Tanoak	72%	28%	-61.8	72%	29%	-59.7	72%	29%	-59.5	57%
	Red alder	41%	30%	-26.9	-	-	-	41%	29%	-28.0	-
	Residual redwood	68%	68%	-0.6	68%	68%	0.0	68%	68%	0.0	-
	All species	49%	30%	-37.3	51%	32%	-36.2	49%	31%	-35.7	24%

[a] Other conifers includes grand fir, western red cedar, and western hemlock.

will make up the majority of the trees in the tallest quartile in all scenarios (Figure 7). The South Fork Lost Man Creek Thinning scenario had both an immediate and prolonged effect on the dominant position of Douglas-fir both in IV and canopy position. The majority of the trees removed for this scenario were Douglas-fir in quartile 4 (Figure 7, Table 6). After 50 years of growth, however, CRYPTOS projects that Douglas-fir will persist as the dominant species in the tallest quartile with the second highest IV in the stand. Redwood will increase its presence in the third quartile from 10 to 44% under the South Fork Lost Man Creek Thinning scenario, but it is projected to make up only 5% of the upper quartile which will be mostly Douglas-fir and the other conifer group (64% and 30%, respectively; Figure 7).

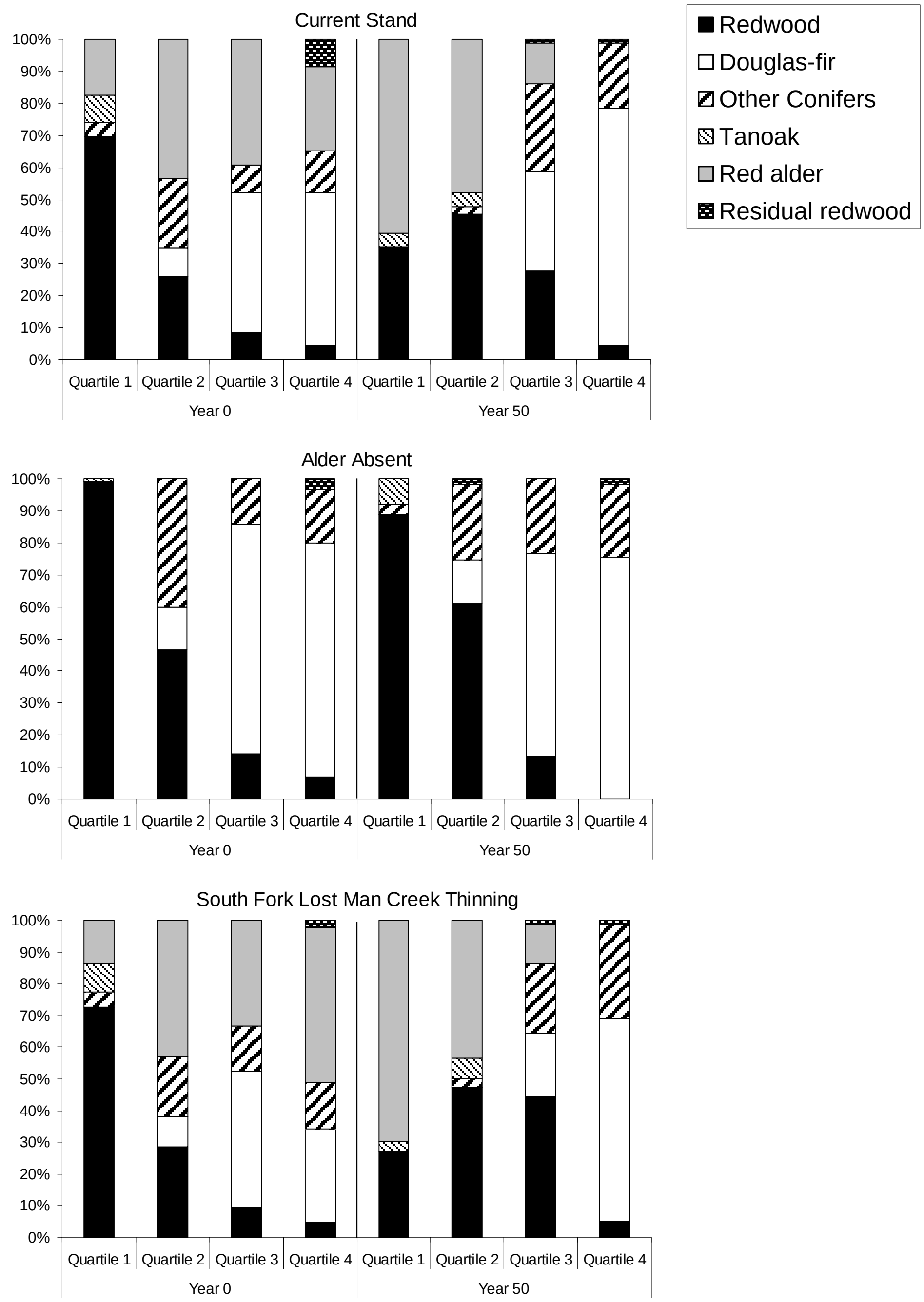

Figure 7. Percent of species present in each height quartile for second-growth riparian forests at Redwood National Park, California at year 0 and after 50 years of CRYPTOS-modeled growth for the Current Stand and under two scenarios: Alder Absent and the South Fork Lost Man Creek Thinning. The other conifer group includes grand fir, western red cedar, and western hemlock.

DISCUSSION

The structure and composition of second-growth riparian forest at Redwood National Park contrasts with the old-growth riparian forest. Further, in growth projections, CRYPTOS suggests that these stands will continue to differ for decades.

Old-growth riparian forests had much greater basal area than second-growth riparian stands but had fewer than half as many trees ha^{-1} (Table 2). The majority (93%) of the total basal area of the old-growth was redwood, even though it only accounted for 45% of the total stem density (Table 2, Figure 3). Old-growth stands had a high variability in stand structure as evidenced by the high standard deviations in both height and quadratic mean diameter (Table 4). Redwood, in particular, was present in all layers of the canopy in the old-growth and had a very large range in diameters (Figures 4, 5). Other species in old-growth were only present in particular layers of the canopy (Douglas-fir in the mid canopy, tanoak in the lower canopy; Figure 4) or in a narrow range of diameter classes (tanoak; Figure 5).

In contrast, second-growth had much smaller variation in size both among and within tree species (Tables 2, 3, Figure 5). Individual trees were smaller and shorter in second-growth and though there was some difference in which position each species occupied in the canopy, there was a great deal of overlap (Figure 4). The stem density of Douglas-fir, red alder, western hemlock, and tanoak contrasted sharply between old-growth and second-growth riparian forests (Table 2, Figure 3). Red alder and Douglas-fir were absent or nearly so in old-growth (0% and 5% of the relative density, respectively) whereas combined they made up the majority of the relative density in second-growth (31.5% and 25.0%, respectively). Tanoak and western hemlock, in contrast, accounted for 20.0% and 30.0%, respectively, of the relative density in old-growth riparian forest, but only 7.6% and 2.2%, respectively, of the relative density in second-growth riparian forest. Tanoak and western hemlock, both shade tolerant species, are commonly found in older forests throughout the redwood region and the Pacific Northwest (Lenihan 1986, Mahoney and Stuart 2000, Busing and Fujimori 2002, Teraoka 2004, Sawyer 2007, Sillett and Van Pelt 2007, Lorimer et al. 2009, Russell 2009). Loya and Jules (2008) included tanoak as an indicator species for the old-growth forest stage.

Some of the differences between the current old-growth and second-growth riparian forests are consistent with observations in other areas of the redwood region and the Pacific Northwest (Spies and Franklin 1991, Moore et al. 2004, Teraoka 2004, Zenner 2004, Chittick and Keyes 2005, Redwood National and State Parks 2005). These differences include the large numbers of Douglas-fir in second-growth, greater than twice as many trees in second-growth, and greater basal area in old-growth. High variability in diameters has been reported for old-growth forests of the redwood region and the Pacific Northwest (Spies and Franklin 1991, Zenner 2004, Sillett and Van Pelt 2007); similar to the old-growth riparian stands in this study. Lenihan (1986) found average canopy cover of 107.4% (SD 21.9) in old-growth forests in the upper portion of the Little Lost Man Creek watershed which was similar to the canopy cover found in the old-growth riparian forest.

Stem density found in this study in second-growth riparian forest is relatively low compared to other studies in Redwood National Park (Teraoka 2004, Chittick 2005). This is not surprising as riparian forests, especially on stream terraces, have been shown to have lower tree densities than adjacent upland sites in other areas of the Pacific Northwest (Means et al. 1996, Pabst and Spies 1999, Nierenberg and Hibbs 2000).

The clear dominance of redwood in old-growth riparian stands is in striking contrast to second-growth forest where red alder and Douglas-fir dominate. Species dominance is not always easy to identify in a mixed-species stand. IV takes into account the how many trees of the species are in the stand (relative density) as well as how common it is (relative frequency) and it size (relative basal area). However, canopy position (height) also is an important factor in determining which species are currently (and are likely to remain) in a dominant position (Curtis and McIntosh 1951, Bell 1974, Goebel and Hix 1996, Oliver and Larson 1996, Barker et al. 2002, Binkley 2004, Zenner 2004). For example, grand fir had the largest quadratic mean diameter in the second-growth (excluding residual old-growth redwood) and was one of the taller trees found in the stand (Table 3, Figures 4 and 5). However, grand fir was found only in one plot and in very small numbers so its IV was only 6.1% (Table 2), providing a more informed estimate of its rarity.

Red alder, however, was a dominant species in second-growth riparian forest; it had the highest IV and occupied a dominant or co-dominant canopy position in the second-growth stands (Figure 4). This was in stark contrast to the complete absence of red alder in the old-growth riparian forest sampled. The dominance of red alder in second-growth riparian forest is a common theme in disturbed forests throughout the redwood region and Pacific Northwest (Stubblefield and Oliver 1978, Dahm 1981, Hibbs and Bower 2001, Andrus 2008, Russell 2009, Villarin et al. 2009). In Redwood National Park, for example, Urner and Madej (1998) noted a shift in vegetation along Redwood Creek from dense, conifer-dominated stands to hardwood-dominated stands consisting of mostly red alder for decades following timber harvest.

The implications of the presence of red alder in terms of future stand structure were investigated further by modeling the structure and composition of the stand in 50 years in the absence of red alder (the Alder Absent scenario of the growth projection). This was compared to 50 years of growth of the current stand (the Current Stand scenario). In the Current Stand Scenario, red alder had the highest IV (25.5%) followed by Douglas-fir (21.5%), residual redwood, and then second-growth redwood (19.4%; Table 6). After fifty years of growth under the Current Stand scenario, the growth projection indicated that red alder will decrease to an IV of 15.1% (fourth most important species; Table 6) and it will be absent from the tallest quartile (Figure 7). Growth projections show that the three most important species (Douglas-fir, redwood, and the other conifer group) will be the same with the same IV ranks after fifty years of group for both the Current Stand and the Alder Absent scenarios (Table 6). The growth projections also indicate that red alder will decrease in IV and will no longer be in the upper quartile of height for the South Fork Lost Man Creek Thinning scenario.

Red alder tends to exhibit rapid, early height growth and can often overtop and suppress competing species (such as Douglas-fir) in second-growth stands (Stubblefield and Oliver 1978, Muldavin et al. 1981, Harrington et al. 1994, Hibbs and DeBell 1994). Red alder is a short-lived species (60–70 years; Harrington 1990) in comparison to the other species present so it is less likely that alder will persist to become a dominant tree in the future. The rapid early height growth of red alder can often place it into a dominant or codominant canopy position. However, if Douglas-fir is present in a codominant role, its later, sustained height growth can enable the species to surpass red alder over time and make it the dominant species (Stubblefield and Oliver 1978, Muldavin et al. 1981, Harrington et al. 1994, Oliver and Larson 1996). Harrington et al. (1994) saw that Douglas-fir began surpassing red alder in height around 45 years following establishment. Because red alder requires full sunlight (is shade intolerant) and must be in the upper canopy (dominant or codominant crown position) to survive in a mixed species stand (Harrington 1990), it would not likely survive if Douglas-fir were to gain a dominant position in the canopy. Red alder does grow well on extremely wet sites (Harrington 1990, Harrington et al. 1994, Villarin et al. 2009) so future cohorts of red alder may be able to maintain a presence in the stand at the immediate edges of the creeks, or even within the active channel if disturbances such as flooding and bank erosion occur (Trush et al. 1989, Newton and Cole 1994, Nierenberg and Hibbs 2000, Villarin et al. 2009). Red alder made up only a small percentage (4%) of seedlings in the second-growth, and since they do not tolerate shade, it is unlikely that red alder will have a strong presence in the stand in the future. In the absence of any major disturbance, by the time the stand reaches 130 years old, there will likely be little red alder remaining in the second-growth riparian stands (Minore and Weatherly 1994, Newton and Cole 1994, Russell 2009, Villarin et al. 2009).

Redwood in the second-growth occupied a lower canopy position than Douglas-fir and red alder and growth projections suggest that position will last for at least the next 50 years. Redwood is an incredibly long-lived species (over 2000 years) with high tolerance to shade (Olson et al. 1990, Sawyer et al. 2000, Lorimer et al. 2009). Though redwood can endure suppression, it grows best in full sunlight. In a suppressed canopy position, redwood growth will continue, but will be slow which, in the second-growth riparian stand, would allow Douglas-fir to maintain its higher position in the canopy. Redwoods can grow from seeds or by sprouting from stumps or damaged trees (Olson et al. 1990). Redwoods have rapid, early height growth. However, trees that originated from seeds may not begin rapid growth for at least 10 years (Olson et al. 1990, Lorimer et al. 2009). This may allow for red alder and Douglas-fir in the stand to gain a higher canopy position. The origins of the redwood in second-growth riparian stand are not known, though it is likely that the majority of the trees originated from seeds. Stumps of large, old trees, like the ones present in the stand before it was cut, tend to sprout less often than smaller, younger trees (Olson et al. 1990, Sawyer et al. 2000, O’Hara et al. 2007). Redwood responds to thinning and will grow rapidly if released from shade (Teraoka 2004, Chittick 2005, Plummer 2008, O’Hara et al. in press).

Douglas-fir appears to have a much greater likelihood of continuing to dominate these second-growth riparian forests for the immediate future. Douglas-fir had the second highest IV in the second-growth (21.5%) and co-dominated the upper canopy with red alder. Douglas-fir grows relatively slowly for the first several years, but then its growth begins to accelerate and it is able to maintain a rapid rate of height growth over a long period of time (Hermann and Lavender 1990). As its height continues to increase, Douglas-fir is likely to gain a more dominant canopy position than red alder and become the primary species in the second-growth (Harrington et al. 1994, Plummer 2008). Coastal Douglas-fir can live for 500 to 1000 years or more (Hermann and Lavender 1990) and it can maintain a dominant position in a stand for decades or centuries (Sawyer 2007, Lorimer et al. 2009).

The 50-year growth projections for both the Current Stand and the Alder Absent scenarios suggest that Douglas-fir will have the highest IV in the stand followed by redwood (Table 6). The only scenario where redwood is projected to have the highest IV after 50 years is the South Fork Lost Man Creek Thinning. However, growth projections indicate that Douglas-fir will be in a higher canopy position than redwood after 50 years for all three scenarios (Figure 7). In the absence of management or a large disturbance, the second-growth riparian forest in the future will likely be dominated by Douglas-fir whereas redwood will continue to be present in a codominant or intermediate role.

The majority (59%) of the overstory trees in second-growth had H:D ratios that exceeded 80:1 (Figure 6), the threshold that indicates a higher probability of damage due to wind and snow (Wonn and O'Hara 2001). These higher H:D ratios in the second-growth stands can be attributed to the dense spacing and due to natural regeneration (Wonn and O'Hara 2001). Closely spaced trees often grow rapidly in height but not in diameter and can be more susceptible to buckling or tipping. The average H:D in nearby upland sites in the Lost Man Creek Watershed were lower than in the riparian areas, ranging from 44.9 in redwood to 65.2 in Douglas-fir (Redwood National and State Parks 2005). These sites had few red alder which could be one reason the riparian site H:D are so high. Newton and Cole (1994) found H:D ratios of greater than 100:1 in dense stands of alder-dominated second-growth in the Oregon coast range. Species with rapid, prolonged height growth such as red alder and Douglas-fir often have high H:D ratios (Table 3; Oliver and Larson 1996). High H:D ratios could cause problems for the stand in the future. Trees with lower H:D ratios (<60:1) are more likely to have enough girth to support the tree whereas trees with higher H:D ratios can have support problems, low vigor, a shallow root system, and may topple during wind storms (Emmingham et al. 2000). Douglas-fir had the highest average H:D ratio in the second-growth whereas the average H:D ratio for redwood was below 80:1 (Table 3). This may indicate that redwood would be stable enough to avoid blowdown in the event of a thinning or other disturbance that opens up the canopy (Wonn and O'Hara 2001). However, any redwoods in the stand that have grown from stump sprouts may have inherent instability even with a low H:D ratio (Olson et al. 1990).

The similar percentage live crown in old-growth and second-growth were surprising since closely spaced trees tend to have lower crown ratios as the crowns recede when light is only available to branches in the upper portion of the canopy (Oliver and Larson 1996). Chittick (2005) found that the percentage of live crown increased as stand stem density decreased in thinned upland second-growth in the headwaters of Lost Man Creek. The average percentage live crown in nearby upland second-growth sites of similar age in the Lost Man Creek Watershed were considerably lower than in the riparian areas, ranging from 26.0 in redwood to 24.7 in Douglas-fir (Redwood National and State Parks 2005). The spacing of trees within the second-growth riparian forest in this study was not as dense as in other parts of Redwood National Park (Teraoka 2004, Chittick 2005) which could be a reason for the higher percentage live crown.

It is also possible that the canopy had only recently closed in the second-growth and the percentage live crown will decrease in the near future. The high snag density in the second-growth suggests that the canopy had closed fairly recently in the second-growth and the stand was just starting to enter stem-exclusion (Oliver and Larson 1996). If the stand is not thinned either naturally through stem exclusion or via anthropogenic causes the percentage live crown will decrease and trees will decrease in vigor (Oliver and Larson 1996, Bailey and Tappeiner 1998, O'Hara and Oliver 1999, Chittick 2005). Growth projections suggest that all three scenarios will have a greater than 30% decrease in percentage of live crown over the fifty-year growth projections. The high percentage of live crowns in the second-growth indicate potential for successful release if the stand were to be thinned in the near future (Emmingham et al. 2000), an advantageous feature that will fade as these stands develop.

The similar understory communities in old-growth and second-growth are not typical of other studies of upland forests in other areas of the redwood region or the Pacific Northwest. Typically, young forests have foliage concentrated high in the canopy with little to no understory, whereas old-growth forests have a diverse understory with a continuous distribution of foliage from the ground to the canopy (Franklin et al. 2002). An understory community with low species richness is a natural characteristic of young stands in stem exclusion (Oliver 1981). The similar total understory percentage cover between old-growth and second-growth riparian forest was also atypical of other studies in the redwood region. Chittick (2005) found understory cover ranging from 0 to 20% in unmanaged second-growth and 45 to 95% in thinned second-growth in the headwaters of Lost Man Creek; cover of the understory decreased as the stem density of overstory trees increased. Average understory cover ranged from 24 to 93 percent in the thinned stands of the Whisky-40 located on the ridge above Little Lost Man Creek and 12% in the unthinned control whereas adjacent old-growth understory cover ranged from 73 to 164% (Teraoka 2004). Lenihan (1986) found average understory cover of 149% (range 77.5–215%) in old-growth forests in the upper portion of the Little Lost Man Creek watershed.

The similarity in the old-growth and second-growth plant communities and average understory plant cover could be due to several factors including similar overstory canopy cover and site quality. Klinka et al. (1996) showed that forest canopy cover and site quality had a strong influence on the percentage cover and species composition of understory communities. Differences from other areas in Redwood National Park could be attributed to wider tree spacing in riparian second-growth forest or increased soil moisture in riparian areas compared to more xeric upland sites. Riparian areas have been shown to have higher plant species diversity than upland areas throughout the Pacific Northwest (Gregory et al. 1991, Naiman et al. 1998). Soil moisture has been shown to have a strong influence on species composition in the redwood region (Lenihan 1986, Mahoney and Stuart 2000, Mahoney and Stuart 2007). The presence of red alder in second-growth could also be affecting the understory vegetation composition. Deal (1997) found most understory plant species had a higher percentage cover under canopies dominated by red alder than those dominated by conifers. Red alder in crowded, pure stands tends to have a very low percentage live crown with a narrow, domelike crown (Harrington 1990) with an understory dominated by *Polystichum munitum* (Newton and Cole 1994). In southeastern Alaska, lightly stocked, mixed alder-conifer riparian stands maintained species-rich understories for up to 45 years after logging (Deal 1997). Alaback (1982) reported rapid declines in understory biomass in spruce hemlock forests once the canopy closed and the stand entered the stem-exclusion phase (Oliver and Larson 1996).

The differences in the shrub and herbaceous percentage cover between old-growth and second-growth was, however, consistent with other studies. Loya and Jules (2008) found significantly higher shrub cover in old-growth redwood stands than in second-growth stands and higher herbaceous plant cover in young second-growth stands than old-growth stands. *Rhodendron occidentale*, *Trillium ovatum* Pursh, and *Oxalis oregana* had IV ranks in the top 10 in the old-growth, but low IV in the second-growth (Table 4). In contrast, *Carex* spp., *Dryopteris* sp., and *Equisetum* sp. all had IV ranks in the top 10 in the second-growth, but were absent or had low IV in the old-growth. *Trillium ovatum* and *Oxalis oregana* are common in old-growth redwood forests and have been described as old-growth stage indicator species (Lenihan 1986, Sawyer 2007, Sillett and Van Pelt 2007, Loya and Jules 2008, Russell 2009).

As with all modeling, there are limitations to CRYPTOS for projecting the structure and composition of the riparian second-growth stand after 50 years (Ritchie 1999). The diameter and height distributions generated by the three different scenarios project a more normal distribution after fifty years of growth. However, CRYPTOS only projects the growth of trees that are currently in the stand and greater than 10 cm DBH. Ingrowth of seedlings and saplings is not taken into account during CRYPTOS growth projections (Wensel et al. 1987). A large number of young trees in the second-growth could have an effect on future stand dynamics by limiting available water resources or by changing the species composition as more redwood grow into the middle stratum of the canopy.

Another limitation of CRYPTOS is the positive effect of red alder on other species in the stand. Red alder has root nodules that can fix atmospheric nitrogen and add it to the soil (Harrington 1990). Other species in the stand, in particular Douglas-fir, can benefit from the nitrogen fixed by red alder (Weetman et al. 1992, Bormann et al. 1994, Hermann and Lavender 1990, Footen et al. 2009). Nitrogen has been shown to be the only nutrient limiting growth of Douglas-fir in the Pacific Northwest (Miller et al. 1992, DeBell et al. 1997, Hermann and Lavender 1990) so the red alder is likely promoting long-term development of Douglas-fir, and perhaps other species.

Goebel and Hix (1996) used old-growth forests as a benchmark with which to compare the structure and composition of nearby second-growth forests. They then used this information to aid in the management of the second-growth. If we are to use the old-growth riparian forest of Little Lost Man Creek as a benchmark for second-growth riparian forest of Lost Man Creek, the compositional goal for the second-growth would be a redwood-dominated stand with only a small component of Douglas-fir and no red alder. Red alder will decrease in importance and likely die out over time on its own, so the primary management concern should be removal of Douglas-fir.

The South Fork Lost Man Creek Thinning scenario shows promise in increasing dominance of redwood (Table 6), but even after 50 years of projected growth, Douglas-fir remained the most common species in quartile 4 with the highest canopy position (Figure 7). Because the South Fork Lost Man Creek Thinning scenario retains the largest trees in the stand, there is little difference in percentage of redwood in quartile 4. Targeting the tallest Douglas-firs for removal would be necessary if the goal is to shift compositional dominance to emulate old-growth stands, specifically to increase redwood's potential for dominance. Analysis of an upland redwood second-growth thinning project at Redwood National Park yielded a similar conclusion (Teraoka 2004). It would also allow the understory trees to ascend and create a multi-layered canopy structure, similar to the Little Lost Man Creek structure and other old-growth forests in the Pacific Northwest (Oliver and Larson 1996, Chittick and Keyes 2005).

Girdling large Douglas-fir could also be implemented to alter canopy dominance. Girdling would also increase future large woody debris inputs to Lost Man Creek (Schuler et al. 2002) while avoiding a pulse of large woody debris to the stream common after timber harvest in riparian zones (Lisle and Napolitano 1998, Welsh et al. 2000). Constant input of large woody debris is important to the health of a stream, both in the immediate area and throughout the rest of the system (Vannote et al. 1980, Sedell et al. 1988, Bilby and Bisson 1992, Andrus 2008). Red alder debris is smaller and decomposes faster than Douglas-fir, western red cedar, and other conifer debris (Bilby 1988, Harmon et al. 1986, Minore and Weatherly 1994, Andrus 2008). Thus, measured contributions of large Douglas-fir entering the stream channel may be beneficial over the coming decades. Girdling to create snags can also provide habitat for cavity-nesting birds and other wildlife (Thornburg et al. 2000, Brandeis et al. 2002). Girdled trees will die and slowly decay before they fall; a process that could take decades (Cline et al. 1980; Brandeis et al. 2002). Girdling can be done by hand, minimizing soil disturbance in the riparian zone by avoiding the need for roads, vehicles, and large equipment.

All of the large trees in the study area (those growing within 10 m of the stream channel) have a 20% chance of contributing large woody debris to the stream, assuming they fall in a random direction (Van Sickle and Gregory 1990). Thinning with directional falling could increase the number of trees within the stream and girdling of trees nearest the stream could increase the number of snags in the stand and the potential for future large woody debris inputs.

Trees with high H:D ratios may be more susceptible to buckling or tipping should other trees be removed from the stand (Oliver and Larson 1996, Wonn and O'Hara 2001) so managers should be aware that thinning these second-growth stands may result in a rapid decline in remaining trees; though as already stated, the lower H:D ratios of redwood may allow it to withstand the increased potential of blowdown after a thinning.

CONCLUSIONS

The potential for redwood to dominate the riparian second-growth forest of Lost Man Creek is limited over the next century. If it continues its height growth, Douglas-fir has the greatest potential to become the long-term dominant species in the second-growth stands with redwood relegated as a subordinate species. Though redwood can remain in a suppressed state almost indefinitely, its growth rate will be slow and it will remain in the lower stratum of the canopy until it is released (Lorimer et al. 2009). If the desired future condition of Redwood National Park's riparian forests is redwood-domination comparable to remnant old-growth, some form of active restoration treatment targeting the upper canopy Douglas-fir (that is more aggressive than the South Fork Lost Man Creek Thinning simulated here) will be necessary in order to alter projected stand development over the foreseeable future.

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