Ecological Basis for Old-Growth Redwood Forest Restoration: 25-Year Assessment of Redwood Ecosystem Response to Restorative Thinning: A Report to Save-the-Redwoods League

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Recommended Citation:
Keyes, Christopher R. 2005. Ecological basis for old-growth redwood forest restoration: 25 year assessment of redwood ecosystem response to restorative thinning: A report to Save-the-Redwoods League. Humboldt State University. Arcata, CA.

Ecological Basis for Old-growth Redwood Forest Restoration: 25-Year Assessment of Redwood Ecosystem Response to Restorative Thinning

Save-the-Redwoods League Research Grant #25 Final Report

June 1, 2005

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PART I:

Stand Structure and Development Following Thinning in a Second-Growth Forest, Redwood National Park

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INTRODUCTION

When Redwood National Park was expanded in 1978, over 20,000 hectares out of 42,900 hectares was regenerating second-growth forest. The regeneration of stands within Redwood National Park following timber harvest resulted in a forested landscape that is composed of extremely high tree densities with uniform structure, diminished understory vegetation, and suppressed growth and development. These areas are dominated by Douglas-fir (*Pseudotsuga menziesii* [Mirbel] Franco) and tanoak (*Lithocarpus densiflorus* [Hook and Arn.] Redh.) in what was predominately an upland coast redwood (*Sequoia sempervirens* [D. Don.] Endl.) old-growth forest (Veirs 1986). The desire to restore these forests to conditions more similar to nearby old-growth stands has been stated most recently in the Redwood National and State Parks General Management Plan (USDI National Park Service 1999), but dates back to the initial park acquisition in 1968 (Stone et al. 1969). The Holter Ridge Thinning Study, located in the headwaters of Lost Man creek within Redwood National Park, is an experiment initiated in 1978 to determine the effects of low thinning with varying levels of residual stand densities on the development of old-growth characteristics and successional development (Veirs 1986). The stated goal is to alter the successional pathway to more closely resemble the pre-existing vegetation and accelerate the development of old-growth characteristics typical of upland redwood forests preceding European settlement

The fire ecology of redwood forests in Redwood National Park, for pre-European disturbance regimes, suggests that stand replacing events were extremely rare with very little analogy to clearcutting (Veirs 1979, (Sawyer et al. 2000). It has been theorized that in well stocked forests following stand replacing events it will take several centuries in order to develop old-growth characteristics such as multiple age structures, multi-layered or continuous vertical canopies, large branches, large snags, and coarse woody debris (Veirs 1986, (Oliver and Larson 1996, (Franklin et al. 2002). Furthermore, it has been noted that second-growth stands with high initial densities and uniform structure might not necessarily develop old-growth characteristics similar to the stands which had previously existed (DeBell et al. 1997, (Tappeiner et al. 1997). However, theories that describe stand development following stand replacing events can provide a framework to understand how second-growth forests develop after clearcutting (Long and Smith 1984, (Oliver and Larson 1996, (Franklin et al. 2002).

The successional sere that these second-growth forests now exhibit is the stem exclusion stage described by Oliver (1981) in which density-dependent tree mortality is the dominant process and recruitment of understory vegetation is excluded. As the main cause of mortality shifts from density-dependent to density-independent, re-initiation of the understory vegetation, including establishment of shade-tolerant species, will occur as gaps in the canopy become wider (Oliver and Larson 1996). Due to overstory tree decadence along with increasing overstory gap creation, vertical stratification of the canopy will proceed among shade-tolerant trees and epicormic branches on the lower portion of the stem will increase (Franklin et al. 2002). Gap processes dominate older stands and are the main creative force behind increasing spatial heterogeneity and regeneration (Sugihara 1989, (Franklin et al. 2002). Initial disturbance intensity, type of disturbance, and amount and type of legacy structures, such as live or dead standing trees, all effect the resulting forest composition and structure (Muldavin et al. 1981, (Halpern 1988, (Franklin et al. 2002). Low-intensity disturbances during stand succession, such as fire or thinning, can accelerate or delay the development of any of these processes throughout a stands development (e.g. tree seedlings being killed and/or regenerated following surface fires) (Franklin et al. 2002).

Silvicultural treatments, such as thinning and gap creation, have gained increasing attention as a way to alter a stand's successional pathway in order to increase near-term old-growth associated characteristic (Newton and Cole 1987, (DeBell et al. 1997, (Curtis et al. 1998). The majority of the research on enhancing old-growth characteristics has focused on the western hemlock zone of Oregon and Washington. Results are that thinning from below enhances the development of multi-storied stands (Barbour et al. 1997, (Bailey and Tappeiner 1998, (Busing and Garman 2002), increases understory vegetation (Bailey et al. 1998, (Thomas et al. 1999, (He and Barclay 2000, (Thysell and Carey 2001, (Lindh and Muir 2004), increases recruitment and survival of understory trees (Tappeiner and Zasada 1993, (Bailey and Tappeiner 1998, (Brandeis et al. 2001), increases growth of understory and mid-canopy trees (Bailey and Tappeiner 1998), produces larger tree sizes (Curtis and Clendenen 1994, (Bailey and Tappeiner 1998, (Busing and Garman 2002), and increases branch diameters (Maguire and Bennett 1996, (Maguire et al. 1999). Studies conducted in the coast range of Oregon that analyze growth rings of old-growth stumps indicate that one possible successional pathway toward old-growth structure is in stands with low initial densities (Tappeiner et al. 1997, (Poage and Tappeiner 2002); hence characteristics similar to old-growth forests may be achieved more quickly when stands have low densities either initially or through thinning.

Understory vegetation consisting of herbaceous, shrub, and tree species are at their lowest levels during canopy closure and may take up to 100 years following stand replacement events for levels to increase (Oliver and Larson 1996). The primary factor limiting understory vegetation in Coast Range forests is the amount of light reaching the forest floor, which thinning can directly alter (Bailey 1996). Thinning dense stands has been shown to increase species richness, diversity, density, and cover of understory vegetation (Bailey et al. 1998, (Bailey and Tappeiner 1998, (Thysell and Carey 2001), and regeneration of shrubs (Fried et al. 1988). Reductions in overstory stand densities have also increased biomass and density of salal (*Gaultheria shallon* Pursh.) (Huffman et al. 1994), and both seedling emergence and survival for salal, salmonberry (*Rubus spectabilis* Pursh.), vine maple (*Acer cicinatum* Pursh.), and big-leaf maple (*Acer macrophyllum* Pursh.) in the central Oregon Coast Range (Tappeiner and Zasada 1993). Understory vegetation possesses the ability to persist in severe shade following canopy closure and flourish upon opening of the canopy (Halpern 1988, (Halpern and Franklin 1990, (Halpern and Spies 1995),.

Due to the ability of redwood to sprout after being thinned, a multi-cohort stand is likely. Density of redwood sprouts following thinning was positively related to the number of redwood stumps while height growth of sprouts was inversely related to overstory density (Barrett 1988, Oliver et al 1994). Factors affecting rates of tree establishment include disturbance of forest floor, presence of downed woody debris, rates of shrub growth, canopy gap size and structure (Bingham 1984, (Gray and Spies 1996, (Bailey and Tappeiner 1998). Tanoak regeneration following cutting is prolific but height growth is negatively affected by overstory cover (Tappeiner and MacDonald 1984, (McDonald and Tappeiner 1987, (Wilkinson et al. 1997). Due to its high shade-tolerance, tanoak can maintain itself as a persistent component in the understory (Tappeiner and MacDonald 1984).

During the stem-exclusion stage the principal issue concerning mortality and species composition in mixed dense young stands is the silvical response of different species to density-dependent competition (Oliver and Larson 1996). Redwood's longevity and ability to persist in shade, combined with the moderate shade tolerance of Douglas-fir and exclusion of disturbances such as fire, indicates that Douglas-fir can be expected to decrease in dominance over time (Olson et al. 1990, (Oliver and Larson 1996). Without the use of silvicultural activities or disturbance, the redwood /Douglas-fir ratio of second-growth forests and associated structure may eventually approach those of old-growth stands over many hundreds or thousands of years. Mortality of tanoak due to competition is assumed to be less than Douglas-fir or redwood, but the specific effects of density on mortality are lacking for tanoak (Tappeiner and MacDonald 1984).

Growth responses due to stand density reductions show that redwood has a high capacity for increased growth following thinning. Research includes the effect of density on stand volume growth (Barnes 1924, (Fritz 1958, (Lindquist and Palley 1967, (Allen et al. 1996), growth following thinning (Carr 1958, (Oliver et al. 1994), and group selection on residual tree growth and regeneration (Adams et al. 1996, (Helms and Hipkin 1996).

Descriptions of stand structure characteristics and development in second-growth mixed-species redwood stands following thinning are limited. In 1995, the Whiskey-40 study was established in Redwood National Park to determine the effect of a low thinning on 30-32 year old stands that had been aerially seeded with Douglas-fir and were now composed of Douglas-fir, redwood, and tanoak. Teraoka (2004) reported that 7 years following thinning there was an increase in understory vegetation cover, prolific redwood and tanoak sprouting but a weak relationship to the number of stems cut, and that tanoak had begun to be overtopped by redwood and Douglas-fir but exhibited a lack of separation into a multi-strata overstory. The light thinning did not have an appreciable effect on basal area growth of the remaining trees but has opened the canopy enough for the understory to increase in cover.

Descriptions of stand development following thinning with regards to old-growth attributes in dense stands are needed to guide management decisions within Redwood National Park. However, unlike the western hemlock zone of Oregon and Washington, an ecological basis for thinning specifically to enhance old-growth forest development has not been established in the coast redwood region. Several issues this study addressed are the effect of thinning and stand density on: 1) understory species cover, richness, and diversity; 2) redwood and tanoak regeneration; 3) mortality and changes in species composition over time; and 4) stand structural attributes such as tree size, growth, and live crown ratio and vertical canopy stratification. Future stand development and succession is also considered with regards to desirable ecological characteristics.

MATERIALS AND METHODS

Study Site

This study was located in the Holter Ridge area in the headwaters of Lost Man Creek, a tributary to Prairie Creek, in the area known as the Holter Ridge Thinning Study (Appendix A). Latitude is 41 degrees North, longitude 123 degrees West, and elevation averages 450 m. Site aspect is north, west, and south but individual plot aspect can vary due to local topography (Appendix B). Angle of slope varies from 10% to 70%. Slope position ranges from ridge top to creek bottom with the majority occupying the mid-slope. Total rainfall for the year averages 200 cm with the majority falling between November and March.

The study consists of a 200 acre, approximately 50 year old stand of second-growth redwood, Douglas-fir, and tanoak (Veirs 1986). Regenerated from natural seeding in 1954 using the seed tree harvest method, an average of 1 dominant redwood per acre was left (Veirs 1986). In 1978, stand densities averaged more than 2500 stems/hectare, with some plots having 8000 stems/hectare. Species composition ratios of redwood to Douglas-fir were recorded at 1:1 on xeric sites and 12:1 on mesic sites within the study area. Old-growth stands nearby were found to be dominated by redwood, with densities ranging from 25-90 trees/hectare for redwood and 3-10 trees/hectare for Douglas-fir; considerably different from the second-growth now present. Associated tree species present include western hemlock, madrone (*Arbutus menziesii* Pursh.), cascara (*Rhamnus purshiana*), and golden chinquapin (*Castanopsis chrysophylla* {Dougl.] A. DC.). Understory vegetation is dominated by salal, rhododendron (*rhododendron* *macrophyllum* D. Don), evergreen huckleberry (*Vaccinium ovatum* Pursh.), red huckleberry (*Vaccinium parviflorum* Sm.), and swordfern (*Polystichum munitum* [Kaulf.] C. Presl).

Methods

The thinning study established by Veirs (1986) consists of six thinning treatments based upon residual tree spacing, retention of hardwoods (cut, no cut, or inclusion of hardwoods in the spacing), and the treatment of the slash (Table 1, Appendix B). In all units the number of redwood stump sprouts was to be thinned to 30-50% of the dominant sprouts. An upper limit of diameters to be cut was established at 45 cm dbh for redwood sprouts, 25 cm for free standing redwood, and 30 cm for Douglas-fir. The result was a range of post-thinning densities ranging from 370 to 8470 stems/ha and 8.9 to 57.8 m^2/ha of basal area.

Immediately after thinning, four 1/24.7-hectare circular plots were systematically established in each treatment unit for a total of 28 plots. For each unit the plots were arranged along two randomly chosen bearing lines with two plots randomly located on that line. For each tree, the following attributes were recorded: species, height, height to base of live crown, diameter at breast height, and diameter at stump height. Trees cut during thinning were measured for stump diameter and regressions were used to reconstruct the stand prior to thinning. From each plot center two photographs were taken in each of four cardinal directions. Tree locations were mapped by measuring the distance and azimuth for each tree from the plot center. Re-measurements were conducted in 1984-5 following the same methods. Additionally in 1984, percent cover of understory

Table 1. Treatment unit delineations based upon spacing, hardwood treatment, and slash treatment (Veirs 1986).

Treatment Unit	Spacing (m)	Hardwoods	Slash
1-A	3 - 3.6	Cut	Lopped
1-B	4.9 - 5.5	Cut	Lopped
2-A	3 - 3.6	Uncut	Lopped
2-B	3 - 3.6	Included in Spacing	Lopped
3-A	3 - 3.6	Included in Spacing	Lopped
3-B	3 - 3.6	Included in Spacing	Not Lopped

vegetation was estimated into six cover classes: 0-1%, 1-5%, 5-25%, 25-50%, 50-75%, and 75-100%. Diameter was remeasured in 1995, but the individual trees were not accounted for and therefore only plot level data are available.

The plots were measured during 2003-4 to determine changes in diameter at breast height, height to base of live crown, and total tree height. All ingrowth of seedlings (<1.37 m tall) and sapling (>1.37 m tall) regenerated since thinning was tallied. Regeneration greater than 5 cm in diameter at breast height was measured for diameter, height, and height to live crown. Understory vegetation was classified by species into modified Braun-Blanquet cover classes with percent covers of: 0.001-0.01%, 0.01-0.1%, 0.1-1%, 1-5%, 5-25%, 25-50%, 50-75%, and 75-100%. The median of each class is the value given for observation. Species were then classified into growth forms based on size and functional traits: tree, tall shrub, low shrub/fern, and herbaceous. Trees were those species with the ability for height growth >15 m, tall shrubs were between 1.5–15 m in height, low shrubs/ferns 0.5–1.5 m in height (ferns are included because of their size and similar functional traits), and herbs <0.5 m and lacking aboveground woody stems. Total cover values were calculated by summing the total of all species per plot and for each growth form. Notice was taken of any damage to the top of the tree and bear damage to the bole.

Analysis

Two methods were used to analyze the data: linear regression analysis and histograms using post-hoc treatment groupings. For regression analysis, three measurements of density were tested for their ability to predict the various response variables: number of stems/ha, stand density index (Reineke 1933), and basal area/ha. Stems/ha being the best fit of the data was then transformed to create a normal distribution and correct for unequal variances. Two transformations were used depending upon which one transformed the data the best: log of stems/ha and stems/ha^{-1}. Significance was determined with an alpha of 0.05.

Post-hoc treatment groups were created because the post-treatment stand densities did not always meet with the intended treatment thereby making it difficult to analyze with the original treatment units. This discrepancy is due to several factors, namely because of poor contractor performance in meeting desired species and density targets and the establishment of study plots after thinning had occurred. I therefore separated the plots into four groups based on density and species composition: Control, Low-Density, Mid-Density, and Redwood. Mean and standard error values by group for the number of stems/ha are listed in Table 2 and the basal area/ha are listed in Table 3.

Understory Vegetation

Linear regression was used to assess whether or not there exists a significant relationship between post-thinning stand densities and the current understory response variables. Understory response variables include: percent cover of understory vegetation, understory trees, tall shrubs, low shrubs/ferns, herbs, and species richness, and Shannon-Weiner diversity index (H'). Shannon-Weiner diversity index is based upon the proportion of cover each species had in relation to the total cover. Additionally, density was compared to changes in the response variables from 1984 to 2003 using linear regression. The number of redwood and tanoak seedlings and saplings were compared to

Table 2. Mean and standard error values of the number of stems/ha for the Control, Low-Density, Mid-Density, and Redwood groups.

Group	Mean ± S.E. number of stems/ha 1979 (post-thinning)				N
	redwood	Douglas-fir	tanoak	Total	
Control	2760 ± 1314	1605 ± 466	1260 ± 255	5631 ± 1137	4
Low-Density	193 ± 36	237 ± 20	69 ± 14	520 ± 49	5
Mid-Density	642 ± 158	339 ± 90	236 ± 40	1217 ± 149	7
Redwood	951 ± 30	91 ± 24	29 ± 15	1074 ± 41	6

Table 3. Mean and standard error values of the basal area (m^2)/ha for the Control, Low-Density, Mid-Density, and Redwood groups.

	Mean ± S.E. sq. m of basal area/ha 1979 (post-thinning)				N
Group	redwood	Douglas-fir	tanoak	Total	
Control	20.7 ± 4.9	17.9 ± 2.5	13.0 ± 1.9	51.5 ± 4.6	4
Low-Density	14.6 ± 4.4	8.3 ± 0.6	1.0 ± 0.4	23.9 ± 4.3	5
Mid-Density	15.4 ± 4.6	8.6 ± 2.6	2.0 ± 0.4	26.0 ± 3.9	7
Redwood	28.3 ± 5.4	2.8 ± 0.8	0.8 ± 0.3	31.9 ± 5.7	6

both stand density and the number of redwood and tanoak cut using forward stepwise regression with a probability to enter of 0.20.

Mortality and Species Composition

Mortality was analyzed using linear regression to test for significant relationships between density and percent mortality for redwood, Douglas-fir, tanoak, and all species combined. Changes in species composition were assessed by graphing the number of stems/ha and the basal area/ha by species over time for the four groups.

Stand Structure

Stand structure was analyzed by means of relating density to measures of tree size, tree growth, and crown ratios. In order to distinguish differences in growth and crowns among canopy layers, three strata were established for 2003 heights: lower (<15 m), middle, (15 to 25 m), and upper (>25 m). Linear regression was used to observe if any significant relationships exist between density and quadratic mean diameter (post-thinning, 2003, and changes over time), and average tree growth and average live crown ratio for lower, middle, and upper canopies. In order to assess the degree of diversification and stratification, a histogram of 1979 and 2003 tree height distributions was created for the Control, Low-Density, Mid-Density, and Redwood groups. An index of stand structural diversity was created based on diameter, height, and species. The proportion of basal area/ha by 5 cm diameter classes was calculated using Shannon's index. This was repeated for basal area/ha by 3 m height classes and by species, and then an average taken of all three. In order to contrast methods, the coefficient of variation of tree heights was also calculated. These were repeated for 1979, 2003, and differences between 1979 and 2003.

RESULTS

Understory Vegetation

A total of 45 species were recorded in the understory: 5 trees, 3 tall shrubs, 11 low shrubs/ferns, and 26 herbs (Table 4). Nine species were gained from 1984 to 2003 while eight species were lost. Only two species were considered invading exotics, bull thistle *(Cirsium vulgare)* and Cutleaf burnweed *(Erichtites minima)*, and they had disappeared from the plots by 2003. Total understory cover ranged from 15% to 95% with all of the thinned plots having 45% or greater cover while the controls were less than 20% cover. Total understory vegetation cover showed a significant negative relationship to log of stems/ha (R^2=0.73, P<0.0001) (Figure 1), but the relationship varied between growth forms. There were significantly negative relationships between stems/ha^{-1} and cover of tall shrubs (R^2=0.67, P<0.0001), cover of low shrubs/ferns (R^2=0.26, P=0.0148) (Figure 1), and between log of stems/ha and Shannon's diversity index (R^2=0.30, P=0.0052) (Figure 2, Table 5). The effect of slash disposal (lopping vs. non-lopping) on understory vegetation was not discernable after 25-years.

Over time, plots at lower densities increased total understory cover while those greater than 2000 stems/ha lost cover. Significant negative relationships existed in 1984 between stems/ha^{-1} and cover of understory vegetation (R^2=0.24, P=0.0152) (Figure 1) and cover of tall shrubs (R^2=0.28, P=0.0084), and between log of stems/ha and species richness (R^2=0.24, P=0.0158) and Shannon's diversity index (R^2=0.23, P=0.0172) (Figure 2, Table 5). Differences in cover from 1984 to 2003 showed significant negative relationships between stems/ha^{-1} and cover of understory vegetation (R^2=0.47, P=0.0002)

Table 4. Vascular plant species list. Growth forms: tree (T), tall shrub (TS), low shrub/fern (LS/F), and herbaceous (H). Classification of native, colonizer, and harsh site occupier taken from Muldavin et al. (1981).

Species	Common name	Growth form	Native	Colonizer	Harsh Site Occupier	Presence 1984	Presence 2003
Lithocarpus densiflorus	tanoak	T	X		X	X	X
Pseudotsuga menziesii	Douglas-fir	T	X		X	X	X
Rhamnus purshiana	cascara	T	X				X
Sequoia sempervirens	redwood	T	X			X	X
Tsuga heterophylla	western hemlock	T	X			X	X
Rhododendron macrophyllum	rhododendron	TS	X			X	X
Vaccinium ovatum	evergreen huckleberry	TS	X			X	X
Vaccinium parvifolium	red huckleberry	TS	X			X	X
Athyrium filix-femina	lady fern	LS/F	X			X	X
Berberis nervosa	littleleaf Oregon-grape	LS/F	X			X	X
Blechnum spicant	deer fern	LS/F	X			X	X
Carex obnupta	sedge	LS/F	X			X	X
Dryopteris expansa	wood fern	LS/F	X			X	X
Equisetum telmateia	horsetail	LS/F	X	X		X	X
Gaultheria shallon	salal	LS/F	X			X	X
Polystichum munitum	sword fern	LS/F	X			X	X
Pteridium aquilinum	bracken fern	LS/F	X			X	X
Rubus spectabilis	salmonberry	LS/F	X				X
Rubus ursinus	pacific blackberry	LS/F	X			X	X
Boykinia occidentalis	coastal brookfoam	H	X			X	
Campanula prenanthoides	bluebell	H	X			X	
Cardamine californica	toothwort	H	X				X
Cirsium vulgare	bull thistle	H		X	X	X	
Claytonia sibirica	candyflower	H	X			X	X
Corallorhiza maculata	spotted coralroot	H	X			X	X
Disporum hookeri	Hooker's fairy-bells	H	X			X	
Erichtites minima	Cutleaf burnweed	H		X	X	X	
Gallium trifollium	gallium	H	X			X	X
Goodyera oblongifolia	rattlesnake plantain	H	X				X
Hierochloe occidentalis	vanilla grass	H	X			X	
Iris douglasiana	Douglas' iris	H	X	X	X	X	X
Juncus spp.	rush	H	X				X
Lilium colombianum	columbia lily	H	X				X
Lonicera hispidula	hairy honeysuckle	H	X				X
Oxalis oregana	redwood oxalis	H	X			X	X
Poaceae spp.	grass	H	?			X	X
Polypodium glycyrrhiza	licorice fern	H	X			X	X

Table 4. Vascular plant species list. Growth forms: tree (T), tall shrub (TS), low shrub/fern (LS/F), and herbaceous (H). Classification of native, colonizer, and harsh site occupier taken from Muldavin et al. (1981). (Muldavin et al. 1981) (continued)

Species	Common name	Growth form	Native	Colonizer	Harsh Site Occupier	Presence 1984	Presence 2003
Trientalis latifolia	star flower	H	X			X	X
Trillium ovatum	trillium	H	X			X	X
Vancouveria hexandra	redwood ivy	H	X			X	
Veronica americana	brooklime	H	X			X	
Viola sempervirens	redwood violet	H	X		X	X	X
Whipplea modesta	modesty	H	X	X	X	X	X

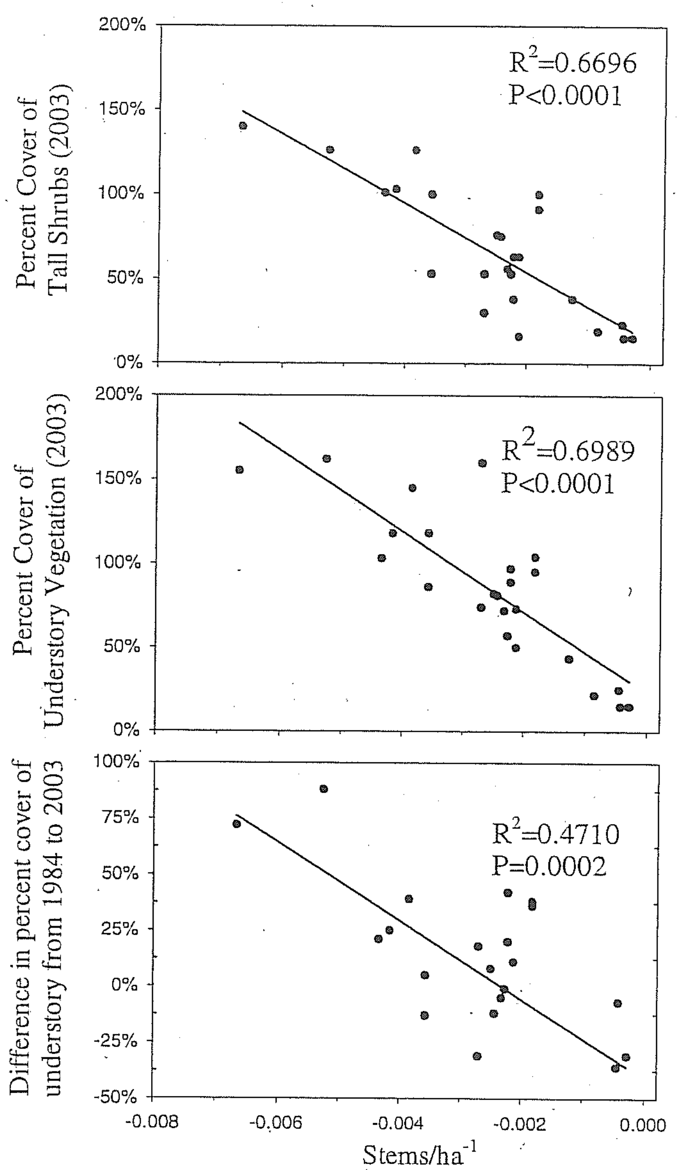

Figure 1. Percent cover of tall shrubs in 2003, percent cover of all understory vegetation in 2003, and differences from 1984 to 2003 versus the number of stems/ha^{-1}. Values are a cumulative total for all species.

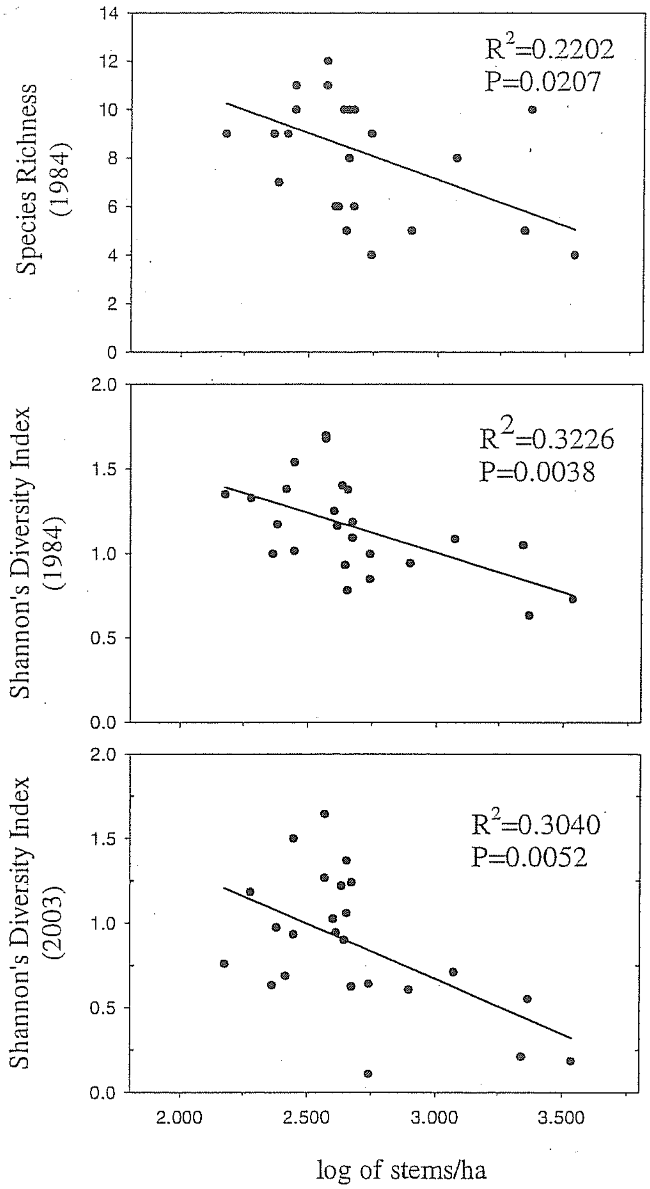

Figure 2. Species richness for 1984 and Shannon's Diversity Index for 1984 and 2003 versus the log of stems/ha.

Table 5. Linear regression analysis of understory response variables versus stems/ha.

Response variable	Stems/ha		
	R^2	P	slope
1984			
Cover of understory vegetation	0.2395	0.0152*a	-0.39
Cover of trees	0.0597	0.2613	-0.14
Cover of tall shrubs	0.2762	0.0084**b	-71.66
Cover of low shrubs/ferns	0.0224	0.4851a	-0.10
Cover of herbs	0.0003	0.9425	0.00
Species richness	0.2202	0.0207*a	-3.82
Shannon's diversity index (H')	0.3226	0.0038**a	-47.10
2003			
Cover of understory vegetation	0.6989	0.0000***b	-240.17
Cover of trees	0.0258	0.4530b	-15.30
Cover of tall shrubs	0.6696	0.0000***b	-203.74
Cover of low shrubs/ferns	0.2625	0.0148*b	-35.73
Cover of herbs	0.0641	0.2325a	-0.01
Species richness	0.0464	0.3121a	-1.88
Shannon's diversity index (H')	0.3040	0.0052**a	-0.65
1984-2003			
Ch. in cover of understory veg.	0.4710	0.0002***b	-176.03
Ch. in cover of trees	0.0039	0.7713b	-8.50
Ch. in cover of tall shrubs	0.4606	0.0003***a	-0.58
Ch. in cover of low shrub/ferns	0.0414	0.3401a	-0.14
Ch. in cover of herbs	0.0603	0.2589a	-0.01
Ch. in species richness	0.1357	0.0838b	-753.49
Ch. in Shannon's index (H')	0.0760	0.1924a	1.94

[a] log of stems/ha

[b] stems/ha^{-1}

*p<0.05

**p<0.01

***p<0.001

(Figure 1), and between log of stems/ha and tall shrubs (R^2=0.46, P=0.0003) (Table 5).

For all plots there were 21 new trees over 5 cm in diameter: 17 redwood, 3 Douglas-fir, and 1 tanoak. All but 4 of these trees occurred on two plots, both had large openings nearby and heavily thinned redwood sprout clumps. The sprouting response of redwood from thinning ranged from 0 to 7800 stems/ha while the number of redwood thinned ranges from 0 to 2400 stems/ha. Tanoak sprouts range from 0 to 1080 stems/ha while the thinning ranged from 0 to 890 stems/ha. Due to multiple sprouts per stump, total numbers of sprouts can be misleading. Cover of redwood sprouts approached 40% in several plots, but cover of tanoak was above 1% in only three plots. The number of redwood thinned/ha was the best predictor of the number redwood seedlings (R^2=0.51, P=0.0013), saplings (R^2=0.36, P=0.0115), and total number of regeneration (R^2=0.41, P=0.0057) (Table 6). Tanoak regeneration was neither related to density nor the number of stems thinned (Table 6).

Mortality and Species Composition

At stand densities less than 2000 stems/ha, mortality for all species combined was less than 25% over the 25-years with 10 plots having less than 10%. Mortality averaged 65% at densities above 5000 stems/ha, which resulted in stand densities averaging 2000 stems/ha in 2003. A significant positive relationship between density and percent mortality was observed for all species (Figure 3). Total percent mortality had the best prediction to log stems/ha (R^2=0.80 and P<0.0001) followed by redwood and Douglas-fir (R^2=0.67, P<0.0001 and R^2=0.65, P<0.0001, respectively) and then tanoak (R^2=0.46, P=0.0007) (Table 7). Percent mortality between redwood and Douglas-fir were not

Table 6. Linear regression analysis of the number of redwood or tanoak sprouts/ha versus the number of redwood or tanoak thinned/ha.

	Number of redwood or tanoak thinned/ha		
Response variable	R^2	P	slope
Number of redwood seedlings/ha	0.5095	0.0013*	0.4081
Number of redwood saplings/ha	0.3560	0.0115*	0.9377
Number of redwood sprouts/ha	0.4093	0.0057*	1.3458
Number of tanoak seedlings/ha	0.0234	0.4968	0.0359
Number of tanoak saplings/ha	0.1098	0.1319	0.0762
Number of tanoak sprouts/ha	0.0803	0.2014	0.1121

*p<0.05

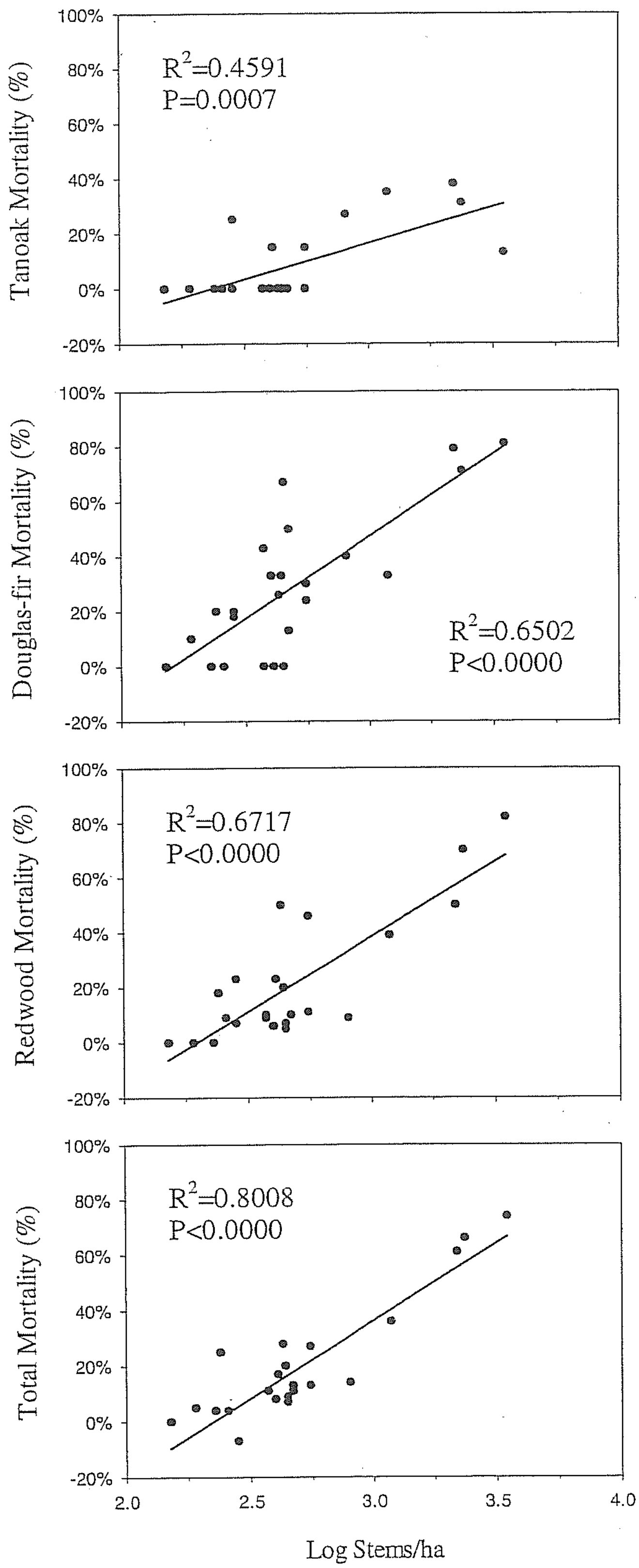

Figure 3. Relationship of tanoak, Douglas-fir, redwood, and total percent mortality for the log stems/ha.

Table 7. Linear regression analysis of percent mortality for tanoak, Douglas-fir, redwood, and total versus the log of stems/ha.

	Log of stems/ha		
Response variable	R^2	P	slope
Percent total mortality	0.8008	0.0000***	0.563
Percent redwood mortality	0.6717	0.0000***	0.549
Percent Douglas-fir mortality	0.6502	0.0000***	0.591
Percent tanoak mortality	0.4591	0.0007***	0.259

*p<0.05

**p<0.01

***p<0.001

significantly different at an alpha equal to 0.05.

Species composition changed only imperceptibly at all levels of thinning, but it changed in the Control plots substantially, marked by a large reduction in the number redwood and Douglas-fir relative to tanoak (Figure 4). The mean ratio of redwood to tanoak in the Control was 2.2:1 in 1979, but was 0.8:1 in 2003. The Douglas-fir to tanoak ratio in the Control was 1.3:1 in 1979, but the proportion of Douglas-fir had decreased to 0.5:1 in 2003. In the thinned plots, the median ratio of redwood to Douglas-fir is 2.2:1 with a range from 0.3:1 to 40:1. Species composition in the Low-Density, Mid-Density, and Redwood plots did not change substantially following thinning (Figure 4).

Changes in basal area by species shows that Douglas-fir increased its dominance over time in the Control and Low-Density and to a lesser extent in the Mid-Density group (Figure 5). Reductions in basal area due to thinning are similar to the reductions in number of stems/ha in that the relative proportions of each species were maintained immediately after thinning.

Stand Structure

Quadratic mean diameters for the lowest densities were almost twice as much as the controls, 44 cm and 23 cm respectively, with an increase from 1979 to 2003 of 18 cm and 10 cm respectively. Mean live crown ratios were at 40% for the lowest densities and 25% in the controls. Significant negative relationships were observed between density and quadratic mean diameter (Figure 6), mean conifer diameter growth (Figure 7), and mean conifer live crown ratios (Figure 8). Stems/ha^{-1} was negatively related to quadratic mean diameter for 1979 (R^2=0.45, P=0.0003), in 2003 (R^2=0.61, P<0.0001), and changes

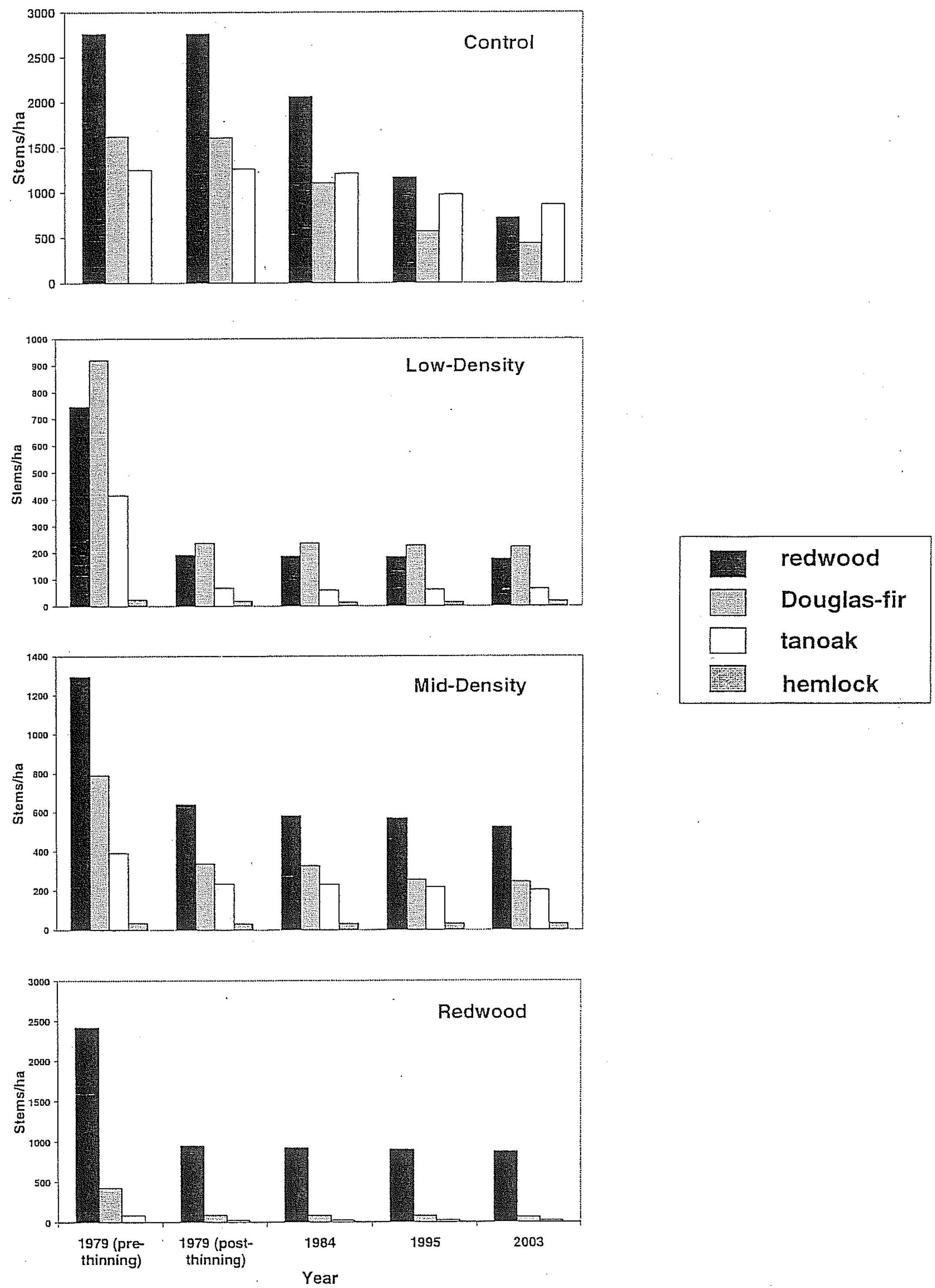

Figure 4. Changes in the number of stems/ha by species from 1979 (pre-thinning) to 2003 for the Control, Low-Density, Mid-Density, and Redwood groups.

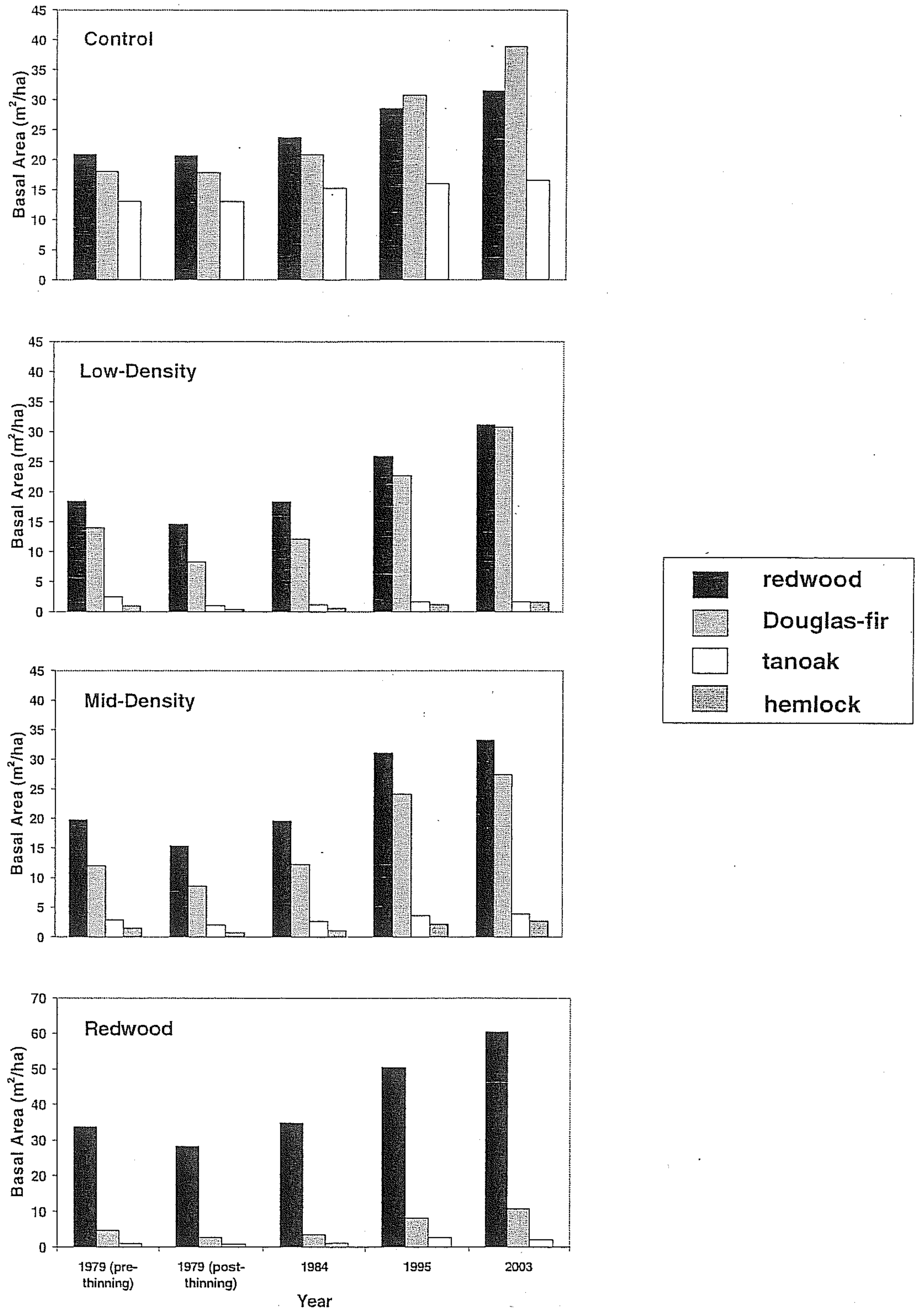

Figure 5. Changes in the basal area (m^2/ha) by species from 1979 (pre-thinning) to 2003 for the Control, Low-Density, Mid-Density, and Redwood groups.

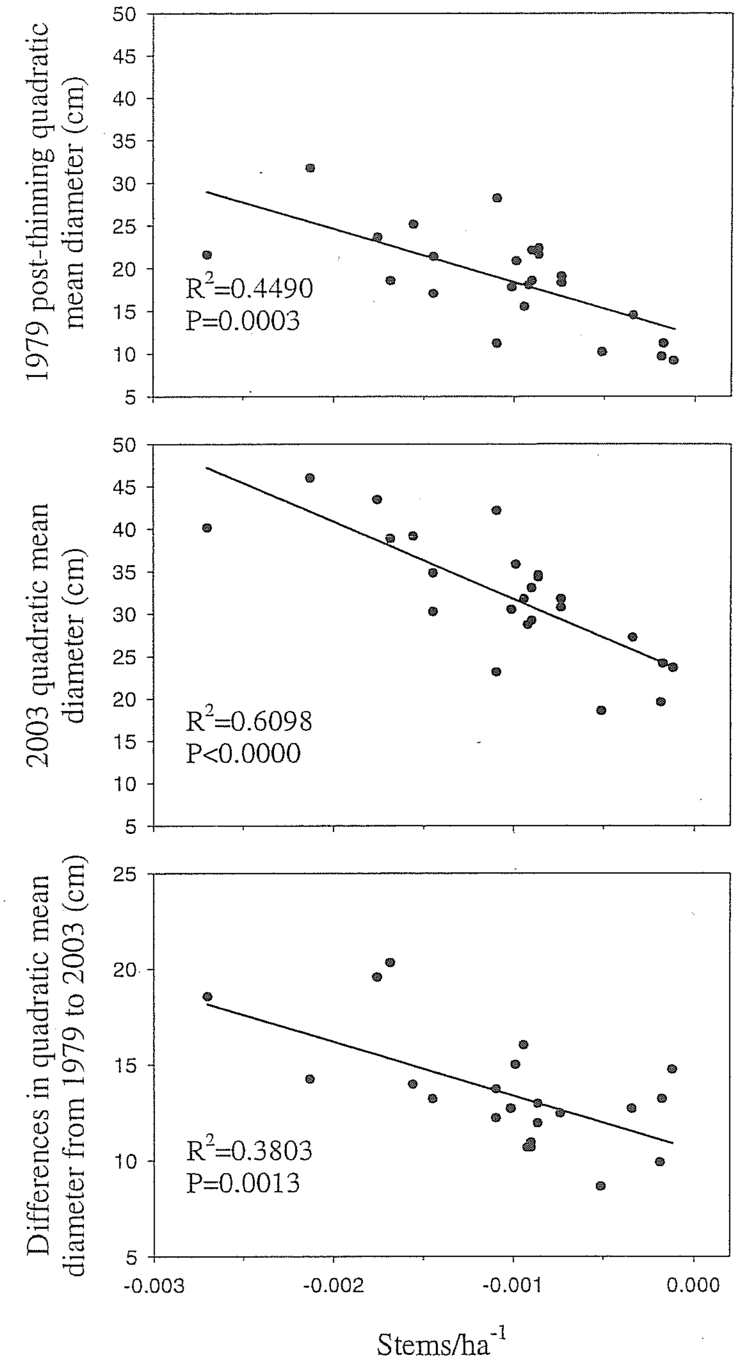

Figure 6. Quadratic mean diameter for 1979, 2003, and change from 1979 to 2003 versus the number of Stems/ha^{-1}.

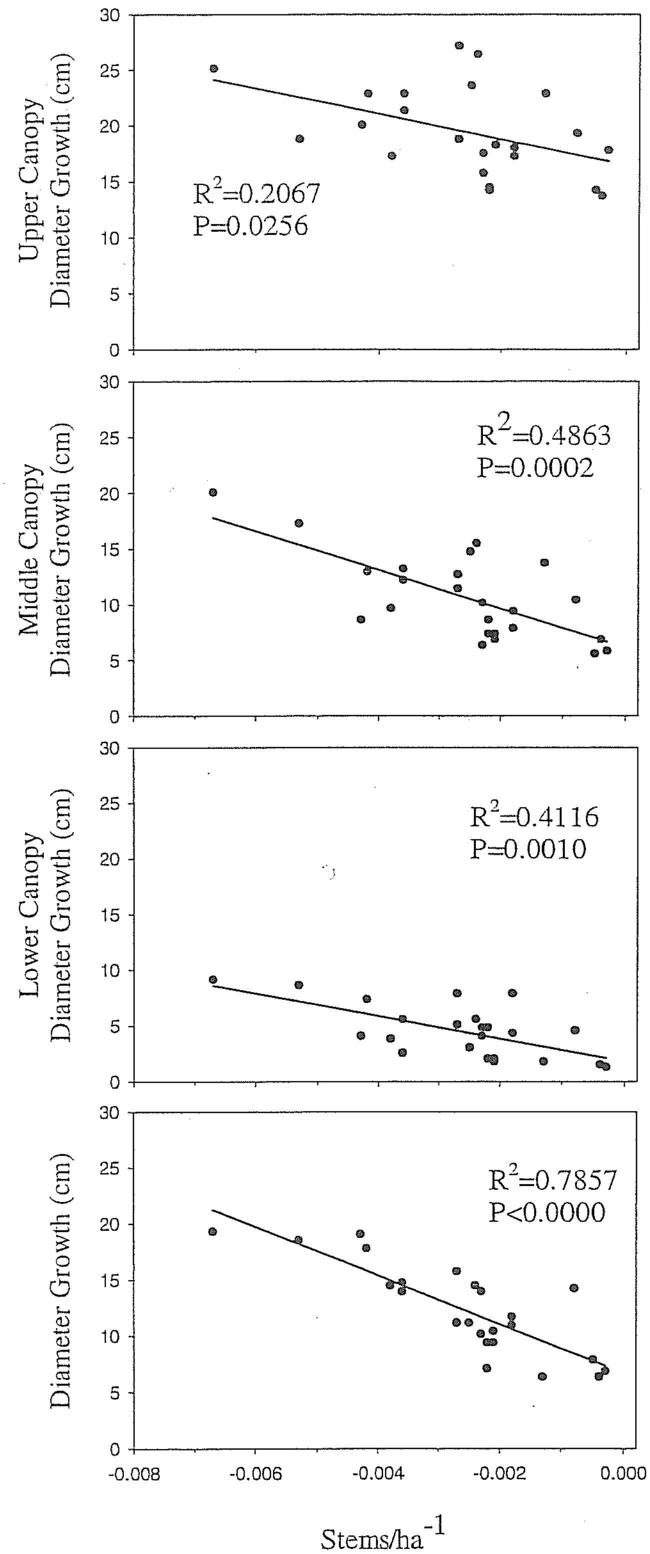

Figure 7. Mean conifer diameter growth for upper, middle, lower, and all canopy layers versus the number of stems/ha^{-1}.

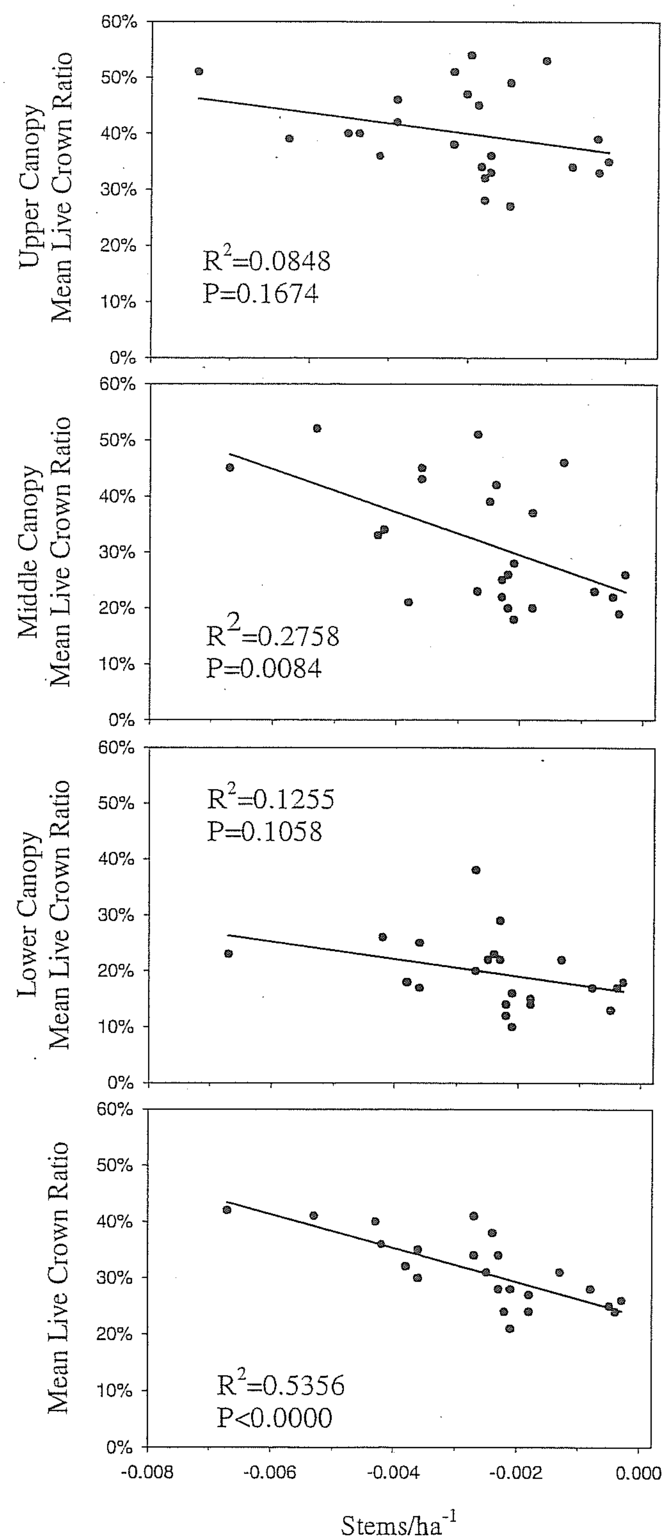

Figure 8. Mean live crown ratio for lower, middle, upper, and all canopy layers versus the number of stems/ha^{-1}.

from 1979 to 2003 (R^2=0.38, P=0.0013) (Table 8). Mean conifer diameter growth was negatively related to stems/ha^{-1} for lower, middle, and upper canopy layers (R^2=0.41, P=0.0010; R^2=0.49, P=0.0002; R^2=0.21, P=0.0256, respectively) with all layers combined having the most significance (R^2=0.79, P<0.0001) (Table 8). Mean live crown ratios among conifers were only significant in the middle canopy (R^2=0.28, P=0.0084) and for all layers combined (R^2=0.54, P<0.0001) (Table 8). When basal area growth/ha was compared to density, no significant relationship was observed.

Significant positive relationships exist between stand densities and structural diversity index for diameter and height distributions but not by species (Figure 9). The positive slope indicates that according to Shannon's index, stands at the highest densities were the most diverse in their distributions of basal area across diameter and height classes. Cumulative diameter and height structure index in 1979 were positively related to stems/ha^{-1} (R^2=0.57, P<0.0001), and in 2003 (R^2=0.384, P=0.0014) (Table 8). Differences in index values from 1979 to 2003 yielded no significant relationships. Coefficient of variation of tree heights also yielded no significant relationships.

By 2003 there are noticeable differences in the canopy positions occupied by various species with a strong influence of density upon stratification for the Control, Low-Density, Mid-Density, and Redwood groups. (Figure 10, Figure 11, Figure 12, and Figure 13, respectively). In all groups, Douglas-fir is most prevalent in the co-dominant/dominant class and a minor component of the intermediate or suppressed. Tanoak occupied mostly the suppressed and intermediate positions; co-dominants of

Table 8. Linear regression analysis of quadratic mean diameter, mean conifer growth, and mean live crown ratios versus the number of stems/ha^{-1}.

	Stems/ha^{-1}		
Response variable	R^2	P	slope
Quadratic mean diameter (1979)	0.4490	0.0003***	-999.7
Quadratic mean diameter (2003)	0.6098	0.0000***	-1455.2
Change in quadratic mean diameter	0.3803	0.0013**	-455.5
Lower canopy diameter growth	0.4116	0.0010**	-399.5
Middle canopy diameter growth	0.4863	0.0002***	-681.5
Upper canopy diameter growth	0.2067	0.0256*	-452.2
Total diameter growth	0.7857	0.0000***	-943.3
Lower canopy live crown ratio	0.1255	0.1058	-16.0
Middle canopy live crown ratio	0.2758	0.0084**	-37.9
Upper canopy live crown ratio	0.0848	0.1674	-14.8
Total live crown ratio	0.5356	0.0000***	-29.9
Diameter Structure (1979)	0.2486	0.0131*	71.5
Height Structure (1979)	0.4846	0.0002***	99.7
Cumulative Structure (1979)	0.5671	0.0000***	85.6
Diameter Structure (2003)	0.3694	0.0016**	80.0
Height Structure (2003)	0.2182	0.0214*	96.6
Cumulative Structure (2003)	0.3778	0.0014**	88.3

*$p<0.05$

**$p<0.01$

***$p<0.001$

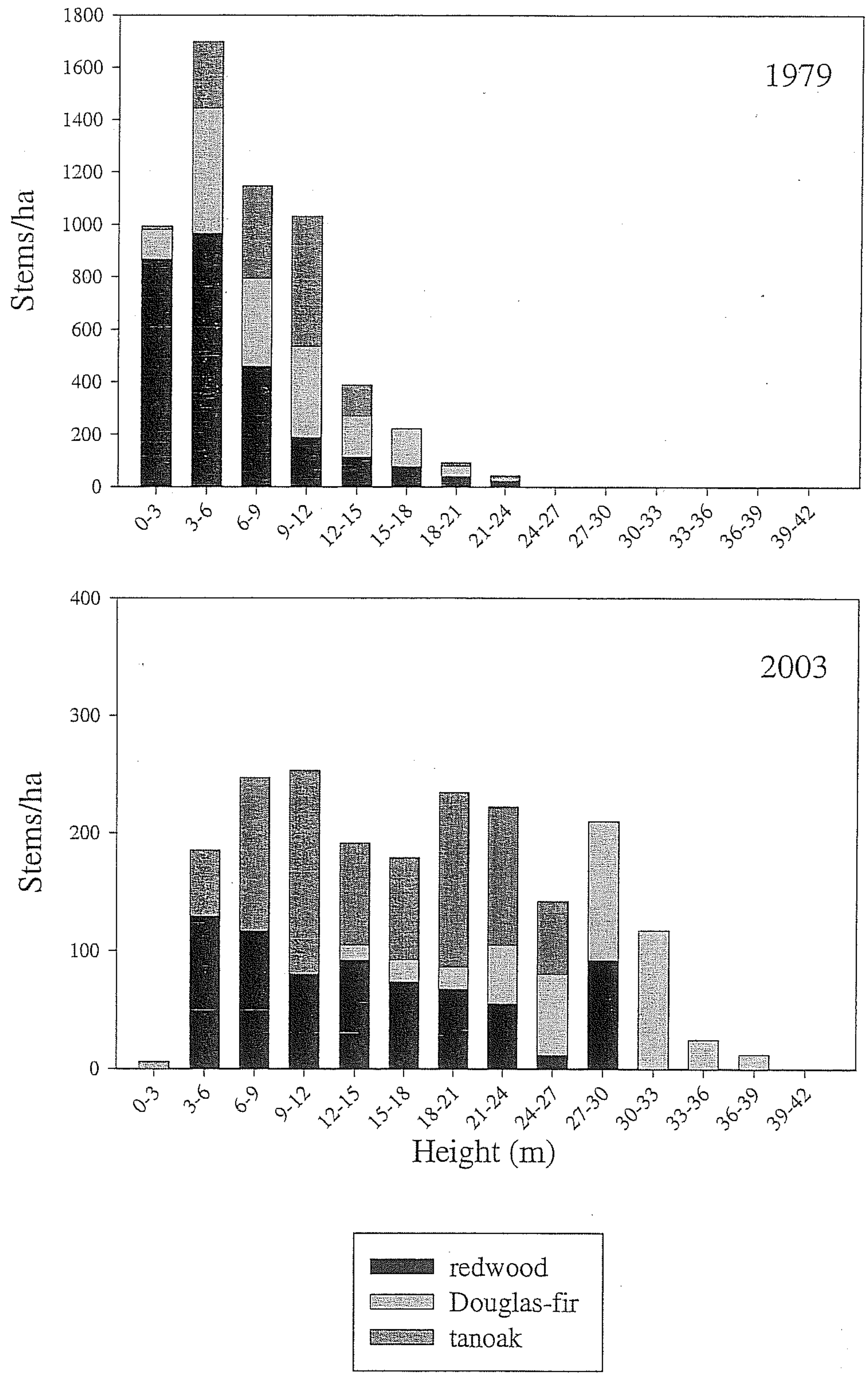

Figure 10. Height distributions of Control plots in 1979 and 2003. Scale of y-axis differ.

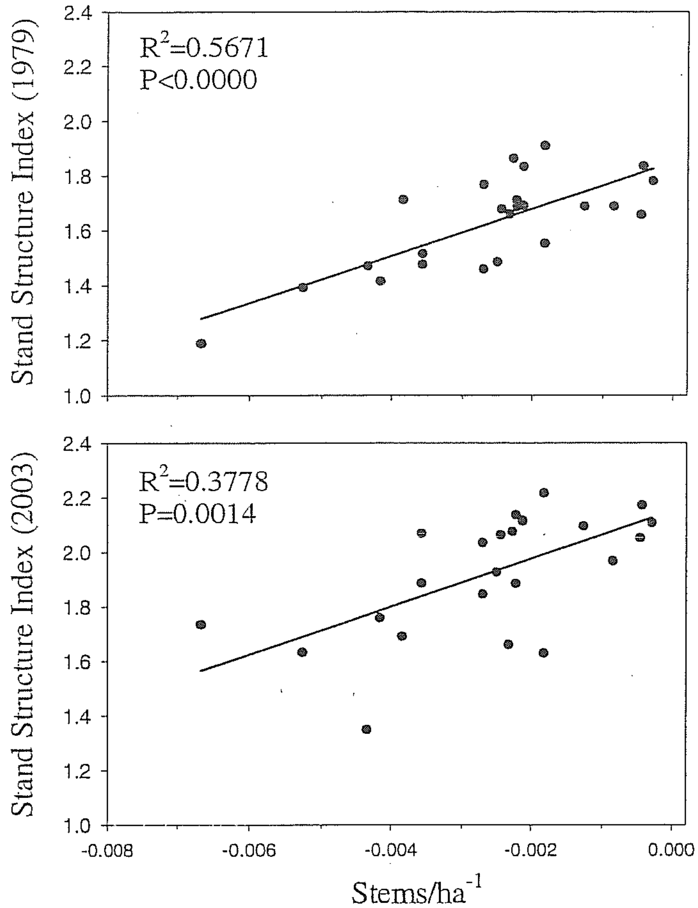

Figure 9. Stand structural diversity index of basal area/diameter and height class for 1979 and 2003 versus the number of stems/ha^{-1}.

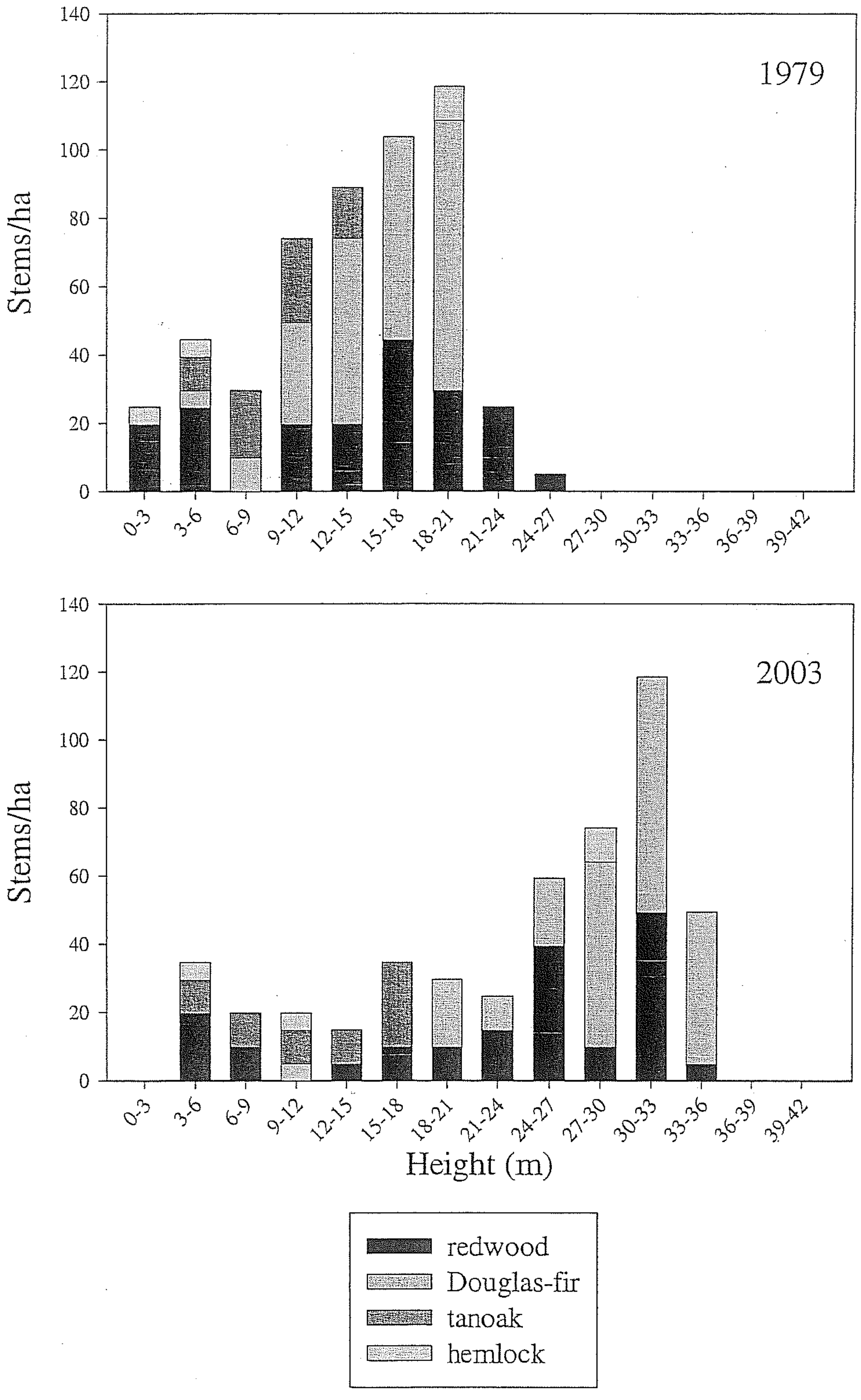

Figure 11. Height distributions of Low-Density plots in 1979 and 2003.

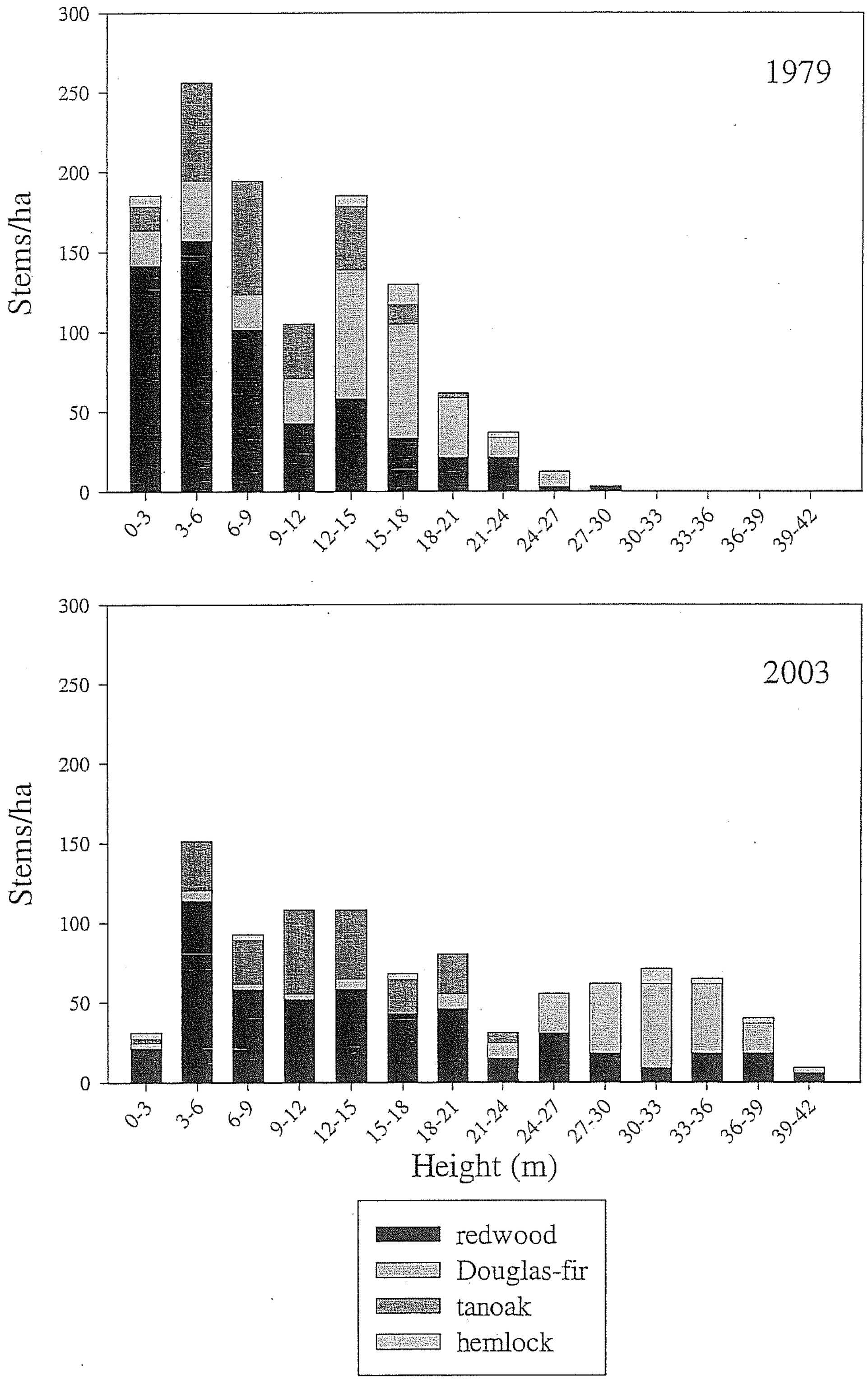

Figure12. Height distributions of Mid-Density plots in 1979 and 2003.

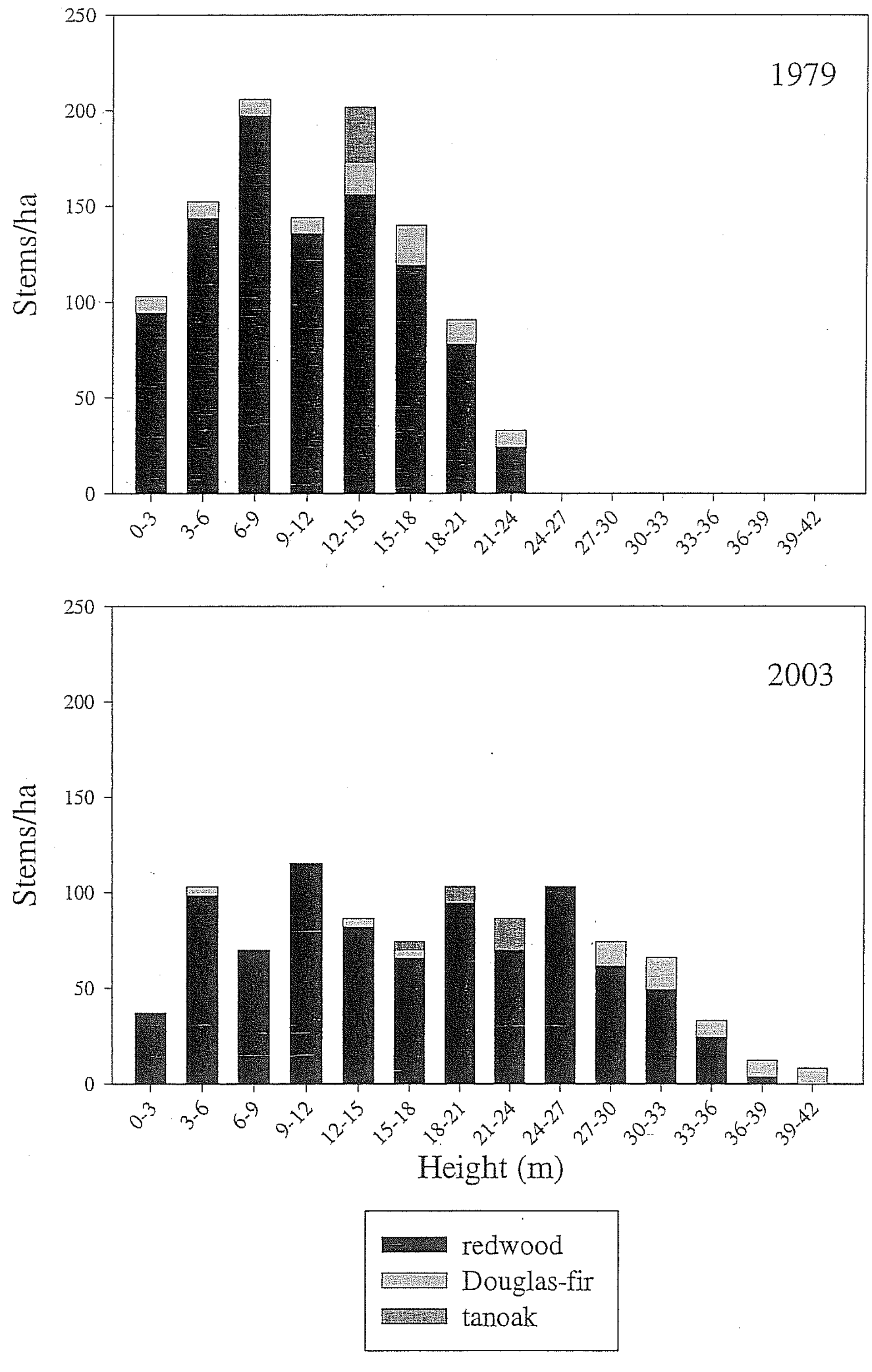

Figure 13. Height distributions of Redwood plots in 1979 and 2003.

tanoak were infrequent with the greatest occurrence in the Controls followed by the Mid-Density. The distribution of redwood is unique in its presence at all heights for all groups. The major differences between Low- and Mid-Density are seen in the numbers of redwood and tanoak in the lower height classes.

DISCUSSION

Models of stand dynamics (Oliver and Larson 1996, (Franklin et al. 2002) predict that within 50-years following stand replacing disturbances and with full site occupancy by tree species, 1) self thinning due to density-dependent mortality will increase, 2) understory herbaceous and shrub species will diminish in relative abundance, 3) recruitment of new trees will cease, and 4) the stratification of shade-tolerant trees into a separate strata will be beginning. Incumbent with these processes is the effect of density on stand development and the influence of thinning on stand density. The effects observed in this study are similar to those found in other studies of thinning to increase old-growth characteristics and processes (Newton and Cole 1987, (Barbour et al. 1997, (Bailey et al. 1998, (Bailey and Tappeiner 1998, (Thomas et al. 1999, (Thysell and Carey 2001, (Busing and Garman 2002, (Lindh and Muir 2004). While most of these studies focus on conifer thinning, few have examined the effect of density in mixed conifer—hardwood forests (Tappeiner and McDonald 1984, (McDonald and Tappeiner 1987, (Deal et al. 2004) let alone mixed-redwood forests (Veirs 1986, (Cussins 1996, (Teraoka 2005). The important results observed this study are the relationships between overstory stand densities, and species composition, understory vegetation, sprout regeneration of shade-tolerant trees, and stand structural development.

Understory Vegetation

Thinning generally causes increased growth of understory vegetation (Lindh and Muir 2004). In this study I found, following thinning, understory vegetation to increase in cover of tall and low shrubs/ferns, increase in species diversity, and increase sprouting of redwood and tanoak (Table 5). The changes seen are due to an increase in available light resources with effects that persisted past canopy re-closure (Thomas et al. 1999). Many understory species can maintain and expand in shaded forest due to rhizomatous spreading and/or clonal growth (Halpern and Spies 1995). Species favored following thinning may include early successional and exotics (Thysell and Carey 2001), shade-tolerant herbs, especially under lower light levels, (Lindh and Muir 2004), tall-stature shrubs (Thomas et al. 1999), and clonal growth forms (Tappeiner et al. 1991). In this study, tall shrubs showed the greatest response to density followed by the low shrubs/ferns (Table 5).

He and Barclay (2000) in a 51-year old stand 27-years after thinning observed cover of only two species to be significantly related to density. Salal and Oregon beaked moss (*Kindbergia oregano* (Sull.) Ochyra) dominated the understory causing the herbaceous and other shrubs to show no response to thinning. Species richness was not affected by thinning. In several studies, species richness increased after thinning (Bailey et al. 1998, (Thomas et al. 1999, (Thysell and Carey 2001). This is similar to results 5-years after thinning where species richness initially was related to density but the relationship diminished following thinning as shrubs and sprouts dominated the understory (Table 5). Generally, species richness rose over the 20-years but some plots did experience significant reductions in species richness. Thomas et al. (1999) found that in stands thinned to similar densities as this study, although only 27-years old, that species richness increased with heavier thinnings. Discrepancies between studies may be due to the age at time of thinning, time since thinning, and pre-existing shrub cover (He and Barclay 2000). Commercial thinning and associated ground disturbance that occurred due to yarding of logs are also likely factors.

In this study, five species accounted for over 90% of the cover observed in 2003: evergreen huckleberry, rhododendron, salal, redwood, and sword fern; all of which are highly disturbance resilient species capable of rapid expansion. Species diversity was negatively correlated to density 5-years after thinning and did not significantly change over time (Table 5). That none of these stands had completely entered into stem exclusion (i.e. before complete canopy closure) at the time of thinning is partly responsible for this increase cover (Halpern and Spies 1995).

Thysell and Carey (2001) observed dramatic increases in cover, species diversity, and presence of exotic species 3-years after thinning. Dominance of the understory by shrubs was not observed, possibly due to the older age of the stand. Bailey et al. (1998) examined commercially thinned and unthinned stands and found thinned stands had greater low shrub, herbaceous, and total understory cover. Tall shrubs were not greater in the thinned stands, and two species, salal and bracken fern (*Pteridium aquilinum*), dominated the low shrubs. Thomas et al. (1999) reported higher thinning levels increased dominance by a few species but did not result in a decline in species diversity. Alaback and Herman (1988) suggest that light to moderate thinnings increase understory species diversity, but it declines under heavier thinnings. This study showed that increased thinning increased dominance of tall shrubs but did not preclude the effects on species diversity (Figure 1 & Figure 2).

Herbaceous species were the most highly variable component with over half of the plots losing herbaceous cover over the 20-year period. Herbaceous cover was not related to overstory density (Table 5) and is likely due to increase shrub growth (He and Barclay 2000). According to Muldavin (1981), dominance of understory vegetation within Redwood National Park was generally shifted from herbaceous to shrub species within three years following logging. Related research in the Cascade Range has shown a similar trend from herbaceous to shrub dominance, but generally at a slower pace (Halpern 1989, (Halpern and Franklin 1990) and the dominance of shrubs at the expense of herbaceous species (Tappeiner et al. 1991, (Huffman et al. 1994). Theoretical models and research demonstrate that although certain species are most abundant in old-growth forests, most are able to survive catastrophic disturbances (Halpern 1989). Thinning prior to canopy closure is thought to reduce the period of, or eliminate, the stem exclusion stage (Tappeiner et al. 1997, (Franklin et al. 2002).

The numbers of redwood sprouts/ha were significantly related to the number of redwood thinned (Table 6). These findings are similar to other studies in which the number of redwood sprouts is related to the number of stems cut, but not to stand density (Barrett 1988, (Lindquist 1989). Oliver at al. (1994) reported height growth of redwood sprouts at 15-years to be 9.4 m at 150 trees/ha and 3.3 m at 475 trees/ha. In this study there were only 4 sprouts with heights over 10 m and only 21 over 5 m. The growth of redwood sprouts >5 cm was only accomplished through the inadvertent creation of relatively large gaps in the overstory or as part of a thinned redwood sprout clump. Density-dependent mortality cannot be expected to recruit new trees into the upper canopies as it eliminates the lowest trees. The development of the remaining sprouts out of the understory is now dependent upon overstory gaps being created or thinning to densities below those in this study (Oliver et al. 1994, (Gray and Spies 1996).

The sprouting response of tanoak due to thinning is not as uniform as redwood nor did it attain the same height or diameter growth (Table 6). That so few tanoak reached sapling size indicates that in the short-term following thinning, tanoak sprouts will not enter out of the understory regardless of the numbers thinned while there is still sufficient overstory competition (McDonald and Tappeiner 1987). Tanoak sprouts have been shown to remain as a shrub in the understory for an indefinite period of time with limited height growth (Tappeiner and MacDonald 1984, (Wilkinson et al. 1997). Given tanoaks over representation in these stands, selective thinning of tanoak can achieve the goals of restoring species composition and altering stand development without increasing the relative abundance of tanoak.

Mortality and Species Composition

Density-dependent mortality was a major predictor in the development of these stands as density accounted for 80% of the mortality (Table 7). Half of all plots had <15% mortality with the remaining thinned plots being between 15% and 30% mortality suggesting that density-dependent mortality after thinning had a moderate influence on most thinned plots, was a slight factors in others and even nonexistent in a few (Figure 3). Mortality levels between Douglas-fir and redwood did not significantly differ (Figure 3) nor did the ratios of redwood to Douglas-fir (Figure 4) change as had been expected at the beginning of the study (Muldavin et al. 1981, (Veirs 1986). Oliver et al. (1994) reported minimal to no mortality in thinned second-growth redwood (45 to 50-years old at time of thinning) with the controls (850 stems/ha >11.3 cm dbh) averaged less than 1 percent annual mortality.

The development of species ratios similar to old-growth stands was not achieved either immediately after thinning or through the ensuing 25-years (Figure 4). In nearby old-growth stands, Veirs (1986) estimated an overstory redwood to Douglas-fir ratio of 8:1, with a range of 1.5:1 to 20:1. Muldavin et al. (1981) report old-growth redwood to Douglas-fir ratios from 3:1 to 10:1. Given the range of elevation and topography within the study area, we could expect that the original species ratio to encompass the entire range reported. Key differences do exist between thinned second-growth and old-growth in that the median ratio was only 2.2:1 versus a mean of 8:1, respectively. Redwood is thought of as a shade-tolerant species and would be expected to have less mortality than the intermediate shade-tolerance of Douglas-fir (Helms 1995). Generally, Douglas-fir height growth was greater than or equal to redwood. This height growth may have helped Douglas-fir overcome shading enough to survive the initial competition (Wensel and Krumland 1986, (Olson et al. 1990). Overstory dominance of Douglas-fir increased during the study period as evidenced by an increase in basal area relative to redwood (Figure 5). However, in the long-term redwood should increase due to its longevity.

Stand Structure

The main ecological benefit of larger trees is that they provide higher quality habitat (i.e. larger snags, coarse woody debris, branches, microhabitats, and bark fissures) due to their size (Franklin et al. 2002). Low-thinning, by its effect on the removal of the smallest trees, increases individual tree growth and increases the quadratic mean diameter of a stand (Drew and Flewelling 1979, (Curtis and Clendenen 1994). The effects of thinning and stand density on radial growth (Figure 8) are similar to other studies (O'Hara 1990, (Curtis and Clendenen 1994, (Oliver et al. 1994, (Bailey and Tappeiner 1998). The findings of larger tree diameters (Figure 6) and increased live crown ratios (Figure 7) are also similar to other studies (Curtis and Reukema 1970, (Curtis and Clendenen 1994, (Oliver and Larson 1996). Because increasing growth of individual trees is of concern, not total growth of the stand, the lowest densities, combined with a low-thinning, provide for the largest possible tree sizes (Drew and Flewelling 1979, (Busing and Garman 2002).

For 50-120 year old stands that had 8 to 60 percent of volume removed, Bailey and Tappeiner (1998) determined that overstory trees in thinned stands had diameters, live crown ratios, crown radii, and radial growth greater than in unthinned stands, and were approaching those values found in old-growth forests. More importantly, trees located in the middle canopy exhibited higher radial growth rates and live crown ratios leading to the establishment of multi-storied canopies found in old-growth forests. This study found comparable results where the higher crown ratio of middle canopy trees was the only canopy layer to be significantly related to density (Figure 7). When diversification of a stand is present, a low-thinning will have little effect on the crown ratio of the dominant trees (Smith et al. 1997). Likewise, suppressed trees are either unable to respond or there is not sufficient light to increase their crown lengths. Thinning to lower densities heavier than reported in this study may increase live crown ratio of suppressed/intermediate trees enough to survive (Bailey and Tappeiner 1998). Under simulated computer models proportional thinning also caused a lengthening of crowns but had diminished large tree sizes. Thinning-from-above, it is theorized, will lead to the development of uneven-age structure in redwood (Helms 1995).

The use of a structural diversity index to quantify stand structure is widespread with many variables being used. Indices generally involve the analysis of the distribution of tree diameters and heights (Latham et al. 1998, (Staudhammer and LeMay 2001, 2004) and can include a horizontal spatial component (Zenner and Hibbs 2000). Using Shannon's index as a measure of structural diversity, the low-thinning produced a more simple structure as densities decreased (Figure 9). Higher densities, and those with a more continuous vertical distribution, had higher structural diversity (Figure 12 & Figure 13). Staudhammer and LeMay (2001) showed a lower structural diversity with a decrease in range and variability of diameter and heights with Shannon's index. Latham et al. (1998) reported that during stem exclusion, Shannon's index was negatively correlated to the number of vertical strata. I found the coefficient of variation of tree heights not correlated to the structural diversity found by Shannon's index, conflicting with the correlation found by Latham et al. (1999).

In the thinned plots, stratification was highly evident (Figure 11 & Figure 12). This created a Douglas-fir—redwood upper strata, a tanoak—redwood middle strata, and, where present, a redwood—tanoak seedling/sapling lower strata. Development of multiple strata with hardwoods present in the lower-canopy and conifers in the upper-canopy is evident in upland old-growth redwood forests (Sawyer et al. 2000). Several studies, including this one, have shown that under overstory canopies, redwood sprout height growth is minimal (e.g. Barrett 1988). The lack of sufficient numbers of lower-canopy redwoods at low-densities (Figure 11), along with minimal growth of redwood sprouts gives concern for the long-term structure. The control plots showed the least canopy stratification, least understory vegetation, and had no recruitment of understory trees (Figure 10). Without disturbance, the control will eventually stratify into a Douglas-fir—redwood upper strata and redwood—tanoak lower strata but be devoid of the smaller diameter trees and any significant understory vegetation (Franklin et al. 2002).

Thinning to low densities (400 to 600 stems/ha) produced a vertical structure that was comprised mostly of dominant overstory trees (Figure 11). Stands with higher densities (600 to 1100 stems/ha) had a vertical distribution that more closely resembles old-growth forests (Figure 12). The Redwood plots (Figure 13), due to a more even vertical distribution, have the potential to diversify the most thereby more closely resembling old-growth stands. This is partly due to the retention of mid- and lower-canopy redwood and tanoak (Sawyer et al. 2000).

Damage to the branches and leaders of redwood often results in the formation of reiterated trunks thereby increasing the complexity of the canopy (Sawyer et al. 2000, (Sillett xxxx). Observations of bole damage consisted of two main types: damage to the leader and bear scraping of the cambium. As observed from the ground, the most common growth form due to damage was a flat top where no leader was present. The next most common damage form was the occurrence of multiple tops (i.e. reiterations).

Decaying dead tops, another feature of old-growth forests, were also observed, presumably due to past scraping of the cambium by bears. Veirs (1986) indicated that following thinning several redwoods lost their leaders due to girdling, presumably by woodrats (*Neotoma fuscipes*) and porcupines (*Erethizon dorsatum*). These occurred within a meter from the top where the diameter was 5-10 cm. No mention is made of bear damage indicating that the scraping of the cambium, and its resulting effects, are less than 20 years old.

In a related study on the same plots, Lombardi and King (2004) found that branch diameters on dominant redwoods with damaged tops had significantly larger branches than trees without damage. When damage was present, the largest branches on that tree were always directly below the damage. No relationship was found to exist between stand density and branch diameter, however, there was a positive relationship between diameter at breast height and branch diameter. The authors reported numerous cases where damage to the leader, resulting in multiple reiterations, was not visible from the ground leading to the conclusion that crown structure in second-growth redwoods is more diverse than previously assumed.

CONCLUSIONS

Thinning dense stands at an early age is a productive means of enhancing the desired ecological and aesthetic values. Future near term development of the canopy (i.e. ~50 to 100 years from present) will entail changes depending upon the initial starting conditions of the stand (Tappeiner et al. 1997, (Franklin et al. 2002) which this study has demonstrated. Low-thinning, while mimicking natural self-thinning, produces in the short-term a simplified structure. If future stand development is a product of present composition and structure, then disturbance processes, whatever they may be, must produce more diverse structure rather than simpler.

Take as an example the recruitment of intermediate and even suppressed redwoods into co-dominant positions. This requires several processes, 1) available regeneration sites for redwood seedlings, 2) retention of lower- and mid-canopy redwood, and 3) overstory densities low enough to provide adequate growth of lower- and mid-canopy trees. This self-perpetuation of redwood may be accomplished by the reintroduction of "natural" disturbances (i.e. fire), girdling of larger trees to create gaps and reduce overstory densities, or the limited use of proportional thinning. The use of variable-density thinning along with gap and anti-gap creation, should provide for within-stand and between-stand diversity.

Following thinning, stand development is no longer dominated by competition-induced mortality and understory exclusion. Instead, processes such as the retention of understory vegetation, regeneration of shade-tolerant trees, and density-independent tree mortality become more important. Characteristics of stand structure and ecological processes are the traits used to classify forests (e.g. old-growth) and encompasses the distribution of trees on a spatial scale, their age distribution, their relative sizes, and positions in the canopy (Smith et al. 1997). Processes interact with the structure and in turn affect how the structure will develop over time. Management for processes (e.g. the recruitment of understory trees) will insure that the target characteristics will self-perpetuate as long as the requisite initial structure, composition, and historic disturbance regimes are present. Future management will be required to pay attention to the resulting structure following thinning, processes that are currently operating, and the structure that is likely to develop from those processes.

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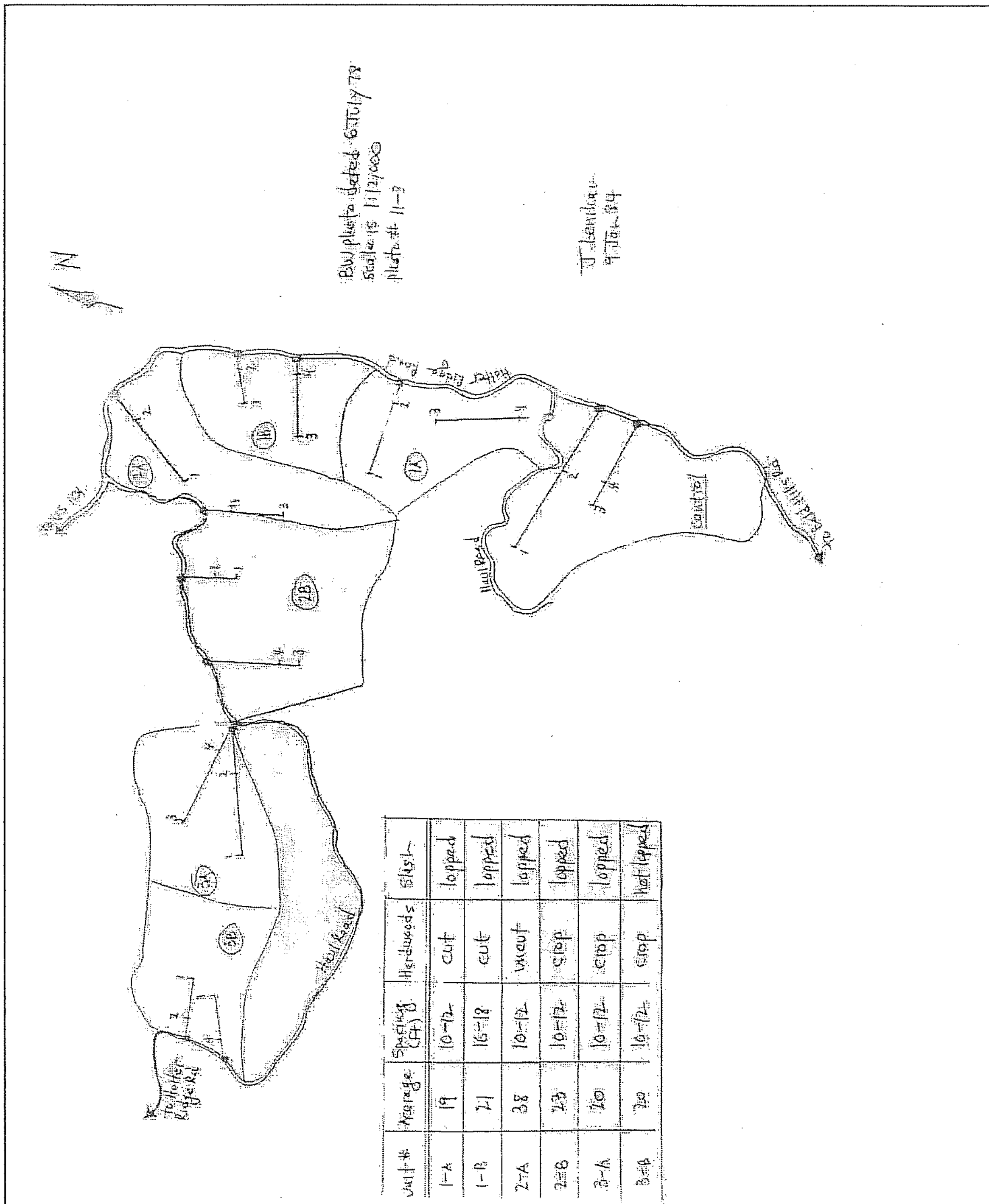
Appendix A. Map location of the Holter Ridge Thinning Study. Taken from Veirs (1986).



Appendix B. Plot level attributes.

The first step in separating the plots into treatment groups was to label the control plots, and one plot that had high initial density with only a few trees removed, as the Control group. One treatment unit (3-B) is dominated almost exclusively by redwood thereby making it considerably difficult to include with other plots and is labeled Redwood. The remaining individual plots were grouped according to post-treatment stand densities and species composition using a K-Means hierarchical clustering from the program NCSS (Hintze 2001). These groups are now labeled: Control, Low-density, Mid-density, and Redwood.

Treatment	Plot	Elevation (m)	General Aspect	Plot Aspect	Slope (degrees)	Post-Thinning Spacing (m)	Post-Thinning Density (stems/ha)	Thinning Group
Control	C1	480	N	NNW	20	2.7	1729	n/a
	C2	500	N	N	10	1.6	5730	Control
	C3	510	N	NE	10	1.4	8472	Control
	C4	530	N	E	14	1.6	5409	Control
Thinned at 3 to 3.6 m spacing, hardwoods cut, slash lopped	1A1	450	W	WSW	30	3.4	1062	Mid
	1A2	510	W	SSW	20	3.0	1359	Mid
	1A3	480	W	SW	35	2.2	2841	n/a
	1A4	480	W	SW	35	2.1	2915	Control
Thinned at 4.9 to 5.5 m spacing, hardwoods cut, slash lopped	1B1	480	W	WSW	17	5.8	371	Low
	1B2	510	W	SW	10	4.3	642	Low
	1B3	460	W	W	30	5.2	469	Low
	1B4	510	W	SW	15	4.4	593	Low
Thinned at 3 to 3.6 m spacing, hardwoods uncut, slash lopped	2A1	480	S	NE	20	4.5	568	Low
	2A2	510	S	S	30	2.8	1606	n/a
	2A3	480	S	ESE	30	4.2	692	n/a
	2A4	480	S	SE	25	4.2	692	Mid
Thinned with hardwoods included at 3 to 3.6 m spacing, slash lopped	2B1	480	S	E	22	3.3	1087	Mid
	2B2	460	S	SE	23	3.0	1359	Mid
	2B3	410	S	WSW	25	3.5	1013	Mid
	2B4	440	S	SSW	25	2.5	1951	Mid
Thinned with hardwoods inclluded at 3 to 3.6 m spacing, slash lopped	3A1	440	NW	NNW	10	3.3	1062	n/a
	3A2	470	NW	NW	5	3.6	914	Redwood
	3A3	440	NW	ENE	22	3.7	914	n/a
	3A4	470	NW	W	23	3.6	988	Redwood
Thinned with hardwoods included at 3 to 3.6 m spacing, slash not lopped	3B1	440	NW	NW	18	3.3	1112	Redwood
	3B2	410	NW	WNW	18	3.2	1161	Redwood
	3B3	440	NW	WNW	15	3.2	1161	Redwood
	3B4	410	NW	NW	20	3.2	1112	Redwood

PART II:

Exploratory Assessment of Redwood Branch Dimensions at the Holter Ridge Thinning Study, Redwood National Park

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Introduction

An abundance of young second-growth forests throughout the redwood region has encouraged a growing interest in restorative thinning techniques that may advance the development of old-growth characteristics, including aspects of tree crown architecture. Like other characteristics of old-growth forest structure, such as spatial heterogeneity, tree age diversity, multi layered canopies, large woody debris and snags (Franklin et al. 2002), branch dimensions and crown morphologies play an important role in providing habitat for species associated with late-successional forests. Stand density / branch size relationships in Douglas-fir, another species of substantial interest for restorative thinning in the Pacific Northwest, are well documented: thinning intensity has been shown to have a strong relationship with crown development in Douglas-fir (Briegleb 1952, Maguire et al. 1991), and spacing has been shown to directly affect crown development and branch size and distribution (Curtis and Reukema 1970, Grah 1961). Such information is lacking for redwood.

In 1978, Redwood National Park acquired 51,000 acres of second-growth stands that were even-aged and overstocked with suppressed growing conditions (Cussins 1996). That same year, the Holter Ridge Thinning Study (HRTS) was initiated within a portion of the park's newly acquired land. The study was implemented in a 200 acre, 25-30 year old second-growth upland mixed even-aged stand of redwood (Sequoia sempervirens (Lamb. ex D. Don) Endl.), Douglas-fir (Pseudotsuga menziesii (Mirbel) Franco), and tanoak (Lithocarpus densiflorus (Hook. & Arn.) Rehd.). Trees had originated from sprouts and seedfall to densities that typically exceeded 1,000 trees per acre. The HRTS was established to assess the effects of thinning on the development of old-growth structural properties at varying levels of residual stand density (Cussins 1996). The HRTS treatments presented a range of densities suitable to the current study. The primary objective of this study, conducted 26 years after the thinnings, was to assess the relationship between stand density and branch diameter among the stand's redwoods. This relationship was investigated in both damaged and un-damaged trees. An additional objective was to report on the correlation between damage and branch size and to note where in the crown the largest branches occurred.

Study Area

Holter Ridge is located approximately six miles inland from the coast in the headwaters of Lost Man Creek in Humboldt County, California. The soils of the study area are deep, brown/reddish brown, moderately acid loam/clay loams and are classified as Mendocino soils (Veirs 1986). Annual precipitation is approximately 80 inches per year, mostly occurring as winter rainfall. As much as 16.7 inches of annual fog drip has been reported in coastal California forests, but is not reported as part of the annual precipitation total. The forest overstory is dominated by redwood and Douglas-fir, with minor components of tanoak, western hemlock (*Tsuga heterophylla*), and madrone (*Arbutus menziesii*). The understory is dominated by shrubs such as evergreen huckleberry (*Vaccinium ovatum*), red huckleberry (*Vaccinium parviflorum*), salal (*Gaultheria shallon*), Pacific rhododendron (*Rhododendron macrophyllum*) and swordfern (*Polysticum munitum*).

In the Holter Ridge Thinning Study, six operational low thinning prescriptions were applied, resulting in a post-treatment density range of 140 to 2470 tree per acre (including the control unit). Following treatments, four 1/10 acre circular plots were systematically located and permanently monumented in each treatment area.

Methods

Among the permanent plots of the Holter Ridge Thinning Study, 10 plots were chosen for analysis in this study, which was conducted during fall, 2004. The chosen plots were selected to minimize variability in site factors (such as slope, aspect, and slope position) and presence of residual old-growth trees, in order to better isolate second-growth stand density as a varying factor. The ten plots ranged in density from 150-1180 trees per acre.

In each plot, a subset of the three largest redwoods, as determined by diameter at breast height (dbh), were selected. Large trees exhibiting past bole or crown damage were not excluded due to their ubiquitous presence in the study plots. All sample trees were ascended using established climbing techniques (Figure 1). Trees were primarily ascended using spurs and lanyards. Climb lines were set in the upper crown of some trees for maneuvering and descents. Climbers passed from crown to crown, where possible, using throw lines and ground assistance.

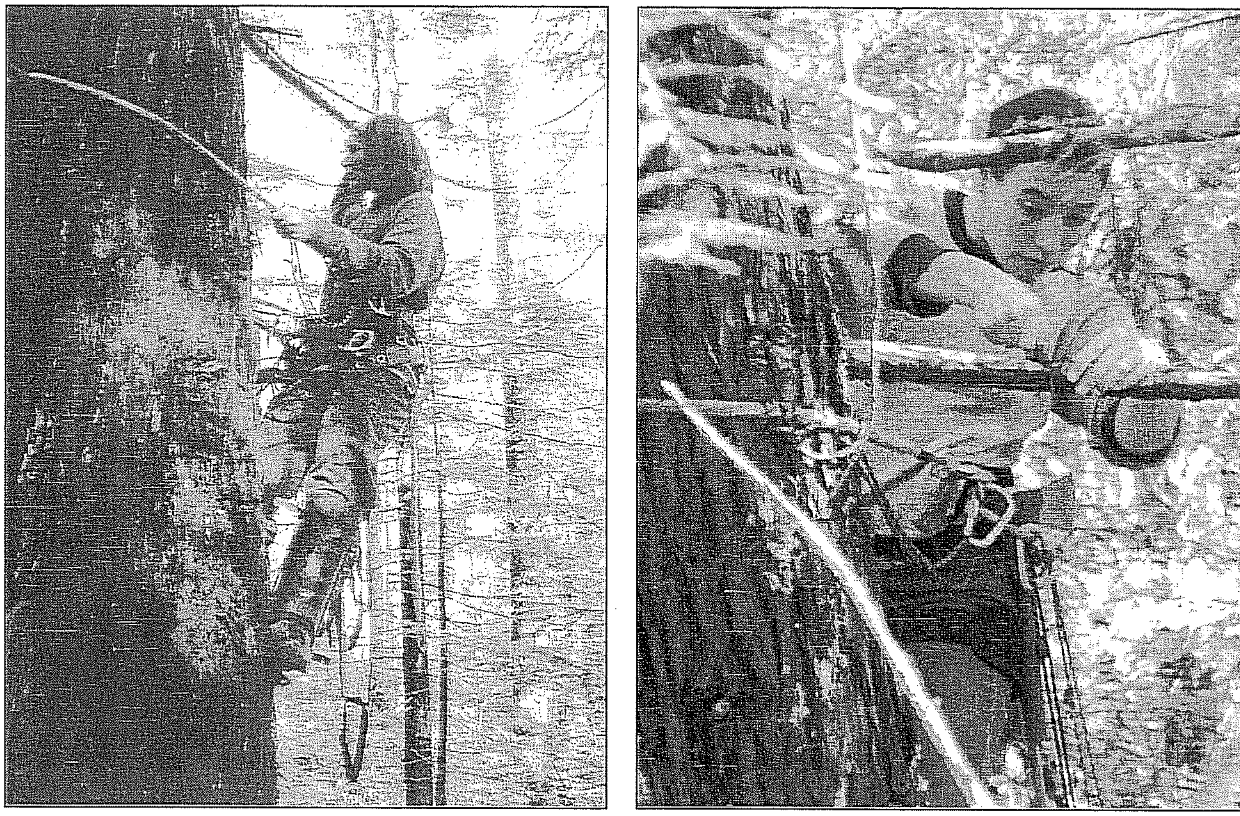

Figure 1. Tree climbing and branch measurement techniques.

Diameters of the four largest branches in the live crown of each tree were measured. Branch diameters were measured at a distance of one foot outward from the bole, in order to avoid the typically variable shape and size of branches at the bole juncture. Each branch diameter was recorded as the average of two measurements taken with a caliper from the side and the top of the branch to the nearest 0.01 inch (Figure 1). Consistent with previous studies of branch and crown analysis (e.g. Maguire et al. 1991), the diameters of these four branches were averaged to provide an average largest branch diameter, or BD4. Statistical analyses based on two-sample t-tests and simple linear regression were applied to test for the presence or absence of relationships between branch diameter and stand density (plot-level estimates of trees per acre and basal area per acre), tree size (diameter at breast height), and damage presence (as a binomial factor).

Results & Discussion

The BD4s of the 28 sampled trees averaged 2.0 inches and ranged from 0.9 to 3.4 inches. Nearly half the trees exhibited some form of crown or bole damage. BD4s were significantly greater among trees with visible evidence of previous bole damage than among undamaged trees (Figure 2).

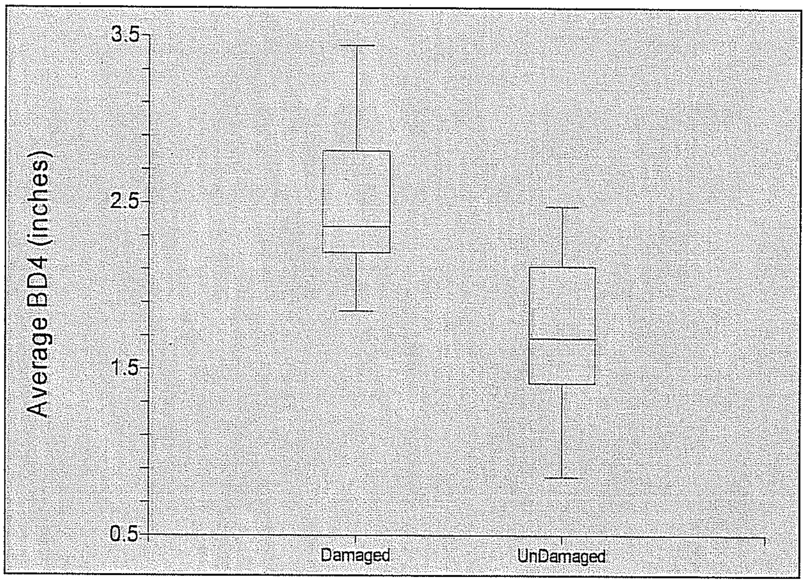

Figure 2. BD4s of damaged trees significantly greater than undamaged trees at α=0.05.

No relationship between BD4 and plot density (expressed as trees per acre) was observed (Figure 3). The result was similar when plot basal area was used as a density measure rather than trees per acre. However, positive relationships between BD4 and dbh were observed among both undamaged trees (Figure 4) and damaged trees (not shown).

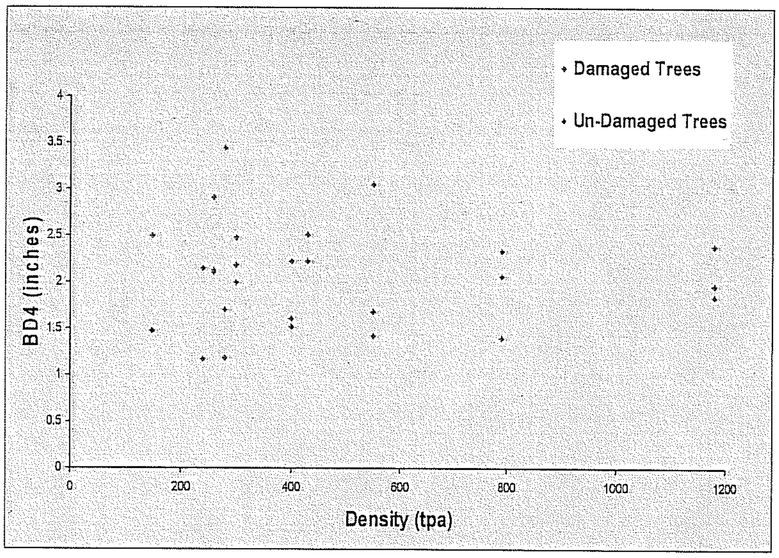

Figure 3. BD4 vs. plot-level density (expressed as trees per acre) suggesting no apparent density-size relationship.

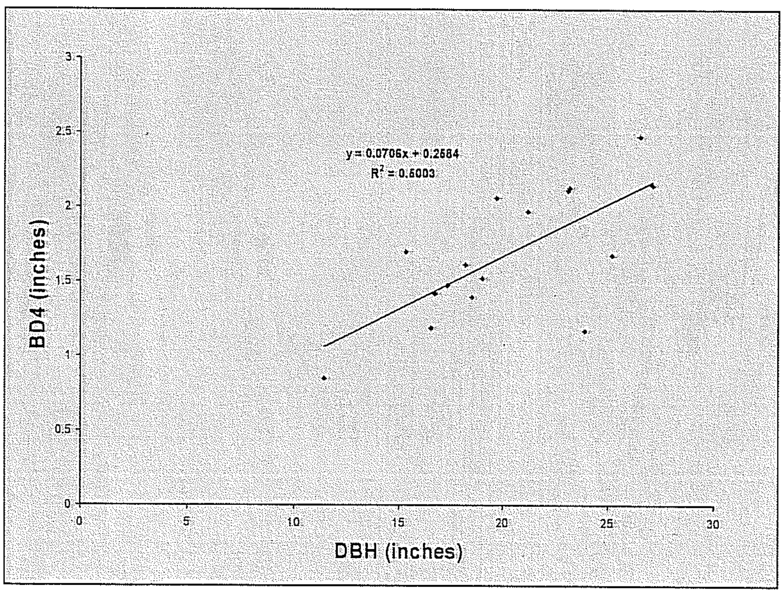

Figure 4. BD4 vs. DBH for un-damaged trees (relationship is similar among damaged trees).

This result was unanticipated, since plot density should correlate to tree diameters and because a BD4-density relationship was not found. The greater variation in BD4s that was observed at lower plot densities than at higher plot densities (Figure 3) could indicate more uniform competition within the latter plots. Such spatial variability of trees was lost in the plot-level density measures. Among undamaged trees, there was no detectable trend regarding the location of the largest branches within the crown (Figure 5). This result is in contrast to findings from other conifer species, where largest branches are typically found in the lower crown. In damaged trees the largest branches consistently occurred directly below the point of damage, irrespective of crown location (Figure 6).

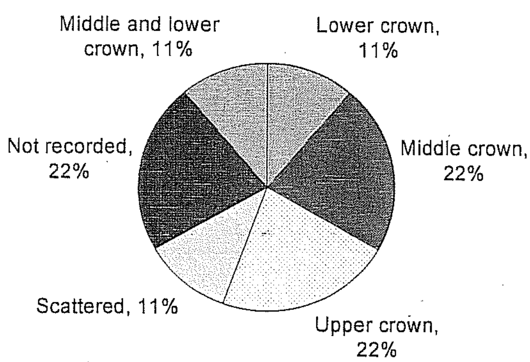

Figure 4. Location of largest branches in undamaged trees, suggesting no particular trend between branch size and crown location.

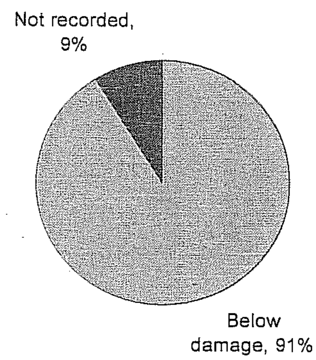

Figure 5. Location of four largest branches in damaged trees. Largest branches occurred directly below the damaged areas in every instance that location was recorded. None occurred above damage.

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