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GREEN-TREE RETENTION: CONSEQUENCES FOR TIMBER PRODUCTION IN FORESTS OF THE WESTERN CASCADES, OREGON

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Abstract. National Forest management in the Pacific Northwest is adopting ecosystem management, in which the entire forest ecosystem is considered, as well as commodity production. Silvicultural prescriptions in ecosystem management often include retention of some live trees following timber harvest (green-tree retention) with the primary goal of maintaining biodiversity. How green-tree retention will affect growth and tree species composition of future forests is an important question. We took a retrospective approach to this question by using past disturbance as an analogue to green-tree retention following timber harvest. We used United States Department of Agriculture (USDA) Forest Service timber inventory plot data from the Cascade Mountains of Oregon and southwest Washington (western hemlock zone). We selected 132 unmanaged stands with a tree cohort of 70-110 yr old (regeneration) or a tree cohort of 70-110 yr old with an overstory of large trees 200+ yr old (remnants), representing clearcuts and stands harvested with green-tree retention, respectively. Regeneration basal area (BA) across species and for Pseudotsuga menziesii tended to decline with increasing remnant density ($R^2 = 0.51$ and 0.60, respectively), but only after remnant densities reached ≈ 15 trees/ha; the relationships were roughly sigmoidal. Part of the effect of remnants on regeneration results from remnants' occupation of space, making it unavailable to the regeneration. After adjusting regeneration BA to account for remnants' space occupation, the relationship between regeneration BA and remnant density weakened by about half, implying that remnant effects resulted from both space occupancy and other factors associated with remnants. Total-stand BA was relatively constant across remnant densities. Remnant density was not related to tree-species diversity in the regeneration.

Key words: Cascade Mountains; ecosystem management; forest management; green-tree retention; new forestry; Pseudotsuga menziesii; remnant trees; retrospective study; Tsuga heterophylla.

INTRODUCTION

Competition between commodity and nonconsumptive uses of U.S. National Forests has illuminated the need to change management practices in these forests. In the U.S. Pacific Northwest, timber-oriented management on Federal lands is yielding to an ecosystem approach to forest management in which the entire ecosystem is considered (Swanson and Franklin 1992). Ecosystem management involves recognizing that provision of diverse benefits from forests may be facilitated by allowing natural processes to occur or mimicking natural processes through management. Forest management schemes that mimic natural disturbance regimes leave standing dead and green trees, as well as fine and coarse woody debris on site.

In the U.S. Pacific Northwest, clear-cutting has been traditionally justified by asserting that it mimics the stand-replacing fires typical of the region (noted in

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Franklin and DeBell 1973). However, recent studies have shown that before ≈ 1910 (when fire suppression began in earnest), fire regimes in the Pacific Northwest were variable, ranging from long-rotation, stand-replacing fires in the Olympic Mountains, to high-frequency, variable-intensity fires in southwest Oregon (Agee 1990). Furthermore, even where stand-replacing fires were considered the norm, pockets of live trees were often left following a fire (Franklin and Waring 1979, Morrison and Swanson 1990). This natural regime of patchy fires that leave live trees as individuals and in clumps is one basis for green-tree retention following timber harvest on U.S. federal lands as mandated in the Forest Ecosystem Management Assessment Team's (FEMAT) Selected Alternative Plan (FE-MAT 1994). Green-tree retention is an aspect of ecosystem management that involves leaving live large trees following timber harvest.

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Remnant trees (those that survive disturbance or that are retained following harvest) probably affect the recovering ecosystem. Together with dead wood, remnant trees bridge past and future forests (FEMAT 1994). These trees provide a seed source, shade, and amelioration of temperature and surface desiccation for the

postdisturbance regenerating cohort. Remnants also compete with the regeneration for deeper soil moisture and nutrients. By providing a source for snags and promoting a multistoried canopy, remnants provide habitat and structural diversity that appear to favor many organisms associated with old-growth forests (FEMAT 1994). Over decades, remnant trees may well influence the species composition and growth rates of the developing tree cohort in Douglas-fir (Pseudotsuga menziesii [Mirbel] Franco; nomenclature follows Hitchcock and Cronquist 1973) dominated systems. For example, as compared to clearcuts, stands with relatively great numbers of remnants may be associated with higher relative densities of shade-tolerant trees such as western hemlock (Tsuga heterophylla [Raf.] Sarg.) and western red cedar (Thuja plicata [Donn.]) and lower abundance of less tolerant Douglas-fir in the regeneration.

Information on effects of green-tree retention on biodiversity or conifer growth and yield over decades or centuries is lacking. Managers have no direct way of determining the long-term impacts of alternative harvest methods on forest ecosystems without studies that would take decades to complete. Simulation models can provide some insights into these consequences (e.g., McComb et al. 1993, Hansen et al. 1995), and retrospective studies also have potential utility for predicting the results of different harvest regimes (Swanson and Franklin 1992).

Retrospective studies are based on the assumption that a past disturbance (such as fire) can be used as an analogue for timber harvest. While analogies between timber harvest and fire can be made, fires do differ from timber harvests in several ways. Compared to fires (and most other natural disturbances), traditional timber harvests followed by slash burning generally: (1) remove more large wood, (2) decrease coarse and fine woody debris on the forest floor, and (3) increase soil compaction and associated erosion losses (Agee and Huff 1987, USDA Forest Service 1990, Brooks et al. 1991). Alternative forestry practices associated with ecosystem management more closely resemble results of fire than timber harvest by clearcutting, in that standing trees and woody debris are left on site, ameliorating erosion losses, particularly when coupled with aerial harvest methods. Planting of tree seedlings often follows harvest, as opposed to natural regeneration after natural disturbances. Planted seedlings often have advantages over those naturally regenerated, introducing complications into the comparison of postfire and postharvest regeneration. Finally, no natural process is equivalent to herbicide treatment of competing herbs and shrubs following harvest. Despite imperfections in the analogy between timber harvest and fire, retrospective studies offer insights into the future of ecosystem management harvests.

We used natural disturbance as an analogue to timber harvest in an attempt to determine, retrospectively, how leaving large green trees on a site will affect stand development over a rotation period of 70-110 yr. Using data from timber inventories on U.S. National Forests from southern Washington to central Oregon, we analyzed yield (basal area; BA, m²/ha) and species composition of 70-110 yr old regeneration growing under varying numbers of remnant trees (>200 yr old). Use of these data saved thousands of dollars and hours compared to those required to conduct the research as a field study. Information previously available on effects of remnant trees on conifer growth included rough estimates in reports by the Willamette National Forest (Jim Mayo, Willamette National Forest, personal communication) and Washington Department of Natural Resources (Hoyer 1993), and simulation models (Birch and Johnson 1992, Long and Roberts 1992, McComb et al. 1993, Hansen et al. 1995), which generally predict yield losses at levels of retention as low as 5 remnants/ ha (e.g., see Hansen et al. 1995).

METHODS

Study area

The study area is the lower-to-moderate elevations (450-1250 m) of the western Cascade Mountains from southern Washington to central Oregon, USA, including portions of the Gifford Pinchot (32 plots) Willamette (83 plots), and Umpqua (17 plots) National Forests (≈43-46° N, 122° W). The area encompasses much of the Tsuga heterophylla zone within the central part of the Western Cascades Province described by Franklin and Dyrness (1973). The maritime climate is relatively mild and wet, with summers receiving only 6-9% of the mean annual precipitation (Franklin and Dyrness 1973). Annual precipitation varies primarily along an elevational gradient ranging from ≈ 150 cm at the lower elevations to \geq 250 cm higher in the mountains (Oregon Climate Service 1993). Average January temperatures at the lower elevations range from $\approx 0^{\circ}$ to 2°C, while mean July temperatures range from ≈17° to 19°C (Franklin and Dyrness 1973). Soils tend to be moderately acidic with a well-developed organic layer and include Dystrochrepts, Haplumbrepts, Haplorthods, Xerumbrepts, and Vitrandepts (Franklin and Dyrness 1973).

Source of data

Data came from the timber inventories that are used to estimate timber volume and growth on National Forests of the Pacific Northwest. These inventories establish or revisit (on an 8–10 yr cycle) thousands of plots on which trees are measured and physiographic conditions (e.g., elevation, aspect, percentage slope, etc.) are recorded. We used data from four inventories: the 1981 inventories on the Gifford Pinchot and Willamette National Forests, the 1980 Umpqua National Forest inventory, and the 1970 Willamette National Forest inventory. For the 1980–1981 inventories, each NaFebruary 1997

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tional Forest was stratified into vegetation types with enough inventory plots established in each type to estimate timber volume within $\pm 10\%$. In 1970, plots were chosen at random from a grid covering the entire forest (USDA Forest Service 1980; Jim Mayo, Willamette National Forest, *personal communication*).

Each timber inventory plot consisted of 10 sample points distributed over ≈0.40 ha (see USDA Forest Service 1980 and Rose 1994 for details). Because each plot represents a relatively homogeneous unit of forest, we will use "stand" in lieu of "plot" throughout. A basal area factor (BAF) 80 wedge prism or angle gauge (Husch et al. 1972, USDA Forest Service 1980) was used to tally all trees ≥ 18 cm diameter at breast height (dbh) at each point. Trees <18 cm dbh were tallied in a 2.07-m fixed-radius (13.46 m²) subplot at each point. Data on tree size (dbh), age, and species were collected for every salvable tree (live and dead) at each point. Age was derived by counting rings on cores of a "representative number" of trees of each species (i.e., 10-20 trees per stand across all species). Age was recorded in 10-yr increments up to 200 yr, then one age class for trees 200-299 yr and one for age 300+ yr; we added years to ages at breast height to approximate more closely the true age for trees of each species (Rose 1994).

Stand selection criteria

We selected only stands: (1) between 450 and 1250 m elevation, (2) in the western hemlock zone (Franklin and Dyrness 1973), (3) with Douglas-fir and western hemlock as dominants, and (4) that were fairly evenaged between 70 and 110 yr old or that had an overstory of remnant trees ≥ 200 yr old over a cohort of trees 70–110 yr old. One hundred thirty-two stands were included in analyses. Although we considered remnants to be all trees ≥ 200 yr, in practice few were <300 yr. Henceforth, we refer to the cohort of 70–110 yr old trees as "regeneration." We assume that fire was the regeneration-initiating disturbance in most cases, and comments on several of the data sheets indicated the presence of fire scars on trees or charcoal in the soil.

We chose stands with a 70-110 yr regeneration cohort because this age range encompasses rotations common on National Forests of the Pacific Northwest (USDA Forest Service 1990) and is narrow enough to allow comparisons between stands. While there were seedlings, young saplings, and occasionally older trees in these stands, the mean age of the dominant regeneration cohort was 70-110 yr for almost every stand, and we avoided truly multiple-aged stands. We excluded seedlings and young saplings from analyses because we were interested in remnants' effects on trees of merchantable size.

Remnant densities ranged from 0 to 125 trees/ha, although most stands had \leq 50 remnants/ha (Table 1). The FEMAT Selected Alternative mandates retention of 15% of green trees on each cutting unit on the matrix TABLE I. Stand characteristics. (A) Basal area (BA, m²/ha) and tree density (trees/ha). (B) Species composition of study stands. Grand fir = Abies grandis (Dougl.) Forbes, western white pine = Pinus monticola Dougl.

A) Basal area and tre	e density			
Characteristic	Mean	SE	Min.	Max.
Stands without remna	nt trees (N	= 51)		
Regeneration BA	60.88	2.47	23.82	108.09
Stands with live and o	dead salvat	ole remn	ants (<i>N</i> =	= 81)
Regeneration BA	39.99	2.16	3.66	81.31
Remnant density	29.31	3.09	0.77	125.39
Remnant BA	28.24	2.67	1.83	97.10

B) Species composition, stands without remnants

		BA across stands (%)			
Tree type		Western hemlock	Grand fir	Western white pine	
Regeneration	90.19	4.23	1.30	1.26	

C) Species composition, stands with remnants

		BA across stands (%)			
73.74	14.18	3.97 10.92	2.24		
	las fir	las fir hemlock 73.74 14.18	15.11 11.10		

lands (sites of most harvesting) on National Forests of the western Oregon and Washington Cascades (USDA and USDI 1994). Henceforth, "management-level" remnant densities range from 0 to 45 trees/ha, a range spanning the traditional number of trees left after harvesting (zero after clear-cutting) through the maximum number likely to be left under alternative management strategies.

Calculation of stand parameters

We calculated total BA for each stand, and for regeneration, remnants, and each species within each stand (Husch et al. 1972, Avery and Burkhart 1983, Bell and Iles 1991, Rose 1994). Summing the BA of all trees in the regeneration cohort produced the basic unit used for most analyses (henceforth "regeneration BA," Table 1). Regeneration BA includes both live and salvable dead trees; salvable dead trees comprised 6.49% of the regeneration BA across all stands, or 5.7% of the stems in the regeneration. We included salvable dead trees because they would likely be harvested in a timber sale, and we wished to focus on effects of remnants on merchantable trees.

Relationships of remnants to regeneration BA, rather than to regeneration volume, were analyzed because height data were lacking from many plots. Regeneration BA is not a perfect surrogate for regeneration volume; for example, on stands with the lowest regeneration densities, BA to volume ratios will likely be higher than on stands with medium-to-high regeneration densities, because free-growing trees allocate more photosynthate to diameter growth (and hence BA) than trees growing with side shade (Oliver and Larson 1990). However, on stands where height data were available (N = 86), stand volume (in cubic meters per hectare) was highly correlated (R = 0.90) with stand BA. Thus, general inferences about remnant effects on regeneration BA may be extendable to effects on regeneration volume.

Remnant tree density (number of trees per hectare) was calculated for each stand by dividing the total BA of all remnants on a stand (in square meters per hectare) by the mean BA (square meters) of remnants in that stand (Bell and Iles 1991). We use remnant-tree density as an independent variable instead of remnant BA for two reasons. First, harvest guidelines (e.g., USDA Forest Service 1990, USDA and USDI 1994) often specify a density of remnant trees to be left, rather than specifying the BA to be retained on site. Second, because each remnant represents the same BA with variable radius sampling (Husch 1972, Bell and Iles 1991), relationships of regeneration BA to remnant BA and to remnant density are nearly identical (see Results and Discussion). Regeneration density could not be estimated reliably due to the large BAF used in sampling.

Remnants currently on a site were present when regeneration was initiated, but in the 70-110 yr or more since the disturbance, other remnants may have died. Thus, the number of currently living remnants may not provide a good indication of growing conditions over the life of the regeneration. Because some dead remnants were undoubtedly influential over the regeneration's history, we used three different remnant densities in analyses: (1) live remnants only; (2) live remnants plus salvable snags (all sizes; ≥ 200 yr); and (3) the combination of live remnants, salvable snags, and nonsalvable snags (nonsalvable snags ≥60 cm dbh). Large Douglas-fir snags in western Oregon are probably salvable for up to 18 yr (see Maser et al. 1988). Thus, salvable remnants likely influenced the regeneration during most of its 70-110 yr of development. Salvable dead remnants made up 8.72% of the combined BA of live plus salvable dead remnants across stands. The heartwood of a large Douglas-fir snag may last ≥125 yr (Maser et al. 1988). Therefore, nonsalvable snags may or may not have lived during part of the regeneration's development. Their inclusion may improve the estimation of remnant effects on plots where these snags were alive at stand initiation, but may decrease the accuracy of estimated remnant effects when these snags were dead at stand initiation. When included, nonsalvable snags (≥60 cm dbh) made up 15.95% of the combined BA of all remnants across stands.

Data analyses

We ordinated stands in species space (Bray-Curtis ordination, Euclidean distance measure, and varianceregression endpoint selection [Beals 1984], matrix of plots by tree species BA in the regeneration) to try to understand the basic patterns of species composition

and relative abundance in the regeneration (using PCORD, McCune 1993). We examined correlations be tween ordination axes and species, remnant density and elevation, as well as overlays of physiographic class (1 = upper and middle west-, southwest- and south-facing slopes; 2 = upper and middle southeas and northwest-facing slopes; 3 = upper and middlenorth-, northeast-, and east-facing slopes; 4 = bottom lands and lower slopes) and aspect on the ordination Univariate methods included regression and correlation analysis using SPSS/PC+ Version 4.0 (Norusis, M. J., SPSS 1988). The dependent variable in regressions (usually regeneration BA) was square-root transformed to improve linearity of relationships between variable: except where indicated. Most regressions involved examining relationships of remnant density to regenera tion BA. We also used regression to examine relation ships of regeneration BA to elevation, regeneration density and age, and proportion of Douglas-fir in the regeneration.

Douglas-fir is a good competitor (Wierman and Oliver 1979) and dominated most stands (Table 1), thue regeneration BA across all species might simply reflec how much Douglas-fir is in the regeneration. Hence we calculated the proportion of Douglas-fir in the regeneration (henceforth "Douglas-fir proportion"; = Douglas-fir regeneration BA/ [Douglas-fir regeneration BA + western hemlock regeneration BA]). Only Douglas-fir and western hemlock were included because they dominated every stand (Table 1) and are most important from a management perspective. Douglas-fir proportions were arcsine square-root transformed prior tc analyses to improve homogeneity of variances (Sokal and Rohlf 1981).

Remnant tree distribution (spacing) may have modified remnant-tree relationships to regeneration. For example, if remnants were clumped, their influence would be restricted to a small part of a stand and probably have less effect on the regeneration than if the same number of remnants were scattered across the stand. We computed an aggregation index to indicate the spatial distribution of remnant trees in each stand. This index was computed by dividing the variance in the number of trees per point by the mean number of trees per point for each stand (adapted from Greig-Smith 1983). A variance/mean ratio of 1 implies a random distribution, a ratio <1 implies a regular, evenly spaced distribution, and a ratio >1 implies a clumped distribution. We did not test for statistical significance of deviations from randomness; rather we added the aggregation index (as a continuous variable) into the regression of regeneration BA on remnant-tree density to test whether spatial distribution of remnants explained any of the residual variance.

Remnant trees affect regeneration by occupying space, making it unavailable. To attempt to distinguish this space occupancy effect from other remnant effects (shading, water use, etc.), we created an adjusted regeneration BA that at least partially controlled for the proportions of each stand occupied by remnants. Proportions of each stand occupied by remnants were calculated based on the mean density of \geq 200-yr-old trees in 33 old-growth stands ("old-growth" here meaning average tree age \geq 200 yr with no other clear cohort of trees) selected from the timber inventory data for this study area. From this mean old-growth tree density, we derived an estimate of the proportion of old-growth stand that remained after the regeneration-initiating disturbance for each stand used in this study, and thus the proportion of the stand theoretically available to the regeneration. The mean density of salvable trees (live and snags) 200+ yr of age in the old-growth stands was 144 trees/ha, with a standard deviation of 61 trees/ha. (This density should not be confused with densities reported elsewhere by tree size; for example the mean density of live Douglas-fir >100 cm dbh in old-growth stands in western Oregon and Washington was 19 trees/ha [Hansen et al. 1991]. In the old-growth plots we identified, the mean density of live Douglasfir >100 cm dbh was comparable, at 22 trees/ha [SE = 2.43].)

For each two-aged stand, we then calculated the proportion of old growth remaining based on the mean density from the old-growth stands. For example, a plot with a remnant density of 37 trees/ha had 0.25 of an old-growth density remaining, because one-fourth (37/ 144) of the tree density in an average old-growth stand remained. In this example, the adjusted regeneration BA would be computed by dividing the regeneration BA by the proportion of the stand available (=1 -0.25), because the regeneration essentially had only 75% of the stand available in which to develop. This adjustment may overestimate the proportion of a stand unavailable for the regeneration because the mean oldgrowth density probably does not represent the highest potential stocking level in these stands. Therefore, adjusted regeneration BA values may be overestimated. A sensitivity analysis involved calculating an adjusted regeneration BA based on mean old-growth density plus (and minus) one standard deviation. When these adjusted BAs were used as the dependent variable, results were qualitatively and quantitatively similar to those based on the adjustment using mean density (Rose 1994). While imperfect, the adjustment based on mean density should compensate somewhat for the remnant space occupancy effect, and hereafter "adjusted regeneration BA" refers to adjustment based on mean old-growth tree densities. Adjusted regeneration BA was then regressed against remnant density to infer remnant effects relatively independently of space occupancy. Cases where regeneration BA was adjusted are specified; all other regeneration BA values are unadjusted.

RESULTS AND DISCUSSION

Community composition

A shade gradient was apparently the main trend in the community data, as stands were ordered from high-

TABLE 2.	Pearson	correlations	of species	(BA), remnant
density ((trees/ha),	and elevatio	n (m) with	Bray-Curtis or-
		= 127 stands		

Species and site variables	Axis 1† (R)	Axis 2† (R)
Abies amabilis	.276	.913
Abies concolor	042	.113
Abies grandis	.155	001
Abies procera	.136	.342
Acer macrophyllum	070	.009
Alnus rubra	.001	.082
Arbutus menziesii	073	.071
Calocedrus decurrens	.034	.126
Castanopsis chrysophylla	047	.040
Picea engelmannii	.025	.264
Pinus lambertiana	037	.073
Pinus monticola	.037	.140
Pseudotsuga menziesii	982	433
Populus trichocarpa	036	025
Taxus brevifolia	008	.064
Thuja plicata	.423	.094
Tsuga heterophylla	.961	.102
Tsuga mertensiana	.224	.067
Remnant density	.669	.189
Elevation	.121	.362

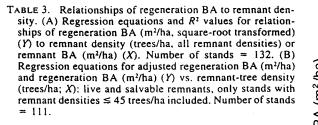
 \dagger Percentage variance explained = 83.03% for Axis 1 and 5.26% for Axis 2.

er abundance of relatively shade-intolerant Douglas-fir to higher abundance of relatively shade-tolerant western hemlock on the first ordination axis (Table 2). Remnant density was positively correlated with the first axis (R = 0.67), and thus negatively correlated with shadeintolerant species in the regeneration. An elevation gradient was also apparent, as indicated by the positive correlations of the second axis with elevation and BA of Pacific silver fir (*Abies amabilis* (Dougl.) Forbes), a high-elevation species in this data set.

Regeneration BA vs. remnant-tree density

Regeneration BA declined with remnant density, whether or not salvable and/or nonsalvable dead remnants were included (Table 3A, Fig. 1), with up to 51% of the variation in regeneration BA apparently explained by remnant density. There was approximately a negative exponential relationship between regeneration and remnant density across all remnant densities, with a large variance in the regeneration BA for most remnant densities. However, within the management density range of remnants (0-45 trees/ha) the relation was roughly sigmoidal (Fig. 2), with no significant decline in regeneration growth until remnant densities were greater than ≈15 trees/ha. Further, the explanatory power of remnant density diminished when only stands with management-level remnant densities were included in regressions (Table 3B, R^2 decreased to 0.34). Apparently, remnants do not capture sufficient resources to impact stand-level regeneration yield (BA) at remnant-tree densities below ~15 remnants/ha.

If salvable remnant (≥ 200 yr) snags had been living for much of the time since the regeneration-initiating disturbance, the relationship of salvable remnants (live

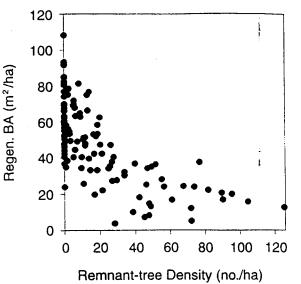


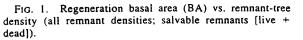
A)			
Type of remnants		Regression equation	R²
Live remnants only (densit Salvable, live, and dead (d. Salvable, live, and dead + nonsalvable ≥ 60 cm	ensity)	Y = 7.52 - 0.0 Y = 7.55 - 0.0	
(density) Salvable, live, and dead (B	A)	Y = 7.64 - 0.0 Y = 7.52 - 0.0	
B) Dependent variable (square-root transformed)		gression quations	R ²
Adj. regeneration BA Regeneration BA		7.78 – 0.05X 7.77 – 0.07X	0.18 0.34

and dead) to regeneration BA should have been stronger than the relationship to live remnants alone. However, there was little difference between these relationships (Table 3A). There were salvable snags (≥ 200 yr old) on only 39 out of the 132 stands, and numbers were generally low ($\bar{X} = \text{six}$ salvable snags/ha, sE =0.88, range 1–26 per stand). This compares with a mean of seven snags/ha (all decay classes, >50 cm dbh) found in old-growth stands in the Oregon Cascades (Spies and Franklin 1991). Apparently most remnant influence was associated with those remnants that were alive when sampled, probably because numbers of now dead remnants (salvable snags) were generally small.

Sixty-one stands had nonsalvable snags $\geq 60 \text{ cm dbh}$. When these were added to remnant densities, the strength of the relationship between remnant density and regeneration BA diminished (Table 3A). This weakening suggests that these snags had been dead for decades, often predating the regeneration, and thus had minimal impact on its growth. Henceforth, "remnant density" includes only salvable, live, and dead remnants.

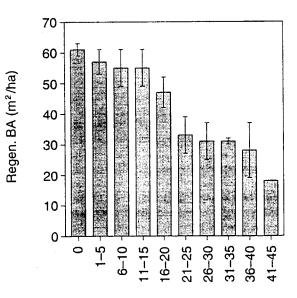
Regeneration BA values adjusted for remnant space occupancy were little different from unadjusted values at management-level densities (0-45 remnants/ha;compare Figs. 1 and 3). However, the fit of the regression of regeneration BA on remnant-tree density at management-level remnant densities was poorer when regeneration BA was adjusted than when it was not adjusted (Table 3B). This reduction in explanatory power implies that a considerable proportion of remnant tree effects at management-level remnant densities results from physical space occupancy rather than from other suppressive effects.





Other factors related to regeneration BA

No factor other than remnant density was significantly related (increased R^2 by >0.05) to regeneration BA when added to the regression equation after remnant density. The Douglas-fir proportion in the regeneration added little to the regression equation, probably because this proportion was strongly correlated with remnant density (R = -0.68). Thus, once remnant density was in the regression, little additional explanatory



Remnant-tree Density (no./ha)

FIG. 2. Mean regeneration basal area (BA) (± 1 SE) vs. remnant-tree density (≤ 45 remnant trees/ha; salvable remnants [live + dead]).

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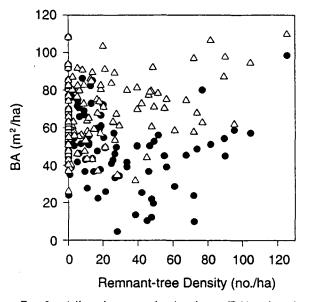


FIG. 3. Adjusted regeneration basal area (BA) and total stand BA vs. remnant-tree density (salvable remnants [live + dead]). \bullet = adjusted regeneration BA, \triangle = total stand BA.

power remained for the Douglas-fir proportion. Regeneration BA did increase with the proportion of Douglas-fir in the regeneration (R = 0.71). However, most pure Douglas-fir stands had no remnant trees, making it impossible to separate clearly the effects of regeneration species mix from those of remnant density.

We had anticipated that, given the same numbers of remnants, regeneration BA would be greater when remnants were clumped than when they were scattered, because remnant effects would be more concentrated when clumped. However, the degree of remnant aggregation was apparently unrelated to regeneration growth (R^2 increased by 0.04 when aggregation index was added to the regression equation after remnant density). These results must be interpreted cautiously, however, because this data set contained few stands with a high degree of clumping, as could occur under a management scenario. In most cases, stands with relatively high aggregation indices had several trees on one or more points in the stand, but also scattered remnants, which may have obscured any differences attributable to aggregation.

Mean ages of the regeneration differed somewhat among stands (minimum within-stand mean regeneration age = 70 yr, maximum = 129 yr, mean regeneration age across stands = 95 yr). Thus, it seemed that relationships between regeneration age and regeneration BA could potentially confound interpretation of remnant effects. However, there was no relationship between mean regeneration age and regeneration BA $(R^2 = 0.01)$, hence regeneration age did not account for any of the variability in the relationship of regeneration BA to remnant density. While stand elevation was apparently unrelated to regeneration BA ($R^2 = 0.01$ after remnant density was in the regression model), stand aspect was indirectly related to regeneration growth by affecting the number of remnant trees. Stands on cooler aspects (i.e., north-facing slopes) tended to have more remnants than those on warmer aspects (Rose 1994). These differences may be due to aspect-influenced differences in growing conditions or disturbance regimes.

Total stand BA vs. remnant density

There was no relationship between total BA (regeneration + remnant) and remnant density across all remnant densities (salvable live and dead remnants; $R^2 =$ 0.13). This result corresponds to the concept that a site can sustain a certain BA, whether in remnants, regeneration, or a combination of both. Adjusted regeneration BAs were often lower than total BAs, particularly at remnant densities >15-20 trees/ha (Fig. 3), which may suggest that remnants exert suppressive effects beyond space occupancy. If space occupancy were the only remnant effect, adjusted regeneration BAs should have been closer to total BAs, because conceptually removing remnants should allow regeneration to fully occupy sites. Our adjusted BAs are, however, a coarse approximation (see Methods), hence this result should be interpreted with caution.

Douglas-fir BA vs. remnant density

Douglas-fir regeneration BA was above 25 m²/ha (except in one plot) until remnant densities exceeded \approx 15 trees/ha, above which it tended to decrease ($R^2 =$ 0.60 across all remnant densities; 0.55 for ≤45 remnants/ha). Similarly, Douglas-fir proportions in the regeneration decreased with increasing remnant densities $(R^2 = 0.42 \text{ and } 0.46 \text{ for regressions including all rem-}$ nant densities and \leq 45 remnants/ha, respectively; Rose 1994). As was the case for regeneration BA across all species, no tested factor other than remnant density was related to Douglas-fir regeneration BA (maximum R^2 increment after remnant density was in the model = 0.05). The decreases in Douglas-fir regeneration BA and proportions above remnant densities of ~15 trees/ ha may have resulted from shading by remnants. While 1st-yr Douglas-fir seedlings survive and grow best under light shade, older seedlings require nearly full sunlight (Hermann and Lavender 1990).

Other species vs. remnant density

We expected that relative abundance of shade-tolerant species would increase with increasing remnant density; however, western hemlock BA was basically unrelated to remnant density ($R^2 = 0.16$). (There were many plots with small amounts of western hemlock BA, but only a few plots with relatively high amounts, creating a skewed distribution of western hemlock BA across stands. Hence, parametric statistics involving western hemlock should be interpreted with caution.) Western hemlock did tend to replace Douglas-fir in the regeneration as remnant density increased (R = -0.45for correlation between Douglas-fir regeneration BA and western hemlock regeneration BA). However, as Douglas-fir regeneration BA decreased, regeneration BA across all species decreased as well (R = 0.87 for)correlation of Douglas-fir regeneration BA with regeneration BA across species), indicating that decreases in Douglas-fir regeneration BA were not compensated fully by increases in regeneration BA of other species, such as western hemlock. (Other species occurred sparsely [Table 1B], hence conclusions regarding their relationships to remnant density cannot be made with any confidence.) Douglas-fir regeneration tended to be slightly older than that of western hemlock ($\tilde{X} = 95$ and 85 yr, respectively, excluding seedlings and young saplings), which may account partially for the decrease in regeneration BA with the decrease in Douglas-fir proportions. Douglas-fir may often have established more rapidly after the regeneration-initiating disturbance, perhaps owing, in part, to its greater abundance in the remnant overstory (Table 1B).

Diversity and remnant-tree density

We expected that tree species diversity would be highest at relatively low (but nonzero) to medium remnant densities, because of the potential for various microclimates under canopies, canopy edges, and full sun. However, neither species richness nor Shannon diversity index (H'; Shannon and Weaver 1949) of tree regeneration was related to remnant density ($R^2 = 0.01$ and 0.07, respectively). Removing stands with no remnants (which were dominated by Douglas-fir) did not strengthen these relationships. Given that most stands had only three or four tree species, variation in diversity was limited. Relationships of species diversity to remnant density would be better tested if herb, shrub, and nonvascular plant species were included.

CONCLUSIONS

Regeneration BA (trees 70-110 yr) was apparently not affected by remnant trees (≥200 yr) below remnant densties of \approx 15 trees/ha, and tended to decline as the density of remnants increased above this. Most of the decline came from a reduction in Douglas-fir regeneration BA at higher remnant densities. The decline in regeneration BA across all species and in Douglas-fir at management-level remnant densities of ≤45 trees/ha was probably a combined effect of shading (or other suppressive effects) and space occupancy by remnants. Basal area of western hemlock regeneration tended to increase as that of Douglas-fir decreased. No strong relationships were found between regeneration BA and other stand features (e.g., remnant aggregation index, regeneration age, elevation). However, aspect may have affected regeneration BA indirectly by affecting number of remnant trees.

Further research is needed to form generalizations

about relationships between green-tree retention and conifer growth throughout the region. Our results indicate that ≈ 15 remnants/ha can be retained following timber harvest without significant reductions in regeneration growth and that total stand BA remains fairly constant across remnant densities. The geographic scope and sample size of this study suggest that this is a reasonable general estimate of effects of green-tree retention on lower to mid-elevation sites in the central western Cascade Mountains. Our results differ, however, from those based on simulation models (e.g., Hansen et al. 1995), which predict reductions in regeneration growth and total stand BA at lower levels of retention; further work is needed to reconcile such differences.

Silvicultural techniques could moderate the decline of both Douglas-fir regeneration BA and regeneration BA across all species with increasing remnant density. For example, Douglas-fir could be planted in the more open areas of a site harvested with green-tree retention, while regeneration of western hemlock or other relatively shade-tolerant species could be facilitated in areas with more canopy cover. These techniques might enable fuller use of growing space, higher yields, higher species diversity and more resistance to wind, insect, and disease damage than found in the near-monospecific stands that resulted from more traditional harvest and replanting.

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