



Growth reduction in harvest-age, coniferous forests with residual trees in the western central Cascade Range of Oregon

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Abstract

To evaluate the relationship of overstory residual trees to the growth of unmanaged young-to-mature understory Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), the basal area and volume of 14 paired plots with and without residual trees were examined in the Willamette National Forest, Oregon. Residual trees were large survivors of the fires that initiated the understory between 55 and 121 yr ago. Understory stands were naturally regenerated and not managed in any way. High residual tree and understory densities were negatively associated with understory volume. The relation of density of residual trees to total understory and Douglas-fir basal areas and volumes was best described by a negative logarithmic function. The rate of decrease in total understory and Douglas-fir basal areas and volumes per individual residual tree became smaller with increasing residual-tree density. Predicted total understory volume reduction was 23% with five residual trees/ha and 47% with 50 residual trees/ha, averaging 4.6% and 0.9% per residual tree, respectively. After including the estimated volume growth of residual trees since initiation of the understory, stand volume was still 19% lower with five residual trees/ha and 41% lower with 50 residual trees/ha than in stands with no residual trees, averaging a reduction of 38% and 0.8% per residual tree, respectively. In mixed stands of Douglas fir and western hemlock, predicted Douglas-fir basal area and volume declined more rapidly than did total understory basal area and volume when residual-tree densities exceeded about 15 trees/ha. This difference was probably due to the relative shade-intolerance of Douglas fir. Predicted Douglas-fir volume reduction was 13% with five residual trees/ha and 75% with 50 residual trees/ha, averaging 2.6% and 1.5% per residual tree, respectively. The southern aspects had more than 150% the total understory basal area and volume and more than 200% the Douglas-fir volume and basal area of the northern aspects. Lower density and basal area of understory trees, particularly of dominant and codominant Douglas fir, were associated with increasing residual-tree densities. Given the same diameter at breast height (DBH), heights of Douglas fir were not related to residual trees. Regardless of understory age, understory volume was greatest in stands with the lowest understory densities. These results suggest that timber production in unthinned green-tree retention units may be reduced and may depend on the density of leave-trees. Thinning of understory trees is recommended to reduce growth loss from intraspecific competition. © 1998 Elsevier Science B.V.

Keywords: Green-tree retention; New forestry; Structure; Growth and yield; Douglas fir; Western hemlock

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1. Introduction

In recent decades, timber management in the Pacific Northwest has been dominated by clearcutting and short rotations (i.e., 40–80 yr, Scott, 1980), leading to concerns that ecological functions and biological diversity may not be maintained in managed forest ecosystems. Natural disturbances, in contrast to clearcutting, often do not result in complete stand mortality (Teensma, 1987; Morrison and Swanson, 1990; Agee, 1991). Intended to mimic natural patterns of disturbance and succession (Hansen et al., 1991; Spies and Franklin, 1991) through silviculture, the retention of biological legacies after timber harvest has become a focus of forest management in the Pacific Northwest (Swanson and Franklin, 1992; Thomas et al., 1993; McComb et al., 1993). Such legacies of natural disturbances include coarse woody debris, standing dead trees and large, live residual trees. Although many potential benefits of the retention of live, green trees and lengthened rotations in managed forests have been hypothesized, actual effects of green-tree retention on tree regeneration growth are unknown. Stand growth models have recently been used to compare the likely effects of green-tree-retention on tree regeneration growth to the growth in stands without retention (Birch and Johnson, 1992; Long and Roberts, 1992; Hansen et al., 1995). Although these studies suggest reduced timber production due to leave-trees, corroborating information from field studies is generally lacking. Because long-term experimental records of understory growth under residual trees do not exist, a retrospective approach was used in this field study to estimate understory growth responses. This retrospective approach is limited by a lack of detail about the disturbances initiating the stands, subsequent tree mortality and by our inability to establish cause-and-effect relations. However, assuming that residual trees left by patchy natural disturbances are analogous to leave-trees in green-tree retention cuts, this method gives timely estimates of whether, and to what extent, residual trees modify the timber volume of the 60- to 120-yr-old stands that have regenerated and developed beneath them. This study was part of an interdisciplinary project aimed at assessing the relationship of residual trees to understory herbs and shrubs (e.g., Traut, 1994), to canopy lichen commu-

nities (e.g., Peck and McCune, 1997), arthropods (e.g., Moldenke, 1995), mycorrhizal fungi (e.g., Cazares et al., 1995), ectomycorrhizal mats (e.g., Griffiths et al., 1995) and understory-tree growth.

2. Study area

This study was done in the western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) zone (Franklin and Dyrness, 1973), the most important vegetation zone for timber production in western Oregon and Washington (Franklin, 1979). 14 pairs of plots in young to mature forests, with and without large residual trees, were established in the Willamette National Forest in Oregon's western central Cascade Range, between 520 to 850 m in elevation (Table 1). The western Cascade Range consists of Tertiary (Oligocene and Miocene) basaltic lava flow and pyroclastic rock (Franklin and Dyrness, 1973), which has formed into mountainous, steep, deeply dissected terrain (Peck et al., 1964). Soils can be divided into two groups according to parent material. Soils derived from pyroclastic parent materials (tuffs and breccias) are often deep, fine textured, but poorly drained on gentle slopes (Haploixerulpts), and less-developed, stony and gravelly clay loams (Haplumbrepts and Xerumbrepts) on steeper slopes. Soils derived from basic igneous rocks (basalt and andesite) are well-drained, stony and coarse textured (Agriixerolls, Haplohumults or Xerumbrepts) (Franklin and Dyrness, 1973). The maritime climate is characterized by moderate temperatures, abundant rainfall (1500 to 2000 mm; Oregon Climate Service, 1993) cool and wet winters, and dry summers (Franklin, 1979); 72% of the precipitation occurs between November and March and 6–9% between June and September (Franklin and Dyrness, 1973). Mean annual and mean July temperatures in the Western Cascades range from 9–10°C and 17–19°C, respectively (Franklin and Dyrness, 1973).

3. Methods

Paired plots were established to compare well-stocked stands containing scattered residual trees to adjacent stands without residual trees. Residual trees

Table 1
Environmental attributes and stand characteristics

Pair number	Elevation (m)	Slope (%)	Aspect (°)	Understory				Residual			
				Age (yr)	Trees/ha	Relative density	Basal area (m ² /ha)	Basal area of Douglas fir (%)	Basal area of western hemlock (%)	Volume (m ³ /ha)	Basal area (m ² /ha)
1	820	85	14	104	860	0.38	35.6	0	99	435	33.3
	820	60	29	121	1380	0.99	79.7	65	28	1207	24.9
2	820	75	350	110	1480	0.54	42.8	23	65	421	56.7
	820	80	343	111	1920	0.79	61.0	39	61	674	23.8
3	670	75	210	62	900	0.70	51.3	99	0	599	13.3
	670	68	217	76	600	0.77	63.7	100	0	983	15.7
4	850	73	225	65	900	0.65	46.7	100	0	567	23.3
	850	77	230	58	1040	0.84	63.3	92	0	831	26.8
5	640	30	143	90	680	0.79	64.0	99	0	896	16.7
	640	40	153	67	860	0.88	68.6	100	0	916	13.9
6	730	62	128	61	940	0.52	39.9	64	36	508	36.7
	730	55	120	55	1240	0.79	56.4	91	1	668	26.0
7	700	28	102	83	460	0.40	38.1	35	57	585	53.3
	700	17	110	84	860	0.79	65.2	78	22	1022	51.7
8	700	50	288	84	480	0.50	47.3	48	49	863	10.0
	700	35	282	87	920	0.76	65.6	55	45	1094	23.0
9	520	62	128	92	660	0.59	47.4	84	16	724	13.3
	520	17	142	94	800	0.91	82.0	66	29	1551	79.5
10	790	60	124	81	860	0.67	52.0	85	15	725	10.0
	790	57	112	85	680	0.89	74.5	100	0	1195	43.0
11	700	32	220	84	480	0.92	84.7	100	0	1861	26.8
	700	32	230	73	440	0.68	59.7	99	0	989	9.5
12	670	33	180	87	620	0.72	58.6	98	1	870	10.0
	670	25	193	95	740	1.02	86.5	99	0	1577	21.1
13	670	53	181	80	860	0.94	75.7	97	0	1182	6.7
	670	70	172	81	1000	1.05	83.0	100	0	1173	7.0
14	640	30	194	74	1200	0.64	47.2	68	32	556	13.3
	640	30	199	76	860	0.76	60.2	84	14	843	17.7

The paired stands were in the following ranger districts: stands 1–4 in Blue River, stand 5 in Detroit, stands 6–10 in Lowell, stands 11–12 in McKenzie and stands 13–14 in Sweet Home.

^aVolume growth of residual trees since initiation of the understory under the assumption of no height growth.

were large survivors of the fires that initiated the understory. Sites were chosen to assure similarity of aspect, slope, elevation and topographic position of the pairs (Table 1). Understocked stands with shrub dominance or with excessive recent mortality of the understory were excluded from the study.

The understory was measured in a circular plot (detection plot), with a slope-corrected radius of 12.6 m (500 m²). Detection plots were nested in plots, one with and one without large residual trees, with a slope-corrected radius of 30.9 m (3000 m²). The larger plot created an 18.3-m buffer zone around the detection plot to exclude the influences of peripheral residual trees. The size of the buffer zone was chosen based on the report of Hoyer (1993), stating that the influence of residual trees on the height growth rates of Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) was minimal beyond 18.3 m. Residual trees were measured in the larger plot.

Tree species, diameter at breast height (DBH), canopy class for all live trees over 5 cm in DBH and the decay class (Cline et al., 1980) for dead trees, were recorded. Tree heights and crown lengths were measured on all residual trees and at least two randomly selected, undamaged understory trees for each combination of species and canopy class. Canopy class was determined relative to the general

canopy layer formed by all understory trees. Heights were measured for 303 Douglas fir, 158 western hemlock, 22 *Castanopsis chrysophylla* (Dougl.) A. DC., 13 *Thuja plicata* Donn, eight *Acer macrophyllum* Pursh, seven *Cornus nuttallii* Audubon, five *Libocedrus decurrens* Torr., three *Arbutus menziesii* Pursh and one *Taxus brevifolia* Nutt. Total stand volume (wood volume without bark) was estimated from equations in Means et al. (1994).

For age estimation, increment cores were obtained at breast height from a subsample of understory trees and mostly residual trees. Age of the understory was defined as the average breast-height age of dominant and codominant trees. Ignoring the current year's growth, past diameter increment of residual trees from the time of the understory initiation was measured with the aid of a dissecting microscope to the nearest 1/10th of a millimeter on all 86 residual trees. The entire past radial growth was estimated for six residual trees and growth periods of 5 to 30 yr were estimated for eight residual trees from which either no cores were obtained because trees were rotten, or cores were of such poor quality that exact growth measurements could not be performed. In these cases the average radial growth of residual trees of the same species in the same plot was used as our estimate for radial growth.

Table 2

Results of independent *t*-tests of basal area (BA), the proportion of basal area in dominant and codominant understory trees, the quadratic mean diameter (QMD) of the understory and trees/ha in different crown classes in 14 pairs of stands with and without residual trees

Variable	Residual trees				Degrees of freedom	<i>t</i> -ratio	Probability > <i>t</i>			
	Present		Absent							
	MEAN	SE	MEAN	SE						
BA (m ² /ha, all trees)	52.2	3.8	69.2	2.7	26	-3.68	0.0011 ^a			
BA (% d/c ^b)	36.8	4.3	51.8	2.8	26	-2.94	0.0068 ^a			
BA (% i/s ^c)	15.4	1.3	17.4	1.2	26	-1.15	0.2613			
QMD (cm, all trees)	29.7	2.0	31.8	1.6	26	-0.81	0.4266			
QMD (cm, d/c ^b)	42.1	1.6	42.2	1.3	26	-0.03	0.9739			
QMD (cm, i/s ^c)	19.9	1.1	21.0	1.1	26	-0.72	0.4750			
Trees/ha (all trees)	813	76	953	99	26	-1.12	0.2714			
Trees/ha (d/c ^b)	254	17	374	19	26	-4.72	0.0001 ^a			
Trees/ha (i/s ^c)	559	78	593	90	26	-0.28	0.7762			

^aSignificant at the 0.05 level.

^bDominant and codominant understory trees.

^cIntermediate and suppressed understory trees.

Due to the lack of past height growth records, we based our volume growth estimates of residual trees since initiation of the understory on the assumption that residual trees did not add significant height growth. The assumption of no height growth of residual trees follows from the advanced age of residual trees (e.g., most residual trees were several hundred years old) and the common occurrence of broken and dead tops (e.g., 39%) of residual trees (Acker et al., in prep.). Aspect readings were transformed to a more biologically meaningful continuous variable according to the following formula (Kaiser, 1986):

$$\text{adjusted aspect} = 180 - |180 - \text{azimuth}| \quad (1)$$

Adjusted aspect equals 0 for north, 90 for east or west and 180 for south.

From the actual tree density and the quadratic mean diameter for each plot, the stand density index (SDI) of Reineke (1933) was calculated and converted to relative density (RD) as a percentage of the maximum possible SDI for each plot (after Long, 1985). The maximum possible SDI was calculated as a weighted average of each species' contribution to the understory basal area.

t-tests were performed to test for structural differences between stands with and without residual trees (Table 2). Multiple linear regression analysis was used in this study to test for the effect of residual trees on total understory and Douglas-fir height, basal area, and volume (Table 3). We did not, however, use the paired plot design. All 28 plots were treated as independent samples that covered a range of residual-tree densities with many data points at zero-residual density. Stepwise variable selection (SAS Institute, 1987) was used to determine which independent variables to include in multiple linear regression models. Where indicated, natural logarithmic transformations were applied to dependent and independent variables to linearize regression models; backtransformed data were not corrected for logarithmic bias (Flewelling and Pienaar, 1981). Predicted values were plotted against observed values to ensure that residuals were centered around zero, and no systematic trends were detected.

To illustrate how much each independent variable

in the regression models influences understory growth, we defined values of independent variables that maximize the values of the response variables. By examining how response surfaces of independent variables decrease from their maximal values (Tables 3 and 4, Fig. 2), we can predict expected growth losses in the understory. Setting residual-tree density to zero trees/h, understory density to 500 trees/ha, and the adjusted aspect to 180° results in maximal growth within the ranges of these independent variables in this study. Departures from these values

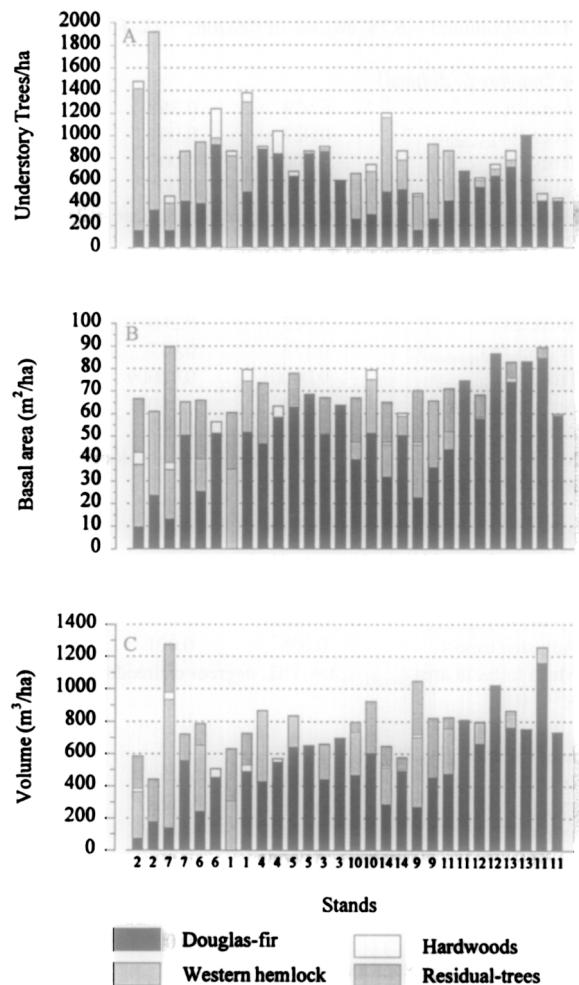


Fig. 1. (a) Understory-tree density, (b) basal area, (c) volume/ha. Stands are ordered by decreasing residual-tree density; within pairs, plots with residual trees are listed first.

Table 3
Selected regression models

Parameter	Standard error	t for H_0 : Parameter = 0	Probability > T	Partial R^2
<i>ln(total understory volume)</i>				
Intercept	6.012	0.421	14.29	0.0001
$\ln(\text{trees/ha}_{\text{residual}})$	−0.163	0.026	−6.28	0.0001
$\text{Trees/ha}_{\text{understory}}$	−0.0004	0.0001	−3.10	0.005
Adjusted aspect	0.003	0.001	2.70	0.013
Age	0.012	0.003	3.59	0.002
Mean $\ln(\text{volume})$ = 6.74, degrees of freedom = 23, F = 18.70, coefficient of variation = 2.97, root mean square error = 0.20, R^2 = 0.76				
<i>ln(stand volume)</i>				
Intercept	6.150	0.424	14.50	0.0001
$\ln(\text{trees/ha}_{\text{residual}})$	−0.133	0.026	−5.09	0.0001
$\text{Trees/ha}_{\text{understory}}$	−0.0005	0.0001	−3.36	0.001
Adjusted aspect	0.003	0.001	2.21	0.037
Age	0.011	0.003	3.43	0.002
Mean $\ln(\text{volume})$ = 6.78, degrees of freedom = 23, F = 14.23, coefficient of variation = 2.98, root mean square error = 0.20, R^2 = 0.71				
<i>ln(Douglas-fir volume)</i>				
Intercept	6.679	0.361	18.5	0.0001
$\text{Trees/ha}_{\text{residual}}$	−0.027	0.004	−7.32	0.0001
$\text{Trees/ha}_{\text{understory}}$	−0.0005	0.0002	−2.71	0.033
Adjusted aspect	0.004	0.002	2.57	0.017
Mean $\ln(\text{volume}_{\text{Douglas fir}})$ = 6.48, degrees of freedom = 23, F = 33.85, coefficient of variation = 4.65, root mean square error = 0.30, R^2 = 0.82				
<i>ln(total understory basal area)</i>				
Intercept	3.327	0.280	11.9	0.0001
$\ln(\text{trees/ha}_{\text{residual}})$	−0.113	0.017	−6.58	0.0001
$\text{Trees/ha}_{\text{understory}}$	0.00001	0.00009	0.16	0.8766
Adjusted aspect	0.003	0.0008	3.54	0.0071
Age	0.007	0.002	3.22	0.0038
Mean $\ln(\text{basal area}_{\text{understory}})$ = 4.08, degrees of freedom = 23, F = 18.27, coefficient of variation = 3.28, root mean square error = 0.13, R^2 = 0.76				
<i>ln(Douglas-fir basal area)</i>				
Intercept	3.517	0.304	11.6	0.0001
$\text{Trees/ha}_{\text{residual}}$	−0.022	0.003	−6.76	0.0001
$\text{Trees/ha}_{\text{understory}}$	−0.0001	0.0001	−0.62	0.5399
Adjusted aspect	0.005	0.001	3.70	0.0012
Mean $\ln(\text{basal area}_{\text{Douglas fir}})$ = 3.82, degrees of freedom = 23, F = 31.66, coefficient of variation = 6.64, root mean square error = 0.25, R^2 = 0.81				
<i>ln(understory height)</i>				
Intercept	1.091	0.056		0.0001
DBH	0.155	0.005	812.71	0.0001
DBH^2	−0.003	0.0002	347.84	0.0001
DBH^3	0.00002	0.000001	184.77	0.0001
$\ln(\text{trees/ha}_{\text{residual}}) \times \text{species}$			3.61	0.0278
Douglas fir	−0.004	0.007		0.5536
Western hemlock	−0.022	0.008		0.0077
$\text{Trees/ha}_{\text{understory}} \times \text{species}$			20.67	0.0001
Douglas fir	−0.0002	0.00003		0.0001
Western hemlock	−0.0001	0.00003		0.0001
Median $\ln(\text{height})$ = 3.19, degrees of freedom = 455, F = 543.96, coefficient of variation = 5.84, root mean square error = 0.19, R^2 = 0.893				

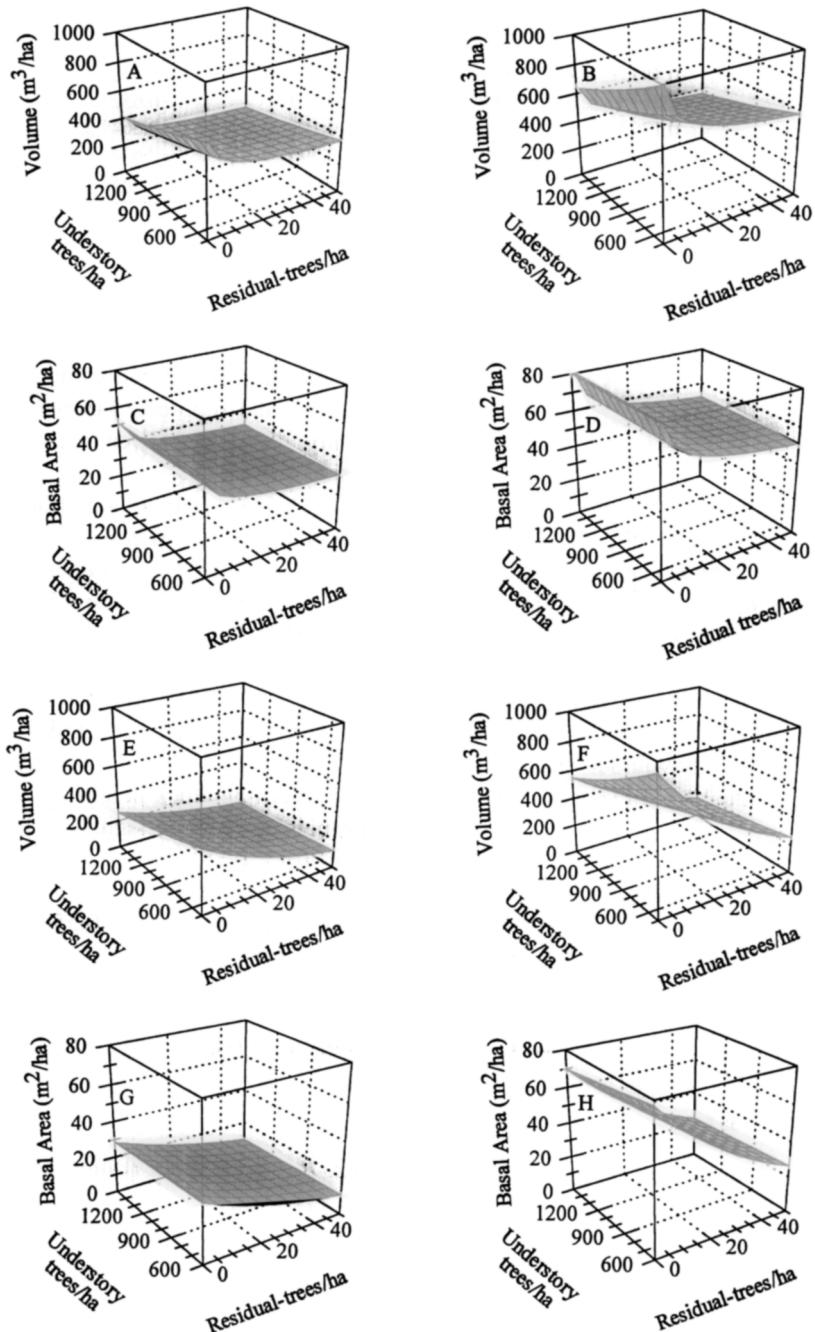


Fig. 2. Understory stand growth reductions. (a) Total understory volume (aspect = 0°), (b) total understory volume (aspect = 180°), (c) total understory basal area (aspect = 0°), (d) total understory basal area (aspect = 180°), (e) Douglas-fir volume (aspect = 0°), (f) Douglas-fir volume (aspect = 180°), (g) Douglas-fir basal area (aspect = 0°), (h) Douglas-fir basal area (aspect = 180°). For volumes, an age of 80 yr is assumed.

Table 4

Correlation coefficients for dependent and independent variables of selected regression models

	Residual	ln(residual)	Understory	Adjusted Aspect	Age
ln(understory volume)	-0.602 ^a	-0.581 ^a	-0.322	0.309	0.109
ln(understory basal area)	-0.775 ^a	-0.772 ^a	-0.026	0.356	0.126
ln(volume _{Douglas fir})	-0.583 ^a	-0.478 ^a	-0.421 ^a	0.512 ^a	-0.020
ln(basal area _{Douglas fir})	-0.777 ^a	-0.587 ^a	-0.319	0.652 ^a	-0.242
ln(volume _{western hemlock})	0.176	-0.021	0.161	-0.664 ^a	0.486 ^a
ln(basal area _{western hemlock})	0.348	0.197	0.290	-0.634 ^a	0.626 ^a
Understory density	0.019	-0.120	1.000	-0.488 ^a	0.301

^aSignificant at the 0.05 level.

resulted in growth reductions. Table 5 presents some predicted percentages of growth reductions.

4. Results

4.1. Understory structure

Total basal area and volume (i.e., understory plus residual trees) were generally greater in stands with residual trees (Table 1, Fig. 1b and c). Understory basal area and volume were generally greater in stands without residual trees. Basal area and density of dominant and codominant understory trees were significantly greater in stands without residual trees than in stands with residual trees (Table 2). In con-

trast, understory density and quadratic mean diameters of all understory trees and trees by crown classes (i.e., dominant and codominant trees only and intermediate and suppressed trees only) were not significantly different between stands with and without residual trees.

Understory height (\log_e -transformed) was poorly associated with residual tree (partial $r^2 = 0.001$, $p < 0.03$, $n = 461$) and understory densities (partial $r^2 = 0.01$, $p < 0.001$, $n = 461$) after accounting for DBH (DBH: partial $r^2 = 0.67$, $p < 0.0001$; DBH²: $r^2 = 0.17$, $p < 0.0001$; DBH³: $r^2 = 0.04$, $p < 0.0001$, $n = 461$). Understory height increased sigmoidally with increasing DBH. Given the same diameter, residual-tree density was negatively related to western-hemlock height ($p < 0.01$), but Douglas-fir height was not significantly related to residual trees ($p = 0.55$).

RD's ranged from 0.38–1.05, and 23 out of 28 stands had RD's above 0.55 (Table 1). Stands with the lowest understory densities had the greatest volumes. In turn, recent understory mortality (decay class 1; data not shown) was positively related to understory density; stands with the greatest understory density had the highest recent mortality.

4.2. Basal area and volume of the total understory

Basal area and volume of the understory (both \log_e -transformed) were inversely related to residual-tree density (\log_e -transformed, partial $r^2 = 0.60$, $p < 0.0001$, $n = 28$; partial $r^2 = 0.45$, $p < 0.0001$, $n = 28$, respectively). As the density of residual trees increased, basal area and volume decreased logarithmically, resulting in smaller rates of decrease with

Table 5
Predicted growth reductions (in %); baseline is zero residual and 500 understory trees/ha

	Residual trees/ha			Understory trees/ha	
	5	15	50	600	1000
Stand volume	19.2	30.2	40.5	4.6	20.9
Understory volume	23.0	35.6	47.1	4.2	19.3
Douglas-fir volume	13.0	34.3	75.3	4.7	21.5
Understory basal area	16.7	26.4	35.8	N.S. ^a	N.S. ^a
Douglas-fir basal area	10.3	27.8	66.2	N.S. ^a	N.S. ^a
Douglas-fir height	0.7	1.2	1.7	1.3	6.2
Western-hemlock height	3.5	5.8	8.2	1.7	8.2

^aNot significant.

each additional residual tree at higher residual-tree densities. Understory volume was also inversely related to the density of the understory (partial $r^2 = 0.18$, $p < 0.001$, $n = 28$), but understory basal area was not significantly related to density ($r = -0.026$, $p = 0.88$, $n = 28$). Understory basal area and volume were both positively related to the southern aspects (partial $r^2 = 0.06$, $p < 0.01$, $n = 28$; partial $r^2 = 0.07$, $p = 0.013$, $n = 28$, respectively) and age of the understory (partial $r^2 = 0.11$, $p < 0.01$, $n = 28$; partial $r^2 = 0.06$, $p = 0.015$, $n = 28$, respectively).

4.3. Basal area and volume of Douglas-fir and western-hemlock understory

Basal area and volume of Douglas fir (both \log_e -transformed) were inversely related to residual-tree density (partial $r^2 = 0.59$, $p < 0.0001$, $n = 27$; partial $r^2 = 0.59$, $p < 0.0001$, $n = 27$, respectively). Increased residual-tree density resulted in smaller rates of decrease with each additional residual tree. Similar to total understory volume and basal area, Douglas-fir volume was also inversely related to the density of the understory (partial $r^2 = 0.06$, $p < 0.01$, $n = 27$), but Douglas-fir basal area was not significantly related to density ($r = -0.32$, $p = 0.54$, $n = 27$). Both Douglas-fir basal area and volume were positively related to the southern aspects (partial $r^2 = 0.21$, $p < 0.01$, $n = 27$; partial $r^2 = 0.18$, $p = 0.017$, $n = 27$, respectively).

Basal area and volume of western hemlock (both \log_e -transformed) were not related to residual-tree density ($r = 0.35$, $p = 0.12$, $n = 21$; $r = 0.18$, $p = 0.44$, $n = 21$, respectively) or understory density ($r = 0.29$, $p = 0.20$, $n = 21$; $r = 0.16$, $p = 0.49$, $n = 21$, respectively). In contrast to the basal areas and volumes of the total understory and Douglas-fir understory, western-hemlock basal area and volume were negatively related to the southern aspects ($r = -0.63$, $p < 0.01$, $n = 21$; $r = -0.66$, $p < 0.01$, $n = 21$, respectively).

4.4. Volume growth of the entire stand since initiation of the understory

The volume growth of the entire stand since understory initiation (\log_e -transformed) was inversely related to residual-tree density (\log_e -trans-

formed, partial $r^2 = 0.34$, $p < 0.001$, $n = 28$) and understory density (\log_e -transformed, partial $r^2 = 0.22$, $p = 0.003$, $n = 28$). As the density of residual trees increased, stand volume decreased logarithmically, resulting in smaller rates of decrease with each additional residual tree at higher residual-tree densities. Stand volume was positively related to the southern aspects (partial $r^2 = 0.06$, $p = 0.04$, $n = 28$) and time since understory initiation (partial $r^2 = 0.09$, $p = 0.002$, $n = 28$).

5. Discussion

In explaining the observed results, it is important to understand the stand dynamics associated with the development of Douglas-fir forests. Briefly, the understory stands involved in this study have undergone a long process of stand differentiation. All stands had well-developed dominance classes with suppressed and dead trees. The RD of 23 out of 28 stands was over 0.55, greatly reflecting advancement to, or through the self-thinning (Drew and Flewelling, 1979) or stem exclusion (Oliver and Larson, 1990) phase. Owing to the nonuniform nature of the mortality process, some stands may be far below their maximum stocking because of recent mortality episodes. Other stands may be approaching their maximum stocking levels. Pairs of stands may be at different stages of development. All of these cycles make a strict interpretation of the results difficult.

Although the retrospective nature of this study does not allow conclusive statements about cause-and-effect, if we assume that the stands in this study were representative for Douglas-fir-dominated forests in the western-hemlock zone in the Willamette National Forest, we can suggest general relationships between residual trees and understory growth in future green-tree retention stands in the area.

5.1. Understory structural changes in stands with residual trees

The most striking change in understory structure related to residual trees was the reduction of both the density and basal area of dominant and codominant understory trees, particularly Douglas fir. The reduction in density of large understory trees may be due

to an influence zone around residual trees because Douglas fir cannot survive and growth of the more shade-tolerant western hemlock is reduced. Such effects are commonly observed in shelterwoods where both density and size of regeneration are reduced within the dripline of shelterwood leave-trees. This would explain why we did not detect height reductions of Douglas fir in stands with residual trees when compared to Douglas fir of the same DBH in stands without residual trees, but did detect height reductions in western hemlock. Douglas fir may have been sufficiently far away from residual trees to preclude influence from residuals. Since height does not reflect competition as well as DBH (Oliver and Larson, 1990), competition is reflected in the lower density of large understory trees in this study. Thus, residual trees may show a gradient of interaction with Douglas fir; whereas the more dominant Douglas fir tend to be more dispersed around residual trees, suppressed Douglas fir may be independently distributed from residual trees. Goslin (1997) found in a similar study in the Cascade Range that the distance of dispersion of Douglas fir relative to residual trees increased with larger size classes of Douglas fir. Dominant Douglas fir were dispersed from residual trees at intermediate distances (e.g., 9–16 m). The distribution of Douglas fir was not influenced by residual trees. Considering the spatial distribution of dominant Douglas fir and residual trees together, their distribution appeared to be regular. Since more dominant trees tend toward a regular spatial distribution (Moeur, 1993) and residual trees reduce the space available for understory trees to grow, it becomes apparent that understory growth reduction may be mainly the result of fewer dominant and codominant Douglas fir.

5.2. Predicted understory basal area and volume reductions in stands with residual trees

The patterns observed in this study suggest the following relationships between residual trees and understory basal area and volume: 1) understory basal area and volume are lower in stands with residual trees; 2) in stands with more than 15 residual trees/ha, basal area and volume are lower in pure Douglas-fir understories than in mixed Douglas-fir/western-hemlock understories; 3) residual

trees have the greatest influence per tree at the lowest residual-tree densities; 4) understory basal area and volume are highest at lowest absolute understory densities; and 5) basal area and volume of the understory are higher on the southern aspects than on the northern aspects.

Based on our regression models, we would expect reduced total understory and Douglas-fir basal areas and volumes in green-tree retention units compared to clearcuts or traditional shelterwoods. Increasing residual-tree density from zero to five residual trees/ha results in a predicted total understory basal area reduction of 17%, averaging 3.3% per residual tree; for 50 residual trees/ha, the predicted reduction is 36%, averaging 0.7% per residual tree. For 5 and 50 residual trees/ha, predicted understory volume reductions are 23% and 47%, averaging 4.6% and 0.9% per residual tree, respectively. Increasing residual-tree density to five residual trees/ha, predicted Douglas-fir basal area reductions are 10% or 2.1% per residual tree, and predicted volume reductions are 13% or 2.6% per residual tree, respectively. The basal area and volume of a pure Douglas-fir understory, however, decrease more rapidly than mixed understories with western hemlock when residual-tree densities exceed 15 residual trees/ha. The more rapid decline for pure Douglas fir may be because the more shade-tolerant western hemlock can compete more successfully with Douglas fir in the high shade of residual trees. At any given level of retention, a more significant hemlock stocking would be expected to further reduce the Douglas-fir understory growth, but western hemlock may also be able to compensate somewhat for expected Douglas-fir growth losses in green-tree retention stands.

The most obvious explanation for the reduction in understory basal area and volume relates to the fact that any site has an upper limit of stocking (in this case basal area). Each large residual tree represents stocking that is unavailable to the understory stand. The stocking that is taken up by residual trees is at the expense of dominant and codominant Douglas fir trees. Both the density and basal area of large understory trees, and consequently the basal area and volume of the total understory, are affected by residual trees.

Differences in understory volume among pairs not accounted for by the influence of residual trees

probably reflect differences in understory age, degree of differentiation and site quality. These differences were best expressed by different understory densities. Except for the oldest stands that were dominated by a dense understory of the shade-tolerant western hemlock, younger, less differentiated stands had the highest understory densities ($RD > 0.55$). In turn, these stands had the lowest understory volumes and the highest recent understory mortality, suggesting stands were undergoing self-thinning. Self-thinning is also reflected in the independence of understory density and understory basal area. Although stands with RD up to 0.25 maximize growth and size of individual trees, understory basal area can be reduced on an area basis (e.g., Long, 1985). Stands with $RD > 0.55$ undergo self-thinning (Drew and Flewelling, 1979) and show stagnating gross stand growth and reduced net stand growth (Long, 1985). Such stands will remain on the plateau (zone 3) of the Langsaeter (1941) curve (as cited in Long, 1985), where different understory densities can result in the same basal area.

The density of the understory and degree of differentiation at a given age further reflect the quality of the site. Low-site stands self-thin slower and differentiate slower than high-site stands. Thus, a combination of lower stocking limits on low sites, and higher understory densities with less differentiated trees of smaller diameters and heights on any site, may explain differences in understory volume among stands not accounted for by the influence of residual trees.

For example, if understory density was 600, rather than 500, trees/ha with all other stand conditions equal, we predict 4.2% and 4.7% less volume for the total understory and Douglas-fir understory, respectively. We believe that understory density management in green-tree retention units is important to prevent stands from self-thinning and therefore further reduced timber production.

Our predictions further suggest that the decrease per retained tree of growth in the understory would become smaller with increasing density of leave-trees. The diminishing effect of residual trees in our data set is within the previously reported limits of simulation studies. Differences in the magnitude of the predicted growth reductions between this study and simulation studies are likely due to assumptions

made in the simulation studies, particularly about differences in understory species composition, rotation ages, blow-down rates, growth rates and site productivity.

Birch and Johnson (1992) found a 5 to 38% decline in understory growth rates, depending on the number of trees left, their sizes and the future rotation age, and a total growth reduction between 8–25% when leave-trees were included in the yield calculation. The effect on understory and total stand growth decreased as the number of leave-trees increased and as the rotation increased. With five and 50 leave-trees/ha, average growth reduction was 1.6 and 0.75% per leave-tree, respectively.

For a mixed stand of grand fir (*Abies grandis* (Dougl.) Forbes) and western hemlock, Long and Roberts (1992) estimated that retention of five and 35 trees/acre (12 and 87 trees/ha) would result in a growth reduction in the understory between 26% and 56%, respectively, after an 80-yr rotation. The effect on understory growth decreased from 5.1% to 1.6% per leave-tree as the number of leave-trees increased. When growth and mortality of leave-trees were included in the yield calculation, Long and Roberts (1992) estimated a long-term growth reduction of 20%.

A possible explanation for the diminishing effect of additional residual trees is that as the density of residual trees increases, there is an increased likelihood of overlap among the influence areas by individual residual trees. Although we did not assess the spatial distribution of residual trees in this study, Goslin (1997) found irregular or clumped spacing in his natural, multistoried stands, which may also have been the case in the present study and may account for some of the observed diminishing effect of additional residual trees. Thus, the same ground area may be under the influence of more than one residual tree, reducing the overall effect of additional residual trees on the understory. Moreover, residual trees may compete with each other and limit one another's crown area. As Oliver and Larson (1990) reported, compared to trees in clumps, free-grown conifers do not prune their lower branches and therefore generally have denser crowns that cast more shade. Further studies are needed to investigate whether lower rates of growth loss per additional residual tree is related to clumped and aggregated spatial distribu-

tions of residual trees and the decrease of light penetration with increased residual-tree density.

Given the same densities of residual and understory trees in green-tree retention stands, we expect greater total understory and Douglas-fir basal areas and volumes on the southern aspects than on the northern aspects. For all understory and residual-tree densities, predicted total understory basal area and volume are 163% and 174%, respectively, and Douglas-fir basal area and volume are 237% and 210%, respectively, and greater on the southern aspects than on the northern aspects. Similar findings on the influence of aspects have been reported previously. Douglas fir is more common on south slopes in the northern part of its range (Williamson and Twombly, 1983). Stage (1976) and Youngberg and Ellington (1982) observed higher basal-area growth on southern aspects. Grier and Logan (1977) found higher biomass of old-growth Douglas fir on the southern aspects than on the northern aspects in the Cascade Range of Oregon.

On north slopes, Douglas fir may be outcompeted by the more shade-tolerant western hemlock. Comparing a north- and a south-facing old-growth, Goslin (1997) found that suppressed Douglas fir were able to survive on the southern aspects where western hemlock was absent. The stands on the northern aspects, however, were dominated by western hemlock and Douglas fir was almost entirely absent. Greater Douglas-fir volume on the southern aspects may be due to light availability. Assuming equal stand conditions, the amount of light received in the understory is highest on the southern aspects, which would favor Douglas fir, because light is one of the major growth constraints for Douglas fir (Minore, 1979). Less available soil moisture on south slopes would reduce competition from western hemlock, which is more limited by moisture stress than Douglas fir. Western hemlock die due to loss of hydraulic conductivity at higher water potentials than do Douglas fir (Brix, 1978). The stomata of western hemlock tend to close at 10 mb vapor pressure deficit (Marshall and Waring, 1984), whereas the stomata of Douglas fir close at 20 mb (Waring and Franklin, 1979). Consequently, we expect that retained trees may have less of a negative effect on Douglas fir at the southern aspects than on the northern aspects. It may thus be possible to retain

more residual trees on the southern aspects than on the northern aspects without the risk of losing Douglas fir from the understory.

5.3. Predicted stand volume reductions in stands with residual trees

Although most residual tree stands in this study had higher stand basal area and volume after including the residual trees's basal area and volume in the yield calculation, an overall effect of residuals on stand timber volume can only be shown after accounting for the growth of residual trees since understory initiation. Based on our regression models, increasing residual-tree density from zero to five residual trees/ha results in a predicted stand volume reduction of 19%, averaging 3.8% per residual tree: for 50 residual trees/ha the predicted value is 41%, averaging 0.8% per residual tree. Despite some uncertainty about the volume residual trees added to the stand since understory initiation 55 to 121 years ago, it appears that residual trees could not compensate for growth losses in the understory.

5.4. Management implications

Characteristics of retained trees in green-tree retention harvest units are likely to be somewhat different than the residual trees in this study. Residual trees in this study were large (DBH ranged from 71–167 cm), and generally slow-growing (e.g., radial growth of 1–3 mm/yr). Even when the growth of residual trees was included in the yield calculation, total stand volume was reduced compared to stands without residual trees. Residual trees older than 200 yr are, however, increasingly rare on the landscape and residual trees in green-tree retention stands are likely to be only one or two rotations older than the understory. Smaller residual trees will probably have less of an influence on the understory at the beginning of the understory initiation than was shown for residual trees in this study. Because residuals may be younger and smaller, they may also have higher growth rates than residuals in this study. Douglas fir has been shown to retain high growth potential for well over 100 yr without a significant loss in mean annual increment (e.g., Curtis and Marshall, 1993). Younger residual trees may thus be

able to compensate for growth losses in the understory to a greater extent than the residual trees in this study. The potential of younger residual trees to compensate for understory growth losses may be extremely important because of the preponderance of young residual trees and the extent to which green-tree retention is now being practiced in the Pacific Northwest. Whether or not younger and smaller residual trees may provide for additive growth or cause growth losses in green-tree retention stands may depend on the density, spatial distribution and growth potential of future residual trees. Better understanding of the effects of different spatial distributions (e.g., dispersed or aggregated) on the growth dynamics of residual trees and the understory is critical in considering the role of younger and smaller residual trees in the compensation for expected growth losses in the understory. Furthermore, very high understory densities in this study were associated with understory growth reductions. Understory density management in green-tree retention stands is thus recommended to reduce competitive pressure within the understory and prevent the understory from self-thinning.

6. Conclusions

With residual trees, understory timber volume was reduced and depended on the density of residual trees in unthinned stands. Total understory volume was reduced by both high understory and residual-tree densities. After accounting for residual-tree density effects, understory growth was also strongly affected by the density of the understory and adjusted aspect. The decrease in total understory and Douglas-fir basal areas and volumes per residual tree were largest at lower residual-tree densities. Above 15 residual trees/ha, however, Douglas-fir basal area and volume were reduced more than the total understory basal area and volume. Total understory and Douglas-fir basal areas and volumes were higher on the southern aspects than on the northern aspects. This is the first field study to investigate the potential consequences of different retention levels of residual trees on understory growth in the Pacific Northwest region. This study suggests that green-tree retention has important consequences for understory structure and timber production.

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