

DO REMNANT OLD-GROWTH TREES ACCELERATE RATES OF SUCCESSION IN MATURE DOUGLAS-FIR FORESTS?

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Abstract. Biological legacies left by natural disturbances provide ecological functions throughout forest stand development, but their influences on processes of ecological succession are not completely understood. We investigated the successional role of one type of biological legacy: remnant old-growth trees persisting in mature *Pseudotsuga menziesii* (Douglas-fir) forests in the U.S. Pacific Northwest. We tested the hypothesis that remnant old-growth *Tsuga heterophylla* (western hemlock) and *Thuja plicata* (western red cedar) trees enhance the reestablishment of shade-tolerant conifers by increasing the availability of seed. Reestablishment of shade-tolerant conifers is a key process in late-successional forest development because it leads to vertical differentiation of the canopy and eventual codominance of shade-tolerant species. Two study areas were selected in the southern Washington Cascade Range, USA. Both had an unfragmented, mature forest cover that was regenerated naturally following wildfire. Twelve study sites were selected, including sites with and without remnant *T. plicata* and *T. heterophylla*. Overstory structure and composition, microsite variables, and conifer regeneration were systematically sampled using nested belt transects and quadrats. Sites with remnant *T. heterophylla* and *T. plicata* had significantly higher densities of conspecific seedlings. Multivariate analyses showed remnant *T. heterophylla* and *T. plicata* presence and density to be the strongest predictors of seedling densities, although the basal area of mature conspecific trees, relative density, aspect, stand age, and microsite characteristics were important secondary predictors. Microsite variations explained regeneration patchiness. Seedling densities were strongly correlated with proximity to remnant trees, exhibiting a negative exponential decline with distance. Shade-tolerant conifers are likely to reestablish faster at sites with remnant seed trees, but canopy disturbances are probably necessary for subsequent height growth. Remnant shade-tolerant conifers are an important biological legacy and seed source influencing rates of ecological succession in mature *P. menziesii* stands. Successional and stand development models should explicitly incorporate this dynamic.

Key words: biological legacies; ecological succession; old-growth; forest trees; Pacific Northwest forests (USA); *Pseudotsuga menziesii*; regeneration; remnant trees; residual trees; seed source; stand development; *Thuja plicata*; *Tsuga heterophylla*.

INTRODUCTION

Biological legacies left by natural disturbances provide ecological functions throughout forest stand development (Franklin et al. 2002), but their influences on rates and pathways of ecological succession are not completely understood. Biological legacies have been defined as “the organisms, organic materials, and organically-generated patterns that persist through a disturbance and are incorporated into the recovering ecosystem” (Franklin et al. 2000:11). In this paper we examine the successional role of one type of biological legacy: remnant old-growth trees persisting in fire-originated, mature *Pseudotsuga menziesii* (Mirbel) Franco (Douglas-fir) forests in the southern Washington Cas-

cade Range, USA. Specifically, we explore the reproductive role of remnant shade-tolerant conifers, which we hypothesize influences rates of late-successional forest development.

Over 20 years of research in the U.S. Pacific Northwest have brought new appreciation for the array of ecological functions provided by biological legacies (Franklin et al. 2002). Much of this research relates to early successional dynamics (Franklin et al. 1985, Halpern 1989) or recovery from high-magnitude disturbances (Franklin 1990, Turner et al. 1998). More recently, researchers have focused on remnant live trees as a biological legacy influencing later stages of forest development. For instance, research has explored the effects of remnant trees on stand productivity (Acker et al. 1998, Zenner et al. 1998) and structural complexity in mature forests (Zenner 2000). However, the possible influence of remnant old-growth trees on understory reestablishment of shade-tolerant conifers (a key process of late-successional compositional and

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PLATE 1. (Top) A group of remnant old-growth trees (rough canopy, center of photo) embedded within a matrix of mature trees (smooth, homogeneous canopy) in the Bourbon Creek Roadless Area, part of our Trapper Creek study area, on the Gifford Pinchot National Forest, Washington, USA. (Bottom) Close-up of remnant old-growth trees shown in the top photo. Field assistant Dan Donato stands next to a remnant western hemlock (foreground), while Eric Tilkens (back left) stands in front of one of several remnant Douglas-firs. Photo credit: W. Keeton.

structural development) in *P. menziesii*-dominated stands has remained unexplored.

In the southern Washington Cascade Range, remnant living and dead trees are common in stands established after disturbances that resulted in partial or incomplete canopy mortality (Spies et al. 1988, Gray and Franklin 1997; see Plate 1). In a sere initially dominated by *P. menziesii*, and transitioning to late-successional co-dominance with *Tsuga heterophylla* (Raf.) Sarg. (western hemlock) and *Thuja plicata* Donn. (western red

cedar), these remnant trees represent a significant source of variation in structure between stands. Sere with and without large components of remnant living trees are possible, depending on disturbance magnitude and the age and structure of the stand at the time of disturbance (Franklin and Spies 1991). We hypothesize that remnant shade-tolerant conifers represent a particularly important source of variability in rates of successional development because they provide a seed source for late-successional species.

Mature *P. menziesii*-dominated stands (i.e., stands 80–200 years old) vary widely in the rate at which shade-tolerant conifers are established in the understorey (Spies and Franklin 1991). Some mature Douglas-fir stands have abundant seedlings, saplings, and poles of western hemlock and western red cedar by the time that they are 80–120 years old, while other stands have very little shade-tolerant representation after even 150–175 years of development. This variability in abundance and development of shade-tolerant tree species is important in controlling redevelopment of functional old-growth forests across a landscape. Mature *P. menziesii* stands differ from old-growth forests in being predominantly composed of a single cohort (or two, where remnant trees have survived), having a canopy that consists of a single layer (until shade-tolerant species become established), and having other structural and compositional differences (Franklin et al. 2002). Establishment of shade-tolerant conifers is an essential step in development of the multilayered and, eventually, vertically continuous canopy characteristic of old-growth coastal Douglas-fir forests (Franklin et al. 1981, 2002). As a result, establishment of shade-tolerant species can limit successional and habitat development in moist temperate *P. menziesii* forests.

In this paper, we hypothesize that remnant trees accelerate reestablishment rates of shade-tolerant conifers in mature, *P. menziesii*-dominated stands. This is probable for several reasons. First, seed availability strongly limits shade-tolerant conifer reestablishment in both coniferous and hardwood-dominated stands (Schrader 1998, Beach and Halpern 2001). Lack of seed sources may explain regeneration deficiencies noted in some areas (Edwards and Leadem 1987). Regeneration deficiencies are especially prevalent where widespread clear-cutting of late-successional/old-growth forests has reduced the relative abundance of shade-tolerant conifers at landscape scales (Schrader 1998). Remnant trees are likely to increase the availability of seed because they are typically well distributed throughout large, fire-originated stands (Keeton and Franklin 2004).

Second, remnant *T. heterophylla* and *T. plicata* are likely to be prolific cone producers because reproduction in these species increases with size, age, (Minore 1979, Burns and Honkala 1990), and access to light above the canopy (Owens and Molder 1984, 1985), reaching its peak in emergent trees, such as remnants (Schrader 1998). Remnants are thus likely to elevate regeneration levels above that associated with subdominant, mature *T. heterophylla* and *T. plicata* that sometimes comprise a minor component of *P. menziesii*-dominated stands.

Third, regeneration of *T. heterophylla* and *T. plicata* is limited by seed dispersal (Beach and Halpern 2001). Maximum effective dispersal distance for *T. heterophylla* under a closed canopy, in contrast to open conditions, is only ~160 m, but most seeds fall close to

the base of parent trees (Gashwiler 1969). *Thuja plicata* seed flight is the shortest of any northwestern conifer (Graham et al. 1987) and is <100 m under a closed canopy (Heatherington 1965). *Thuja plicata* regenerates vegetatively and asexual propagules can outnumber sexual propagules in some stands (Parker and Johnson 1987). But the resulting “vegtings” do not negate the need for seed sources, since they establish only immediately adjacent to existing trees. Their growth rates also tend to be very slow, according to research in vestigial *Thuja* stands in Idaho that are structurally and compositionally similar to *Tsuga*–*Thuja* forests in the Cascade Range (Parker 1979). Finally, remnant old-growth trees have greater seed release heights, which result in disproportionately longer dispersal distances compared to shorter, mature trees (Isaac 1930, Johnson et al. 1981).

METHODS

Study areas

We selected two study areas that are representative of mature, fire originated, naturally regenerated *Pseudotsuga menziesii*-dominated forests. They are located on the Gifford Pinchot National Forest in the southern Washington Cascade Range. The majority (~2000 ha) of the first, the Trapper Creek Wilderness Area, consists of a single stand that is ~135 years old. The second study area, the Siouxon Creek Roadless Area, is dominated by a cohort established following a 16 000-ha wildfire in 1902 (Gray and Franklin 1997). Continuous mature forest cover in the Siouxon Creek study area covers >7000 ha. Plant associations at low to mid elevations in the study areas are characteristic of the *T. heterophylla* zone described in Franklin and Dyrness (1988). Within this zone *P. menziesii* is the primary seral species, although *T. heterophylla* is codominant or dominant on some sites. *Thuja plicata*, while abundant within remnant old-growth stands at low to mid elevations (Keeton 2000), is a minor component of the mature cohorts.

Selection of study sites

We selected study sites at mid-slope positions with elevations <700 m above sea level and plant associations indicative of mesic sites with moderate to high productivity following Topik et al. (1986). We used additional site-matching criteria to ensure similarity in disturbance history, canopy closure, aspect (north and south), and remnant tree patch size. We identified 28 candidate sites with and without *T. heterophylla* and *T. plicata* >200 years old. Twelve study sites were randomly selected from this pool (Table 1). In our study areas shade-tolerant remnants occur predominately in concavities (Keeton and Franklin 2004). Consequently, all sites were centered on concavities, such as first order and ephemeral stream channels. Sites were classified as either “remnant sites” (sites with live shade-tolerant

TABLE 1. Descriptive information for study sites.

Study area	Site number	Stand age (yr)	Aspect	Remnant density (no. stems/ha) [†]		Basal area (m ² /ha)		
				<i>Tsuga</i>	<i>Thuja</i>	All species [‡]	Mature <i>Tsuga</i> [§]	Mature <i>Thuja</i> [§]
Trapper Creek	1	130	north	0	0	65.2	5.4	2.4
	2	130	north	5	2	63.9	6.9	1.9
	3	130	south	0	3	74.2	2.3	1.7
	4	130	south	3	1	68.5	2.0	1.4
	5	130	south	0	0	66.0	2.0	1.6
	6	130	south	2	2	57.9	3.6	1.5
	7	130	south	0	0	68.8	3.3	1.8
	8	130	south	0	6	69.4	3.0	1.6
Siouxon Creek	1	96	north	2	2	60.7	3.9	0.3
	2	96	north	0	0	63.0	4.7	0.1
	3	96	south	0	0	60.5	2.2	0.1
	4	96	south	3	2	61.8	2.6	0.1

[†] Density includes live trees >5 cm dbh. Density estimation is at the scale of individual sites. Within sites, remnant stems were clustered in close proximity (<40 m separation) to one another.

[‡] Includes all live trees >5 cm dbh.

[§] Includes all live trees >10 cm dbh.

remnants) or “non remnant” (sites with no live shade-tolerant remnants). All sites, including “non-remnant sites,” had live remnant *P. menziesii*. In total, there were seven remnant and five non-remnant sites for *T. plicata*; there were five remnant sites and seven non-remnant sites for *T. heterophylla*.

Data collection

We used a systematic sampling design with a randomized point of origin. At each study site we established four, 150-m-long (horizontal distance) belt transects separated by 150 m. The transects ran perpendicular to the center of each concavity. No canopy gaps were sampled.

Each transect consisted of several nested belts. Conifer regeneration (0.1–3 m tall and <5 cm dbh) was sampled within a 5-m-wide belt. Species, height, transect position, and substrate were recorded for individual seedlings. The litter layer around all *T. plicata* regeneration was excavated to expose buried stems and branches in order to determine the number of genets vs. the number of vegetative shorts/stems. Regeneration data for *T. plicata* represent the number of genets. All live trees >5 cm dbh were sampled within a 3.8-m-wide belt. Species, diameter at breast height, and transect position were recorded.

The spatial coordinates of all remnant *T. heterophylla*, *T. plicata*, and *P. menziesii* old-growth trees, both living and dead, were surveyed within a 50-m-wide belt. Remnant trees were defined as trees >200 years of age. Live *T. heterophylla* and *T. plicata* were cored at breast height (1.37 m) with an increment borer to confirm that age exceeded 200 years; precise aging was not necessary for this purpose. Remnant *P. menziesii* were easily distinguishable based on size and morphology. Cut stumps within the study areas indicated that these size classes belonged to locally com-

mon ~300-yr-old and ~500-yr-old age classes. Dead remnants were assigned a decay stage (1–9). Age and height were also determined for four dominant, mature *P. menziesii* on each transect ($n = 16/\text{site}$). Approximate ages were determined in the field from increment cores taken at breast height with correction for coring height. Only cores that included pith were examined. One increment core per site was returned to the laboratory and rings were counted using a microscope to provide an estimate of field error (mean of ± 3 yr, $n = 12$). We calculated *P. menziesii* site class₁₀₀ following McArdle et al. (1961).

Microsite characteristics were sampled within 1-m² plots. We estimated percent cover for shrubs, tall herbs, dominant ground cover, and substrate types (fine litter, coarse woody debris, and mineral soil). Litter depth (humus and O horizon) was measured at four points in each 1-m² plot. Canopy closure was measured using a spherical densiometer. Expected (or null) distributions were estimated from six plots placed at 25-m intervals along each transect. Observed frequency distributions were calculated from plots centered on randomly selected seedlings (<60 cm tall). This method facilitated statistical tests comparing microsite availabilities (expected distributions) within sites to the microsite characteristics at locations where seedlings actually occurred (observed distributions). Coarse woody debris (CWD; downed logs ≥ 15 cm diameter at intercept) volume was estimated using a line intercept method following Warren and Olsen (1964), as modified by Shivers and Borders (1996). Decay class (1–5) determinations followed Sollins (1982).

Data analysis

The data analysis consisted of three parts. Part 1 differentiates the study sites based on the presence or absence of remnant shade-tolerant conifers. Differen-

es in regeneration density are described by species and height class. Part 2 explores variability in regeneration densities within sites as a function of distance from remnant seed trees, alternate seed sources, hypothesized stream moisture gradients, and microsite characteristics. Part 3 then uses multivariate analysis to model the relative predictive strength across all sites of multiple independent variables. All statistical results were considered significant at the $\alpha = 0.05$ level.

Part 1. Regeneration differences between sites.—Regeneration data were grouped into three height classes, hereafter referred to as “short” (0.10–0.50 m tall), “medium” (0.51–1.0 m tall), and “tall” (1.1–3.0 m tall). We used these groupings because they positively correlate with age (Christy 1986, Daniels et al. 1995). We used cumulative height classes to analyze total regeneration both with (≤ 3 m cumulative height class) and without (≤ 1 m cumulative height class) small saplings assumed to include some suppressed mature trees. Two-sample *t* tests were used to test for differences in seedling abundances.

Part 2. Regeneration variability within sites.—We analyzed several spatial relationships to determine whether regeneration densities are correlated with distance from remnant seed trees and other factors within individual sites. Analyses of spatial relationships were restricted to the ≤ 1 -m height class. Regeneration in this height class had the highest probability of having established following a period of self thinning and thus was likely to include few suppressed mature trees. This determination was based on cross-sectional aging, observed morphology, and previous demographic research relating height to age for both species under similar stand conditions (Christy 1986, Daniels et al. 1995).

Spatial relationships were tested for each site individually and using mean values for remnant and non-remnant groups. Data for regeneration, mature basal area (trees > 10 cm dbh) by species, and downed coarse wood debris (CWD) volume were grouped into fifteen 0.005-ha plots per transect. Because of the sampling design, transect distances also represented distances from stream channels, and by proxy, potential soil moisture gradients associated with riparian influence. The Kolmogorov-Smirnov goodness-of-fit test for continuous data was used to test for departures from uniformity in distance-referenced distributions. Linear regression analysis was used to examine the spatial distribution of mature basal area by shade-tolerant species.

A weighted average distance was calculated for each seedling representing its average distance from all remnant seed trees on the same transect. Distance weighting was performed using $1/\text{distance}$ based on the assumption of a negative exponential seed rain pattern (Caspersen et al. 1999). The weighting results in closer remnant trees having a greater influence on average distance values. Distance-referenced regeneration data

needed to be normalized because the geometry of the sampling design sometimes resulted in unequal sampling of average distance values. To normalize the data an expected distance distribution was calculated for each transect. The expected distribution was derived from the weighted ($1/\text{distance}$) average distance from every point sampled to every remnant seed tree. Expected and observed regeneration distributions were converted to frequency distributions. We calculated a ratio of observed to expected frequency at each plot along transects and then converted these to normalized frequency distributions for individual transects. Normalized frequency distributions were averaged for each site and then pooled for remnant and non-remnant site groups.

Linear regression analysis was used to test for relationships between regeneration density and distance from remnant seed trees. Alternate transformations of the dependent variable (distance) were employed. Linear, logarithmic, polynomial, and negative exponential curves were fitted in this way. In all but one case, negative exponential curves had the best fit.

We performed additional analyses of microsite controls to determine whether these influenced regeneration patterns at within-site scales. Observed and expected distributions for shrub cover, canopy closure, and substrate associations (by species) were calculated from random and systematically collected data, respectively. Two-sample Kolmogorov-Smirnov (continuous data) or chi-square goodness-of-fit (discrete data) tests were used for statistical testing of observed vs. expected distributions. We used linear regression analysis to determine whether CWD abundance covaried with distance from streams and whether this might explain spatial trends in *T. heterophylla* regeneration. This species is known to establish most successfully on CWD (Harmon and Franklin 1989). We also used two-sample *t* tests to test for differences in CWD volume between remnant and non-remnant sites.

Part 3. Multivariate predictive modeling.—Descriptive statistics (means and sample variances) for overstory and microsite variables were generated for each site (Table 2). Each independent variable was regressed against the dependent variables (regeneration densities by species and height class). The number of independent variables was reduced to 11 (*T. heterophylla*) and 12 (*T. plicata*) by eliminating redundant variables (Table 2). Redundant variables with lower correlation coefficients were eliminated in this way. Regeneration processes related to distance from remnant trees and streams (explored in Part 2 of the analysis), as continuously varying spatial patterns within sites, could not be included; the models predict mean regeneration density at the site level (by assessing variability among, not within, sites). Normality was confirmed ($\alpha = 0.05$) for all dependent variables (regeneration densities) using the Wilk-Shapiro test. We used a two-part multivariate analysis to model regeneration density by height

TABLE 2. Description of independent and dependent variables. Variables in italics were not selected for multivariate analyses.

Independent variables		Dependent variables
Variable	Data type	
Stand age	continuous	Density (no. trees/ha) per regeneration class:†
Aspect (315°–45° N vs. 135°–225° S)	categorical, discrete	Short regeneration (10–50 cm tall)
Site class (1–5)	categorical, ordinal	Medium regeneration (51 cm to 1 m tall)
Conspecific remnant tree presence/absence	categorical, discrete	Tall regeneration (1.1–3.0 m tall)
Live conspecific remnant tree density (per ha)	continuous	Cumulative regeneration (≤ 1 m tall)
<i>Dead conspecific remnant tree density (per ha)</i>	continuous	Cumulative regeneration (≤ 3 m tall)
Live + dead <i>Thuja</i> remnant tree density (per ha)‡	continuous	
Live <i>Pseudotsuga</i> remnant tree density (per ha)	continuous	
Conspecific basal area (m ² /ha) of mature trees (>10 cm dbh)	continuous	
<i>Stem density: trees >5 cm dbh</i>	continuous	
Relative density (per ha): trees >5 cm dbh	continuous	
Canopy closure (%)	continuous	
Shrub percent cover	continuous	
Litter layer depth (cm)‡	continuous	
CWD volume (m ³ /ha): all decay classes§	continuous	
<i>CWD volume (m³/ha): decay classes 3 and 4</i>	continuous	
<i>Percent CWD cover</i>	continuous	

Note: CWD = coarse woody debris.

† Segregated by species.

‡ *Thuja* modeling only.

§ *Tsuga* modeling only.

class and species as a function of the independent variables (Table 2). The first part consisted of Classification and Regression Tree (CART) analysis, performed using S-Plus statistical software (Statistical Sciences 2000). Cost-complexity pruning was used to eliminate nonsignificant nodes.

For the second step we used multiple regression analysis. This provided a useful contrast with the CART analysis. Multiple regression analyses assess predictive strength and variability across all sites. This contrasts with CART where variance is partitioned hierarchically into smaller and smaller groups of sites. This results in secondary independent variables having predictive strength for only a subset of sites (or values of the dependent variable). Thus, the two methods are likely to select the same primary predictor variable (e.g., if the variable has high predictive strength across all sites), but may select different secondary variables due to the difference in how variance is examined (Breiman et al. 1984). For this reason we used multiple regressions primarily to validate the strongest predictor variables selected in CART. Wilk-Shapiro tests and Rankit plots were used to confirm assumptions of normality and independence. Multiple least squares regression analyses were run in S-Plus for each regeneration height class by species. Initial regression models included all independent variables identified in CART output for the corresponding species. We used a single term deletion, forwards and backwards stepwise modeling procedure. Dummy variables were used to model categorical data. Final regression models were produced with regression coefficients estimated using the maximum likelihood method.

RESULTS

Regeneration densities and demographics

Sites with remnant *Tsuga heterophylla* or *Thuja plicata* had significantly greater densities of conspecific seedlings ≤ 1 m tall than sites with no remnants (Figs. 1–2). *Tsuga heterophylla* seedlings were an order of magnitude greater at sites with remnants (mean ± 1 SD, 3313 ± 1367 /ha) than at sites without remnants (332 ± 193 /ha). *Thuja plicata* regeneration density was 6.5 times greater at sites with remnants (169 ± 60 /ha) than at sites with no remnants (27 ± 23 /ha). Variability in *T. plicata* seedling densities was 2.4 times greater among non-remnant sites. Densities of *T. heterophylla* regeneration were an order of magnitude or more greater than densities of *T. plicata* at all sites. Remnant *T. plicata* sites were strongly associated with higher densities of *T. plicata* regeneration in all three height classes. For *T. heterophylla*, however, remnant sites were not significantly correlated with the density of tall regeneration, although they were significantly correlated with short and medium height classes.

If there were positive correlations between regeneration densities in different height classes it would be an indication that seed source effects are not negated by density-dependent mortality. *Thuja plicata* regeneration densities were significantly correlated across all height class combinations ($P < 0.01$). For *T. plicata*, therefore, having a greater regeneration density within all shorter height classes conferred a high probability of having greater density within all taller height classes. For *T. heterophylla*, by contrast, there was a statistically significant correlation ($P = 0.004$) only between the medium and tall height classes; there was a positive

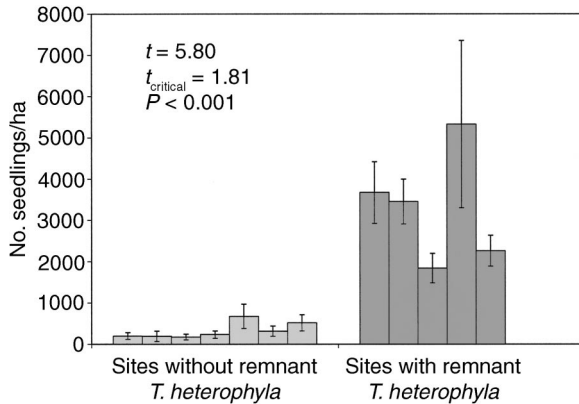


FIG. 1. Comparison of *Tsuga heterophylla* regeneration density (seedlings ≤ 1 m tall) between sites with and without remnant *T. heterophylla*. The critical value of t for the test is 1.81, given: (1) the significance level (95%, or $\alpha = 0.05$), (2) that the test is one-tailed, and (3) the degrees of freedom (or $n - 2$; in this case $12 - 2 = 10$). Bars represent means ± 1 SE.

though nonsignificant ($P = 0.106$) relationship between the short and medium height classes.

Proximity to remnant old-growth trees

Densities of regeneration ≤ 1 m tall were strongly associated with proximity to conspecific remnant old-growth trees within study sites. Regeneration densities exhibited a strong negative exponential relationship with increasing distance from remnant trees (Figs. 3, 4). For remnant sites collectively, negative exponential curves explained a high degree of variability in regeneration densities for *T. heterophylla* ($R^2 = 0.812$, $P < 0.001$) and *T. plicata* ($R^2 = 0.614$, $P < 0.001$).

Proximity relationships were more variable within individual sites, but showed similarly strong declines in regeneration density with distance. At the within-site scale, variability explained by negative exponential models ranged from 74% to 86% for *T. heterophylla* and from 38% to 81% for *T. plicata*. Negative exponential models were significant at all remnant sites ($P < 0.010$ for all sites except one *T. plicata* site, where $P < 0.050$). Negative exponential curves, rather than alternate transformations, resulted in the strongest statistical relationships.

Tsuga heterophylla regeneration (≤ 1 m tall) declined to minimal densities (< 160 seedlings/ha) at 100–110 m weighted average distance from remnant trees at all sites. *Thuja plicata* regeneration (≤ 1 m tall) also declined with distance to a minimum threshold at all sites, but the distance and density of the threshold was more variable. Minimal densities (ranging from 0 to 60 seedlings/ha) were reached at distances ranging from 90 m to 130 m, with a mean distance of 110 m. *Thuja plicata* regeneration patterns were significantly more variable than *T. heterophylla*. For both species abrupt discontinuities in density with distance from remnant trees

occurred on all transects and were clearly related to tightly clumped regeneration patches. Variability around regression curves for both species reflected this patchy spatial distribution.

Riparian influence

Remnant seed trees at the study sites were generally located within 40 m of streams. Consequently, before regeneration patterns within sites can be attributed to remnant trees it is necessary to determine whether regeneration patterns might also or more strongly reflect riparian influences. Correlations between regeneration densities and proximity to riparian areas varied widely between remnant and non-remnant sites. *Tsuga heterophylla* regeneration was correlated ($P < 0.001$) with proximity to riparian areas at all remnant sites, but only at two of seven non-remnant sites ($P < 0.020$ and $P < 0.050$). Statistically significant correlation coefficients were almost 50% weaker for individual non-remnant compared to remnant sites. Aggregating site data resulted in a negative exponential relationship with distance from riparian areas for *T. heterophylla* regeneration at remnant sites ($R^2 = 0.488$, $P < 0.001$), but this relationship was linear and much weaker at non-remnant sites ($R^2 = 0.149$, $P < 0.001$; Fig. 5).

Thuja plicata regeneration was significantly correlated with proximity to riparian areas (negative exponential curve) at four of seven remnant sites but was unrelated at all non-remnant sites. At three of the sites with significant relationships, the strength of the correlations was 18% lower, on average, than distance-from-remnant-tree correlations; it was 20% higher at one site. Aggregated site data for *T. plicata* were statistically correlated for remnant sites ($R^2 = 0.327$, $P < 0.001$), but not for non-remnant sites ($R^2 = 0.010$, $P = 0.388$; Fig. 6).

We conclude that regeneration densities decrease with distance from riparian areas within sites, but that this trend is generally weaker than the trend associated

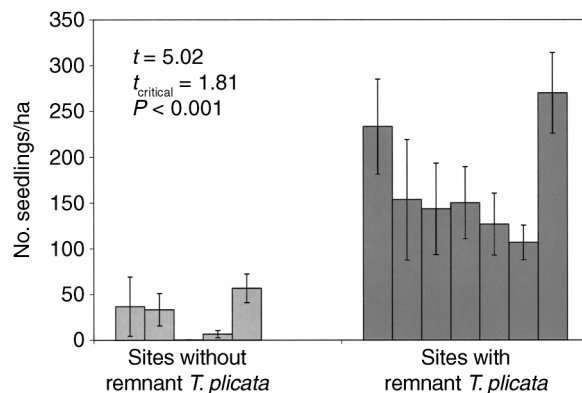


FIG. 2. Comparison of *Thuja plicata* regeneration density (seedlings ≤ 1 m tall) between sites with and without remnant *T. plicata* (see Fig. 1 legend for explanation of $t_{critical}$). Bars represent means ± 1 SE.

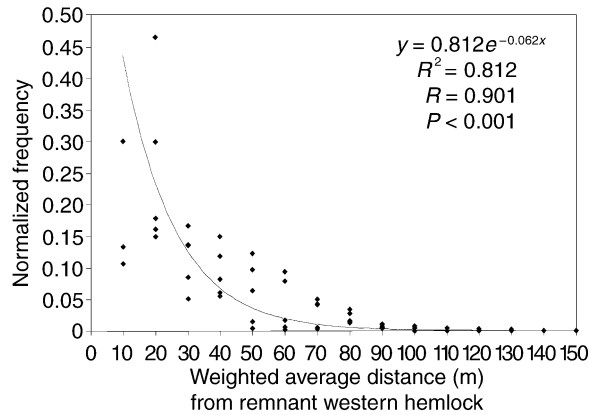


FIG. 3. Normalized frequency of *Tsuga heterophylla* regeneration (seedlings ≤ 1 m tall) vs. weighted average distance from remnant *T. heterophylla* for all remnant sites ($n = 5$).

with remnant trees. While riparian proximity correlations were significant for remnant sites, these correlations were 40% and 47% weaker, respectively, than correlations between *T. heterophylla* and *T. plicata* regeneration and proximity to remnant trees.

Mature tree spatial patterns

Relationships between regeneration abundance and proximity to remnant trees or riparian areas could not have been due to a covarying effect from mature seed trees within sites. No relationship was found between the distribution of mature *T. heterophylla* and *T. plicata* trees (>10 cm dbh) and distance from streams (i.e., distance along sampling transects; Fig. 7). This held for sites both with (*T. heterophylla*, $R^2 < 0.001$, $P = 0.960$; *T. plicata*, $R^2 = 0.014$, $P = 0.675$) and without (*T. heterophylla*, $R^2 = 0.077$, $P = 0.317$; *T. plicata*, $R^2 = 0.003$, $P = 0.849$) remnant trees. Additional evidence that mature trees were not clustered at one end or point along sample transects came from Kolmogorov-Smirnov goodness-of-fit tests, which showed that there were no statistically significant departures from spatially uniform distributions of mature *T. heterophylla* and *T. plicata* at any of the study sites (Fig. 7).

Microsite associations

Microsite factors did influence the spatial distribution of *T. heterophylla* and *T. plicata* seedlings within the study sites (Fig. 8). Both *T. heterophylla* ($D_{\max} = 0.15$, $P < 0.001$) and *T. plicata* ($D_{\max} = 0.15$, $P < 0.001$) were negatively associated with shrub cover at within-site scales. Substrate associations differed dramatically between *T. heterophylla* and *T. plicata*. After controlling for the relative availability of substrates at study sites, we found *T. heterophylla* seedlings to be closely associated ($\chi^2 = 108.53$, $P < 0.001$) with coarse woody debris (CWD), although 23% did occur on fine litter. Of *T. plicata* seedlings, 86% were found on fine

litter; the remainder were on CWD. However, after controlling for substrate availability, there was no statistically significant association ($\chi^2 = 0.186$, $P = 0.600$) with substrate type for *T. plicata*. Thus, variations in shrub cover, and CWD availability in the case of *T. heterophylla*, influenced regeneration patterns at scales smaller than transect distances. Neither *T. heterophylla* ($D_{\max} < 0.01$, $P = 0.960$) nor *T. plicata* ($D_{\max} < 0.001$, $P = 0.990$) seedlings (10–60 cm tall) were statistically related to the slight variations in canopy closure we found within individual mature forest sites based on the results of Kolmogorov-Smirnov goodness-of-fit tests. Gross differences in average canopy closure, which were more variable between sites, may influence differences in regeneration densities at larger scales.

Spatial distribution of coarse woody debris

An effort was made to determine whether *T. heterophylla* regeneration patterns attributed to remnant seed trees might reflect spatial covariance in CWD substrate availability within sites. Based on field observations, it was determined that *T. heterophylla* seedlings at the study sites occurred overwhelmingly on decay classes 3 and 4. Therefore, analysis of CWD spatial distributions was restricted to these classes.

Coarse woody debris (>15 cm diameter) was abundant at both remnant and non-remnant sites. There also was no significant difference in CWD volume between sites with remnant *T. heterophylla* and non-remnant sites (which did have remnant *Pseudotsuga menziesii*). This held true for all decay classes ($t = 0.590$, $P = 0.569$) and for just decay classes 3 and 4 ($t = 0.388$, $P = 0.707$). However, there was a weak, though significant, positive correlation ($R^2 = 0.095$, $P = 0.007$) between CWD availability and proximity to riparian areas at remnant sites, and a somewhat stronger correlation at non-remnant sites ($R^2 = 0.149$, $P < 0.001$). Concave, riparian influenced or moist landforms tend to accumulate coarse woody debris through down slope debris movement, higher rates of biomass production,

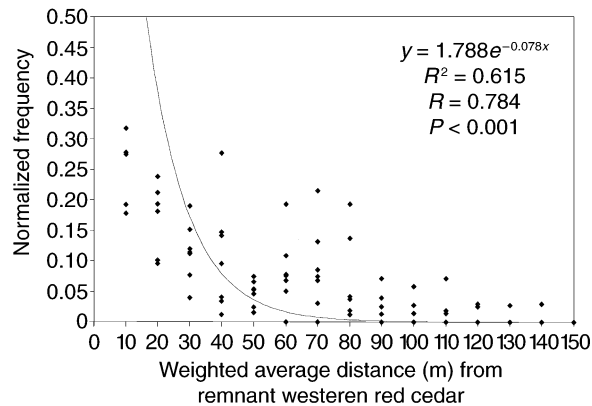


FIG. 4. Normalized frequency of *Thuja plicata* regeneration (seedlings ≤ 1 m tall) vs. weighted average distance from remnant *T. plicata* for all remnant sites ($n = 7$).

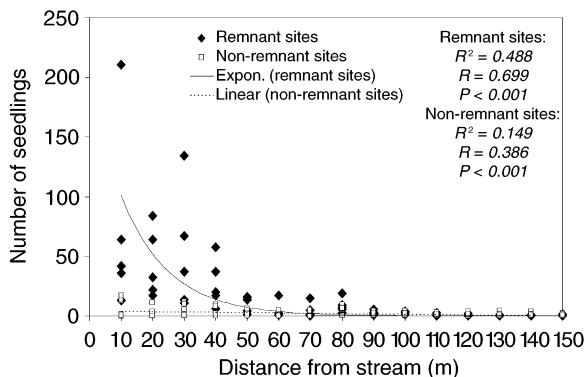


FIG. 5. Relationship between *Tsuga heterophylla* regeneration (seedlings ≤ 1 m tall) abundance and distance from streams for remnant vs. non-remnant sites.

and slower rates of decay (Spies et al. 1988). However, because the correlation coefficients are very low, at our sites they may or may not represent an actual mechanistic relationship; statistical significance, in this case, may be an artifact of a relatively large number of data points ($n = 12$ for each of 15 distance classes; total data points = 180). The correlation coefficient for CWD availability at remnant sites is almost an order of magnitude lower than that found between *T. heterophylla* regeneration and proximity to remnant seed trees. Thus the slight decrease in CWD availability with distance along sample transects is insufficient to explain the observed regeneration trends.

Predictive modeling using multiple variables

Remnant tree presence or density were the strongest predictors of conspecific regeneration differences among sites based on Classification and Regression Tree (CART) results (Fig. 9). A density of three or more trees per ha was the strongest partitioning point for variance in medium and tall *T. heterophylla* regeneration. Remnant *T. heterophylla* presence alone was the strongest partitioning point for variance in both the short and cumulative height classes. Remnant *T. plicata* presence was the strongest predictor of regeneration abundance in the medium and ≤ 3 m height classes. Density of remnant *T. plicata* was the strongest predictor of regeneration abundance in the tall and ≤ 1 m height classes. The combined density of live and dead remnant *T. plicata* was the strongest predictor of short regeneration abundance, suggesting that a portion of the dead *T. plicata* may have died relatively recently. That 45% of remnant *T. plicata* snags were decay stages 3 or 4 (recently deceased) supports this conclusion. Remnant presence and combined (live and dead) density also explained secondary deviance partitions in the short and medium classes, respectively.

Classification and Regression Tree (CART) analyses identified several secondary predictors that contributed to regeneration differences among sites (Fig. 9). How-

ever, due to the limited sample size ($n = 12$) these had lower statistical rigor compared to primary predictors. Secondary predictors of *T. heterophylla* regeneration included aspect, relative density, canopy closure, and coarse woody debris volume. The importance of mature conspecific basal area differed between height classes. For tall regeneration, mature *T. heterophylla* basal area was the strongest secondary variable explaining variation between sites falling below a minimum density of remnant *T. heterophylla*. For regeneration ≤ 3 m tall, a threshold for mature *T. heterophylla* basal area explained the most variation in regeneration between remnant sites. Sites with remnant *T. heterophylla* and a mature *T. heterophylla* basal area above $3.06 \text{ m}^2/\text{ha}$ had the greatest density of total conspecific regeneration ≤ 3 m tall. Highest abundances of *T. heterophylla* regeneration ≤ 1 m tall occurred on south-facing remnant sites.

Secondary variables selected in classification trees for *T. plicata* included mature conspecific basal area, litter layer depth, stand age, relative density, shrub cover, and density of live remnant *P. menziesii*. For short regeneration and both cumulative height classes, there was strong interaction between either remnant tree presence or density and mature *T. plicata* basal area. Highest regeneration abundances occurred on sites with remnant trees, or falling above a remnant density threshold, and having a basal area of mature *T. plicata* above $1.66 \text{ m}^2/\text{ha}$.

Final multiple regression models for most of the response variables were consistent with CART results; they included either remnant presence or remnant tree density as the strongest predictors of regeneration abundance. The only exception was tall *T. plicata* regeneration, for which the multiple regression results did not validate the CART results. For this height class relative density, shrub cover, stand age, and mature *T. plicata* basal area were slightly stronger predictors than remnant *T. plicata* density; all of these variables were strongly significant ($P < 0.001$). Remnant *T. hetero-*

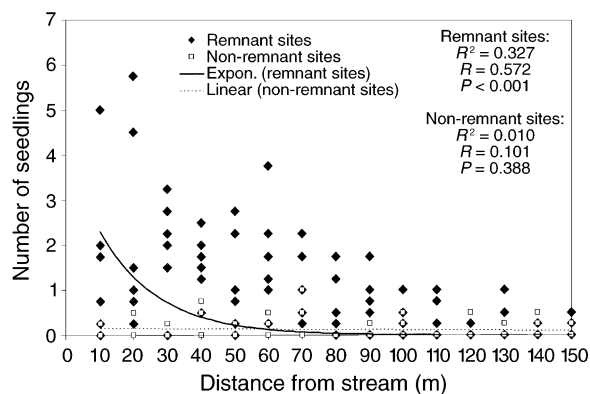


FIG. 6. Relationship between *Thuja plicata* regeneration (seedlings ≤ 1 m tall) abundance and distance from streams for remnant vs. non-remnant sites.

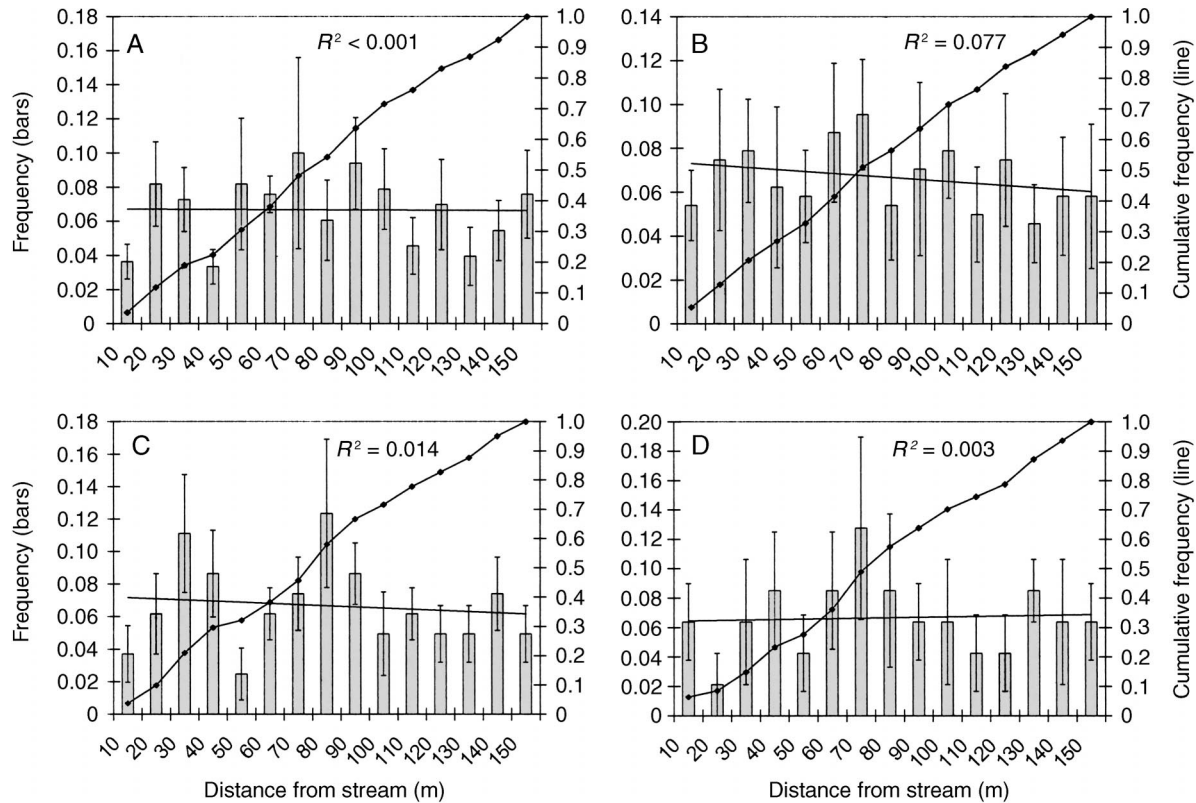


FIG. 7. Spatial distributions of mature trees (>10 cm dbh) with distance from stream: (A) mature *Tsuga heterophylla* at remnant sites, $n = 5$; (B) mature *T. heterophylla* at non-remnant sites, $n = 7$; (C) mature *Thuja plicata* at remnant sites, $n = 7$; and (D) mature *T. plicata* at non-remnant sites (bottom right), $n = 5$. R^2 values pertain to linear trend lines. Cumulative frequency distributions showed no statistically significant departure from uniformity. Bars represent means \pm 1 SE.

phylla density was the only final predictor variable for regeneration in the medium height class.

The multiple regression models resulted in a reduced set or different combination of secondary independent variables depending on species and height class. This was expected due to the differences between multiple regression analysis and CART in terms of how variance among sites is assessed, as explained previously. Thus the primary conclusion from multiple regression modeling is that, for all but one case of the dependent variable, the CART-selected primary predictors are validated.

The ecological relevance of the general set of secondary variables selected by CART was also supported by the multiple regression models. That, in some cases, these were selected in different combinations or reduced sets is again related to differences between the tests. In the regression models, mature conspecific basal area was significantly predictive in most cases of the dependent variable, including all cumulative height classes for both species. Other secondary variables in predictive models included aspect for short *T. heterophylla* regeneration and both cumulative height classes and relative density for tall regeneration, although it was not statistically significant ($P = 0.089$). Re-

gression models for *T. plicata* regeneration included stand age, litter depth, and/or shrub cover for two of the discrete height classes, but not for the cumulative height classes.

The regression models achieved high statistical significance ($P < 0.01$) and predictive power with >80–90% of the variability in regeneration abundance between sites accounted for in most cases. There were two exceptions. Only 50% of the variability was accounted for in the model for *T. heterophylla* regeneration in the medium height class, which included remnant *T. heterophylla* density as the only predictor variable. Only 59% of the variability was explained by the model for tall *T. heterophylla* regeneration, and this model was not statistically significant ($P = 0.055$), albeit by a slim margin.

DISCUSSION

Remnant old-growth trees as seed sources

Remnant old-growth trees accelerate rates of shade-tolerant conifer reestablishment in mature *Pseudotsuga menziesii*-dominated stands in the southern Washington Cascade Range. This conclusion is supported by three lines of evidence. First, sites with remnant shade-tol-

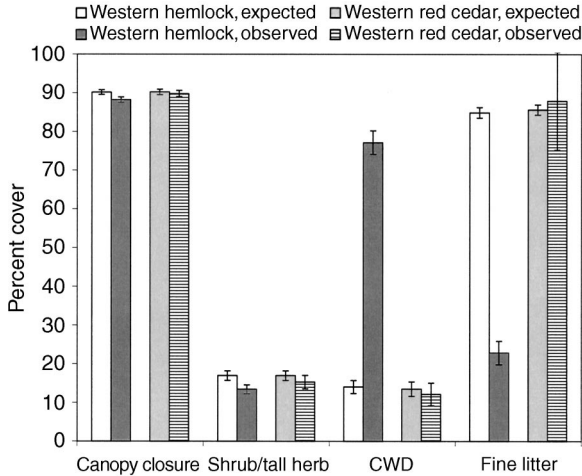


FIG. 8. Microsite associations for western hemlock (*Tsuga heterophylla*) and western red cedar (*Thuja plicata*) seedlings (10–60 cm tall). CWD = coarse woody debris. Bars represent means \pm 1 SE.

erant trees had significantly higher densities of seedlings than sites lacking remnants. Second, the presence and/or density of remnant *Tsuga heterophylla* or *Thuja plicata* were the strongest predictors, relative to other stand structure and microsite variables, of regeneration differences between sites. The third reason pertains to the distinct clustering of regeneration around remnant seed trees. In the absence of canopy openings, seedling densities declined with distance from remnant shade-tolerant conifers, reaching background levels at distances between 90 m and 130 m. These distances are similar to the maximum within-closed-canopy dispersal distances reported for these species (Heatherington

1965, Gashwiler 1969, Mair 1973). Seedling densities followed a negative exponential density curve typical of wind-dispersed seed rain. This strong correlation, though not a direct measure of seed fall or paternity, does support an inference that seedling densities reflected remnant tree seed rain patterns and dispersal limitations.

The conclusion that seed source (i.e., seed producing trees), in general, can be a major limiting factor for shade-tolerant conifers in mature *P. menziesii*-dominated stands is supported by our results. *Tsuga heterophylla* and *T. plicata* establishment patterns clearly reflect dispersal limitations within a closed canopy, such that sites even a relatively short (e.g., >130 m) distance from seed trees may have significantly lower or minimal seedling densities. Consequently, it is probable that seedling densities have a high degree of spatial variability within mature stands as a function of the spatial distribution and heterogeneity of seed sources.

Secondary controlling factors

Remnant old-growth seed sources have an overriding effect on shade-tolerant conifer regeneration patterns in the understory despite finer scale variability associated with microsite heterogeneity. This conclusion is consistent with previous research on seed source effects in the Pacific Northwest, for instance in hardwood-dominated forests (Beach and Halpern 2001), and our understanding of the many factors that control variability in shade-tolerant conifer reestablishment (Christy and Mack 1984, Harmon and Franklin 1989, Adams and Mahoney 1991, Gray and Spies 1997). The stand structure and microsite factors identified as predictor variables in our models either influence directly (e.g.,

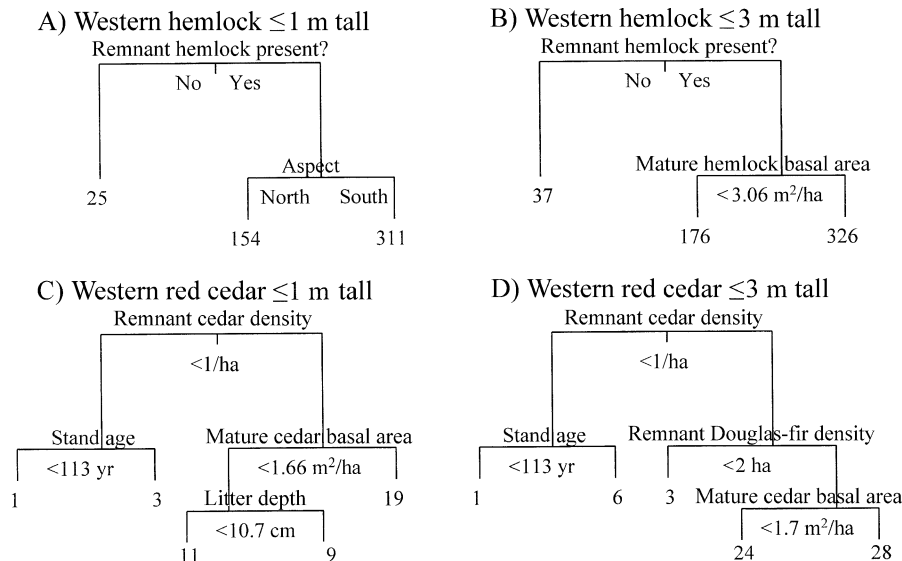


FIG. 9. Classification and regression trees, showing independent variables selected, split values, and partitioned mean values of the dependent variable, for cumulative height classes of western hemlock (*Tsuga heterophylla*) and western red cedar (*Thuja plicata*) regeneration. Minimum observations required for each split = 2; minimum deviance = 0.01; $n = 12$.

relative density) or correlate with (e.g., stand age) important limiting factors, such as light, substrate availability, and competition with shrubs. However, our results suggest that microsite controls are secondary to seed availability and operate at spatial scales smaller than *T. heterophylla* and *T. plicata* seed dispersal distances. Gap dynamics, through effects on microsite controls, also interact with rates of regeneration establishment, survival, and release (Stewart 1986a, Spies and Franklin 1989, Gray and Spies 1996). As stated previously, our research excluded areas with gaps in an effort to control for this source of variability.

There were two unexpected results. First, higher densities of *T. heterophylla* seedlings densities in the short and ≤ 1 m height classes occurred on south-facing aspects. This was surprising because north-facing aspects are less prone to moisture stress. The association with south-facing aspects may reflect riparian influences at the study sites. Riparian effects were operative at the sites on both north and south aspects. It is possible, however, that on south aspects they may reduce summer moisture stress sufficiently to allow seedlings to take advantage of greater light availability and a longer growing season. The second unexpected finding was an apparent positive association between *T. plicata* regeneration ≤ 3 m tall and the density of remnant old-growth *P. menziesii*. The mechanism linking these variables is unclear. The density of remnant *P. menziesii* can be negatively correlated with stem density (Acker et al. 1998), and can be positively correlated with tree diameter variation (Zenner 2000). Consequently, remnant *P. menziesii* may positively influence aspects of stand structure, such as light availability, that, in turn, affect *T. plicata* regeneration under a closed canopy.

We conclude that while remnant old-growth trees have a seminal influence on regeneration processes, secondary microsite and stand structure variables explain the spatial variability or "patchiness" in regeneration patterns emanating away from remnant trees. Safe sites for *T. heterophylla* and *T. plicata* seedlings are determined by shrub cover, light availability, substrate (in the case of *T. heterophylla*), soil nutrients, and soil moisture. However, these factors operate at finer spatial scales than seed rain, excepting possibly soil moisture, and may have little effect on seedling densities in the absence of seed sources. *Tsuga heterophylla* and *T. plicata* seeds do not persist in a seed bank (Archibold 1989). For regeneration to occur, seeds must be wind borne to the site. Consequently, seed must arrive first in order for other factors to influence seedling establishment and survival.

Mature seed trees

The inferred remnant tree seed rain pattern cannot be attributed to spatial covariation with mature potential seed trees. Mature trees were distributed uniformly along transects and thus were not spatially correlated with, or clustered around, conspecific remnant trees at

the scales investigated. This result can be attributed to greater seed dispersal distances (e.g., *T. heterophylla* > 600 m) in open canopy conditions compared to under a closed canopy (e.g., *T. heterophylla* < 160 m; Keeton 2000). Mature *T. heterophylla* may have originated from seed sources nearby (e.g., remnant trees) and farther away (e.g., at the periphery of the stand-initiating burn area). *Thuja plicata* disperses farther (> 120 m) in an open canopy compared to a closed canopy (< 100 m), but is far more limited in this regard because it has a heavy seed (Keeton 2000). Nevertheless, mature *Thuja* originating from remnant tree seed sources, and established at stand initiation, are unlikely to cluster at the scale investigated in this study.

The basal area of mature conspecific trees was identified as a secondary variable in multivariate models for both cumulative height classes of *T. heterophylla* and all height classes of *T. plicata*. Thus, we can infer that mature shade-tolerant conifers also act as seed sources and influence regeneration densities. This conclusion is consistent with the results of previous studies (Ruth and Harris 1979, Schrader 1998). However, the inference that remnant old-growth trees are more prolific seed sources is supported by the strong correlation between regeneration densities and proximity to remnant trees. Our results also suggest an interaction between remnant and mature tree seed sources. Regeneration densities were highest on sites that had both remnant seeds trees and a greater proportion of shade-tolerant conifers in the mature cohort.

There may be "diminishing returns" in terms of increasing *T. heterophylla* regeneration with increasing density of mature and remnant *T. heterophylla*. Stewart (1989) found a logarithmic decline in *T. heterophylla* seedling abundance with increasing density of dominant *T. heterophylla* in old-growth stands, which he attributed to the measurably lower light levels beneath the dense crowns typical of *T. heterophylla*. Canopy gaps become increasingly important for the establishment and release of regeneration under these conditions (Stewart 1986a, b). However, Stewart's (1989) regression model predicts that regeneration densities will not decline until *T. heterophylla* crowns occupy $> 30\%$ of the canopy. These relatively high densities of codominant *T. heterophylla* contrast with the sites we investigated, where mature *T. heterophylla* comprised only 5% of total basal area, on average. It remains probable, therefore, that regeneration levels increase with increasing densities of remnant and mature seed trees as long as the latter do not reduce light availability to the point where seedling establishment and growth is inhibited.

Riparian influence

A logical criticism of attributing the observed regeneration patterns to seed rain is that these patterns might also reflect riparian effects. Seedlings of both *T. heterophylla* and *T. plicata* are sensitive to soil mois-

ture stress because they have short root systems (Minore 1979, Krasowski and Owens 1991); soil moisture and relative humidity gradually decline with distance from riparian areas in Pacific Northwest forests (Gregory et al. 1991, Chen et al. 1999). Set against these favorable environmental conditions are greater competition with herbaceous vegetation and higher potential for litter burial due to the abundance of hardwood trees and broadleaved shrubs. However, a relationship between seedling densities and proximity to streams is probable. This relationship may covary with density trends projecting away from remnant trees clustered near streams and moist concavities.

There may be an interaction between seed rain and riparian influence. Seedling densities were significantly correlated with distance from streams, although this relationship was evident primarily at sites with remnant seed trees and was not consistent among remnant *T. plicata* sites. Our results suggest that seedling densities are highest where there are both favorable soil moisture conditions and the greatest availability of seed. Where seed availability is significantly lower, the pulse of increased regeneration near streams may be substantially less or, as at all but two of the non-remnant sites, may not occur. Distance-from-remnant tree correlations were almost twice as strong as distance-from-stream correlations. Thus, while seedling densities are more strongly associated with proximity to remnant trees, the strength of these correlations may partially reflect a confounding riparian influence. However, it remains likely that density decay rates were accurately estimated because the majority of remnant seed trees were located 20–40 m upslope on most sampling transects. Seedling densities peaked near these locations rather than near streams and declined to minimal levels at distances from remnant trees that are close to reported dispersal distances.

Do remnant trees increase rates of vertical development?

Given the strong positive relationship between remnant seed trees and the density of shade-tolerant conifer seedlings <1 m tall, an important question is whether this effect translates into accelerated rates of vertical development (i.e., vertical movement of shade-tolerant regeneration into the lower canopy). Alternatively, does density-dependent mortality negate such effects?

It is not possible to make a definitive statement about vertical development based on our results. While seedling densities were correlated either in full (*T. plicata*) or in part (*T. heterophylla*) among height classes, densities declined precipitously for both species with height increase from ≤ 1 m to 1.1–3.0 m. Thus density-dependent mortality was operative even with enhanced net survivorship at remnant sites. Intraspecific competition and mortality will prevent or inhibit accelerated vertical development to at least some degree. We should not conclude, however, that rates of develop-

ment are unaffected by remnant seed trees. Rather, it signals the importance of canopy disturbances in late-successional developmental processes. Canopy openings or gaps caused by fine-scale natural disturbances increase light availability and free up rooting space and other belowground resources (Stewart 1986a, Gray and Spies 1996). These effects promote seedling establishment in gaps and release advanced regeneration (Stewart 1989, Moeur 1997, Van Pelt and Franklin 1999).

Gap formation, therefore, is an important means by which regeneration is released and allowed to develop vertically. Therefore, by increasing rates of reestablishment of shade-tolerant conifers, remnant trees are increasing the potential for vertical development through release, but canopy disturbances help translate this effect into accelerated development of multilayered canopies. We found background regeneration densities, in the absence of remnant trees, to be very low on average (*Tsuga*, <200/ha; *Thuja*, <60/ha), suggesting a limited capacity to exploit new gaps. The elevated densities found at remnant sites, conversely, would increase (a) the proximity of regeneration to new gaps, and (b) the ability of shade-tolerant conifers to compete with herbaceous vegetation, which is a critical limiting factor in gap dynamics (Gray and Spies 1997). Regeneration can respond to low angle sunlight from openings in the forest canopy that are offset spatially (Van Pelt and Franklin 2000), such that regeneration need not be located directly below a gap to experience release effects. Furthermore, even where advanced regeneration is limited, remnant trees may increase the potential for gaps to seed in rapidly.

Ongoing research using data from permanent sample plots in the Pacific Northwest is finding very low levels of mortality over many years within sapling/pole-sized western hemlock cohorts in the mature Douglas-fir stands; vigor of the advanced shade-tolerant regeneration is high. Thus some degree of vertical development can occur due to high canopy self thinning alone (Franklin et al. 2002), even in the absence of gap formation. Increased densities of vigorous advanced regeneration is likely to both accelerate this process and provide the capacity for gap exploitation.

Seed rain related spatial patterns in stand development

An interesting question is whether spatially clustered conifer reestablishment might affect patterns of late-successional forest development across larger areas. This question has been addressed in other forest ecosystems via simulation modeling. For instance, SORTIE (Pacala et al. 1996) simulations of mixed northern hardwood/coniferous forest dynamics in New England, where modeled tree dispersal distances are shorter than in the Pacific Northwest, result in significant clustering and species segregation at scales of 25 m after 500 years of succession (Caspersen et al. 1999). Density trends from the regression models in Figs. 3 and 4

would result in similar clustering of *T. heterophylla* and *T. plicata* around remnant trees in mature stands, although the scale of the clustering would be larger.

Spatial patterns related to seed rain may diminish over time as the shade-tolerant species become dominant in the canopy and increase seed production; patches with codominant shade-tolerant species would expand outward and gradually coalesce, because *P. menziesii* would not be regenerating. Areas of higher seedling densities around remnant trees would form nuclei from which understory reestablishment of shade-tolerant conifers initiates and expands most rapidly. Remnant seed trees are likely, therefore, to have a strong effect on the spatial dynamics of succession in mature *P. menziesii* forests. Gap occurrence will become increasingly important (i.e., in old-growth forests) to structural development and compositional dynamics as shade-tolerant regeneration becomes more ubiquitous, such that light availability, rather than reproduction or seed dispersal, becomes the primary factor limiting the demography of shade-tolerant conifers.

Applications to stand development models

Widely used conceptual models of stand development based on studies of successional development in secondary forests (i.e., developed from logged over areas and/or abandoned farm land) in the eastern United States (Bormann and Likens 1979, Peet and Christensen 1980) or plantation forestry (Oliver and Larson 1996) typically do not include biological legacies, such as live remnant trees, as structural elements or as sources of variation in rates and pathways of development. By contrast, much ecological research in the U.S. Pacific Northwest has focused on stand dynamics in primary forest systems where biological legacies are common. As a consequence, successional ecology in that region often stresses the structural, compositional, and functional influences of biological legacies on stand development (Hansen et al. 1991, Spies 1997, Franklin et al. 2002). Researchers working in other forest systems, including old-growth forests in the eastern United States, the U.S. Rocky Mountain region, and Australia also have found biological legacies to be common features of natural disturbance-originated stands (Lindenmayer and Franklin 1997, Foster et al. 1998, Turner et al. 1998).

The strong influence of remnant old-growth trees on understory reestablishment of shade-tolerant conifers represents an important successional role played by biological legacies. This study adds to a growing body of research (Hansen et al. 1995, Acker et al. 1998, Zenner 2000) on the role of biological legacies in late-successional processes. However, our results are among the first to show that legacies can directly accelerate rates of late-successional forest development. Thus, successional and stand development models should include, where appropriate, large remnant structures as sources of ecological variability throughout stand de-

velopment, not just at stand initiation and during early succession.

In coastal Douglas-fir forest of the Pacific Northwest, shade-tolerant conifer reestablishment strongly limits rates of late-successional structural and compositional development in mature stands (Franklin et al. 2002). Factors that influence reestablishment rates are thus central to our understanding of old-growth forest ecosystem recovery from both anthropogenic and natural disturbances. Remnant old-growth trees have a previously unrecognized and important role in this regard. Spatial and temporal reestablishment dynamics appear to be influenced by interactions among multiple factors, including remnant trees, mature seed trees, riparian influences, gaps and canopy architecture, and microsite controls. If stand development models are to incorporate biological legacies and multiple rates and pathways of succession, it will be necessary to account for these interacting sources of variability.

CONCLUSION

Remnant old-growth seed trees increase rates of understory reestablishment of shade-tolerant conifers in mature *Pseudotsuga menziesii*-dominated stands in the southwestern Washington Cascades. Sites with remnant *Tsuga heterophylla* and *Thuja plicata* are likely to have higher densities of conspecific seedlings. Seedling densities decline exponentially with distance from remnant conspecific trees, reaching background levels at maximum effective within-stand dispersal distance. Stand density, riparian influences, and mature seed trees also affect regeneration densities, while microsite factors control densities and patterns at a fine scale. Remnant shade-tolerant conifers, however, represent a source of spatial variability in rates of seedling establishment that is detectable and stronger than these sources of variability. Despite accelerated reestablishment rates, substantially increased rates of vertical compositional and structural development are unlikely to occur in the absence of canopy mortality and disturbances. Remnant shade-tolerant conifers have an important seed source influence on the development of late-successional characteristics in mature stands that should be explicitly addressed by stand development models.

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