Controls on conifer regeneration in managed riparian forests: effects of seed source, substrate, and vegetation

Eric W. Beach and Charles B. Halpern

Abstract: Red alder (*Alnus rubra* Bong.) commonly dominates the overstory in managed riparian forests of the Pacific Northwest. Although it is assumed that competition with a dense shrub layer inhibits succession from hardwoods to shade-tolerant conifers within these forests, this assumption has not been explicitly tested. We hypothesized that seed availability rather than competitive interactions largely shape patterns of conifer regeneration in managed riparian forests. At nine locations in western Washington, we established paired transects in riparian sites adjacent to abundant versus few or no sources of seed to examine the importance for conifer regeneration of dispersal limitation, rooting substrate, and vegetation cover. Frequency and density of regeneration were significantly greater in transects within 100 m of remnant forest patches than in paired sites at greater distances (mean frequencies of 59 vs. 18% and densities of 0.23 vs. 0.16 trees/m^2, respectively). Where seed sources were present, regeneration was positively associated with coarse woody debris and negatively associated with fine litter. Regeneration was most abundant in plots with <10% herb or shrub cover; however, for most species, recruitment occurred across the full range of understory plant cover. We detected no relationship between regeneration density and overstory conifer or hardwood cover. Our results suggest that, in managed forests, conifer regeneration is largely limited by seed availability and only secondarily by competitive interactions or substrate conditions. In managed landscapes, conventional strategies of vegetation control are not likely to be as effective in increasing conifer regeneration in riparian forests as managing for seed sources through green-tree retention.

Résumé : L’aulne rouge (*Alnus rubra* Bong.) domine généralement l’étage dominant dans les forêts ripariennes aménagées du nord-ouest de la région du Pacifique. Même si on assume que la compétition due à un étage dense d’arbustes empêche les conifères ombrophiles de succéder aux feuillus, cette hypothèse n’a pas été explicitement vérifiée. Nous émettons l’hypothèse selon laquelle la régénération des conifères dans les forêts ripariennes aménagées serait surtout influencée par la disponibilité des graines plutôt que par la compétition. À neuf endroits dans l’ouest de l’état de Washington, nous avons établi des transects appariés sur des sites ripariens adjacents où les sources de graines étaient soit abondantes, soit limitées ou inexistantes. Le but de cette étude consistait à vérifier l’importance des contraintes de dispersion, du substrat d’enracinement et du couvert végétal pour la régénération des conifères. La fréquence et la densité de la régénération sont significativement plus élevées dans les transects situés à moins de 100 m d’îlots de forêt résiduelle que dans les sites correspondants plus éloignés (les fréquences moyennes sont respectivement de 59 et 18% et les densités de 0,23 et 0,16 arbres/m^2). Dans les endroits où des sources de graines sont présentes, la régénération est corrélée positivement avec les débris ligneux grossiers et négativement avec la litière fine. La régénération est la plus abondante dans les parcelles avec moins de 10% de couverture herbacée ou arbustive. Pour la plupart des espèces par contre, le recrutement s’est produit dans toutes les conditions de couvert végétal de sous-étage. Nous n’avons observé aucune relation entre la densité de la régénération et le couvert feuillu ou résineux dans l’étage dominant. Nos résultats indiquent que dans les forêts aménagées, la régénération des conifères est largement limitée par la disponibilité des graines et, seulement accessoirement, par la compétition ou la nature du substrat. Dans les paysages aménagés, les stratégies conventionnelles de maîtrise de la végétation ont peu de chances d’être aussi efficaces pour augmenter la régénération des conifères dans les forêts ripariennes que le serait un aménagement axé sur la disponibilité des graines par la conservation d’arbres vivants.

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E.W. Beach.[1,2] Weyerhaeuser Timberlands Research, WTC 1A3, P.O. Box 2999, Tacoma, WA 98477, U.S.A.
C.B. Halpern. Division of Ecosystem Sciences, College of Forest Resources, Box 352100, University of Washington, Seattle, WA 98195-2100, U.S.A.

[1] Corresponding author (e-mail: eric.beach@ci.seattle.wa.us).

[2] Present address: Seattle Public Utilities, Watershed Management Division, 19901 Cedar Falls Road S.E., North Bend, WA 98045, U.S.A.

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Introduction

The riparian zone is an integral part of the forest–stream ecosystem complex (Swanson et al. 1982). The composition and structure of riparian forests can shape ecosystem processes and biological conditions within stream channels. For example, in temperate coniferous forests, the abundance of large woody debris, as it influences channel properties, determines the availability of habitat for many species of salmonids (Hicks et al. 1991; Inoue and Nakano 1998). Thus, it is in the riparian zone where forest management practices may have the greatest effect on fish habitat. In the Pacific Northwest region of North America, a focal point of riparian forest management is the production of large coniferous trees that contribute woody debris to stream channels (U.S. Fish and Wildlife Service et al. 1999). Coniferous species are superior to hardwoods as sources of woody debris because of their larger size and longer persistence within stream channels (Fetherston et al. 1995). Historically, however, in the absence of requirements for stream buffers, riparian areas were routinely logged as part of adjacent upland harvest units, with the consequential loss of most or all of the coniferous overstory. In coastal regions of the Pacific Northwest, red alder (*Alnus rubra* Bong.) quickly exploited this niche and now comprises a significant portion of the streamside vegetation in managed forests (Hibbs and Giordano 1996). In this study we investigated some of the factors that influence conifer regeneration in riparian areas in managed forests of western Washington State, focusing in particular on the effects of distance to upland seed sources, rooting substrate, and possible interactions with vegetation.

In this region, a commonly held hypothesis is that, in alder-dominated riparian areas, a dense, competitive shrub layer, typically composed of salmonberry (*Rubus spectabilis* Pursh), prevents succession toward shade-tolerant conifers (Minore and Weatherly 1994; Hibbs and Giordano 1996). Following senescence of the relatively short-lived (ca. 100-year-old) alder, shrubs may dominate these communities, creating a “successional bottleneck” (Carlton 1988). Inhibition of tree establishment by lesser vegetation has been documented in many ecosystems, including old fields (DeSteven 1991; Gill and Marks 1991; Riege 2000), power-line rights-of-way (Niering and Goodwin 1974), and mountain meadows (Magee and Antos 1992; Prach et al. 1996). However, we suspect that, where sources of seed are sufficient, competitive interactions play a relatively minor role in coastal riparian forests. For example, successful regeneration of shade-tolerant conifers has been observed in alder-dominated riparian areas in southeastern Alaska (Hanley and Hoel 1996; Deal 1997). The current study was designed to test the fundamental hypothesis that seed dispersal is the primary factor shaping conifer regeneration in managed riparian stands of western Washington.

The coniferous species most suited to establishment under alder are shade-tolerant trees such as Sitka spruce (*Picea sitchensis* (Bong.) Carrière), western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), and western redcedar (*Thuja plicata* Donn ex D. Don); these are the dominant overstory species in undisturbed coastal Pacific Northwest forests (Franklin and Dyrness 1973). In managed forests of this region, traditional clear-cut logging has removed most sources of seed of these species, and upland areas adjacent to the riparian zone have been planted to Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), which is relatively shade intolerant and managed on short rotations (40–60 years). More recently, however, landscape-level plans for managed forests incorporate the retention of remaining patches of older forest to provide habitat for wildlife and other ecological services (USDA and USDI 1994; Weyerhaeuser Co. 1996). These relatively undisturbed remnant patches contain large shade-tolerant trees that have the potential to disperse seed into adjacent riparian areas.

Provided that sources of seed are present, regeneration also may vary as a function of local biotic and abiotic factors. Previous studies suggest that substrate (Soos and Walters 1963; Minore 1972; Christy and Mack 1984; Harmon and Franklin 1989; LePage et al. 2000), competition with herbs (Adams and Mahoney 1991) or shrubs (Niering and Goodwin 1974; Walker and Chapin 1986; Hibbs and Giordano 1996), and overstory canopy cover (Ruth 1967; Alaback and Tappeiner 1991; LePage et al. 2000) may individually or jointly influence regeneration success. However, the ability to detect such effects requires that seed sources are present.

The objectives of this study were threefold: to determine if distances to dispersal sources, rather than competing vegetation, limit conifer regeneration; if dispersal is limiting, to quantify relationships between dispersal distance and regeneration for the major shade-tolerant species; and to quantify the relative importance of local biotic and abiotic factors for conifer recruitment. We posed four specific hypotheses.

(1) The frequency and density of conifer regeneration will be higher in hardwood-dominated riparian areas within seed-rain distance of mature, shade-tolerant conifers than in riparian areas with few or no such sources of seed.
(2) Density of regeneration will decrease with distance from potential seed sources.
(3) Regeneration will be positively associated with the presence of coarse woody debris.
(4) Regeneration density will vary inversely with the cover of competing vegetation, including herbs, shrubs, and overstory trees (conifers and hardwoods).

Methods

Study areas

Sampling was conducted at nine locations on timberlands owned by Weyerhaeuser Co. and on adjacent state and federal lands (Table 1). All were adjacent to second- to fourth-order streams and were dominated by stands of 15- to 50-year-old red alder. Although current forest practices require retention of unharvested “leave areas” of 20–30 m width on each side of the stream channel, all riparian locations had been harvested once or twice prior to establishment of the current stand (typically at a 45- to 50-year interval). Adjacent to each site were either individual trees or remnant patches (2–250 ha) of mature, shade-tolerant conifers; size, density, and species composition of remnant trees varied among locations (Table 1).

Study locations represent two geographic regions in Washington State, U.S.A.: southwestern Washington and the Cascade Range (Fig. 1). Sample sites fall within the *Tsuga heterophylla* and *Picea sitchensis – Tsuga heterophylla* forest zones (Franklin and Dyrness

Table 1. Physical features, age of the riparian overstory, and seed source characteristics for the nine sample locations.

				Potential seed sources				
Transect	Stream order	Elevation (m)	Overstory age (years)	Density* (no./ha)	Species[†]	Distance[‡] (m)	Mean diameter (cm)	Maximum diameter (cm)
1a	2	400	25	17	Hemlock	65	60	165
					Spruce	80	185	200
					Redcedar	82	78	230
1b	2	400	25	≤1	Hemlock	85	70	90
					Spruce	35	90	90
2a	2	350	30	42	Redcedar	55	80	155
					Hemlock	39	65	110
2b	2	350	30	<1	Hemlock	53	50	60
					Redcedar	67	60	60
3a	3	300	20	18	Hemlock	37	75	90
					Redcedar	35	120	170
3b	3	300	20	<1	Hemlock	54	80	80
					Redcedar	56	80	80
4a	3	200	28	61	Hemlock	66	66	105
					Spruce	77	90	150
					Redcedar	73	95	150
4b	3	200	20	0	—	>200	—	—
5a[§]	3	200	28	1	Hemlock	30	80	90
					Spruce	28	70	80
5b	2	150	30	<1	Spruce	90	40	60
					Hemlock	90	50	70
6a	3	400	25	5	Redcedar	28	60	90
					Hemlock	30	50	55
6b	3	400	25	<1	Hemlock	90	45	55
					Redcedar	90	60	90
6c	3	400	25	<1	Hemlock	29	60	105
					Doug-fir	43	25	30
					Redcedar	60	80	80
7a	3	800	15	26	Douglas-fir	45	110	165
					Hemlock	47	50	65
					Redcedar	43	80	110
7b	3	800	15	0[¶]	Douglas-fir	141	110	165
					Hemlock	112	50	65
					Redcedar	141	80	110
8a	4	400	20	9	Redcedar	44	83	150
					Hemlock	31	35	100
					Douglas-fir	51	40	60
					Spruce	90	90	150
8b	4	400	20	0	—	>200	—	—
9a	4	450	40	35	Hemlock	35	50	85
					Redcedar	50	40	70
9b	4	450	40	<1	Redcedar	72	95	120
9c	2	800	48	10	Hemlock	52	70	120
					Redcedar	84	70	165

Note: Paired transects share the same number: a, with seed sources; b, with few or no seed sources. Unpaired transects (c; see Methods) were excluded from tests of hypothesis 1 (paired *t* tests).

*Total density of remnant trees (dominant or co-dominant individuals >50 years old).

[†] Listed in decreasing order of abundance.

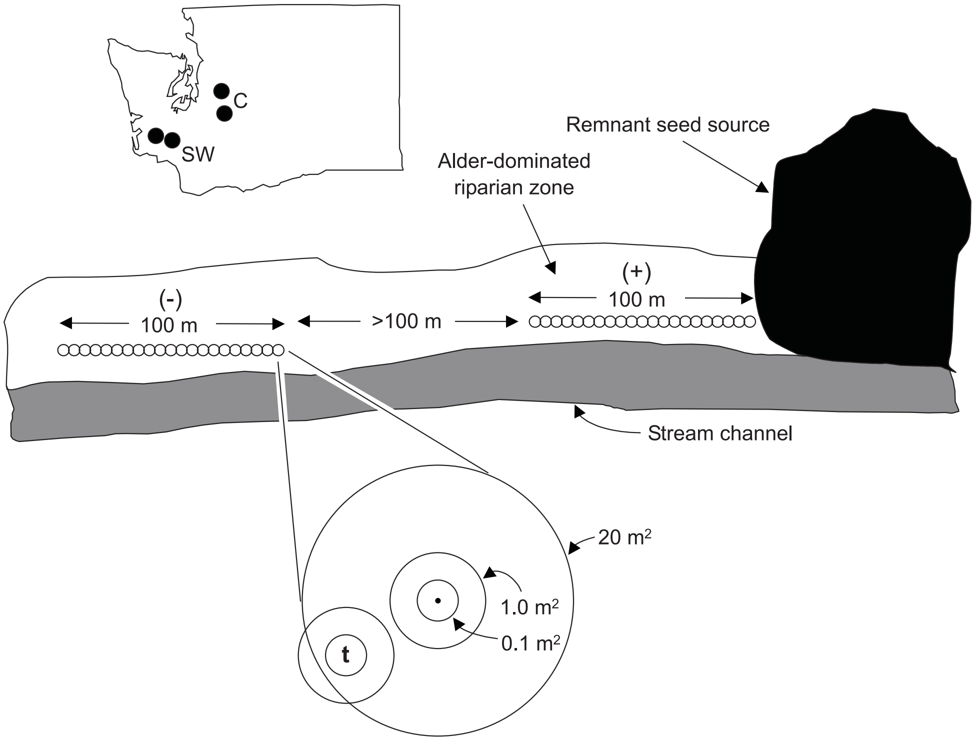
[‡] Mean distance (in m) of sample plots to the nearest potential seed tree.

[§] Sampled with 31 plots in two parallel transects (see Methods).

[¶] Density is defined as zero because potential seed sources were >100 m from all sample plots (see Methods).

1973). Climate is maritime with mild wet winters and cool moist summers. Mean maximum daily temperatures range from 21.1 to 25.6°C in August and from 4.6 to 7.2° C in January. Annual precipitation averages 255–288 cm and is highly seasonal, with 70–80% falling between 1 November and 30 April (Naselle, Centralia, and Cedar Lake meteorological stations; Natural Resource Conservation Service 1999). Riparian shrub layers are dominated by dense communities of *Rubus spectabilis*, *Rubus parviflorus* Nutt.,

Fig. 1. The locations of study regions (SW, southwestern Washington; C, Cascades) and basic sampling design of paired transects: (+) with seed sources; (–) with few or no seed sources. Each transect contained twenty-one 20-m^2 circular plots. Substrate type was recorded at the center of each circular plot (a point sample). Herb and shrub cover were visually estimated in nested plots of 0.1 and 1.0 m^2, respectively; cover of overstory hardwoods and conifers was estimated at each plot center using a spherical densiometer. Similar measurements were recorded at the locations of each regenerating conifer (t) within each 20-m^2 plot (see Methods for details).



Acer circinatum Pursh, *Oplopanax horridum* (Torr. & Gray) Miq., *Vaccinium parvifolium* Smith, and *Ribes bracteosum* Dougl. The most common herbs include *Polystichum munitum* (Kaulf.) Presl, *Oxalis oregana* Nutt., *Montia sibirica* (L.) Howell, *Tolmiea menziesii* (Pursh) Torr. & Gray, and *Stachys cooleyae* Heller. Logging in these areas dates to the late 19th century.

Field methods

Site selection and sampling design

Sampling locations were selected using aerial photo stereo pairs (1 : 12 000 scale). Historical aerial photos were used to ensure that distances to potential sources of conifer seed had not changed since the current riparian stands became established. At each location, we established a pair of 100 m long transects parallel to the stream channel and 5 m upslope from the stream at the point closest to stream-bankfull width (Fig. 1). One of each pair of transects was established adjacent to a source of conifer seed, hereafter termed the transect "with seed sources." The origin of the transect was placed at the edge of the seed source (i.e., at the base of the outermost tree in the remnant forest patch) (Fig. 1). The second transect, the transect "with few or no seed sources," was established >100 m upstream or downstream from the first, in similar hardwood-dominated riparian forest. At two locations a third, unpaired transect was established downstream (6c) or upstream (9c) from the paired transects, to increase the sample size for particular analyses (see Table 1). With one exception, all transects were comprised of twenty-one 20-m^2 circular plots (2.5 m radius) with plot centers spaced at 5-m intervals (Fig. 1); however, transect 5a was sampled with 31 plots in two parallel transects (because of the presence of a road at the 75-m point).

Densities and ages of regenerating conifers

At each location during summer 1998, regenerating conifers (i.e., all individuals younger than the alder overstory, including first-year seedlings) were tallied and measured for height within each of the 20-m^2 sample plots. To ensure that only recent regeneration was tallied and not suppressed trees that predated establishment of the alder overstory, ca. 40% of the tallied individuals were aged. Depending on the species and size of tree, ages were determined either from increment cores taken at the base of the stem (trees >5 cm diameter at breast height (DBH)), counts of terminal bud-scale scars, or counts of annual rings from basal cross sections (trees <5 cm DBH). Species-specific regression models (age as a function of height) were developed and ages of the remaining tallied trees were then predicted. The age of the overstory (primarily alder) was estimated from an increment core taken at the base of a dominant individual of each species. Regenerating conifers found to be older than the alder overstory were omitted from subsequent analyses.

Seed source density and distance

Orthophotographs, geographic information system (GIS), and direct field measurements were used to quantify the composition and density of potential seed trees adjacent to each transect. Transects were superimposed on orthophotographs and the program ARCVIEW® was used to delineate an area within 100 m of any sample plot, a distance assumed to encompass most potential seed trees. This distance was chosen because previous studies suggest that: (*i*) the maximum effective dispersal distances for western hemlock and spruce are 160 and 200 m, respectively, (Garman 1951; Gashwiler 1969; Timony and Peterson 1996), and for western redcedar and silver fir, <100 m (Heatherington 1965), and (*ii*) the vast majority of seeds of all species fall much closer to the

Fig. 2. Age-class distributions of the primary species of regenerating conifers. Data are pooled among transects. *n*, total number of individuals.

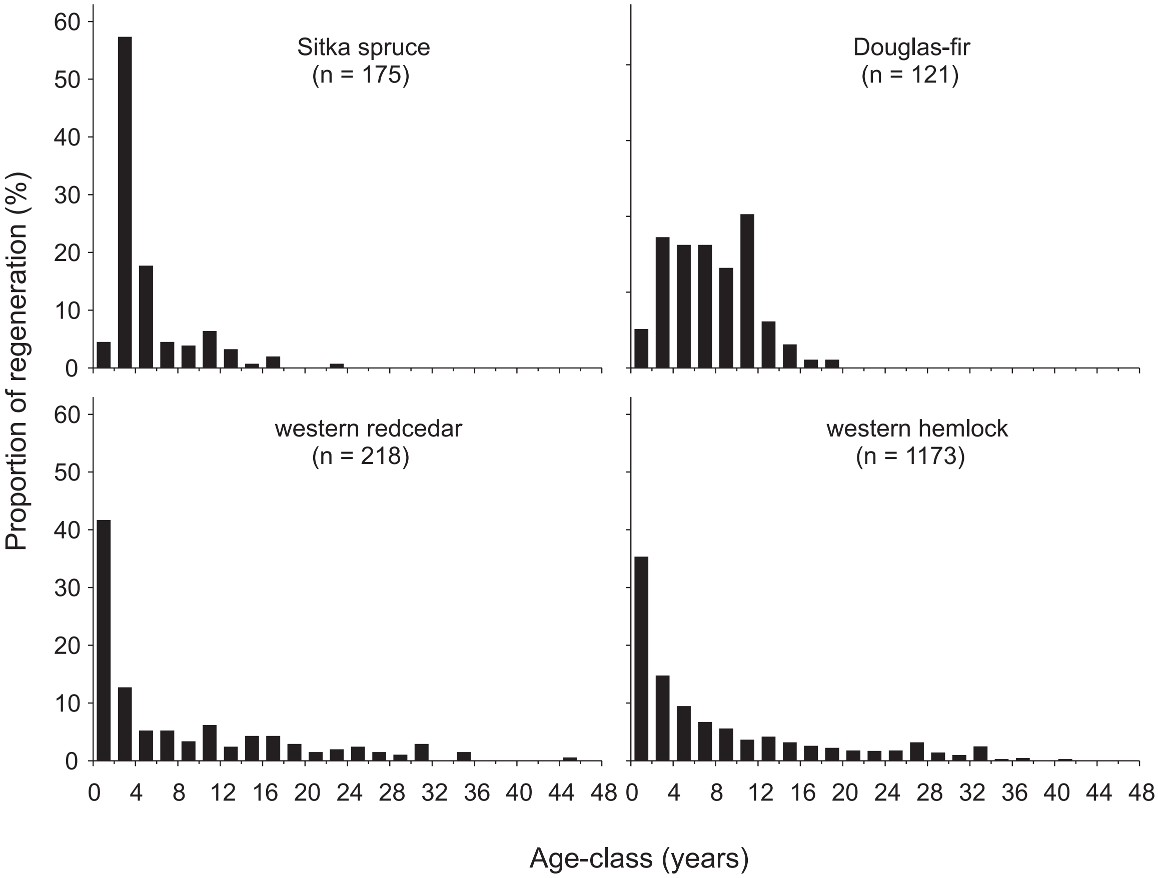


Table 2. Age–height relationships for regenerating conifers.

	Height (cm)					Coefficients		
Species	Mean	Range	r^2	*n*	*F*	b_0	b_1	*P*
Western hemlock	46.0	1–400	0.88	453	3548.85	0.9212	0.6316	<0.001
Western redcedar	42.0	2–500	0.89	112	905.58	0.6714	0.6770	<0.001
Sitka spruce	58.7	2–600	0.71	80	202.15	1.2619	0.4472	<0.001
Douglas-fir	112.1	2–600	0.81	94	406.02	1.0086	0.4589	<0.001

Note: Heights and *n* values represent the subset of tallied individuals used to develop regression models (see Methods); sample sizes for silver and grand fir were too small to develop models. Equations are of the following form: total age = $b_0 \times \text{height}^{b_1}$.

source tree, i.e., within 20 m (Heatherington 1965; Mair 1973; LePage et al. 2000). Within the area defined for each transect, the composition, density, and size (diameter and height) of potential seed trees were either subsampled using one or two 0.05-ha circular plots (50% of the locations) or were extracted from a site-specific forest-inventory data base (FIRS, which contains density and size data for all coniferous species). Seed trees were defined as dominant or codominant individuals >50 years old at the time of sampling; this threshold was chosen to differentiate residual from plantation trees, which are typically harvested by 45 years.

Distances from individual sample plots to potential seed trees of each regenerating species present within a plot were estimated with a Criterion® laser in the following manner. The bearing and horizontal distance to the leading edge of the remnant forest patch (or to the individual remnant) was measured from known points along each transect. These were used to calculate the horizontal distance from the center of each plot to the edge of the remnant forest patch (or to the individual remnant). Each regenerating conifer within a plot was then assigned this species-specific, minimum distance.

Within-stand abiotic and biotic factors

To examine relationships with rooting substrate and vegetation cover, we sampled as follows. For each regenerating conifer in each of the 20-m^2 plots we recorded rooting substrate as coarse woody debris (>10 cm in diameter), organic (litter or humus), or mineral soil. Total herb and shrub cover were estimated in circular plots of 0.1 and 1.0 m^2 (0.18 and 0.54 m radius, respectively) centered on each regenerating conifer (Fig. 1). Cover of coniferous and deciduous overstory trees (>10 cm DBH) were measured with a spherical densiometer (Lemmon 1957) at the center of the plot. In similar fashion, we recorded substrate type, and estimated herb, shrub, and coniferous and hardwood tree cover at the center of each of the twenty-one 20-m^2 plots per transect. These systematically obtained data provided null models of substrate type and

Table 3. Frequency and density of conifer regeneration in transects with seed sources and with few or no seed sources.

	With seed sources		With few or no seed sources	
Transect	Frequency (%)	Density (no./m^2)	Frequency (%)	Density (no./m^2)
1	86	0.28	81	1.38
2	33	0.15	5	<0.01
3	71	0.35	24	0.02
4	62	0.17	0	0.00
5	34	0.09	0	0.00
6	48	0.12	0	0.00
7	86	0.64	33	0.06
8	81	0.16	19	0.01
9	33	0.08	0	0.00
Mean	59	0.23	18	0.16

Note: Frequency is the proportion of plots supporting regenerating conifers. Paired t test (frequency): $t = 6.765$, $P < 0.0001$; Wilcoxon signed-rank test (density): $Z = -1.599$, $P = 0.110$ for all transects and $Z = -2.521$, $P = 0.012$ with transect 1 removed (see Discussion).

plant cover used in subsequent analyses of the observed distributions of regenerating conifers.

Data analysis

Relationships with dispersal distance

To test for differences in the frequency and density of conifer regeneration between transects with seed sources and those with few or no seed sources (hypothesis 1), a mean density (seedlings/m^2) and frequency (proportion of plots with regeneration) were calculated for each transect. $F_{\max}$ tests were used to assess homogeneity of variances between groups and the choice of statistical tests was made accordingly: a paired t test for frequency data and the nonparametric Wilcoxon signed-rank test for density data (Sokal and Rohlf 1981).

To explore relationships between regeneration density and dispersal distance (hypothesis 2), separate species-level analyses were conducted. For each species, only those transects with an adjacent seed source were used (see Table 1), yielding the following sample sizes: western hemlock (16 transects), western redcedar (14), Sitka spruce (6), and Douglas-fir (4). Data were pooled among transects, and density of regenerating conifers was plotted against minimum dispersal distance (i.e., the number of trees per area sampled within each distance class).

Relationships with substrate and vegetation cover

To quantify relationships between conifer regeneration and substrate (hypothesis 3), contingency tables and G tests of goodness of fit (Sokal and Rohlf 1981) were used to test for species' associations with substrates, expressed as significant differences between expected frequencies (samples at plot centers) and observed frequencies (rooting substrates of conifers). To examine relationships with herb and shrub cover (hypothesis 4), Kolmogorov–Smirnov tests (Sokal and Rohlf 1981) were used to test for significant differences between the frequency distributions of cover measured at plots centers and those associated with conifer regeneration. Because of possible negative effects of larger regenerating conifers on herb or shrub cover, these analyses were limited to plots centered on trees ≤1.0 m tall. To assess relationships with overstory cover, plot-level seedling densities were regressed against conifer and hardwood canopy cover. As with analyses of dispersal distance, each of these species-level tests included only those transects adjacent to a potential seed source (see above).

Relative strength of relationships with independent variables

Spearman rank-order correlation was used to assess the relative strengths of relationships between species' regeneration densities at the scale of 100 m long transects and the full suite of abiotic and biotic variables considered above. All 20 transects were included in these analyses. Distance to a seed source was expressed as the mean distance among plots to the nearest potential seed tree (Table 1). For transects where no sources of seed were found, this distance was assigned a value of 200 m. The abundance of each substrate (CWD, organic, and mineral soil) was represented by its frequency among the 21 sample points per transect. Herb, shrub, and tree cover (hardwoods and conifers) were each expressed as means of the 21 plot values per transect.

Results

We observed a total of 1714 regenerating conifers; these occurred in 170 of 431 plots and 16 of 20 transects. Western hemlock was by far the most abundant species (68% of the total number of individuals). Western redcedar (13%), Sitka spruce (10%), and Douglas-fir (7%) were also common, but Pacific silver fir (*Abies amabilis* (Dougl.) Forbes) and grand fir (*Abies grandis* (Dougl.) Forbes) were not frequent enough (a total of 27 individuals) to be included in species-specific analyses. Nearly 40% of the individuals were ≤5 cm tall and nearly 50% were ≤2 years old; the remaining stems represented a broad range of heights (up to 6 m) and ages (Fig. 2). Relationships between seedling height and age were best described by curves of the form: total age = $b_0 \times \text{height}^{b_1}$. Coefficients varied by species, and r^2 values were generally high (Table 2).

Presence and distance to dispersal sources

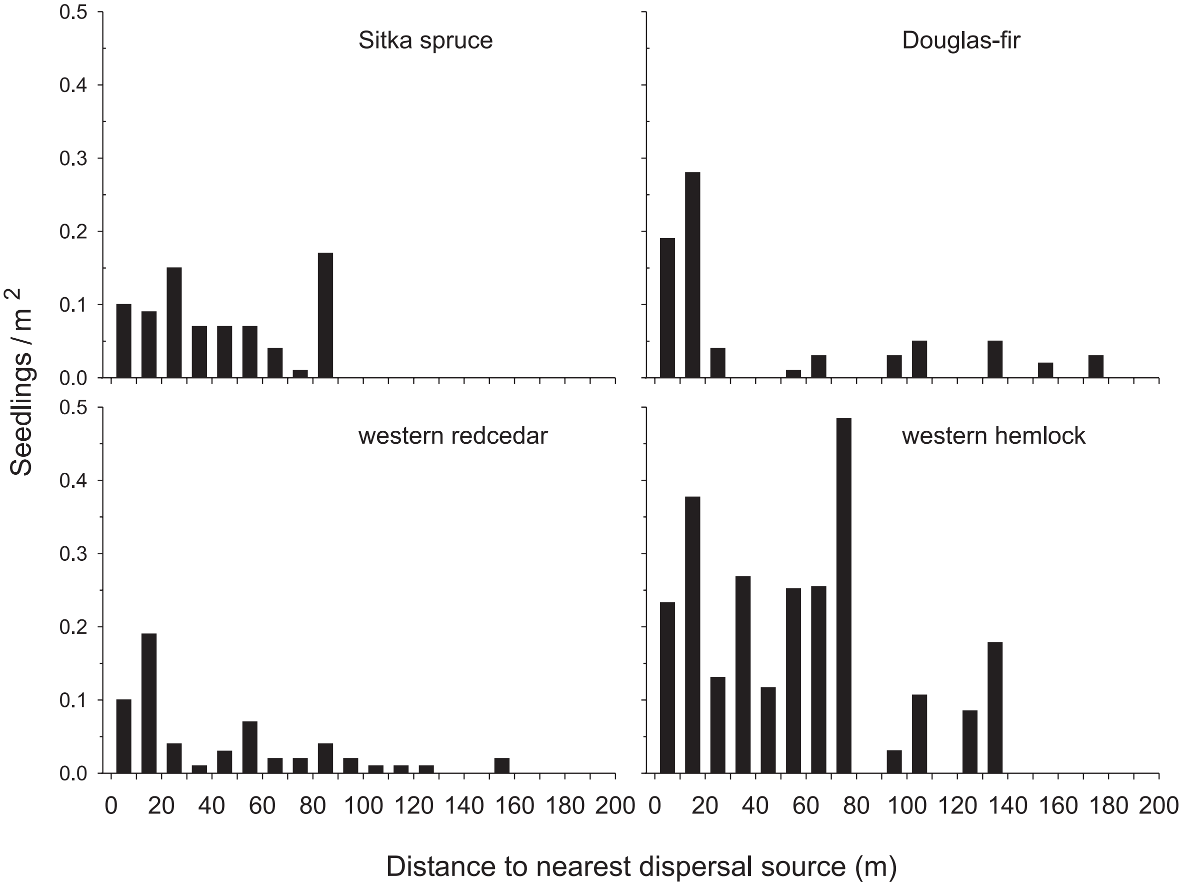
The frequency of plots with regeneration was significantly greater in transects with seed sources than in those with few or no sources of seed (paired t test, $t = 6.765$, $P < 0.001$; Table 3). With one exception, mean density of regeneration was also greater in transects with seed sources, although this difference was not statistically significant (Wilcoxon signed-rank test, $Z = -1.599$, $P = 0.11$; Table 3). However, a highly significant result was observed if the anomalous location (transect 1) was removed from the analysis (Wilcoxon signed-rank test, $Z = -2.521$, $P = 0.012$) (see Discussion).

The vast majority (92%) of all regeneration was found within 80 m of the nearest potential seed tree, and densities were much reduced beyond that distance (Fig. 3). No regeneration was found in plots >170 m from the nearest potential seed source (although distances in excess of 300 m were considered). With one exception (transect 1b), regeneration densities were greatest in transects that bordered remnant forest patches with less than five mature conifers per hectare. In comparison, regeneration was relatively low in transects adjacent to individual remnant trees or to young plantation forests.

Substrate

Across all sites 52% of regenerating conifers were found on coarse woody debris (CWD) (Fig. 4), although CWD comprised, on average, only 16% of the available rooting substrate. Mineral soil and other organic substrates (litter, humus) comprised 53 and 31% of the available forest floor,

Fig. 3. Density of regeneration as a function of distance to nearest dispersal source. Sample sizes are western hemlock, 16 transects; western redcedar, 14; Sitka spruce, 6; and Douglas-fir, 4.



respectively. All species except for Douglas-fir showed a significant positive association with CWD (Fig. 4). Both Sitka spruce and Douglas-fir showed a significant, positive association with mineral soil, and western hemlock, a significant negative association with mineral soil. All species were found significantly less often than expected on other organic substrates (litter, humus).

Vegetation cover

Total herb and shrub cover were significantly lower in plots centered on regenerating conifers than in the systematic sample plots (Kolmogorov–Smirnov tests for all species, $P < 0.001$; Figs. 5 and 6). For all species, most (50–90%) regeneration was found in plots with herb and shrub cover <10%, far in excess of the proportion of systematic plots with similar cover. However, for most species, regeneration was found in plots supporting the full range of plant cover values. In contrast, we could detect no relationship between regeneration density and the cover of overstory conifers or hardwoods (linear regression: $r^2 = 0.08$, $P = 0.23$ and $r^2 = 0.01$, $P = 0.69$, respectively).

Relative strength of relationships with independent variables

Spearman rank-order correlation supported, in large part, the results of the previous analyses. Dispersal distance had the strongest correlation (negative in sign) with regeneration density for all coniferous species (Table 4). Other significant correlations, in decreasing strength were coarse woody debris (+), mineral soil (–), and hardwood tree cover (–) for western hemlock; coarse woody debris (+) for Sitka spruce; and coniferous tree cover (+), shrub cover (–), and herb cover (–) for Douglas-fir. Beside dispersal distance, we detected no other significant correlations for western redcedar.

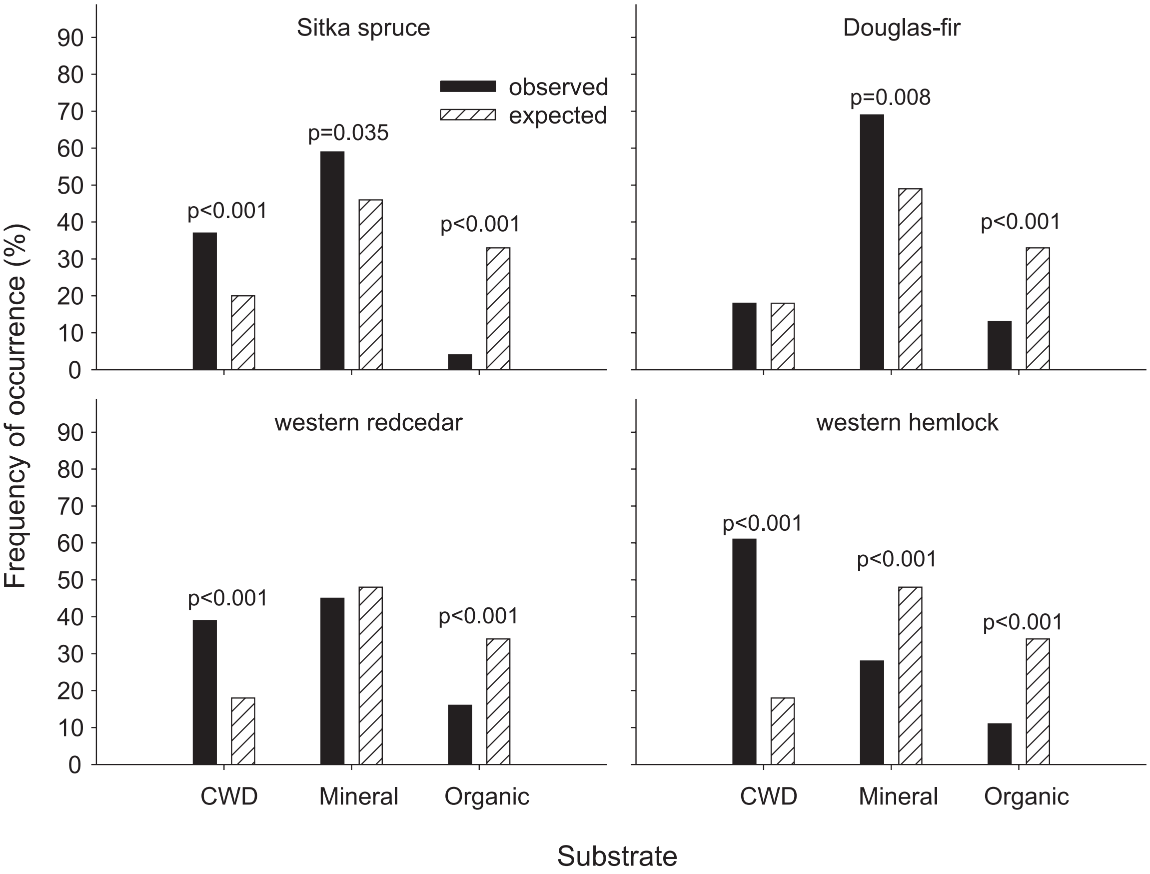
Discussion

Previous studies in alder-dominated riparian zones of the Oregon Coast Range suggest that recruitment of conifers is largely controlled by biotic interactions, namely competition with a tall, dense shrub layer (Henderson 1970; Carlton 1988; Minore and Weatherly 1994; Hibbs and Giordano 1996). Surprisingly, however, there has been little explicit consideration of the role of seed availability. Our study, in contrast, illustrates the simple but fundamental importance of dispersal limitation for conifer regeneration and, only secondarily, the effects of other biotic or abiotic factors (see also LePage et al. 2000).

Dispersal limitation

Natural regeneration of conifers in these managed, riparian forests is clearly limited by seed dispersal. With one exception, both the proportion of plots supporting regeneration and the mean density of trees were considerably higher at locations within 100 m of a remnant forest patch than in adja-

Fig. 4. Frequency of rooting substrates associated with plot centers (expected) and regenerating conifers (observed). See Fig. 3 caption for species' sample sizes.



cent areas more distant from seed sources. Where regeneration was more abundant at greater distance, the anomalous transect (1b) supported a fresh deposit of alluvial silt and the vast majority of seedlings were recent germinants (<1 year old), probably transported by fluvial processes. Although conditions for germination were optimal (moist silt free of competing vegetation or litter), short-term survival may be significantly reduced (see below) and the contrast in density between transects should diminish with time.

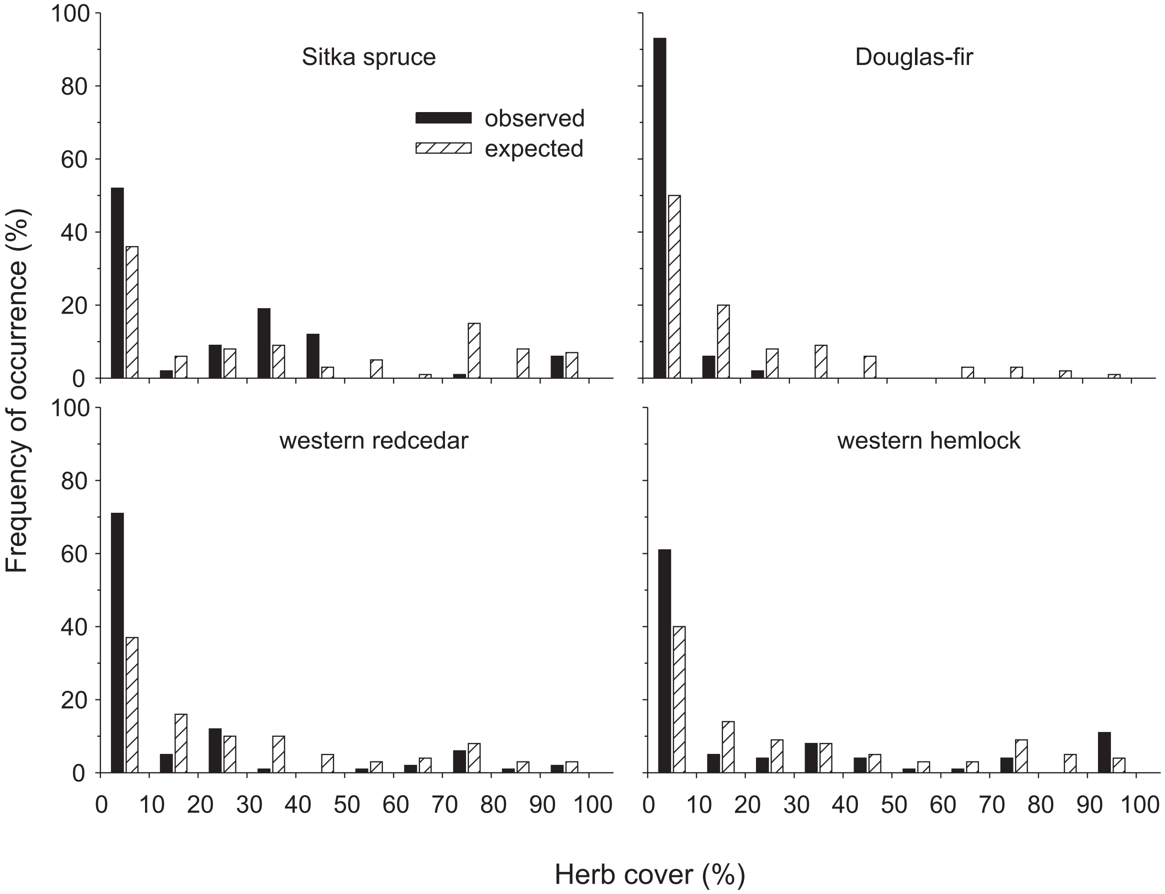
Conifer seeds have short-term viability (Williamson 1986; Archibold 1989) and do not form a persistent seed bank. Thus, following harvest of upland and riparian forests, seeds must derive from adjacent stands. However, in intensively managed landscapes without residual trees, the paucity of such seed sources and the large distances between them suggest that few riparian areas experience sufficient seed rain for successful conifer regeneration. Our data on the spatial distributions of regeneration are consistent with previously published figures for seed dispersal (Garman 1951; Heatherington 1965; Gashwiler 1969; Mair 1973; Sato and Hiura 1998; LePage et al. 2000): regeneration was extremely low beyond 80 m and was absent at distances >170 m. Similar patterns of dispersal limitation have been described in other boreal and temperate ecosystems both during primary succession (Halpern and Harmon 1983; Fastie 1995) and regeneration of secondary forests (Timony and Peterson 1996; LePage et al. 2000).

Our data also illustrate that the density of residual trees increases the likelihood of successful regeneration. Regeneration was most abundant in transects adjacent to remnant forests with less than five trees per hectare and relatively sparse or absent in transects that bordered either individual seed trees or young plantations. Even if shade-tolerant conifers were present in adjacent plantations, seed production would be relatively limited under short-rotation harvest. For example, western hemlock may begin to produce seed at 30 years (Ruth 1974), but peak production occurs much later (Burns and Honkala 1990), increasing with age and stem diameter (Green and Johnson 1994).

Abiotic and biotic controls on regeneration

Where sources of seed are present, additional abiotic and biotic conditions appear to mediate local patterns of conifer establishment. Of the available substrates, CWD supported the highest density of regeneration. Similar patterns have been observed in upland forests of the Pacific Northwest, where it is postulated that seedlings that establish on logs can escape competition with the ground-layer community and can take advantage of the greater moisture-retaining capacity of CWD (Christy and Mack 1984; Harmon and Franklin 1989). Interestingly, decay condition did not appear to have an effect on seedling establishment: regeneration densities were high on both sound and rotten logs (E.W. Beach, personal observation). Although residual logs can persist for 270 years or more (Daniels et al. 1997), short-

Fig. 5. Frequency distribution of herb cover at plot centers (0.1 m^2) (expected) and similar sized plots associated with conifer regeneration (observed). Expected and observed distributions are significantly different for all species ($P < 0.001$, Kolmogorov–Smirnov test). Only regeneration ≤1.0 m tall were considered. See Fig. 3 caption for species' sample sizes.



term replenishment of large, persistent material is not likely in hardwood-dominated stands. However, if CWD is currently abundant within the riparian zone, seedbed conditions may remain adequate until developing populations of conifers can contribute to CWD through mortality.

Mineral soil, derived from fluvial deposits on floodplain surfaces, was the most abundant substrate at these sites, supporting regeneration of all coniferous species. In contrast, regeneration on fine organic substrates (accumulations of alder leaves) was relatively rare. Thick accumulations of litter are known to limit tree establishment by physically impeding seedling emergence (e.g., Wagg 1964; Caccia and Ballaré 1998); a similar process is likely to occur in riparian forests dominated by broad-leaved shrubs and trees.

Competitive interactions with understory strata, as inferred from the relationships between regeneration density and shrub and herb cover, were detectable, but the effect appears to be less pronounced than that suggested by previous studies (Henderson 1970; Carlton 1988; Minore and Weatherly 1994; Hibbs and Giordano 1996). Although regeneration of shade-tolerant conifers occurred more often than expected in plots with low herb and shrub cover, individuals of all ages were observed across the full range of plant cover (including dense patches of shrubs). Despite relatively low densities of conifers under higher shrub cover, individuals may, in time, outcompete dominant shrubs such as salmonberry. In contrast with the shade-tolerant conifers, however, Douglas-fir was rarely observed where herb or shrub cover exceeded 10%. This relatively shade-intolerant species may have difficulty regenerating beneath an alder canopy.

Age distributions of the shade-tolerant conifers suggest that, as in upland forests, most mortality occurs within 2 years of germination (Christy and Mack 1984; Cui and Smith 1991; Feller and Klinka 1998). Thereafter, it appears that rates of mortality are low. Although ca. 50% of regeneration was ≤2 years old, the numerous remaining individuals spanned a broad range of age and height classes, with many stems emerging from the herb and shrub layers. Thus, beyond effects on initial establishment, interspecific competition does not appear to be a major factor in the survival of shade-tolerant species, although many individuals exhibited signs of suppressed growth (e.g., small annual rings or closely spaced whorls of branches). However, if the period of suppressed growth is not too protracted, shade-tolerant conifers are capable of responding to increased levels of light with increased diameter and height growth (Stewart 1986). Moreover, because alder is relatively short lived (maximum age ca. 100 years; Franklin and Halpern 1999) and does not recruit without major disturbance, as overstory individuals die, suppressed conifers may ascend into the canopy (Kabzems 1952; Franklin and Pechanec 1968). Ulti-

Fig. 6. Frequency distribution of shrub cover at plot centers (1.0 m^2) (expected) and similar sized plots associated with conifer regeneration (observed). Expected and observed distributions are significantly different for all species ($P < 0.001$, Kolmogorov–Smirnov test). Only regeneration ≤1.0 m tall were considered. See Fig. 3 caption for species' sample sizes.

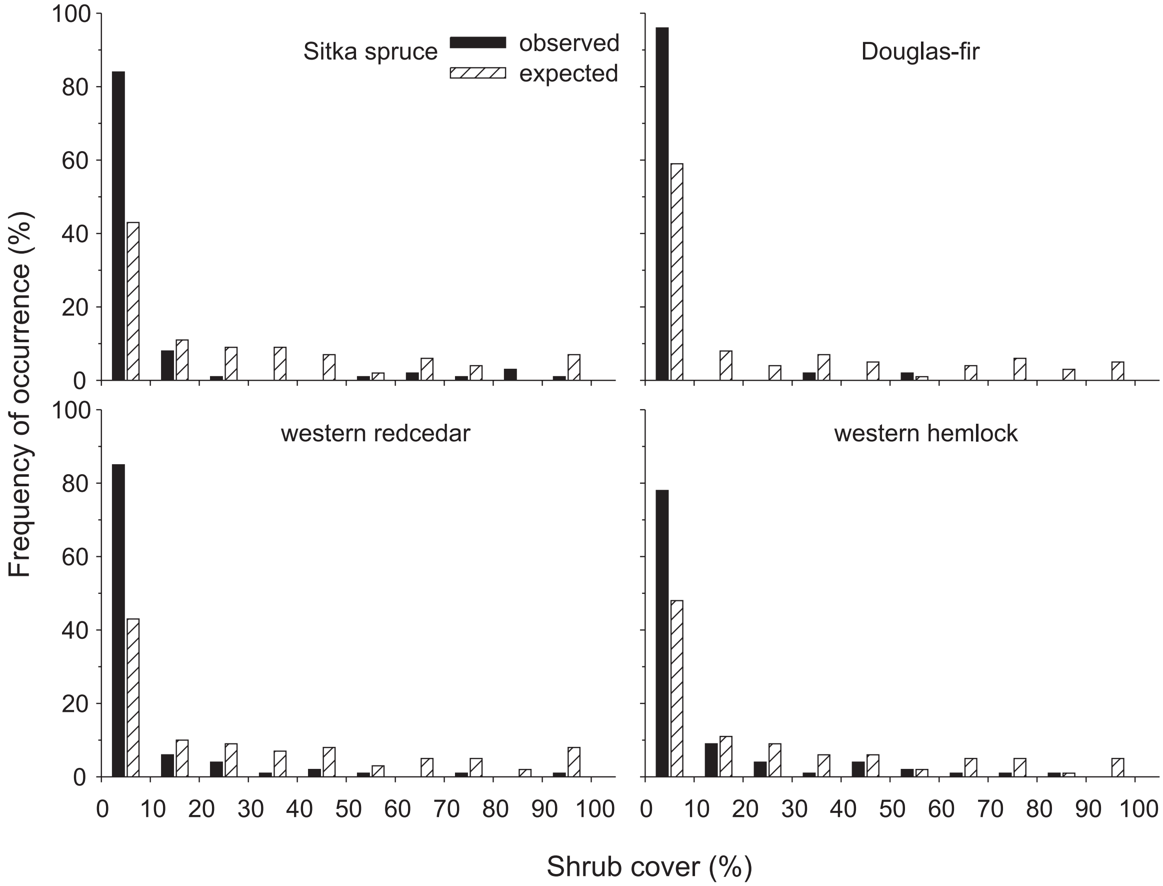


Table 4. Spearman rank-order correlation coefficients (r_s) and significance levels (P) for conifer regeneration density and measured abiotic and biotic variables (n = 20 transects; see Methods for details).

	Western hemlock		Western redcedar		Sitka spruce		Douglas-fir	
Variable	r_s	P	r_s	P	r_s	P	r_s	P
Mean minimum dispersal distance	–0.54	0.01	–0.55	0.01	–0.93	<<0.01	–0.82	<<0.01
Coarse woody debris	0.54	0.01	0.30	0.18	0.44	0.05	–0.06	0.79
Mineral soil	–0.51	0.02	–0.17	0.46	–0.30	0.19	0.05	0.83
Organic (litter, humus)	0.32	0.15	0.03	0.89	0.08	0.72	0.07	0.77
Shrub cover	–0.27	0.23	–0.11	0.64	–0.08	0.75	–0.49	0.03
Herb cover	–0.09	0.68	–0.33	0.14	0.04	0.86	–0.44	0.05
Hardwood overstory cover	–0.45	0.04	–0.26	0.25	–0.07	0.76	–0.25	0.27
Coniferous overstory cover	0.23	0.32	0.18	0.44	–0.10	0.68	0.54	0.01

Note: Correlations are significant at $P \le 0.5$. P values have not been adjusted for multiple comparisons.

mately, if sources of seed are present, eventual replacement of alder by shade-tolerant conifers is likely.

Management implications

Management strategies designed to increase the abundance of conifers in riparian forests should naturally focus on those factors that have the greatest influence on successful regeneration. Our results suggest that conventional riparian management strategies, such as understory vegetation control (Zasada and Tappeiner 1991), may not be as effective in increasing conifer regeneration as managing for seed sources through green-tree retention. Retaining large trees in and adjacent to riparian areas has the potential to alter successional trends toward conifer dominance. Our size and age-structure data suggest that, given sufficient time, retention of relatively low densities of mature trees (<5 trees/ha) is sufficient to shift canopy dominance toward shade-tolerant species. Retained trees could be selected by the characteristics most likely to contribute to successful recruitment beneath a dense alder overstory, namely physiology (e.g., shade-tolerant species such as western hemlock or western redcedar), size (individuals with the greatest height and diameter), and proximity to the riparian zone. Because the physical form of the tree has little bearing on seed production (Perry 1994), individuals with a high degree of defect (and lower economic value) could be selected for retention, thus providing additional ecological benefit as wildlife habitat. Green-tree retention has been incorporated into current Habitat Conservation Plans on private lands (Weyerhaeuser Company 1996) and is mandated on federal "matrix" lands within the range of the northern spotted owl (USDA and USDI 1994). Management plans that provide for retention of green trees as local sources of conifer seed may accelerate the successional development of riparian forests, enhancing stream habitat quality with minimal loss of timber value.

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