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Abundance of natural regeneration and growth comparisons with planted seedlings 10–13 years after commercial thinning in 50-year-old Douglas-fir, Douglas-fir/western hemlock, Oregon Coast Range

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ABSTRACT

Post-thinning natural regeneration in the Pacific Northwest of USA was evaluated 13 years after thinning 50-year-old Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco var. *menziesii*) stands on a drier, interior Coast Range site (McDonald) and 10 years after thinning 50- to 55-year-old Douglas-fir/western hemlock (*Tsuga heterophylla* [Raf.] Sarg.) stands on a moister, coastal site (Blodgett) as part of a long-term study of late-seral habitats following commercial thinning. At each site, thinning varied in residual stand density (ranging from 17 to 34 m^2/ha) and pattern (uniform thinning or thinning with the incorporation of 0.06- and 0.1-ha gaps). Effects of understory vegetation control were also evaluated. McDonald had minor components of grand fir (*Abies grandis* [Dougl. ex D. Don.] Lindl.); Blodgett had substantial overstory stocking of western hemlock. Natural seedling densities and heights of natural and underplanted seedlings were recorded where stands had been thinned to four (McDonald) and three (Blodgett) residual densities. Densities of natural Douglas-fir seedlings ranged from 55 to 980/ha at McDonald (13 years after thinning) and from 887 to 1566/ha at Blodgett (10 years after thinning). Douglas-fir abundance was inversely related to overstory density at McDonald after thinning and was greater at both sites where understory had been chemically controlled. Natural regeneration of grand fir at McDonald was limited by proximity to seed source, but more abundant than Douglas-fir where it occurred. Regeneration of western hemlock 10 years after thinning at Blodgett averaged 44,058–56,845/ha and did not vary across overstory densities or with vegetation control. Heights of hemlock and Douglas-fir regeneration were greatest where overstories were least dense. Hemlock was consistently taller than Douglas-fir at the site (Blodgett) where regeneration of both species occurred. However, Douglas-fir was preferentially browsed, which limited height growth. Canopy gaps did not consistently increase density or height of natural regeneration at either site, but many of the tallest seedlings recorded were found within gaps. Heights and recent height growth rates for western hemlock at Blodgett were similar between natural and planted seedlings. Natural Douglas-fir were shorter than planted Douglas-fir at both sites. Reliance on natural Douglas-fir regeneration in thinned stands provided variable stocking, with uncertain futures where post-thinning overstory basal area exceeded 28 m^2/ha in 50-year-old stands.

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1. Introduction

In many parts of the world, forest management has been shifting from a single-use objective of timber management toward multiple-objective management, which incorporates societal values of biodiversity and ecosystem management (Spiecker, 2003; Puettmann and Ammer, 2007). Of major concern globally is the loss of "old-growth" forests (Bauhus et al., 2009). Forest managers in the Pacific Northwest (USA), especially in the public sector, have expressed a growing interest in managing for old-growth-like stand structure aimed toward late-seral habitat while maintaining a sustainable supply of timber (USDA and USDI, 1994; Oregon Department of Forestry, 2001). Many of the areas targeted for this type of management within the Coast Range of western Oregon are now dominated by Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco var. *menziesii*), the region's most widely grown commercial species, often in <60-year-old plantations. Managers are seeking ways of progressing these stands towards late-seral habitat. The federal Northwest Forest Plan and State of Oregon Northwest Oregon State Forests Management Plan provide general directions for late-seral management on public lands within parts of the Coast Range.

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Bauhus et al. (2009) suggested the need to identify and prioritize structural elements within forests that are important and to manage towards those. A moderately heavy "structural" thinning (Schütz, 2002) has been suggested as a means to shorten the time to develop some structural features (Choi et al., 2007; Davis et al., 2007). The creation of a multilayered canopy has been identified as a key element in the development of late-successional structure (Spies and Franklin, 1991; McComb et al., 1993) in the Douglas-fir region. Depending upon specific objectives and forest types, multilayered canopies may consist of conifer, hardwood, and/or shrub species. Initiation of subsequent canopy layers under an established overstory may follow underplanting or reliance on natural regeneration coupled with overstory thinning.

Several studies in the Douglas-fir region of western Oregon and Washington have evaluated the survival and growth of underplanted conifers in young, even-aged stands (Brandeis et al., 2001; Maas-Hebner et al., 2005; Chan et al., 2006; Harrington, 2006). These studies compared several shade-tolerant species to the more shade-intolerant Douglas-fir. Results from underplanting studies generally support a need for overstory thinning prior to underplanting to provide for survival and growth of underplanted seedlings (Maas-Hebner et al., 2005; Chan et al., 2006).

Studies that have assessed the establishment of naturally-regenerated conifers under thinned stands generally found higher seedling densities and frequencies (number of sample points containing at least one seedling) in thinned stands versus unthinned stands (Bailey and Tappeiner, 1998; Prévost and Pothier, 2003; Chan et al., 2006; McDonald et al., 2009; Otto et al., 2012), but partial cuttings have not always resulted in increased conifer density (Man et al., 2009). Stands of low overstory density also recruited higher numbers of natural Douglas-fir seedlings than higher density stands (Bailey and Tappeiner, 1998; Jerra and Vogt, 1998; Miller and Emmingham, 2001). These studies demonstrated that natural regeneration of shade-intolerant coastal Douglas-fir benefits from both logging-created ground disturbance and increased light intensity. Kneeshaw et al. (2002) observed processes by which relatively more shade-tolerant interior Douglas-fir seedlings adapt to partial overstory removal when provided with increased light. Few studies (Bailey and Tappeiner, 1998; Karlsson and Nilsson, 2005) evaluating natural regeneration have provided comparative data of shade-tolerant versus shade-intolerant species when the prevalent forest type was dominated by a shade-intolerant species.

Most studies of natural regeneration of shade-intolerant species in understories have occurred on sites with predominantly single-species overstories (Bailey and Tappeiner, 1998; Miller and Emmingham, 2001; Zhu et al., 2003; Chan et al., 2006; Otto et al., 2012). Not surprisingly, with the exception of a few sites reported in Bailey and Tappeiner (1998), most naturally-regenerated seedlings were of the species that dominated the overstory due to seed tree prevalence. Little research on natural Douglas-fir regeneration has been conducted on sites where a dominant Douglas-fir overstory also contained a significant component of shade-tolerant western hemlock (*Tsuga heterophylla* [Raf.] Sarg.) or other shade-tolerant species, a common condition in much of the Coast and Cascade Ranges of Oregon and Washington. In Sweden, when shelterwoods were dominated by shade-intolerant Scots pine (*Pinus sylvestris* L.) but comprised of up to 25% shade-tolerant Norway spruce (*Picea abies* (L.) Karst.), similar levels of Scots pine and Norway spruce regeneration were reported (Karlsson and Nilsson, 2005), Conversely, when Norway spruce dominated stands (comprising 90% of stand basal area), Scots pine had much lower seedling densities than spruce (Nilsson et al., 2002), indicating that shade tolerance, in addition to seed tree prevalence, may impact natural regeneration.

Very few studies in the Pacific Northwest have explored the role of understory shrubs on the establishment and growth of natural seedlings, especially under different prescribed levels of overstory cover. Studies from other regions indicated understory vegetation can limit natural regeneration through direct and indirect effects, such as competition and habitat impacts on seed predation (MacLean and Morgan, 1983; Caccia and Balleré, 1998; Roberts et al., 2005; O'Brien et al., 2007; Yildiz et al., 2007; Dodet et al., 2011; Sarr et al., 2011). A preliminary investigation of natural regeneration on one of the sites used in this study showed higher conifer seedling densities 4 years after thinning where residual stands were least dense and understory vegetation had been controlled (Jerra and Vogt, 1998). They also reported an inverse relationship between abundance of natural regeneration after thinning and overtopping by shrubs and ferns. The specific objectives for this study were to determine how (1) overstory stand density, (2) overstory tree distribution (uniform thinning versus thinning with gaps), and (3) reduction of understory vegetation affect the density and height class distribution of naturally-regenerated Douglas-fir and shade-tolerant associates 10–13 years after thinning treatments and understory site preparation. This account provides a snapshot observation of natural conifer regeneration 10–13 years after control of overstory density and understory vegetation in 50-year-old Douglas-fir-dominant stands in two climatic regions of the Oregon Coast Range, USA. We compare performance of natural regeneration with planted seedlings established immediately after overstory thinning, using data from Cole and Newton (2009).

2. Methods

2.1. Study site description

This study included two sites located within the Coast Range Province of western Oregon (Franklin and Dyrness, 1988; Table 1).

2.1.1. McDonald

The McDonald site was located on the eastern flanks of the Coast Range, 8 km north of Corvallis, Oregon. This site is influenced by the warm-summer climate of the Willamette Valley, which is also the source of many exotic and invasive plant species. The warm climate with long, dry summers and low relative humidity provides high moisture stress for planted and naturally-regenerated conifer seedlings. Franklin and Dyrness (1988) postulated that the natural successional sequence of this forest entailed colonization by Oregon white oak (*Quercus garryana* [Douglas ex Hook]), transitioning to Douglas-fir and finally to grand fir (*Abies grandis* [Douglas ex. D. Don] Lindl.) and bigleaf maple (*Acer macrophyllum* Pursh).

The overstory at McDonald was comprised mostly of planted 50-year-old Douglas-fir, with widely scattered groups of naturally regenerated grand fir and scattered bigleaf maple. Prior to planting in about 1940, the site was an open savanna with scattered old growth Douglas-fir and Oregon white oak. At the time of the study-related thinning in 1993, basal areas ranged from 26.7 to 45.1 m^2/ha, averaging 33.9 m^2/ha. Fully stocked Douglas-fir stands (i.e. near culmination of basal area at this age) at this site would have been 48.0–49.0 m^2/ha at age 50 (McArdle et al., 1961). All stands were previously thinned in 1964 and 1980. Although specific details of the thinnings were not available, conventional thinning during those times removed 25–30% of basal area from below. Dominant trees at the time of seedling evaluation ranged from 38 to 44 m in height and were growing vigorously.

Immediately prior to thinning for this study, understory vegetation was generally well-developed and consisted of western sword fern (*Polystichum munitum* [Kaulf] C. Presl.), western bracken fern (*Pteridium aquilinum* (L.) Kuhn), trailing blackberry (*Rubus ursinus* Cham. & Schldl.), Himalaya blackberry (*R. discolor* Weihe and Nees),

Table 1
Description of study sites.

Descriptor	McDonald	Blodgett
County	Benton	Columbia
Location	44°39′N, 123°16′W	46°4′N, 123°21′W
Annual precip (cm)	102–152 (80–85% October–April)	152–200 (80–85% October–April)
Site index$_{50}$ (m)[a]	33.5–39.6	36.6–42.7
Elevation (m)	245–395	270–370
Aspect	NW–N	N–E
Slope (%)	0–60	0–70
Soil series	Price-Ritner complex, Jory silty clay loam	Scaponia-Braun silt loams, Tolke silt loam
Soil subgroup (class)	Dystric Xerochrepts (Price and Ritner), Xeric Haplohumults (Jory),	Umbric Dystochrepts (Scaponia), Dystric Eutochrepts (Braun), Mesic Haplumbrepts (Tolke)
Soil texture	Silty clay loam	Silt loam
Previous thin	1964, 1980	1987
Overstory composition (% BA)	88% *Pseudotsuga menziesii*, 8% *Acer macrophyllum*, 1% *Abies grandis*, 1% *Arbutus menziesii*, 1% *Prunus emarginata*	55% *P. menziesii*, 41% *Tsuga heterophylla*, 3% *Alnus rubra*, 1% *Thuja plicata*
Study planted	January 1994	February 1997

[a] See King (1966).

Pacific poison oak (*Toxicodendron diversilobum* [Torr. & Gray] Greene), hazel (*Corylus cornuta* Marsh.), and ocean spray (*Holodiscus discolor* [Pursh.] Maxim.), with a variety of other species intermixed (Brandeis et al., 2001). Scattered advance regeneration of Douglas-fir and grand fir occurred across the site.

2.1.2. Blodgett

The second site, Blodgett, was located in the northern Oregon Coast Range, 10 km west of Clatskanie, Oregon, and 3 km south of the Columbia River. The Blodgett site is strongly influenced by coastal climate, with a short dry season (July through mid-September). Blodgett typically has higher humidity than McDonald and more total rainfall during the dry season (Johnsgard, 1963). This site is classified by Franklin and Dyrness (1988) as *T. heterophylla* with succession from Douglas-fir to western hemlock/*P. munitum*.

Stands at Blodgett contained 50- to 55-year-old Douglas-fir and western hemlock with widely scattered western redcedar. Red alder was present in small amounts and mostly concentrated along old skid trails. Species mixtures ranged from nearly pure Douglas-fir (95% of overstory BA) to mostly western hemlock (60% of overstory BA). Stands regenerated naturally in old growth clearcuts harvested in the late-1930s. Prior to the study-related thinning in 1995–1996, basal areas ranged from 31.4 to 55.8 m^2/ha, averaging 42.9 m^2/ha. At this age and level of site productivity, stands are considered fully stocked at 48.0–51.4 m^2/ha (McArdle et al., 1961) for Douglas-fir and 66.6–67.5 m^2/ha (Barnes, 1962) for western hemlock. Most stands used for this study were previously thinned in 1987. At the time of seedling evaluation, height of dominant overstory trees ranged from about 44 to 49 m for Douglas-fir and 40–44 m for hemlock. Some advance regeneration of western hemlock was present at the time of study inception, but seedlings were generally <50 cm tall and patchily distributed. Advance regeneration of other conifer species was nearly non-existent. Other understory vegetation included western sword fern, salal (*Gaultheria shallon* Pursh), Oregon grape (*Berberis nervosa* Pursh), vine maple (*Acer circinatum* Pursh), western bracken fern, salmonberry (*Rubus spectabilis* Pursh), deer fern (*Blechnum spicant* (L.) Roth), and red huckleberry (*Vaccinium parvifolium* Smith), with several other species also present.

2.2. Experimental design and treatments

The study was laid out in a randomized complete block, split–split plot design that included three 15-ha (Blodgett) or 20-ha (McDonald) blocks at each site (Fig. 1a). At McDonald, the blocking factor was approximate site quality defined by slope position, with soil depth and site quality increasing on lower slopes. The blocking factor at Blodgett was the level of hemlock present in the overstory, which varied from 16% to 55% of total basal area after thinning.

Each block included two 7.5-ha (Blodgett) or 10.0-ha (McDonald) whole plots (Fig. 1b), and each whole plot was randomly assigned to either a uniform or "gap" thinning pattern. In the uniform thinning, residual trees were relatively evenly spaced throughout the whole plot. The gap thinning incorporated the creation of nine (Blodgett) or twelve (McDonald) 0.10-ha gaps and the same number of 0.06-ha gaps per whole plot into a surrounding "matrix" of relatively evenly spaced trees. Gaps comprised about 20% of the total area in gap-thin plots. The 0.10-ha and 0.06-ha gap sizes corresponded to gap diameter-to-tree height ratios of 0.99 and 0.77, respectively, at McDonald, and 0.86 and 0.67, respectively, at Blodgett, reflecting differences in sites.

Each whole plot contained three (Blodgett) or four (McDonald) 2.5-ha subplots (Fig. 1b), and each subplot was randomly assigned to be thinned from below (i.e. leaving dominant trees) to one of three (Blodgett) or four (McDonald) overstory retention levels (Table 2). Thinning, including gap creation, occurred in fall 1993 at McDonald and in fall/winter of 1995–1996 with yarding completed in fall 1996 at Blodgett using a combination of cable- and ground-skidding equipment. The thinning was designed so that overall basal area for a given retention level was the same in gap-thin and uniform subplots. If insufficient cut was removed from the gaps, then trees were thinned on a uniform spacing around the gaps (matrix areas). This resulted in the "matrix" areas between gaps of a gap-thin subplot being roughly 25% denser than the corresponding uniform subplot, but gap edges received some sidelight from gaps.

The average basal area associated with each retention level differed slightly between sites to account for the higher productivity and greater potential for windthrow at Blodgett (Table 2). The comparatively lower Relative Density Index (RDI; Drew and Flewelling, 1979) at Blodgett reflects the substantial component of western hemlock in the overstory. While relative densities were calculated the same regardless of species mix, the maximum stand density index ($SDI_{max;}$; Reineke, 1933) used to calculate RDI was weighted proportionally by species as described in Shaw (2006). An SDI_{max} of 598 was used for Douglas-fir while 850 was used for western hemlock (Tappeiner et al., 2007), leading to basal areas at Blodgett designed to be slightly higher than at McDonald. No attempts were made to minimize damage to advance regeneration during forest operations and no damage data were collected on advance regeneration following operations.

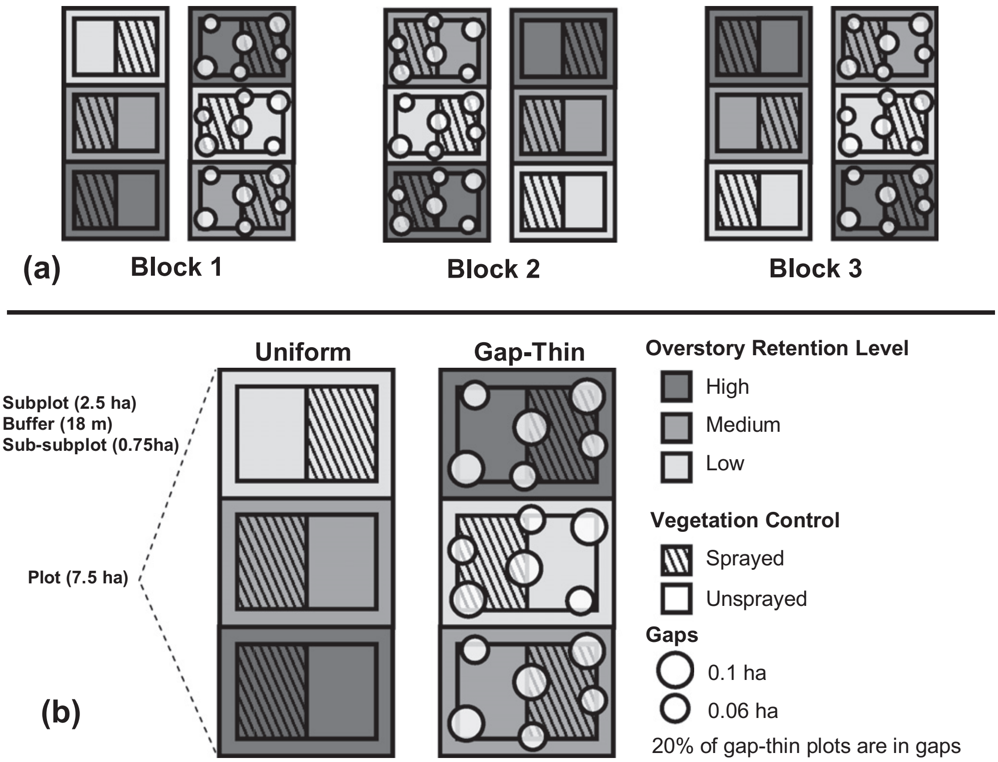

Fig. 1. Study layout at Blodgett. A similar layout was used at McDonald except at McDonald, a fourth overstory retention level (med-high) was included.

Table 2
Post-thinning stand basal areas (BA), relative densities (Curtis, 1982) and relative density index (RDI) (Reineke, 1933) at McDonald and Blodgett Forest installations.

Overstory retention level	McDonald			Blodgett		
	BA (m^2/ha)	Relative density	RDI	BA (m^2/ha)	Relative density	RDI
Low	16.7–18.8	2.6	0.18	18.6–21.1	3.0	0.17
Medium	19.3–25.1	3.3	0.23	24.5–28.2	3.9	0.23
Med-High	26.9–29.6	4.0	0.27	–	–	–
High	27.7–32.9	4.6	0.31	30.8–33.5	4.9	0.27

Each subplot was subdivided into two 0.75-ha (Blodgett) or 0.5-ha (McDonald) sub-subplots plus an 18-m buffer (Fig. 1b). Understory vegetation control treatments were installed in a randomly selected sub-subplot to evaluate the influence of shrubs, herbs, and ferns as competitors as of the time thinning was completed (pre-harvest spray versus no-spray). Herbicide application occurred in late summer 1993 at McDonald and late summer 1995 at Blodgett, at least 1 month prior to thinning. The herbicide treatment applied to most vegetation control sub-subplots at both sites contained a mixture of glyphosate (1.6 kg/ha) and imazapyr (0.14 kg/ha at McDonald or 0.20 kg/ha at Blodgett); sulfometuron (0.16 kg/ha) was added to the mixture at Blodgett and triclopyr (3.3 kg/ha) was also included on plots at Blodgett where evergreen shrubs, primarily salal and Oregon grape, were abundant. All herbicide applications were broadcast uniformly using the "waving wand" method (Newton et al., 2009). Some top kill of advance regeneration of hemlock at Blodgett was noted after application, but little mortality of advance regeneration was observed at either site. Unsprayed sub-subplots and the 18-m buffer had no vegetation manipulation beyond the effects of harvesting.

Vegetation control at Blodgett was, to an unknown extent, somewhat affected by halted logging that necessitated partial repetition of spraying. Although all overstory trees were felled in fall/winter of 1995–1996, saturated soils prevented yarding in ground-skidded units until the following fall. Immediately after completion of yarding in October 1996, we applied sulfometuron at 0.16 kg/ha plus a mixture of butoxy ethanol esters of 2,4-D and diclorprop at a rate of 1.1 kg/ha to each previously sprayed plot to ensure that vegetation control was maintained despite the delay in yarding. Plots with remaining competitive levels of salal also received triclopyr in the spray mixture at 2.2 kg/ha. All herbicide treatments were broadcast applied as uniformly as possible to ensure that understory cover was minimal in all treated plot areas.

Subplots were underplanted at a 3 × 3-m spacing in January 1994 (McDonald) and at 3 × 4-m spacing in February 1997 (Blodgett). At McDonald, the plantations consisted of randomized double rows of Douglas-fir, western hemlock, western redcedar, and grand fir. Randomized double rows of Douglas-fir, western hemlock, and western redcedar were planted at Blodgett. All seedlings were Plug +1 transplants except for western redcedar at McDonald, which were Plug +2 transplants. See Cole and Newton (2009) for a detailed description of planted seedlings and methods of data collection.

The study was originally designed to include future thinnings. The medium and medium–high overstory retention levels at McDonald were re-thinned 8 years after the initial study thinning because seedlings were being suppressed at that time (Cole and Newton, 2009). Across all blocks, these two intermediate retention levels were re-thinned to their original post-thinning density as described in Newton and Cole (2006). The lowest retention level was not re-thinned because seedlings were growing satisfactorily. The highest retention level was not re-thinned because seedlings showed high mortality, and we were concerned about damaging the remaining seedlings with re-thinning. We also wanted to maintain the higher range of densities for monitoring understory development. Damage to natural seedlings was not recorded following the re-thinning but 40% of planted seedlings were damaged by logging (Newton and Cole, 2006). None of the subplots at Blodgett were re-thinned.

2.3. Measurements

Sampling of natural regeneration at both sites was conducted in fall 2006, 13 years after initial study thinning at McDonald and 10 years after thinning was completed at Blodgett. Seedlings >30 cm tall were tallied to evaluate the rate of understory conifer establishment less mortality. Individuals were tallied by 1-m height classes within a fixed distance of previously established, systematically placed (evenly spaced) permanent sample points within each sub-subplot. Five sample points within each sub-subplot at McDonald and seven or eight sample points within each sub-subplot at Blodgett were used during seedling tallies. Within the gap thinning, location of point, gap or matrix, was noted. Numbers of sample points were 22 gap, 98 matrix, and 120 uniform at McDonald, and 28 gap, 111 matrix, and 134 uniform at Blodgett.

Reflecting a principle of variable plot sampling, plot size around each sample point varied somewhat by species and between sites to adapt to large differences in densities of regeneration and of species. At McDonald, seedling tallies were conducted for all species within a 5-m radius of each sample point. At Blodgett, where establishment rates were higher, tallies for Douglas-fir and western redcedar were conducted within a 3-m radius of each sample point, while tallies for western hemlock were limited to a 1.5-m radius following preliminary inspection of a range of these points; different radii for different species reflected orders of magnitude differences in abundance of hemlock and Douglas-fir seedlings.

While conducting seedling tallies, no attempt was made to differentiate between seedlings that established shortly before or after the time of thinning. However, individual saplings over 50 mm diameter had been tagged after thinning and included with overstory tallies. Smaller understory trees obviously greater than 20 years old within the regeneration layer (based on visual observations of branch whorls and bud scars) were also excluded from the tally (understory trees >20 years old were widely scattered at both sites and had minimal influence on the development of the regeneration layer that established around the time of thinning). All others were tallied as natural regeneration for this evaluation, including those that may have been present at the time of thinning. Although many understory trees in this study were greater than 1.37 m tall at the time of measurement, all understory trees in this paper will be referred to as seedlings.

The tallest naturally regenerated seedling of each species on each sample point was measured for total height, and height at each of the previous three annual-height increments (nodes) was recorded to reflect recent growth. Damage was also recorded. In rare instances where the tallest seedling was severely damaged or unhealthy, measurements may have been collected from a slightly shorter seedling if it was determined to be significantly healthier with higher potential for future dominance. Despite this flexibility, many Douglas-fir seedlings measured on both sites had suffered some level of browsing damage. Only seedlings estimated to have established within 2 years of thinning (±2 years) on each sample point were used for height and recent height growth analyses in this paper. These data provided the basis of comparison to growth rates of 10-year-old planted seedlings reported by Cole and Newton (2009). The same measurements as those described above were performed on planted seedlings except seedlings were located along grids rather than on points (see Cole and Newton, 2009, for a full description of the sampling design for underplanted seedlings). Even though natural regeneration data at McDonald were collected 13 years after thinning, to aid comparisons to planted seedlings and between sites, branch whorls were used to estimate year 10 heights.

2.4. Statistical analysis

Analysis of variance (ANOVA) was used to evaluate the effects of thinning pattern, overstory retention level, and vegetation control on the density and frequency of occurrence (percentage of sample points with one or more individuals) of natural seedlings. Height and 3-year height growth rates were analyzed for both natural and planted Douglas-fir and western hemlock. We used PROC MIXED and PROC GLIMMIX in SAS 9.2 (SAS Institute, 2002–2008) to fit a three-way ANOVA model to the data for each species. Means for gaps and the surrounding forest matrix were nested within the gap-thin treatment to determine differences between gaps and the matrix within gap-thin treatments. Analyses were weighted based on the number of points or sample seedlings within the gap, matrix (gap-thin treatments), and uniform areas. Poor survival of both natural and planted Douglas-fir seedlings in the highest density at McDonald Forest eliminated feasibility of analyses of seedlings at this density; hence it was not a part of our analyses for height and height growth, but was included for density and frequency of natural seedlings. Due to differences in the study design and year of study inception between the two sites used in this study, all statistical analyses were conducted independently for each site. Because of differences in sampling methods, natural and planted seedlings within each site could not be compared directly. When applicable, comparisons between sites and between natural and planted seedlings are considered in Section 4.

Several data transformations were necessary to correct issues with non-constant variance (Sabin and Stafford, 1990), which were detected using PROC UNIVARIATE and GPLOT in SAS. Variance in seedling density data at Blodgett tended to increase around larger expected values, requiring a square root transformation. Seedling density data at McDonald included numerous low values leading to non-constant variance that could not be corrected with log or square root transformations. As a result, for Douglas-fir density data at McDonald, sub-subplot averages were ranked and an ANOVA was carried out on ranked data using Friedman's test. An arcsine square root transformation was used on frequency data because a high percentage of data points at both sites fell near zero or one. Because variance increased around larger expected values for height and recent height growth rate, PROC GLIMMIX was used for these variables. For each variable, we tested the following null hypotheses: (1) thinning pattern, (2) overstory retention level, and (3) understory vegetation control have no effect on the (a) density or (b) frequency of occurrence for naturally-regenerated conifers or the (c) height or (d) recent height growth of naturally-regenerated or planted conifers, and (4) no interactions exist between treatments and effects on understory regeneration.

After running each ANOVA to check for treatment effects and interactions, we used the same model to generate least-squares means for transformed seedling density and frequency data within each treatment level. A Tukey HSD adjustment was used to derive p-values and confidence intervals from all multiple comparisons. Although most analyses were conducted on transformed data, to aid comparisons to other studies, seedling densities and frequencies presented in this paper are untransformed means, and seedling heights and recent height growth rates are presented on the original scale.

3. Results

3.1. Seedling densities

3.1.1. McDonald

Thirteen years after initial study thinning at McDonald, natural conifer regeneration was dominated by Douglas-fir, the principal conifer seed source, accounting for 73% of all naturally-regenerated seedlings. Across the study site, an average of 449 naturally-regenerated Douglas-fir seedlings/ha were present 13 years after initial study thinning. At year 4, Jerra and Vogt (1998) observed that most Douglas-fir seedlings (76%) were established within 2 years of thinning for this study, and that eight percent of seedlings (52/ha) had been established before the study thinning. Distribution was variable, with only 44% of 5-m radius sample points containing at least one Douglas-fir seedling. Douglas-fir natural regeneration was affected by overstory density and vegetation control (Table 3), with generally higher densities and frequencies under lower overstory densities and where vegetation had been controlled (Tables 4 and 5). However, the net effect of vegetation control tended to decrease under the highest overstory density (overstory density x vegetation control interaction), where seedling densities and frequencies were low in both sprayed (51 seedlings/ha) and unsprayed sub-subplots (59 seedlings/ha). Thinning pattern (uniform versus gap-thin, whole plot basis) did not have a statistically significant effect on Douglas-fir densities (Table 3). In the absence of vegetation control, a lower proportion of Douglas-fir was generally found in gaps than in the surrounding matrix, but virtually no difference existed when vegetation was controlled (Fig. 2), although this trend was not significant due to high variability.

The shade-tolerant grand fir accounted for 27% of natural regeneration at McDonald, averaging 167 seedlings/ha across the study site despite occurring on only 15% of 5-m radius sample points. Grand fir regeneration was associated with presence of grand fir seed trees, and was irregular and independent of thinning and vegetation control treatment. On sub-subplots where grand fir was present in the overstory (11 of 48 sub-subplots), grand fir dominated understory natural regeneration, comprising 72% of all such seedlings at those locations, with densities ranging from 25 to 2600 seedlings/ha. This relative abundance of grand fir regeneration occurred despite grand fir comprising only 0.1–15% of overstory basal area (4–39 trees/ha) on these sub-subplots. The low rate and irregularity of establishment for grand fir precluded a useful statistical comparison of treatment effects on the density and frequency of this species. Therefore, data are not presented.

The effect of the re-thinning on seedling densities could not be assessed. Observations in the first years after re-thinning indicated that re-thinning did not result in additional establishment of seedlings. Fewer seedlings were found in year 13 than in year 4 (Jerra and Vogt, 1998). Some of the mortality in the re-thinned area (the two middle densities) was attributable to damage from logging operations, especially on plots that were ground skidded. Although we have no information on re-thinning mortality for natural regeneration, 18% of planted Douglas-fir and 8% of planted grand fir seedlings were killed, and an additional 11% and 10%, respectively, were lodged or buried (Newton and Cole, 2006). Although actual numbers of naturally-regenerated seedlings may have been reduced in the medium and medium–high densities by re-thinning, trends across the densities would be maintained, even considering 30% mortality during the re-thinning.

Table 3
ANOVA table for year 10 (Blodgett) or 13 (McDonald) seedling densities and frequency of occurrence. Bold indicates statistical significance at $\alpha = 0.05$. *P*, thinning pattern; *O*, overstory retention level; *V*, vegetation control; *N*, numerator; *D*, denominator.

Effect	d*f*	Density		Frequency	
	N,D	*F*	Pr > *F*	*F*	Pr > *F*
McDonald					
Douglas-fir					
P	2,4	2.02	0.2474	1.44	0.3389
O	3,15	**14.02**	**0.0001**	**8.91**	**0.0012**
P * *O*	6,15	0.51	0.7911	0.17	0.9804
V	1,18	**17.97**	**0.0005**	**8.82**	**0.0082**
P * *V*	1,18	2.00	0.1646	0.48	0.6280
O * *V*	3,18	**3.19**	**0.0484**	1.60	0.2238
P * *O* * *V*	6,18	2.21	0.0903	1.90	0.1367
Blodgett					
Douglas-fir					
P	2,4	0.12	0.8913	0.29	0.7659
O	2,12	0.53	0.6009	0.67	0.5307
P * *O*	4,12	1.26	0.3394	0.72	0.5931
V	1,16	8.11	**0.0116**	**21.04**	**0.0003**
P * *V*	2,16	1.25	0.3136	0.10	0.9092
O * *V*	2,16	0.34	0.7174	0.39	0.6811
P * *O* * *V*	2,16	0.60	0.6655	0.29	0.8783
Western hemlock					
P	2,4	0.77	0.5212	0.29	0.7599
O	2,12	0.46	0.6414	0.05	0.9527
P * *O*	4,12	0.22	0.9214	0.17	0.9486
V	1,16	2.37	0.1436	1.84	0.1933
P * *V*	2,16	0.52	0.6031	0.32	0.7276
O * *V*	2,16	1.33	0.2927	0.54	0.5911
P * O * V	2,16	1.81	0.1767	0.56	0.6963

3.1.2. Blodgett

At Blodgett, shade-tolerant western hemlock regenerated prolifically, reflecting the abundance of this species in the overstory to serve as a seed source; Douglas-fir natural regeneration was present in far lesser amounts. The Blodgett site averaged 1208 Douglas-fir seedlings/ha 10 years after thinning. This species was detected on 68% of 3-m radius sample points. Of the treatments, only vegetation control significantly influenced Douglas-fir seedling numbers (Table 3), with a higher density and frequency of occurrence in sprayed sub-subplots (Tables 4 and 5). Overstory density and thinning pattern had no apparent effect on the density or frequency of occurrence of Douglas-fir 10 years after thinning (Table 3). Although high variability in Douglas-fir densities resulted in non-significant differences between gaps and the surrounding matrix across the study site as a whole, a higher proportion of Douglas-fir seedlings occurred in gaps as overstory densities within the surrounding matrix increased (Fig. 3).

Western hemlock regeneration averaged 51,580 seedlings/ha across the study site 10 years after the study thinning, with 78% of 1.5-m radius sample points containing at least one hemlock seedling. Overstory density, vegetation control and thinning pattern did not have statistically significant effects on hemlock densities or on the frequency of hemlock occurrence 10 years after thinning (Table 3).

Only one 3-m radius sample point contained a single naturally-regenerated western redcedar seedling, suggesting negligible establishment of this species even in the presence of seed sources.

Overall, western hemlock accounted for 98% of all naturally-regenerated conifer seedlings at Blodgett. We found it noteworthy though that in one whole plot where hemlock constituted only five percent of overstory basal area (as compared to 48% across the rest of the study site), equal amounts of hemlock (1722 seedlings/ha) and Douglas-fir (1778 seedlings/ha) natural regeneration were present. This was the only plot with a southwestern exposure, hence drier-than-average microclimate.

Table 4
Comparison of seedling densities per ha across treatment levels 13 (McDonald) or 10 (Blodgett) years after thinning. The numbers shown are untransformed means, but statistical analyses were conducted on ranked (McDonald) or square-root transformed (Blodgett) data. Different letters indicate values within a given factor (i.e., thinning pattern) on each line are significantly different ($p < 0.05$).

	Thinning pattern			Overstory retention level				Vegetation control	
	Gap-Thin								
	Gap	Matrix	Uniform	Low	Medium	Med-Hi	High	Yes	No
McDonald									
Douglas-fir	253 a	515 a	409 a	980 a	486 abc	276 bc	55 c	647 a	261 b
Blodgett									
Douglas-fir	1087 a	1432 a	1055 a	1566 a	1173 a	–	887 a	1649 a	768 b
Western hemlock	23299 a	46161 a	61889 a	44058 a	53840 a	–	56845 a	44648 a	58515 a

Table 5
Frequency of occurrence of at least one seedling on sample points 13 (McDonald) or 10 years (Blodgett) after thinning. The numbers shown are untransformed means, but an arcsine (square root) transformation was used for statistical analyses. Sample points had a 5-m radius at McDonald, a 3-m radius at Blodgett for Douglas-fir and 1.5-m radius at Blodgett for western hemlock. Different letters indicate values within a given factor (i.e., thinning pattern) on each line are significantly different ($p < 0.05$).

	Thinning pattern			Overstory retention level				Vegetation control	
	Gap-Thin								
	Gap	Matrix	Uniform	Low	Medium	Med-Hi	High	Yes	No
McDonald									
Douglas-fir	0.48 a	0.53 a	0.34 a	0.77 a	0.40 bc	0.43 b	0.15 c	0.55 a	0.33 b
Blodgett									
Douglas-fir	0.73 a	0.67 a	0.68 a	0.74 a	0.73 a	–	0.56 a	0.88 a	0.48 b
Western hemlock	0.84 a	0.82 a	0.75 a	0.77 a	0.81 a	–	0.78 a	0.83 a	0.74 a

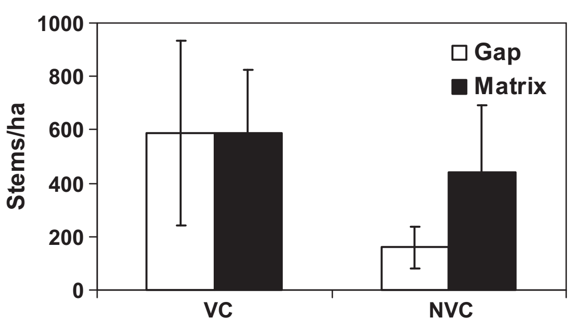

Fig. 2. Mean seedling densities of naturally-regenerated Douglas-fir in gaps and the surrounding forest matrix 13 years after overstory thinning at McDonald. This graph highlights differences in the proportion of Douglas-fir in gaps versus matrix depending on whether competing understory vegetation was controlled. VC, vegetation control; NVC, no vegetation control. Error bars represent ±1 standard error of the mean.

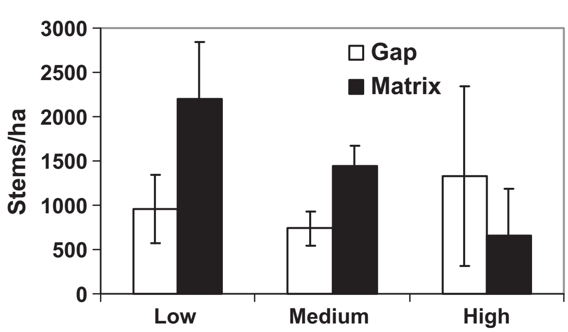

Fig. 3. Mean seedling densities of naturally-regenerated Douglas-fir in gaps and the surrounding forest matrix 10 years after overstory thinning at Blodgett. This graph highlights differences in the proportion of Douglas-fir in gaps versus matrix depending on the level of overstory retention (low, medium, high). Error bars represent ±1 standard error of the mean.

3.2. Height and recent height growth rates of natural and planted seedlings

Statistical comparisons between natural and planted seedlings were not feasible due to differences in sampling protocol. Comparisons are made based upon trends and apparent differences in height and recent height growth.

The height class distribution of natural Douglas-fir at McDonald showed a reverse J-shaped curve, with lowest frequencies in the tallest classes; few trees exceeded 4 m in height 13 years after thinning, and most of those were where vegetation had been controlled, in gaps, or under the lowest overstory density (Fig. 4). Mean heights of the dominant natural Douglas-fir seedlings and all surviving planted Douglas-fir within the same treatment responded about equally to overstory treatments, but planted seedlings were consistently taller than natural seedlings (Table 6). Recent height growth rates appeared similar between natural and planted Douglas-fir (Table 7).

The height class distribution for natural Douglas-fir at Blodgett indicated that this species was favored by vegetation control and low overstory densities, but not by gaps (Fig. 5). Douglas-fir seedlings greater than 2 m tall were not recorded under the highest overstory density. Mean heights of dominant natural Douglas-fir (Table 6) were consistently lower than those of planted Douglas-fir. Both natural and planted Douglas-fir were shorter and had lower recent height growth rates as overstory density increased, but only planted Douglas-fir showed a positive growth response to vegetation control (Tables 6 and 7).

Browsing by black-tailed deer (*Odocoilueus hemionis columbiana*, both sites) and Roosevelt elk (*Cervus elaphus*, Blodgett only) was prevalent and limited height growth of both natural and planted Douglas-fir (see Nabel, 2008). At McDonald, 51% of natural seedlings and 43% of planted seedlings suffered browsing damage within the past 3 years. At Blodgett, browsing damage was observed on 28% of natural seedlings and 29% of planted seedlings. Recent height growth rates of browsed seedlings were significantly lower than undamaged seedlings for all but natural Douglas-fir at Blodgett (Nabel, 2008).

For western hemlock natural regeneration at Blodgett, the height class distribution curve appeared relatively unaffected by

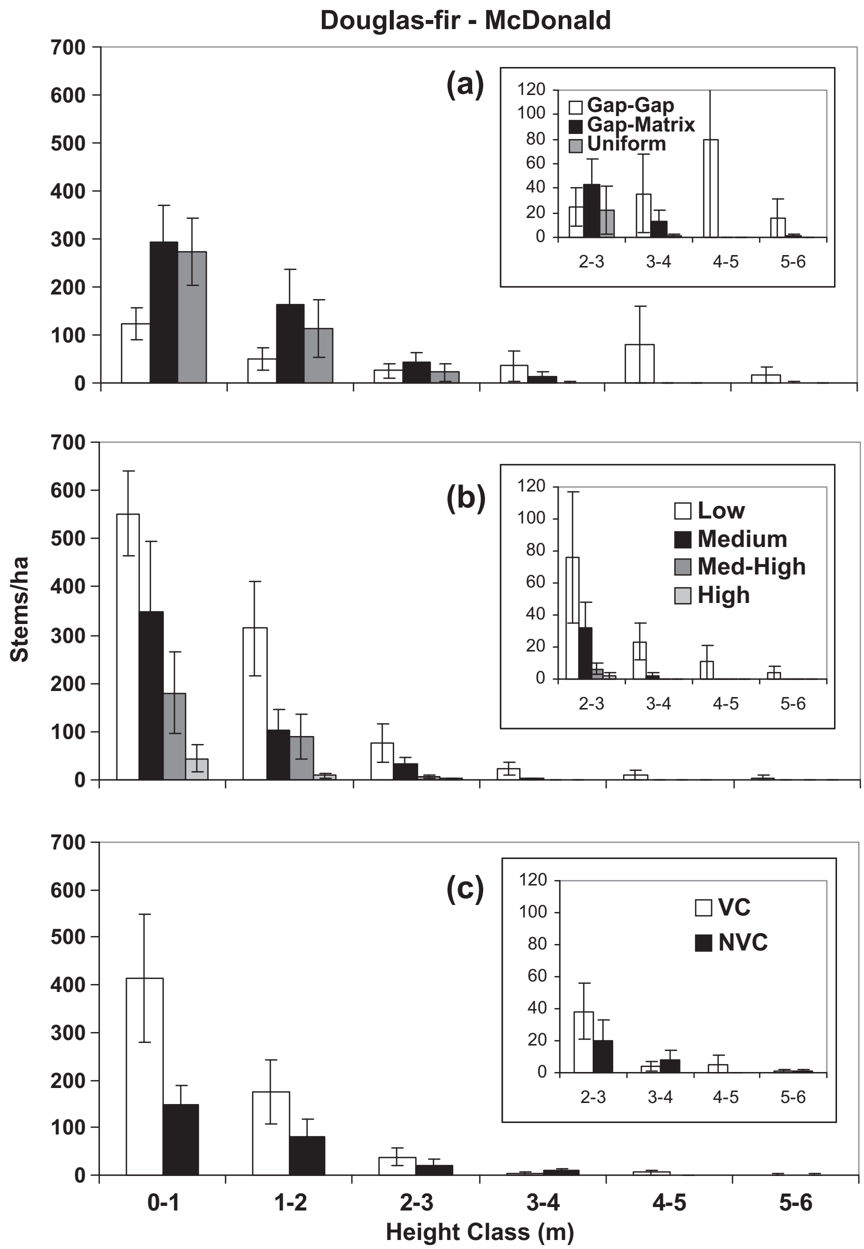

Fig. 4. Height class distribution of naturally-regenerated Douglas-fir at McDonald 13 years after overstory thinning. Comparisons are made between (a) gap-thin and uniform thinning patterns, (b) low, medium, med-high, and high overstory retention levels, and (c) vegetation control and no vegetation control. Insets expand the *y*-axis for taller height classes. Error bars represent ±1 standard error of the mean.

any treatment, except that the relative frequency of the largest height classes appeared greater under lower overstory densities and in gaps (Fig. 6). Heights and recent height growth rates for western hemlock at Blodgett were similar between natural and planted seedlings, as were responses to overstory treatments. Only planted western hemlock responded positively to vegetation control. Browsing damage was minimal (<5%) on natural and planted hemlock. Heights and height growth rates for hemlock appeared higher than Douglas-fir regardless of regeneration method.

4. Discussion

4.1. Species composition

Perhaps the most important of our findings was that, while thinning intensity (McDonald) and vegetation management (both sites) had an influence on Douglas-fir understory regeneration recruitment, differences between sites had a much greater effect on understory structure. Natural regeneration of western hemlock at Blodgett was abundant and vigorous, and far exceeded natural regeneration of Douglas-fir. Although the occurrence of the relatively shade-tolerant grand fir was lower than Douglas-fir at McDonald overall, in areas where grand fir was present in the overstory, even in small amounts, grand fir comprised a higher percentage of the natural regeneration, as was found by Miller and Emmingham (2001). Natural regeneration studies where prevailing cover was dominated by shade-tolerant species have often reported high densities of natural regeneration of those species (Youngblood and Zasada, 1991; re: *Picea glauca* [Moench.] Voss; Newton et al., 1992, re: *Abies balsamea* (L.) Mill. and *Picea rubens* Sarg.; Smith et al., 1997, re: mixtures of northern hardwood species; and Nilsson et al., 2002, re: *Picea abies* (L.) Karst.).

The abundance of western hemlock natural regeneration relative to Douglas-fir at Blodgett was likely caused by a greater number of germinants and a more favorable environment for continued

Table 6
Comparison of mean heights (cm) of 10-year-old planted and 8- to 12-year-old dominant naturally-regenerated conifers across treatment levels. Different letters indicate values within a given factor (i.e., thinning pattern) on each line are significantly different ($p < 0.05$).

	Thinning pattern			Overstory retention level				Vegetation control	
	Gap-Thin								
	Gap	Matrix	Uniform	Low	Medium	Med-Hi	High	Yes	No
McDonald									
Douglas-fir									
Natural	117 a	94 a	86 a	121 a	91 ab	78 b	–	103 a	87 a
Planted	232 a	164 ab	137 b	185 a	163 a	146 a	–	165 a	162 a
Blodgett									
Douglas-fir									
Natural	155 a	120 a	101 a	151 a	117 ab	–	92 b	122 a	113 a
Planted	248 a	182 b	189 b	233 a	201 b	–	171 c	214 a	187 b
Western hemlock									
Natural	393 a	238 a	246 a	354 a	275 ab	–	211 b	287 a	262 a
Planted	334 a	225 a	266 a	336 a	283 b	–	207 c	320 a	228 b

Table 7
Comparison of recent mean annual height growth rates (cm), averaged over the past 3 years, for planted and dominant naturally-regenerated conifers. Different letters indicate values within a given factor (i.e., thinning pattern) on each line are significantly different ($p < 0.05$).

	Thinning pattern			Overstory retention level				Vegetation control	
	Gap-Thin								
	Gap	Matrix	Uniform	Low	Medium	Med-Hi	High	Yes	No
McDonald									
Douglas-fir									
Natural	17 a	16 a	13 a	18 a	15 a	11 a	–	18 a	12 a
Planted	26 a	15 b	11 b	20 a	14 ab	12 b	–	16 a	14 a
Blodgett									
Douglas-fir									
Natural	22 a	16 a	13 a	22 a	14 b	–	12 b	17 a	14 a
Planted	27 a	16 b	18 b	27 a	20 b	–	14 c	23 a	17 b
Western hemlock									
Natural	52 a	31 a	33 a	51 a	37 ab	–	26 b	40 a	33 a
Planted	42 a	25 a	29 a	41 a	33 a	–	21 b	38 a	24 b

survival. Western hemlock produces many more seeds than Douglas-fir, with about 4.5 times as many viable seeds per kg (USDA, 1974). Christy and Mack (1984) reported that western hemlock seeds comprised 84% of the seed rain in stands containing a nearly equal proportion of overstory western hemlock and Douglas-fir. Both species disperse and germinate well in humid sites, but western hemlock germinates more readily under heavier shade (Minore, 1979). Douglas-fir seedling survival is high on a range of sites if competition is slight in the first few years; competition from overstory trees, understory shrubs, and other understory seedlings for light and available soil moisture greatly reduces survival and limits growth (Carter and Klinka, 1992; Brandeis et al., 2001; Drever and Lertzman, 2001; Maas-Hebner et al., 2005; Devine and Harrington, 2008). Hemlock survival is adversely affected by dry conditions, reflecting small seed and a shallow rooting habit (Packee, 1990).

The reproductive potential of shade-tolerant western hemlock in coastal environments can exceed 10,000 seedlings/ha on sites with ground cover and precipitation similar to Blodgett (Berntsen, 1955; Ruth and Harris, 1979; Newton and Cole, 2012). Within 4 years of clearcutting an area surrounded by Sitka spruce (*Picea sitchensis* [Bong.] Carr.), western hemlock, and scattered Douglas-fir seed sources, Berntsen (1955) reported natural seedfall of roughly a million viable seeds per hectare. A small fraction of the seed was Douglas-fir, but most was hemlock (1.0 kg/ha/yr) or spruce (0.9 kg/ha/yr). From this seed-fall emerged 38,816 seedlings/ha, of which half were hemlock. Only 309 Douglas-fir seedlings/ha were observed. This proportion of western hemlock to Douglas-fir is very similar to what we observed in our study. The moisture regimes in the study area described by Berntsen (1955) would have resembled the sites at Blodgett other than one southwest slope on which we observed equality of Douglas-fir and hemlock where Douglas-fir presence as a seed source was far more abundant. Douglas-fir is generally considered more drought-tolerant than western hemlock (Minore, 1979; Sarr et al., 2011), and this coupled with greater Douglas-fir seed sources likely contributed to greater abundance of Douglas-fir regeneration relative to hemlock in that area. In addition, many other factors affect seedling establishment (Burton et al., 2000; Kozlowski, 2002).

The proportionally higher rate of grand fir versus Douglas-fir regeneration at McDonald when grand fir was present in the overstory occurred even though grand fir seeds are twice as heavy as Douglas-fir and have less than a third as many germinants per kg (USDA, 1974). The abundance of grand fir may have been linked to a good seed crop, which occurs more frequently for grand fir than Douglas-fir (Minore, 1979). Also, the adaptable rooting habit of grand fir allows it to survive and grow under a wide range of shade and moisture conditions (Foiles et al., 1990) and compete favorably with Douglas-fir under partial overstories (Maas-Hebner et al., 2005). The heavy seed of grand fir limits dispersal distances (Foiles et al., 1990), explaining the close proximity of grand fir nat-

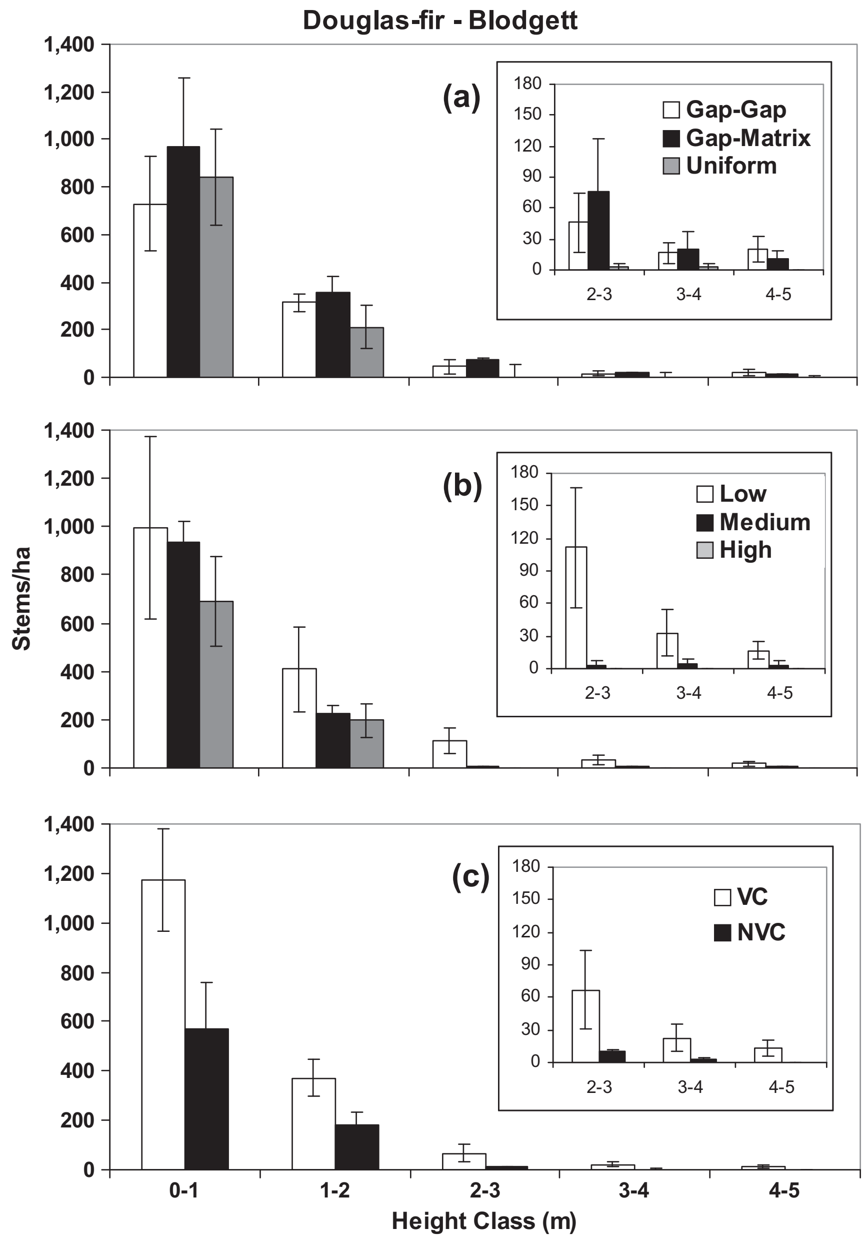

Fig. 5. Height class distribution of naturally-regenerated Douglas-fir at Blodgett 10 years after overstory thinning. Comparisons are made between (a) gap-thin and uniform thinning patterns, (b) low, medium, and high overstory retention levels, and (c) vegetation control and no vegetation control. Insets expand the *y*-axis for taller height classes. Error bars represent ±1 standard error of the mean.

ural regeneration to overstory seed sources in our study. Other studies have also shown the importance of proximity to seed source and seed dispersion mechanisms in controlling regeneration of less common overstory species (Karlsson and Nilsson, 2005; Solarik et al., 2010).

4.2. Overstory effects

Higher overstory densities resulted in lower numbers of Douglas-fir regeneration 13 years after thinning at McDonald, but the effect of overstory density on the abundance of natural Douglas-fir regeneration at Blodgett was not significant 10 years after thinning. Other studies have also shown inconsistent early patterns of understory Douglas-fir regeneration, but generally emphasize importance of reduced overstory densities (Miller and Emmingham, 2001; Chan et al., 2006). Williamson (1973) observed regeneration in 21 stands in the western Cascades of Oregon where shelterwood harvesting to a residual density of 12–112 stems/ha had occurred. Most of these stands were harvested to a lower range of overstory stocking than those in our study. Within this range, natural regeneration of Douglas-fir was generally abundant (550–5000 stems/ha) and inversely related to residual stand densities. Bailey and Tappeiner (1998) also reported higher Douglas-fir densities and frequencies following overstory thinnings with low residual stand densities, but noted low levels of regeneration in some stands with RDI values around 0.25, possibly due to greater presence of competing vegetation, under which natural regeneration was generally absent. In other forest types, Noguchi and Yoshida (2004) and O'Brien et al. (2007) reported declines in conifer regeneration as canopy cover decreased. Regeneration declines in these studies were associated with highly aggressive understory species that thrive under lower levels of canopy cover. Other factors, such as substrate and microsite characteristics, also determined regeneration success.

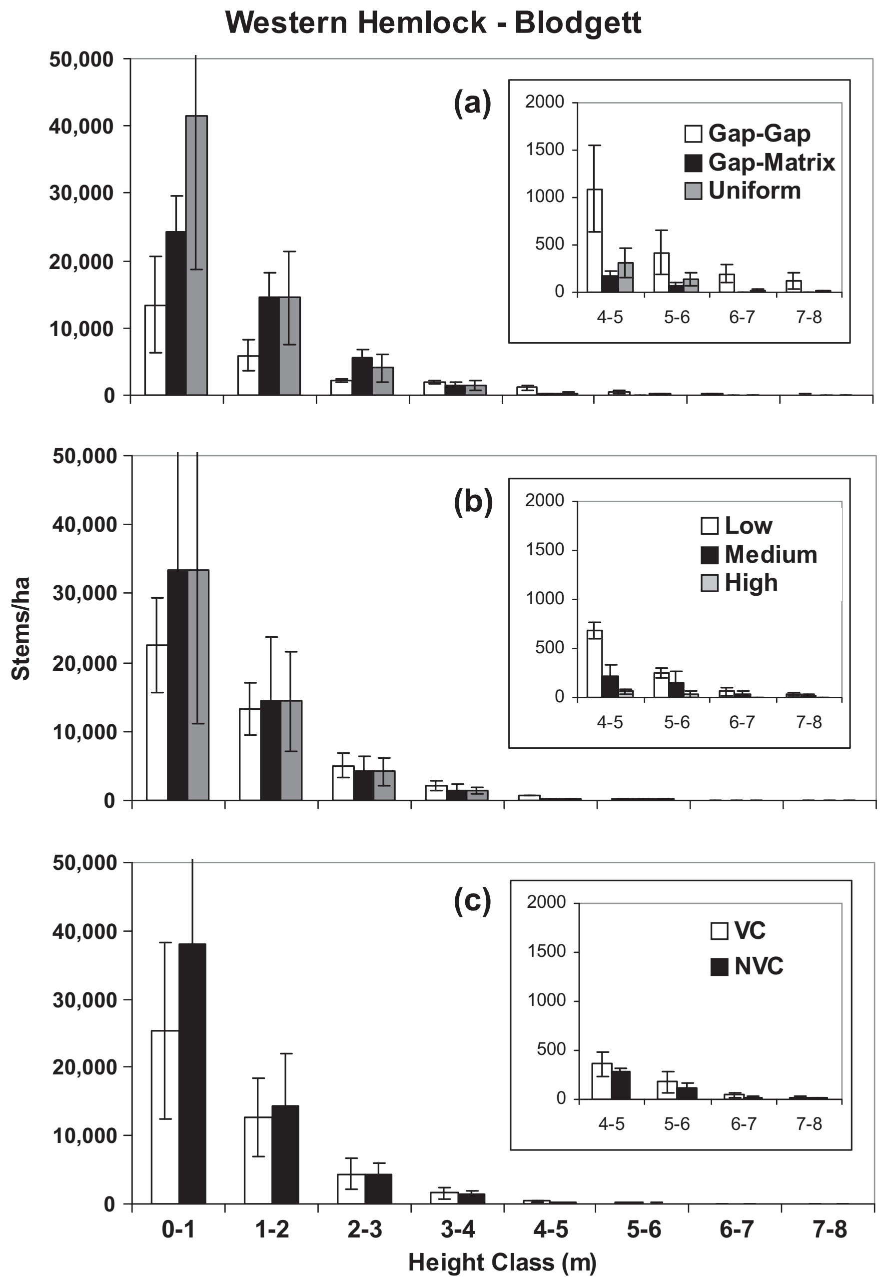

Fig. 6. Height class distribution of naturally-regenerated western hemlock at Blodgett 10 years after overstory thinning. Comparisons are made between (a) gap-thin and uniform thinning patterns, (b) low, medium, and high overstory retention levels, and (c) vegetation control and no vegetation control. Insets expand the *y*-axis for taller height classes. Error bars represent ±1 standard error of the mean.

In a study looking specifically at western hemlock regeneration in western Washington, Williamson and Ruth (1976) noted abundant and potentially excessive levels of regeneration following all levels of overstory thinning, much as we observed at Blodgett. They reported the greatest number of hemlock seedlings under basal areas of 23–44 m^2/ha, a range similar to Blodgett (17–34 m^2/ha), with decreasing seedling densities outside of this range. The lack of a significant overstory density response observed in our study may be due to the apparent ability of western hemlock to establish on a wide range of substrates provided adequate moisture and temperature conditions are maintained during the early stages of seedling development (Packee, 1990).

Net growth of understory conifers is influenced by combinations of overstory density, tolerance of low light, available moisture, and other factors. Heights of both natural and planted Douglas-fir in our study showed positive growth responses to canopy openness (Miller and Emmingham, 2001; Buermeyer and Harrington, 2002), but the degree of response varied somewhat by regeneration method. Although statistical comparisons could not be made, planted Douglas-fir seedlings at both sites were taller than dominant natural Douglas-fir across all levels of overstory competition. The inferior height of natural Douglas-fir relative to its planted counterpart may be a function of the length of time required for a new germinant to achieve seedling status and may also reflect the early competitive advantage of planted seedlings in capturing resources (Pitt et al., 2011).

Contrary to Douglas-fir, no height differences were observed between dominant natural and underplanted western hemlock across the range of overstory densities used in our study. The lack of observed height differences may have resulted in part from our inclusion of natural seedlings that established shortly prior to study inception. It may also have been attributable to the sheer abundance of seed rain and early establishment of hemlock, increasing the probability that seeds with superior genetics found superior microsites and experienced rapid early growth (Solarik et al., 2010). The inverse relationship between overstory density and height was similar between natural and planted hemlock in our study, and corresponds to the findings of other studies (Williamson and Ruth, 1976; Harrington, 2006).

Mason et al. (2004) evaluated several species, including Douglas-fir and western hemlock in underplanting experiments in Great Britain. They demonstrated that under varying levels of overstory, dry weights of hemlock were consistently greater than Douglas-fir, and both species increased with increasing openness of canopy. Harrington (2006) reported greater relative growth rates for hemlock than Douglas-fir for a given level of overstory basal area. Douglas-fir generally requires more light to maintain growth than western hemlock (Carter and Klinka, 1992; Drever and Lertzman, 2001), indicating that western hemlock, whether natural or planted, is the more likely species to achieve dominance in the understory. The competitive growth disadvantage of Douglas-fir was likely compounded in our study by its comparatively limited abundance. These reports all suggest that the ratio of Douglas-fir to hemlock in our study will decline as overstory canopies continue to close and individual hemlock trees establish positions of dominance within the understory.

Reductions in overstory cover in our study led to temporary effects, depending on level of residual cover. Prior to the initial study thinning, crown cover was 40–50% at McDonald (Cole and Newton, unpublished data). Crown cover in stands at McDonald ranged from 28% to 37% following thinning and increased to 40–67% in the first 5 years after thinning. Re-thinning decreased crown cover by 10–20%, and all densities ranged from 43% to 72% 10 years after initial study thinning, indicating that crown cover had returned to or exceeded levels that were present at the time of initial study thinning. Blodgett crown cover at the time of thinning was somewhat greater (55–60%), did not drop as sharply with thinning (33–57%), and ranged from 46% to 63% 10 years after thinning. Our stands were initially thinned to 30–60% of "normal" stocking (McArdle et al., 1961). Only stands thinned to the lowest residual basal areas have retained canopy cover below 50% through the first decade after initial study thinning. Crown expansion and rapid re-occupation of growing space by vigorous 50- to 55-year-old overstory trees in our study demonstrated the challenge of recruiting a second canopy layer during the stem exclusion stage of stand development. At present, all Douglas-fir seedlings are growing at rates reflecting severe suppression when compared to open grown seedlings on similar sites (Harrington et al., 1995; Stein, 1997; Rose et al., 2006). In our study, rates of overstory canopy development even at the lowest densities may well preclude midstory development that maintains a significant component of Douglas-fir, whether planted or natural, especially on drier sites.

In addition to affecting light levels, presence of an overstory can also affect competition for belowground resources. Although competition for nitrogen was not considered limiting, Devine and Harrington (2008) found that competition for soil water from edge trees limited Douglas-fir sapling growth in Washington. Our study was not designed to separate the confounding effects of the overstory on light and moisture competition, but the overstory was certainly having effects on soil water availability.

4.3. Role of gaps in overstory

In our study, gaps favored high frequencies of tall Douglas-fir seedlings at McDonald, but not overall abundance 13 years after gap creation (Fig. 4). Ten years after gap creation at Blodgett, Douglas-fir showed little response to gaps, but gaps led to high frequencies of tall hemlock (up to 8 m, Fig. 6). The high frequency of tall hemlock occurred despite consistently fewer seedlings overall (1.4–2.1 times fewer) in gaps proper relative to the surrounding forest matrix (Table 4), perhaps the result of self-thinning among the larger individuals in gaps or lower recruitment initially.

Several studies have compared seedling establishment and/or growth between gaps with total overstory removal to surrounding stands with partial or no overstory removal (Gray and Spies, 1996, 1997; Wright et al., 1998; Coates, 2002; Zhu et al., 2003; Grassi et al., 2004; Prévost et al., 2010; Otto et al., 2012). In the Pacific Northwest, Coates (2002) noted higher seedling recruitment for western hemlock and other species in canopy gaps than in the adjacent undisturbed forest 5 years after thinning. Gray and Spies (1996) reported higher Douglas-fir and western hemlock establishment in gaps and higher growth rates than under neighboring closed canopy forest 2 years after gap creation. Wright et al. (1998) observed that gaps of only 0.06 ha favored western hemlock emergence over several species in the first year emergence for hemlock was lower in the second year of that study. Emergence was greatest on the shady (south) side of the gaps. Sample points in our study were not located as transects across gaps, so we were not able to examine if microsite differences, such as distance from gap edge, affected seedling regeneration or growth as has been found in other studies (Gray and Spies, 1996; Wright et al., 1998; Coates, 2002; Zhu et al., 2003; Grassi et al., 2004; Prévost et al., 2010; Otto et al., 2012).

Results from our study and from the aforementioned studies demonstrate the important role gaps play not only in perpetuating shade-intolerant species, but also in promoting the rapid growth of climax species into positions in the midstory, leading to greater structural diversity (Wang and Liu; 2011). In managing gaps over time, Schütz (2002) highlighted the importance of expanding gaps when trees reach the pole stage to maintain H:D ratios capable of handling heavy snow loads.

4.4. Understory vegetation management

Douglas-fir natural regeneration was more abundant at both sites where sprayed (except under the highest overstory density), but hemlock natural regeneration was not favored significantly where vegetation control occurred. The greater abundance of Douglas-fir following spraying was not surprising given the general negative relationship between understory vegetation cover and seedling establishment reported in other studies (Bailey and Tappeiner, 1998; Caccia and Balleré, 1998; O'Brien et al., 2007; Yildiz et al., 2007; Man et al., 2009). Both of our study sites had abundant sword fern cover before herbicide application and little in following years where treated (Newton et al., 2009). Sword fern often dominates understory cover on rich sites, producing heavy deposits of frond litter annually that could limit conifer seedling establishment (Jerra and Vogt, 1998), especially beneath low-density overstories.

Vegetation control in the context of interactions with other treatments provided initial growth-benefits most prominently for planted hemlock at Blodgett, but planted Douglas-fir seedlings at Blodgett were also significantly larger at age 10 where vegetation had been controlled. Understory vegetation can negatively affect growth of both natural and planted seedlings growing under canopies (Harrington, 2006; Nilsson et al., 2006; Man et al., 2009; O'Brien et al., 2007; Pitt et al., 2011), and studies (Brandeis, 1999; Harrington, 2006; Devine and Harrington, 2008) examining light and water relations indicated complex interactions that vary with overstory, understory vegetation, and species of regeneration. For instance, Harrington (2006) reported that overstory competition would limit the growth responses of Douglas-fir seedlings to vegetation control, but response of western redcedar and hemlock would be largely unaffected. Benefits to soil water availability from vegetation control decreased as overstory increased, although competition for light was considered the primary factor affecting seedling growth.

4.5. Other factors

Height and recent height growth of Douglas-fir appeared lower than western hemlock at both sites. Although the relative shade tolerance of the two species was a factor, Douglas-fir was heavily browsed by deer and/or elk, whereas browsing on hemlock was minimal (Brandeis et al., 2001; Nabel, 2008; Cole and Newton, 2009). Browsing levels on Douglas-fir and western hemlock on different sites in Oregon were highly localized. Maas-Hebner et al. (2005) reported <10% of underplanted seedlings browsed, while Burney and Jacobs (2011) found that first-year browsing ranged from 12% to 70% for western hemlock and from 1% to 52% for Douglas-fir on three or four sites, respectively, in western Oregon. Impacts on growth have been related to severity of browsing, with year 4 Douglas-fir volume decreases ranging from 23% to 45% (Newton and Cole, 2005). Browsing can be severe enough to minimize the effects of light and moisture competition and alter species composition (Ammer, 1996). On our sites, planted seedlings were mostly taller than 1.5 m and out of range of browsing, but natural Douglas-fir were still within reach and may continue to be affected by browsing.

Scarification improves germination of natural regeneration (Wurtz and Zasada, 2001; Nilsson et al., 2006; Prévost et al., 2010; Solarik et al., 2010), and ground disturbance during logging impacts regeneration. Although ground disturbance due to logging varied based on thinning intensity on our study sites, it was also related to the use of ground- versus cable-yarding systems. At each of our study sites, two whole plots (one each in the gap and uniform thinning) were thinned using ground-based equipment, with the exception of one subplot at McDonald. Although ground disturbance may have been a factor in initial seedling establishment, we did not find greater numbers of seedlings 10 and 13 years after thinning associated with subplots that were yarded using ground-based equipment versus cable systems. Observations indicated that the additional ground disturbance from the re-thinning at McDonald did not result in additional regeneration, but we do not know if that was due to inadequate seed fall, seed predation, poor germination conditions, or other factors affecting seedling survival.

Douglas-fir seedling populations have apparently decreased slowly in the 9 years since Jerra and Vogt (1998) summarized natural regeneration at McDonald. Both seedling densities and the proportion of inventory points with at least a single Douglas-fir seedling have declined by about one-third. Recruitment apparently came in a wave that lasted less than 3 years. Newton et al. (2009) observed that understory vegetation had not fully re-established in 3 years, hence limits on further recruitment beyond that are unknown.

5. Summary and conclusions

Results from our study demonstrated varying potentials for natural conifer regeneration to contribute to the development of a multilayered canopy in thinned second-growth Douglas-fir-dominant stands. The patchy distribution and slow growth of natural Douglas-fir regeneration, especially under higher overstory densities, suggested this species was unlikely to contribute many individuals to a position in the midstory outside of gaps. Even the most vigorous Douglas-fir seedlings found in gaps in our study were growing at approximately half of site potential. Gaps larger than those used in our study would be required to expedite the growth of Douglas-fir, and management of other species of understory trees (i.e., western hemlock) in gaps may be required unless the seed source is removed from the overstory prior to gap creation. Underplanting Douglas-fir and/or controlling competing understory vegetation may increase the contribution of this species to the midstory, given appropriate management of the overstory.

Attainment of a multilayered coniferous canopy is more likely in stands containing a western hemlock seed source. In our study, western hemlock regenerated prolifically across all levels of overstory thinning regardless of whether competing vegetation was controlled. Many individuals, especially those under lower overstory densities and in gaps, were >5 m tall 10 years after thinning and still adding >50 cm of height growth annually. If these growth rates continue, stands could be approaching the Oregon Department of Forestry definition of "layered" within 30 years (Oregon Department of Forestry, 2001). Underplanted hemlock performed similarly to natural hemlock, suggesting little benefit to planting this species in stands where natural regeneration is expected. Pre-commercial thinning of an overly dense understory hemlock layer may enhance the growth of prospective crop trees and promote a more diverse shrub and herbaceous layer. If a mix of understory hemlock and Douglas-fir is desired, an overstory comprised of 95% Douglas-fir and 5% western hemlock showed potential for recruiting near equal amounts of these species on a southwestern exposure with drier-than-average microclimate.

The relative shade tolerance and low palatability of grand fir offer the possibility for this species to establish a midstory in stands containing a more significant seed source than those used in our study. Incidental observation of grand fir at one of our study sites suggested this species would regenerate readily under lower overstory densities with a well-distributed seed source.

Growth of the overstory at this point will set the stage for future development of understory conifers. Seedlings under all overstory conditions were growing under a relatively young, vigorous canopy that exhibited rapid change and increasing crown closure following thinning. Development of a canopy is predictable, with level of closure dependent on overstory stocking, tree age, and site quality. Data from Newton and Cole (1987) suggested that future overstory growth under all retention levels used in our study will eventually suppress understory conifer growth to levels associated with high mortality (Brandeis et al., 2001; Cole and Newton, 2009). In that study, stands thinned more heavily than ours at ages 50–70 reached >70% full stocking at age 140 or earlier, at which time understory conifers were virtually absent and remain so. Additional thinning to reduce overstories, concentrating overstories in clumps, or creation of substantial gaps would be required to maintain minimal levels of vigor in understory conifers. Such thinning would require strategies to fell trees away from locations where regeneration exists to avoid excessive damage to future structural trees (Newton and Cole, 2006). Consideration of the desired composition, density, distribution, and growth rate of understory trees over a term of several decades would be important when planning additional overstory thinnings designed to release regeneration.

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