

Understory vegetation response to thinning disturbance of varying complexity in coniferous stands

Ares, Adrian^{*1}; Berryman, Shanti D.^{1,2} & Puettmann, Klaus J.^{1,3},

¹Department of Forest Ecosystems and Society, 321 Richardson Hall, Oregon State University, Corvallis, Oregon, USA 97331;

²E-mail berryman@fastmail.fm;

³E-mail klaus.puettmann@oregonstate.edu;

*Corresponding author; Fax +1 5417371393; E-mail adrian.ares@oregonstate.edu

Abstract

Question: Can augmented forest stand complexity increase understory vegetation richness and cover and accelerate the development of late-successional features? Does within-stand understory vegetation variability increase after imposing treatments that increase stand structural complexity of the overstory? What is the relative contribution of individual stand structural components (i.e. forest matrix, gaps, and leave island reserves) to changes in understory vegetation richness?

Location: Seven study sites in the Coastal Range and Cascades regions of Oregon, USA.

Methods: We examined the effects of thinning six years after harvest on understory plant vascular richness and cover in 40- to 60-year-old forest stands dominated by Douglas-fir (*Pseudotsuga menziesii*). At each site, one unthinned control was preserved and three thinning treatments were implemented: low complexity (LC, 300 trees ha⁻¹), moderate complexity (MC, 200 trees ha⁻¹), and high complexity (HC, variable densities from 100 to 300 trees ha⁻¹). Gaps openings and leave island reserves were established in MC and HC.

Results: Richness of all herbs, forest herbs, early seral herbs and shrubs, and introduced species increased in all thinning treatments, although early seral herbs and introduced species remained a small component. Only cover of early seral herbs and shrubs increased in all thinning treatments whereas forest shrub cover increased in MC and HC. In the understory, we found 284 vascular plant species. After accounting for site-level differences, the richness of understory communities in thinned stands differed from those in control stands. Within-treatment variability of herb and shrub richness was reduced by thinning. Matrix areas and gap openings in thinned treatments appeared to contribute to the recruitment of early seral herbs and shrubs.

Conclusions: Understory vegetation richness increased 6 years after imposing treatments, with increasing stand complexity mainly because of the recruitment of early seral and forest herbs, and both low and tall shrubs. Changes in stand density did not likely lead to competitive species exclusion. The abundance of potentially invasive introduced species was much lower compared to other plant groups. Post-thinning reductions in within-treatment variability was caused by greater abundance of early seral herbs and shrubs in thinned stands compared with the control. Gaps and low-density forest matrix areas created as part of spatially variably thinning had greater overall species richness. Increased overstory variability encouraged development of multiple layers of understory vegetation.

Keywords: Ecological disturbance; Forest density management; Plant species richness; Stand structural complexity; Understory vegetation.

Nomenclature: USDA-NRCS (2005).

Abbreviations: DBH = Diameter at breast height; DMS = Density management study; HC = High complexity treatment; ISA = Indicator species analysis; IV = Species indicator values; LC = Low-complexity treatment; MC = Moderate-complexity treatment; MRPP = Blocked multi-response permutation procedure; NMS = Non-metric multi-dimensional scaling ordination; PNW = Pacific Northwest.

Introduction

Human interventions into forest landscapes often lead to increased structural, compositional and functional homogeneity (Halpern & Spies 1995; Peltzer et al. 2000; Wikstrom & Eriksson 2000).

Forests regenerated after clear-cut harvest commonly lack the variability found in stands that developed after natural disturbance. Thus, forest structure, diversity and function are commonly simplified in managed stands following conventional silvicultural practices (McComb et al. 1993; deMaynadier & Hunter 1995). Adoption of new forest ecosystem paradigms world-wide has brought forward the need for management strategies that mimic natural succession dynamics and enhance biodiversity (Attiwill 1994; Bergeron & Harvey 1997; Humphrey 2005; Puettmann & Ammer 2007). Knowledge about consequences of these alternative silvicultural practices on forest ecosystems is still limited and long-term field testing is needed to evaluate rate and quality of the response to novel management approaches (Poage & Tappeiner 2002; Schuler et al. 2002; Vallauri et al. 2002; Larsen & Nielsen 2006).

Understory vegetation is a major contributor to plant diversity in forests. Changes in forest overstory composition, structure and spatial complexity would have significant effects on understory species richness and abundance because of the consequent shifts in resource availability and competitive relationships (e.g. release response of clonal shrubs and other species) (Berger & Puettmann 2000; McKenzie et al. 2000; Thysell & Carey 2001; Beggs 2005). Stand density reductions may contribute to increased recruitment of early-seral and disturbance-related species and/or increased introduced species that would alter the understory composition and diversity (Puettmann & Berger 2006; Davis et al. 2007; Macdonald & Fenniak 2007). Post-harvest residual fine and coarse woody detritus accumulation combined with ground disturbance may also affect the understory vegetation (Halpern & Spies 1995; Roberts & Gilliam 1995; Fahey & Puettmann 2007).

Thinning regimes of varied intensity and spatial configuration have produced different effects on understory richness and abundance (often indexed by plant cover). Understory plant diversity sometimes increases following thinning (Wienk et al. 2004; Metlen & Fiedler 2006), supposedly through reduced competition of overstory trees. Only in a few cases, however, was this increase linked to increased light availability (Harrington & Edwards 1999; Son et al. 2004). Time lags in vegetation response to understory light conditions and physical disturbance during thinning may be responsible for a lack of relationship between increased light and understory vegetation diversity (Thomas et al. 1999). In other cases, thinning influenced plant species diversity negatively because of the effects of

harvesting on specific plant groups such as forbs (Nagai & Yoshida 2006) or increased dominance by a few species (Alaback & Herman 1988). In studies with simultaneous surveys of understory vegetation richness and cover, thinning led to increased richness but not cover (Dodson et al. 2008), both richness and cover (Thysell & Carey 2001; Zenner et al. 2006), neither cover nor richness (Nelson et al. 2008) and cover but not richness (Bauhus et al. 2001). In other instances, invasions of introduced species could be accelerated by thinning (Davis et al. 2000; Harrod 2001).

In the Pacific Northwest (PNW) region of the US, forest management has changed to incorporate ecological goals into management plans. Historically, forests were managed primarily for timber with the purpose of maximizing economic value. As a consequence, a vast area of the PNW is covered by regenerated plantations that are relatively homogeneous and typically dominated by young Douglas-fir (*Pseudotsuga menziesii* (Mirb) Franco) (USFS 2002). These dense forests do not provide much habitat for understory plant species and other organisms (Spies 1991; Rambo & Muir 1998; Drever & Lertzman 2003). The Density Management Study (DMS; Cissel et al. 2006) aims to determine if alternative silvicultural thinning treatments improve biodiversity at the stand level and accelerate the development of late-successional structural characteristics in young Douglas-fir stands of western Oregon. Such features include large trees, multiple vegetation layers, standing dead wood (e.g. snags), downed coarse woody detritus and well developed and diverse understory vegetation (Franklin & Spies 1991).

Based on the underlying assumption of the DMS that increased diversity and abundance of the understory layer results in improved wildlife habitat and higher overall stand-level biodiversity (Muir et al. 2002; Sullivan et al. 2005; Hagar 2007), the first objective of this study was to determine the understory vascular plant vegetation response to different thinning intensities 6 years after thinning treatments that resulted in a range of variability in overstory conditions. We therefore examined treatment effects on (1) mean cumulative richness and cover of understory herbs and shrubs in four plant groups (early seral, forest understory, late seral and introduced species); and (2) understory community composition. The second objective was to test whether understory communities were more variable within more spatially variable treatments. To address this objective, we compared the within-treatment variability in understory plant richness

and cover among the treatments. The third objective was aimed at understanding stand variability (as described for objective (2) and compare the relative contribution of individual stand structural components such as forest matrix (i.e. thinned forest area that surrounds permanent openings), gaps, and leave island reserves to changes in community composition and diversity.

Methods

Study area and design

This study encompasses seven sites located in western Oregon on Bureau of Land Management lands (Fig. 1). Four sites are in the Oregon Coast Range, two sites are in the foothills of the Cascade Range and one site is in the Willamette Valley near the fringe of the Coastal Range (Table 1). Mean annual rainfall in this study area ranges from 1351 to 2192 mm with little precipitation in the summer months (June-August) (USDA NRCS 1999). Selection criteria included homogenous conifer dominated stands (mainly by Douglas-fir) in the age class 40-60 years and a minimum of 81 ha of contiguous forest. These sites were treated as replicates and defined the scope of inference of the study. As a tradeoff, among-site and within-site variation in topography (especially aspect and slope) and in the

dominant understory plant communities was quite large. The two sites in the Cascade Foothills (Delph Creek and Keel Mt) have more western hemlock, *Tsuga heterophylla* (Raf.) Sarg., than sites on the Coast Range. Hardwood trees were a minor component of the overstory stands and were preferentially reserved during harvest. Common hardwoods were *Acer macrophyllum* Pursh, *Alnus rubra* Bong, *Corylus cornuta* Marsh, *Arbutus menziesii* Pursh, *Frangula purshiana* (DC.) Cooper and *Chrysolepis chrysophylla* (Douglas ex Hook.) Hjelmq.

Several sites had been thinned 20-40 years ago and/or fertilized (Table 1; see Cissel et al. 2006 for comprehensive site history details). Pre-treatment data or data characterizing actual disturbance from harvesting, such as ground compaction and slash were not available. The effects of thinning treatments were therefore assessed by comparison with an unthinned control. Tree density and tree basal area information are presented in Table 2. One unthinned control was preserved at each site with areas ranging from 16 to 25 ha (Table 2). Three thinning treatments comprising 14-58 ha each were implemented at each site: (1) high density, low complexity (LC, 300 trees ha⁻¹), (2) moderate density and complexity (MC, 200 trees ha⁻¹) and (3) high complexity (HC, variable densities). The LC treatment was lightly thinned and 3-13% of the stand areas (the total area varied by site) were left

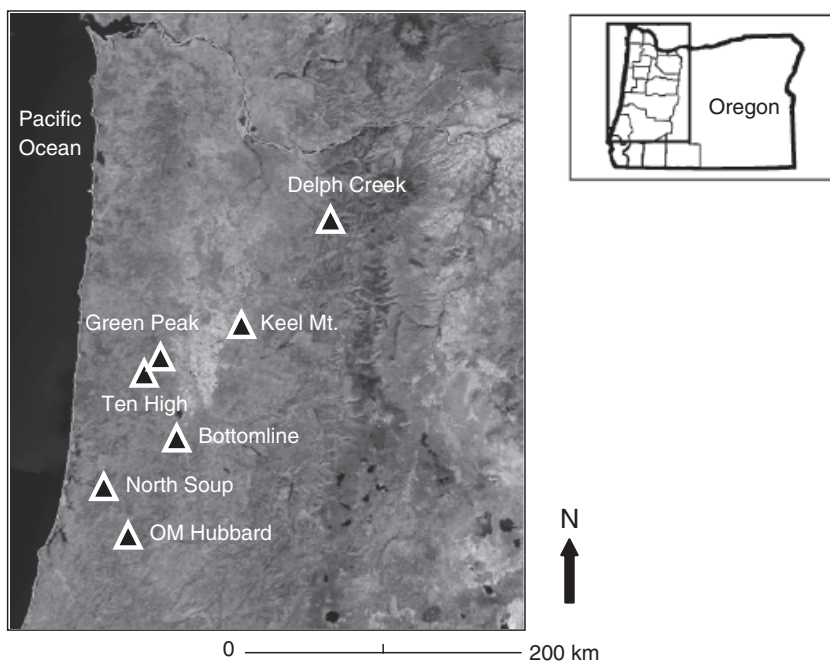


Fig. 1. Location of the study sites in Oregon, USA.

Table 1. Environmental characteristics and pre-harvested features of the experimental sites in Oregon, USA. Ranges represent variation within sites. ^aElevation and slope were measured at the 0.1-ha vegetation plot center. ^bPrecipitation was estimated from PRISM data for the period 1980–2005. ^cPOMU = *Polystichum munitum* Kaulf. C. Presl, VAPA = *Vaccinium parvifolium* Sm., RUUR = *Rubus ursinus* Cham. & Schlecht., GASH = *Gautheria shallon* Pursh, VISE = *Viola sempervirens* Greene, MYMU = *Mycelis muralis* L. Dumort, OXOR = *Oxalis oregana* Nutt., GATR = *Galium triflorum* Michx., MANE = *Mahonia nervosa* (Pursh) Nutt., VIOLA = *Viola* sp., TRBOL = *Trientalis orientalis* spp. *latifolia*, PTAQ = *Pteridium aquilinum* (L.) Kuhn), WHMO = *Whipplea modesta* Torr., HIAL = *Hieracium albiflorum* Hook., FEOC = *Festuca occidentalis* Hook., OXSU = *Oxalis suksdorfii* Trel., LUPA = *Luzula parviflora* (Ehrh.) Desv., COCOC = *Corylus cornuta* Marsh. var. *californica* (A.DC.) Sharp. ^dLC = Low complexity, MD = Medium complexity, HD = High complexity.

	Delph Creek	Keel Mountain	Green Peak	Ten High	O.M. Hubbard	North Soup	Bottomline
Ecoregion	Cascade Foothills	Cascade Foothills	Coast Range	Coast Range	Coast Range	Coast Range	Coast Range, edge of Willamette Valley
Latitude, longitude	45°15'56"N, 122°9'33"W	44°31'41"N, 122°37'55"W	44°22'00"N, 123°27'30"W	44°16'50"N, 123°31'06"W	43°17'30"N, 123°35'00"W	43°33'57"N, 123°46'38"W	43°46'20"N, 123°14'11"W
Elevation (m) ^a	553–725	576–798	514–738	430–710	341–798	162–426	210–528
Mean annual precipitation (mm) ^b	1937	1823	1949	2192	1351	1684	1256
Slope (%) ^a	0–60	3–35	0 to > 60	0 to > 60	3–87	0–60	8–42
Size (ha)	120	90	103	130	89	81	100
Most abundant understory vascular plant species ^c	POMU, VAPA, RUUR, GASH, VISE, MYMU	VAPA, POMU, OXIR, GATR, MANE, VIOLA	GATR, TRBOL, POMU, MANE, GASH, PTAQ	POMU, RUUR, VAPA, TRBOL, MANE, GASH	WHMO, HIAL, RUUR, TRBOL, POMU, FEOC	POMU, GATR, OXSU, RUUR, MANE, LUPA	POMU, RUUR, GATR, PTAQ, VIOLA, COCOC
Harvest date	April 2000	December 1997	January 2000	April 1998 to March 2000	September 1997	August 1998	September 1997
Stand age at harvest (yr)	53	44	56	44	39	48	55
Harvesting method ^d	LC: cable MC: ground HC: ground	LC: cable MC: ground HC: ground	LC: cable MC: cable, ground HC: cable	LC: cable MC: cable HC: cable	LC: cable, ground MC: cable, ground HC: ground, cable	LC: cable MC: cable HC: cable	LC: cable MC: cable HC: cable
Management history	Pre-commercial thin in 1974	Pre-commercial thin in 1964, and 1972	None	Pre-commercial thin in 1972	Pre-commercial thin in 1970, fertilized	Fertilized	None
Site index at year 50 (King 1966)	37	39	37	38	36	40	42

Table 2. Ranges within sites of tree density and basal area 6 yr after harvest in the experimental sites in Oregon, USA. LC = Low complexity, MD = Medium complexity, HD = High complexity.

Treatment	Delph Creek	Keel Mountain	Green Peak	Ten High	O.M. Hubbard	North Soup	Bottomline
Tree density (number ha ⁻¹)							
Unthinned	337–654	376–802	238–762	406–1168	584–1446	159–822	238–525
LC	198–634	158–555	168–584	149–406	178–901	99–564	119–505
MC	139–574	0–772	0–654	0–555	79–832	0–1347	99–327
HC	79–465	20–495	50–495	10–347	20–624	0–545	79–505
Tree basal area (m ² ha ⁻¹)							
Unthinned	57–85	67–83	47–85	52–79	33–57	33–82	22–54
LC	31–108	33–60	39–77	24–62	20–61	17–58	25–86
MC	20–80	0–70	0–62	0–58	13–44	0–66	10–57
HC	18–74	0–81	9–73	0–47	3–38	0–59	19–64

unthinned in circular leave island reserves of 0.1, 0.2 and 0.4 ha. The MC treatment was thinned to a moderate density with 4-18% of the stand cut in circular gap openings and 4-13% of the stand left unthinned in circular leave island reserves (0.1, 0.2 and 0.4 ha in size for both gaps and leave islands). The HC complexity treatment was designed to create maximum spatial variability within the treatment areas and included three densities: 25-30% in light thin, 300 trees ha⁻¹; 25-30% in moderate thin, 200 trees ha⁻¹; and 8-16% in heavy thin, 100 trees ha⁻¹. In addition, 4-18% of the area was in circular gap openings and another 4-18% was left in leave island reserves. Gaps and leave islands in all treatments were 0.1, 0.2 and 0.4 ha in size. Thinning was completed between 1997 and 2000 and thinning treatments were not replicated at each site but across sites.

Vegetation plots

Seventy-seven, permanent 0.1-ha circular overstory plots were installed 6 years after harvest to document the overstory conditions. Plot locations were randomly selected using GIS (ArcGIS, Redlands, CA, US) with 21 plots within the LC, MC and VC treatments and 14 plots in the control. Plots were located to avoid overlapping and were at a minimum distance of 15.2 m from other plots and treatment boundaries. Plots on active roads were shifted to areas adjacent to the road. Inactive roads and skid trails were considered part of the stand and included in the study. Four 0.002-ha circular vegetation subplots were installed permanently at 9.1 m in each cardinal direction from overstory plot centers.

Vegetation measurements were scheduled to be taken 5-6 years after thinning and occurred during June-September 2003 at Keel Mountain, Bottomline and O.M. Hubbard, July-September 2004 at North Soup, and June-October 2005 at Delph Creek, Green Peak and Ten High. All trees in the overstory plot with a diameter ≥ 5 cm at breast height (1.3 m above ground; DBH) were tagged and measured to characterize overstory density, composition and structure. Understory vegetation was measured in the 0.002 ha subplots. Total vegetation cover was visually estimated for each understory plant species in the vegetation subplots to the nearest cover class (i.e. 1% = trace, 5%, 10%, 20% and continuing in 10% increments). Overstory trees and shrubs >6 m tall were not considered part of the understory and excluded from cover measurements. Cover by plant life form and substrate groups were also estimated in

the subplots. Plant taxonomic nomenclature followed the USDA Plant Database (USDA-NRCS 2005).

Data analysis

Stand-scale response of understory vegetation

We tested differences among thinning treatments using a mixed-model ANOVA in SAS 9.0 (Cary, NC, US) for (1) mean understory cumulative cover and richness of herbs and shrubs in four plant groups (Adapted from Halpern 1989): early seral (i.e. species with maximum abundance in disturbed sites), forest understory (i.e. shade-tolerant species associated with young or mature rather than old-growth forests that do not respond positively to canopy opening), late seral (i.e. species, often clonal, that are commonly considered shade tolerant, and have maximum abundance in mature forests) and introduced (i.e. species absent from the native understory vegetation); and (2) mean total understory richness and cover for herbs and shrubs. The response variables were averaged to the treatment level for each site. Pre-treatment data were not collected and therefore, assessment of treatment response was determined in relation to the unthinned controls.

We used non-metric multidimensional scaling ordination (NMS) to assess patterns in understory plant community composition (Kruskal 1964; Mather 1976). Sorensen distance measure was used with the "slow-and-thorough" autopilot settings with 40 runs of 50 iterations each in PC-ORD 4.0 (McCune & Mefford 1999). Stands were ordinated in vascular plant species space for all sites. The ordination was used to assess gradients in understory plant communities and their relationships with the stand density measures, individual species richness and other factors that may influence plant distribution such as elevation, slope, aspect and moss cover. An arbitrary cut-off of $r \geq |0.4|$ (Pearson's correlation coefficient) was used when assessing correlations of environmental variables and abundance of individual species with the ordination axes.

Out of a total of 284 vascular plant species found, species that occurred in <5% of the stands across all sites were excluded from the analyses, eliminating 63 rare species to reduce noise in the data. In addition, the species data were log-transformed using the equation in McCune & Grace (2002). Multivariate analysis of all 28 treatment units found no significant outliers that were greater than three standard deviations from the grand mean

of distances among stands. A NMS was run on the reduced species matrix for all 28 stands representing seven DMS sites each containing four treatments.

Blocked multi-response permutation (MRBP) was performed in PC-ORD 4.0 to test for differences in understory plant community composition among control and thinned stands. This procedure tested for differences in species composition among stand treatment groups based on the average within-group Sorensen distance, and blocking for site-to-site variation (MRBP = blocked multi-response permutation procedure). Indicator species analysis (ISA; Dufrêne & Legendre 1997) was performed in PC-ORD 4.0 to calculate indicator values (IVs) for vascular plant species in the treatments. IVs are measures of the fidelity of a species to a given treatment and are calculated from species' relative frequency and abundance within a given treatment. The indicator species from ISA were linked to the plant groups. Individual species response was not considered because of the lack of pre-treatment data.

Within-treatment variability

A mixed-model ANOVA in SAS 9.0 was used to test for differences in understory plot-to-plot variation within treatments using the coefficient of variation as a measure of understory variability. The coefficient of variation was calculated for cumulative richness and cover of herbs and shrubs by plant groups (described above) within each treatment by site. Other estimates of variability such as species turnover (i.e. half-changes, beta diversity) were examined but there were no significant differences among treatments.

Contribution of stand structural components to treatment response

Non-metric multidimensional scaling ordination was performed separately for each site, to investigate differences in community composition among plots that were located in the forest matrix, gaps, and leave islands. Ordinations of all 77 plots in species space at the site level allowed for more detailed evaluations of the understory patterns within each treatment. The ordination for the O.M. Hubbard site is the only site-level ordination reported here as the patterns and trends at this site are similar to those from the other six sites. Sorensen distance measure was used with 40 runs of 114 iterations as described above. Vascular plant species that occurred in <5% of the stands across all sites were excluded from the analysis, eliminating 42 rare species. The species data were log transformed as indicated, and a cut-off of $r \geq |0.4|$ was used when

assessing correlations of environmental variables and abundance of individual species with the ordination axes.

The site-level NMS ordination was rotated to maximize the correlation of live conifer density of overstory trees with one axis which reflected the thinning gradient. Plots were assigned to one of three structural groups: forest matrix, gap or leave island. A grouping variable was overlaid on the ordination graph to indicate which plots were entirely (all four subplots in one stratum) or partially (two or three subplots in one stratum) located in the gaps, leave islands or openings from harvest of each treatment. The plots in the ordination space were coded by treatment, for which the HC treatment was separated into the three density components (300, 200 and 100 trees ha⁻¹).

Treatment-level responses curves were examined by site for understory herb richness for three plant groups: early seral, forest understory and late seral as defined above. The response curves were separated by the three structural components to compare the relative contribution of each to the overall treatment response. These comparisons allow for discussion of trends only based on the subplot level (0.002 ha) vegetation measurements. As a result of the study design, relatively few sub-plots were sampled in the gaps and leave islands because these features represent a relatively small component of the stands.

Results

Response of plant groups to stand density management

Plant groups responded variedly to the thinning treatments. Richness and cover of understory herbs was greater in thinned stands than in the control. Compared with the control, all herb richness increased in all thinning treatments (Fig. 2a) whereas cover increased only in the MC treatment (Fig. 2e). Forest herb richness was greater in the LC treatment compared with the control (Fig. 2b). Forest herb cover, however, was not affected by thinning (Fig. 2f). Richness and cover of early seral herbs were greater in the thinned treatments (Fig. 2c and g). Late seral herbs were scarce across all sites (typically <1% cover in the 0.002-ha plots) and their richness and cover was not related to the thinning treatments (Fig. 2d and h).

All shrub richness increased in the MC and HC treatments compared with the control (Fig. 3a) but

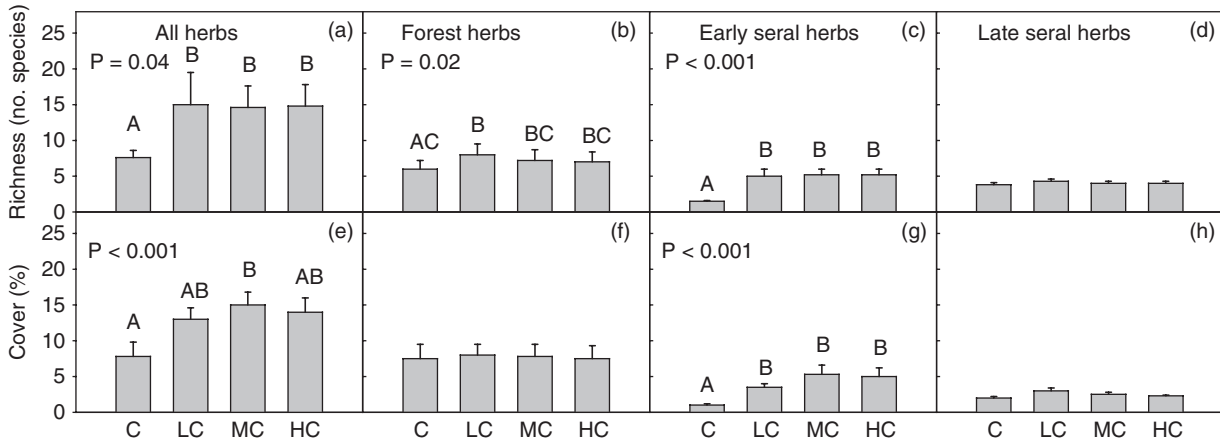


Fig. 2. Mean treatment cumulative richness and cover for understory herbs by seral classes. Means with standard error bars and P -values (when means were significantly different among treatments) are reported. For a given seral class and richness/cover, means with the same letter were not significantly different at $P \leq 0.05$ (Tukey's *post hoc* comparisons).

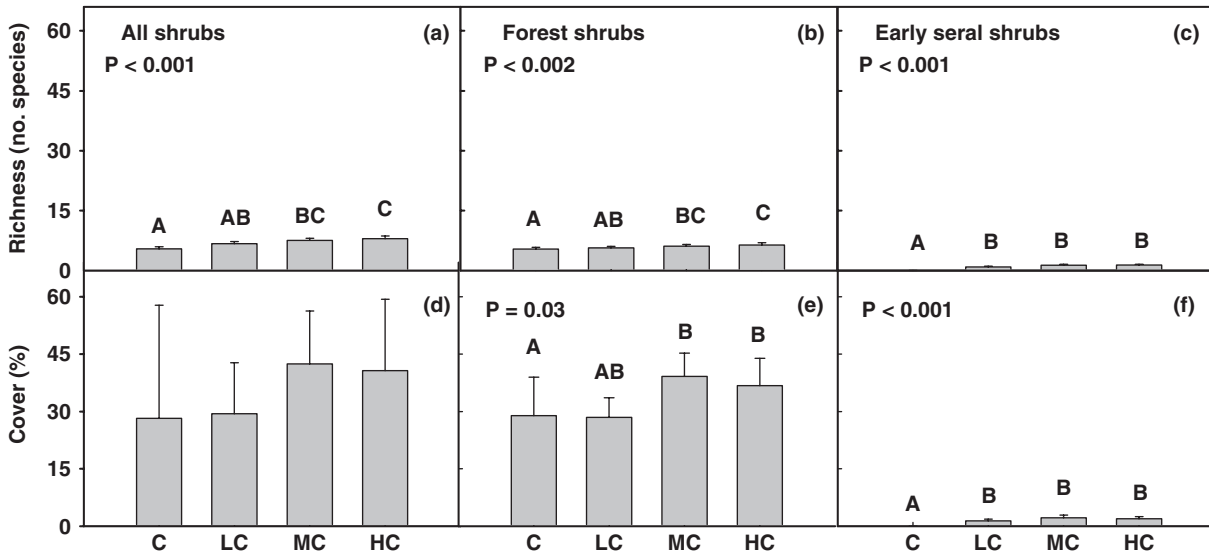


Fig. 3. Mean treatment cumulative richness and cover for understory shrubs by seral classes. Means with standard error bars and P -values (when means were significantly different among treatments) are reported. For a given seral class and cover/richness, means with the same letter were not significantly different at $P \leq 0.05$ (Tukey's *post hoc* comparisons).

all shrub cover did not differ among the treatments (Fig. 2d). Both forest shrub richness and cover were greater in MC and HC treatments than in the control (Fig. 3b and e) indicating recruitment and release responses following harvest. For example, the clonal, native species *Gaultheria shallon* Pursh and *Rubus ursinus* Cham & Schlecht were dominant forest shrubs across sites and their abundance consistently responded to the thinning treatments ($P = 0.02$ and $P < 0.001$, respectively), showing greatest cover in the MC and HC treatments. Early seral shrubs were present in relatively low abundance across stands, but had greater richness and

cover in the thinning treatments compared with the control (Fig. 3c and f).

Introduced species constituted a relatively small component of the understory communities and were present in very low abundance in the thinned stands (mean cover for thinned stands = $2.4 \pm 1.9\%$), with the greatest abundance in the HC treatments stands (mean cover = $2.9 \pm 2.5\%$). Richness of introduced species was greatest in the thinned stands (mean richness for thinned stands 3.2 ± 1.9). Introduced species were often absent or present in very low abundance in the controls (mean cover = $0.1 \pm 0.09\%$). For example, *Cytisus scoparius* L. and

Rubus discolor Weihe & Nees were the only two relatively abundant invasive species found across all sites, reaching a maximum cover of 5-10%.

Response of plant community composition to stand density management

As expected, distinct differences in understory vascular plant community composition were evident among sites. The rotated three-dimensional NMS ordination of 28 treatment units in species space described 86% of the cumulative variance in the community structure (Axis 1 = 16%, Axis 2 = 25%, and Axis 3 = 45%; Fig. 4). Axis 1 was highly correlated with overstory stand density (total live tree density, $r = 0.72$; conifer tree density, $r = 0.69$, Table 3), and represented the patterns of understory vegetation in relation to stand density gradient created by thinning treatments. Axis 3 represented mainly a topographical gradient from the Cascade foothill sites to the Coast Range sites and the associated differences in vegetation community composition (Table 3). Most species with high positive scores were species typical of warm and dry climate while those with high negative values were from cool and moist sites (Table 4). Axis 2 described 25% of the variation in understory communities and was related to differences in community composition

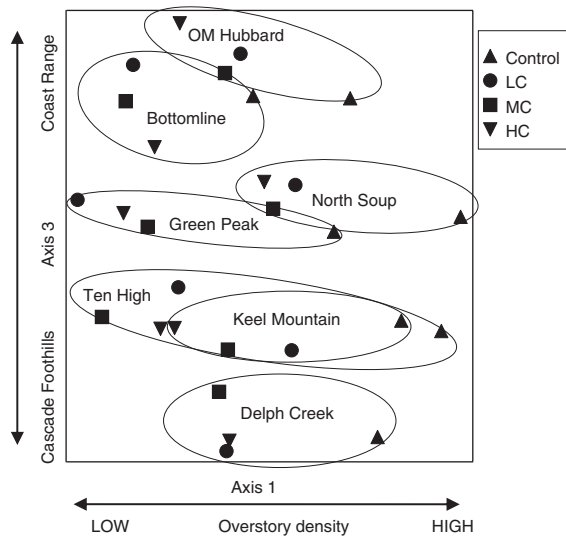


Fig. 4. Rotated NMS ordination of stands ($n = 28$) in understory vascular plant species space. Correlations of species and variables with ordination axes are in Tables 3 and 4. LC = low complexity treatment, MC = moderate complexity treatment, HC = high complexity treatment. Variability explained by axis 1 and 3 were 16% and 45%, respectively.

Table 3. Correlation coefficients (r) of environmental and stand variables with each ordination axis. Correlations for variables with $r \geq |0.4|$ with at least one ordination axis are shown in bold. Cumulative variance in understory composition explained by each axis is indicated in parentheses.

Variable	Axis 1 (16 %)	Axis 2 (25%)	Axis 3 (45%)
Elevation (m)	-0.08	-0.33	-0.49
Slope (%)	0.09	0.63	0.30
Aspect (°)	0.28	-0.21	-0.62
Live tree basal area ($m^2 ha^{-1}$)	0.64	-0.32	-0.40
Live tree density ($trees ha^{-1}$)	0.72	-0.39	0.03
Conifer tree density ($trees ha^{-1}$)	0.69	-0.42	-0.07
Hardwood tree density ($trees ha^{-1}$)	0.20	0.19	0.56
Moss cover (%)	0.17	0.64	-0.14
Seedling density ($number ha^{-1}$)	-0.19	0.02	-0.57

among sites, primarily driven by differences among dryer Coast Range sites and moister Cascades foothills sites (see Table 4 for dominant species associated with Axis 2). The understory community at O.M. Hubbard dominated by species such as *Whipplea modesta* Torr. and *Hieracium albiflorum* Hook, for example, was quite different from communities at the Green Peak, Ten High and North Soup sites.

Despite differences in plant communities among sites, thinning treatments affected understory community composition in a consistent manner (Fig. 4; MRBP; $T = -7.2$, $P < 0.001$, A-stat = 0.11). The most prominent difference in understory community composition was among control and thinned stands (Fig. 4). Understory composition in thinned stands was variable and differentiation among stands was moderate (MRBP; $T = -1.6$, $P = 0.06$, A-stat = 0.01; an A-stat near zero indicates high heterogeneity among stands). The overstory density gradient was reflected in greater abundance of shade-tolerant forest understory species in the dense stands, primarily in the unthinned controls (to the right of Axis 1), and by greater abundance of early seral species and forest shrubs in the thinned stands (left of Axis 1). Eight species of the early seral group were significant indicators of thinning: *Holcus lanatus* L. (introduced) and *Agrostis exarata* Trin., grasses; *Pteridium aquilinum* L. Kuhn, a clonal fern; *Hypochaeris radicata* L. and *Prunella vulgaris* L., both introduced herbs; and the introduced shrub *Ribes sanguineum* Pursh, and the native shrubs *Rubus laciniatus* Willd. and *R. ursinus* Cham. & Schlecht. (Table 5). *Rubus ursinus* was the only species that was a key indicator of thinned stands across all seven sites.

Table 4. Correlation coefficients (r) of individual vascular plant species with each ordination axis. Correlations for species with $r \geq |0.4|$ with at least one ordination axis are shown in bold type. E = early seral species; F = forest understory species; I = introduced species, L = late seral species; UNK = species that did not fit into the preceding groups or were assigned to genera or family species groupings. Cumulative variance in understory composition explained by each axis is indicated in parentheses.

Species	Group	Axis 1 (16%)	Axis 2 (25%)	Axis 3 (45%)
<i>Adenocaulon bicolor</i> Hook.	F, L	-0.35	0.18	0.75
<i>Anaphalis margaritacea</i> (L.) Benth. & Hook. f.	E	-0.65	0.63	0.07
Aster group	E	0.14	0.68	0.20
<i>Blechnum spicant</i> (L.) Sm	F, L	0.22	-0.26	-0.72
<i>Carex hendersonii</i> L. H. Bailey	UNK	0.05	0.76	-0.11
<i>Cirsium</i> sp.	E, I	-0.74	0.62	0.21
<i>Cirsium vulgare</i> (Savi) Ten.	E	-0.59	0.62	0.21
<i>Clinopodium douglasii</i> (Benth.) Kuntze	F	-0.32	-0.19	0.73
<i>Collomia heterophylla</i> Dougl. ex Hook.	E	-0.34	0.82	0.04
<i>Epilobium ciliatum</i> Raf.	E	-0.51	0.69	-0.17
<i>Erechtites minima</i> (Poir.) DC.	E, I	-0.51	0.68	-0.09
<i>Festuca idahoensis</i> Elmer	E	-0.20	-0.36	0.78
<i>Festuca occidentalis</i> Hook.	F	-0.27	0.88	-0.06
<i>Festuca subulata</i> Trin.	F	-0.03	0.84	-0.07
<i>Galium aparine</i> L.	E	-0.26	0.64	0.07
<i>Gautheria shallon</i> Pursh	F, L	-0.69	-0.06	0.14
<i>Hieracium albiflorum</i> Hook.	E, F	-0.66	0.56	0.34
<i>Holodiscus discolor</i> (Pursh) Maxim.	F	-0.39	0.33	0.85
<i>Hypericum perforatum</i> L.	E, I	-0.74	0.33	-0.03
<i>Hypochaeris radicata</i> L.	E, I	-0.80	0.55	0.00
<i>Iris tenax</i> Douglas ex Lindl.	E	-0.65	0.42	0.45
<i>Lotus crassifolius</i> (Benth.) Greene	E	-0.52	0.64	-0.20
<i>Osmorhiza berteroi</i> DC.	F	-0.28	0.33	0.81
<i>Pteridium aquilinum</i> (L.) Kuhn	E	-0.81	0.27	0.22
<i>Rubus leucodermis</i> Dougl. ex Torr. & Gray	E	-0.61	0.65	-0.11
<i>Senecio jacobea</i> L.	E, I	-0.41	0.66	-0.28
<i>Senecio sylvaticus</i> L.	E, I	-0.61	0.65	0.03
<i>Sonchus asper</i> (L.) Hill	E, I	-0.49	0.78	0.08
<i>Stellaria crispa</i> Cham. & Schlecht.	UNK	-0.01	0.65	0.11
<i>Symphoricarpos mollis</i> Nutt.	F	-0.52	-0.00	0.67
<i>Vaccinium parvifolium</i> Sm.	E, F	0.19	-0.39	-0.67
<i>Viola glabella</i> Nutt.	E, F	-0.13	-0.73	0.52
<i>Viola sempervirens</i> Greene.	F, L	-0.01	0.77	-0.48
<i>Viola</i> sp.	UNK	-0.13	-0.73	0.52
<i>Whipplea modesta</i> Torr.	F	-0.04	0.03	0.81
Graminoid group	UNK	-0.39	0.11	0.23

Within-treatment variability in understory vegetation

Within-treatment variability (i.e. plot-to-plot variability measured by the coefficient of variation, CV) in understory vegetation cover and richness was high with the CV often > 100%, and did not differ among the three thinning treatments despite differ-

Table 5. Indicator species for the thinned stands from Indicator Species Analysis performed across all sites. Only species with $P \leq 0.05$ are reported. IV is an indicator value combining the relative abundance and frequency of each species in the unthinned control, low (LC), moderate (MC) and high (HC) complexity treatments. The higher the IV, the greater the association of the species to a given treatment. E = early seral species; F = forest understory species; I = introduced species.

Species	Treatment	Life form	Group	IV	P
<i>Agrostis exarata</i> Trin.	HC	Grass	E, I	45.3	0.02
<i>Holcus lanatus</i> L.	MC	Grass	E, I	40.8	0.04
<i>Hypochaeris radicata</i> L.	HC	Herb	E, I	36.0	0.05
<i>Prunella vulgaris</i> L.	HC	Herb	E, I	40.8	0.03
<i>Pteridium aquilinum</i> (L.) Kuhn	MC	Fern	E	29.4	0.02
<i>Ribes sanguineum</i> Pursh	HC	Shrub	E	39.3	0.05
<i>Rubus laciniatus</i> Willd.	HC	Shrub	E, I	43.0	0.03
<i>Rubus ursinus</i> Cham. & Schlecht.	HC	Shrub	E, F	28.5	0.04

ences in overstory structural complexity. There was greater variability in herb and shrub abundance within the unthinned controls compared with the thinned stands. Thinning reduced within-stand variability of herb and shrub richness, but had no clear effect on variability of herb and shrub cover. Richness of early seral herbs and shrubs tended to have greater abundance in thinned stands resulting in more homogeneous communities within the thinned stands compared with the unthinned control ($P = 0.07$ and $P = 0.004$ for the CV values, respectively).

Within-site differences in understory composition were apparent among thinning treatments (MRPP: $T = -13.76$, $P < 0.001$, A-stat = 0.03), but there was high variability and overlap, especially among the LC and MC treatments for all sites. Patterns of understory community composition within most sites were related to differences in local topography and site-level variations in plant communities. Ordinations at the vegetation-plot level are shown only for the O.M. Hubbard site as an example (Fig. 5). Despite this within-site variability, there was a strong differentiation of understory composition among thinned and unthinned plots. The ordination of plots in species space for O.M. Hubbard resulted in a three-dimensional solution describing 82% of the overall variation in the community structure. Axis 1 represented 49% of this variation and was rotated to maximize its correlation with conifer density ($r = 0.55$) to represent the thinning treatment gradient. The other two gradients in the O.M. Hubbard site ordination were

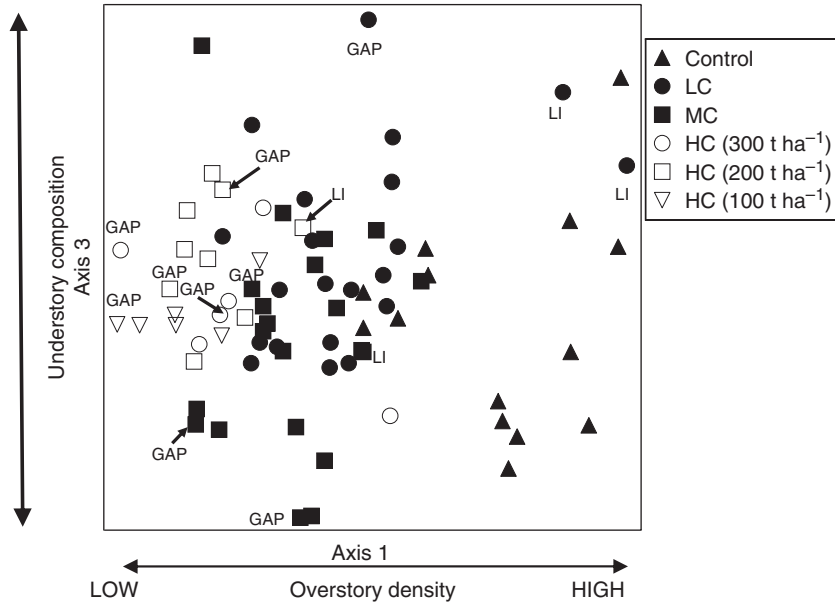


Fig. 5. Rotated NMS ordination for the O.M. Hubbard Coast Range site in understory vascular plant species space ($n = 77$). See Table 6 for correlations of species with ordination axes. Symbols indicate treatments and the high complexity treatment is shown by thinning density (300, 200 and 100 trees ha^{-1}). Gap openings and leave island reserves are labeled while forest matrix plots are not. LC = low-complexity treatment, MC = moderate-complexity treatment, HC = high-complexity treatment, LI = Leave island. Variability explained by axis 1 and 3 were 49% and 23%, respectively.

relatively minor explaining 10% and 23% of the variability for Axes 2 and 3, respectively, and were related to differences in understory composition (see dominant species associated with Axes 2 and 3 in Table 6). Understory communities in the unthinned controls were composed of forest understory species and a few late-seral species, such as *Anemone deltoidea*, *Chimaphila menziesii* R. Br. ex D. Don and *Trillium ovatum*. Thinned stands included early seral, introduced and persistent forest understory species that responded positively to disturbance (Table 6). These trends were similar in the other six sites, although indicator species for each plant group differed.

Contribution of stand structural components to treatment-level response

The contribution of the three stand structural components – forest matrix, gaps and leave islands – to the overall understory response was consistent for all sites; therefore, only results for the O.M. Hubbard site are presented. Matrix areas and gap openings in the MC and VC treatments appeared to accentuate the overall short-term response of understory communities to thinning (Fig. 6). Plots that were completely or partly in gap openings and in the HC, heavy thinning to 100 trees ha^{-1} , had greater

Table 6. Correlation coefficients (r) of individual species with each ordination axis for the O.M. Hubbard Coast Range site. Correlations for species with $r \geq |0.4|$ with at least one ordination axis are shown in bold. E = Early seral species; F = forest understory species; I = introduced species.

Species	Group	Axis 1 (49%)	Axis 2 (10%)	Axis 3 (23%)
<i>Campanula scouleri</i> Hook. ex A. DC	E, F	-0.33	-0.60	-0.16
<i>Claytonia siberica</i> L.	E, F	0.01	-0.12	-0.59
<i>Festuca idahoensis</i> Elmer	E	-0.57	-0.41	-0.08
<i>Galium triflorum</i> Michx.	F, L	0.10	-0.40	-0.60
<i>Hieracium albiflorum</i> Hook.	E, F	-0.62	-0.46	0.03
<i>Hypochaeris radicata</i> L.	E, I	-0.76	0.05	-0.11
<i>Polystichum munitum</i> Kaulf. C. Presl	F, L	-0.05	0.04	-0.65
<i>Rhododendron macrophyllum</i> D. Don. G. Don	F, L	0.55	-0.14	0.46
<i>Rubus ursinus</i> Cham. & Schlecht.	E, F	-0.57	0.002	-0.13
<i>Stachys mexicana</i> L.	E	-0.19	-0.25	-0.57
<i>Whipplea modesta</i> Torr.	F	-0.79	0.04	-0.12

richness than other thinned stands. Gaps and heavily thinned areas tended to have greater abundance of early seral shrubs and herbs (Fig. 6).

The thinned forest matrix components of the treated stands contributed to the majority of the understory herb response, where thinning resulted

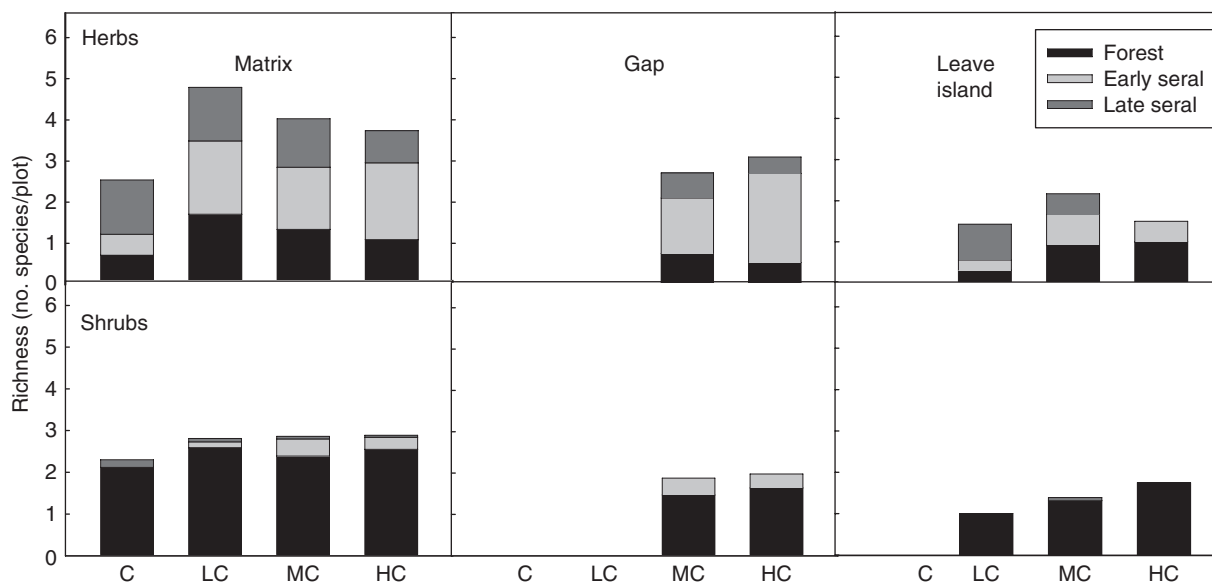


Fig. 6. Herb and shrub richness (number of species per 20-m² understory vegetation subplots) for the O.M. Hubbard site. Richness values are shown by treatment and by strata: forest matrix, gap, and leave island.

in higher herb richness than that in the unthinned control. In particular, early seral species were present in greater abundance in the thinned forest matrix components of the LC, MC and HC stands. Patterns of species richness in leave island reserves were less clear; plots that fell completely or partly in leave islands appeared to have communities similar to the LC treatment or the control (Fig. 6). Leave islands were relatively shaded preserves within the thinned stand and consequently their richness of herbs and shrubs was relatively low (Fig. 6).

Discussion

Changes in understory vegetation 6 years after imposing stand density management treatments likely reflected the “initial effect” of disturbance (Halpern & Spies 1995) on plant communities. At this stage, understory vegetation characteristics are related to resource availability, and below- and above-ground competition for resources (Davis et al. 1999; Grime 2001; Roberts 2004; Barbier et al. 2008), as well as by other factors such as detritus cover, harvesting disturbance, microtopography, and propagule availability (Halpern & McKenzie 2001; Roberts 2004, 2007; Puettmann & Berger 2006; Fahey & Puettmann 2007; Wilson & Puettmann 2007). To accommodate the lack of pre-harvest data, treatment effects on the understory vegetation in the DMS were inferred by differences between treatment and control plots. This is justified

because understory vegetation development is not very dynamic in PNW coniferous forest in the absence of disturbance. Accordingly, richness and cover of understory vegetation species were similar in pre-thinning plots and in control plots measured 3 years after thinning, while the latter differed from the treatment plots at this time (Harrington et al. 2002).

Increased richness in understory response to stand density reduction supports findings from previous studies in temperate forest ecosystems (North et al. 1996; Thomas et al. 1999; Thysell & Carey 2001; Son et al. 2004; Chan et al. 2006; Shields & Webster 2007). Also, a chronosequence study in 6- to 20-year-old Douglas-fir plantations established in western Oregon revealed that stand density was the most important factor influencing understory vegetation composition (Puettmann & Berger 2006). Results from the DMS suggested that thinnings created functional heterogeneity (i.e. spatial and temporal variation in habitat structures) instead of conditions contributing to competitive exclusion (i.e. increased dominance of a few species). It has been proposed that functional heterogeneity can be maintained when high-magnitude disturbances (i.e. fires and landslides) are not too frequent and mild disturbances are not too infrequent (Odion & Sarr 2007). In turn, increased diversity may increase vegetation community function, stability and resilience (Naeem et al. 1999; Tilman 1999).

Increased all herb richness supports the notion that stand density management designed to resemble natural gap dynamics can have a particularly

strong impact on increasing diversity of the herb layer (Halpern & Spies 1995). Furthermore, increased richness of forest herbs in the thinned treatments suggested recruitment of herb species or release of subordinate species by overstory removal (Lindh 2005). Lack of thinning effect on late seral herbs are contrary to findings in other younger coniferous forests 20 years after thinning despite large inter-specific variability in the response (Lindh & Muir 2004). This suggests that the understory vegetation measured 6 years after harvest in our study may be representative of a transient stage. A quicker development of late seral species may require more complex silviculture regimes perhaps similar to the structural complexity enhancement tested for US eastern forests (Smith et al. 2008).

Only cover of early seral herbs and shrubs responded positively to all thinning treatments but their overall cover was generally minor. The lack of a treatment response in forest herb cover could be attributed to the survival of forest herbs following harvest (L.R. Davis and K.J. Puettmann, unpubl. data). Increased forest shrub cover in moderate- and high-complexity treatments likely indicated a release following harvest. The shrub response described an opposite trend to those found in other stand density management studies in the PNW (see review by Wilson & Puettmann 2007), where shrub cover decreased probably because of damage during harvesting operations. Data from Coastal Oregon forests, however, indicated that shrub cover increased with decreased basal area of *T. heterophylla* and density of shade-tolerant trees (Kerns & Ohmann 2004).

Herb responses to thinning (i.e. increased cover), which was only significant in the moderate complexity treatment compared with the control, was mainly driven by increases in early seral herbs. Late seral herbs comprised a small fraction of the understory and responses to thinning were minor. Introduced species were also relatively scarce in most sites; however, their number increased with thinnings. Stand density management studies had shown similar responses for introduced, sometimes invasive species (Wilson & Puettmann 2007), although increased vascular plant richness often relates to a proportionally greater increase in abundance of introduced species (Thysell & Carey 2000, 2001; Griffis et al. 2001). According to the theory of fluctuating resources in plant communities, a plant community is more susceptible to invasion whenever unused resources increase (Davis et al. 2000). Invasive species, however, may encounter intense competition for resources from resident species, and that may have reduced the spread of introduced species at the DMS sites.

The site specificity revealed for plant community composition showed that the study successfully covered a wide inference space as a result of varied site characteristics which were most pronounced among the Cascade and Coast Range sites. Because of the high variability among sites, accounting for site-level differences was necessary to document patterns of understory communities. Environment and treatment effects explained about half of the understory variability each, with treatment effects manifesting more in the high-complexity treatment. In thinned stands, harvest disturbance resulted in overall higher species richness because of the recruitment of early seral herbs and shrubs and both low and tall shrubs, greater cover of early seral herbs and shrubs, a release response of shrubs such as *G. shallon* and *R. ursinus*, and greater abundance of introduced species, many of which are considered early seral species. *R. ursinus* tolerates forest conditions although it acts more like a ruderal species and does most of its sexual reproduction in openings (D. Peter, pers. commun.). This species was also common in Douglas-fir plantations although its cover decreases after about a stand age of 13 years as denser tree canopies develop (Puettmann & Berger 2006). Thus, some species would not persist in the understory communities for long periods of time (except when they are maintained with continued stand density reductions). They might not be permanent or even long-term features of these ecosystems but represent a short-term understory response to resource availability following reductions in overstory density and canopy cover.

Disturbances caused by stand density reduction, fire, herbivory, insect and fungus outbreaks can be followed by the establishment of dense and persistent (i.e. lasting by decades; Mallik 2003) canopies of native understory species (termed "recalcitrant layers"; Royo & Carson, 2006). Recalcitrant layers of species such as *Rubus spectabilis* can occur in the PNW (Tappeiner et al. 1991), greatly reducing plant richness and tree regeneration. In this study, the occurrence of these monodominant plant layers was not evident, suggesting that disturbance was not so intense as to trigger their establishment.

The identification of eight understory species (out of ca. 300 observed species) indicating stand density reductions could serve to monitor and predict initial plant successional trends and changes in other organisms following disturbance (Stolte et al. 2002; Gray & Azuma 2005; Yost 2008). In redwood forests of northern California, 25 species were identified as indicators for the stand initiation stage but

only seven of them were found for the closure, mature and old-growth stages (Loya & Jules 2008). One of the indicator species in this study, the deciduous, introduced shrub *R. laciniatus* was present in 13% of 1127 forest inventory plots in western Oregon forests (Gray 2005). Frequency and cover of this species were negatively associated with overstory canopy cover and stand basal area, respectively.

Within-stand variability of herb and shrub richness was reduced by thinning. This trend was evident despite the within-site variability of understory communities, which was driven by topographic factors and other variables. Topography may have exerted a lingering effect on plant richness. Overall, increasing structural complexity of the overstory does not necessarily result in more spatially variable understory communities in the short term. Disturbance can initially homogenize the vegetation structure, because of the recruitment and increased abundance of early seral herbs and residual forest understory species (Halpern 1989; Beggs 2005), increased light uniformity caused by the development of upper understory layers (Bartemucci et al. 2006), or proliferation of invasive species (McKinney 2004), which may depend on initial site conditions and increased nutrient uptake (Dassonville et al. 2008).

Although the gap openings and heavy-thin components were a small component of the overall treatment areas, they appeared to contribute to the recruitment of early seral species and tall shrubs, resulting in greater overall species richness in these areas than in the forest matrix components of untreated stands. Herb cover, however, did not increase in gaps although field observations suggested that herb biomass did. This early response to thinning has so far supported the contention that gap creation may moderately increase variability in understory vegetation conditions depending upon gap size (Fahey & Puettmann 2007, 2008). While increased plant richness in gaps was somewhat expected, the increased richness in matrix areas of the thinning treatments was less predictable and constituted an interesting phenomenon. Understory vegetation diversity, instead, did not increase in leave island reserves.

Conclusions

Large changes in spatial variability of the overstory were followed by relatively small changes in understory composition 6 years after imposing a variety of thinning treatments on 11 sites of the PNW. Richness and cover of the different plant

groups did not respond consistently to thinnings suggesting a diverse functional heterogeneity. Pre-treatment conditions act in conjunction with facilitative and competitive effects, as well as with physical disturbance to create a diversity of understory conditions. Different responses in species richness and cover suggest that other factors such as propagule availability may have also affected understory development. Forest matrix areas in the thinning treatments appeared to contribute to increased richness of early seral herbs and shrubs; this effect was less expected than a similar trend found for gaps. Greater species richness could be achieved by implementing spatially variable thinning specifications. Continued monitoring of the understory response akin to a “species accounting system” (Brunnell 2008) will determine if plant successional trends and dominance of some plant groups are maintained or change at different time-scales in response to stand density management strategies varying in complexity. Periodic re-measurement in the study plots will document long-term trends of understory vegetation development.

Acknowledgements. We thank the U.S. Department of Interior Bureau of Land Management for continued funding to the DMS, and to BLM research liaisons, site managers and district office personnel for their support. We are grateful to Bruce McCune, Manuela Huso and Lisa Ganio for statistical assistance, and to the numerous people that have participated in field data collection.

References

- Alaback, P.B. & Herman, F.R. 1988. Long-term response of understory vegetation to stand density in *Picea-Tsuga* forests. *Canadian Journal of Forest Research* 18: 1522–1530.
- Attwill, P.M. 1994. The disturbance of forest ecosystems: the ecological basis for conservation management. *Forest Ecology and Management* 63: 247–300.
- Barbier, S., Gosselin, F. & Balandier, P. 2008. Influence of tree species on understory vegetation diversity and mechanisms involved. A critical review for temperate and boreal forests. *Forest Ecology and Management* 254: 1–15.
- Bartemucci, P., Messier, C. & Canham, C.D. 2006. Overstory influences on light attenuation patterns and understory plant community diversity and composition in southern boreal forests of Quebec. *Canadian Journal of Forest Research* 36: 2065–2079.
- Bauhus, J., Aubin, I., Messier, C. & Connell, M. 2001. Composition, structure, light attenuation and nutrient content of the understorey vegetation in a *Eucalyptus*

- sieberi* regrowth stands 6 years after thinning and fertilisation. *Forest Ecology and Management* 144: 275–286.
- Beggs, L.R. 2005. Vegetation response following thinning in young Douglas-fir forests of Western Oregon: can thinning accelerate development of late-successional structure and composition? M.S. thesis. Oregon State University, Corvallis, OR, USA.
- Berger, A.L. & Puettmann, K.J. 2000. Overstory composition and stand structure influence herbaceous plant diversity in the mixed aspen forest of northern Minnesota. *American Midland Naturalist* 143: 111–125.
- Bergeron, Y. & Harvey, B. 1997. Basing silviculture on natural ecosystem dynamics: an approach applied to the southern boreal mixed wood forest of Quebec. *Forest Ecology and Management* 92: 235–242.
- Brunnell, F.L. 2008. Indicators for sustainable biological diversity in Canada's most controversial forest type—Coastal temperate rainforest. *Ecological Indicators* 8: 149–157.
- Chan, S.S., Larson, D.J., Maas-Hebner, K.G., Emmingham, W.H., Johnston, S.R. & Mikowski, D.A. 2006. Overstory and understory development in thinned and underplanted Oregon Coast Range Douglas-fir stands. *Canadian Journal of Forest Research* 36: 2696–2711.
- Cissel, J., Anderson, P., Olson, D., Puettmann, K.J., Berryman, S., Chan, S. & Thompson, C. 2006. BLM density management and riparian buffer study: establishment report and study plan. Scientific Investigations Report 2006–5087. U.S. Department of Interior, U.S. Geological Survey, Corvallis, OR, US.
- Dassonville, N., Vanderhoeven, S., Vanparys, V., Hayez, M., Gruber, W. & Meerts, P. 2008. Impacts of alien invasive plants on soil nutrients are correlated with initial site conditions in NW Europe. *Oecologia* 157: 131–140.
- Davis, L.R., Puettmann, K.J. & Tucker, G.F. 2007. Overstory response to alternative thinning treatments in young Douglas-fir forests in Western Oregon. *Northwest Science* 81: 1–14.
- Davis, M.A., Wrage, K.J., Reich, P.B., Tjoelker, M.G., Schaeffer, T. & Muermann, C. 1999. Survival, growth, and photosynthesis of tree seedlings competing with herbaceous vegetation along a water–light–nitrogen gradient. *Plant Ecology* 145: 341–350.
- Davis, M.A., Grime, J.P. & Thompson, K. 2000. Fluctuating resources in plant communities: a general theory of invisibility. *Journal of Ecology* 88: 528–534.
- deMaynadier, P.G. & Hunter, M.L. 1995. The relationship between forest management and amphibian ecology: a review of the North America literature. *Environmental Reviews* 3: 230–261.
- Dodson, E.K., Peterson, D.W. & Harrod, R.J. 2008. Understory vegetation response to thinning and burning restoration treatments in dry conifer forests of the eastern Cascades, USA. *Forest Ecology and Management* 255: 3130–3140.
- Drever, C.R. & Lertzman, K.P. 2003. Effects of a wide gradient of retained tree structure on understory light in coastal Douglas-fir forests. *Canadian Journal of Forest Research* 33: 137–146.
- Dufrêne, M. & Legendre, P. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs* 67: 345–366.
- Fahey, R.T. & Puettmann, K.J. 2007. Ground-layer disturbance and initial conditions influence gap partitioning of understory vegetation. *Journal of Ecology* 95: 1098–1109.
- Fahey, R.T. & Puettmann, K.J. 2008. Patterns in spatial extent of gap influence on understory plant communities. *Forest Ecology and Management* 255: 2801–2810.
- Franklin, J.F. & Spies, T.A. 1991. Composition, function and structure of old-growth Douglas-fir forest. In: Ruggiero, L.F., Aubry, K.B., Carey, A.B. & Huff, M.F. (eds.). *Wildlife and vegetation of unmanaged Douglas-fir forests*. pp. 71–82. USDA Forest Service Technical Report PNW-GTR-285, USDA Forest Service, Portland, OR, US.
- Gray, A.N. 2005. Eight nonnative plants in western Oregon forests: associations with environment and management. *Environmental Monitoring Assessment* 100: 109–127.
- Gray, A.N. & Azuma, D.L. 2005. Repeatability and implementation of a forest vegetation indicator. *Ecological Indicators* 5: 57–71.
- Griffis, K.L., Crawford, J.A., Wagner, M.R. & Moir, W.H. 2001. Understory response to management treatments in northern Arizona ponderosa pine forests. *Forest Ecology and Management* 146: 239–245.
- Grime, J.P. 2001. *Plant strategies, vegetation processes, and ecosystem properties*. 2nd edn. John Wiley and Sons Ltd, Chichester, UK.
- Hagar, J.C. 2007. Wildlife species associated with non-coniferous vegetation in Pacific Northwest conifer forests: a review. *Forest Ecology and Management* 246: 108–122.
- Halpern, C.B. 1989. Early successional patterns of forest species: interactions of life history traits and disturbance. *Ecology* 70: 704–720.
- Halpern, C.B. & McKenzie, D. 2001. Disturbance and post-harvest ground conditions in a structural retention experiment. *Forest Ecology and Management* 154: 215–225.
- Halpern, C.B. & Spies, T.A. 1995. Plant species diversity in natural and managed forests of the Pacific Northwest. *Ecological Applications* 5: 913–934.
- Harrington, T.B. & Edwards, M.B. 1999. Understory vegetation, resource availability, and litterfall responses to pine thinning and woody vegetation control in longleaf pine plantations. *Canadian Journal of Forest Research* 29: 1055–1064.
- Harrington, C.A., Buermeyer, K.R., Brodie, L.C. & Wender, B.W. 2002. Factors influencing growth and flowering of understory plants in conifer stands in

- western Washington. In: Johnson, A.C., Haynes, R.W. & Monserud, R.A. (eds.) *USFS PNW-General Technical Report*. pp. 159–168, Pacific Northwest Research Station, USDA Forest Service, Portland, OR, US.
- Harrod, R.J. 2001. The effect of invasive and noxious plants on land management in eastern Oregon and Washington. *Northwest Science* 75: 85–89.
- Humphrey, J.W. 2005. Benefits to biodiversity from developing old-growth conditions in British upland spruce plantations: a review and recommendations. *Forestry* 78: 33–53.
- Kerns, B.K. & Ohmann, J.L. 2004. Evaluation and prediction of shrub cover in coastal Oregon forests (USA). *Ecological Indicators* 4: 83–98.
- King, J. 1966. *Site index curves for Douglas-fir in the Pacific Northwest*. Weyerhaeuser Forestry Paper No. 8. Weyerhaeuser Co., Forestry Research Center, Centralia, WA, US.
- Kruskal, J.B. 1964. Nonmetric multidimensional scaling: a numerical method. *Psychometrika* 29: 115–129.
- Larsen, J.B. & Nielsen, A.B. 2006. Nature-based forest management. Where are we going? Elaborating forest development types in and with practice. *Forest Ecology and Management* 23: 107–107.
- Lindh, B.C. 2005. Effects of conifer basal area on understory herb presence, abundance, and flowering in second-grown Douglas-fir forest. *Canadian Journal of Forest Research* 35: 938–948.
- Lindh, B.C. & Muir, P.S. 2004. Understory vegetation in young Douglas-fir forest: does thinning help restore old-growth composition? *Forest Ecology and Management* 192: 285–296.
- Loya, D.T. & Jules, E.S. 2008. Use of species richness estimators improve evaluation of understory plant response to logging: a study of redwood forests. *Plant Ecology* 194: 179–194.
- Macdonald, S.E. & Fenniak, T.E. 2007. Understory plant communities of boreal mixedwood forests in western Canada: natural patterns and response to variable-retention harvesting. *Forest Ecology and Management* 242: 34–48.
- Mallik, A.U. 2003. Conifer regeneration problems in boreal and temperate forests with ericaceous understory: role of disturbance, seedbed limitation, and keystone species change. *Critical Reviews in Plant Science* 22: 341–366.
- Mather, P.M. 1976. *Computational methods of multivariate analysis in physical geography*. J. Wiley and Sons, London, UK.
- McComb, W.C., Spies, T.A. & Emmingham, W.H. 1993. Douglas-fir forests: managing for timber and mature-forest habitat. *Journal of Forestry* 91: 31–42.
- McCune, B. & Grace, J.B. 2002. *Analysis of ecological communities*. MjM Software, Glenden Beach, OR, USA.
- McCune, B. & Mefford, M.J. 1999. *PC-ORD. Multivariate analysis of ecological data. Version 4*. MjM Software, Glenden Beach, OR, US.
- McKenzie, D., Halpern, C.B. & Nelson, C.R. 2000. Overstory influences on herb and shrub communities in mature forests of western Washington, USA. *Canadian Journal of Forest Research* 30: 1655–1666.
- McKinney, M.L. 2004. Measuring floristic homogenization by non-native plants in North America. *Global Ecology and Biogeography* 13: 47–53.
- Metlen, K.L. & Fiedler, C.E. 2006. Restoration treatment effects on the understory of ponderosa pine/Douglas-fir forests in western Montana, USA. *Forest Ecology and Management* 222: 355–369.
- Muir, P.S., Mattingly, R.L., Tappeiner, J.C., Bailey, J.D., Elliott, W.E., Hagar, J.C., Miller, J.C., Peterson, E.B. & Starkey, E.E. 2002. Managing for biodiversity in young Douglas-fir forests of western Oregon. Biological Science Report, USGS/BRD/BSR-200200006. US Geological Survey, Forest and Rangeland Ecosystem Science Center, Corvallis, OR, US
- Naeem, S., Chapin III, F.S., Costanza, R., Ehrlich, P.R., Golley, F.B., Hooper, D.U., Lawton, J.H., O'Neill, R.V., Mooney, H.A., Sala, O.E., Symstad, A.J. & Tilman, D. 1999. *Biodiversity and ecosystem function: Maintaining natural life support processes*. Ecological Society of America, Issues in Ecology No. 4, Washington, DC, US.
- Nagai, M. & Yoshida, T. 2006. Variation in understory structure and plant species diversity influenced by silvicultural treatments among 21- to 26-year old *Picea glehnii* plantations. *Journal of Forest Research* 11: 1–10.
- Nelson, C.R., Halpern, C.B. & Agee, J.K. 2008. Thinning and burning result in low-level invasion by nonnative plants but neutral effects on natives. *Ecological Applications* 18: 762–770.
- North, M., Chen, J., Smith, G., Krakowiak, L. & Franklin, J.F. 1996. Initial response of understory plant diversity and overstory tree diameter growth to a green tree retention harvest. *Northwest Science* 70: 24–35.
- Odion, D.C. & Sarr, D.A. 2007. Managing disturbance regimes to maintain diversity in forested ecosystems of the Pacific Northwest. *Forest Ecology and Management* 246: 57–65.
- Peltzer, D.A., Bast, M.L., Wilson, S.D. & Gerry, A.K. 2000. Plant diversity and the responses following contrasting disturbances in boreal forest. *Forest Ecology and Management* 127: 191–203.
- Poage, N.J. & Tappeiner, J.C. 2002. Long-term patterns of diameter and basal area growth of old-growth Douglas-fir trees in western Oregon. *Canadian Journal of Forest Research* 32: 1232–1243.
- Puettmann, K.J. & Ammer, C. 2007. Trends in North American and European regeneration research under the ecosystem management paradigm. *European Journal of Forest Research* 126: 1–9.
- Puettmann, K.J. & Berger, C.A. 2006. Development of tree and understory vegetation in young Douglas-fir plantations in Western Oregon. *Western Journal of Applied Forestry* 21: 94–101.

- Rambo, T.R. & Muir, P.S. 1998. Forest floor bryophytes of *Pseudotsuga menziesii*-*Tsuga heterophylla* stands in Oregon: influence of substrate and overstory. *Bryologist* 101: 116–130.
- Roberts, M.R. 2004. Response of the herbaceous layer to natural disturbance in North American forests. *Canadian Journal of Botany* 82: 1273–1283.
- Roberts, M.R. 2007. A conceptual model to characterize disturbance severity in forest harvests. *Forest Ecology and Management* 242: 58–64.
- Roberts, M.R. & Gilliam, F.S. 1995. Patterns and mechanisms of plant diversity in forested ecosystems: implications for forest management. *Ecological Applications* 5: 969–977.
- Royo, A. & Carson, W.P. 2006. On the formation of dense understory layers in forests worldwide: consequences and implications for forest dynamics, biodiversity, and succession. *Canadian Journal of Forest Research* 36: 1345–1362.
- Schuler, T.M., Ford, W.M. & Collins, R.J. 2002. Successional dynamics and restoration implications of a montane coniferous forest in the Central Appalachians, USA. *Natural Areas Journal* 22: 88–98.
- Shields, J.M. & Webster, C.R. 2007. Ground-layer response to group selection with legacy-tree retention in a managed northern hardwood forest. *Canadian Journal of Forest Research* 37: 1797–1807.
- Smith, K.J., Keeton, W.S., Twery, M.J. & Tobi, D.R. 2008. Understory plant responses to uneven-aged forestry alternatives in northern hardwood-conifer forests. *Canadian Journal of Forest Research* 38: 1303–1318.
- Son, Y., Lee, Y.Y., Jun, Y.C. & Kim, Z.S. (2004). Light availability and understory vegetation four years after thinning in a *Larix leptolepis* plantation of central Korea. *Journal of Forest Research* 9: 133–139.
- Spies, T.A. 1991. Plant species diversity and occurrence in young, mature, and old-growth Douglas-fir stands in western Oregon and Washington. In: Ruggiero, L.F., Aubry, K.B., Carey, A.B. & Huff, M.F. (eds.) *Wildlife and vegetation of unmanaged Douglas-fir forests*. pp. 111–121. USDA Forest Service General Technical Report PNW-GTR-285. Pacific Northwest Research Station, USDA Forest Service, Portland, OR, US.
- Stolte, K., Conkling, B., Campbell, S. & Gillespie, A. 2002. *Forest Health Indicators. Forest Inventory and Analysis Program*. USDA Forest Service FS-746. USDA Forest Service, Washington, DC, US.
- Sullivan, T.P., Sullivan, D.S., Lindgren, P.M.F. & Ransome, D.B. 2005. Long-term responses of ecosystem components to stand thinning in young lodgepole pine forest. II. Diversity and population dynamics of forest floor small mammals. *Forest Ecology and Management* 205: 1–14.
- Tappeiner, J.C., Zasada, J., Ryan, P. & Newton, M. 1991. Salmonberry clonal and population structure: the basis for a persistent cover. *Ecology* 72: 609–618.
- Thomas, S.C., Halpern, C.B., Falk, D.A., Ligouri, D.A. & Austin, K.A. 1999. Plant diversity in managed stands: understory responses to thinning and fertilization. *Ecological Applications* 9: 864–879.
- Thysell, D.R. & Carey, A.B. 2000. *Effects of forest management on understory and overstory vegetation: a retrospective study*. USDA Forest Service General Technical Report PNW-GTR-488. Pacific Northwest Research Station, USDA Forest Service, Portland, OR, US.
- Thysell, D.R. & Carey, A.B. 2001. Manipulation of density of *Pseudotsuga menziesii* canopies: preliminary effects on understory vegetation. *Canadian Journal of Forest Research* 31: 1513–1525.
- Tilman, D. 1999. The ecological consequences of changes in biodiversity: a search for general principles. *Ecology* 80: 1455–1474.
- USDA-NRCS. 2005. *The PLANTS Database 3.5* (data compiled by Mark W. Skinner. National Plant Data Center, Baton Rouge, LA, US). Available at <http://plants.usda.gov> (accessed 13 March 2008).
- USDA-NRCS, National Water and Climatic Center; Oregon State University, University Spatial Climate Analysis Service (USDA OSU). 1999. Parameter-elevation regressions on independent slopes model (PRISM). <http://www.wcc.nrcs.usda.gov> (accessed 13 March 2008).
- USFS, 2002. Resource Planning Act (RPA) Assessment, Final Statistics. <http://www.fs.fed.us/research/rpa> (accessed 1 June 2009)
- Vallauri, D.R., Aronson, J. & Barbero, M. 2002. An analysis of forest restoration 120 years after reforestation on badlands in the southwestern Alps. *Restoration Ecology* 10: 16–26.
- Wienk, C.L., Sieg, C.H. & McPherson, G.R. 2004. Evaluating the role of cutting treatments, fire and soil seed banks in an experimental framework in ponderosa pine forests of the Black Hills, South Dakota. *Forest Ecology and Management* 192: 375–393.
- Wikstrom, P. & Eriksson, L.O. 2000. Solving the stand management problem under biodiversity-related considerations. *Forest Ecology and Management* 126: 361–376.
- Wilson, D.S. & Puettmann, K.J. 2007. Density management and biodiversity in young Douglas-fir forests: challenges of managing across scales. *Forest Ecology and Management* 246: 123–134.
- Yost, A.C. 2008. Probabilistic modeling and mapping of plant indicator species in a Northeast Oregon industrial forest, USA. *Ecological Indicators* 8: 46–56.
- Zenner, E.K., Kabrick, J.M., Jensen, R.G., Peck, J.E. & Grabner J, K. 2006. Responses of ground flora to a gradient of harvest intensity in the Missouri Ozarks. *Forest Ecology and Management* 222: 326–334.

Received 16 February 2009;

Accepted 20 May 2009.

Co-ordinating Editor: R. Ohlemuller