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Understory Response to Repeated Thinning in Douglas-fir Forests of Western Oregon

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*This study investigated effects of a second-thinning entry on understory vegetation and tree regeneration development and understory vegetation composition. Study sites were located in the Coast Range and Cascade Range mountains of western Oregon and were dominated by Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) forests. Stands were initially thinned between 1975 and 1982 and parts of these same stands were thinned again approximately 20 yr later. Thinning stands a second time resulted in greater amounts of fern, graminoid, and open-site species, but the abundance of tree regeneration was not affected. Despite different site conditions, compositional patterns in the understory consistently shifted toward open-site early seral species following the second thinnings. These results suggest that the initial impacts of a second thinning are not simply predictable from studies in which only a single thinning was implemented. It is important to consider that vegetation trends were already influenced by the*

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previous thinnings, and impacts of the second thinning are thus not as easily detectable. Within these limitations, repeated thinnings may be an effective management tool to maintain early seral species in older forests, while other aspects of understory vegetation and tree regeneration are less influenced in the short term.

KEYWORDS *repeated thinning, understory vegetation, tree regeneration, vegetation community composition*

INTRODUCTION

Discussions about incorporating ecological goals such as biological diversity and wildlife habitat into forest management objectives have contributed to an increased interest in thinning as a management tool in the Pacific Northwest (PNW), especially on public land (Carey, 2003; Franklin, Mitchell, & Palik, 2007; Wilson & Puettmann, 2007). This interest originated from findings that forests dominated by high-density even-aged Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) stands do not support the diversity and abundance of plant and wildlife species that exist in older, unmanaged forests in the PNW (Carey, 1998; Franklin et al., 2002; Chan et al., 2006). Traditionally, managers have used thinning to increase growth rates of desirable trees and to promote stem quality and tree vigor (e.g., Curtis et al., 1998). Refined thinning practices (e.g., variable thinning intensities and spatial patterns) aimed at enhancing structural diversity and composition of understory layers result in increased heterogeneity and improved habitat suitability for many organisms (Hagar, Howlin, & Ganio, 2004; Davis, Puettmann, & Tucker, 2007).

Thinning opens up the overstory canopy (Davis et al., 2007) and, through disturbance of vegetation and soil, alters the microclimate and increases resource availability (Oliver & Larson, 1996; Thomas, Halpern, Falk, Ligouri, & Austin, 1999). The benefits of open canopy conditions following a thinning, however, are temporary because of the high growth potential in Douglas-fir stands. For example, canopy closure after thinning can be quite rapid (Newton & Cole, 2003; Chan et al., 2006; Davis et al., 2007), which impacts resource levels such as light availability for understory vegetation (Lindh, Gray, & Spies, 2003). Thus, it is generally understood that multiple thinnings are necessary to achieve the long-term transition of young, dense stands to stands with greater structural diversity (Tappeiner, 2008) and greater variability in composition of understory layers.

The response of tree growth and mortality to single and multiple thinnings has been documented (Marshall & Curtis, 2002; Chan et al., 2006; Davis et al., 2007). However, studies that investigated the response

of other ecosystem components, such as understory vegetation and tree regeneration, have been limited to a single thinning entry (Bailey, Mayrsohn, Doescher, St. Pierre, & Tappeiner, 1998; Kuehne & Puettmann, 2008; Davis & Puettmann, 2009; but see Shatford, Bailey, & Tappeiner, 2009). For example, Davis & Puettmann (2009) found that initial (5- to 7-yr post-treatment) declines in both low and tall shrubs, followed by subsequent growth and recovery, and shifts in understory composition were related to the release of early seral herbaceous species. Kuehne and Puettmann (2008) reported greater seedling densities initially following a thinning in Douglas-fir dominated stands (5- to 7-yr post-treatment). Longer term impacts of a single-thinning entry have also been documented through retrospective analysis of stands thinned more than a decade ago (Bailey & Tappeiner, 1998; Thomas et al., 1999; Lindh & Muir, 2004). For example, 10 to 24 yr after density treatments, low shrub, tall shrub, and herbaceous cover as well as abundance of conifer regeneration were greater in stands that were commercially thinned than in stands that were not thinned (Bailey & Tappeiner, 1998). In addition, Lindh and Muir (2004) reported increased heterogeneity in understory species composition 2 decades after a single pre-commercial thinning entry. However, when stands are thinned a second time, the question arises as to whether such understory responses are cumulative, and, if so, which trends may be altered or strengthened and which may be slowed or even reversed (e.g., due to physical impacts of the second harvesting operation). In this study, we investigated these questions in terms of the development of understory vegetation in order to assist managers with assessment of the trade-offs between single and multiple thinnings.

Our study objectives were to compare the response of tree regeneration and understory vegetation in stands that were thinned twice (twice-thinned) to stands that were thinned only once (once-thinned). Specifically, we investigated differences between once-thinned areas and twice-thinned areas in (a) cover and frequency of understory plant species, (b) abundance of tree regeneration, and (c) understory plant community composition.

METHODS

Study Description and Design

The study sites were located in the Coast Range and Cascade Range of western Oregon and are within the Coastal Western Hemlock (*Tsuga heterophylla* (Raf.) Sarg) Zone (Franklin & Dyrness, 1973). The area has a maritime climate characterized by mild, wet winters and relatively dry summers. Mean annual precipitation, primarily in the form of rain, varied from 57 to 115 in. Elevations ranged from 447 to 1,673 ft in the Coast Range sites

TABLE 1 Site Characteristics for Selected Study Locations in the Coast and Cascade Range Mountains of Western Oregon

Site	Blue Retro	Little Wolf	Sand Creek	Perkins Creek
Latitude (hddd°mm'ss'')	43°16'49"N	43°25'20"N	44°50'05"N	43°42'51"N
Longitude (hddd°mm'ss'')	124°04'57"W	123°37'45"W	123°35'26"W	122°54'47"W
Elevation range (ft)	1,465–1,668	447–900	1,306–1,673	1,506–2,125
Slope range (%)	5–50	8–93	3–50	10–37
Precipitation (in.)	60	70	115	57
Site index (King, 1966)	133	105	130	107
Dominant soil series	Blachly	Rosehaven	Bohannon	Peavine
Once-thinned area (ac)	15	18	11	99
Twice-thinned area (ac)	48	23	50	90
Once-thinned (yr)	1982	1980	1975	1980
Twice-thinned (month, yr)	March, 1999	Sept., 1998	Nov., 1997	March, 2000

and from 1,506 to 2,125 ft in the Cascade Range site. The dominant soil orders throughout the study area are largely Andisols and Inceptisols.

The study was set up as a large-scale management experiment (*sensu* Monserud, 2002) to minimize the need for extrapolation to operational conditions. To ensure a broad scope of inference, study sites were selected to represent a wide range of physical and environmental conditions (Table 1; Cissel et al., 2006). The sites were located in four naturally regenerated 60- to 90-yr-old stands: BR (Blue Retro), LW (Little Wolf), PC (Perkins Creek), and SC (Sand Creek). Stand areas ranged from 41 to 219 ac and consisted of relatively homogenous, contiguous conifers dominated by Douglas-fir. The stands had been commercially thinned 17 to 22 yr before our study, but the exact logging methods used are not known. Visual assessments of standing and downed wood revealed no indication of high mortality from a stem exclusion phase prior to the first commercial thinning.

At the beginning of our study, each of the four stands was divided into two treatment units, to which one of two treatments was assigned randomly. Thus, each stand contained one replicate of two treatments, providing a total of eight treatment units. The two treatments on each stand consisted of a once-thinned area and a twice-thinned area. The once-thinned areas had been thinned from below between 1975 and 1982 to densities of 110 to 240 trees per acre (tpa) and were not thinned again. The twice-thinned areas were re-thinned from below between 1997 and 2000 to an average density of 40 to 60 tpa. Twice-thinned areas were thinned using cable yarding, with the exception of the Sand Creek site, where tractor yarding was used for 7 ac.

Pre-treatment conditions of understory vegetation and tree regeneration were not assessed prior to the second thinning. Stands were selected to be homogenous and treatments were assigned randomly, with no regard to understory vegetation; therefore, we had no reason to assume a systematic bias in vegetation (see also Shatford et al., 2009).

Sampling Methods

Sample plots were established on a systematic grid to achieve 20 to 25 plots per stand in areas that approximately matched the target residual tree density prescription (Cissel et al., 2006). Quarter-acre circular plots (58.9-ft radius), each with four circular 0.005-ac subplots (8.3-ft radius), were established and permanently marked in the once-thinned (6–12 plots; mean = 9) and twice-thinned (12–13 plots; mean = 12) treatment types. Subplot centers were located 50 ft from plot center in each cardinal direction. Plot aspect and percent slope were recorded and elevation was determined using a handheld GPS unit. Understory vegetation and tree regeneration were sampled in the subplots 1 to 2 yr and 6 to 7 yr after the second-thinning entry (hereafter, Yr 1 and 6, respectively). Absolute percent cover of each vascular plant species within each subplot was visually estimated using cover classes: 1 (trace), 5, 10%, and continuing in 10% increments to 100%. The number of seedlings with a stem height between 6.0 in. and 4.5 ft, and the number of saplings with a stem height ≥ 4.5 ft and a diameter < 2.0 in. were counted for all conifer and hardwood species. Species nomenclature for all vegetation follows the United States Department of Agriculture Natural Resources Conservation Service PLANTS Database (USDA, NRCS, 2005).

Within the quarter-acre circular plots, all live trees with a diameter at breast height (DBH) > 2.0 in. were measured for diameter and a subset (systematically selected) of those trees were measured for total height and live-crown height. For reference, see Table 2 for summary statistics.

Data Analysis

Study sites were selected to allow for a broad scope of inference covering the Cascade and Coast Ranges of Oregon. As a trade-off, we had to account for a high amount of variability among our study sites. The analytical implication of this study design was that it reduced the statistical power to detect trends (Ganio & Puettmann, 2008). Consequently, we were cautious in our interpretations and aware that, due to the sample size representing a broad scope of interest, it was hard to determine whether trends were significantly different. On the other hand, statistically significant trends provide strong evidence for a regionally synchronous response, particularly given site variability and low statistical power. For statistical purposes, sites were treated as replicates ($n = 4$) and trends within sites (data not shown) were examined for consistency with overall trends.

The impact of the second thinning was assessed by comparing vegetation trends in the twice-thinned units with those in the matching once-thinned units (see also Shatford et al., 2009). Thus, we specifically compared the trends over time to document whether the second thinning strengthened, counteracted, or did not influence trends that developed after the first thinning. To account for the lack of pre-treatment vegetation data,

TABLE 2 Summary Statistics for Each Site by Treatment and Year for Basal Area, Trees Per Acre, Diameter at Breast Height, and Live Crown Ratio of all Live Trees (Standard Error in Parentheses)

Site ^a	Yr	Treatment ^b	Basal area (ft ² /ac)	Trees/ac	Diameter at breast height (in)	Live crown ratio (%)
BR	1	OT	232 (11.2)	133 (8.6)	16.8 (0.5)	0.46
BR		RT	149 (10.3)	84 (9.5)	16.6 (0.6)	0.46
BR	6	OT	247 (10.2)	126 (7.8)	17.9 (0.5)	0.39
BR		RT	165 (12.2)	84 (9.2)	17.5 (0.7)	0.49
LW	1	OT	169 (11.9)	144 (13.5)	13.0 (0.7)	0.41
LW		RT	118 (7.5)	71 (8.8)	16.4 (1.0)	0.45
LW	6	OT	182 (12.9)	143 (14.2)	13.5 (0.7)	0.40
LW		RT	131 (8.1)	79 (9.9)	16.2 (1.0)	0.49
PC	1	OT	205 (6.3)	192 (13.3)	12.7 (0.4)	0.46
PC		RT	102 (8.2)	66 (5.4)	15.9 (1.1)	0.47
PC	6	OT	226 (6)	195 (11.7)	13.1 (0.3)	0.42
PC		RT	116 (8.8)	74 (6.3)	15.4 (1.0)	0.52
SC	1	OT	264 (8.1)	102 (6.9)	21.2 (0.7)	0.28
SC		RT	124 (9.5)	54 (6.1)	19.5 (1.0)	0.34
SC	6	OT	275 (7.4)	102 (7.0)	21.6 (1.0)	0.42
SC		RT	144 (12.5)	65 (10.6)	19.4 (1.2)	0.48

^aBR = Blue Retro; LW = Little Wolf; PC = Perkins Creek; SC = Sand Creek. ^bOT = once-thinned; RT = twice-thinned.

we limited our discussions to general trends in species groups rather than single species (Davis & Puettmann, 2009).

UNDERSTORY VEGETATION AND TREE REGENERATION DEVELOPMENT

Treatment effects on understory vegetation were examined after grouping species by growth form (i.e., herb, tall shrub, etc.), habitat (i.e., forest understory, open-site, etc.), and/or origin (i.e., native and exotic). Plants were assigned to these groups based on vegetation characteristics described in the USDA PLANTS Database (see USDA, NRCS, 2005). Plot-level mean percent cover of ferns, graminoids (including grasses, sedges, and rushes), herbs, low shrubs, tall shrubs, forest understory species, open-site species, and exotic species was calculated by averaging the four subplots for each group. Mean plot frequencies of vegetation groups were calculated for each plot as the number of subplots in which a group was present divided by the total number of subplots in a plot. Abundance of tree regeneration was calculated for each plot as the total number of seedlings and saplings in the four subplots and expanded to a per-acre basis. Treatment-level averages for percent cover and frequency of understory vegetation and abundance of tree regeneration were calculated from plot-level means. A mixed-model ANOVA (SAS version 9.0; SAS Institute Inc., Cary, NC, USA) was used to test for the effects of treatment, year, and a treatment-by-year interaction on mean percent cover and mean frequency of each vegetation group, as well

as mean number of seedlings and saplings. Sites were treated as a random effect with treatments nested within sites. Response variables were assessed for agreement with statistical assumptions (i.e., normality and homoscedasticity of residuals) and, where needed, understory data was transformed using log, square root, or power transformations.

UNDERSTORY VEGETATION COMPOSITION

Understory vegetation cover values for each species were averaged for each treatment by site and year. To examine plant community composition, multivariate community analysis was conducted using PC-ORD v. 4.0 (McCune & Medford, 1999). Differences in species composition between once-thinned and twice-thinned treatment groups for each year (Yr 1 and 6 following the second thinning) were tested using multi-response blocked permutation procedure (MRBP; Mielke, 1979). MRBP provides an effect size, A , that measures the chance-corrected within-group agreement, and is a measure of the homogeneity of plant-community composition within treatments—for example, if $A = 1$, all species are identical within groups; if $A = 0$, then homogeneity within groups is random; and if $A < 0$, then homogeneity within groups is less than expected by chance.

To examine patterns in understory plant-community composition and their relationships with stand density measures (e.g., basal area), species abundances, and other environmental variables that may influence plant distribution (e.g., topography), an ordination of treatment units in species space was conducted using non-metric multidimensional scaling (NMS; Kruskal, 1964). Sørensen distance measure was used with the slow-and-thorough autopilot mode (McCune & Grace, 2002). Species occurring in less than 5% of the treatments were excluded from the NMS analysis to reduce noise in the data before running ordinations. In addition, community data were log-transformed to improve multivariate normality.

Indicator species analysis (Dufrêne & Legendre, 1997) was conducted separately by measurement year (Yr 1 and Yr 6) and was used to identify the exclusiveness or the concentration of species to particular treatment types (once-thinned and twice-thinned). This method calculates an indicator value from the relative abundance and relative frequency of each species. Indicator values range from 0 to 100, where 100 is a perfect indication of a species to a treatment (McCune & Grace, 2002).

RESULTS AND DISCUSSION

Understory Vegetation and Tree Regeneration Development

In general, development of understory vegetation was quite dynamic after the second thinning, but responses were not consistent for the various vegetation groups. The second thinning led to increased cover of fern,

TABLE 3 Mean Percent Cover (a) and Frequency (b) of Understory Vegetation Groups 1 Yr and 6 Yr Post-Second Thinning in Once-Thinned and Twice-Thinned Areas (Standard Error in Parentheses)

	Yr 1		Yr 6	
	Once-thinned	Twice-thinned	Once-thinned	Twice-thinned
(a)				
Fern	31 (9.29)	32 (12.00)	30 (7.38)	43 (14.83)
Herb	26 (16.39)	30 (12.94)	15 (8.15)	21 (9.43)
Low shrub	42 (12.64)	30 (8.32)	35 (10.39)	36 (10.38)
Tall shrub	21 (4.87)	15 (0.86)	23 (6.69)	16 (1.49)
Graminoid	2 (1.13)	5 (2.05)	2 (0.51)	3 (0.29)
Forest understory spp.	106 (13.32)	87 (11.94)	95 (7.94)	95 (7.55)
Open-site spp.	12 (4.73)	20 (8.43)	7 (2.10)	20 (7.02)
Exotic	1 (0.40)	2 (0.82)	0.1 (0.02)	1 (0.20)
(b)				
Fern	1.6 (0.16)	1.8 (0.19)	1.6 (0.23)	2.0 (0.16)
Herb	5.0 (0.98)	6.3 (1.18)	5.7 (1.28)	7.1 (1.28)
Low shrub	2.7 (0.87)	2.8 (0.90)	2.9 (0.88)	3.0 (0.96)
Tall shrub	1.8 (0.15)	1.8 (0.14)	2.1 (0.10)	2.3 (0.20)
Graminoid	1.2 (0.39)	1.6 (0.48)	1.3 (0.38)	2.2 (0.12)
Forest understory spp.	9.0 (1.27)	9.1 (0.96)	9.9 (1.03)	10.3 (0.86)
Open-site spp.	1.7 (0.39)	3.2 (0.83)	2.2 (0.53)	4.1 (0.70)
Exotic	0.2 (0.16)	1.0 (0.46)	0.1 (0.02)	0.7 (0.11)

low shrub, tall shrub, and forest understory species; while cover of herb, graminoid, and exotic species decreased over the 6-yr measurement period (Table 3). However, a comparison of vegetation trends between treatment types showed that differences in cover of herb, low shrub, tall shrub, graminoid, and forest understory species were too small to be statistically significant. This contrasts with findings from thinning studies that assessed understory vegetation response to a single thinning entry, which showed that cover of most vegetation groups increased after thinning (Bailey et al., 1998; Thomas et al., 1999). Exceptions to these patterns included tall shrubs, which may be slow to recover from harvest damage (Davis & Puettmann, 2009). In these studies, unthinned stands were used for comparison, whereas our reference conditions were stands that had been thinned previously. The impact of repeated thinnings may account for the difference between our findings and those of previous studies. In contrast to impacts of repeated thinnings on sapling growth (Shatford et al., 2009), it appears that the dynamics of other understory vegetation may still be influenced by the initial thinning to an extent that impacts of a second thinning on vegetation cover were not statistically detectable. However, the lack of a statistically significant response in vegetation cover to the second thinning may also be partially due to our small sample size and high site variability. Further development of our statistical model using basal area (including hardwoods and conifers) as a covariate showed that basal area did not influence understory

vegetation cover (or frequency) beyond the treatment assignment (data not shown, but see Table 2).

Thinning stands twice altered trends in fern cover and marginally affected exotic species cover. The second thinning led to an increase in fern cover, and the difference between once-thinned and twice-thinned stands increased over time (treatment \times year interaction: $p = .010$). This result suggests a release response by rhizomatous species, as bracken fern (*Pteridium aquilinum*) and sword fern (*Polystichum munitum*) were the dominant fern species in these areas. While these species can provide habitat and foraging opportunity for some wildlife species (Haeussler & Coates, 1986; Hagar, 2007), uniform cover of these species can limit diversity by inhibiting the growth and establishment of other species (Tappeiner & Zasada, 1993; Thysell & Carey, 2000; 2001). This may be another explanation for why cover values of most vegetation groups were not statistically different following the second thinning. Thinning stands twice created conditions more favorable for exotic species (treatment: $p = .051$). However, cover was low in both treatment types (<2%), as has been found after thinning and fire treatments (Nelson, Halpern, & Agee, 2008; Dodson, Peterson, & Harrod, 2008). Greater cover of exotic species following the second thinning is likely due to short-term disturbance effects, as evident by their transient occupancy (Thysell & Carey, 2001; Lindh & Muir, 2004; Davis & Puettmann, 2009; Ares, Neill, & Puettmann, 2010) in these areas.

The second thinning increased the frequency of fern, graminoid, open-site species, and exotic species (treatment: $p = .020$; $p = .021$; $p = .028$; $p = .049$, respectively). The type and amount of harvesting disturbance may have influenced these patterns (Thysell & Carey, 2001; Davis & Puettmann, 2009) by creating conditions (e.g., disturbed soil, increased light availability) favorable for invasion (Bailey et al., 1998; Mack et al., 2000; Thysell & Carey, 2000) by opportunistic species that have the ability to quickly colonize such areas. As a result, these species could displace less competitive species in the short term (Grime, 1979), which may help explain why frequencies of herbs, low shrubs, and forest understory species were not influenced by the second thinning. In addition, the species that establish after thinning depend on site history, e.g., the seed bank and propagule availability through invasion (Halpern, Evans, & Nielson, 1999). Although data were not collected following the first thinning, it is likely that some opportunistic species were present in these areas at that time (Halpern et al., 1999). Repeated thinnings may extend or provide a second temporal window for the establishment of opportunistic species (Halpern et al., 1999; Thysell & Carey, 2001; Davis & Puettmann, 2009).

The second thinning had no impact on the frequency of tall shrubs, which may reflect the low shrub cover prior to the second-thinning entry (Wilson, Anderson, & Puettmann, 2009). However, frequencies increased over the measurement period in both treatment types (year: $p = .010$). This

TABLE 4 Mean Density of Seedlings and Saplings 1 Yr and 6 Yr Post-Second Thinning in Once-Thinned and Twice-Thinned Areas at Each Site (Standard Error in Parentheses)

Site ^a	Yr 1		Yr 6	
	Once-thinned	Twice-thinned	Once-thinned	Twice-thinned
Seedlings (number/ac)				
BR	2,125 (858.4)	2,854 (922.8)	900 (360.1)	1,342 (492)
LW	910 (287.8)	508 (126.6)	890 (257.7)	412 (183)
PC	400 (175.3)	245 (76.7)	367 (128.1)	354 (79.2)
SC	425 (143.0)	292 (80.7)	583 (179.7)	854 (173.0)
Saplings (number/ac)				
BR	392 (199.8)	288 (230.4)	725 (288.6)	1,483 (382.6)
LW	250 (137)	435 (102.3)	415 (175.8)	642 (150.4)
PC	175 (84.5)	127 (40.1)	367 (128.1)	354 (79.2)
SC	283 (186.5)	96 (35.1)	425 (172.6)	454 (120.2)

^aBR = Blue Retro; LW = Little Wolf; PC = Perkins Creek; and SC = Sand Creek.

result suggests that tall shrubs may have initially been negatively affected by the second thinning, likely from mechanical damage during the thinning operation. Such initial setbacks may prevent immediate increases in frequencies (and cover) of tall shrubs and recovery thereafter may also be slow (Davis & Puettmann, 2009). Whether or not the long-term impact of the second thinning will increase frequencies of tall shrubs remains unseen and further examination is warranted.

Seedling and sapling densities were quite variable (Table 4), as expected after thinning operations (Kuehne & Puettmann, 2008), but thinning stands a second time did not alter trends in the amount of tree regeneration ($p < .05$). The second thinning may not have created conditions for successful germination and establishment in the short term due to limited soil disturbance during cable harvesting (Bailey & Tappeiner, 1998). Alternatively, the existing understory vegetation and advanced regeneration may have prevented the establishment of a new cohort (Tappeiner, Maguire, & Harrington, 2007). In contrast, growth of established saplings has been shown to benefit rather quickly from a second thinning (Shatford et al., 2009). Thinning also appears to have little influence on composition of the regeneration. In both treatment types, composition of the regeneration was dominated by Douglas-fir and western hemlock (*Tsuga heterophylla*), with other species such as western red cedar (*Thuja plicata*) and giant chinquapin (*Chrysolepis chrysophylla*) also being present. Non-dominant overstory species were left in the second-thinning entry and overstory composition (and thus seed availability) was likely not sufficiently altered to impact regeneration patterns.

Understory Vegetation Composition

Results of the vegetation analysis confirmed that the study sites collectively represented a wide range of ecological conditions because understory

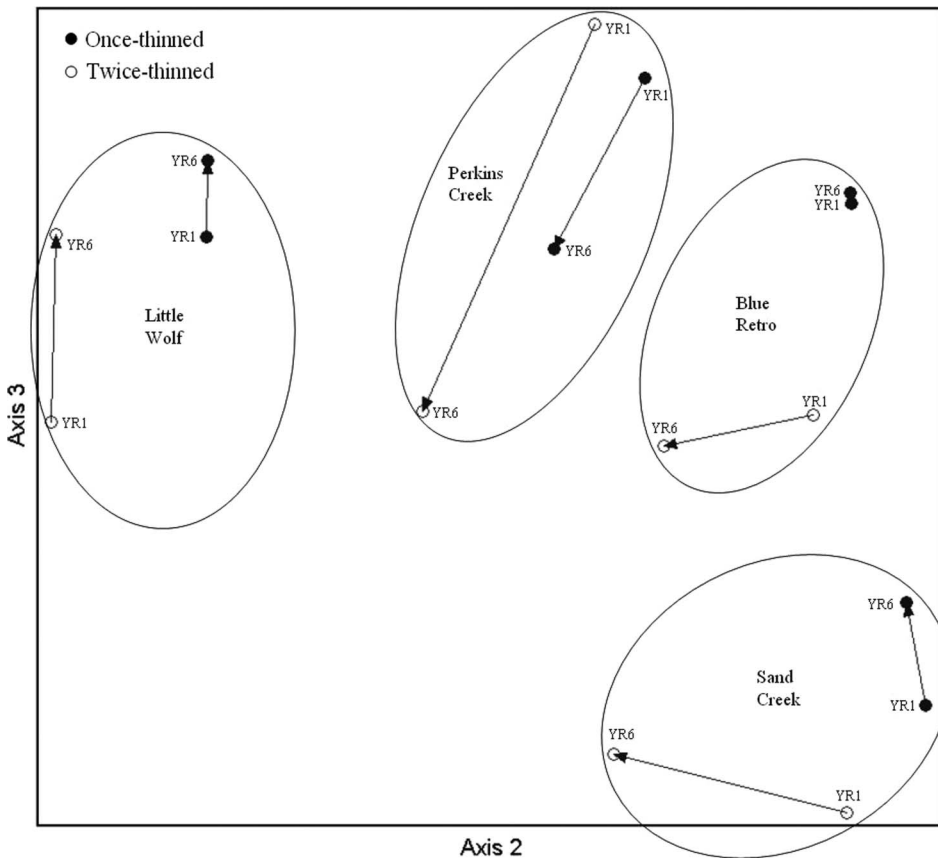


FIGURE 1 Ordination of forest stands in species space for each site for Yr 1 and Yr 6 yielded a three-dimensional solution that explained 93% of the variation in the raw data (NMS ordination, $p = .0196$, final stress = 5.26, final instability = 0.00001, 79 iterations). Points in the ordination graph represent stands and were coded by thinning treatment (once-thinned and twice-thinned). Vectors were used to connect stands from Yr 1 to Yr 6. The magnitude of difference in understory composition in the twice-thinned areas appears much larger than in the once-thinned areas (see vector lengths).

plant community composition was more similar within than among sites. Figure 1 shows the ordination of treatment-level data that illustrates patterns of understory composition. In particular, understory communities were most different at the Little Wolf site, consisting of greater hardwood trees and shrubs (Ordination Axis 2 describes 52% variation in community structure). Axis 3 (describes 26% variation) was related to changes in community composition over time (i.e., grass, $R^2 = .598$ with ordination axis) and Axis 1 (describes 15% variation, not shown) to abiotic factors (i.e., aspect).

Despite the range of site conditions, however, vegetation trends by plant group were consistent across all sites, suggesting that results are applicable to the wide inference scope covered by the range of sites. The second

TABLE 5 Indicator Species Analysis for Yr 1 (a) and Yr 6 (b). Indicator Values (IV) Are Plotted with Letters Indicating the Species' Typical Habitat Association: F—Forest Understories; O—Open or Disturbed Sites; M—Wet Meadows, Rock Outcrops, or Other Types of Natural Openings; and NS—Not Specified or None.

Treatment	Species	Habitat	IV
(a)			
Once-thinned	<i>Campanula scouleri</i>	F	61.7
	<i>Linnaea borealis</i>	F	50.0
	<i>Lilium columbianum</i>	M	50.0
	<i>Mabonia nervosa</i>	F	52.3
	<i>Mycelis muralis</i>	F	50.0
Twice-thinned	<i>Carex</i> sp.	NS	58.0
	<i>Cirsium arvense</i>	O	50.0
	<i>Anaphalis margaritacea</i>	O	61.7
	<i>Athyrium filix-femina</i>	F	58.5
	<i>Epilobium minutum</i>	O	75.0
	<i>Erechtites minima</i>	O	50.0
	<i>Iris tenax</i>	M	52.6
	<i>Lotus corniculatus</i>	O	50.0
	<i>Maianthemum stellatum</i>	F	50.0
	<i>Ribes</i> sp.	O	58.3
	<i>Rubus discolor</i>	O	50.0
	<i>Rubus lasiococcus</i>	F	50.0
	<i>Sanicula crassicaulis</i> var. <i>crassicaulis</i>	F	50.0
	<i>Sambucus racemosa</i>	F	50.0
	(b)		
Once-thinned	<i>Campanula scouleri</i>	F	58.4
	<i>Trillium ovatum</i>	F	59.7
Twice-thinned	<i>Chamerion angustifolium</i>	O	50.0
	<i>Acer circinatum</i>	F	50.6
	<i>Actaea rubra</i>	F	50.0
	<i>Adiantum aleuticum</i>	F	50.0
	<i>Anaphalis margaritacea</i>	O	100*
	<i>Cirsium vulgare</i>	O	50.0
	<i>Dicentra formosa</i>	F	60.3
	<i>Digitalis purpurea</i>	O	50.0
	<i>Epilobium minutum</i>	O	50.0
	<i>Erechtites minima</i>	O	50.0
	<i>Festuca</i> sp.	NS	54.4
	<i>Frangula purshiana</i>	F	54.9
	Grass	O	64.7
	<i>Hieracium albiflorum</i>	F	65.3
	<i>Holcus lanatus</i>	O	50.0
	<i>Hypericum perforatum</i>	O	50.0
	<i>Hypochaeris radicata</i>	O	84.8
	<i>Iris tenax</i>	M	64.6
	<i>Lotus crassifolius</i>	O	62.7
<i>Lotus micranthus</i>	O	50.0	
<i>Luzula comosa</i>	M	61.8	
<i>Luzula parviflora</i>	F	57.8	
<i>Oxalis oregana</i>	F	54.8	

(Continued)

TABLE 5 (Continued)

Treatment	Species	Habitat	IV
	<i>Pteridium aquilinum</i>	O	54.9
	<i>Ribes</i> sp.	O	100*
	<i>Rubus laciniatus</i>	O	50.0
	<i>Rubus leucodermis</i>	O	75.0
	<i>Rubus parviflorus</i>	O	61.0
	<i>Rubus spectabilis</i>	F	55.5
	<i>Rubus ursinus</i>	F	55.3
	<i>Sambucus racemosa</i>	F	50.0

* $p > .05$.

thinning resulted in different compositional patterns after accounting for site-to-site variation in Yr 1 (blocked MRPP: $A = 0.058$, $p = .049$) and in Yr 6 (blocked MRPP: $A = .104$, $p = .037$). Areas that were thinned a second time had greater abundances of open-site early seral species (Table 5), and species such as *Anaphalis margaritacea* and *Ribes* sp. were indicative of these areas 6 yr following treatment (Table 5b). Without the second thinning, more shade-tolerant and persistent forest understory species were dominant (Table 5a and 5b). Thus, the shift in species composition toward early-seral-type species evident after single-thinning entries (Halpern, 1989; Wilson & Puettmann, 2007; Davis & Puettmann, 2009) appears to be repeated in the second entry. This is especially important in a region where early seral habitat is becoming a concern for a variety of wildlife species (Hagar et al., 2004; Swanson et al., 2010). Repeated thinning entries may provide an opportunity to maintain early seral species in older forests for longer time periods. These results also suggest that over the long term, repeated thinnings may counteract the development of late seral understory vegetation. In these instances, such conditions may be achieved by leaving unthinned areas within stands (Franklin et al., 2007; Ares, Berryman, & Puettmann, 2009).

CONCLUSIONS

Thinning stands a second time upheld many trends in understory vegetation that developed after the first-thinning entry, with notable exceptions such as vegetation composition. Our study showed that 2 decades later, the development of understory vegetation after the initial thinning made it difficult to show significant impacts of the second thinning. Consequently, any consideration regarding whether to approach density reductions with a few (or perhaps only one) high-intensity thinnings rather than multiple, lighter thinning entries requires weighing the costs and benefits of repeated thinnings against the trends set in motion by the initial thinning. Furthermore, findings from studies that only used a single-thinning entry cannot simply be

used to predict the responses of understory vegetation following a second thinning (and likely additional thinnings). Lastly, it should be noted that this study only assessed the initial response of the forest understory to a second thinning; whether these trends hold up in the long term requires further study.

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