Understory plant species composition 30–50 years after clearcutting in southeastern Wyoming coniferous forests

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Abstract

To evaluate the long-term effects of clearcutting and slash treatment on understory plant species composition in Rocky Mountain coniferous forests, we collected comparable data from 30- to 50-year-old post-harvest stands and adjacent mature (>100-year-old) stands that originated after wildfire. In general, plant species richness was higher in the post-harvest stands than in adjacent mature stands, due in large part to the presence of species that benefit from disturbance. Species composition in post-harvest and mature stands was more similar in montane forests (2710–2805 m elevation) than in subalpine forests (2800–3164 m elevation), suggesting greater resilience of montane understories. Composition in post-harvest and mature stands was least similar when slash was piled and burned, and most similar when slash was lopped and scattered. Eighty-seven percent of the post-harvest stands had at least one exotic species, but total cover of exotic plant species in all post-harvest stands was $\leq 1\%$. Exotic species were largely absent from mature forests. Our results suggest that understory species of low-elevation montane forests recover more quickly from disturbance than do those of subalpine forests, with slash treatment and species life history traits strongly influencing this recovery.

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1. Introduction

Sustainable forest management requires monitoring the effects of past management practices (Grumbine, 1994). While various studies have investigated understory plant succession after timber harvesting (Corns and LaRoi, 1976; Bormann and Likens, 1979; Stransky et al., 1986; Halpern, 1988, 1989;

Schoonmaker and McKee, 1988; Halpern and Franklin, 1990; De Grandpre et al., 1993; Halpern and Spies, 1995; Gilliam et al., 1995; Roberts and Gilliam, 1995; De Grandpre and Bergeron, 1997; Brakenhielm and Liu, 1998; Bailey et al., 1998; Ruben et al., 1999), none have investigated the long-term effects of clearcutting and slash treatment in the Rocky Mountain region of North America. Our study focuses on 30–50-year-old post-harvest stands in the Medicine Bow Mountains of southeastern Wyoming. We compared post-harvest stands in different environments with different kinds of slash treatment, to adjacent, mature stands that originated after wildfire.

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Although long-term effects of clearcutting on forest understories have not been examined in Rocky Mountain coniferous forests, several studies have examined early successional trends. [Dion \(1998\)](#) compared understory species composition in 7-year-old stands treated with mechanical site preparation (roller-chopping and tractor walking) to that of untreated post-harvest stands and mature uncut stands in the Sierra Madre Mountains to the west of our study area. She found that plant species richness was higher in clearcut than in adjacent mature stands due to invasion of wind-dispersed species (native and non-native), but that species richness did not differ between stands in which slash was treated and untreated. Cover of residual species (i.e., those present before harvesting) declined with disturbance intensity and there was a higher cover of non-native invaders in clearcut stands than in adjacent mature stands. However, exotic species comprised only 1–2% cover and did not differ in treated and untreated post-harvest stands. [Dion \(1998\)](#) also found less vegetation where soil disturbance was greater, although individual understory species responded differently to disturbance.

Similar results were obtained from studies examining effects of slash treatment on lodgepole pine regeneration patterns. [Adams \(1972\)](#) noted a seemingly direct correlation between presence of slash and presence of lodgepole pine seedlings, with piled and burned stands having lower rates of stocking than stands in which slash was compressed into the soil with several passes of a tractor or stands where slash was evenly distributed. [Alexander \(1964\)](#) suggested that higher stocking densities are achieved when slash is left untreated or is evenly distributed, compared to slash that is piled and burned.

Results from a long-term study in the western Cascade Range of Oregon after clearcutting in Douglas-fir forests appear to support the short-term pattern of understory species dynamics documented by [Dion \(1998\)](#) in the Rocky Mountain region ([Halpern, 1988, 1989; Halpern and Franklin, 1990; Halpern and Spies, 1995](#)). Most understory plant species survived disturbance and invading species colonized within 2 years after broadcast burning ([Halpern, 1988](#)). Succession was also affected by intensity of soil disturbance. Understories were dominated largely by residual species in relatively undisturbed sites (i.e., slash and forest floor left intact), and burned sites were domi-

nated by invaders that colonized within two years after disturbance ([Halpern, 1989](#)). Although invaders of burned sites included non-native species, their importance declined with time.

Our study was motivated, in part, to determine if the short-term trends observed by [Dion \(1998\)](#) persist after 30–50 years of succession, and whether patterns in Rocky Mountain forests are similar to those in West Cascade Range forests ([Halpern, 1988, 1989; Halpern and Franklin, 1990; Halpern and Spies, 1995](#)). Our objectives were to examine the differences in species richness, species composition, and total cover of understory vegetation in 30–50-year-old post-harvest stands and adjacent mature post-fire stands, determine the influence of post-harvest slash treatments and elevation on the recovery of understory species, and assess the importance of non-native understory species in developing post-harvest stands. We hypothesized that: (1) elevation would have a significant effect on the recovery of forest understory species assemblages, with higher elevation forests recovering more slowly, (2) more intensive slash treatments (e.g., piling and burning) would negatively impact the long-term recovery of forest understories, and (3) cover of non-native understory species would be higher in 30–50-year-old post-harvest stands than in adjacent mature forest understories.

2. Materials and methods

2.1. Study area

Our study was conducted in the Snowy Range portion of the Medicine Bow National Forest (MBNF; 41°N, 106°W), located in the Medicine Bow Mountains of southeastern Wyoming (50 km west of Laramie). The Snowy Range encompasses approximately 218,600 ha and ranges in elevation from 2500 to 3700 m ([Alexander et al., 1986](#)). Precambrian gneiss and igneous rock underlie most of the Range ([Houston, 1968](#)), and soils in forested areas are usually Typic Cryochrepts and Typic Cryoboralfs ([Knight, 1994](#)). Mean annual precipitation ranges from 40 cm at lower elevations (~2700 m) to as much as 120 cm at higher elevations (~3200 m), with roughly two-thirds of this falling as snow ([Knight, 1994](#)). Mean annual temperature is generally less than 2 °C, with the potential for

freezing temperatures during any month of the year (Martner, 1986).

Lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm. ex Wats.) dominates forests at lower elevations (2500–3000 m) and on more xeric sites, comprising 66% of the forested land on the Snowy Range. Subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) and Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) dominate forests at higher elevations (3000–3300 m) and on more mesic sites, covering 27% of the forested area (Alexander et al., 1986; Kipfmüller and Baker, 1998). All three species often occur together in mixed stands at middle elevations.

Common post-harvest slash-reduction treatments in the 1950s and 1960s included piling and burning, roller-chopping, lop and scatter, and, in selected areas, a combination of piling and burning and roller-chopping (L.T. Cartwright, personal communication; Walter Chesbro, personal communication; Boe, 1956; Alexander, 1964). The pile and burn technique employed a bulldozer with a brush rake rather than a blade to avoid incorporating too much soil into the slash piles. Burning took place within 2 years of harvest. Roller-chopping was common in the early 1960–1980s; a drum weighing approximately 9.2×10^3 kg was towed behind a bulldozer to compress slash into the soil. In the lop and scatter method, logging slash was cut into sections and distributed manually throughout the stand. Tree regeneration usually occurred naturally from seeds contained in logging slash or by seeds dispersed from adjacent uncut areas (Alexander, 1964; Dion, 1998). There is no record of artificial seeding or planting in any of the stands we studied.

We selected post-harvest stands that originated after clearcutting between 1950 and 1969 and that were adjacent to mature forests with similar environmental conditions (slope, aspect, elevation, soil-type). Mature stands were assumed to have initiated after fire, and we did not sample mature stands that had been thinned or had any evidence of selective harvest.

For each post-harvest stand, we determined harvest year, harvest technique, and thinning history using information contained within the Rocky Mountain Resource Information System (RM-RIS) database maintained by the MBNF. Information on the type and timing of slash treatments was not available for clearcuts originating in the 1950s and 1960s, so type of

slash treatment was determined by on-site analysis of logging debris. Remnants of burned slash piles were still evident after 30–50 years (circular areas with low vegetation cover and abundant charcoal and charred coarse woody debris). Distinct chop-marks roughly 60 cm apart on larger woody debris indicated roller-chopping. Stands without evidence of burn-piles and chop-marks on logging debris were assumed to have been lopped and scattered. We assumed that slash treatments were implemented either immediately after harvesting or in the following year.

2.2. Sampling

We sampled 54 forest stands over two field seasons—30 post-harvest stands and 24 adjacent, mature uncut stands (Table 1). Sampling was done from mid-June to late August in 1998 and 1999. Within each stand, we collected data along ten 50 m transect lines distributed at ≥ 10 m intervals and running perpendicular to a subjectively chosen baseline. At 10 m intervals along each transect, a 50 cm $\times$ 100 cm point-frame with 36 points (Floyd and Anderson, 1982; Turner et al., 1997) was used to estimate cover and frequency of understory species and tree seedlings (< 20 cm tall); a total of 50 frames (1800 points) was sampled in each stand. Importance values (IVs) were calculated as the sum of relative cover and relative frequency of each species (range of 0–200; Gilliam et al., 1995). Understory species were grouped into one of four categories for analysis of growth-form composition: tall shrubs, low shrubs, forbs, and graminoids. Non-native species were identified using a list compiled for Wyoming by Fertig (1999).

Tree species taller than 20 cm were sampled with 2 m $\times$ 20 m plots running parallel to each 50 m transect. Tree species were classified into four categories: seedlings (< 20 cm tall; sampled with point-frame), short saplings (≥ 20 cm but < 1.5 m tall), tall saplings (≥ 1.5 m tall but < 4 cm dbh), and canopy trees (≥ 1.5 m tall, ≥ 4 cm dbh); only data for seedlings and canopy trees are presented here. For canopy trees, we recorded species, number, and diameter at breast height (dbh). Density (stems ha^{-1}) and basal area ($\text{m}^2 \text{ha}^{-1}$) was calculated by species for canopy trees. Canopy height was estimated by measuring the height of 10 randomly selected canopy trees within each

Table 1

Location, silvicultural treatments, and environmental characteristics of 30 sampled post-harvest stands^a

Post-harvest stand	USGS 7.5' quadrangle	Year harvested	Slash treatment	Thinned	Elevation (m)	Aspect	Slope (%)	Adjacent mature
FP1	Foxpark	1951	Lop and scatter	Y	2774	SW	5	N
FP2	Foxpark	1951	Lop and scatter	Y	2804	E	5	Y
FP11	Foxpark	1960	Both PB and RC	N	2804	N	8	Y
FP18	Foxpark	1969	Roller-chop	Y	2774	N	24	Y
FP19	Foxpark	1969	Both PB and RC	Y	2773	W	18	Y
FP20	Foxpark	1965	Both PB and RC	Y	2737	E	4	Y
WL2	Woods Landing	1957	Lop and scatter	Y	2710	SW	13	N
WL18	Woods Landing	1957	Lop and scatter	Y	2743	NE	14	Y
WL19	Woods Landing	1957	Lop and scatter	Y	2731	N	15	Y
OH1	Overlook Hill	1965	Roller-chop	Y	2805	NW	30	Y
HR25	Horatio Rock	1959	Pile and burn	Y	2792	SE	5	Y
HR36	Horatio Rock	1956	Pile and burn	Y	2750	NE	8	Y
HR37	Horatio Rock	1961	Roller-chop	N	2712	S	25	Y
KS3	Keystone	1967	Pile and burn	N	2900	SE	5	Y
KS9	Keystone	1965	Lop and scatter	Y	2780	S	15	N
KS12	Keystone	1965	Both PB and RC	Y	2890	E	18	Y
KS13	Keystone	1965	Both PB and RC	N	2919	S	12	Y
KS14	Keystone	1967	Lop and scatter	N	3010	SE	18	Y
TR122	Turpin Reservoir	1957	Pile and burn	Y	2865	SW	5	Y
SL27	Sand Lake	1957	Pile and burn	Y	3070	SE	10	Y
PL102	Phantom Lake	1963	Pile and burn	N	3010	SE	16	Y
PL102a	Phantom Lake	1963	Pile and burn	N	3060	SE	16	Y
PL124	Phantom Lake	1965	Roller-chop	Y	2800	NW	10	Y
PL125	Phantom Lake	1966	Lop and scatter	Y	2877	N	34	Y
PL126	Phantom Lake	1966	Lop and scatter	Y	2896	NW	24	Y
M7	Morgan	1969	Roller-chop	N	3050	NE	12	Y
M9	Morgan	1968	Pile and burn	N	3070	NW	10	Y
MB1	Medicine Bow Peak	1969	Pile and burn	N	3164	NW	12	Y
MB2	Medicine Bow Peak	1969	Pile and burn	N	3152	NW	18	Y
MB3	Medicine Bow Peak	1969	Pile and burn	N	3120	N	14	Y

^a “N” under “adjacent mature” indicates no suitable mature forest stand within the vicinity of the post-harvest stand.

stand using a clinometer and taking the mean of those 10 measurements as the canopy height. Year of origin for post-harvest stands was available from USFS records. For the mature forests, we estimated stand age by counting annual growth rings on cores from five of the largest trees. Stand age was assumed to be the age of the oldest tree. We avoided coring trees that were much larger in diameter (>15–20 cm) or much older than the majority of trees in the stand, as these may have been survivors of the last fire.

Five soil samples were taken from the A horizon (approximately 5 cm below the top of the O horizon) in each stand and were combined. These composite samples were then analyzed for texture (percent sand, silt, and clay) using the hydrometer method (Miller and Kotuby-Amacher, 1998).

2.3. Data analysis

The stands we sampled occurred along a relatively broad elevation range (2710–3164 m; Table 1). We used two-way indicator species analysis (TWINSPAN; Hill, 1979) of mature stand understory IV data to objectively separate stands into two elevation zones: a high elevation, subalpine zone, in which subalpine fir and Engelmann spruce were the dominant canopy species, and a low- to mid-elevation montane zone, in which the forest canopy was dominated by lodgepole pine. We used two-sample *t*-tests to determine if there were statistically significant differences in elevation, soil-texture (percent sand), and stand age between montane and subalpine mature stands as classified by TWINSPAN (α adjusted for the

number of comparisons using the Bonferroni correction; Sokal and Rohlf, 1981).

Non-metric multidimensional scaling (NMS) was used to examine variation in understory composition in post-harvest and adjacent mature forest stands within and between the two elevation zones. NMS is an iterative best-fit technique that seeks to arrange samples (in this case forest stands) so that the distance between each pair of samples in ordination space is in rank order with their similarities in species composition (Clarke, 1993). Multiple iterations are performed to minimize lack of fit, or stress, between ordination distances and measures of dissimilarity based on species composition. We performed NMS on the IV data using the Sorensen (Bray-Curtis) metric as a measure of dissimilarity (Faith et al., 1987; McCune, 1997). Dimensionality was assessed by examining the change in stress as a function of dimension while stepping down from a six- to one-dimensional solution. We used an instability criterion of 1×10^{-5} and performed 40 runs with real data and 50 runs with randomized data. The best solution for each dimensionality was selected as the real run with the lowest final stress on a scale of 0–100 (McCune and Mefford, 1999). Results indicated a two-dimensional solution was most parsimonious. Final stress for the two-dimensional solution was found to be lower than 95% of the randomized runs based on a Monte Carlo test. The ordination was rotated using the varimax method to maximize the elevation gradient along NMS axis 1, the most obvious gradient in the ordination.

We used multi-response permutation procedures (MRPP) to test the hypothesis of no difference in understory species composition between post-harvest stands and adjacent mature forest stands in both the montane and subalpine zones. MRPP is a non-parametric, multivariate method used to make statistical comparisons among two or more a priori groups (Zimmerman et al., 1985). The MRPP test statistic describes the separation between groups based on the weighted mean within-group distance, A (McCune and Grace, 2002). The Sorensen distance metric was used to quantify the compositional distance, as it has been shown to be more robust than other distance measures (Faith et al., 1987; McCune and Mefford, 1999), and because it was used as the distance metric in the NMS ordination. The degree of similarity between post-harvest and mature forest understories,

as measured by Sorensen distance, serves as an indicator of resilience, or the degree of community recovery (Halpern, 1988). The TWINSpan classification, NMS ordination, and MRPP analyses were performed using the PC-ORD software package (PC-ORD v.4.2, 1999 MjM Software, Gleneden Beach, OR).

Differences in understory species richness, total vegetation cover, and cover by growth-form (tall shrubs, low shrubs, forbs, and graminoids) were examined with two-factor analysis of variance (ANOVA) for the main effects of harvesting (post-harvest vs. mature) and elevation zone (montane vs. subalpine), as well as their interaction. All percentage data (e.g., percent cover) were transformed using the arcsine-square root transformation before statistical analysis to approximate normality (Sokal and Rohlf, 1981).

To determine if the type of slash treatment (lop and scatter, roller-chop, pile and burn, or the combination of roller-chopping and piling and burning) had an effect on the degree of similarity between post-harvest and mature forest understory species assemblages, we performed one-factor analysis of covariance (ANCOVA) with Sorensen distance as the response variable and elevation as the covariate. Sorensen distances between paired post-harvest and mature forest stands were calculated independent of one another. Least-squares means of the four slash treatment levels were compared using Tukey's HSD all pairwise comparisons. We used one-factor ANCOVA with elevation as the covariate rather than a two-factor ANOVA in order to maintain an adequate sample size among the four levels of slash treatment.

We summed the importance values of non-native species in each post-harvest stand and used a two-sample *t*-test to determine if the importance of non-native species differed between montane and subalpine post-harvest stands. We also determined if the importance of non-native species in post-harvest stands differed significantly among the four slash treatments using a one-way ANOVA. Statistical analyses were conducted using the SAS JMP IN v.4.0.4 software package (SAS Institute, 2001).

3. Results

Subalpine stands tended to have higher relative densities of Engelmann spruce and subalpine fir

Table 2

Stand characteristics of post-harvest and mature stands in the montane and subalpine zones (data are means $\pm$ 1 S.E.)

	Montane zone		Subalpine zone	
	Post-harvest	Mature	Post-harvest	Mature
Total number of stems (ha^{-1})	1132 (115)	2003 (301)	1445 (310)	2451 (255)
Percentage of total number of stems (by species)				
Lodgepole pine	96 (2)	92 (4)	36 (8)	41 (11)
Subalpine fir	4 (2)	7 (4)	53 (9)	42 (8)
Engelmann spruce	0	1 (0.3)	11 (3)	17 (5)
Total basal area ($\text{m}^2 \text{ha}^{-1}$)	14 (1)	3925 (199)	8 (1)	6390 (990)
Mean dbh (cm)	10 (1)	14 (1)	6 (1)	15 (1)
Stand age (years)	41 (2)	180 (22)	37 (2)	231 (15)

than montane stands, which were dominated by lodgepole pine (Table 2). Subalpine stands were significantly higher in elevation by an average of 227 m ($t = 6.8$, $P < 0.001$), and mature subalpine stands were significantly older than mature montane stands by an average of 70 years ($t = 2.83$, $P = 0.005$). In addition to differences in elevation and mature stand age, subalpine stands had soils with significantly lower sand content ($t = 6.48$, $P < 0.0001$).

Along the first axis of the two-dimensional NMS ordination, understory species composition of forest stands was separated according to elevation and percent soil sand content (Fig. 1 and Table 3), with montane stands representing the lower end of this axis (low elevation, high soil sand content) and subalpine stands representing the upper end (high elevation, low soil sand content). Mature montane stands had a higher proportion of *Shepherdia canadensis*,

Fig. 1. NMS ordination of understory species composition in post-harvest and adjacent mature forest stands. Vectors point in the direction of maximum change of the specified variable, and vector length indicates the degree of correlation between site variables and axes (see Table 3 for correlation coefficients). Ordination space was rotated to maximize the relationship between elevation and axis 1.

Table 3
Correlations between site variables and NMS ordination axis scores^a

Variable	Axis 1	Axis 2
Elevation	0.761	−0.039
Canopy height	0.016	−0.690
Species richness	−0.018	0.698
Stand age	0.188	−0.625
Soil sand content	−0.609	−0.101
Tree basal area	0.187	−0.577
Non-native spp. IVs	0.154	0.546
Tree canopy cover	−0.295	0.118
Slope	0.046	−0.135
Tree density	0.128	−0.130

^a Correlation coefficients (r) were calculated after ordination space was rotated to maximize the relationship between elevation and axis 1.

Juniperus communis, *Arnica cordifolia*, and *Carex geyeri* than mature subalpine forest understories which were dominated by *Vaccinium scoparium* (Table 4). Forest stands separated along the second NMS axis according to factors related to timber harvesting (Fig. 1). NMS axis 2 was negatively correlated with canopy height, stand age, and stand basal area, and positively correlated with plant species richness and summed importance values of non-native species (Table 3). Mature stands represented the lower end of this axis while post-harvest stands represented

the upper end (Fig. 1). Species present in montane post-harvest stands but absent or rare from adjacent mature stands included *Achillea millefolium*, *Anaphalis margaritacea*, *Taraxacum officinale*, *Ceanothus velutinus*, *Purshia tridentata*, and *Trisetum spicatum* (Table 4). Species present in subalpine post-harvest stands more often than in adjacent mature stands included *Phleum alpinum*, *Lonicera involucrata*, *T. spicatum*, *Juncus drummondii*, *Luzula parvifolia*, and several *Carex* species (Table 4).

The NMS ordination also revealed an apparently greater separation between post-harvest and mature stands in the subalpine zone than the montane zone (Fig. 1). MRPP analysis confirmed this pattern: in the subalpine zone there was a significant difference in species composition between post-harvest and mature stands ($A = 0.195$, $P < 0.001$). However, there was no significant difference in species composition between post-harvest and mature stands in the montane zone ($A = 0.025$, $P = 0.064$).

There was a significant interaction effect of harvesting and elevation zone on plant species richness per stand (Table 5), such that timber harvesting at higher elevations resulted in a greater long-term increase in species richness than timber harvesting in the montane zone (Fig. 2). Total cover of understory species did not differ between post-harvest and mature forest stands (Table 5). However, there was a significant effect of elevation zone (Table 5), with mean total vegetation

Fig. 2. Species richness in post-harvest and adjacent mature montane and subalpine forest understories. Data are means + 1 S.E.

Table 4

Mean percent cover of understory species in post-harvest and mature montane and subalpine forest stands^a

Species	Montane		Subalpine	
	Post-harvest	Mature	Post-harvest	Mature
Low shrubs				
<i>Arctostaphylos uva-ursi</i>	0.07	0.09	0.00	0.00
<i>Chimaphala umbellata</i>	0.00	0.01	0.00	0.01
<i>Mahonia repens</i>	0.38	0.32	0.28	0.04
<i>Pyrola chlorantha</i>	0.08	0.05	0.03	0.06
<i>Ribes inerme</i>	0.00	0.00	0.02	0.00
<i>R. woodsii</i>	0.67	0.24	0.24	0.01
<i>Rubus idaeus</i>	0.00	0.00	0.11	0.00
<i>Vaccinium caespitosum</i>	0.21	0.37	0.00	0.00
<i>V. scoparium</i>	8.22	13.94	27.93	52.17
Tall shrubs and tree seedlings				
<i>A. lasiocarpa</i>	0.03	0.15	0.21	0.12
<i>C. velutinus</i>	0.21	0.00	0.00	0.00
<i>J. communis</i>	3.77	1.37	0.68	0.04
<i>L. involucrata</i>	0.00	0.00	0.09	0.00
<i>P. engelmannii</i>	0.00	0.00	0.03	0.09
<i>P. contorta</i>	0.09	0.10	0.05	0.01
<i>P. tridentata</i>	0.12	0.00	0.00	0.00
<i>Salix scouleriana</i>	0.00	0.00	0.03	0.00
<i>S. canadensis</i>	1.60	1.84	0.10	0.00
Forbs				
<i>A. millefolium</i>	0.21	0.00	0.56	0.00
<i>Agoseris aurantiaca</i>	0.01	0.00	0.09	0.00
<i>Agoseris glauca</i>	0.01	0.00	0.16	0.00
<i>A. margaritacea</i>	0.03	0.00	0.37	0.00
<i>Antennaria rosea</i>	0.51	0.09	0.86	0.00
<i>Arabis drummondii</i>	0.02	0.01	0.04	0.00
<i>Arenaria congesta</i>	0.07	0.10	0.00	0.00
<i>A. cordifolia</i>	1.66	1.23	1.53	0.34
<i>Arnica mollis</i>	0.00	0.05	0.15	0.00
<i>Arnica parryi</i>	0.00	0.00	0.57	0.00
<i>Caltha leptosepala</i>	0.00	0.00	0.01	0.00
<i>Castilleja rhexifolia</i>	0.00	0.00	0.02	0.00
<i>Cirsium centaureae</i>	0.01	0.00	0.00	0.00
<i>Draba</i> sp.	0.00	0.00	0.04	0.00
<i>Epilobium angustifolium</i>	0.88	0.05	1.25	0.08
<i>Epilobium halleianum</i>	0.00	0.00	0.04	0.00
<i>Erigeron peregrinus</i>	0.00	0.13	1.46	0.44
<i>Erythronium grandiflorum</i>	0.00	0.00	0.04	0.00
<i>Fragaria virginiana</i>	0.68	0.15	0.35	0.07
<i>Gentianella amarella</i>	0.00	0.00	0.03	0.00
<i>Geranium richardsonii</i>	0.00	0.00	0.03	0.00
<i>Hieracium albiflorum</i>	0.28	0.18	0.26	0.03
<i>Hieracium gracile</i>	0.19	0.02	1.57	0.02
<i>Ligusticum porteri</i>	0.00	0.00	0.20	0.02
<i>L. vulgaris</i>	0.00	0.00	0.04	0.00
<i>Lupinus argenteus</i>	1.17	0.10	2.89	0.01
<i>Orthilia secunda</i>	0.00	0.00	0.00	0.03

Table 4 (Continued)

Species	Montane		Subalpine	
	Post-harvest	Mature	Post-harvest	Mature
<i>Osmorhiza depauperata</i>	0.00	0.01	0.02	0.05
<i>Pedicularis racemosa</i>	0.00	0.00	0.00	0.13
<i>Penstemon saxosorum</i>	0.00	0.00	0.01	0.00
<i>Penstemon whippleanus</i>	0.00	0.00	0.39	0.00
<i>Plantago tweedyi</i>	0.00	0.00	0.04	0.00
<i>Potentilla fissa</i>	0.05	0.01	0.00	0.00
<i>Senecio crassulus</i>	0.00	0.00	1.44	0.00
<i>Senecio cronatus</i>	0.04	0.00	0.19	0.00
<i>Senecio eremophilus</i>	0.00	0.06	0.02	0.05
<i>Sibbaldia procumbens</i>	0.00	0.00	0.86	0.00
<i>Silene menziessii</i>	0.00	0.00	0.01	0.00
<i>Solidago multiradiata</i>	0.09	0.02	0.87	0.00
<i>Solidago parryi</i>	0.05	0.04	0.08	0.00
<i>Taraxacum</i> sp.	0.49	0.00	1.09	0.00
<i>Veronica wormskjoldii</i>	0.00	0.00	0.08	0.00
Graminoids				
Grasses				
<i>Alepocuris pratensis</i>	0.00	0.00	0.09	0.00
<i>Bromus carinatus</i>	0.00	0.00	0.08	0.00
<i>Calamagrostis canadensis</i>	0.00	0.00	0.02	0.01
<i>Calamagrostis inexpansa</i>	0.00	0.01	0.00	0.00
<i>Calamagrostis rubescens</i>	0.00	0.00	0.39	0.00
<i>Danthonia intermedia</i>	0.01	0.00	0.03	0.01
<i>Deschampsia cespitosa</i>	0.00	0.00	0.55	0.03
<i>Elymus glaucodes</i>	0.06	0.01	0.00	0.00
<i>Oryzopsis exigua</i>	0.41	0.06	0.00	0.00
<i>P. alpinum</i>	0.00	0.00	0.90	0.00
<i>Poa fendleriana</i>	0.02	0.01	0.01	0.00
<i>Poa nervosa</i>	0.26	0.14	0.22	0.00
<i>Poa pratensis</i>	0.00	0.00	0.58	0.00
<i>Poa</i> sp.	0.00	0.00	0.07	0.00
<i>Trisetum wolfii</i>	0.00	0.00	0.04	0.00
<i>Trisetum spicatum</i>	0.08	0.01	1.25	0.00
Sedges				
<i>C. geyeri</i>	0.83	1.27	0.37	0.04
<i>Carex haydeniana</i>	0.00	0.02	1.18	0.00
<i>Carex hoodii</i>	0.00	0.00	0.02	0.00
<i>Carex microptera</i>	0.00	0.00	0.15	0.00
<i>Carex occidentalis</i>	0.00	0.00	0.31	0.00
<i>Carex phaeocephala</i>	0.00	0.00	0.03	0.00
<i>Carex raynoldsii</i>	0.00	0.00	0.13	0.00
<i>Carex rossii</i>	1.07	0.55	1.61	0.62
Rushes				
<i>J. drummondii</i>	0.00	0.03	1.62	0.00
<i>L. parvifolia</i>	0.00	0.00	0.04	0.00

^a Fifty quadrats (50 cm × 100 cm) were sampled in each stand.

Fig. 3. Mean percent cover of understory vegetation by growth-form in post-harvest and adjacent mature montane and subalpine forest stands. Error bars represent 1 S.E.

cover of subalpine stands approximately twice that of montane stands (Fig. 3).

Although total understory vegetation cover was similar in post-harvest and adjacent mature forest stands, both harvesting and elevation zone had significant effects on the cover of different growth-forms (Table 5). There was a significant harvest by elevation

zone interaction effect on the cover of both forbs and graminoids (Table 5), such that there was a disproportionately greater long-term increase in forb and graminoid cover from harvesting subalpine stands than from harvesting montane stands (Fig. 3). The effects of harvesting and elevation on the cover of low shrubs (primarily *V. scoparium*; Table 4) and tall

Fig. 4. Sorensen distance between post-harvest and adjacent mature forest understory species assemblages following different post-harvest slash treatments. Data are least-squares means adjusted for elevation $\pm$ 1 S.E. Means with the same letter do not differ significantly based a one-factor ANCOVA and Tukey–Kramer HSD all pairwise comparisons test.

Table 5
ANOVA for species richness, total cover of understory species, and cover by growth-form

Source	d.f.	MS	F	P > F
Species richness				
Harvest	1	1967.84	34.59	<0.0001
Elevation zone	1	2.25	0.04	0.8430
Harvest × elevation zone	1	260.67	4.58	0.0373
Error	48	56.89		
Total cover				
Harvest	1	0.0081	0.28	0.6010
Elevation zone	1	1.6087	55.14	<0.0001
Harvest × elevation zone	1	0.0001	0.01	0.9456
Error	48	0.0292		
Forbs				
Harvest	1	0.5952	41.14	<0.0001
Elevation zone	1	0.0748	5.17	0.0273
Harvest × elevation zone	1	0.1743	12.05	0.0011
Error	48	0.0145		
Graminoids				
Harvest	1	0.2065	14.49	0.0004
Elevation zone	1	0.0195	1.37	0.2477
Harvest × elevation zone	1	0.1254	8.80	0.0046
Error	48	0.0143		
Low shrubs				
Harvest	1	0.4674	12.08	0.0010
Elevation zone	1	1.6762	43.33	<0.0001
Harvest × elevation zone	1	0.1119	2.89	0.0951
Error	48	0.0387		
Tall shrubs				
Harvest	1	0.03224	3.77	0.0477
Elevation zone	1	0.2670	31.23	<0.0001
Harvest × elevation zone	1	0.0035	0.41	0.5242
Error	48	0.0086		

shrubs were additive (Table 5). Low shrub cover was significantly higher in post-harvest stands than in adjacent mature stands, and low shrub cover in subalpine stands was two to fivefold higher than in montane stands (Table 5 and Fig. 3). Tall shrub cover was significantly higher in post-harvest stands than in mature stands, and significantly lower in subalpine stands than in montane stands (Table 5 and Fig. 3). Tall shrub cover in mature subalpine stands was essentially zero (Fig. 3).

When adjusted for elevational differences, compositional dissimilarity between post-harvest and adjacent, mature forests was greater when slash was piled and burned than when it was roller-chopped or lopped

and scattered (Fig. 4). However, there were no significant differences in dissimilarity among stands where slash was lopped and scattered, roller-chopped, or roller-chopped and piled and burned (Fig. 4).

At least one non-native species was present in 26 of the 30 post-harvest stands (87%), but their overall importance was low, with cover values generally less than 1%. Only seven non-native species were encountered in post-harvest stands: *Cirsium arvense*, *Linaria vulgaris*, *Poa compressa*, *P. palustris*, *P. pratensis*, *Taraxacum laevigatum*, and *T. officinale*. Two of these, *C. arvense* and *L. vulgaris*, are considered noxious weeds in Wyoming (Fertig, 1999). Non-native species were essentially absent from mature forests, with only one species, *T. officinale*, found in a single stand with cover and frequency of <1%. Summed non-native IVs were not significantly different, on average, between montane and subalpine post-harvest stands ($t = 0.19$, $P = 0.76$), and there was no significant difference in the importance of non-native species among the different types of slash treatment ($F = 1.44$, $P = 0.253$).

4. Discussion

By comparing 30–50-year-old post-harvest forests to adjacent mature forests across a broad range of environmental conditions, we were able to determine some of the long-term impacts of timber harvesting on forest understory species composition in the Medicine Bow Mountains of southeastern Wyoming. Our primary finding was that montane post-harvest understories were more similar to adjacent mature forests 30–50 years after clearcutting than were comparable subalpine forest understories, suggesting that montane forests recover more rapidly after harvesting. Type of slash treatment also had a long-term effect on forest understory recovery, with the greatest negative impact from piling and burning. Non-native species were encountered more often in clearcut stands than in adjacent mature forests, where they were largely absent. Although present in nearly all the post-harvest stands we studied, non-native plant species were not a significant component of post-harvest understories after 30–50 years of succession.

Montane forest understories appear to recover more rapidly after harvesting than do subalpine forest

understories. The substantial differences in community composition, vegetation density, and physical environment between montane and subalpine forests may have led to differences in resiliency. Climatic effects associated with elevation undoubtedly make some contribution to compositional differences, as higher elevation subalpine forests dominated by Engelmann spruce and subalpine fir are generally cooler and wetter than lower elevation montane forests dominated by lodgepole pine (Martner, 1986; Smith and Knapp, 1990; Knight, 1994). Compositional differences may also reflect differences in fire regime between montane and subalpine forests. Fire return intervals are considerably shorter in montane lodgepole pine than in subalpine spruce-fir forests (Romme and Knight, 1981; Peet, 2000), and thus understory species that can persist in montane forests are most likely better adapted to disturbance. Mature subalpine forest stands tended to be older than mature montane stands (Table 2), further suggesting a shorter fire rotation in lower elevation lodgepole pine forests. Alternatively, post-harvest and mature stands in the montane zone may be more similar simply because they differ less in age than do the comparable subalpine forests (Table 2).

In addition to the influences of climate and fire regime, the resilience of montane vs. subalpine understories may also be affected by the diversity of species present at the time of disturbance. Tilman and Downing (1994) suggested that communities with high species richness are more resilient because they are more likely to contain disturbance-resistant species. Montane mature forest understories tended to be dominated by a combination of species representing a variety of growth-forms (Table 4 and Fig. 3), while one species, *V. scoparium*, comprised >90% of the understory plant cover in subalpine mature stands. Many of the dominant species in montane forests (e.g., *Shepherdia canadensis*, *J. communis*, *A. cordifolia*, *C. geyeri*, and *Rosa woodsii*) show increased regeneration in response to disturbance, either through sprouting, layering, or seedling establishment (Blauer et al., 1975; Mauk and Henderson, 1984; Noble, 1985; Noste and Bushey, 1988; Diotte and Bergeron, 1989; Steele and Geier-Hayes, 1987; Hansen et al., 1990; Stickney, 1990). In contrast, cover of *V. scoparium* often declines in response to disturbance (Zager, 1980; Zager et al., 1983; Lyon, 1984; Dion, 1998).

Seedling establishment is uncommon (Hungerford, 1986; Crossley, 1974), and although it can reproduce vegetatively (Hitchcock et al., 1959; McClean, 1968; Forcella and Weaver, 1977; Steele and Geier-Hayes, 1987), the rhizomes of *V. scoparium* may be easily damaged because of their shallow location between the forest floor and mineral soil (McClean, 1968; Richardson, 1980; Zager, 1980; Zager et al., 1983; Lyon, 1984; Dion, 1998). Survivors of disturbance events are often restricted to protected microsites, such as under fallen logs (Richardson, 1980). We observed that clumps of *V. scoparium* in post-harvest stands were often concentrated under and around logs that appeared to have been less disturbed than adjacent areas.

Slash disposal techniques differed significantly in their long-term impact on understory recovery after timber harvesting, regardless of stand elevation. Piling and burning had the greatest detrimental effect, while roller-chopping and lopping and scattering had less impact on understory species recovery (Fig. 4). In a study of slash disposal techniques in central Montana, Boe (1956) noted that roughly half the soil surface area in block clearcuts was severely disturbed when slash was piled and burned, but there was virtually no surface soil disturbance when slash was lopped and scattered. Roller-chopping has also been found to cause less soil disturbance compared to the soil scarification and intense soil heating associated with piling and burning (Stein, 1995; Kovalchik and Blake, 1972). Our results suggest that more intensive slash disposal techniques such as piling and burning can negatively impact understory species composition for decades after clearcutting, especially in stands dominated by species sensitive to disturbance such as *V. scoparium*.

Reduction of *V. scoparium* due to harvesting and slash treatment in subalpine stands, combined with its apparent inability to rapidly re-colonize disturbed sites from adjacent mature stands, would likely leave large areas of open habitat available for establishment of shade-intolerant species, especially if mineral soil was exposed (McIntyre et al., 1995). As a consequence, succession in subalpine post-harvest stands appears to have been driven primarily by colonization from off-site by non-forest, wind-dispersed graminoids, forbs, and tall shrubs. Tree establishment on high-elevation disturbed sites may be slow due to the

harsh environment, or due to intense competition from graminoid and forb species that establish rapidly after disturbance (Stahelin, 1943; Noble and Ronco, 1978). This delay in canopy closure allows shade-intolerant plant species that are atypical of mature subalpine forests to persist for decades.

Alternatively, succession in montane post-harvest forests appears to have been driven either by residual plants and seeds present at the time of disturbance or by propagule dispersal of forest understory species from adjacent undisturbed stands. Since we have no information on species composition immediately following harvesting and slash treatment, the relative importance of residual plants and seeds vs. off-site invaders is unknown. However, studies of early successional post-fire and post-harvest lodgepole pine forests in Wyoming have shown that, even on moderately to severely disturbed sites, plant cover is dominated by re-sprouting survivors (Turner et al., 1997; Dion, 1998; Doyle et al., 1998). In addition to being well adapted to survive disturbance, several montane species such as *A. cordifolia*, *C. geyeri*, and *R. woodsii* are tolerant of full sun to at least moderate shade, and thus are found in both early and late seral communities (Blauer et al., 1975; Mauk and Henderson, 1984; Steele and Geier-Hayes, 1987; Hansen et al., 1990; Stickney, 1990). The broad tolerance range and disturbance adaptations of many montane understory species may partially explain why montane post-harvest understory composition is not significantly different from that of adjacent mature forests after 30–50 years of succession.

Low-elevation forests dominated by lodgepole pine on the MBNF are more resilient than high-elevation spruce-fir forests. Halpern (1988, 1989) suggested a deterministic component to secondary succession based on the life history traits of individual species. Our study supports this suggestion, in that subalpine stands dominated by *V. scoparium*, with its shallow rhizomes and poor seedling establishment, recover more slowly from disturbance, especially where soil disturbance caused by slash treatment is high. A combination of factors may facilitate the more rapid recovery of montane forests understories, including a longer growing season at lower elevations, higher species richness, and a greater proportion of species with the potential to regenerate or re-colonize after disturbance.

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