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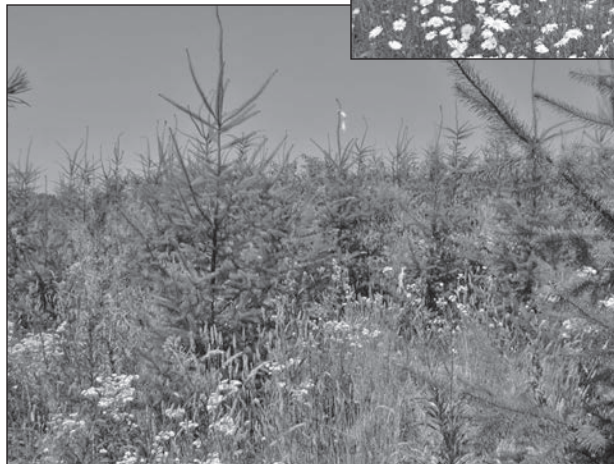
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Relations of Native and Exotic Species 5 Years After Clearcutting With and Without Herbicide and Logging Debris Treatments

David H. Peter and Timothy B. Harrington



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Cover: Photos show the three sites at 5 years of age. The Molalla site is on top, Matlock in the middle, and Fall River on the bottom.

Abstract

Peter, David H.; Harrington, Timothy B. 2012. Relations of native and exotic species 5 years after clearcutting with and without herbicide and logging debris treatments. Res. Pap. PNW-RP-589. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 37 p.

To increase timber production and manage other forest resource values, some land managers have undertaken logging debris and vegetation control treatments after forest harvest. We explored the roles of clearcutting on plant community composition and structure at three sites where logging debris was dispersed, piled, or removed and vegetation was annually treated or not treated with herbicides for 5 years. Without vegetation control, a competitive relation was identified between exotic and native ruderal (i.e., disturbance-associated) species. When exotic ruderal cover changed by 4 percent, native ruderal cover changed by 10 percent in the opposite direction. This relation was independent of site, but site was important in determining the overall dominance of ruderals. Five annual vegetation control treatments increased Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) growth, but decreased richness and cover of other species at the rate of one species per 10 percent reduction in cover. Debris treatment effects were small and found on only one site.

Keywords: Clearcut, invasive species, exotic species, community diversity, community structure.

Summary

Clearcutting of Pacific Northwest (USA) forests results in conversion of the understory plant community from dominance by shade-tolerant native species to dominance by a mixture of native and exotic ruderal (i.e., disturbance-associated) species. To increase timber production and manage for other resource values, some land managers have undertaken subsequent logging debris and vegetation control treatments. We explored the roles of clearcutting with and without logging debris and vegetation control treatments on plant community composition and structure at three sites with different plant communities and productivity. Logging debris was dispersed, piled, or removed. Vegetation was annually treated or not treated with herbicides for 5 years. Without vegetation control, a competitive relation was identified between exotic and native ruderal species in which a 4 percent change in exotic ruderal cover was associated with an opposite 10 percent change in native ruderal cover. This relation was independent of site, but site was important in determining the overall dominance of ruderals. Vegetation control increased Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) growth, while it decreased cover and richness of other species. Richness declined at the rate of one species per 10 percent reduction in cover regardless of site, stand history, or treatment protocol. Nonmetric multidimensional scaling ordination suggested that, although the untreated plant communities were floristically distinct at age 5 years, communities receiving similar herbicide treatments become more alike after treatment. Debris treatment effects were small and found only on the least productive site.

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Introduction

Owing to their high levels of light and nutrient availability, early seral communities in the Pacific Northwest are dominated by ruderals (i.e., plant species associated with disturbance) soon after harvesting, but with some surviving residual forest understory species. The residual forest understory species are “stress tolerant” (*sensu* Grime 1977) in that they tolerate the low levels of light and nutrients typical of later seral communities while surviving in the understory of the predisturbance forest. Thus, while some late-successional species such as western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) may enter the stand much later (relay floristics model), early seral communities in the Pacific Northwest follow an initial floristics model (Egler 1954) in the beginning. Following establishment of the ruderals, succession in these communities is largely driven by canopy development of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*) or other conifers, but the rate of succession and the community composition are affected by site productivity and silvicultural management activities.

Ruderal communities in the maritime Pacific Northwest (USA) have been invaded by many exotic (invasive nonnative) plant species. However, very little is currently known about the competitive relation that exists between these exotic species and native species. Invasive exotic species can alter hydrologic, nutrient, and disturbance regimes (Mack et al. 2000) and may threaten native species (Wilcove et al. 1998). However, exotic species are not always a threat to native plants (Davis 2003), and uncertainty regarding the roles of exotic species in ecosystems hinders our ability to know how or even whether to attempt native community restoration.

Soon after forest harvesting, forest managers may engage in site preparations to benefit planted trees. Thus, early community assembly that was initiated by tree harvesting may be interrupted by a series of disturbances including logging debris treatment and vegetation control for which there are few natural analogues. Because organic matter provides a protective barrier against soil disturbance and influences nutrient cycling (Smethurst and Nambiar 1990), soil moisture, and temperature (Devine and Harrington 2007, Roberts et al. 2005), the recruitment and survival of postharvest species could be affected by debris treatments. Most forestry studies have found only small changes in species diversity and composition of ground layer vegetation with operational use of herbicides (Boyd et al. 1995, Haeussler et al. 2002). For example, in the Pacific Northwest, Stein (1995) found that a single glyphosate application caused a shift toward ruderal species with little effect on diversity. However, we wondered what effect more rigorous herbicide regimes would have on early community composition and structure.

We asked how exotic and native floras interact following clearcutting in the Pacific Northwest. We were also interested in how postclearcutting logging debris and vegetation control treatments further affect plant diversity and composition of the community.

Because wood products are often not the only and sometimes not the most important output desired, land managers need knowledge about the effects of silvicultural treatments on entire plant communities. Thus, we evaluated the relations between native and exotic species in three forest productivity studies that were initiated by clearcutting. Subsequent vegetation control with herbicides and logging debris manipulations were designed to promote Douglas-fir growth in some areas and not others. We examined these sites 5 years after clearcutting. Some of the vegetation control treatments were more stringent than what are typically used in forest management, although no more stringent than are sometimes used for management of road or power line rights-of-way.

We asked how exotic and native floras interact following clearcutting in the Pacific Northwest. We were also interested in how postclearcutting logging debris and vegetation control treatments further affect plant diversity and composition of the community. To this end, we studied three operational studies having similar treatments in western Washington and Oregon. Although it is recognized that disturbance increases opportunities for ruderal species, we asked if the relation of native and exotic ruderals to the residual forest species was similar, and what the relation of the two ruderal groups was to each other. We hypothesized that if exotic species abundance increased as a result of postclearcutting vegetation control or logging debris treatments, there would be a decrease in native species abundance. Similarly, but more generally, we hypothesized that an increase in ruderal species would be accompanied by a decrease in residual species.

Materials and Methods

Study Sites

Our study sites (Matlock, Molalla, and Fall River) were located in the Western Hemlock Zone (Franklin and Dyrness 1988) of western Washington and Oregon. These sites were managed for timber production and initially supported uniformly stocked stands of 40- to 70-year-old Douglas-fir. At Matlock and Molalla, some trees were removed before clearcutting (in a low thinning in 1993 at Molalla and by removal of damaged trees after a 1996 ice storm at Matlock). Each stand was clearcut (in spring 2003 at Matlock and Molalla and spring 1999 at Fall River) and planted with Douglas-fir seedlings (plug+1 stock planted in early 2004 at Matlock and Molalla on a 3-m grid; 2+0 stock planted in March 2000 at Fall River on a 2.5-m grid). Each site was fenced to prevent ungulate browsing of the planted seedlings.

The Matlock site is on nearly level glacial outwash at about 35 m elevation 25 km west of Shelton, Washington. The soil is deep, somewhat excessively

drained, very gravelly loamy sand in the Grove Series with 55 to 75 percent coarse fragments (Dystric Xerorthent; USDA NRCS 2009a). The water-holding capacity of the top 60 cm of soil averaged 55 mm, and the total nitrogen (N) content averaged 3300 kg/ha in the year following forest harvesting (Devine et al. 2011). The average annual precipitation is 2413 mm (USDA NRCS 2000b). The primary plant association of the Matlock site is the *Tsuga heterophylla/Gaultheria shallon* plant association with some occurrences of the *Tsuga heterophylla/Gaultheria shallon-Mahonia nervosa* association (Henderson et al. 1989).

The Molalla site is on a gently rolling ridge and upper west-facing slope (0 to 30 percent slope) between 500 and 570 m elevation about 24 km northeast of Molalla, Oregon. The soil is a deep, well-drained cobbly loam of the Kinney Series derived from igneous tuffaceous agglomerate with 25 to 35 percent coarse fragments (Andic Dystrudept; USDA NRCS Soil Surv. Staff 2009). The water-holding capacity of the top 60 cm of soil averaged 142 mm, and the total N content averaged 7220 kg/ha in the year following forest harvesting (Devine et al. 2011). The average annual precipitation is 1829 mm (USDA NRCS 2009b). The Molalla site has the most topographic variability and correspondingly the most plant associations. The four Molalla plant associations in order of importance are *Tsuga heterophylla/Mahonia nervosa/Polystichum munitum*, *Tsuga heterophylla/Mahonia nervosa-Gaultheria shallon*, *Tsuga heterophylla/Polystichum munitum-Oxalis oregana*, and *Tsuga heterophylla/Polystichum munitum* (Halverson et al. 1986).

The Fall River site is located 33 km west-northwest of Chehalis, Washington, on a gentle (<15 percent), west-facing slope at 335 m elevation. The soil is a uniform, very deep, well-drained, silty clay loam to silty clay of the Boistfort Series derived from volcanic ash and deeply weathered basalt (Typic Fulvudand; USDA NRCS 2009a). The water-holding capacity of the top 60 cm averaged 174 mm, and the total N content averaged 10 188 kg/ha in the year following forest harvesting (Devine et al. 2011). The average annual precipitation is 2159 mm (USDA NRCS 2009b). The main plant association of the Fall River site is *Tsuga heterophylla/Polystichum munitum-Oxalis oregana* (Henderson et al. 1989).

Study Design

We used a randomized complete block design. At Matlock and Molalla, six treatments were replicated four times as a factorial combination of three logging-debris treatments by two vegetation-control treatments. Each treatment was randomly assigned to four 50- by 60-m (0.3-ha) plots, providing a total of 24 plots per site. Blocking was based on aspect (Molalla) and proximity to logging roads (Matlock

and Molalla)—a surrogate for frequency of machine traffic. Machine traffic associated with shovel yarding and the logging debris treatments (described below) at Matlock and Molalla was confined to designated trails placed at 20-m intervals lengthwise through the plots.

At Fall River there were eight replications of three treatments for a total of 24 plots (Ares et al. 2007). Each Fall River treatment was randomly assigned to two 30- by 85-m (0.26-ha) treatment plots in each of four blocks. Blocking was based on preharvest Douglas-fir volume. All of the plots had similar gentle slopes and west exposures. For this study, we looked at only 3 of the 12 treatments conducted at Fall River (Ares et al. 2007).

Treatment

No.	Description
1	Logging debris dispersed without vegetation control: removal of merchantable logs to a 10- (at Fall River) or 12.7-cm diameter (at Matlock and Molalla) top with retention of logging debris in place (Matlock and Molalla: four plots per site; Fall River: eight plots).
2	Logging debris piled without vegetation control (piled/no vegetation control): removal of merchantable logs and moving of logging debris <12.7-cm diameter into piles 3 to 4 m in diameter (Matlock and Molalla: four plots per site).
3	Logging debris removed without vegetation control: removal of aboveground portion of trees (boles, branches, and foliage >5-cm diameter) (Matlock and Molalla: four plots per site).
4	Logging debris dispersed with vegetation control: same as treatment 1, but with five annual herbicide treatments to reduce abundance of competing vegetation (described below) (Matlock and Molalla: four plots per site; Fall River: eight plots).
5	Logging debris piled with vegetation control: same as treatment 2, but with five annual herbicide treatments to reduce abundance of competing vegetation (described below) (Matlock and Molalla: four plots per site).
6	Logging debris removed with vegetation control treatment: same as treatment 3, but with five annual herbicide treatments to reduce abundance of competing vegetation (described below). This treatment occurred at all three sites, but at Fall River, all debris > 0.6-cm diameter was removed (Matlock and Molalla: four plots per site; Fall River: eight plots).

Piling and removing of debris resulted in additional mechanically induced soil disturbance. Where debris was dispersed, there was significantly less exposure of mineral soil (2 to 3 percent of the total area) than where it was piled or removed (4 to 6 percent of the total area) (Harrington and Schoenholtz 2010). The debris piles were about 3 m in diameter and 1 m high. There were 105 piles per hectare at Matlock and 60 piles per hectare at Molalla (Harrington and Schoenholtz 2010).

In addition to reducing competition with Douglas-fir seedlings, a goal of the herbicide treatments at Matlock and Molalla was to reduce cover of herbaceous and woody vegetation to ≤ 20 percent and thereby provide experimental conditions for quantifying debris effects on Douglas-fir growth independent of vegetation abundance. To this end, an initial vegetation control treatment was applied to all plots in late summer 2003 to reduce woody vegetation prior to planting of Douglas-fir (table 1). Annual herbicide treatments were applied in the fall or spring of 2003 through 2008 to the designated vegetation control plots to reduce abundance of herbaceous and woody vegetation (Harrington and Schoenholtz 2010). Douglas-fir was the only species that was deliberately not sprayed. At Matlock, three additional herbicide treatments were applied to all plots to specifically reduce abundance of Scotch broom (*Cytisus scoparius* (L.) Link). These directed applications of triclopyr were made to individual broom plants to minimize effects on other vegetation and eliminated most of the Scotch broom at Matlock. This highly competitive, exotic shrub reproduced prolifically from seed stored in the soil (Bossard 1993) that was probably introduced during the 1998 salvage harvest.

At Fall River, where the goal was to eliminate all vegetation other than the planted trees, vegetation control was achieved by one preplanting herbicide application (dispersed/no vegetation control treatment excepted) and five annual applications of preemergent herbicides in the spring with spot applications of postemergent herbicides as needed (table 1). Herbicides differed by year at all three sites to control selected species as they became dominant and to prevent the development of resistance in any of the species of competing vegetation. Both broadcast and spot treatments were used to ensure that the desired level of control was achieved.

Field Procedures

Circular 176.6-m² (7.5-m-radius) vegetation sample plots were located in the center of treatment plots at Matlock and Molalla and centered 35 m from the west edge of each treatment plot at Fall River. Vegetation measurements were made in year 5 in July (Fall River: 2004, Matlock and Molalla: 2008). Vegetation assessment followed protocols for reconnaissance plots of the USFS Pacific Northwest Region, Area 1 Ecology Program (Henderson et al. 1989). Plant cover was ocularly estimated for all vascular species except Douglas-fir. Douglas-fir cover was calculated from the product of mean cover per tree (based on two crown diameter measurements of each tree taken at right angles) and the total count of trees on the plot. Ten systematically selected trees per plot were measured at Fall River. All trees on the plot were measured at Matlock and Molalla. Each measured tree was also measured for height.

Table 1—Vegetation control treatment information by year for the three study sites

Site	Month/year	Study year ^a	Herbicide(s) active ingredient	Herbicide rate(s)	Method of application
Matlock	09/2003	0	Triclopyr ester	2.8 kg a.i. ha ⁻¹ with surfactant ^b	Broadcast
	12/2003	0	Sulfometuron	0.2 kg a.i. ha ^{-1c}	Broadcast
	10/2004	1	Triclopyr ester	2.5 percent solution in water ^d	Directed foliar
	04/2005	2	Glyphosate + clopyralid	1.5 percent + 0.75 percent solution in water ^c	Broadcast
	04/2006	3	Glyphosate + clopyralid	1.5 percent + 0.75 percent solution in water ^c	Broadcast
	04/2007	4	Glyphosate + clopyralid	1.5 percent + 0.75 percent solution in water ^c	Broadcast
	06/2007	4	Triclopyr ester	20 percent solution in crop oil ^d	Directed basal stem
	05/2008	5	Glyphosate + clopyralid	1.5 percent + 0.75 percent solution in water ^c	Broadcast
	05/2008	5	Triclopyr ester	20 percent solution in crop oil ^d	Directed basal stem
	Molalla	08/2003	0	Glyphosate	2.2 kg a.i. ha ⁻¹ in water with surfactant ^b
10/2003		0	Sulfometuron	0.2 kg a.i. ha ⁻¹ in water ^c	Broadcast
10/2004		1	Glyphosate + Sulfometuron	1.1 + 0.2 kg a.i. ha ⁻¹ in water ^c	Broadcast foliar
05/2006		3	Glyphosate + atrazine	1 percent solution in water + 4.9 kg a.i. ha ^{-1c}	Broadcast
05/2007		4	Clopyralid + atrazine	0.8 + 4.9 kg a.i. ha ⁻¹ in water ^c	Broadcast
05/2008		5	Triclopyr ester + 2, 4-D ester	2 percent + 2 percent suspension in water with surfactant ^c	Broadcast
Fall River	03/2000	1	Sulfometuron	0.2 kg ha ^{-1c}	Broadcast 2 weeks before planting
	03/2000	1	Glyphosate	4.67 L ha ^{-1c}	Broadcast 2 weeks before planting
	03/2001	2	Atrazine	9.3 L ha ^{-1c}	Broadcast
	04/2001	2	Glyphosate	0.75 percent in water ^c	Spot
	03/2002	3	Atrazine	9.3 L ha ^{-1c}	Broadcast
	03/2002	3	Sulfometuron	0.17 kg ha ^{-1c}	Broadcast
	04–05/2002	3	Clopyralid	1 percent in water ^c	Spot
	06/2002	3	Glyphosate	0.75 percent in water ^c	Spot
	03/2003	4	Hexazinone	7.0 L ha ^{-1c}	Directed band between rows
	04–05/2003	4	Clopyralid	1 percent in water ^c	Spot to shrubs
	06/2003	4	Glyphosate	0.75 percent in water ^c	Spot
04/2004	5	Hexazinone	5.85 L ha ^{-1c}	Directed band between rows	

^a Growing seasons since planting Douglas-fir seedlings in early 2004.

^b Applied to all plots.

^c Applied to annual vegetation control plots only.

^d Applied to Scotch broom only.

Analysis

We analyzed site and treatment effects on diversity (species richness, Simpson, Shannon, and evenness indexes) and canopy cover of plants in three species groups or in total. The three species groups were exotic ruderal (ER), native ruderal (NR), and native residual forest (RF) species. Ruderal species respond favorably to disturbances such as overstory removal and perform poorly in dense shade. Exotics (as contrasted with natives) are species that are now naturalized but were not originally present in the Pacific Northwest and were introduced in conjunction with the spreading of old-world culture into the area. Most exotic species come from Europe or Asia. Most NR species are perennials, whereas most ER species are annuals, biennials, or short-lived perennials. Residual forest species are native shade-tolerant species typically associated with interior forest settings and are generally long-lived perennials. Many of these species regenerated from residual stumps, rhizomes, or roots in the clearcut environment. For analyses of canopy cover, individual species' canopy covers were summed for each species group (i.e., ER, NR, RF, and total understory) by plot.

We used PC-Ord computer software (McCune and Mefford 1999) to calculate several indicators of species diversity per 176.6-m² plot (i.e., species richness, Simpson, Shannon, and evenness indexes). Richness is expressed as the number of vascular plant species on a plot by species group (ER, NR, RF) or as an overall total (all species on a 176.6-m² plot regardless of group).

Community composition—

To examine plant community floristics before and after treatment, we used PC-Ord to conduct two nonmetric multidimensional scaling (NMS) ordinations (McCune and Mefford 1999) (table 2). One ordination included only plots that had not received vegetation control (n = 32). A second ordination included only plots that received vegetation control (n = 40). The response variables were estimated canopy covers for all understory species. We set the PC-Ord NMS autopilot for thoroughness, specified use of the Sorensen distance measure, and otherwise used default

Table 2—Nonmetric multidimensional scaling model performance for the two ordinations described in the text^a

Data set	Final		Number of		
	Stress	Instability	Iterations	Plots	Species
No vegetation control	13.5	<0.00001	74	32	116
Vegetation control	10.3	0.007	500	40	90

^a Douglas-fir was not included in these ordinations.

We analyzed site and treatment effects on diversity and canopy cover of plants in three species groups or in total. The three species groups were exotic ruderal (ER), native ruderal (NR), and native residual forest (RF) species.

settings. Default settings included 6 axes, 400 (maximum) iterations, random starting coordinates, reduction in dimensionality of 1 at each cycle with a 0.2 step length (rate of movement toward minimum stress), random number of seeds, 40 runs with real data, 50 runs with randomized data, and a stability criterion of 0.000010 standard deviations in stress over the last 15 iterations. We superimposed on our ordinations joint plots (McCune and Mefford 1999) of 5-year tree height and crown width (measures of productivity) and seven measures of diversity including number of NR, ER, and RF species; total richness; Shannon's index; Simpson's index; and evenness. Joint plots show the direction (angle) and strength (line length) of relations of variables to the ordination scores (correlations). The lines of the joint plots emanate from the centroid of all the species data used in the ordination.

Analysis of variance (diversity and canopy cover)—

We used analysis of variance (ANOVA) to test the hypothesis that the ordination centroids of the three sites were not distinct on each axis of each ordination. We analyzed site-specific effects in canopy cover and diversity variables with two factor mixed-model ANOVA (SAS PROC MIXED) (SAS Institute Inc. 2003) to evaluate debris and vegetation control treatments (fixed effects), blocking (random effect), and treatment interactions within each site.

Cover relations among the species groups—

We used linear regression to test for differences among sites in the cover relations of NR and native RF species versus ER species. For each relation, plot values were pooled across sites for each of the debris treatments without vegetation control ($n = 8, 12,$ and 12 for Fall River, Matlock, and Molalla, respectively). Indicator variables were specified to test for differences in slopes and intercepts among sites using the extra-sums-of-squares approach (Neter et al. 1989). Stepwise regression in PROC Reg was used to compare a full model with reduced models having common intercepts, slopes, or both (SAS 2003).

Relation of richness to total cover—

We used linear regression to test for site differences in the relation of richness to total understory cover. Total understory cover (summed over all species except Douglas-fir) was used as the measure of intensity of vegetation control as well as an indicator of site productivity. Plot values of richness, pooled across sites for each of the debris treatments with and without vegetation control ($n = 24$ for each site), were regressed against associated plot values for total understory cover. The extra-sums-of-squares approach was used similarly as described above to test for differences in slopes and intercepts among sites for each relation (Neter et al. 1989).

Results

Species Composition and Diversity

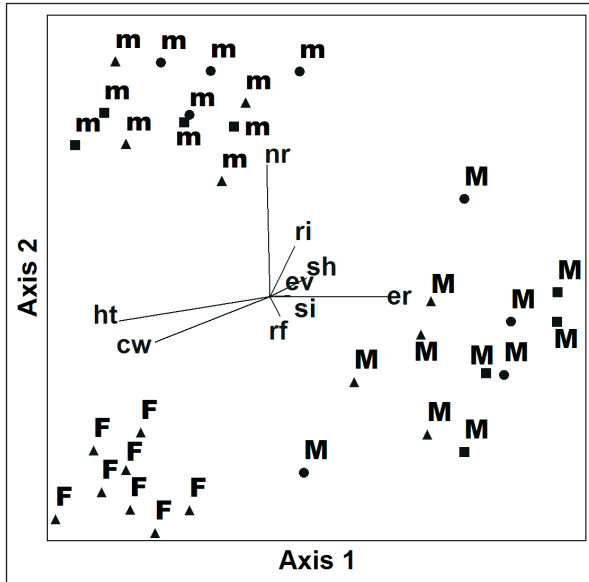
Over all plots regardless of treatment at each site ($n = 24$ per site), we found 82 species at Matlock, 91 species at Molalla, and 52 species at Fall River. On the debris-dispersed treatment plots where no herbicide was used, we found 80 species at Matlock ($n = 4$), 89 species at Molalla ($n = 4$), and 49 species at Fall River ($n = 8$). Thus, Fall River was the least diverse site, Molalla had a few more species than Matlock, and nearly all species at each site were found in the debris-dispersed plots.

The dominant species differed among the treatments that lacked vegetation control. At Matlock, the three most abundant species were oxeye daisy (*Leucanthemum vulgare* Lam.; 28 percent cover), hairy cat's ear (*Hypochaeris radicata* L.; 27 percent), and Douglas-fir (8 percent). The most abundant species at Molalla were California blackberry (*Rubus ursinus* Cham. & Schltldl.; 55 percent cover), velvet grass (*Holcus lanatus* L.; 27 percent), and Douglas-fir (12 percent). At Fall River, the most abundant species were Douglas-fir (53 percent), hairy cat's ear (34 percent), and velvet grass (27 percent). The vegetation control treatments were mostly dominated by the same species, but with much lower covers except for Douglas-fir, which had higher cover.

Our NMS ordinations separated the three sites floristically (fig. 1). Overall NMS model performance is provided in table 2 and correlation values (tau) for each variable in the joint plots with each axis are given in table 3. Without vegetation control, the average location of points from any two sites on either axis was significantly different with the exception of Molalla and Fall River on axis 1. However, with vegetation control, all possible site comparisons were significantly different. The community floristic affinities are further indicated by the unique sharing of 10 species between Fall River and Molalla, but only 3 species were uniquely shared between Fall River and Matlock. However, Matlock and Molalla had 32 species uniquely in common, suggesting even closer affinities between these sites. There were no clear patterns in our ordinations attributable to debris treatments except for the partial separation of debris removed versus debris dispersed plots at Fall River where vegetation control was used (fig. 1b).

The joint plot in figure 1 (correlation values presented in table 3) suggests that two indicators of productivity (crown width and tree height) correlate with the floristic differences that separate the three sites in the ordination. Thus, Fall River and Molalla (with the largest tree sizes) are separated on axis 1 from Matlock with the smallest tree size (fig. 1a). Molalla is further separated from the other sites by higher NR species diversity as is Matlock by higher ER species diversity. Figure 1b shows that the more severely herbicide treated Fall River community separates

A. Plots without vegetation control



B. Plots with vegetation control

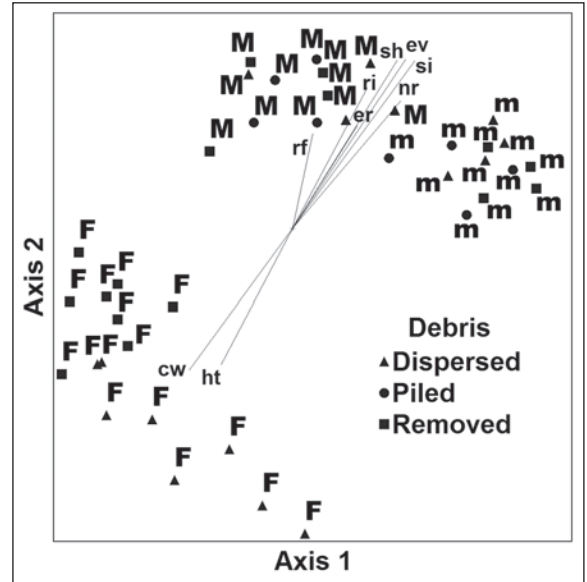


Figure 1—Nonmetric multidimensional scaling ordinations by treatment type at Matlock (M), Molalla (m), and Fall River (F) for (a) plots without vegetation control and (b) plots with vegetation control. Superimposed are joint plots showing the direction (angle) and strength (line length) of relations of tree size and species diversity measures to the ordination scores. Included are Douglas-fir height (ht), Douglas-fir crown width (cw), number of native ruderal (NR) species, number of exotic ruderal (ER) species, number of residual forest (RF) species, total richness (ri), Shannon’s index (Sh), Simpson’s index (Si), and evenness (ev). In “a,” Simpson’s index, and exotic ruderal (er) count fall on the same angle but are different lengths. Similarly, evenness and Si fall on another line. Douglas-fir was not included in these ordinations.

Table 3—Correlation (tau) of each productivity and diversity indicator with each ordination axis

Axis	No vegetation control		Vegetation control	
	1	2	1	2
Crown width	-0.47	-0.26	-0.48	-0.43
Tree height	-0.59	-0.12	-0.55	-0.37
Richness	0.26	0.33	0.62	0.34
Evenness index	0.24	0.06	0.67	0.32
Shannon index	0.30	0.23	0.70	0.28
Simpson index	0.22	0.09	0.69	0.33
Exotic ruderal count	0.52	0.04	0.53	0.39
Native ruderal count	-0.01	0.56	0.55	0.51
Residual forest count	0.07	-0.21	0.58	0.19

Debris treatments have only modest effects on diversity and little if any effect on Douglas-fir productivity.

from the Matlock and Molalla communities on the basis of lower diversity, which is inversely correlated with tree size.

Our data suggest that debris treatments have only modest effects on diversity and little if any effect on Douglas-fir productivity as measured by 5-year height and canopy cover growth (table 4). No debris treatment effect was found for any richness or diversity index at Molalla. The Matlock Shannon index was higher for the debris-piled treatment than for the debris-removed treatment. At Fall River

Table 4—Mean 5-year treatment cover and diversity index values with P-values for comparisons that were significantly different ($\alpha = 0.05$)^{a b c}

Matlock								
	LDD	LDP	LDR	Debris P	NVC	VC	VC P	VC x Debris P
n	8	8	8		12	12		
Douglas-fir height	195.3	170.6	175.3		163.7	197.1	0.00	
Douglas-fir cover	13.3	10.4	10.7		7.7	15.2	0.00	
Exotic ruderal cover	38.8	45.9	57.2	0.04*	79.8	14.9	0.00	
Native ruderal cover	23.2	13.1	13.2		19.8	13.2		
Residual forest cover	30.5	19.4	14.1	<0.01**	22.0	20.7		
Total understory cover	92.5	78.4	84.5		121.5	48.8	0.00	
Exotic ruderal richness	7.8	8.6	8.1		10.0	6.3	0.00	
Native ruderal richness	9.0	8.5	8.0		9.8	7.2	0.01	
Residual forest richness	13.6	12.4	11.4		12.7	12.3		
Evenness index	0.7	0.7	0.7		0.7	0.7		0.05
Shannon index	2.4	2.5	2.2	0.04***	2.4	2.3		0.01
Simpson index	0.9	0.9	0.8		0.8	0.8		
Molalla								
	8	8	8		12	12		
n								
Douglas-fir height	227.4	323.1	227.2		217.3	240.5	0.05	
Douglas-fir cover	13.3	15.3	13.8		12.4	15.9	0.01	
Exotic ruderal cover	39.6	33.7	40.3		54.2	21.5	0.01	
Native ruderal cover	56.3	55.2	57.3		89.3	23.2	0.00	
Residual forest cover	21.7	22.7	23.9		32.0	13.5	0.00	
Total understory cover	117.6	111.6	121.5		175.6	58.3	0.00	
Exotic ruderal richness	6.3	6.3	6.5		7.0	5.7		
Native ruderal richness	11.4	11.6	11.0		15.1	7.6	0.00	
Residual forest richness	8.9	9.8	8.4		10.7	7.3	0.00	
Evenness index	0.6	0.7	0.6		0.6	0.7		
Shannon index	2.1	2.2	2.1		2.3	2.0	0.00	
Simpson index	0.8	0.8	0.8		0.8	0.8		
Fall River								
	16	0	8		8	16		
n								
Douglas-fir height	323.9		344.8		310.4	341.1	0.00	
Douglas-fir cover	62.5		70.6		53.1	71.3	0.00	
Exotic ruderal cover	33.0		2.9		64.8	2.0	0.00	
Native ruderal cover	25.5		1.0		50.6	0.7	0.00	
Residual forest cover	14.7		1.0		28.1	1.2	0.00	
Total understory cover	73.1		4.9		143.5	3.9	0.00	
Exotic ruderal richness	4.1		2.5		5.8	2.5	0.00	
Native ruderal richness	4.3		2.5		6.9	2.1	0.00	
Residual forest richness	8.4		5.0		11.5	5.2	0.00	
Evenness index	0.4		0.1	0.03	0.6	0.1	0.00	
Shannon index	1.1		0.3	0.04	2.0	0.3	0.00	
Simpson index	0.4		0.1	0.01	0.8	0.1	0.00	

^a Where three values are compared (as in the case of debris treatments), mean separations according to Tukey Honestly Significant Difference tests ($\alpha = 0.05$) are provided at the end of the table.

^b Douglas-fir is not included in the richness values.

^c LDD = logging debris dispersed, LDP = logging debris piled, LDR = logging debris removed, NVC = no vegetation control, and VC = vegetation control.

Note: * LDD < LDR, ** LDD > (LDR = LDP), *** LDP > LDR.

Exotic ruderal species compete with residual forest species to a lesser extent than with native ruderal species. A lack of a relation between residual forest cover and native ruderal cover suggests little interaction at age 5 between these two groups.

the Evenness, Shannon and Simpson indexes were higher for the debris-dispersed treatment than for the debris-removed treatment. Thus, removal of organic matter sometimes decreased diversity, but never increased it.

Herbicide treatments decreased diversity while increasing Douglas-fir growth (table 4). All indicators of richness and diversity decreased significantly at Fall River. Matlock ruderal richness (exotic and native) decreased, but at Molalla native species richness (ruderal and RF) decreased. At Matlock, none of the diversity indexes changed (evenness, Shannon, Simpson), but at Molalla the Shannon index decreased.

Relations Among Native and Exotic Species Groups

In the absence of vegetation control, there was a strong negative relation ($R^2 = 0.77$; $P < 0.01$, slope = -0.43) between NR cover and ER cover suggesting that species in these two groups have overlapping resource requirements resulting in competition (fig. 2, table 5). Intercepts, but not slopes, differed among sites for the NR and ER relation (fig. 2a), but a common intercept and slope were found for all three sites in the relation of RF cover and ER cover (fig. 2b). A weaker relation ($R^2 = 0.27$; $P < 0.01$, slope = -0.27) between RF cover and ER cover suggests that ER species compete with RF species to a lesser extent than with NR species. Conversely, a lack of a relation between RF cover and NR cover suggests little interaction at age 5 between these two groups (fig. 2c).

Canopy Cover and Productivity

Douglas-fir cover and height were greater with than without vegetation control at all three sites (table 4). At Matlock ER cover was higher where logging debris was removed than where it had been dispersed. Also, RF species cover was significantly higher where logging debris was dispersed than where it had been piled or removed at Matlock. No such relation was found among debris treatments at Molalla, and owing to experimental design differences, this comparison could not be made at Fall River. On debris-dispersed plots without vegetation control, Douglas-fir height and canopy cover were greatest at Fall River and least at Matlock (table 4).

Relation of Richness to Total Cover

Over all plots with or without vegetation control, richness had a strong, positive linear relation with total understory cover ($R^2 = 0.88$, $P < 0.01$; fig. 3). Although the site determined the overall level of richness (regression intercepts differed significantly among sites), the rate of species loss owing to vegetation control (regression slope) was independent of site, herbicides used, and application protocols that were

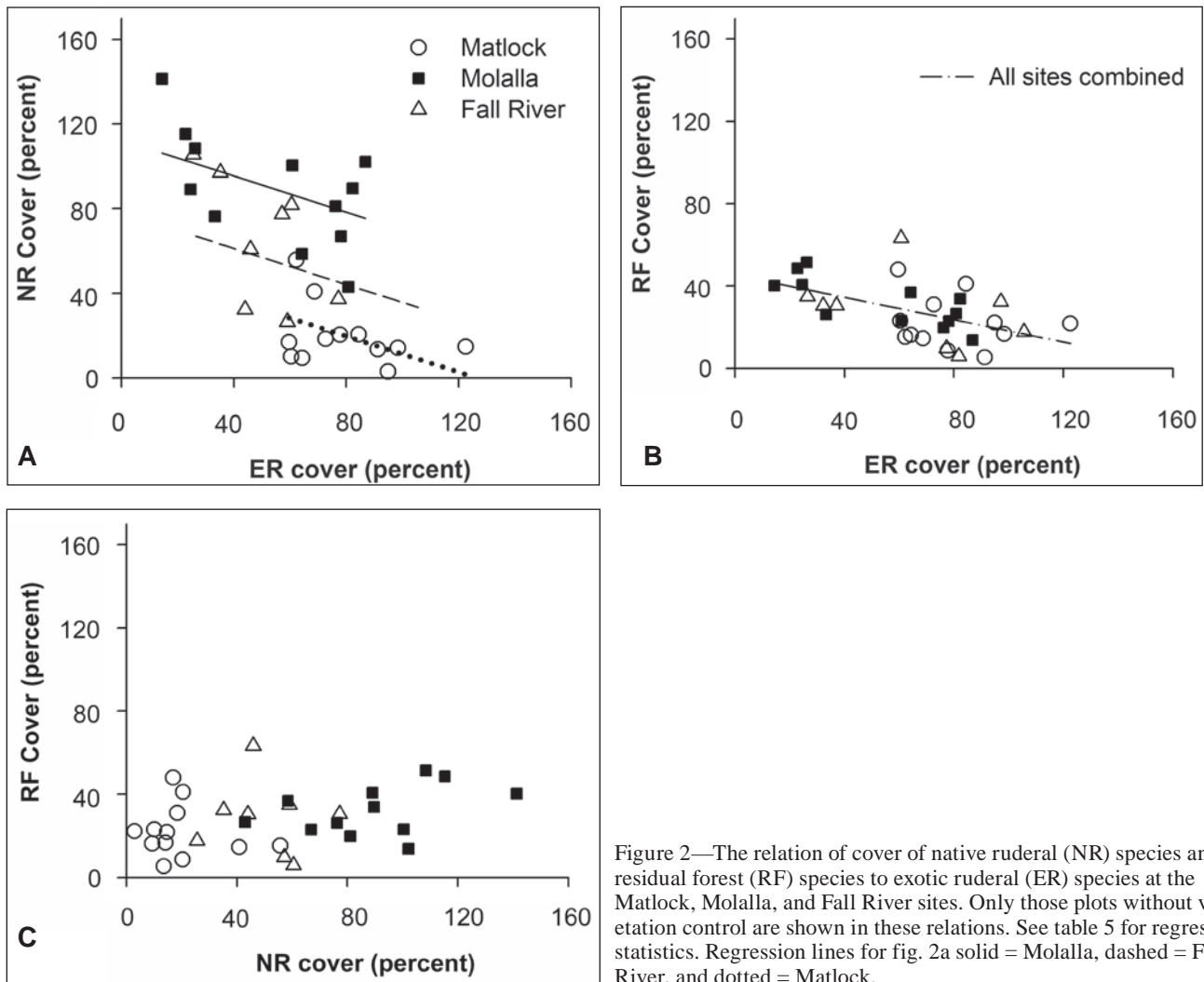


Figure 2—The relation of cover of native ruderal (NR) species and residual forest (RF) species to exotic ruderal (ER) species at the Matlock, Molalla, and Fall River sites. Only those plots without vegetation control are shown in these relations. See table 5 for regression statistics. Regression lines for fig. 2a solid = Molalla, dashed = Fall River, and dotted = Matlock.

Table 5—Regression statistics for the relations of native ruderal cover to exotic ruderal cover (see fig. 2), and residual forest cover to exotic ruderal cover (see fig. 2) and species richness to total cover (see fig. 3) at the Matlock, Molalla, and Fall River sites

Site	Y	X	Equation	R^2	$S_{y,x}$	n
Matlock	Native ruderal cover	Exotic ruderal cover	$Y = 53.8 - 0.43X$	0.77	17.5	32
Molalla			$Y = 112 - 0.43X$			
Fall River			$Y = 78.2 - 0.43X$			
All sites combined	Residual forest cover	Exotic ruderal cover	$Y = 45.3 - 0.27X$	0.27	12.2	32
Matlock	Species richness	Total cover	$Y = 20.7 - 0.098X$	0.88	3.23	72
Molalla			$Y = 15.4 - 0.098X$			
Fall River			$Y = 9.6 - 0.098X$			

Note: Each regression coefficient is significant ($p \leq 0.05$). R^2 is the coefficient of determination, $S_{y,x}$ is the standard error of the estimate, and n is the sample size.

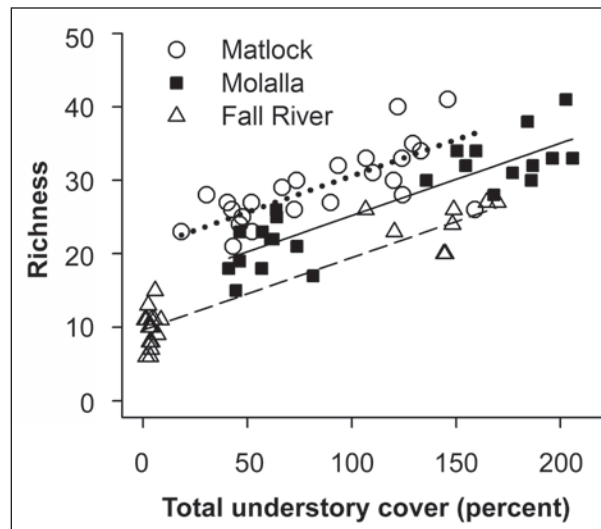


Figure 3—The relation of richness to total understory cover for combined plots with and without vegetation control at three study sites. Douglas-fir was not included in either richness or cover as it was deliberately not treated with herbicide. See table 5 for regression statistics. Regression lines: dotted = Matlock, solid = Molalla, and dashed = Fall River.

used. Species loss was proportional to the amount of total understory canopy cover remaining after treatment (approximately one species lost for each 10 percent reduction of cover).

Discussion

Community Structure and Composition

Our three Western Hemlock Zone (Franklin and Dyrness 1988) sites had distinctive environments, floras, and levels of productivity. Indicator species (Halverson et al. 1986, Henderson et al. 1989) and our ordinations floristically separate each site from the others, but suggest closer floristic affinities between Matlock and Molalla than between either of these sites and Fall River. However, based on the ordinations, Molalla and Fall River are floristically more similar than are Matlock and Fall River. The joint plot suggests that high NR diversity helps to distinguish Molalla from Matlock and Fall River while high ER diversity helps to distinguish Matlock from the Molalla and Fall River communities.

The balance of evidence suggests a site productivity gradient of Matlock < Molalla < Fall River, which follows the observed ranking in soil water and N availability among the three sites. Matlock had the highest precipitation, but also the lowest soil water-holding capacity and the lowest soil N. Fall River had the highest soil N, as well as a very deep clay-loam soil providing the largest soil water-holding

capacity. Site index values (King 1966) from the preharvest stands suggest Fall River is the most productive site (Fall River 41 to 43 m) (Terry et al. 2001), but do not distinguish between Matlock and Molalla (both 36 m) (Harrington and Schoenholtz 2010). However, published site index (McArdle and Meyer 1930, base 100 years) values for the plant associations present on these sites are 38 m for Matlock, 43 m for Molalla, and 54 m for Fall River (Halverson et al. 1986, Henderson et al. 1989). Also, the mean 5-year postharvest Douglas-fir tree heights and covers were least at Matlock and greatest at Fall River.

Trends in species richness approximated the inverse of the productivity gradient as suggested by the Intermediate Disturbance Hypothesis (Huston 1979). Although total richness was greatest at Molalla, richness per unit of canopy cover was greatest at Matlock (least productive) and least at Fall River (most productive) with or without vegetation control (fig. 3). Also, all three diversity indexes were apparently higher on debris-dispersed plots at Matlock than the other two sites, and total richness was lowest at Fall River (table 6). Exotic species were especially important contributors to the diversity at Matlock.

The negative relation of ER and RF species covers contrasts with the lack of a relation between NR and RF covers, suggesting that ER and NR species groups are not only functionally different but have fundamentally different relations to RF species as a result. In general, ruderal species (native or exotic) rapidly occupy space not already occupied by RF species during early succession. The more RF cover surviving the disturbance, the less ruderal cover and thus an inverse relation

Table 6—Comparison of means and standard deviations (SD) for Douglas-fir height, cover, and plant community diversity indicators for logging debris dispersed without vegetation control plots at the three sites

n	Matlock 4		Molalla 4		Fall River 8	
	Mean	SD	Mean	SD	Mean	SD
Douglas-fir height (cm)	169	20.6	219	9.3	310	16.0
Douglas-fir cover	8.5	0.8	11.4	2.2	53.1	5.3
Exotic ruderal cover	69.7	11.3	58.6	30.7	64.8	30.4
Native ruderal cover	27.9	18.6	87.9	42.7	50.6	16.3
Residual forest cover	33.8	14.2	28.2	8.2	28.1	17.9
Exotic ruderal richness	10.3	1.7	6.8	1.5	5.8	1.4
Native ruderal richness	10.8	2.6	15.8	3.2	6.9	1.5
Residual forest richness	14.8	2.1	10.5	2.4	11.5	3.1
Richness (w/o Douglas-fir)	35.8	6.0	33.0	3.7	24.1	2.9
Evenness index	0.7	0.03	0.6	0.03	0.6	0.03
Shannon index	2.6	0.16	2.2	0.16	2.0	0.13
Simpson index	0.9	0.02	0.8	0.02	0.8	0.02

A change of 4 percent cover of exotic ruderal species was accompanied by an opposite change of 10 percent cover of native ruderal species. Niche overlap of these groups is sufficient for native ruderal species to have lost some growing space to exotic ruderal species; however, they appear to differ enough in habitat requirements that coexistence is possible.

develops. However, chronosequence data from Fall River clearly show ER species establishing dominance more quickly than NR species (Peter and Harrington 2009). The rapid occupancy of open space by ER species obscures what might otherwise have been a similar relation of NR to RF species in the past before the invasion of ER species. Thus, in the past, a negative relation of NR and RF species probably developed, albeit more slowly. The ability of ER species to more rapidly occupy these sites than NR species is key to their invasion success and the reason for the current obscure relation of NR and RF species. Native ruderal species appear to invade and grow more slowly, gradually taking space left as shorter lived ER species senesce. Thus, NR cover shows little relation to RF cover at this point in succession.

The inverse relation between NR and ER cover suggests niche overlap and competition. Regardless of site, a change of 4 percent cover of ER species was accompanied by an opposite change of 10 percent cover of NR species. However, there was apparently no consistent dominance of one group by the other, and, to our knowledge, no localized extinction has resulted, suggesting that our communities are not species saturated. Antos and Halpern (1997) found lower root-to-shoot ratios of invading annuals (including some ER species) than in NR perennials like fireweed (*Chamerion angustifolium* (L.) Holub). Greater belowground resource allocation of NR species suggests a strategy of superior competitiveness for soil resources, but at the expense of rapid reproductive capacity and capture of aboveground growing space and thus a difference in their niche space relative to ER species. Apparently, niche overlap of these groups is sufficient for NR species to have lost some growing space to ER species; however, they appear to differ enough in habitat requirements that coexistence is possible provided species in both groups have access to the site.

Differences in site characteristics or land use history determined the representation of ruderals. Based on productivity, Fall River might have been expected to have the greatest total ruderal cover; however, Douglas-fir attains dominance so rapidly on this site that light and root competition partly suppressed the ruderal plants by age 5 years, suggesting that high productivity compresses the window of availability of suitable habitat for ruderal species. Higher richness of ER species at Matlock and the inverse relation of NR to ER species suggests that Matlock is more susceptible to invasion by ER species than the other sites. This may result from a slower rise in dominance of trees, a slower rate of colonization by NRs owing to their more conservative reproductive strategy, and to the slow recovery rate of RF species.

Debris Treatments

Ground disturbance, disruption of the litter layer, and top damage to perennial native plants associated with logging debris removal and piling likely favored fast-growing ERs at the expense of native species. Differences in cover among debris treatments were significant at Matlock (ER species: debris dispersed < debris removed; RF species: debris dispersed > debris removed or piled). Scotch broom also increased where debris was removed at Matlock relative to where debris was dispersed (Harrington and Schoenholtz 2010). Ground disturbance also promoted ER species invasion elsewhere (Marshall and Buckley 2008, Sumners and Archibald 2007). However, at Molalla and Fall River, the debris treatments had little effect on abundance of the species groups, similar to some other studies where organic matter removal caused only small changes in soil carbon and N (Powers 2004, Sanchez et al. 2006), microbial communities (Busse et al. 2006), species richness (Alban et al 1994, Hauesler et al. 1999) and conifer growth (Fleming et al. 2006). We suggest that the low N content and water-holding capacity of soil at Matlock slowed recovery or increased mortality of damaged RF species making more and longer lasting openings available to invasive exotic species. This also accounts for Matlock's higher ER cover in the debris-removed treatment compared to the debris-dispersed treatment.

Vegetation Control

Similar to other studies involving high rates or repeated applications of herbicides (Pitt et al. 2004, Wilkins et al. 1993), our vegetation control treatments increased tree growth but caused a loss of diversity and plant cover. The more extreme Fall River vegetation control treatments clearly overwhelmed all species groups unlike the Matlock or Molalla treatments, but even at these sites, cover and diversity were lost. The similarity of the richness response to loss of cover at all three sites regardless of substantial differences in flora, productivity, and treatments (one species lost for each 10 percent reduction in cover) suggests robustness for this relationship in Pacific Northwest forests.

Concern over Scotch broom competition with planted Douglas-fir at Matlock prompted an effort to control the broom with individual-plant applications of tricopyr in years 1, 4, and 5 on all plots (Harrington and Schoenholtz 2010). Observations by the authors and others (Wearne and Morgan 2004) indicate that Scotch broom commonly attains high densities that suppress species diversity. Scotch broom would likely turn the predominantly herbaceous-to-tree-dominated succession at Matlock (potentially at the other sites too), into a shrub-to-tree-dominated succession while delaying the time required for Douglas-fir to attain dominance.

The extra control measures prevented excessive loss of diversity and tree mortality (Harrington and Schoenholtz 2010), and thwarted a potential change in successional state. Scotch broom was present at the other sites, but did not achieve high levels of dominance there owing to differences in previous stand history, aggressiveness of previous control efforts, and possibly differences in soil N. Controlling this shrub at Matlock provided a more favorable comparison of the remaining, mostly herbaceous ruderal communities. However, it is important to recognize the potential of this and some other species such as red alder (*Alnus rubra* Bong.) for changing the outcome of this study and succession in general with severe consequences to the timber crop. Red alder has the potential to be an aggressive competitor at Molalla and Fall River, but probably not at Matlock because of limited soil water availability.

Plant community composition at Matlock and Molalla, but not Fall River, became more similar (shown by ordination) after vegetation control owing to differential reductions in ruderal richness and dominance. The ER richness at Matlock and the NR richness at Molalla (and both groups at Fall River) were reduced significantly, thus there does not appear to be any tendency of either group toward greater herbicide resistance. While Matlock and Molalla vegetation became more similar, herbicide treatment decreased their similarity to Fall River. Reduction of richness and diversity indexes at Fall River with vegetation control indicates that representation of the fewer remaining species became more unequal. Exotic ruderals, although much diminished on vegetation control plots, had more than twice the cover of native RF species and four times that of the NRs suggesting a superior ability to colonize and grow between herbicide applications.

The Intermediate Disturbance Hypothesis (IDH) predicts that an optimal frequency and intensity of disturbance produces the highest diversity for a given community (Connell 1978, Grime 1973). This theory is mainly premised on two observations: (1) highly competitive species suppress less competitive species, and (2) disturbance may injure or kill highly competitive species as much or more than others, thus reducing the advantage that they have. Thus, when the forest overstory is removed, the understory is released and space is made available for invaders. Damage done to the understory vegetation during timber harvest and site preparation (e.g., debris treatments) creates space for ruderal invasion but rarely eliminates the original understory flora, resulting in an increase in diversity. This was the case for the plots that did not receive vegetation control. Although we do not have preharvest data for our stands, casual observation of adjacent intact forest and species lists accumulated for mature and old-growth stands of the plant associations we identified (Halverson et al. 1986, Henderson et al. 1989) strongly suggest that

diversity increased after forest harvesting at all three of our sites wherever vegetation control was not used. Thus, harvesting and debris treatments by themselves tend to promote community diversity and thus do not greatly exceed the optimal level of disturbance predicted by the IDH.

Foresters typically plant vigorous seedlings of a highly competitive tree species (e.g., Douglas-fir) often with vegetation control treatments. This allows the planted trees to achieve dominance more rapidly than during natural succession, thereby reducing the time that the community spends in a diverse early successional state over what would naturally occur. The inverse relation of productivity and diversity among our sites suggests that tree growth, even by year 5, may be reducing community diversity at Fall River but not at Matlock. This is also suggested by the relation of tree size to community composition in the ordination joint plots and is suggested in the findings of Peter and Harrington (2009). Thus, when intermediate levels of disturbance stop, or when a single species is allowed to escape the effects of disturbance and grow to dominance, the IDH predicts that species diversity will decline. The resulting condition that develops in forests has been referred to as the stem-exclusion stage (Oliver 1980) and is widely recognized as having low diversity. It is therefore especially important in systems managed on short timber rotations to understand how silvicultural treatments affect ephemeral developing understory communities where most of the diversity of the developing forest resides.

The vegetation control treatments were effective in accelerating Douglas-fir dominance. Douglas-fir responded to reduced competition by growing faster, and at Matlock with higher survival (Harrington and Schoenholtz 2010). The magnitude of the effect (34 percent increase in crown area) in the productive and predominantly herbaceous community at Fall River was notable; however, Douglas-fir benefited from vegetation control most at Matlock (56 percent increase in crown area). Even so, owing to lower productivity, it will be years before Douglas-fir at Matlock achieves the level of dominance expressed at Fall River in year 5, which means that early successional diversity will be expressed for a longer period of time at this site. However, by accelerating Douglas-fir dominance, ruderal species will be suppressed more rapidly with potential landscape-level implications for ruderal diversity and wildlife habitat quality where these practices are widespread.

Our annual herbicide treatments reduced richness of three different plant communities at the rate of one species per 10 percent loss of canopy cover regardless of site or treatment differences, suggesting a degree of generality for this relation. As expected, the more intensive Fall River treatments suppressed diversity and cover more than the Matlock or Molalla treatments, but at the same rate relative to

Our annual herbicide treatments reduced richness of three different plant communities at the rate of one species per 10 percent loss of canopy cover regardless of site or treatment differences, suggesting a degree of generality for this relation.

canopy cover. In the context of the IDH, the powerful effects of herbicide applications pushed the community beyond an “intermediate” level of disturbance and thus compromised diversity.

Although herbicides have few natural analogues, like other disturbances they create new growing space, which is colonized by ruderals. Therefore, we expect that ruderals, especially ERs will increase upon cessation of herbicide treatments. While our research does not indicate what effect more typical single applications of herbicides would have on diversity, Stein (1995) found a compositional shift toward more ruderal species and little effect on diversity with a single application of glyphosate. Stein (1995), however, did not identify all taxa to species, so loss of rare species might have been overlooked. Peter and Harrington (2009) found that a single treatment at Fall River decreased richness in the year of application while further annual applications prevented recovery. Elsewhere, few effects of vegetation control with herbicides on diversity have been reported (Boyd et al. 1995, Haeussler et al. 2002). However, these and most other forestry herbicide studies monitored diversity years after treatment, unlike ours, which monitored diversity during the first growing season following treatment. The lesson from these other studies appears to be that diversity does recover in time. We plan to continue monitoring these sites in the future to measure recovery of diversity and composition in the absence of further treatments.

The RF species group was somewhat tolerant of the herbicide control measures used. Over all three sites, vegetation control treatments reduced RF species cover and richness proportionately less than that of ruderal species. Residual forest species are mostly stress tolerators (Grime 1977) that cope with intense shade and root competition from the dominant arboreal overstory as succession proceeds. Many RF species have a large root (and rhizome)/shoot ratio, compared to ruderals (Antos and Halpern 1997, Lezberg et al. 1999), which is common for stress-tolerant plants (Chapin 1980) and an important strategy for surviving unpredictable top loss (Iwasa and Kubo 1997). The large underground investment in root and rhizome tissue, and the ability to regrow from these organs, allows many forest species to survive a variety of disturbances (Halpern 1988). We believe that these characteristics reduce the susceptibility of RF species to herbicides by reducing the proportion of tissue available for herbicide absorption compared to the total plant biomass (relative to most ruderals), resulting in a lower dose received. However, their ability to avoid herbicide injury was largely overcome at Fall River by more frequent applications, and therefore a higher dose, of herbicides.

Conclusions

Although ER and NR species have considerable niche overlap, ER species are more successful at initially occupying disturbed sites. While the response of NR species to ER species cover was independent of site or stand history, the overall ruderal representation was not. We believe that the kind and quantity of the original forest understory together with the level of damage incurred during harvest operations and the time sites are open and available (owing to differences in site productivity) are largely responsible for differences in the overall ruderal representation after clearcutting. Because ER species rapidly invade space not occupied by RF species, minimizing damage to the forest understory should decrease ER colonization. Intensive debris removal, which also involves ground disturbance further encouraged ER establishment on our least productive site. But the lack of such an effect on our other sites suggests that this kind of activity has less impact than clearcutting on ruderal representation. The ability of ERs to rapidly invade after herbicide treatments suggests that limiting such activity would favor native species. Early successional species diversity is partly an expression of site potential because species richness is inversely proportional to site productivity (Huston 1979), but the degree of species saturation may also be important. Intensive vegetation control measures aimed at increasing tree productivity reduced richness at the rate of one species per 10 percent understory canopy cover reduction regardless of site or treatment differences. Understory dominance relations were also changed because of a superior ability of ERs to colonize and grow between herbicide treatments and less herbicide susceptibility of RF species compared to ruderals.

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Although exotic ruderal and native ruderal species have considerable niche overlap, exotic ruderal species are more successful at initially occupying disturbed sites.

English Equivalent

When you know:	Multiply by:	To find:
Millimeters (mm)	0.0394	Inches
Centimeters (cm)	.394	Inches
Meters (m)	3.28	Feet
Kilometers (km)	.621	Miles
Hectares (ha)	2.47	Acres
Kilograms (kg)	2.205	Pounds
Kilograms per hectare (kg/ha)	.893	Pounds per acre

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Appendix

Table 7—Species with mean cover by site and treatment for the three study sites ^{a b c}

			Study site, treatment, number of plots, and species richness																				
			Fall River				Matlock						Molalla										
Scientific name	Common name	Group	LDD	LDD	LDR	VC	LDD	LDP	LDR	LDD	LDP	LDR	NVC	VC	LDD	LDP	LDR	LDD	LDP	LDR	NVC	VC	
			NVC	VC	VC	VC	NVC	NVC	NVC	VC	VC	VC	NVC	VC	NVC	NVC	NVC	VC	VC	VC	NVC	VC	
			8	8	8	16	4	4	4	4	4	4	12	12	4	4	4	4	4	4	12	12	
			43	29	25	36	62	51	57	45	42	44	73	58	63	61	61	38	38	37	84	51	
<i>Abies grandis</i> (Douglas ex D. Don) Lindl.	grand fir	RF					0	0	0		0	0	0	0								0	0
<i>Abies procera</i> Rehder	noble fir	NR																1					0
<i>Acer circinatum</i> Pursh	vine maple	RF	0				6	1	1	11	5	2	2	6	0		0	0				0	0
<i>Acer macrophyllum</i> Pursh	bigleaf maple	NR												0	0								
<i>Achlys triphylla</i> (Sm.) DC.	sweet after death	RF		0		0								0	0		0						0
<i>Adenocaulon bicolor</i> Hook.	American trailplant	RF																					
<i>Agoseris retrorsa</i> (Benth.) Greene	spearleaf agoseris	NR						0		0												0	
<i>Agrostis capillaris</i> L.	colonial bentgrass	ER	0				1	3	3		1	0	2	0	5	1	1	1	0	0		2	0
<i>Aira caryophyllea</i> L.	silver hairgrass	ER														0	1	0				0	0
<i>Aira praecox</i> L.	yellow hairgrass	ER							0	1	0	0	0	0	0								
<i>Alnus rubra</i> Bong.	red alder	NR																1		1			1
<i>Amelanchier alnifolia</i> (Nutt.) Nutt. ex M. Roem.	saskatoon serviceberry	RF						5	3	1	3	3	2	3	3								
<i>Anaphalis margaritacea</i> (L.) Benth.	western pearly everlasting	NR	8	0	0	0		2	0		0	1	3	1	1		0	0	0			0	

Table 7—Species with mean cover by site and treatment for the three study sites ^{a b c} (continued)

			Study site, treatment, number of plots, and species richness																																																		
			Fall River				Matlock						Molalla																																								
Scientific name	Common name	Group	LDD	LDD	LDR		LDD	LDP	LDR	LDD	LDP	LDR				LDD	LDP	LDR	LDD	LDP	LDR																																
			NVC	VC	VC	VC	NVC	NVC	NVC	VC	VC	VC	NVC	VC	NVC	VC	NVC	NVC	NVC	VC	VC	VC	NVC	VC	NVC	VC																											
			8	8	8	16	4	4	4	4	4	4	12	12	4	4	4	4	4	4	4	12	12	43	29	25	36	62	51	57	45	42	44	73	58	63	61	61	38	38	37	84	51										
<i>Chamerion angustifolium</i> (L.) Holub	fireweed	NR	25	0	0	0		4	2	0	1	3	0	2	1	1	1	4			0	2	0																														
<i>Cirsium arvense</i> (L.) Scop.	Canada thistle	ER						0	0	0				0		0	0	0			0	0	0																														
<i>Cirsium vulgare</i> (Savi) Ten.	bull thistle	ER	0						0					0		0						0																															
<i>Claytonia sibirica</i> L. var. <i>sibirica</i>	Siberian springbeauty	RF		0		0									1	1	1		0		0	1	0																														
<i>Clinopodium douglasii</i> (Benth.) Kuntze	yerba buena	RF						0		0				0		1						0																															
<i>Collomia heterophylla</i> Douglas ex Hook.	variableleaf collomia	NR								0				0		0	0		0	0		0	0																														
<i>Cornus canadensis</i> L.	bunchberry dogwood	RF								0	0			0		0						0																															
<i>Cornus nuttallii</i> Audubon ex Torr. & A. Gray	Pacific dogwood	RF														1																																					
<i>Corylus cornuta</i> Marsh. var. <i>californica</i> (A. DC.) Sharp	California hazelnut	RF														0						0	0																														
<i>Crepis capillaris</i> (L.) Wallr.	smooth hawksbeard	ER				3		5	12	2	2	2	7	2		1		0	3	2		1	0	2																													
<i>Cytisus scoparius</i> (L.) Link	Scotch broom	ER				0		1	0	0	0	0	1	0				0					0																														
<i>Dactylis glomerata</i> L.	orchardgrass	ER							1		0		0	0																																							
<i>Danthonia spicata</i> (L.) P. Beauv. ex Roem. & Schult.	poverty oatgrass	NR				0		0	0	0		0	0	0																																							

Table 7—Species with mean cover by site and treatment for the three study sites ^{a b c} (continued)

		Study site, treatment, number of plots, and species richness																							
		Fall River				Matlock								Molalla											
Scientific name	Common name	Group	LDD	LDD	LDR	VC	LDD	LDP	LDR	LDD	LDP	LDR	NVC	VC	LDD	LDP	LDR	LDD	LDP	LDR	NVC	VC			
			NVC	VC	VC	VC	NVC	NVC	NVC	VC	VC	VC	NVC	VC	NVC	NVC	NVC	VC	VC	VC	NVC	VC			
		8		8		16		4		4		4		12		4		4		4		12			
		43		29		25		36		62		51		57		45		42		44		73		58	
		4		4		4		63		61		61		38		38		37		84		51			
<i>Dicentra formosa</i> (Haw.) Walp.	Pacific bleedingheart	RF	0	0	0	0																			
<i>Digitalis purpurea</i> L.	purple foxglove	ER	2	0		0			0	0			0		2	3	2		0			2	0		
<i>Dryopteris expansa</i> (C. Presl) Fraser- Jenkins & Jermy	spreading woodfern	RF	0		0	0																			
<i>Elymus glaucus</i> Buckley	blue wildrye	NR						1	3	7			0	4	0		1	3	2			2			
<i>Epilobium ciliatum</i> Raf.	fringed willowherb	NR	0	0		0		1	0	0	0	0	0	0	0		0	0		0	0	0	0		
<i>Epilobium minutum</i> Lindl. ex Lehm.	chaparral willowherb	NR						1		0				0											
<i>Equisetum arvense</i> L.	field horsetail	NR			0	0																			
<i>Erechtites minima</i> (Poir.) DC.	coastal burnweed	ER	1																						
<i>Festuca occidentalis</i> Hook.	western fescue	RF		0		0	1	1	2	1	1	0	1	1	2	5	1	1	2	1	3	1			
<i>Fragaria vesca</i> L.	woodland strawberry	NR					0	0	0	0	0		0	0		3	8	2				4			
<i>Frangula purshiana</i> (DC.) Cooper	cascara buckthorn	RF	0	0	0	0	0	0		1	0	1	0	0	6	10	10	2	2	7	9	3			

Table 7—Species with mean cover by site and treatment for the three study sites ^{a b c} (continued)

			Study site, treatment, number of plots, and species richness																			
			Fall River				Matlock						Molalla									
Scientific name	Common name	Group	LDD	LDD	LDR		LDD	LDP	LDR	LDD	LDP	LDR	NVC	VC	LDD	LDP	LDR	LDD	LDP	LDR	NVC	VC
			NVC	VC	VC	VC	NVC	NVC	NVC	VC	VC	VC	VC	VC	VC	NVC	NVC	NVC	VC	VC	VC	VC
			8	8	8	16	4	4	4	4	4	4	12	12	4	4	4	4	4	4	12	12
			43	29	25	36	62	51	57	45	42	44	73	58	63	61	61	38	38	37	84	51
<i>Galium aparine</i> L.	stickywilly	NR							0	0				0	0		0	0		0	0	2
<i>Galium triflorum</i> Michx.	fragrant bedstraw	RF					0	0	0	0	0	0	0	0	2	2	3	0	0	0	2	0
<i>Gaultheria shallon</i> Pursh	salal	RF					7	4	2	9	6	3	4	6	12	11	12	11	4	3	11	6
<i>Geranium carolinianum</i> L.	Carolina geranium	NR													0							0
<i>Hieracium albiflorum</i> Hook.	white hawkweed	NR	2		0	0			0	0	0		0									
<i>Holcus lanatus</i> L.	common velvetgrass	ER	27	0	0	0	3	8	2	0	1	0	4	0	31	13	38	11	14	15	27	13
<i>Holodiscus discolor</i> (Pursh) Maxim.	oceanspray	RF					0	0	0		0	0	0	0		0	2				1	
<i>Hypericum perforatum</i> L.	common St. Johnswort	ER									0		0		0		0	0	0	0	0	0
<i>Hypochaeris radicata</i> L.	hairy cat's ear	ER	34	1	3	2	28	26	28	4	10	12	27	9	2	1	0	1	5	1	1	2
<i>Ilex aquifolium</i> L.	English holy	EF													0	0			0	1	0	0
<i>Iris tenax</i> Douglas ex Lindl.	toughleaf iris	NR		0	0	0									1	2	2	0		0	1	0
<i>Juncus tenuis</i> Willd.	poverty rush	NR														0						0
<i>Lapsana communis</i> L.	common nipplewort	ER															0			0	0	0
<i>Leucanthemum vulgare</i> Lam.	oxeye daisy	ER					25	23	35	1	4	3	28	3	17	25	17	5	3	2	20	3
<i>Ligusticum apiifolium</i> (Nutt. ex Torr. & A. Gray) A. Gray	celleryleaf licorice-root	NR													0		0					0
<i>Lilium columbianum</i> Leichtlin	Columbia lily	NR					0	0	0		0	0	0	0								

Table 7—Species with mean cover by site and treatment for the three study sites ^{a b c} (continued)

			Study site, treatment, number of plots, and species richness																				
			Fall River				Matlock								Molalla								
Scientific name	Common name	Group	LDD	LDD	LDR		LDD	LDP	LDR	LDD	LDP	LDR				LDD	LDP	LDR	LDD	LDP	LDR		
			NVC	VC	VC	VC	NVC	NVC	NVC	VC	VC	VC	NVC	VC	NVC	VC	NVC	VC	VC	VC	VC	VC	NVC
			8	8	8	16	4	4	4	4	4	4	12	12		4	4	4	4	4	4	12	12
			43	29	25	36	62	51	57	45	42	44	73	58		63	61	61	38	38	37	84	51
<i>Linnaea borealis</i> L.	twinflower	RF					3	1	0	0	0			1	0								
<i>Lonicera ciliosa</i> (Pursh) Poir. ex DC.	orange honeysuckle	RF						1	1	0	1	1	1	1									
<i>Lotus aboriginus</i> Jeps.	rosy bird's-foot trefoil	NR					1	2	0	0		0	1	0	6	3	7	0	0	0	5	0	
<i>Lotus micranthus</i> Benth.	desert deervetch	NR										0	0				0	1			0		
<i>Luzula comosa</i> E. Mey.	Pacific woodrush	NR					0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Luzula parviflora</i> (Ehrh.) Desv.	smallflowered woodrush	RF	0	0		0									0	0	0					0	
<i>Mahonia nervosa</i> (Pursh) Nutt.	Cascade barberry	RF					1	1	1	0	1	1	1	1	3	0	0	1	2	1	1	1	
<i>Maianthemum racemosum</i> (L.) Link	feathery false lily of the valley	RF															0					0	
<i>Maianthemum stellatum</i> (L.) Link	starry false lily of the valley	RF						0			0		0		0	0		0	0		0	0	
<i>Malus fusca</i> (Raf.) C.K. Schneid.	Oregon crab apple	NR						0						0									
<i>Menziesia ferruginea</i> Sm.	rusty menziesia	RF	0																				
<i>Mycelis muralis</i> (L.) Dumort.	wall-lettuce	NR						0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Oemleria cerasiformis</i> (Torr. & A. Gray ex Hook. & Arn.) Landon	Indian plum	RF						0					0				0				0		

Table 7—Species with mean cover by site and treatment for the three study sites ^{a b c} (continued)

			Study site, treatment, number of plots, and species richness																						
			Fall River				Matlock						Molalla												
Scientific name	Common name	Group	LDD	LDD	LDR		LDD	LDP	LDR	LDD	LDP	LDR				LDD	LDP	LDR	LDD	LDP	LDR				
			NVC	VC	VC	VC	NVC	NVC	NVC	VC	VC	VC	NVC	VC	NVC	VC	NVC	NVC	NVC	VC	VC	VC	NVC	VC	NVC
			8	8	8	16	4	4	4	4	4	4	12	12		4	4	4	4	4	4	12	12		
			43	29	25	36	62	51	57	45	42	44	73	58		63	61	61	38	38	37	84	51		
<i>Oplopanax horridus</i> (Sm.) Miq.	devilsclub	RF			0	0																			
<i>Osmorhiza berteroi</i> DC.	sweet cicely	RF						0		0					0	0		0	0				0	0	
<i>Oxalis oregana</i> Nutt.	redwood-sorrel	RF	14	1	0	1									0	1								0	
<i>Petasites frigidus</i> (L.) Fr. var. <i>palmatus</i> (Aiton) Cronquist	arctic sweet coltsfoot	NR													1									0	
<i>Phacelia hastata</i> Douglas ex Lehm.	silverleaf phacelia	NR						0	0				0												
<i>Poa compressa</i> L.	Canada bluegrass	NR													0	1	0	1	2	0			1	1	
<i>Poa pratensis</i> L.	Kentucky bluegrass	NR													0			0	0				0	0	
<i>Polystichum munitum</i> (Kaulf.) C. Presl	western swordfern	RF	2	0		0	0	1	0	1	0	0	0	0	1	2	4	1	2	1		2	1		
<i>Prosartes smithii</i> (Hook.) Utech, Shinwari & Kawano	largeflower fairybells	RF	0	0	0	0		0	0	0	1	0	0	0											
<i>Prunella vulgaris</i> L.	common selfheal	NR						1	1	2	0	0		2	0			0		0					
<i>Prunus avium</i> (L.) L.	sweet cherry	EF																	0					0	
<i>Prunus emarginata</i> (Douglas ex Hook.) D. Dietr.	bitter cherry	NR	0		0	0		1	1	0	0	0	0	1	0	1	1	4	1	0		2	0		

Table 7—Species with mean cover by site and treatment for the three study sites ^{a b c} (continued)

		Study site, treatment, number of plots, and species richness																					
		Fall River				Matlock								Molalla									
Scientific name	Common name	Group	LDD	LDD	LDR		LDD	LDP	LDR	LDD	LDP	LDR			LDD	LDP	LDR	LDD	LDP	LDR			
			NVC	VC	VC	VC	NVC	NVC	NVC	VC	VC	VC	NVC	VC	NVC	NVC	NVC	VC	VC	VC	NVC	VC	
			8	8	8	16	4	4	4	4	4	4	12	12	4	4	4	4	4	4	4	12	12
			43	29	25	36	62	51	57	45	42	44	73	58	63	61	61	38	38	37	84	51	
<i>Pseudognaphalium canescens</i> (DC.) W.A. Weber ssp. <i>thermale</i> (E.E. Nelson) Kartesz	Wright's cudweed	NR											0		0								
<i>Pseudotsuga menziesii</i> (Mirb.) Franco	Douglas-fir	NR	53	72	71	71	9	8	7	18	13	15	8	15	11	12	14	15	18	14	12	16	
<i>Pteridium aquilinum</i> (L.) Kuhn	western brackenfern	NR	2	0		0	6	4	1	7	1	7	4	5	16	10	4	1	1	2	10	1	
<i>Ranunculus occidentalis</i> Nutt.	western buttercup	NR	0												0	1						0	
<i>Ribes sanguineum</i> Pursh	redflower currant	NR										0			0		0		1			0	
<i>Rosa gymnocarpa</i> Nutt.	dwarf rose	RF							0	0	0	0		0	0		0					0	
<i>Rubus armeniacus</i> Focke	Himalayan blackberry	ER														0	1					0	
<i>Rubus laciniatus</i> Willd.	cutleaf blackberry	ER	1	0		0			0					0		1	0	1		0	0	0	

Table 7—Species with mean cover by site and treatment for the three study sites ^{a b c} (continued)

			Study site, treatment, number of plots, and species richness																						
			Fall River				Matlock						Molalla												
Scientific name	Common name	Group	LDD	LDD	LDR		LDD	LDP	LDR	LDD	LDP	LDR				LDD	LDP	LDR	LDD	LDP	LDR				
			NVC	VC	VC	VC	NVC	NVC	NVC	VC	VC	VC	NVC	VC	NVC	NVC	NVC	VC	VC	VC	NVC	VC	NVC	VC	NVC
			8	8	8	16	4	4	4	4	4	4	12	12	4	4	4	4	4	4	4	12	12	4	4
			43	29	25	36	62	51	57	45	42	44	73	58	63	61	61	38	38	37	84	51			
<i>Rubus leucodermis</i> Douglas ex Torr. & A. Gray	whitebark raspberry	NR	0												1	0	1	0	0	1	0				
<i>Rubus parviflorus</i> Nutt.	thimbleberry	NR						0					0		0	0	1					1			
<i>Rubus spectabilis</i> Pursh	salmonberry	RF	1	0	0	0																			
<i>Rubus ursinus</i> Cham. & Schtdl.	California blackberry	NR	12	0	1	0	9	5	1	9	2	3	5	5	53	59	55	18	12	24	55	18			
<i>Rumex acetosella</i> L.	common sheep sorrel	ER					0	0	1				0		0	0	0						0		
<i>Salix scouleriana</i> Barratt ex Hook.	Scouler's willow	NR	1																						
<i>Sambucus racemosa</i> L.	red elderberry	RF	4	0	0	0		1	0		0		0		0		0	0	1			1			
<i>Senecio jacobaea</i> L.	stinking willie	ER	0	0		0												0	0			0			
<i>Senecio sylvaticus</i> L.	woodland ragwort	ER	0	0	0	0		1	4	5	0		3		0						0	0	0		
<i>Stachys mexicana</i> Benth.	Mexican hedgenettle	NR	1																						
<i>Stellaria longipes</i> Goldie	longstalk starwort	NR						0					0				0					0			

Table 7—Species with mean cover by site and treatment for the three study sites ^{a b c} (continued)

			Study site, treatment, number of plots, and species richness																				
			Fall River				Matlock						Molalla										
Scientific name	Common name	Group	LDD	LDD	LDR		LDD	LDP	LDR	LDD	LDP	LDR	NVC	VC	LDD	LDP	LDR	LDD	LDP	LDR	NVC	VC	
			NVC	VC	VC	VC	NVC	NVC	NVC	VC	VC	VC	VC	VC	NVC	VC	NVC	NVC	NVC	VC	VC	VC	NVC
			8	8	8	16	4	4	4	4	4	4	12	12	4	4	4	4	4	4	12	12	
			43	29	25	36	62	51	57	45	42	44	73	58	63	61	61	38	38	37	84	51	
<i>Veronica chamaedrys</i> L	germander speedwell	ER	0				1	1	1	1	1	1	1	1									
<i>Vicia americana</i> Muhl. ex Willd.	American vetch	NR													0		1	0		0	0	0	
<i>Vicia nigricans</i> Hook. & Arn. ssp. <i>gigantea</i> (Hook.) Lassetter & C.R. Gunn.	giant vetch	NR													1	0	0					0	
<i>Viola sempervirens</i> Greene	evergreen violet	RF	3	0	0	0		0	0		0	0	0	0	0		0	0	0		0	0	

^aValues shown as “0” are positive values smaller than 1 percent.

^bLDD = logging debris dispersed, LDR = logging debris removed, LDP = logging debris piled, VC = vegetation control, NVC = no vegetation control.

^cColumns labelled simply “VC” or “NVC” incorporate all debris treatments either receiving or not receiving vegetation control respectively. For Fall River only; LDD = NVC.

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