# Six years of plant community development after clearcut harvesting in western Washington

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Abstract: What roles do ruderals and residuals play in early forest succession and how does repeated disturbance affect them? We examined this question by monitoring plant cover and composition on a productive site for 6 years after clear-cutting and planting Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco). The replicated experiment included three treatments: vegetation control with five annual herbicide applications superimposed over two levels of slash removal (bole only or total tree plus most other wood) and an untreated control. Three species groups were analyzed: native forest, native ruderals, and exotic ruderals. Without vegetation control, the understory was rapidly invaded by exotic ruderals but was codominated by native and exotic ruderals by year 6. Douglas-fir cover surpassed covers in the three species group covers at least 3 years sooner with herbicide treatments than without. Species richness and coverage were lower for all species groups with vegetation control than without vegetation control. The effects of organic matter removal were much less than that of vegetation control. As predicted by the Intermediate Disturbance Hypothesis, repeated vegetation control resulted in declining cover and richness; however, native forest species were surprisingly resilient, maintaining as much or more cover and richness as the ruderal groups.

Resume: Quels rôles jouent les espèces résiduelles et rudérales en debut de succession forestière et de quelle façon sont-elles affectées par des perturbations répétées? Nous avons étudié cette question en faisant le suivi de la composition et du couvert vegetal dans une station productive pendant 6 ans après une coupe à blanc et la plantation de douglas de Menzies (*Pseudotsuga menziesii* (Mirb.) Franco). L'expérience qui a ete répétée comprenait trois traitements : la maitrise de la vegetation avec cinq applications annuelles d'herbicide superposée à deux intensité d'élimination des résidus de coupe (Ie tronc seulement ou l'arbre en entier ainsi que la plupart des autres pieces de bois) et un témoin non traité, Trois groupes d' espèces ont ete analysées : les espèces forestières indigenes, les espèces rudérales indigenes et les espèces rudérales exotiques. Sans maitrise de la vegetation, Ie sous-bois a rapidement ete envahi par les espèces rudérales exotiques mais les deux groupes d'espèces rudérales étaient codominants après 6 ans. Le couvert de douglas de Menzies a surpassé Ie couvert des trois groupes d'espèces au moins 3 ans plus tot dans les traitements avec un herbicide comparativement aux traitements sans herbicide. La maitrise de la vegetation a réduit la couverture et la richesse en espèces chez tous les groupes d'espèces. Les effets de I'éllmination de la matiere organique étaient beaucoup moins importants que ceux de la maitrise de la vegetation. Tel que Ie prédit l'hypothèse de perturbation intermédiaire, la maitrise répétée de la vegetation a entrainé une diminution de la richesse et de la couverture. Cependant, les espèces forestières indigenes étaient étonnamment résilientes et ont maintenu une couverture et une richesse similaires ou supérieures aux groupes d'espèces rudérales,

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## Introduction

Ecosystem management, biodiversity conservation, and maintenance of long-term productivity are major objectives of forest managers who recognize that harvesting and regeneration practices have substantial effects on these values. Ecological theory is yielding promising models to aid in biodiversity management (Odion and Sarr 2007). Nonequilibrium theories such as the Intermediate Disturbance Hypothesis predict broad trends of forest succession (Grime 1977; Huston 1979); for example, Pacific Northwest forest succession is predicted to begin with residuals and ruderals, then becomes dominated by shade-intolerant trees, then shade-tolerant trees. Intermediate levels of disturbance reduce dominant species, allowing less competitive early successional and shade-intolerant species to coexist with later successional species, thus increasing diversity (Grime 1973). The greatest diversity occurs between the initiating disturbance and overstory crown closure, or much later owing to age-associated gaps (Franldin and Spies 1991). At the beginning of this sequence, less understood processes take place, which although entrained into the overall successional model, are not adequately described. Thus, we asked what successional adjustments are made by the native flora in response to the exotic ruderal flora. Trees inevitably dominate, facilitating a transition to a shade-tolerant herb, fern, and shrub understory, but what are the roles of ruderals and residuals in this transition and how do further perturbations affect these roles?

Herbicides have been extensively evaluated for their potential to release crop trees from competing vegetation (Brodie and Walstad 1987; Newton and Comeau 1990), but minimal attention has been paid to the effects of herbicide applications on Pacific Northwest floral diversity (e.g., Stein

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1995). Stein (1995) found that a single glyphosate application caused a shift toward ruderal species with little effect on diversity. Studies examining vegetation development after herbicide use in other regions also reported only small or temporary changes in diversity and composition (Freedman et al. 1993; Boyd et al. 1995; Haeussler et al. 2002). While greater effects were observed with higher rates or repeated applications (Wilkins et al. 1993; Pitt et al. 2004), there is an emerging consensus that operational forestry herbicide use produces only small, temporary changes in plant communities.

Regeneration harvests remove merchantable tree boles but may remove branches, needles, and nonmerchantable wood, too. Organic matter influences nutrient cycling (Smethurst and Nambiar 1990), soil moisture, and temperature (Roberts et al. 2005) and provides a protective barrier against soil disturbance. Repeated harvests, combined with the trend of some ownerships toward higher wood utilization, reduce organic matter, possibly affecting recruitment and survival of understory species. Also, site preparation scenarios, such as whole-tree or biomass harvesting, remove additional organic matter from the site. Thus, it is worthwhile to examine treatments that differ in organic matter removal.

The Fall River Long-Term Site Productivity Study (Terry et al. 2001) offered a unique opportunity to study the effects of common management techniques, applied at controlled but uncommon intensities and frequencies. A coniferous forest dominated by *Pseudotsuga menziesii* (Mirb.) Franco (Douglas-fir) was clearcut, replanted with Douglas-fir, and then grown naturally or subjected to five annual herbicide applications to eliminate competition with planted seedlings, with or without removal of most organic matter. We contrasted succession at the limits of floral survival with a more natural stand succession and revealed competitive and survival strategies, which we interpret in the context of successional theory.

We examine the utility of the Intermediate Disturbance Hypothesis, which assumes a competitive hierarchy among species resulting in dominance by a subset of species in the absence of disturbance (Sarr et al. 2005), for predicting early postclearcutting successional events with and without further disturbance on a highly productive site. We expected the herbicide treatments to eliminate forest residuals and maintain habitat for annual ruderals-the only plants capable of completing their life cycles between applications. Thus, we wanted to know how floral membership changed among ruderals (theoretically poor competitors) and native forest species (theoretically good understory competitors) across treatments, using measures of diversity, dominance, and composition. Since our study did not include a treatment with organic matter removal without herbicide application, it is not possible to separate the effects of the harvest from the interaction of the harvest plus organic matter removal and herbicide application. But extensive organic matter removal could damage roots and tops of forest residuals resulting in greater loss or slower recoveries for these species compared with treatments without organic matter removal. This might favor ruderals capable of rapidly occupying open sites (Haeussler et al. 1999), but reduced nitrogen from the organic matter loss might hinder the invasion of this group purported to invade more aggressively with abundant nitrogen (Burke and Grime 1996). Thus, we asked if the nature of the disturbance mattered (annual herbicide application with or without organic matter removal). We also asked if there is a logical progression of species loss, and if so, what would this tell us about competitive strategies? Also, what is the combined effect of the seral vegetation on the rate at which Douglas-fir (presumed best precrown closure competitor) reclaims dominance, and as dominance is reclaimed what is the effect on the seral community membership across treatments?

## Methods

### Study site

The study site is located 33 km west-northwest of Chehalis, Washington, USA (46°43'N, 123°25'W), on a gentle (<15%), west-facing slope at 335 m elevation with very uniform soil, topography, and plant vegetation potential. The soil is a very deep, well-drained, silty clay loam to silty clay, derived from volcanic ash and deeply weathered basalt in the Boistfort Series (USDA Natural Resources Conservation Service Soil Survey Staff 2006), Orthic Sombric Brunisol (Soil Classification Working Group 1998). The climate is maritime with 2260 mm of precipitation per year, and more than 80% falls between 1 October and 30 April mostly as rain (USDA Natural Resources Conservation Service, National Water and Climate Center; and Oregon State University Spatial Climate Analysis Service 2005).

The potential natural vegetation of the site is the *Tsuga heterophylla* - *Polystichum munitum* - *Oxalis oregana* plant association (Henderson et al. 1989). A pretreatment vegetation survey recorded 16 understory species, from 481m² plots, each randomly placed within each treatment plot (12 per block; see below). A bootstrap estimate of species richness from these data indicates that about 21 understory species were likely present within the stand (Beach 2000). The three species with the highest percent covers were *Oxalis oregana* Nutt. (redwood-sorrel) (36%), *Polystichum munitum* (Kaulf.) C. Presl (6%) (western swordfern), and *Dryopteris expansa* (C. Presl) Fraser-Jenkins & Jermy (1%) (spreading woodfern). All 16 species were native perennials and only one could be considered ruderal (*Rubus ursinus* Cham. & Schltdl. (California blackberry)). There were 15 understory species recorded on a 177 m² plot (7.5 m radius) immediately south of the study site. The most common species were redwood-sorrel (85%), *Polystichum munitum* (25%), *Viola sempervirens* Greene (1%) (evergreen violet). All 15 were native perennials and only two could be considered ruderals (*Hieracium albiflorum* Hook. (white hawkweed) and *Pteridium aquilinum* (L.) Kuhn (western brackenfern)). Combining species lists from these two sources yields a list of 20 native perennial species, three of which could be considered native perennial ruderals.

The preharvest stand was planted with Douglas-fir seedlings in the winter of 1953-1954 and a substantial component of *Tsuga heterophylla* (Raf.) Sarge (western hemlock) seeded in naturally. This stand was clearcut in 1999; trees were directionally felled to retain tops within the treatment boundary. Merchantable wood was removed by cable yarding to minimize soil disturbance. The site was planted in spring 2000 with 2-year-old Douglas-fir seedlings. Large western hemlock seedlings were manually removed from the entire study area to maintain Douglas-fir dominance in the tree layer. The study site was fenced through January 2005 to protect the trees from deer and elk browse.

### Study design and treatments

The Fall River study uses a randomized complete-block design with 12 treatments and four blocks (Ares et al. 2007). Each treatment plot was 30 m by 85 m. Blocks 1 and 2, with 58%-69% preharvest Douglas-fir by volume, respectively, were higher on the slope than blocks 3 and 4, which had 43%–49% Douglas-fir, respectively. Our study uses a subset of the larger study's treatments. For the three treatments we report, there were two treatment units per block. The three treatments were as follows:

- Removal of only tree boles to a 10 cm top and no vegetation control (BO/-VC).
- Removal of only tree boles to a 10 cm top and five annual herbicide applications for vegetation control (BO/+VC).
- Removal of the total tree (boles, branches, and foliage), plus removal of other woody material >0.6 cm diameter using a shovel harvester operating from outside the plot to prevent soil compaction. Organic matter removal was followed with five annual herbicide applications for vegetation control (TTP/+ VC).

We analyzed herbicide application versus no herbicide application and bole wood-only wood removal versus total tree plus legacy wood organic matter removal. We were not able to assess a treatment with total tree plus organic matter removal but without herbicide application. We could not statistically separate the effects of the total tree plus organic matter removal from the herbicide effect because of the limitations of the larger study's design.

Vegetation control was achieved by one preplanting herbicide application and five annual applications of preemergent herbicides in the spring and spot applications of postemergent herbicides as needed. Herbicide applications differed by year to prevent development of resistance to a single herbicide. Herbicide treatments were as follows:

- Oust® (sulfometuron methyl at 0.2 $kg \cdot ha^{-1}$) and Accord Concentrate® (glyphosate at 4.67 $L \cdot ha^{-1}$) were manually applied in two passes 2 weeks prior to planting in spring 2000.
- Atrazine® (atrazine at 9.3 $L \cdot ha^{-1}$) was uniformly applied in March 2001, followed by spot applications of Accord Concentrate® (0.75% in water).
- Atrazine® (9.3 $L \cdot ha^{-1}$) and Oust® (0.17 $kg \cdot ha^{-1}$) were uniformly applied in March 2002, followed by spot applications of Transline® (1% clopyralid in water) in April and May and Accord Concentrate® (0.75% in water) in June.
- A directed-band of Velpar® (hexazinone at 7.0 $L \cdot ha^{-1}$) was applied between rows in March 2003, followed by spot applications of Transline® (1% in water) to shrubs in April and May and Accord Concentrate® (0.75% in water) in June.
- Velpar® (5.85 $L \cdot ha^{-1}$) was applied in a directed band between rows in April 2004.

Oust targets forbs and some grasses, Transline principally targets forbs, Atrazine targets grasses, Accord Concentrate and Velpar are broad spectrum herbicides.

### Field procedures

Circular, 176.6 $m^2$ (7.5 m radius) vegetation sample plots were located 20 m from the west edge of each of the 24 sampled treatment units (Fig. 1). Vegetation measurements were made in July of 2000 to 2005 (referred to as years 1 through 6). Canopy cover by species was assessed each year except in 2003. Plant taxonomy is consistent with the USDA Natural Resources Conservation Service (2005). Vegetation assessment generally followed protocols for reconnaissance plots of the US Forest Service Region 6, Area 1, Ecology Program (Henderson et al. 1989). Cover was ocularly estimated for all vascular species (at 0.1% intervals below 1%, at 1% intervals from 1%-10%, and at 5% intervals above 10%).

Douglas-fir were planted on a 2.5 m grid (32 per plot). The 10 sample trees selected for measurement included the four trees nearest to the sample plot center, the two trees approximately 2.5 m from the east and west sample plot boundaries, and the four trees approximately 2.5 m from the north and south sample plot boundaries. Tree crown diameter was measured and used to calculate each sample tree's cover. Tree covers were summed for a plot canopy cover.

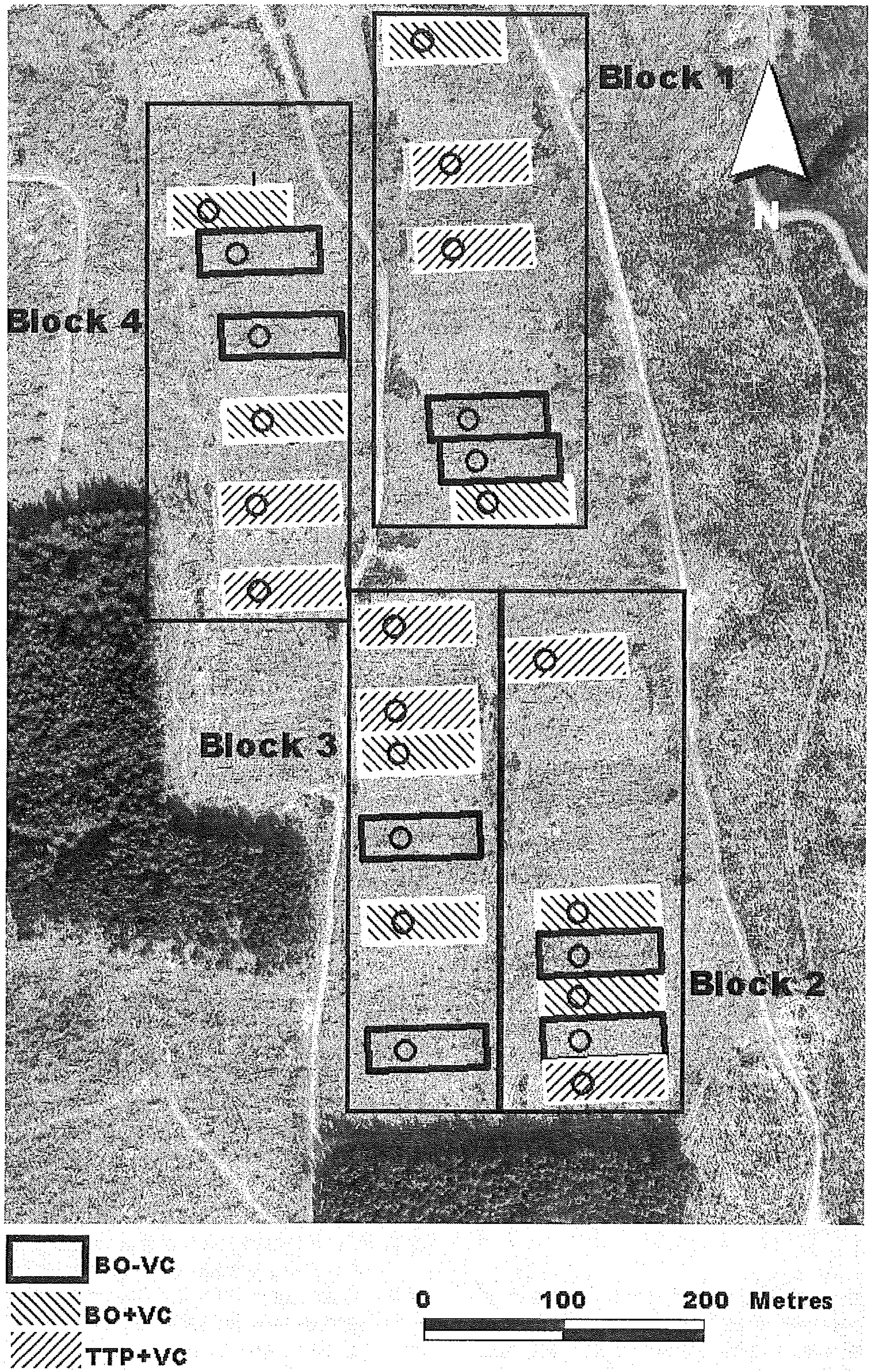
### Statistical analysis

Most statistical manipulations were carried out with SAS version 9.1 (SAS Institute Inc. 2003) software. Statistical significance was declared at $P = 0.05$. Species in the sample plots were divided into three species analysis groups: exotic ruderal, native ruderal, and native forest species. Ruderal species are species that respond favorably to disturbance, such as overstory removal, and are usually shade intolerant. Forest species are defined as shade-tolerant species typically associated with interior forest settings. Three species, California blackberry, white-flowered hawkweed, and brackenfern, are sometimes considered to be tolerant forest species; however, they are vegetatively more aggressive in open environments, rarely flower in shaded environments, and are minor species in surrounding forest stands, so here are classified as native ruderals.

### Repeated-measures ANOVA

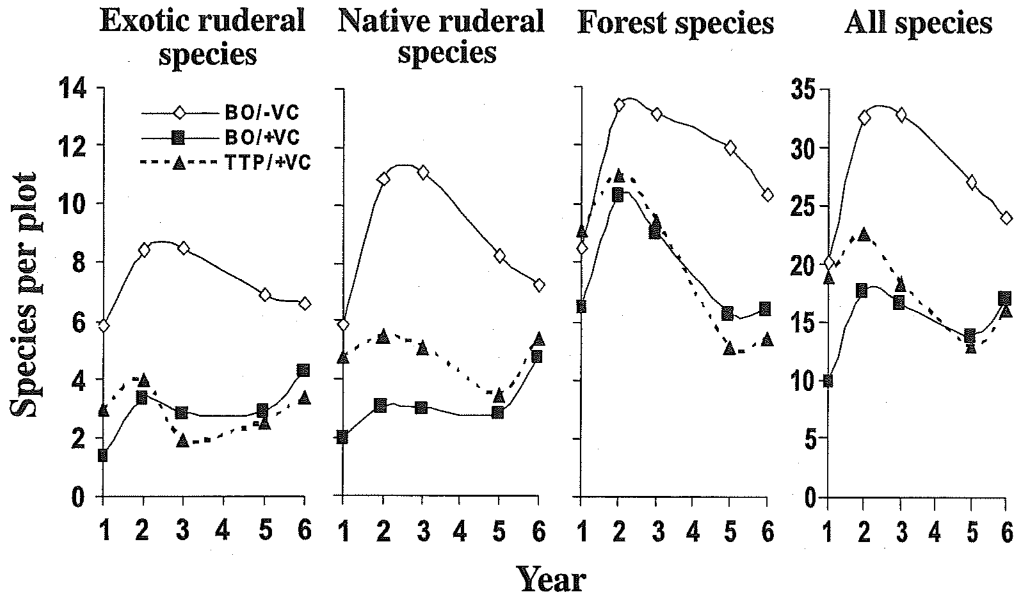
We used repeated-measures ANOVA, with year as the repeated variable (5 years), and block as a random variable (4 blocks) to compare the three treatments (two subsamples in each block = eight total). We evaluated species richness (three analysis groups and all combined) and summed species cover (each analysis group and Douglas-fir separately) per plot over years. This analysis compared numbers of species (or covers) per plot among years within treatment and number of species (or covers) per plot among treatments within year for each species analysis group. Sources of variation included block, treatment, and the block x treatment interaction. Tukey's Honestly Significant Difference (HSD) comparisons were made when significant differences were found between years for each treatment (within each species analysis group) and between treatments for each year (within each species analysis group).

**Fig. 1.** The arrangement of blocks, plots, and sample plots at Fall River. Large rectangles are blocks, and small rectangles represent the treatment units (plots) used in this study. Circles represent the vegetation sample plots.




We used a separate two-factor ANOVA to evaluate covers per sample plot among species analysis groups, within year and treatment. The independent variables were species analysis group (four groups including Douglas-fir cover) and block (four blocks). Since block effects were not significant, block was dropped from the design and single factor ANOVA with species analysis group as the independent variable was used for the summary analyses. Significant differences were located with Tukey's HSD tests.

Fig. 2. Annual change in the mean number of species per plot ($n$ = 8) in each treatment and plant analysis group.




### Diversity

In addition to species richness, we used PC-ORD (McCune and Mefford 1999) to calculate Shannon's ($H' = -\sum_i^s p_i \log p_i$) and Simpson's ($D = 1 - \sum_i^s p_i^2$) diversity indexes for each plot in each year based on species coverage values by plot (where $Pi$ is percent canopy coverage). Simpson's diversity index is less sensitive than Shannon's index to the presence of rare species (Peet 1974). We then used repeated-measures ANOV A to compare diversity in treatments overall and by year, and used Tukey's HSD for mean separations between treatments by year.

### Survival of initial species

To compare the overall effect of the treatments on the initial postharvest plant community composition, we calculated the mean number of species per plot present in year 1 or 2 that survived to year 6. We used Kruskal-Wallis ANOV A to compare the distributions of numbers of surviving species between treatments within analysis groups and Dunn's tests to locate differences between treatments when significance was found. We also tallied the total number of species initially present in each treatment that survived to year 6.

## Results

Plant cover developed rapidly on this productive site, with the total coverage of species other than Douglas-fir averaging more than 80% by year 2 in the treatment without vegetation control. By year 5, the only understory canopy openings were associated with large logs and stumps. The early seral plant community was primarily herbaceous in terms of diversity and cover. Variation from plot to plot within a treatment in vegetation development and tree growth was generally low. Since herbicides were carefully applied under "no drift" conditions, there were no apparent edge effects due to adjacent treatments.

### Repeated-measures ANOVA-species diversity

The BO/-VC plots had the highest species richness in all years and groups (Fig. 2). Species richness for all three species groups in the BO/- VC plots peaked in years 2 or 3 when richness was significantly higher than in other years. The same pattern occurred for forest species in the two vegetation control treatments. However, one year after herbicide treatments ended (year 6), ruderal species richness in both vegetation control treatments was as high or higher than in other years. Forest species richness in all treatments was significantly lower in years 5 and 6 compared with years 2 and 3 and in some cases lower than in year 1 as well.

The TTP/+ VC plots began with significantly higher ruderal species richness than the BO/+VC plots, but richness in the two treatments converged to similar levels by year 5, resulting in a significant treatment x year interaction. The divergence of forest species richness between the BO/-VC treatment and the herbicide treatments also caused a significant treatment x year interaction, but forest species richness did not differ between the two herbicide treatments in any year. A slight tendency towards higher diversity of native ruderals in the blocks higher on the slope resulted in a significant block effect for this group.

### Repeated-measures ANOVA—canopy. coverage

In nearly every year, canopy coverage in the plots with BO/-VC treatment was significantly higher for ruderals and forest species than in the two treatments with vegetation control (Fig. 3). Canopy coverage in the BO/-VC treatment increased significantly from year 1 to years 5 and 6 for the ruderal groups and Douglas-fir, but forest residual coverage changed little. The BO/-VC ruderal covers strongly diverged over time from the other two treatments, resulting in significant treatment x year interactions. In year 6, covers were 96% for total understory and 61% for trees. After year 2, Douglas-fir coverage was significantly lower in the BO/-VC plots than in the BO/+VC and TTP/+VC plots.

Fig. 3. Annual change in the mean summed covers for each plant analysis group ($n$ = 8).

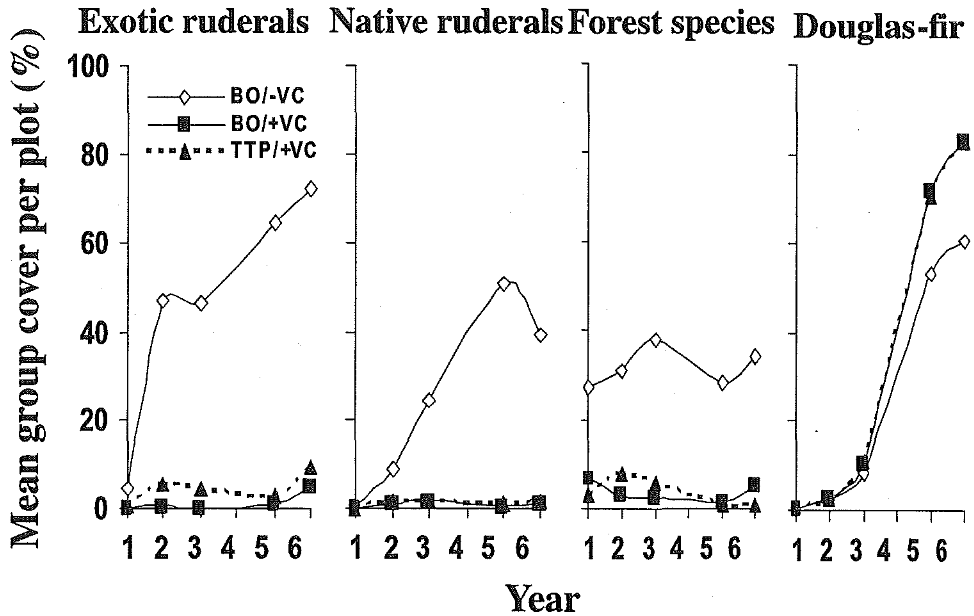
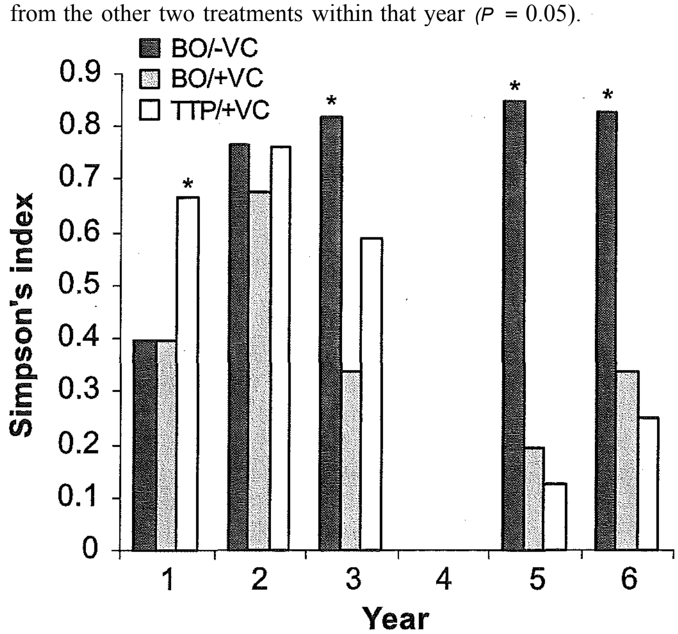



Fig. 4. Simpson's Diversity Index by year and treatment. An asterisk (*) over a bar indicates the treatment is significantly different from the other two treatments within that year ($P$ = 0.05).




With the BO/+ VC treatment, both ruderal groups had about 1% or lower cover through year 5. Exotic, but not native ruderals, increased significantly in year 6, one year after herbicide treatments ended (Fig. 3). In year 6, covers were 9% for the understory and 83% for trees.

With the TTP/+ VC treatment, the ruderal groups had less than 6% cover through year 5. Ruderal and forest residual canopy coverage tended to be higher with the TTP/+VC treatment than with the BO/+VC treatment at least through the period of herbicide application. However, in year 6, forest residual coverage ended significantly higher in the BO/+VC plots. In year 6, one year after the last herbicide treatment, covers were 11% for the understory and 83% for trees.

## Diversity indexes

Shannon's and Simpson's diversity indexes produced similar results (with or without Douglas-fir). Overall, Shannon's and Simpson's Indexes indicated significantly more diversity with the BO/-VC treatment than with the other two treatments. There were also significant differences in most years between treatments. Because of the high degree of similarity between these analyses, we graphically present only the Simpson's Index (with Douglas-fir) in Fig. 4, but in each case, the index for the TTP/+ VC treatment was significantly higher than that for the other two treatments in year 1, and the BO/-VC treatment was more diverse than the other two treatments in years 5 and 6.

## Dominance

Forest species had significantly higher coverage in all three treatments in year 1 than ruderals, although the first herbicide application apparently reduced their cover by a factor of 4 to 9 (Fig. 3). Thereafter, ruderals dominated the understory in the BO/-VC plots, with exotics tending to have higher coverage. Native forest species cover in the BO/+VC plots was significantly higher in years 1 and 2 than ruderal cover, and remained as high or higher through year 6. However, no understory species group expressed clear dominance after year 2 in either of the two treatments with vegetation control. Douglas-fir cover significantly surpassed the cover of the other groups in year 3 with the herbicide treatments and year 5 with the BO/-VC treatment, and thereafter continued to increase at a faster rate than any other group.

## Survival of initial species

Overall, survival through year 6 of species present in the first or second year was significantly lower with both vegetation control treatments than with the BO/- VC treatment

Table 1. Mean number of species per sample plot and the percentage of species per plot surviving to year 6 by analysis group and treatment.

| | Exotic ruderal | | Native ruderal | | Native forest | | All species | |
|---|---|---|---|---|---|---|---|---|
| Treatment | Mean | % | Mean | % | Mean | % | Mean | % |
| BO/–VC | 4.4a | 78 | 3.9a | 92 | 6.8a | 86 | 15.1a | 86 |
| BO/+VC | 0.4b | 33 | 1.5b | 57 | 4.0a | 81 | 5.9b | 66 |
| TTP/+VC | 1.5ab | 33 | 2.8ab | 31 | 3.6a | 59 | 7.9b | 44 |

Note: Letters in mean column indicate statistically different treatments within each vegetative group based on post Kruskal-Wallis Dunn's tests $(P = 0.05)$. BO/-VC, Removal of only tree boles to a 10 cm top and no vegetation control; BO/+VC, removal of only tree boles to a 10 cm top and five annual herbicide applications for vegetation control; TTP/+VC, removal of the total tree (boles, branches, and foliage), plus removal of other woody material >0.6 cm diameter using a shovel harvester operating from outside the plot to prevent soil compaction. Organic matter removal was followed with five annual herbicide applications for vegetation control.

(Table 1). In the BO/-VC plots, 86% of the species present in years 1 and 2 were still present in year 6 compared with 66% in the BO/+VC plots and 44% in the TTP/+VC plots. Survival in the BO/-VC plots was highest for native ruderal species and lowest for exotic ruderals. Survival was higher for forest species than ruderals in both herbicide treatments. With the BO/+VC treatment, survival was lowest for exotic ruderals, but both ruderal groups had similarly low survival with the TTP/+VC treatment.

There were 57 species initially present in the plots treated with BO/-Ve, 51 with TTP/+VC, and 44 with BO/+VC (Table 2). Thus, there were 11%-23% fewer species in herbicide-treated plots than in the plots treated with BO/- VC. In the first 6 years, the BO/-VC treatment lost 20 species, but gained seven others after year 2; the BO/+VC lost 18 and gained seven, and the TTP/+VC lost 26 and gained one (Table 2). Only five (of 25) forest species present in years 1 or 2 were lost from the BO/-VC plots, but eight (of 23) were lost from the BO/+VC and nine (of 22) from the TTP/+VC plots.

The forest species lost from plots were minor in terms of dominance in the native understory of this plant association except for western swordfern, which averages 25% cover in mature stands of this plant association (Henderson et al, 1989) (also 6% site estimate and 25% in adjacent forest). In year 1, western swordfern was present in all except one TTP/+VC sample plot. In years 5 and 6, western swordfern was present in all the BO/-VC plots, half of the BO/+VC plots, and none of the TTP/+VC sample plots. Western swordfern cover declined from 0.1% per plot in year 1 to 0% after year 3 in the TTP/+VC plots, but in contrast, it increased from 1.8% in year 1 to 3% by year 6 in the BO/-VC plots. *Athyrium filix-femina* (L.) Roth (common ladyfern), a less common fern, was also lost only from the TTP/+VC plots.

## Discussion

Studies intended to test diversity theory in forestry settings where herbicides have been used have not been carried out, but herbicide impacts on floristics in a variety of forest ecosystems are consistent with the Intermediate Disturbance Hypothesis. For example, Wilkins et al. (1993) found that herbicide effects on species richness and diversity depend on application rate, edaphic factors, adaptive strategies of resident species, and herbicide tolerance, suggesting that disturbance severity and site productivity are important. Our study is unique in that we focussed on the effects of extreme disturbance on understory dynamics while permitting the major overstory species (Douglas-fir) to increase in dominance. We believe our results are interpretable as a special case within the framework of the Intermediate Disturbance Hypothesis. Thus, at higher levels of disturbance (our BO/+VC and TTP/+VC plots), some species were unable to recover and were eliminated, while at lower disturbance frequencies (our BO/-VC plots) competitive exclusion reduced diversity (Huston 1979). Although competitive exclusion is more rapid on highly productive sites (Grime 1973) such as ours, our study examined the earliest part of succession before competitive exclusion was fully expressed.

By reducing competition, the herbicide treatments accelerated Douglas-fir dominance, which will ultimately result in the loss of ruderal habitat. It seems likely that the growing dominance of Douglas-fir was already affecting competitive relationships in the understory towards the end of our study. This might explain some loss of species between years 3 and 5 in all three treatments, but might have been a principal cause in the BO/-VC plots.

Without herbicide treatment, the Fall River community tracked the "normal" postclearcutting successional pathway described elsewhere in the Pacific Northwest (Schoonmaker and McKee 1988; Halpern 1989). Diversity was likely higher after clearcutting because ruderal invasion offset residual species loss (Dyrness 1973). The total of 43 species found a year after harvest in the BO/-VC plots is well above what could be estimated for the forest community from Table 2 or from the preharvest survey. Most forest species survived clearcutting, and although some increased and others decreased, there was little change in group cover over 6 years. Ruderals rapidly invaded in the first 2 years (especially exotics) to become the dominant groups.

Following year 3, overall richness declined, but diversity leveled off in the BO/-VC plots. Diversity indexes such as Simpson's and Shannon's are determined both by richness and the evenness of species distributions (Peet 1974). The species were probably initially distributed in a patchy fashion, reflecting former forest patterns, slash deposition, and logging damage. By year 3, widespread ruderal species were common and some forest residuals recovered sufficiently to be more widely detected; both of these factors would have increased evenness and maintained diversity even while some minor species were lost.

Table 2. Vascular flora present at the Fall River study site by species analysis group and treatment.

| Species | Observations by treatment† | | |
|---|---|---|---|
| | BO/–VC | BO/+VC | TTP/+VC |
| **Forest species** | | | |
| *Acer circinatum** | 1, 6, 6 | 2, 3, 2 | –, –, 0 |
| *Achlys triphylla** | –, –, 0 | 1, 6, 6 | 1, 3, 3 |
| *Angelica genuflexa** | –, –, 0 | 1, 1, 1 | –, –, 0 |
| *Athyrium filix-femina** | 1, 6, 6 | 1, 6, 6 | 1, 3, 3 |
| *Blechnum spicant** | 1, 6, 6 | 3, 6, 2 | 2, 6, 4 |
| *Carex deweyana** | 2, 5, 4 | –, –, 0 | –, –, 0 |
| *Claytonia sibirica** | 1, 6, 6 | 2, 5, 4 | 1, 3, 3 |
| *Dicentra formosa** | 1, 6, 6 | 1, 6, 6 | 1, 6, 6 |
| *Disporum smithii** | 1, 6, 6 | 1, 6, 6 | 1, 6, 6 |
| *Dryopteris expansa** | 1, 6, 6 | 2, 3, 2 | 1, 5, 2 |
| *Festuca occidentalis** | 1, 1, 1 | 5, 5, 1 | –, –, 0 |
| *Festuca subuliflora** | 3, 3, 1 | –, –, 0 | –, –, 0 |
| *Frangula purshiana** | 1, 6, 6 | 2, 6, 5 | 1, 6, 6 |
| *Galium triflorum** | 2, 3, 2 | 1, 1, 1 | 2, 2, 1 |
| *Luzula parviflora** | 1, 6, 6 | 5, 6, 2 | 1, 2, 2 |
| *Mahonia nervosa** | –, –, 0 | 1, 6, 6 | –, –, 0 |
| *Maianthemum dilatatum** | 1, 6, 6 | –, –, 0 | –, –, 0 |
| *Menziesia ferruginea** | 1, 6, 6 | –, –, 0 | –, –, 0 |
| *Oplopanax horridus** | –, –, 0 | 1, 3, 3 | 1, 6, 6 |
| *Oxalis oregana** | 1, 6, 6 | 1, 6, 6 | 1, 6, 6 |
| *Polystichum munitum** | 1, 6, 6 | 1, 6, 6 | 1, 3, 3 |
| *Rosa gymnocarpa** | –, –, 0 | 2, 3, 2 | –, –, 0 |
| *Rubus spectabilis** | 1, 6, 6 | 2, 6, 5 | 2, 6, 5 |
| *Sambucus racemosa** | 1, 6, 6 | 1, 6, 6 | 1, 6, 6 |
| *Trientalis borealis** | 1, 6, 6 | 1, 6, 6 | 2, 6, 5 |
| *Trillium ovatum** | 1, 1, 1 | –, –, 0 | 1, 3, 3 |
| *Tsuga heterophylla** | 2, 6, 5 | 1, 6, 6 | 1, 6, 6 |
| *Vaccinium ovalifolium** | 1, 2, 2 | 2, 2, 1 | 2, 2, 1 |
| *Vaccinium parvifolium** | 1, 6, 6 | 1, 6, 6 | 1, 6, 6 |
| *Vancouveria hexandra** | 1, 6, 6 | 1, 6, 6 | 1, 6, 6 |
| *Viola sempervirens** | 1, 6, 6 | 1, 6, 6 | 1, 6, 6 |
| **Native ruderal species** | | | |
| *Agrostis exarata* | 2, 3, 2 | –, –, 0 | –, –, 0 |
| *Anaphalis margaritacea* | 1, 6, 6 | 1, 6, 6 | 1, 6, 6 |
| *Campanula scouleri* | 2, 2, 1 | 1, 3, 3 | 2, 3, 2 |
| *Carex hendersonia* | 1, 6, 6 | –, –, 0 | 1, 3, 2 |
| *Carex rossii* | 2, 6, 5 | 2, 6, 3 | 1, 5, 5 |
| *Chamerion angustifolium* | 1, 6, 6 | 2, 6, 5 | 1, 6, 6 |
| *Cirsium edule* | 1, 3, 3 | 1, 1, 1 | 1, 1, 1 |
| *Deschampsia elongata* | 2, 2, 1 | –, –, 0 | –, –, 0 |
| *Epilobium ciliatum* | 1, 6, 6 | 2, 5, 2 | 5, 5, 1 |
| *Equisetum arvense* | –, –, 0 | –, –, 0 | 2, 6, 2 |
| *Hieracium albiflorum** | 1, 6, 6 | 6, 6, 1 | 1, 6, 3 |
| *Iris tenax* | 2, 3, 2 | 2, 6, 5 | 1, 5, 5 |
| *Lactuca biennis* | 2, 3, 2 | 1, 2, 2 | 1, 2, 2 |
| *Luzula comosa* | 1, 6, 6 | 6, 6, 1 | 1, 6, 2 |
| *Prunus emarginata* | 2, 6, 5 | –, –, 0 | 1, 5, 4 |
| *Pseudotsuga menziesii** | 1, 6, 6 | 1, 6, 6 | 1, 6, 6 |
| *Pteridium aquilinum** | 1, 6, 6 | 1, 6, 6 | 1, 3, 3 |
| *Ranunculus occidentalis* | 3, 5, 3 | –, –, 0 | –, –, 0 |
| *Rubus leucodermis* | 3, 5, 3 | –, –, 0 | –, –, 0 |
| *Rubus ursinus** | 1, 6, 6 | 1, 6, 6 | 1, 6, 6 |
| *Salix scouleriana* | 1, 6, 6 | –, –, 0 | –, –, 0 |
| *Stachys mexicana* | 1, 6, 6 | –, –, 0 | 2, 2, 1 |
| *Stellaria calycantha* | 2, 6, 3 | –, –, 0 | –, –, 0 |
| **Exotic ruderal species** | | | |
| *Agrostis capillaris* | 1, 6, 6 | 6, 6, 1 | 2, 6, 2 |
| *Agrostis scabra* | 2, 3, 2 | 6, 6, 1 | –, –, 0 |
| *Agrostis* sp. | 1, 2, 2 | –, –, 0 | –, –, 0 |
| *Anthoxanthum odoratum* | 3, 3, 1 | –, –, 0 | –, –, 0 |
| *Cirsium arvense* | 1, 3, 3 | 2, 2, 1 | 2, 3, 2 |
| *Cirsium vulgare* | 1, 6, 6 | 1, 6, 3 | 1, 3, 3 |
| *Crepis capillaris* | 3, 3, 1 | 3, 3, 1 | –, –, 0 |
| *Digitalis purpurea* | 1, 6, 6 | 1, 6, 6 | 1, 6, 3 |
| *Erechtites minima* | 1, 6, 6 | 1, 6, 4 | 1, 2, 2 |
| *Holcus lanatus* | 1, 6, 6 | 3, 6, 3 | 1, 6, 6 |
| *Hypochaeris radicata* | 1, 6, 6 | 1, 6, 6 | 1, 6, 6 |
| *Leucanthemum vulgare* | 3, 6, 4 | 1, 3, 3 | 2, 2, 1 |
| *Ranunculus repens* | 6, 6, 1 | –, –, 0 | –, –, 0 |
| *Rubus laciniatus* | 2, 6, 5 | 2, 5, 4 | 2, 3, 2 |
| *Senecio jacobaea* | 1, 6, 6 | 1, 5, 5 | 1, 3, 2 |
| *Senecio sylvaticus* | 2, 6, 5 | 2, 6, 5 | 2, 6, 3 |
| *Solanum dulcamara* | –, –, 0 | –, –, 0 | 2, 3, 2 |
| *Trifolium repens* | –, –, 0 | –, –, 0 | 2, 2, 1 |
| *Veronica chamaedrys* | 3, 6, 4 | –, –, 0 | –, –, 0 |

*Species present or assumed present in the preharvest stand.
†Data for each species indicate the first year, last year, and number of years a species was observed by treatment. –, Not observed.

Statistical inference from our study is limited because it was done at a single site. However, the Trait Convergence Hypothesis (Grime 2006) (determinants of productivity such as soil and climate control many spatial patterns in vegetation) and the Intermediate Disturbance Hypothesis suggest that it is probably reasonable to assume that similar activities in similar vegetation will produce similar results.

**Forest** species

Logging slash and mechanical damage during harvesting initially reduced detection of some forest species, which subsequently recovered, so year 2 provided a better indication of which forest species survived clearcutting than year 1. Our failure to detect these survivors in year 1 reflects the stochastic nature of logging damage and slash burial on forest vegetation, delaying occupancy of some areas and possibly leaving some plants more vulnerable to subsequent disturbances and competition.

Forest species in the BO/+VC plots had higher covers and species retention than ruderals in all 6 years, while in the TTP/+VC plots, forest species cover declined below that of exotic ruderals only in years 5 and 6. These patterns suggest a general strategy for surviving disturbance. All but four of the surviving forest species produce rhizomes or large root structures. Pacific Northwest native perennials tend to have a larger proportion of underground biomass than shorter lived ruderals (Antos and Halpern 1997; Lezberg et al. 1999), which may limit the ratio of herbicide reception area to total biomass, thus providing an advantage. Lezberg et al. (1999) found that 6 of 11 forest understory species had more than half of their biomass underground. Two forest species at Fall River, *M. dilatatum* and *O. oregana* have the ability to produce long rhizomes permitting them to forage laterally for shifting resource pools under the forest canopy (Lezberg et al. 1999). This may also be important in recovering from disturbance, as the position a plant occupies under a forest canopy may not be a desirable place once the canopy is removed, especially considering the liability of being buried under logging debris. Damaged shrubs such as vine maple (*Acer circinatum* Pursh) and red elderberry (*Sambucus racemosa* L.) grew rapidly, overtopping other plants. Such rapid growth is probably only possible with the help of stored reserves in large residual root systems. Since plants generally have physiological barriers that prevent equal performance in very different environments (Smith and Huston 1989) (e.g., clearcuts and forests), these strategies provide insurance against stochastic damage and temporary changes in environment.

Many forest species regenerated from underground organs for one or more years, but redwood-wood sorrel, *Vancouveria hexandra* (Hook.) C. Morren & Decne. (white insideout flower), and *Viola sempervirens* Greene (evergreen violet) were also able to exploit "spray shadows" next to logs, or under slash or live tree branches because of their short stature and shade tolerance. The ability to spread laterally underground into "spray shadows" may have helped maintain some of these species.

Usually, the more dominant forest species either never disappear or are able to reestablish when conditions are suitable (Halpern and Spies 1995). Some minor forest species were lost even without herbicide treatments, but species richness without herbicide treatment remained higher than with herbicide treatment in all years. The ability of these minor species to return to the system is not understood, although two forest species (*Festuca occidentalis* Hook. (western fescue) and *Luzula parviflora* (Ehrh.) Desv. (small-flowered woodrush) ) reinvaded the BO/+VC plots a year after herbicide treatments ended.

### Ruderals

The herbicide treatments were clearly stressful, as these treatments caused a loss of species richness and precipitously declining cover. Annual herbicide application maintained receptive conditions for ruderal propagules, while largely preventing their establishment. Although ruderals maintained as much or more representation in the understory throughout the period of observation as forest species, they suffered the largest loss of species.

Without herbicide use, ruderal diversity peaked in years 2 or 3 and ruderal cover surpassed forest species cover in year 2. Logging slash probably delayed establishment of ruderals in some areas, but seed for some species probably did not arrive until later. As found by others (West and Chilcote 1968; Halpern et al. 1997), some exotic ruderals, including species of *Senecio* L., and *Erechtites minima* (Poir.) DC. (coastal burnweed), initially increased rapidly but declined in dominance after 2-3 years. Ruderals are generally more competitive on disturbed, nitrogen-rich soils (Burke and Grime 1996). Clearcutting temporarily increases soil nitrogen from slash and forest floor decomposition (Redding et al. 2004; Strahm et al. 2005). While this may have benefited some ruderals, the soil nitrogen pool was already large (13 140 kg·ha$^{-1}$ in the 0-80 cm mineral soil (Ares et al. 2007)), so other factors (e.g., mineral soil exposure, soil temperature, competitive relationships) were probably more important determinants, especially since there was more exotic ruderal cover in the TTP/+VC than in the BO/+VC plots. Generally high soil nitrogen likely accelerated succession, shortening the "window" for ruderal occupancy.

Antos and Halpern (1997) found that root-to-shoot ratios of invading annuals were much lower than that of ruderal perennials like *Chamerion angustifolium* (L.) Holub (fireweed), which suggests a fundamental difference in the invasion strategy of these two ruderal groups. Many Fall River native ruderals were perennials that increase in dominance from buds on roots and rhizomes; this strategy allows them to increase in dominance over time from a slower start.

Although native ruderals were slower to establish than exotics, ruderal group covers converged by year 5, suggesting that in time, native ruderals might dominate annual and biennial exotics, but fence removal in year 6 resulted in ungulate browse on fireweed and a drop in ruderal cover. Assuming that exotic ruderals have partially displaced native ruderals, the rapid closing of the ruderal establishment window by increasing Douglas-fir cover suggests that the rapid response of exotics is a more effective ruderal strategy on highly productive sites. Slower to establish and mature native ruderals reproductive time is "squeezed" between rapidly establishing exotics and rapidly growing Douglas-fir. Cultural treatments that shorten the window of occupancy may favor exotic ruderals.

### Organic matter removal

Our study design did not permit us to separate the effects of the harvest alone from the interaction of the harvest plus organic matter removal combined with herbicide application. But, the effect of organic matter removal appears to be small compared with the herbicide effect. This might be expected, since other studies indicate organic matter removal has only small effects on soil carbon and nitrogen (Powers et al. 2004; Sanchez et al. 2006), microbial communities (Busse et al. 2006), tree seedling survival (Fleming et al. 2006), or species richness (Alban et al. 1994; Haeussler et al. 1999). Nitrogen loss was probably not a factor at Fall River because of the large mineral soil nitrogen pool (Ares et al. 2007).

We expected the combined effect of organic matter removal and herbicide application, representing two almost simultaneous disturbances, to produce a greater effect than just the herbicide application. More species were lost with the TTP/+VC treatment than with the BO/+VC treatment, but the difference was not significant. But, only with this combination of treatments was a major species lost (western swordfern). Ladyfern was also lost only from this treatment. Possible reasons why these two ferns were eliminated include the following. (l) Both have short, erect rhizomes that may be vulnerable to mechanical damage from moving logs. (2) Without logging slash, they may have been more visible to herbicide applicators in the TTP/+VC plots. (3) Warmer, drier surface soils in the TTP/+ VC plots (Roberts et al. 2005) may have added stress. But, since diversity and canopy cover by species group were not significantly different between these treatments, herbicide treatment and not organic matter removal appears to be the primary factor in the loss of diversity. Western swordfern was reduced with the BO/+VC treatment, but increased with the BO/-VC treatment, also suggesting an herbicide effect. Thus, organic matter removal effects were largely overshadowed by the rigorous herbicide regime.

## Conclusions

The Intermediate Disturbance Hypothesis suggests that disturbance beyond an intermediate level reduces diversity. The largest annual loss of richness probably occurred in the first year after clearcutting. Although supported by significant differences in richness between the BO/-VC and BO/+VC treatments, this interpretation requires caution, since we have little pretreatment data. However, a loss of diversity is expected on a theoretical basis, since this herbicide treatment, unlike the others, closely followed clearcutting, thus, two disturbances (three in the case of organic matter removal) were closely spaced, exceeding what could be termed an "intermediate" level of disturbance.

Our expectation that forest residuals would be eliminated by our rigorous herbicide regime proved wrong. In fact, a higher percentage of forest residual species than ruderal species survived the herbicide treatments; we attribute this response to the larger ratio of underground to aboveground tissues in forest species. While ruderals are better adapted to rapidly exploit punctuated, severe disturbances, the ability of forest species to survive these disturbances also conferred an ability to tolerate multiple herbicide exposures.

Douglas-fir clearly benefited from vegetation control, surpassing the cover of the other groups at least 3 years sooner with vegetation control than without. A loss of richness after year 3 with the BO/-VC treatment (and other treatments) may be due to mounting competitive exclusion by Douglas-fir, but this cannot be confirmed without a control that does not have Douglas-fir present. A warming climate in the last few years may also be a contributing factor.

Our study is consistent with the disturbance model of Haeussler et al. (2002), which suggests that as disturbance intensity increases, the residual plant community is progressively replaced by species that regenerate from the budbank, seedbank, and newly dispersed exogenous seed. Clearcutting initiated a succession from all three of these regeneration sources, but herbicide treatments gradually caused a larger proportion of regeneration to come from seed sources and less from the budbank. Continued herbicide treatments would probably eliminate both bud and seed banks, leaving only exogenous seed for regeneration.

The effect of organic matter removal was much smaller than the effect of annual herbicide treatments and difficult to detect. However, there were differences in survival of large fern species, which suggests cumulative effects occurred.

It is difficult to compare our multiple treatments with single operational treatments; however, it appeared that the first herbicide treatment had a large impact on species cover and survival, while subsequent treatments maintained low covers and further decreased survival. Since the forest species lost were largely minor subordinate species, it seems unlikely future community function will be measurably affected (Grime 1998). It is not clear to what extent future community succession has been altered; however, it appears that most species characteristic of the previous mature forest will be present as crown closure occurs on all three treatments.

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