

The Soil Seed Bank of an Oregon Montane Meadow:
Consequences of Conifer Encroachment and Implications for Restoration

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Abstract

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Nicole L. Lang

Chair of the Supervisory Committee:
Research Professor Charles B. Halpern
College of Forest Resources

In this study, I examine the soil seed bank of an Oregon montane meadow that has experienced encroachment of *Pinus contorta* and *Abies grandis* for more than a century. I use a chronosequence approach to investigate whether the composition and abundance of seeds in the soil change as meadows are gradually replaced by forest, and by implication, whether the seed bank can serve as a source of propagules for restoration once trees are removed or sites are burned. Litter and soil samples (10 cm depth) were collected from 209 locations representing the transition from open meadow to old (>130 yr) forest. Light availability, forest structure, and understory species composition were also measured at each location. Density and composition of viable seeds were estimated using the greenhouse emergence method. Density of germinants averaged 2,332 m⁻². Forty-four species were identified, including 29 forbs, 10 graminoids, 3 shrubs, and 2 trees. Ruderal species dominated the seed bank (15 species, 71% of germinants); meadow species were less abundant (12 species,

21% of germinants) and forest species were uncommon (12 species, 3% of germinants). Exotics (7 species) comprised 7% of all germinants. Species richness of the seed bank was greatest in old forest, but total density of germinants and density of meadow species did not vary during the transition from open meadow to old forest. Seed bank composition differed significantly from the above-ground vegetation. Only 32% of species found in meadow locations were present in the seed bank, and only the dominant sedge, *Carex pensylvanica*, was frequent in the germinant pool (51% of samples). Our results suggest that there is limited potential for the seed bank to contribute to restoration of meadow communities following tree removal or prescribed fire. Natural reestablishment of many species will require dispersal from adjacent openings or gradual vegetative spread; however, competitive interactions with forest understory plants and dominance of the seed bank by ruderal species may pose problems for successful recruitment.

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DEDICATION

To those who inspired and encouraged me in science: David Clements, Eric Menges, Carl Weekley, Pedro Quintana-Ascensio, Rick Anderson, David Pilliod, Carol Miller, and Charlie Halpern.

And to my parents, who inspired and encouraged me in life.

Introduction

Soil seed banks contribute to the diversity and dynamics of most plant communities. In some systems they are critical for maintenance of species' populations (e.g., Kemp 1989; Harrod & Halpern 2005), or for restoration of native plant communities (Graham & Hutchings 1988; van der Valk & Pederson 1989). Similar to the above-ground community of plants, seed banks are dynamic in their composition and abundance and are responsive to factors that influence seed inputs and losses. Moreover, because seed longevity varies greatly among taxa, the composition and diversity of the seed bank can differ substantially from that of the local vegetation (see reviews in Leck et al. 1989).

Where human activities have resulted in loss or degradation of natural or semi-natural communities, the seed bank can contribute to restoration, but using the seed bank can be challenging. For example, in the agricultural landscapes of Europe, considerable attention has been devoted to the role of the seed bank in restoring species-rich grasslands degraded by intensive cultivation or other human activities (e.g., Bekker et al. 1997; Bakker & Berendse 1999; Bossuyt & Hermy 2001; Jongepierova et al. 2004; Walker et al. 2004). Under conditions in which seed banks are highly impoverished, attempts at restoration have included removal of sod or topsoil to reduce nutrient inputs and to expose seeds of target species buried at depth (Blomqvist et al. 2003; Walker et al. 2004).

Afforestation or natural succession to scrub or woodland also threatens the integrity of many natural or semi-natural grassland or prairie ecosystems worldwide (e.g., Knight et al. 1994; Bakker et al. 1996; Davies & Waite 1998; Van Auken 2000; Lett & Knapp 2005). In these situations, the potential for restoration via the seed bank is typically low (e.g., Bekker et al. 1997; Laughlin 2003; Bisteau & Mahy 2005). Species characteristic of grasslands primarily reproduce by vegetative means; although sexual reproduction can contribute to species' persistence, seed longevity in the soil is typically short (Milberg & Hansson 1993; Bisteau & Mahy 2005; but see Rice 1989; Bakker & Berendse 1999; Thompson 2000). Some grassland taxa do retain viable seed banks for decades under woody plant cover (Donelan & Thompson 1980; Bakker et al. 1996; Davies & Waite 1998; Kalamees & Zobel 1998), but seeds of most species are quickly depleted once reproductive plants are lost.

Ruderal or weedy species dominate the persistent seed banks of many ecosystems (Archibold 1989; Baker 1989; Halpern et al. 1999; Willson & Traveset 2000, Korb et al. 2005). They persist as legacies of earlier successional stages (e.g., agricultural fields or clearcut forests), or accumulate over time via dispersal, thus proximity to source populations can determine their abundance in the seed bank. Because germination is cued to disturbance and growth is typically rapid, they have the potential to compete with target species in restoration efforts (Baskin & Baskin 1998; Matus et al. 2003; Bisteau & Mahy 2005).

Loss of mountain meadows to conifer encroachment is a widespread and fairly recent (20th century) phenomenon in western North America. The timing and causes of encroachment vary among ecosystems and locations, but generally reflect three types of causes: changes in climate (temperature and rainfall), elimination of sheep grazing, and/or long-term suppression of wildfire (Vale 1981; Arno & Gruell 1986; Magee & Antos 1992; Rochefort & Peterson 1996; Miller & Halpern 1998; Lepofsky et al. 2003). In the Pacific Northwest (USA), loss of montane meadows to encroachment has important implications for local and regional patterns of diversity, because these relatively small and isolated habitats support floras and faunas distinctly different from those of the surrounding forest matrix (Hickman 1976; Halpern et al. 1984; Franklin & Halpern 1999; Miller et al. 2003). Land managers have begun to experiment with tree removal and prescribed fire to slow habitat loss and restore community structure and diversity. However, the potential for restoration remains uncertain where trees have been present long enough to cause local extinction of meadow species and replacement by forest herbs.

In this study, I use a chronosequence approach to examine changes in the composition of the soil seed bank, and by implication, its potential for use in restoration following encroachment of *Pinus contorta* and *Abies grandis* over nearly two centuries into a dry montane meadow in western Oregon. Forest development has been accompanied by major declines in cover and diversity of

meadow species and concomitant increases in forest herbs (R. Haugo, unpublished data), suggesting limited potential for vegetative reproduction to contribute to restoration. My objectives are three-fold: (1) to identify the contributions of meadow, forest, and ruderal species to the seed bank in these montane ecosystems; (2) to describe changes in species composition and in the abundance and richness of these functional groups during the transition from meadow to old forest; and (3) to test whether local patterns of composition, density, or richness of the seed bank can be explained by variation in forest structure or in the composition of above-ground vegetation.

Study Area

The study area, Bunchgrass Ridge (hereafter, Bunchgrass), lies on a broad, gently sloping plateau at an elevation of ca. 1350 m in the Willamette National Forest, Oregon (lat. 44°17'N, long. 121°57'W). It occupies a transitional position between the geologically older and deeply dissected slopes of the western Cascade Range and the younger gentler slopes that comprise the High Cascade Province (Franklin & Dyrness 1988). Bunchgrass supports a mosaic of dry, montane meadow and coniferous forest. Meadows are dominated by graminoids (primarily *Festuca idahoensis* and *Carex pensylvanica*) and forbs (*Achillea millefolium*, *Fragaria* spp., and *Lupinus latifolius*) and are structurally and floristically similar to *Festuca*-dominated communities throughout the western Cascade Range (Halpern et al. 1984; Franklin & Halpern 1999). *Abies grandis* is the principal tree species, although *Pinus contorta* is locally abundant and typically the first to establish in open meadow. Understory composition varies with stand age and structure (R. Haugo, unpublished data) and is comprised of species characteristic of rich, mesic forests at this elevation (Hemstrom et al. 1987). Common herbs include *Smilacina stellata*, *Galium oregonum*, and *Anemone oregana*. The surrounding landscape is comprised of mature and old-growth forests of mixed species composition and young stands originating from clearcuts dating from the 1970s and 1980s.

Soils grade from Vitric Melanocryands in open meadow to Aquic Vitricryands in older forests (D. Lammers, unpublished data). Profiles suggest centuries of soil development under grassland, even in locations that currently support old forest. All are deep (>170 cm), fine to very fine sandy loams derived from andesitic basalt and tephra deposits, with a large and highly variable component of glacially derived cobbles, stones, and boulders.

The climate is maritime, with cool, wet winters and warm, dry summers. At the primary meteorological station at the nearby Andrews Experimental Forest (420 m), average air temperatures range from 0.6°C in January to 17.8°C in July. Annual precipitation averages 2300 mm, 70% of which falls between November and March (Bierlmaier & McKee 1989). At Bunchgrass, temperatures are colder and precipitation is higher, with snow accumulations commonly exceeding 2 m and persisting into late spring.

Methods

Site selection and sampling design

Historical aerial photographs were used to select the locations of four 1-ha (100 x 100 m) plots that included open meadow, recent conifer encroachment, and older forest (Fig. 1). Two plots were directly adjacent, otherwise distances among plots ranged up to 300 m. In July 2003, permanent plot corners were established relative to reference trees identified in the aerial photographs. Within each plot, a 10 x 10 m grid was then surveyed to create 100 subplots, the sampling units for this study. Twelve additional subplots were surveyed on the outer margins of two plots to ensure sufficient representation of open meadow.

Forest age, overstory structure, and vegetation composition

All trees ≥ 1.4 m tall within the subplots ($n = 5,486$) were identified to species, spatially mapped to the nearest 0.1 m, and measured for diameter at breast height (dbh). Trees were aged in one of three ways. Larger trees (greater than ca. 10 cm dbh; $n = 1,965$) were cored as close to the ground as possible and coring height was measured. Smaller trees ($n = 3,521$) were felled and a basal section was taken; height of the cut surface was recorded. Cores and basal sections were sanded and annual rings were counted under 10-40x magnification. A series of ring-pattern templates was used to estimate missing rings when pith was not present in core samples. Adjustments for age-to-coring height were

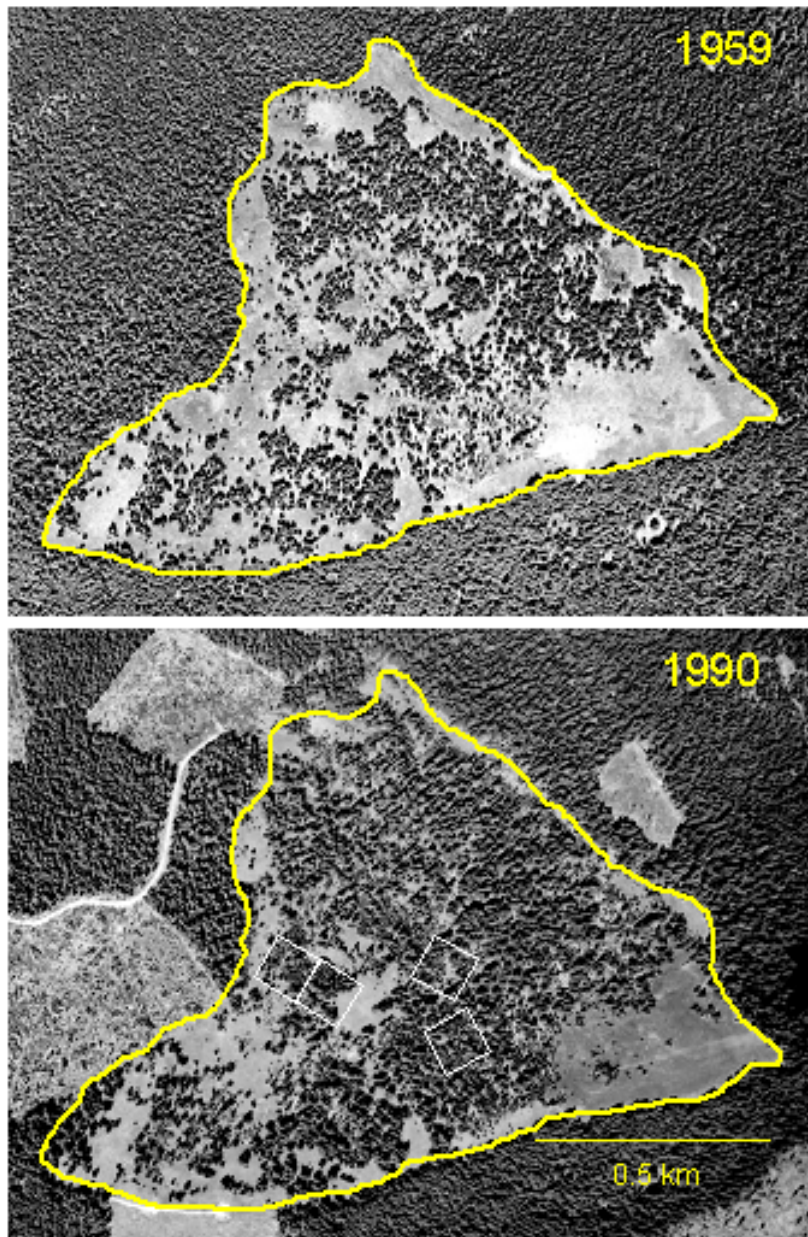


Figure 1. Aerial photographs of Bunchgrass Ridge from 1959 and 1990. The meadow boundary is outlined in yellow and the four 1-ha sample plots in white.

based on regression equations developed from a destructive sample of 30-40 seedlings per species (C. Halpern, unpublished data). Ages of trees with rotten or incomplete cores ($n = 135$) were estimated from diameters based on species-specific regression equations; these were developed from the larger pool of aged cores and basal sections (C. Halpern, unpublished data). Dead stems ≥ 5 cm dbh ($n = 1386$) were also identified to species and measured for diameter.

Total transmitted light, an index of light availability, was estimated at the center of each subplot from hemispherical photographs. Photographs were taken at a height of 1.65 m using a Nikon Coolpix 990 digital camera with FC-E8 fisheye converter. Photos were taken before 08:00 or after 18:00 hr, or under uniformly cloudy conditions to minimize direct exposure to sun. Total transmitted light averaged over the year (expressed as a percentage of full sun) was calculated using the image analysis software, Gap Light Analyzer 2.0 (GLA; Frazer et al. 1999).

Composition of ground vegetation (including trees < 1.4 m tall) was sampled between 5 July and 16 August 2004. Four 1 x 1 m quadrats were placed within the central 6 x 6 m area of each subplot, spaced at 1-m intervals along the NW-SE diagonal. Within each quadrat we visually estimated the cover of each vascular plant species. Several taxa (*Disporum*, *Fragaria*, and *Listera*) were recorded at the generic level because species identification was difficult at the time of sampling. In addition, *Festuca viridula*, present in small amounts, could not be

distinguished from the dominant, *F. idahoensis*, when it was not in flower, and was grouped with the latter. Nomenclature follows Hitchcock & Cronquist (1973).

Soil seed bank samples

Soil seed bank samples were collected between 22 and 25 May 2004, immediately after snowmelt. To sample a broad range of forest ages and structures, 50 subplots per plot were selected as a stratified random sample of tree basal area (see *Statistical analyses*, below). Within each plot, subplots were first assigned to one of five basal-area classes (class ranges varied among plots). From each class, 10 subplots were then chosen randomly. To ensure adequate sampling of open meadow, nine additional subplots were selected randomly from the pool of subplots that contained no trees, yielding a total of 209 subplots. To allow for this level of replication in the greenhouse, samples were not stratified by depth, thus limiting our ability to distinguish between transient and persistent seeds.

From each subplot, three soil samples spaced 2 m apart were collected from areas between the four vegetation quadrats. At each sampling point, the litter layer circumscribed by a bulb planter (6 cm diameter) was measured for depth, removed, and retained. The bulb planter was then used to extract mineral soil to a depth of 10 cm (volume of ca. 283 cm³). The three soil and litter samples from each subplot were combined (total soil volume of ca. 849 cm³ per subplot), placed

in coolers, and transported to refrigerators at the University of Washington (UW), Seattle.

Greenhouse methods

On 30 May 2004, samples were mixed and spread in plastic germination flats (25 x 25 cm) to a depth of 2 cm; twigs, roots, and rhizome fragments were then removed. Flats were arranged randomly on two greenhouse benches (Department of Biology, UW) and sub-irrigated using a capillary-mat system. Natural lighting was supplemented with 1000 watt, metal-halide lamps to provide a 16-hr light, 8-hr dark photoperiod. To reduce possible contamination by wind-dispersed seeds, remay cloth was draped over a PVC frame constructed above each bench. Twelve flats of potting soil were also randomly distributed among the samples as controls. Germination was monitored weekly at first, then bi-weekly. Germinants were marked upon emergence with color-coded wire, identified, and removed. If identification was not possible, seedlings were transplanted to larger pots and grown until leaf morphology or flowers permitted identification. On 29 July 2004 (after 2 mo), soils were turned to expose new surfaces. On 15 September 2004 (3.5 mo), samples were allowed to dry for approximately 1 wk. Samples were then stirred and rewetted. Monitoring was terminated on 3 January 2005 (ca. 7 mo after initiation).

Data manipulation

Subplot classification, overstory structure, and vegetation composition

A composite age structure was developed from the full set of trees sampled in the four 1-ha plots. This revealed two broad, but distinct periods of conifer establishment: ca. 1810 to 1910 and a more recent and intensive period of invasion from ca. 1930 to 1980 (Fig. 2). Based on this bimodal age structure and the density and ages of trees within each subplot, subplots were assigned to one of three stages of conifer encroachment: (1) open meadow (no to few trees), (2) young forest (many trees, ages <75 yr), or (3) old forest (fewer and larger trees, ages >95 yr). Because most of the study area supported recent invasion, sample size for young forest ($n = 160$) was much larger than that for open meadow and old forest ($n = 24$ and 25 , respectively).

Overstory structure was also quantified for each subplot. I computed the density and basal area of all live and dead stems, and of the primary tree species, *Pinus contorta* and *Abies grandis*. For each understory plant species, mean cover per subplot was computed from the four quadrats.

Seed bank density, richness, and functional group composition

For each subplot, I calculated total germinant density and richness. To compare density and richness of species representing different functional types, each taxon was classified, *a priori*, in two ways. First, each species was assigned

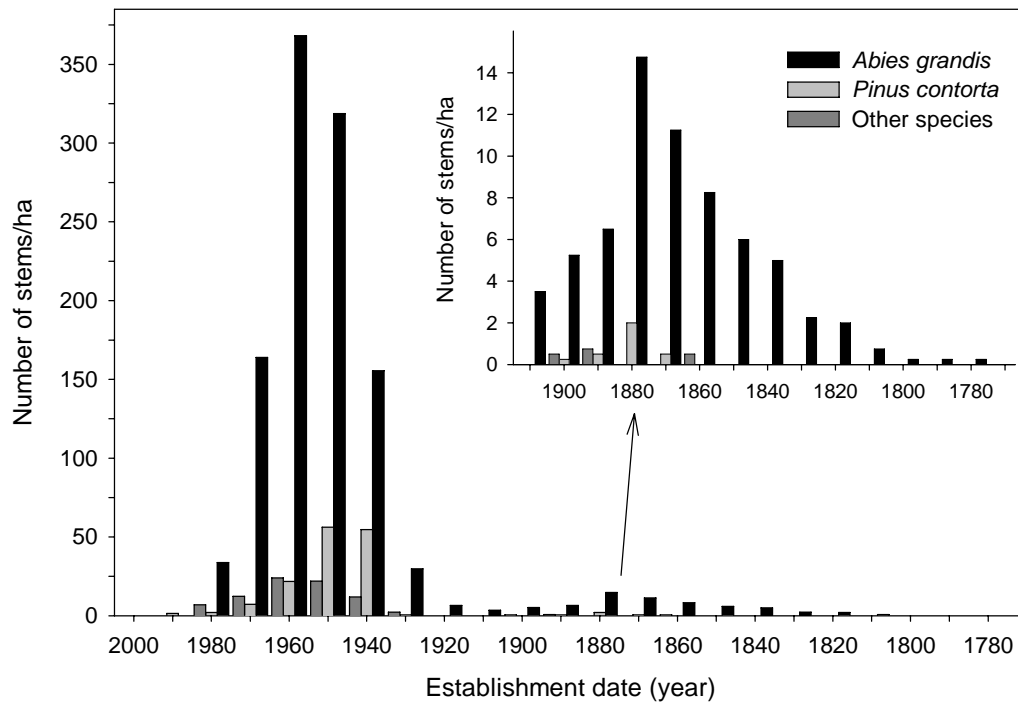


Figure 2. Composite age structure of trees ≥ 1.4 m tall in the four 1-ha plots. Establishment dates represent 20-yr age classes. The age structure for the early period of establishment is rescaled and enlarged for clarity.

to one of three groups reflecting habitat preference: meadow, forest, or ruderal (disturbed sites) (Hitchcock et al. 1969; Halpern et al. 1984; Halpern 1989; Franklin & Halpern 1999). Several taxa could not be classified; these were either habitat generalists or generic-level taxa that could not be assigned unambiguously. Second, each taxon was classified as native or exotic based on geographic origin (Hitchcock et al. 1969, Hitchcock & Cronquist 1973).

The 12 control flats yielded very few germinants: one unknown graminoid, two *Carex* species, and one *Oxalis corniculata* (a common greenhouse weed). A total of 27 germinants of *O. corniculata* also emerged in non-control flats and were removed from subsequent analyses. Given limited presence of contaminants in the controls, no further data adjustments were made.

Statistical analyses

To verify the spatial independence of seed bank samples and permit use of subplots as replicates in statistical analyses, a series of Mantel's tests (Mantel 1967) were run. For each of the four 1-ha plots, a matrix of geographic distances among subplot centers was correlated with a matrix of compositional dissimilarity (Euclidean distance) among subplots. Randomization (Monte Carlo) tests were used to assess the significance of the correlations between matrices (McCune & Grace 2002). All correlation coefficients were very low (r of 0.016 to 0.169) and were non-significant for three plots; thus, subplots were treated as independent samples in subsequent analyses.

Changes in seed bank density, richness, and composition

To test for differences in the density or richness of germinants among open meadow, young forest, and old forest subplots, one of two methods was used. For data that met the assumptions of analysis of variance, one-way ANOVA was run. When a significant main effect was detected ($p \leq 0.05$), means were compared with the GT2-method that accommodates unequal sample sizes (Sokal & Rohlf 1981). Alternatively, when variance among groups was heterogeneous, a non-parametric, Kruskal-Wallis (K-W) test was used (followed by a Mann-Whitney U test for *post-hoc* comparisons). Separate tests were run for (1) density and richness of all taxa combined; (2) density and richness of meadow, forest, and ruderal taxa; and (3) density of native and exotic taxa (the number of exotic taxa was too small to test richness).

Detrended correspondence analysis (DCA; Hill & Gauch 1980) was used to portray gradients in seed bank composition associated with stage of encroachment. Germinant density was used as the measure of abundance. Samples without germinants were removed from the analysis, as were species present in fewer than 5 subplots; this yielded a total of 195 samples and 22 species. Default settings of PC-Ord ver. 4.0 were used (McCune & Mefford 1999).

Multi-response permutation procedure (MRPP; Biondini et al. 1988) was used to test whether species composition of the seed bank differed among

subplots representing open meadow, young forest, and old forest. This nonparametric test compares the average within-treatment similarity among groups to an expected average (i.e. the chance-corrected within-group agreement) for all possible partitions of the data of the same size. Sorensen's coefficient was used as the distance measure. Following a test that compared all stages of encroachment, separate pairwise comparisons were made between stages.

Indicator species analysis (ISPAN; Dufrêne & Legendre 1997) was used to identify species in the seed bank that showed fidelity to a particular stage of encroachment. This method computes a maximum indicator value (IV_{max}) for each species based on its proportional abundance and frequency of occurrence within *a priori* groups (in this case, encroachment stages) and evaluates the statistical significance of IV_{max} through a Monte Carlo simulation that randomly assigns sample units to groups; 1000 randomizations were used in this analysis. Only those species present in five or more subplots were considered.

Relationships with overstory structure

I used simple linear regression to explore relationships of the density and richness of taxa in the seed bank to measures of forest structure. Predictors included total transmitted light, and density and basal area of all live stems, of *Abies grandis*, and of *Pinus contorta*. Response variables included the density and richness of functional types (see above). Transformations of response variables were necessary to meet the assumptions of regression, but even with

transformations, the proportion of variation explained was uniformly poor; thus regression results are not shown. However, visual inspection of simple scatterplots suggested that several attributes of forest structure constrained the *maximum* density of germinants in the seed bank. Although we don't develop maximum-response models to quantify these thresholds or limits (e.g., Guo et al. 1998, Cade et al. 1999), we illustrate the relationships graphically.

Canonical correspondence analysis (CCA; ter Braak 1986) was used to explore relationships between seed bank composition and forest structure. The community matrix was that used in DCA; the environmental (secondary) matrix included mean litter depth, total transmitted light, and density and basal area of live and dead *Pinus contorta* and *Abies grandis*. Ordination axes explained a small percentage of the variance in the community matrix and a Monte Carol test indicated no significant correlation between matrices (results not shown). Thus, interpretations of compositional gradients in the seed bank were made indirectly by correlating axis scores of subplots from DCA to associated values of forest structure (Økland 1996; McCune & Grace 2002); rank correlation (Kendall's *tau*) was used.

Relationships with above-ground vegetation

I used a series of Mantel's tests to determine whether compositional patterns in the seed bank correlated to those in the above-ground vegetation. Dissimilarity values in both matrices were based on Euclidean distances among subplots. The

first test included all subplots in which germinants emerged ($n = 196$). Three separate tests were then run for subplots representing each stage of encroachment (open meadow, young forest, and old forest).

I also tested whether presence of individual species in the seed bank was associated with presence in the above-ground vegetation. Fisher's exact test was employed on 2 x 2 contingency tables of species' presence or absence within subplots (Sokal & Rohlf 1981). One-tailed probability values were used to test for positive associations. Only those species that occurred in the seed bank in at least five subplots were tested.

All univariate analyses were performed with SPSS ver. 12.0 (SPSS Inc. 2003) and multivariate analyses with PC-Ord ver. 4.0 (McCune & Mefford 1999).

Results

Changes in overstory structure

The three encroachment stages differed substantially in vegetation structure and environment (Table 1). In open meadow, total transmitted light was more than twice that in young forests. Meadow subplots either had no trees or a few small individuals of *Pinus contorta* and/or *Abies grandis*. In contrast, tree densities were high in young forest (mean of 1,552 ha⁻¹); *Abies grandis* was dominant, but live and dead *Pinus contorta* were also common. Densities were 25% lower in old forest, but basal area was three time greater, reflecting presence of large-diameter (70 to >130 cm) *Abies grandis*.

Seed bank density, richness, and composition

A total of 4,130 germinants emerged from 196 of the 209 soil samples; 13 samples (6%) yielded no germinants. Density of germinants ranged from 0 to 254 per sample (0 to 29,918 m⁻²) with a mean of 19.8 per sample (2,332 m⁻²). Forty-four species representing 23 families and 43 genera were identified (Table 2). Families with the greatest number of species were the Compositae (8) and Gramineae (7). Eighty-five germinants (2% of the total) could not be identified and were recorded as unknown dicots or graminoids. Forbs (30 taxa) and graminoids (9 taxa) were more common than woody plants (3 shrub and 2 tree species) (Table 2). A large proportion of the seed bank was comprised of

Table 1. Total transmitted light, stem density, and basal area (mean and SE) in subplots representing open meadow, young forest, and old forest at Bunchgrass Ridge. n is the number of subplots.

Structural variable	Open meadow ($n = 24$)		Young forest ($n = 160$)		Old forest ($n = 25$)	
	Mean	SE	Mean	SE	Mean	SE
Transmitted light (%) ^a	46.3	4.5	21.7	0.9	17.2	0.8
Stem density (no. ha ⁻¹)						
Live (≥ 1.4 m tall)						
<i>Pinus contorta</i>	16.7	9.8	180.0	17.1	28.0	10.8
<i>Abies grandis</i>	70.8	20.4	1268.1	63.0	1108.0	114.5
Other species ^b	8.3	8.3	103.7	10.8	36.0	11.4
Total	95.8	27.9	1551.9	74.1	1172.0	120.8
Dead (≥ 5 cm dbh)						
<i>Pinus contorta</i>	4.2	4.2	235.6	26.1	64.0	19.0
<i>Abies grandis</i>	29.2	18.5	166.9	17.9	192.0	34.6
Other species ^b	0.0	0.0	0.0	0.0	0.0	0.0
Total	33.3	18.7	402.5	29.4	256.0	43.2
Basal area (m ² ha ⁻¹)						
Live (≥ 1.4 m tall)						
<i>Pinus contorta</i>	0.2	0.1	5.8	0.7	2.1	1.7
<i>Abies grandis</i>	5.6	3.6	28.9	2.4	111.4	13.8
Other species ^b	0.0	0.0	1.7	0.5	2.0	1.5
Total	5.8	3.6	36.3	2.4	115.5	13.4
Dead (≥ 5 cm dbh)						
<i>Pinus contorta</i>	0.1	0.1	6.6	0.7	4.8	2.0
<i>Abies grandis</i>	4.1	2.5	3.8	1.0	24.5	10.1
Other species ^b	0.0	0.0	0.0	0.0	0.0	0.0
Total	4.1	2.5	10.5	1.1	29.2	10.5

^a Some canopy photographs were missed thus sample sizes are lower for transmitted light: open meadow ($n = 14$), young forest ($n = 155$), and old forest ($n = 24$)

^b Other species are *Abies amabilis*, *Calocedrus decurrens*, *Castanopsis chrysophylla*, *Pinus monticola*, *Pseudotsuga menziesii*, *Taxus brevifolia*, *Tsuga heterophylla*, and *Tsuga mertensiana*.

Table 2. Frequency of occurrence (% of subplots) and abundance (mean cover or germinant density) of plant species found in the above-ground vegetation (Veg) and seed bank (Seed). Habitat preference (F = forest, M = meadow, and R = ruderal) was assigned *a priori* (see Methods: Data manipulation); species that could not be classified are coded as “–”. Origin is native (N) or exotic (E). Within a growth form, species are arranged in descending order of frequency in the seed bank. Values for tree species are for stems <1.4 m tall.

Growth form/Species	Habitat	Origin	Frequency (%)		Mean cover (%)	Germ. density (no. m ⁻²)
			Veg	Seed		
Graminoids						
<i>Agrostis scabra</i>	R	N	<1	71	<0.01	1331.15
<i>Carex pensylvanica</i>	M	N	83	51	11.18	389.03
Unknown graminoids	–	–		22		13.02
<i>Festuca idahoensis</i> ^a	M	N	37	4	3.40	3.94
<i>Danthonia intermedia</i>	M	N	11	3	0.14	3.94
<i>Elymus glaucus</i>	M	N	53	2	4.48	2.82
<i>Luzula campestris</i>	R	N	2	1	0.01	2.25
<i>Bromus vulgaris</i>	F	N	72	<1	3.27	2.25
<i>Melica subulata</i>	F	N	45	<1	1.04	0.56
<i>Stipa occidentalis</i>	M	N	4	<1	0.03	0.56
<i>Bromus carinatus</i>	M	N	27		1.20	
<i>Trisetum canescens</i>	F	N	8		0.05	
<i>Agropyron repens</i>	M	E	3		0.08	
Unknown Gramineae	–	–	3		0.02	
<i>Carex pachystachya</i>	M	N	2		0.08	
<i>Poa pratensis</i>	M	E	2		0.01	
<i>Agrostis</i> sp.	–	N	1		0.01	
<i>Bromus</i> sp.	–	N	1		<0.01	
<i>Carex deweyana</i>	–	N	1		0.01	
<i>Carex hoodii</i>	M	N	<1		0.18	
Herbs and Ferns						
<i>Epilobium watsonii</i>	R	N	6	33	0.02	119.48
<i>Lactuca muralis</i>	R	E	44	23	1.44	130.18
<i>Ranunculus uncinatus</i>	–	N	15	20	0.03	65.37
<i>Fragaria</i> spp. ^b	M	N	89	17	4.20	33.81
Unknown dicots	–	–		17		33.81
<i>Galium triflorum</i>	F	N	61	13	1.09	26.49
<i>Senecio sylvaticus</i>	R	E		7		9.02
<i>Circaea alpina</i>	F	N	32	6	1.19	11.83
<i>Achillea millefolium</i>	M	N	66	5	2.24	10.14
<i>Arenaria macrophylla</i>	F	N	77	5	0.97	6.20

Table 2. Continued.

Growth form/Species	Habitat	Origin	Frequency (%)		Mean cover (%)	Germ. density (no. m ⁻²)
			Veg	Seed		
Herbs and Ferns (cont.)						
<i>Campanula scouleri</i>	F	N	54	5	1.77	9.02
<i>Stellaria crispa</i>	R	N	1	5	<0.01	22.54
<i>Cirsium callilepis</i>	M	N	44	4	1.06	5.64
<i>Cerastium arvense</i>	M	N		3		24.80
<i>Gnaphalium microcephalum</i>	R	N		3		3.94
<i>Rumex acetosella</i>	R	E	1	3	0.01	21.42
<i>Veronica americana</i>	M	N		3		15.78
<i>Conyza canadensis</i>	R	N		2		2.25
<i>Hieracium albiflorum</i>	F	N	70	2	0.95	3.38
<i>Montia sibirica</i>	R	N	5	2	0.19	3.38
<i>Iris chrysophylla</i>	M	N	61	1	1.73	1.13
<i>Viola glabella</i>	F	N	82	1	1.34	1.69
<i>Asarum caudatum</i>	F	N	33	<1	1.47	0.56
<i>Cardamine</i> sp.	R	N		<1		1.13
<i>Comandra umbellata</i>	M	N	8	<1	0.05	0.56
<i>Phacelia heterophylla</i>	R	N	1	<1	<0.01	0.56
<i>Prunella vulgaris</i>	R	E	1	<1	0.01	0.56
<i>Sonchus</i> sp.	R	E		<1		0.50
<i>Sagina procumbens</i>	R	E		<1		0.56
<i>Vicia americana</i>	M	N	27	<1	0.60	0.56
Unknown forb 1	–	–		<1		1.13
<i>Osmorhiza chilensis</i>	F	N	83		1.20	
<i>Anemone deltoidea</i>	F	N	74		1.21	
<i>Anemone oregana</i>	F	N	57		0.54	
<i>Erigeron aliceae</i>	M	N	57		1.77	
<i>Adenocaulon bicolor</i>	F	N	56		1.62	
<i>Smilacina stellata</i>	F	N	56		5.68	
<i>Galium oreganum</i>	F	N	53		2.85	
<i>Achlys triphylla</i>	F	N	39		2.07	
<i>Rubus lasiococcus</i>	F	N	37		1.04	
<i>Lupinus latifolius</i>	M	N	34		1.40	
<i>Lathyrus nevadensis</i>	M	N	32		2.38	
<i>Tiarella trifoliata</i>	F	N	28		0.53	
<i>Hieracium gracile</i>	M	N	25		0.57	
<i>Listera</i> spp. ^c	F	N	25		0.06	
<i>Viola nuttallii</i>	M	N	25		0.08	
<i>Rubus ursinus</i>	F	N	22		0.38	

Table 2. Continued.

Growth form/Species	Habitat	Origin	Frequency (%)		Mean cover (%)	Germ. density (no. m ⁻²)
			Veg	Seed		
Herbs and Ferns (cont.)						
<i>Phlox diffusa</i>	M	N	17		0.94	
<i>Clintonia uniflora</i>	F	N	14		0.34	
<i>Trientalis latifolia</i>	F	N	14		0.17	
<i>Agoseris</i> sp.	M	N	13		0.08	
<i>Anemone lyallii</i>	F	N	13		0.04	
<i>Aster radulinus</i>	M	N	13		0.42	
<i>Aster ledophyllus</i>	M	N	11		0.23	
<i>Lilium columbianum</i>	–	N	11		0.07	
<i>Aster occidentalis</i>	M	N	10		0.21	
<i>Agoseris aurantiaca</i>	M	N	9		0.08	
<i>Anaphalis margaritacea</i>	M	N	8		0.08	
<i>Calochortus subalpinus</i>	M	N	7		0.01	
<i>Linnaea borealis</i>	F	N	7		0.17	
<i>Orthocarpus imbricatus</i>	M	N	7		0.08	
<i>Goodyera oblongifolia</i>	F	N	6		0.02	
<i>Pteridium aquilinum</i>	M	N	6		0.96	
<i>Corallorhiza maculata</i>	F	N	5		0.01	
<i>Viola orbiculata</i>	F	N	5		0.04	
<i>Pyrola secunda</i>	F	N	4		0.04	
<i>Chimaphila menziesii</i>	F	N	3		0.03	
<i>Polystichum munitum</i>	F	N	3		0.02	
<i>Trillium ovatum</i>	F	N	3		0.02	
<i>Disporum</i> spp. ^d	F	N	2		0.03	
<i>Penstemon procerus</i>	M	N	2		0.01	
<i>Actaea rubra</i>	F	N	1		0.01	
<i>Aquilegia formosa</i>	–	N	1		<0.01	
<i>Chimaphila umbellata</i>	F	N	1		0.01	
<i>Corallorhiza striata</i>	F	N	1		<0.01	
<i>Dryopteris austriaca</i>	F	N	1		<0.01	
<i>Epilobium angustifolium</i>	R	N	1		0.02	
<i>Microsteris gracilis</i>	M	N	1		<0.01	
<i>Pyrola picta</i>	F	N	1		0.01	
<i>Agoseris glauca</i>	M	N	<1		<0.01	
<i>Cerastium vulgatum</i>	M	E	<1		<0.01	
<i>Claytonia lanceolata</i>	M	N	<1		0.04	
<i>Corallorhiza</i> sp.	F	N	<1		<0.01	
<i>Cornus canadensis</i>	F	N	<1		0.03	

Table 2. Continued.

Growth form/Species	Habitat	Origin	Frequency (%)		Mean cover (%)	Germ. density (no. m ⁻²)
			Veg	Seed		
Herbs and Ferns (cont.)						
<i>Delphinium menziesii</i>	M	N	<1		0.02	
<i>Lomatium triternatum</i>	M	N	<1		<0.01	
<i>Polygonum douglasii</i>	M	N	<1		<0.01	
Shrubs						
<i>Rubus leucodermis</i>	R	N		3		3.94
<i>Rubus parviflorus</i>	–	N		<1		0.56
<i>Sambucus racemosa</i>	F	N		<1		0.56
<i>Symphoricarpos mollis</i>	F	N	23		0.65	
<i>Amelanchier alnifolia</i>	F	N	10		0.06	
<i>Rosa gymnocarpa</i>	F	N	3		0.03	
<i>Berberis nervosa</i>	F	N	2		0.01	
<i>Vaccinium membranaceum</i>	F	N	2		0.02	
<i>Haplopappus greenei</i>	M	N	1		0.07	
<i>Vaccinium caespitosum</i>	M	N	1		<0.01	
<i>Acer circinatum</i>	F	N	<1		0.11	
<i>Berberis aquifolium</i>	F	N	<1		<0.01	
<i>Berberis</i> sp.	F	N	<1		<0.01	
Trees						
<i>Abies grandis</i>	F	N	36	3	0.66	3.38
<i>Pseudotsuga menziesii</i>	F	N	<1	1	0.02	1.13
<i>Rhamnus purshiana</i>	F	N	3		0.01	
<i>Abies procera</i>	F	N	2		0.10	
<i>Sorbus sitchensis</i>	F	N	5		0.04	
<i>Taxus brevifolia</i>	F	N	1		0.03	
<i>Pinus monticola</i>	F	N	1		0.02	
<i>Castanopsis chrysophylla</i>	F	N	1		0.01	
<i>Pinus contorta</i>	F	N	1		0.01	
<i>Tsuga heterophylla</i>	F	N	1		0.01	
<i>Tsuga mertensiana</i>	F	N	1		<0.01	
<i>Prunus emarginata</i>	F	N	<1		<0.01	

^a May include *Festuca viridula*

^b Includes *Fragaria vesca* and *F. virginiana*

^c Includes *Listera caurina* and *cordata*

^d Includes *Disporum hookeri* and *D. smithii*

ruderal species (15 species, 71% of germinants). By comparison there were 12 meadow species (21% of germinants) and 12 forest species (3% of germinants). Five species of germinants were exotic (7% of germinants; all forbs). Among these, *Lactuca muralis* was the most common (23% of subplots, 6% of germinants).

Transition from open meadow to old forest

Richness and density of germinants

Species richness (number per subplot) of all germinants was greatest in old forest (Fig. 3a), whereas density tended to decline with forest age, but did not differ significantly among groups (Fig. 3b). Richness and density of meadow species (Figs. 3c,d) did not vary with stage of encroachment. Richness and density of forest species (Fig. 3e,f) tended to increase with forest age, but differences among groups were not significant. For ruderal species — the most diverse functional type — richness was greatest in old forest (Fig. 3g), whereas density of germinants tended to decline, although not significantly, with forest age (Fig. 3h). Density of native germinants tended to be lowest in old forest, but differences were not significant among groups (Fig. 4a). However, density of exotic germinants (largely *Lactuca muralis*) was greatest in old forest (Fig. 4b, Table 3).

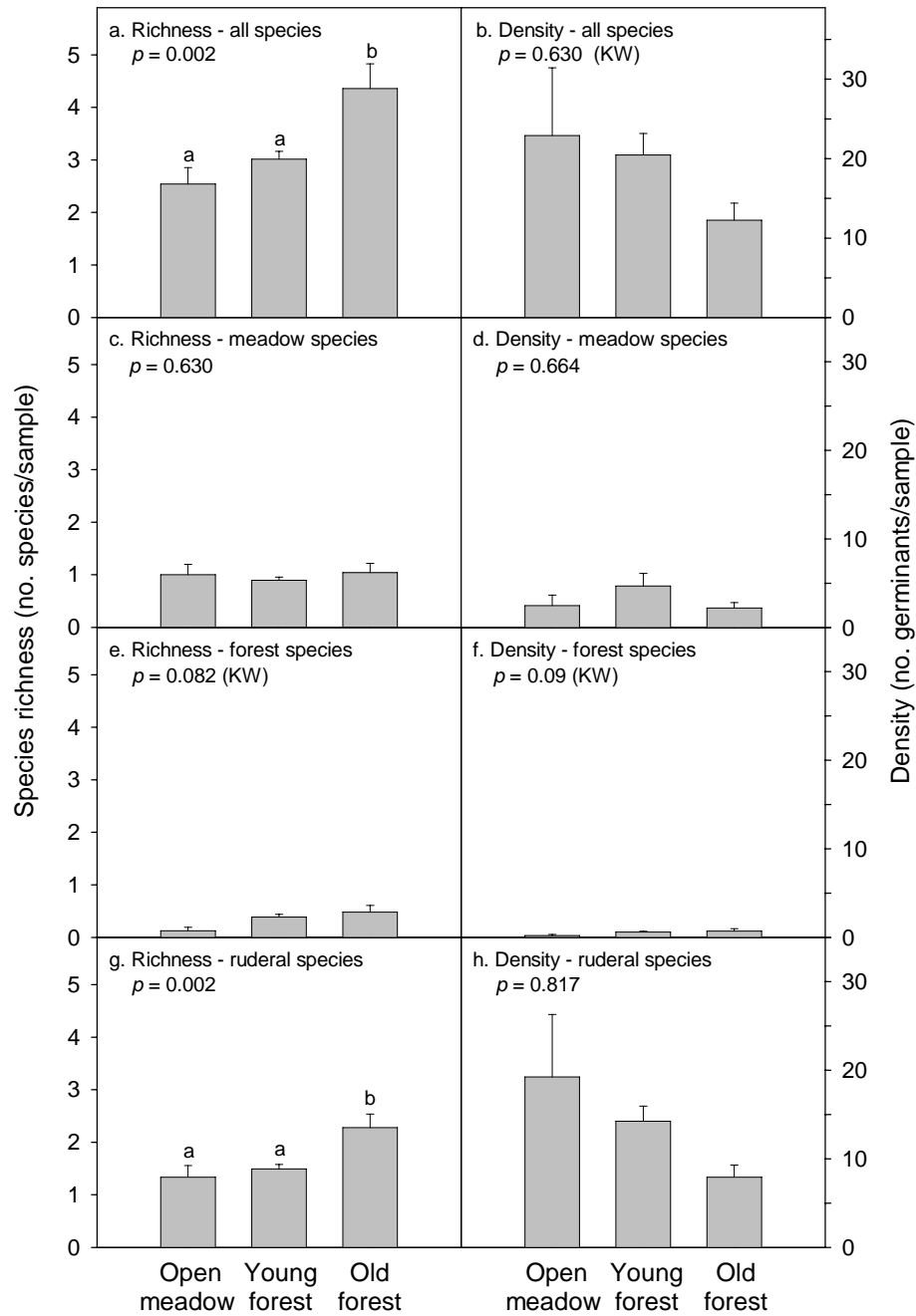


Figure 3. Mean (+1SE) density (number/sample) and richness (number of species/sample) of germinants of all, meadow, forest, and ruderal species for the three stages of encroachment. p values are from ANOVA or Kruskal-Wallis (KW) tests, as noted. Differing letters above bars indicate stages that differ significantly.

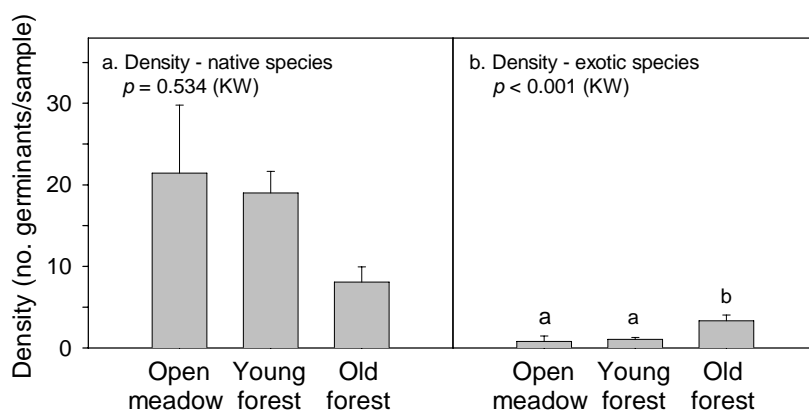


Figure 4. Mean (+1 SE) density (number sample⁻¹) of germinants of native and exotic species for the three stages of encroachment. p values are from Kruskal-Wallis (KW) tests. Differing letters above bars indicate stages that differ significantly.

Table 3. Frequency of occurrence (% of subplots) and density of germinants emerging from soil samples representing the three stages of encroachment. Sample sizes are: open meadow ($n = 24$), young forest ($n = 160$), and old forest ($n = 25$).

Growth form/Species	Frequency (%)			Density (no. m ⁻²)		
	Open meadow	Young forest	Old forest	Open meadow	Young forest	Old forest
Graminoids						
<i>Agrostis scabra</i>	70.8	71.9	68.0	2041.6	1377.4	353.4
<i>Bromus vulgaris</i>		1.9			2.9	
<i>Carex pensylvanica</i>	29.2	53.1	60.0	108.0	464.5	160.2
<i>Danthonia intermedia</i>	16.7	1.3	4.0	19.7	1.5	4.7
<i>Elymus glaucus</i>	4.2	1.3	4.0	4.9	2.2	4.7
<i>Festuca idahoensis</i> ^a	4.2	3.1	8.0	4.9	4.5	9.4
<i>Luzula campestris</i>	4.2	0.6	4.0	4.9	1.5	4.7
<i>Melica subulata</i>		0.6			0.7	
<i>Stipa occidentalis</i>	4.2			4.9		
Unknown graminoids	25.0	7.5	16.0	29.3	7.5	16.1
Herbs and Ferns						
<i>Achillea millefolium</i>	20.8	3.8		49.1	5.9	
<i>Arenaria macrophylla</i>		5.6	4.0		7.3	4.7
<i>Asarum caudatum</i>		0.6			0.7	
<i>Campanula scouleri</i>		6.3			11.8	
<i>Cardamine sp.</i>		1.3			1.5	
<i>Cerastium arvense</i>	4.2	3.1	4.0	78.6	12.5	51.8
<i>Circaea alpina</i>		5.0	16.0		12.5	18.8
<i>Cirsium callilepis</i>	4.2	4.4	4.0	4.9	5.9	4.7
<i>Comandra umbellata</i>			4.0			4.7
<i>Conyza canadensis</i>		2.5			2.9	
<i>Epilobium watsonii</i>	25.0	33.1	40.0	98.1	123.7	113.1
<i>Fragaria spp.</i> ^b	16.7	16.3	20.0	19.7	37.6	23.6
<i>Galium triflorum</i>	4.2	13.1	24.0	4.9	25.1	56.5
<i>Gnaphalium microcephalum</i>	16.7	1.3	4.0	19.7	1.5	4.7
<i>Hieracium albiflorum</i>	4.2	1.3	4.0	14.7	1.5	4.7
<i>Iris chrysophylla</i>		1.3			1.5	
<i>Lactuca muralis</i>	8.3	18.8	64.0	14.7	108.2	381.6
<i>Montia sibirica</i>	4.2	0.6	8.0	4.9	0.7	18.8
<i>Phacelia heterophylla</i>		0.6			0.7	
<i>Prunella vulgaris</i>		0.6			2.9	
<i>Ranunculus uncinatus</i>	4.2	20.0	36.0	39.2	67.7	75.4
<i>Rumex acetosella</i>	4.2	3.1	4.0	83.4	14.7	4.7
<i>Sagina procumbens</i>		0.6			0.7	

Table 3. Continued.

Growth form/Species	Frequency (%)			Density (no. m ⁻²)		
	Open meadow	Young forest	Old forest	Open meadow	Young forest	Old forest
Herbs and Ferns (cont.)						
<i>Senecio sylvaticus</i>		6.3	16.0		8.1	23.6
<i>Sonchus</i> sp.			4.0			4.7
<i>Stellaria crispera</i>		5.0	8.0		27.2	14.1
<i>Veronica americana</i>		3.1	4.0		19.9	4.7
<i>Vicia americana</i>	0.6			0.7		
<i>Viola glabella</i>	1.3			2.2		
Unknown dicots	16.7	15.6	24.0	235.6	30.9	47.1
Unknown forb 1			8.0			9.4
Shrubs						
<i>Rubus leucodermis</i>		3.1	8.0		3.7	9.4
<i>Rubus parviflorus</i>			4.0			4.7
<i>Sambucus racemosa</i>		0.6			0.7	
Trees						
<i>Abies grandis</i>	4.2	3.1		4.9	3.7	
<i>Pseudotsuga menziesii</i>		1.3			1.5	

^a May include *Festuca viridula*

^b Includes *Fragaria vesca* and *F. virginiana*

Table 4. Frequency of occurrence (proportion of subplots) and mean cover of vascular plant species in subplots representing the three stages of encroachment. Values for tree species are for stems <1.4 m tall. Sample sizes are: open meadow ($n = 24$), young forest ($n = 160$), and old forest ($n = 25$). Cover <0.1% is reported as “t” (trace).

Growth form/Species	Frequency (%)			Mean cover (%)		
	Open meadow	Young forest	Old forest	Open meadow	Young forest	Old forest
Graminoids						
<i>Agropyron repens</i>	16.7	1.3		0.4	t	
<i>Agrostis scabra</i>	8.3	0.6		0.1	t	
<i>Agrostis</i> sp.		0.6			t	
<i>Bromus carinatus</i>	75.0	20.0	28.0	3.9	0.9	0.5
<i>Bromus</i> sp.		1.3			0.0	
<i>Bromus vulgaris</i>	45.8	73.8	84.0	0.8	3.7	3.0
<i>Carex deweyana</i>		0.6	4.0		t	0.1
<i>Carex hoodii</i>		0.6			0.2	
<i>Carex pachystachya</i>		2.5			0.1	
<i>Carex pensylvanica</i>	87.5	85.6	60.0	18.6	11.4	2.4
<i>Danthonia intermedia</i>	54.2	5.0	4.0	0.9	0.1	t
<i>Elymus glaucus</i>	95.8	50.0	32.0	14.6	3.2	2.8
<i>Festuca idahoensis</i> ^a	91.7	30.6	24.0	18.9	1.9	1.5
Gramineae sp.		3.8	4.0		t	t
<i>Luzula campestris</i>	12.5	0.6	4.0	t	t	t
<i>Melica subulata</i>	25.0	45.0	68.0	1.2	1.0	1.5
<i>Poa pratensis</i>	16.7			0.1		
<i>Stipa occidentalis</i>	25.0	1.3		0.2	t	
<i>Trisetum canescens</i>		3.1	4.0		t	t
Herbs and Ferns						
<i>Achillea millefolium</i>	100.0	65.6	32.0	6.9	1.8	0.6
<i>Achlys triphylla</i>		0.6	4.0		t	0.1
<i>Actaea rubra</i>	4.2	38.8	76.0	0.1	1.9	4.8
<i>Adenocaulon bicolor</i>	4.2	64.4	56.0	t	1.9	1.5
<i>Agoseris aurantiaca</i>	25.0	7.5		0.2	0.1	
<i>Agoseris glauca</i>		0.6			t	
<i>Agoseris</i> sp.	16.7	13.8	8.0	0.1	0.1	t
<i>Anemone deltoidea</i>	20.8	82.5	68.0	0.1	1.5	0.7
<i>Anemone lyallii</i>	4.2	16.3		t	t	
<i>Anaphalis margaritacea</i>	12.5	8.8		0.1	0.1	
<i>Anemone oregana</i>	33.3	57.5	80.0	0.2	0.6	0.6
<i>Aquilegia formosa</i>		1.3			t	
<i>Arenaria macrophylla</i>	58.3	79.4	80.0	0.3	1.1	0.8

Table 4. Continued.

Growth form/Species	Frequency (%)			Mean cover (%)		
	Open meadow	Young forest	Old forest	Open meadow	Young forest	Old forest
Herbs and Ferns (cont.)						
<i>Asarum caudatum</i>	4.2	35.6	44.0	0.3	1.6	1.7
<i>Aster ledophyllus</i>	33.3	9.4	4.0	0.9	0.1	0.1
<i>Aster occidentalis</i>	29.2	8.1		0.7	0.2	
<i>Aster radulinus</i>	12.5	13.1	16.0	0.3	0.4	0.5
<i>Campanula scouleri</i>	8.3	61.3	48.0	0.3	2.0	1.7
<i>Calochortus subalpinus</i>	20.8	5.6		0.1	t	
<i>Cerastium vulgatum</i>			4.0			t
<i>Chimaphila menziesii</i>		3.8			t	
<i>Chimaphila umbellata</i>		0.6	4.0		t	t
<i>Circaea alpina</i>	8.3	26.3	88.0	0.1	0.7	5.1
<i>Cirsium callilepis</i>	91.7	40.0	28.0	3.9	0.8	0.2
<i>Claytonia lanceolata</i>		0.6			0.1	
<i>Clintonia uniflora</i>	4.2	16.3	12.0	t	0.4	0.3
<i>Comandra umbellata</i>	20.8	5.6	8.0	0.2	t	t
<i>Cornus canadensis</i>		0.6			t	
<i>Corallorhiza maculata</i>		5.0	8.0		t	t
<i>Corallorhiza</i> sp.		0.6			t	
<i>Corallorhiza striata</i>		1.3			t	
<i>Delphinium menziesii</i>		0.6			t	
<i>Disporum</i> spp. ^b		0.6	12.0		t	0.1
<i>Dryopteris austriaca</i>	4.2	0.6		t	t	
<i>Epilobium angustifolium</i>		1.9			t	
<i>Epilobium watsonii</i>	4.2	7.5		t	t	
<i>Erigeron aliciae</i>	83.3	58.8	20.0	5.1	1.5	0.3
<i>Fragaria</i> spp. ^c	95.8	91.9	60.0	6.3	4.4	1.1
<i>Galium oreganum</i>	33.3	55.6	56.0	2.0	3.1	2.4
<i>Galium triflorum</i>	16.7	63.1	88.0	0.3	0.8	3.9
<i>Goodyera oblongifolia</i>		6.3	12.0		t	0.1
<i>Hieracium albiflorum</i>	29.2	81.3	40.0	0.2	1.1	0.4
<i>Hieracium gracile</i>	37.5	26.3	8.0	0.9	0.6	t
<i>Iris chrysophylla</i>	33.3	68.8	40.0	0.8	2.1	0.4
<i>Lactuca muralis</i>	12.5	43.1	80.0	0.9	1.0	5.0
<i>Lathyrus nevadensis</i>	50.0	26.3	52.0	9.4	1.0	4.6
<i>Linnaea borealis</i>	4.2	6.9	8.0	t	0.2	0.1
<i>Lilium columbianum</i>	4.2	11.9	8.0	t	0.1	t

Table 4. Continued.

Growth form/Species	Frequency (%)			Mean cover (%)		
	Open meadow	Young forest	Old forest	Open meadow	Young forest	Old forest
Herbs and Ferns (cont.)						
<i>Listera</i> spp. ^d		32.5			0.1	
<i>Lomatium triternatum</i>		0.6			t	
<i>Lupinus latifolius</i>	75.0	32.5	4.0	6.5	0.9	t
<i>Microsteris gracilis</i>		1.9			t	
<i>Montia sibirica</i>	4.2	1.9	28.0	0.6	t	0.9
<i>Orthocarpus imbricatus</i>	16.7	6.3		0.4	t	
<i>Osmorhiza chilensis</i>	29.2	88.1	100.0	0.3	1.1	2.7
<i>Penstemon procerus</i>	4.2	2.5		t	t	
<i>Phacelia heterophylla</i>		1.9			t	
<i>Phlox diffusa</i>	25.0	17.5	4.0	3.2	0.7	0.3
<i>Polygonum douglasii</i>	4.2			t		
<i>Polystichum munitum</i>		3.1	4.0		t	0.1
<i>Prunella vulgaris</i>		1.3			t	
<i>Pteridium aquilinum</i>	41.7	1.9		7.5	0.1	
<i>Pyrola picta</i>		1.9			t	
<i>Pyrola secunda</i>		5.6			t	
<i>Ranunculus uncinatus</i>	16.7	11.9	32.0	0.1	t	0.1
<i>Rubus lasiococcus</i>	4.2	44.4	24.0	0.1	1.3	0.2
<i>Rubus ursinus</i>		25.0	20.0		0.4	0.9
<i>Rumex acetosella</i>		1.3	4.0		t	t
<i>Smilacina stellata</i>	12.5	56.9	92.0	0.7	5.1	14.2
<i>Stellaria crispa</i>		0.6	4.0		t	t
<i>Tiarella trifoliata</i>		30.0	40.0		0.6	0.4
<i>Trientalis latifolia</i>	4.2	6.9	16.0	t	t	0.1
<i>Trillium ovatum</i>	8.3	11.3	36.0	0.3	0.1	0.3
<i>Vicia americana</i>	54.2	20.0	44.0	2.0	0.4	0.7
<i>Viola glabella</i>	50.0	86.3	84.0	0.7	1.5	0.9
<i>Viola nuttallii</i>	4.2	31.9	4.0	t	0.1	t
<i>Viola orbiculata</i>		6.9			t	
Shrubs						
<i>Acer circinatum</i>		0.6			0.1	
<i>Amelanchier alnifolia</i>		10.6	12.0		0.1	0.1
<i>Berberis aquifolium</i>			4.0			t
<i>Berberis nervosa</i>		1.9	4.0		t	t
<i>Berberis</i> sp.		0.6			t	
<i>Haplopappus greenei</i>	4.2	0.6		0.2	0.1	

Table 4. Continued.

Growth form/Species	Frequency (%)			Mean cover (%)		
	Open meadow	Young forest	Old forest	Open meadow	Young forest	Old forest
Shrubs (cont.)						
<i>Rosa gymnocarpa</i>		2.5	12.0		t	0.2
<i>Symphoricarpos mollis</i>		27.5	20.0		0.8	0.4
<i>Vaccinium caespitosum</i>	4.2	0.6		t	t	
<i>Vaccinium membranaceum</i>		3.1			t	
Trees						
<i>Abies grandis</i>	4.2	46.3	4.0	0.1	0.8	t
<i>Abies procera</i>		2.5			0.1	
<i>Castanopsis chrysophylla</i>		1.9			t	
<i>Pinus contorta</i>		1.9			t	
<i>Pinus monticola</i>		1.3			t	
<i>Prunus emarginata</i>		0.6			t	
<i>Pseudotsuga menziesii</i>		0.6			t	
<i>Rhamnus purshiana</i>		3.1	4.0		t	t
<i>Sorbus sitchensis</i>		5.6	4.0		t	t
<i>Taxus brevifolia</i>		0.6	4.0		t	t
<i>Tsuga heterophylla</i>		1.3	4.0		t	t
<i>Tsuga mertensiana</i>		1.3			t	

^a May include *Festuca viridula*

^b Includes *Disporum hookeri* and *D. smithii*

^c Includes *Fragaria vesca* and *F. virginiana*

^d Includes *Listera caurina* and *L. cordata*

Compositional trends

Detrended correspondence analysis based on germinant density revealed a gradual transition from open meadow subplots (high scores on axis 1) to old forest subplots (low scores on axis 1; gradient length of 4.5 SD units; Fig. 5a). Species with the highest scores on axis 1 included *Danthonia intermedia* and *Achillea millefolium* (Fig. 5b), both common in open meadow (Table 4). Species with the lowest scores included the exotic forb, *Lactuca muralis* (common in old forest subplots; Table 4) and the forest herb, *Circaea alpina* (Fig. 5b).

Results of MRPP indicated no difference in seed bank composition between open meadow and young forest ($A = 0.00283$, $p = 0.089$), but significant differences between young and old forest ($A = 0.0130$, $p < 0.0001$) and between open meadow and old forest ($A = 0.0472$, $p < 0.0001$). Despite statistical significance, however, the A-statistic (a measure of effect size) for these tests suggests that compositional differences were small.

Indicator species analysis (ISPAN) yielded five taxa in the seed bank that showed a positive association with a particular stage of encroachment (Table 5). *Danthonia intermedia* and *Achillea millefolium* (both meadow species) and *Gnaphalium microcephalum* (a ruderal species) were associated with open meadow subplots. *Lactuca muralis* and *Senecio sylvaticus* (both exotic, ruderal species) were associated with old forest. However, maximum indicator values were low except for *Lactuca*.

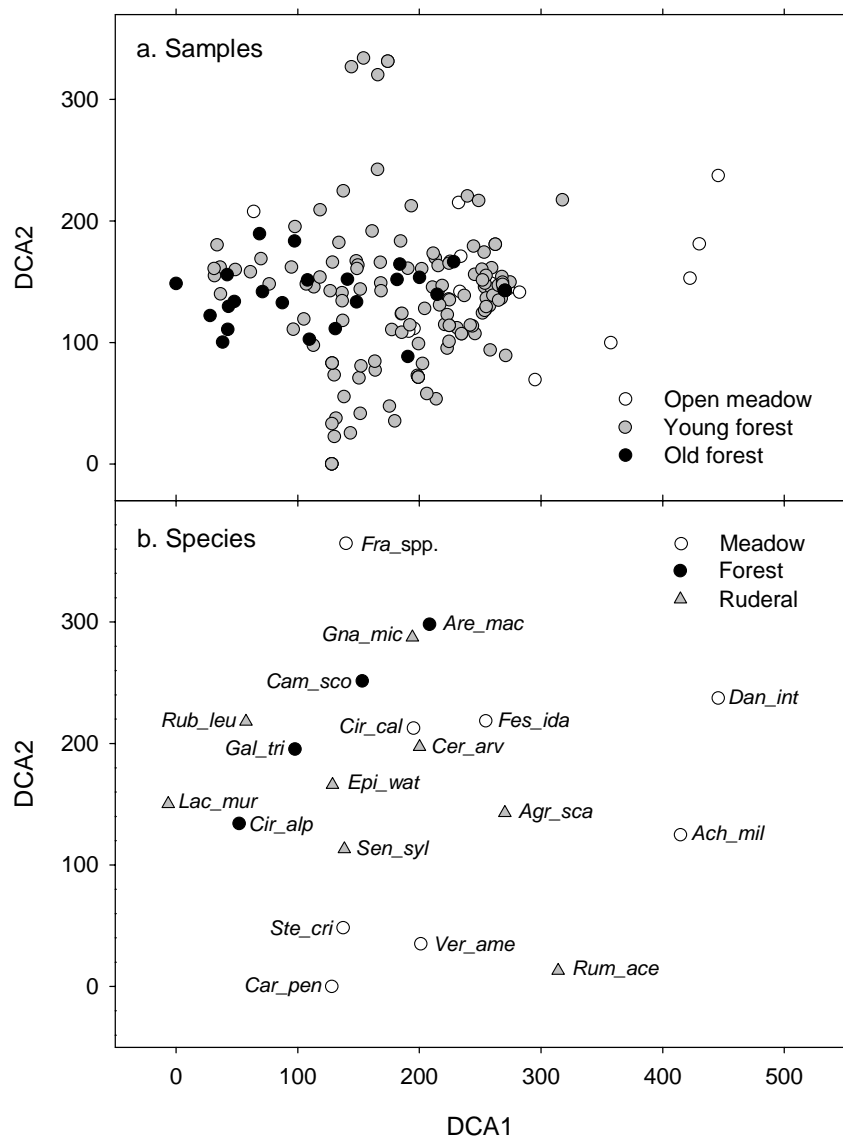


Figure 5. DCA ordination of seed bank (a) samples and (b) species. Germinant density was used as the measure of species abundance. Species codes are: *Ach_mil* = *Achillea millefolium*, *Agr_sca* = *Agrostis scabra*, *Are_mac* = *Arenaria macrophylla*, *Cam_sco* = *Campanula scouleri*, *Car_pen* = *Carex pensylvanica*, *Cer_arv* = *Cerastium arvense*, *Cir_alp* = *Circaea alpina*, *Cir_cal* = *Cirsium callilepis*, *Dan_int* = *Danthonia intermedia*, *Epi_wat* = *Epilobium watsonii*, *Fes_ida* = *Festuca idahoensis*, *Fra_spp* = *Fragaria vesca*/*F. virginiana*, *Gal_tri* = *Galium triflorum*, *Gna_mic* = *Gnaphalium microcephalum*, *Lac_mur* = *Lactuca muralis*, *Rub_leu* = *Rubus leucodermis*, *Rum_ace* = *Rumex acetosella*, *Sen_syl* = *Senecio sylvaticus*, *Ste_cri* = *Stellaria crispa*, *Ver_ame* = *Veronica americana*. Two unclassified species are not shown.

Table 5. Results of indicator species analysis (ISPAN) for seed bank taxa present in five or more samples. Species are grouped by the stage of encroachment in which they exhibited the maximum observed indicator value, IV_{max} . p is the proportion of randomized trials with an IV equal to or exceeding the observed IV. Significant values ($p \leq 0.05$) are in bold.

Seed bank species	IV_{max}	p
Open meadow		
<i>Agrostis scabra</i>	39.5	0.134
<i>Achillea millefolium</i>	19.3	0.004
<i>Danthonia intermedia</i>	13.2	0.008
<i>Gnaphalium microcephalum</i>	13.2	0.010
<i>Rumex acetosella</i>	3.5	0.452
<i>Abies grandis</i>	2.4	0.645
<i>Cerastium arvense</i>	2.4	0.828
Young forest		
<i>Carex pensylvanica</i>	36.9	0.215
<i>Fragaria</i> spp. ^a	8.3	0.776
<i>Campanula scouleri</i>	6.8	0.203
<i>Arenaria macrophylla</i>	3.8	0.691
<i>Stellaria crispa</i>	3.6	0.684
<i>Veronica americana</i>	2.8	0.655
<i>Cirsium callilepis</i>	1.8	1.000
Old forest		
<i>Lactuca muralis</i>	50.0	0.001
<i>Galium triflorum</i>	16.2	0.059
<i>Ranunculus uncinatus</i>	15.3	0.199
<i>Epilobium watsonii</i>	13.9	0.838
<i>Senecio sylvaticus</i>	12.3	0.046
<i>Circaea alpina</i>	9.9	0.086
<i>Rubus leucodermis</i>	5.9	0.226
<i>Festuca idahoensis</i> ^b	4.1	0.523

^a Includes *Fragaria vesca* and *F. virginiana*

^b May include *Festuca viridula*

Relationships with overstory structure

Correlations between overstory structural variables and germinant density or richness within subplots were generally weak. However, I observed strong relationships of live stem density (or basal area) with the *maximum* densities of total germinants (Figs. 6a,b), ruderals (Fig. 6c,d) and exotics (Fig. 6e). At low stem density (or basal area), germinant density ranged from very low to very high; however, as stem density and basal area increased, maximum density of germinants declined sharply.

Rank correlations between overstory structural attributes and subplot scores in DCA space suggest only weak relationships between seed bank composition and overstory structure. Among the variables considered, basal area of live *Abies grandis* showed the strongest correlation to Axis 1 (Kendall's $\tau = -0.27$); all correlations with Axis 2 were poor (Kendall's $\tau < 0.09$).

Relationships with above-ground vegetation

A total of 114 taxa were recorded in the above-ground vegetation. Of these, 40 were classified as meadow, 55 as forest, and 10 as ruderal species (Table 2). Thirteen (32%) of the meadow species and 12 (22%) of the forest species were represented in the seed bank. In contrast, all of the ruderal taxa were present in the seed bank. The most abundant was *Agrostis scabra* (71% of subplots, 57% of germinants); however, it was present in the above-ground vegetation in only 1% of the subplots. In general, most species in the seed bank showed limited

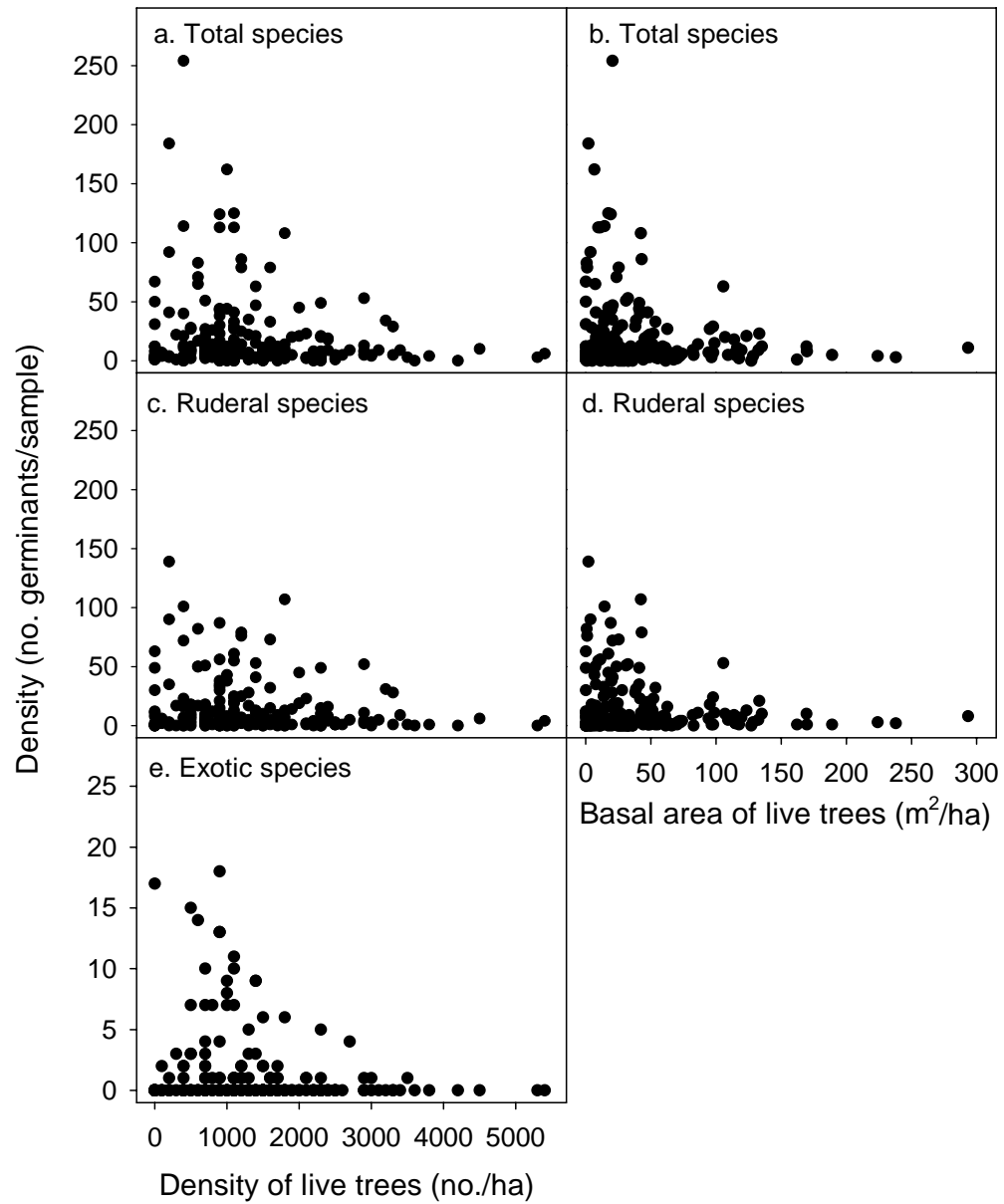


Figure 6. Examples of relationships between the density of germinants and the density or basal area of live trees.

occurrence in the vegetation. *Carex pensylvanica*, the dominant meadow sedge, was the exception, with a high frequency in both the seed bank (51%) and vegetation (83%) (Table 2).

A Mantel's test to compare the correlation between compositional dissimilarity among subplots for the seed bank and the above-ground vegetation yielded a significant ($p = 0.03$), but low correlation ($r = 0.13$). Separate Mantel's tests for subplots representing each stage of encroachment revealed a significant correlation ($p = 0.003$) in young forests, but similar to the full set of data, the correlation was low ($r = 0.19$).

Fisher's exact test of the correspondence between species' occurrence in the seed bank and the above-ground vegetation yielded strong positive associations for half of the species tested. Of 10 species with sufficient frequency in the seed bank, five showed a significant result (p of <0.001 to 0.002). These included three forest species, *Circaea alpina*, *Campanula scouleri*, and *Galium triflorum*; one ruderal species, *Lactuca muralis*; and one unclassified or "generalist" species, *Ranunculus uncinatus*.

Discussion

The greenhouse emergence method is a common and efficient approach for quantifying the density and diversity of viable seed in the soil (Gross 1990; Brown 1992; Thompson et al. 1997). Yet caution is necessary in drawing inferences about the seed bank from the density and composition of germinants. In particular, greenhouse conditions may not stimulate emergence of species with specific germination requirements (e.g., heating above a threshold temperature; Clark & Wilson 1994). Physical extraction can provide a more accurate estimate of seed density and diversity, but has notable limitations: it is labor intensive which limits the number of samples that can be processed, seeds must be tested for viability, and a reference collection is required for seed identification. Greenhouse emergence provides a reasonable basis for comparing the abundance of species with readily germinable seeds, which are the species of particular relevance to restoration activities.

Seed bank density, richness, and composition

Soils in both meadow and forest supported a well-developed and diverse community of viable seeds. Germinants occurred in 94% of samples with densities averaging $>2,300$ seeds m^{-2} . Although data for similar types of meadows or forests do not exist for this region, germinant densities appear of comparable magnitude to those reported from other western grassland and

coniferous forest ecosystems (e.g., Pratt et al. 1984; Rice 1989). In a California *Festuca* prairie, density averaged 8,230 m⁻² (Major & Pyott 1966). Densities ranged from 222 to 1,724 m⁻² in a low elevation, western Cascade forest dominated by *Pseudotsuga* (Harmon & Franklin 1995) and from 189 to 1,154 m⁻² in *Abies grandis* forests of central Idaho (Kramer & Johnson 1987).

Ruderal taxa dominated the seed bank both in richness (34% of taxa) and number (>70% of germinants), greatly exceeding the contributions of meadow and forest species. This is not surprising, as early successional species are prominent in the seed banks of most grassland and forest soils (Kellman 1970; Pratt et al. 1984; Rice 1989; Halpern et al. 1999; Bossuyt & Hermy 2003). In this system, where ruderal species had limited occurrence in the vegetation, presence in the seed bank generally reflects dispersal from off-site sources rather than persistence from an earlier successional stage (e.g., as in old field seres; Oosting & Humphreys 1940; Livingston & Alessio 1968). The one exception is the shade-tolerant exotic herb, *Lactuca muralis*, which was common in old forest subplots (see below). Many of these ruderals possess plumed or comose seeds for long-distance dispersal (e.g., *Conyza canadensis*, *Epilobium watsonii*, *Gnaphalium microcephalum*, and *Senecio sylvaticus*) and are ubiquitous colonists of early seral forests throughout the region (Kellman 1970, 1974; Schoonmaker & McKee 1988; Halpern 1989; Halpern et al. 1997, 1999). Dominance of the seed bank by *Agrostis scabra* (>70% of samples, >50% of germinants), however, was

surprising. Although wind dispersal is possible and seed trapping has confirmed its dispersal ability (Harmon & Franklin 1995), *Agrostis* does not possess traits for long-distance transport. Proximity to roads and adjacent clearcuts (where it can colonize soon after disturbance; Klinka et al. 1985) may have allowed for abundant dispersal and accumulation in meadow and forest soils.

In contrast, seeds of meadow species were poorly represented in these communities. Only 20% of germinants were classified as meadow taxa and 80% of these were of a single species, *Carex pensylvanica*. In addition, nearly 70% of meadow species were absent from the seed bank; even common grasses that are prolific seed producers and potential seed bankers (e.g., *Elymus*, *Bromus*, and *Festuca*; Strickler & Edgerton 1976; Pratt et al. 1984; Pitschel 1988) were sparse in the germinant pool. Only *Achillea millefolium* and *Danthonia californica* showed a significant (but weak) association between germinant density and encroachment class (open meadow). None of the meadow species had a positive association between presence in the vegetation and presence in the seed bank. The high dissimilarity of above- and below-ground floras is consistent with that observed in many grassland ecosystems (e.g., Major & Pyott 1966; Davies & Waite 1998; Bakker & Berendse 1999; Bisteau & Mahy 2005). It appears that population persistence occurs primarily through vegetative means and not maintenance of a viable seed bank in systems dominated by perennial grasses and forbs (Rice 1989).

The poor representation of forest herbs in the seed bank was expected. Trends in richness and density suggest a gradual accumulation of seeds, but at extremely low rates. It is notable, however, that three forest herbs were among the five species for which there was a positive association between presence in the vegetation and presence in the seed bank. In most forest ecosystems, the characteristic understory species do not maintain a viable seed bank (Archibold 1989; McGee & Feller 1993; Halpern et al. 1999; Bossuyt & Hermy 2001); many are clonal (Sobey & Barkhouse 1977; Antos & Zobel 1984), and rely on vegetative growth for persistence and spread. Although establishment from seed is infrequent in many forest herbs (Bierzychudek 1982), the disjunct distributions of newly forming forest patches indicate that at least the initial stages of understory development have occurred through seed dispersal and establishment. However, this establishment may occur without an intervening period of seed dormancy. Similarly, the rarity of tree species from the seed bank is consistent with observations in other coniferous forests (Oosting & Humphreys 1940; Kramer & Johnson 1987; Harmon & Franklin 1995). Conifers tend to exhibit high annual variation in cone production and short-term viability of seed (Archibold 1989; Burns & Honkala 1990), however dispersal is not likely to be limiting, given the intensity of recent establishment.

Temporal gradients in the seed bank

Variation in the seed bank among encroachment stages was small, despite the

temporal duration of the chronosequence. Density and richness of meadow taxa were low but comparable among stages. For the few meadow species present in the seed bank, temporal trends suggest that local inputs and short-distance dispersal, rather than long-term persistence, underlie the distributions of viable seeds. Few meadow species showed declines in density among successive stages suggestive of a gradual senescence of viable seed (*cf.* Milberg 1995; Bakker et al. 1996; Davies & Waite 1998; Bossuyt & Hermy 2001). *Achillea millefolium* was an exception: seed density declined dramatically in young forest and seeds were absent from old forest soils. For the dominant sedge, *Carex pensylvanica*, and for *Fragaria* spp., abundant seed in young forests may simply reflect persistence of flowering plants in the understory. For other meadow species that were lost from the local vegetation, presence of low densities of seed in forest soils may reflect proximity to propagule sources: most patches of young and old forests lie adjacent to large meadow openings or include small meadow remnants from which dispersal may occur (e.g., Dutoit & Alard 1995; Bisteau & Mahy 2005). In general, the limited representation of meadow species in the seed bank leads to the conclusion that most taxa are not dependent on a strategy of seed banking, thus limiting the potential for *in situ* restoration (Rice 1989; Bakker & Berendse 1999; Stöcklin & Fischer 1999; Bossuyt & Hermy 2003).

Given the limited contributions of meadow and forest species, the dynamics of the seed bank were largely shaped by ruderal species. Richness of ruderals

increased significantly in old forest, but density tended to decline. It is commonly observed that the density and diversity of seeds of weedy species decrease over successional time in forest ecosystems, reflecting the combined effects of reduced inputs and gradual losses to decay, predation, or germination (Oosting & Humphreys 1940; Livingston & Allessio 1968; Leck et al. 1989). In montane meadows of the Pacific Northwest, however, ruderals are uncommon components of the flora; thus, the apparent temporal decline in density is likely to reflect differential inputs in “space,” rather than gradual decay of a persistent seed bank (as commonly observed in old-field seres). At Bunchgrass, trends among ruderals were strongly influenced by the distribution of *Agrostis scabra*, which dominated the seed bank. Significant declines from meadow to old forest may reflect both proximity of meadows to adjacent clearcuts (where *Agrostis* may have been abundant soon after logging) and poorer dispersal into forests where wind speeds are typically lower (e.g., Chen et al. 1995). Seeds of the exotic ruderal, *Lactuca muralis*, showed a very different trend, increasing in old forest in parallel with its abundance in the vegetation. In fact, *Lactuca* showed a highly significant association (IV_{max}) with old forest subplots and was one of the few species to show a strong spatial association between presence in the seed bank and the vegetation. *Lactuca muralis* is one of the few exotic forbs in this region that can persist and reproduce within shaded habitats (e.g., Clabby & Osborne 1997; Parendes & Jones 2000).

Correlations with forest structure

To what extent was variation in the seed bank explained by local variation in overstory structure? Multivariate analyses (CCA) of seed bank composition and correlations of forest structural variables with germinant density and richness yielded generally poor relationships, suggesting limited ability to predict seed bank characteristics from overstory attributes. Samples from young and old forest were particularly variable, showing complete overlap in ordination space.

However, I observed fairly strong relationships between the tree density or basal area and the maximum density of germinants (total, ruderal, or exotic). Forest structure can influence seed dispersal or accumulation either directly — as a barrier to movement (Willson & Crome 1989) — or indirectly via effects on species composition and local seed production. Indirect effects of structure may explain patterns of seed density among exotics: abundance of *Lactuca muralis* was markedly lower in dense, young forest than in old forest. However, for the seed bank as a whole it appears that direct effects of forest structure, limiting lateral dispersal and vertical descent through the canopy, become increasingly important at greater stand densities or basal areas.

Implications for restoration

Conifer encroachment at Bunchgrass Ridge has been accompanied by dramatic changes in community structure, including marked declines in the abundance and diversity of meadow species and conversion to forest understory

species. Thus in addition to tree removal, successful restoration will require re-introduction or rejuvenation of species that have been locally extirpated or severely reduced in abundance. My results indicate that re-establishment of most species will not occur through a relictual seed bank. Lack of a persistent seed bank limits the potential for *in situ* restoration of other grassland ecosystems (Bakker & Berendse 1999; Bossuyt & Hermy 2003; Bisteau & Mahy 2005; Lett & Knapp 2005), and leads to a common conclusion that community recovery requires seed dispersal into the target ecosystem (Dutoit & Alard 1995; Schott & Hamburg 1997; Poschlod et al. 1998; Bakker & Berendse 1999).

Restoration efforts should thus focus on forest-meadow boundaries or tree islands to maximize propagule pressure and the potential for vegetative spread of clonal species. Soils in ecotonal areas are also likely to be more similar to those of open meadows (e.g., Griffiths et al. 2005), thus providing edaphic conditions that are more likely to be conducive to germination and establishment of target meadow species. Where local propagule sources or seed dispersal are known to be limiting, artificial seeding can be used to re-introduce species (e.g., McDonald 1993; Maret & Wilson 2000); however, this approach requires access to abundant sources of seed, as well as consideration of the genetic and ecological consequences of introducing non-endemic genotypes (Lesica & Allendorf 1999; Jones 2003).

Even where dispersal of target species is not limiting, dominance of the seed

bank by ruderal species poses a potential problem. Activities that expose or heat mineral soils will facilitate germination and growth of disturbance-dependent annuals and short-lived perennials (e.g., Schoonmaker & McKee 1988, Halpern 1989) that can compete with species targeted for restoration. Strategies that minimize soil disturbance (e.g., tree removal on snow) or consumption of organic matter by fire (e.g., spring burning), may reduce these impacts, as depth of soil disturbance and duration of heating can result in differential expression of the seed bank (Moore & Wein 1977; Morgan & Neuenschwander 1988; Halpern 1989; McGee & Feller 1993). However, some disturbance of the soil may be necessary for establishment of target species.

Release of forest understory plants may also limit recruitment of meadow species. Although many shade-tolerant herbs are sensitive to increases in solar radiation and are likely to decline after overstory removal, some woody species (e.g., *Symphoricarpos mollis* and *Rubus ursinus*) show vigorous release and can dominate post-harvest understories for many years (e.g., Halpern 1989). When these species are abundant, attempts at restoration may produce shrub fields rather than grass- and forb-dominated meadow.

Encroachment of conifers in these ecosystems may represent a transition to an alternative stable state (e.g., Petraitis & Latham 1999), triggered by a change in climate or disturbance regime, and reinforced by a positive feedback between trees and the chemical and biological properties of soils (Griffiths et al. 2005).

Clearly, tree removal is a necessary precursor to meadow restoration. Whether prescribed fire is needed (or desirable) remains an open question. Although natural or anthropogenic burning may have contributed to the origin or maintenance of these ecosystems (Burke 1979; Vale 1981), anecdotal evidence from this and nearby meadows suggests that prescribed burning may not be an effective strategy once forests have developed. In tree islands that have been experimentally burned, *Abies* seedlings are likely to reestablish quickly and at high density: seed sources are locally abundant and consumption of forest litter by ground fire provides an ideal substrate for germination. Repeated entries to remove seedlings would be possible, but impractical at the spatial scales at which restoration treatments are likely to be implemented. Given the loss of meadow species, the depauperate nature of the seed bank, and the challenges of redirecting succession, the most effective strategy for conservation of these dry montane meadows is one that targets tree removal during the initial stages of encroachment.

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