The soil seed bank of a montane meadow: consequences of conifer encroachment and implications for restoration

Nicole L. Lang and Charles B. Halpern

Abstract: We examined changes in the soil seed bank associated with conifer encroachment of montane meadows in the western Cascade Range of Oregon. We asked whether, and over what period of time, meadow species maintain viable seeds in the soil, and by implication, whether the seed bank can contribute to restoration if conifers are removed. Seed bank composition, ground vegetation, and forest age structure were quantified for 209 samples representing a chronosequence of open meadow, young forest (<75 years), and old forest (95 to >200 years). The seed bank was substantial (44 taxa and 2332 germinants/m^2), but dominated by native ruderals (16 species comprising 71% of germinants). Greater than 70% of meadow species were absent from the seed bank. Thirteen meadow species accounted for 21% of all germinants, but most of these were the dominant sedge, *Carex pensylvanica* Lam.. Seed density, richness, and composition showed weak relationships to forest age, and little resemblance to the ground vegetation, which changed markedly with forest development. Our results suggest that there is limited potential for recovery of most meadow species via the seed bank. Natural reestablishment of these species will require seed dispersal or gradual vegetative spread from existing openings, but competitive interactions with ruderal or forest species may limit recruitment or recovery.

Key words: dispersal, meadow dynamics, meadow restoration, seed longevity, species richness, tree invasion.

Résumé : Les auteurs ont examiné les changements dans la banque de graines du sol, associés à la colonisation des prairies montagnardes par des conifères, dans l'ouest du Cascade Range, en Oregon. On a cherché à déterminer si, et au cours de quelle période de temps, les espèces de prairie maintiennent des graines viables dans le sol, et conséquemment, si la banque de graines peut contribuer à la restauration lorsqu'on enlève les conifères. On a quantifié la composition de la banque de graines, la végétation au sol, et la structure d'âge de la forêt, dans 209 échantillons représentant une chronoséquence, allant de la prairie à la jeune forêt (<75 ans), et à la forêt âgée (95 à >200 ans). La banque de graines est substantielle (44 taxons et 2332 germinats/m^2), mais dominée par des espèces indigènes rudérales (16 espèces constituant 71 % des germinats). Plus de 70 % des espèces de prairies sont absentes dans la banque. Treize espèces de prairies constituent 21 % de tous les germinats, mais la plupart de ceux-ci appartiennent au carex dominant, *Carex pensylvanica* Lam. La densité, la richesse et la composition des graines montrent une faible relation avec l'âge de la forêt, et il y a peu de ressemblance avec la végétation au sol, qui se modifie considérablement avec le développement de la forêt. Les résultats suggèrent que le potentiel de recouvrement des espèces de prairie via la banque de graines est limité. Le rétablissement naturel de ces espèces nécessitera la dispersion de graines, ou encore un étalement graduel à partir des ouvertures existantes, mais les interactions compétitives avec les espèces rudérales et forestières pourraient limiter le recrutement ou le recouvrement.

Mots-clés : dispersion, dynamique des prairies, restauration de la prairie, longévité des graines, richesse en espèces, invasion par les arbres.

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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 (Kemp 1989; Harrod and Halpern 2005), or for restoration of native plant communities (Graham and Hutchings 1988; van der Valk and Pedersen 1989). Seed banks are dynamic and responsive to factors that influence seed input and loss. Moreover, because seed longevity varies greatly among taxa, the composition of the seed bank can differ substantially from the resident flora (Leck et al. 1989).

Considerable attention has been devoted to the role of the seed bank in restoring grasslands degraded by intensive cultivation or other human activities (e.g., Bekker et al. 1997; Bakker and Berendse 1999; Bossuyt and Hermy 2001). Many natural or semi-natural grassland or prairie ecosystems are also threatened by afforestation or succession to scrub or woodland (e.g., Bakker et al. 1996; Davies and Waite 1998; Van Auken 2000; Lett and Knapp 2005). However, potential for restoration via the seed bank may be limited. Seed longevity is typically short (Milberg and Hansson 1993), although some grassland species retain viable seeds

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under woody plant cover for decades (Donelan and Thompson 1980; Bakker et al. 1996; Davies and Waite 1998). Moreover, seed banks are often dominated by ruderal taxa (native and exotic) that persist as legacies of earlier successional stages or accumulate via dispersal (Archibold 1989; Baker 1989; Halpern et al. 1999; Willson and Traveset 2000). Because germination is cued to disturbance and growth is rapid, ruderal species can compete with target species in restoration efforts (Matus et al. 2003; Bisteau and Mahy 2005).

Loss of grass- and forb-dominated meadows to the expansion of coniferous forest has become increasingly apparent in mountain landscapes throughout western North America. In some instances it may reflect natural processes associated with changes in climate (e.g., Rochefort and Peterson 1996; Miller and Halpern 1998), but it may also be an unintended consequence of past management, such as sheep grazing or fire suppression in the surrounding forest landscape (e.g., Vale 1981; Arno and Gruell 1986; Miller and Halpern 1998). In the Pacific Northwest, loss of meadows to forest encroachment can reduce local and regional diversity. These small, often isolated openings, support floras and faunas distinctly different from those of the surrounding landscape (Hickman 1976; Franklin and Halpern 1999; Miller et al. 2003; Haugo and Halpern 2007). As a consequence, federal land managers have begun to experiment with tree removal and prescribed fire as tools for restoration. However, forest encroachment has resulted in major loss of meadow species, necessitating their reestablishment. This leads to questions about the potential of the soil seed bank for restoration. Do species that characterize these meadows retain viable seeds in the soil? How does seed-bank composition and density change over time as meadows are gradually replaced by forest?

In this study, we use a chronosequence approach to address these questions in a montane meadow of western Oregon into which lodgepole pine, *Pinus contorta* Dougl. ex Loud., and grand fir, *Abies grandis* (Dougl. ex D. Don) Lindl. have colonized for nearly two centuries. This study is one of a series of retrospective and experimental studies examining spatial and temporal patterns of encroachment, associated changes in vegetation, and the potential for restoration through tree removal and prescribed burning (Haugo 2006; Haugo and Halpern 2007; C. Halpern, unpublished data, 2007). The objectives of this study are (*i*) to identify the contributions of meadow, forest, and ruderal species to the soil seed bank; (*ii*) to document changes in the composition, abundance, and richness of these functional types during the transition from open meadow to old forest; (*iii*) to determine the degree of correspondence between the seed bank and the local vegetation; and (*iv*) to discuss the implications of these findings for meadow restoration.

Study Area

Physical environment and vegetation

The study area, Bunchgrass Ridge (hereinafter, Bunchgrass), occurs on a broad, gently sloping plateau at an elevation of ca. 1300–1350 m in the Willamette National Forest, Oregon (44°17′N, 121°57′W) between the geologically older western Cascade Range and the younger, High Cascade Province to the east (Franklin and Dyrness 1988). Bunchgrass supports a 100 ha mosaic of dry, montane meadow and coniferous forest. Meadows are comprised of graminoids (primarily *Festuca idahoensis* Elmer and *Carex pensylvanica* Lam.) and herbs (*Achillea millefolium* L., *Fragaria* spp. L., and *Lupinus latifolius* Agardh.), and are floristically similar to *Festuca*-dominated communities throughout the western Cascade Range (Halpern et al. 1984; Franklin and Halpern 1999). Forests are dominated by *Abies grandis*, although *Pinus contorta* is locally abundant and typically the first to establish in open meadow. The forest understory is composed of species characteristic of rich, mesic sites at this elevation (Hemstrom et al. 1987), including *Smilacina stellata* (L.) Desf., *Galium oreganum* Britt., and *Anemone oregana* Gray. The surrounding landscape consists of mature- and old-growth forests of mixed species composition and young stands originating from clearcut logging in the 1970s and 1980s.

Soil profiles from areas of open meadow and old forest indicate centuries of development beneath grassland vegetation (D. A. Lammers, unpublished data, 2005); soils grade from Vitric Melanocryands in open meadow to Aquic Vitricryands in older forests. All are deep (>170 cm), fine to very fine sandy loams derived from andesitic basalt and tephra, 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 a.s.l.), 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 and McKee 1989). At Bunchgrass, temperatures are colder and precipitation is higher, with snow accumulations commonly exceeding 2 m and persisting into late spring.

Disturbance history

Information on fire and grazing history are lacking for Bunchgrass. Natural fires at this elevation are infrequent (>100 years; Teensma 1987). Although Native Americans are thought to have used fire to maintain meadow openings throughout the Pacific Northwest (Boyd 1999), stumps in recently cut experimental plots at Bunchgrass showed no evidence of fire scars, and previous archeological surveys yielded no artifacts originating from Native American use of the meadow (E. Bergland, personal communication, 2004). Grazing by sheep is likely to have occurred during the early part of the 20th century, synchronous with widespread grazing in the Cascade Range (Burke 1979; Johnson 1985; Rakestraw and Rakestraw 1991). However, historical records documenting use of Bunchgrass are not present in US Forest Service archives (Johnson 1985, E. Bergland, personal communication, 2004).

Methods

Sampling design

We selected four, from a set of nine, 1 ha experimental units (plots) that comprise the broader restoration experiment; these would subsequently be logged. Each plot included areas of open meadow, recent conifer encroachment, and older forest. In July 2003, a permanent grid was established within each plot to create 100 subplots, measuring 10 m × 10 m each. To ensure that a diversity of locations and vegetation conditions (open meadow to old forest) were sampled, 50 subplots were selected from each plot. Subplots were chosen as a stratified random sample of five forest structural (basal area) classes — 10 subplots per class (see the tree measurements below). To ensure adequate sampling of open meadow, nine additional subplots were randomly selected from those subplots that had no trees, yielding a total of 209 sampling locations.

Forest age, overstory structure, and vegetation composition

Within each subplot, species and diameter at breast height (dbh) were recorded for all trees ≥1.4 m tall. From these data we computed the local density and the basal area of stems. Each tree was also aged. Larger trees (ca. >10 cm dbh) were cored as close to the ground as possible; smaller trees were felled and a basal section was taken. Samples were sanded and annual rings were counted under 10–40× magnification. Ring-pattern templates were used to estimate missing rings if the pith was absent in a core. Adjustments for age-to-coring height were based on regression equations developed from a sample of 30–40 seedlings per species.

To characterize light availability associated with changes in forest structure, total transmitted light was estimated at the center of each subplot from a hemispherical photograph. 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 0800 or after 1800 h, 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).

Ground vegetation (including trees <1.4 m tall) was sampled between 5 July and 16 August 2004. Four 1 m × 1 m quadrats were placed within the central 6 m × 6 m area of each subplot, spaced at 1 m intervals along the northwest–southeast diagonal. Within each quadrat we visually estimated the cover of each vascular plant species; a subplot mean was then generated for each plant species. Nomenclature follows Hitchcock and Cronquist (1973).

Soil seed bank samples

Soil seed bank samples were collected from each of the 209 subplots between 22 and 25 May 2004, immediately after snowmelt. Three soil samples spaced 2 m apart were collected from areas between the four vegetation quadrats. At each point, the litter layer circumscribed by a bulb planter (6 cm diameter) was removed and retained. The bulb planter was then used to extract mineral soil to a depth of 10 cm (volume of ca. 283 cm^3). The three soil and litter samples from each subplot were combined (total soil volume of ca. 849 cm^3 per subplot), placed in coolers, and transported to refrigerators at the University of Washington, Seattle, Washington.

Greenhouse methods

On 30 May 2004, samples were mixed and spread in germination flats (25 cm × 25 cm) to a depth of 2 cm; roots and rhizome fragments were then removed. Flats were arranged randomly on two greenhouse benches and subirrigated using a capillary-mat system. Natural lighting was supplemented with 1000 W, metal-halide lamps to provide a 16 h light, 8 h dark photoperiod. To reduce possible contamination by wind-dispersed seeds, remay cloth was draped over a PVC frame above each bench. Twelve flats of potting soil were randomly distributed among samples as controls. Germination was monitored weekly at first, then bi-weekly. Germinants were marked 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 (after 2 months), soils were turned to expose new surfaces. On 15 September (after 3.5 months), samples were allowed to dry for ca. 1 week; samples were then stirred and rewetted. Monitoring was terminated on 3 January 2005 (ca. 7 months after initiation).

Classification of subplots and species

Trees were placed in 10-year age classes from which a composite age structure was developed. This revealed two broad but distinct periods of conifer establishment: ca. 1810–1910 and a more recent and intensive period of invasion from ca. 1930–1980 (Fig. 1). Based on local age structure, subplots were assigned to one of three stages of encroachment: (*i*) open meadow (characterized by no to few trees), (*ii*) young forest (high density of stems <75 years old), or (*iii*) old forest (fewer, but larger trees with ages of 95 to >200 years). Because most of the study area supported recent invasion, the sample size for young forest (n = 160) was much larger than that for open meadow (n = 24) or old forest (n = 25).

Each taxon was classified, a priori, by habitat affinity and geographic origin. Habitat affinity included meadow, forest, or ruderal (Hitchcock et al. 1969; Halpern et al. 1984; Halpern 1989; Franklin and Halpern 1999). Several taxa that were habitat generalists or identified only to genus could not be assigned to a group. Origin was native or exotic (Hitchcock et al. 1969; Hitchcock and Cronquist 1973).

Statistical analyses

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

To assess how well our 209 samples captured the diversity of species in the seed bank we generated species-accumulation curves and first-order jackknife estimate of richness (Heltsche and Forrester 1983; Palmer 1991) for all species and for the subset of meadow species.

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) was run. For each plot, 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 (McCune and Grace 2002). Correlation coefficients were uniformly low ($r = 0.016–0.169$) and nonsignificant for three of the four plots. Given that not more than 3% of the variation in composition was explained by proximity in space, subplots were treated as independent samples in subsequent analyses.

Changes in the seed bank with stage of encroachment

To test for differences in richness or density 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 and Rohlf 1981). Alternatively, when variance among groups was heterogeneous, a nonparametric, Kruskal–Wallis (K–W) test was used (followed by a Mann–Whitney U test for post-hoc comparisons). Separate tests were run for (*i*) richness and density of all taxa combined; (*ii*) richness and density of meadow, forest, and ruderal taxa; and (*iii*) density of native and exotic taxa (the number of exotic taxa was too small to test richness).

Detrended correspondence analysis (DCA; Hill and Gauch 1980) was used to portray gradients in seed bank composition. Germinant density was log-transformed and used as the measure of species abundance. Samples without germinants as well as species present in fewer than five subplots were removed from the analysis, yielding a total of 195 samples and 22 species. Default settings of PC-Ord version 4.0 were used (McCune and Mefford 1999). Multi-response permutation procedures (MRPP; Biondini et al. 1988) were then used to test whether seed bank composition differed among open meadow, young forest, and old forest subplots. MRPP is a nonparametric, Monte Carlo method that compares a weighted average within-group similarity to an expected average based on all possible partitions of the data for groups of the same size (McCune and Grace 2002). It produces an A-statistic (the chance-corrected within-group agreement, a measure of effect size) and a probability of statistical significance. Sørensen's coefficient was used as the distance measure. After an initial MRPP that included all stages of encroachment, separate pairwise comparisons were made. Indicator species analysis (ISPAN; Dufrêne and Legendre 1997) was used to identify species in the seed bank that showed fidelity to a specific stage of encroachment; 1000 randomizations were used to test the significance of maximum indicator values (IV_{max}) (McCune and Mefford 1999). Only species present in at least five subplots were considered.

Relationships with ground vegetation

We used several approaches to assess similarity between the ground vegetation and seed bank. For species composing both floras we calculated the frequency of occurrence (proportion of subplots) and the average abundance (cover or germinant density) at each stage of encroachment. For each subplot we also calculated the similarity of species composition using Sørensen's index (proportion of species common to both floras; Mueller-Dombois and Ellenberg 1974). We then calculated a mean similarity for each stage of encroachment. Finally, we tested whether the presence of individual species in seed bank samples was associated with presence in the vegetation. Fisher's exact test was employed on 2 × 2 contingency tables of species' presence or absence (Sokal and Rohlf 1981). One-tailed probability values were used to test for positive associations. Only species present in at least five seed bank samples were tested. All univariate analyses were conducted with SPSS version 12.0 (SPSS 2003) and multivariate analyses with PC-Ord version 4.0 (McCune and Mefford 1999).

Results

Changes in overstory structure

The three encroachment stages differed markedly in 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* or *Abies*. In young forests, stem densities were high (mean of 1552/ha); *Abies* was dominant, but *Pinus* was also common. Stem densities were 25% lower in old forests, but basal area was three times greater, reflecting presence of large-diameter (70 to >130 cm) *Abies*. Old forests were also characterized by stratification of the canopy into distinct overstory and understory layers.

Seed bank density, floristics, and representation of functional types

A total of 4130 germinants emerged from 196 of 209 soil samples; 13 samples (6%) yielded no germinants. The density of germinants ranged from 0 to 254 per sample (0–29 918/m^2) with a mean of 19.8 (2332/m^2) and a median of 8.0 (942/m^2). Forty-four species representing 23 families and 43 genera were identified (Table 2). The greatest number of species were from families Compositae and Gramineae (eight and seven, respectively). Only 85 germinants (2%) could not be identified and they were recorded as unknown dicots or graminoids.

Herbs (30 taxa) and graminoids (9 taxa) were more common in the seed bank than were shrubs or trees (3 and 2 species, respectively) (Table 2). Ruderals were dominant (16 species, 71% of all germinants). By comparison, there were 13 meadow species (21% of all germinants of which 80% were *Carex pensylvanica*), and 11 forest species (3% of all germinants). Five species were exotic (7% of germinants) of which *Lactuca muralis* (L.) Fresen. was the most common (6% of all germinants, 23% of samples). Species-accumulation curves (not shown) and jackknife estimates of richness (55 total species, 16 meadow species) suggest that our sample of 209 cores was sufficient to observe the vast majority of species in the seed bank, but that we may have missed a number of very infrequent taxa.

Changes in seed bank richness, density, and composition

Trends in total richness and density of germinants (Figs. 2*a* and 2*b*) were largely shaped by ruderals. Richness of ruderals was greatest in old forest (Fig. 2*c*); germinant density tended to decline with forest age, but did not differ significantly among stages (Fig. 2*d*). Richness and density of meadow species did not vary with stage of encroachment (Figs. 2*e* and 2*f*). Richness and density of forest species

Fig. 1. Composite age structure of trees ≥1.4 m tall. Ages are mid-points of 10 year classes. The age structure of trees representing old forest is rescaled and enlarged for clarity.

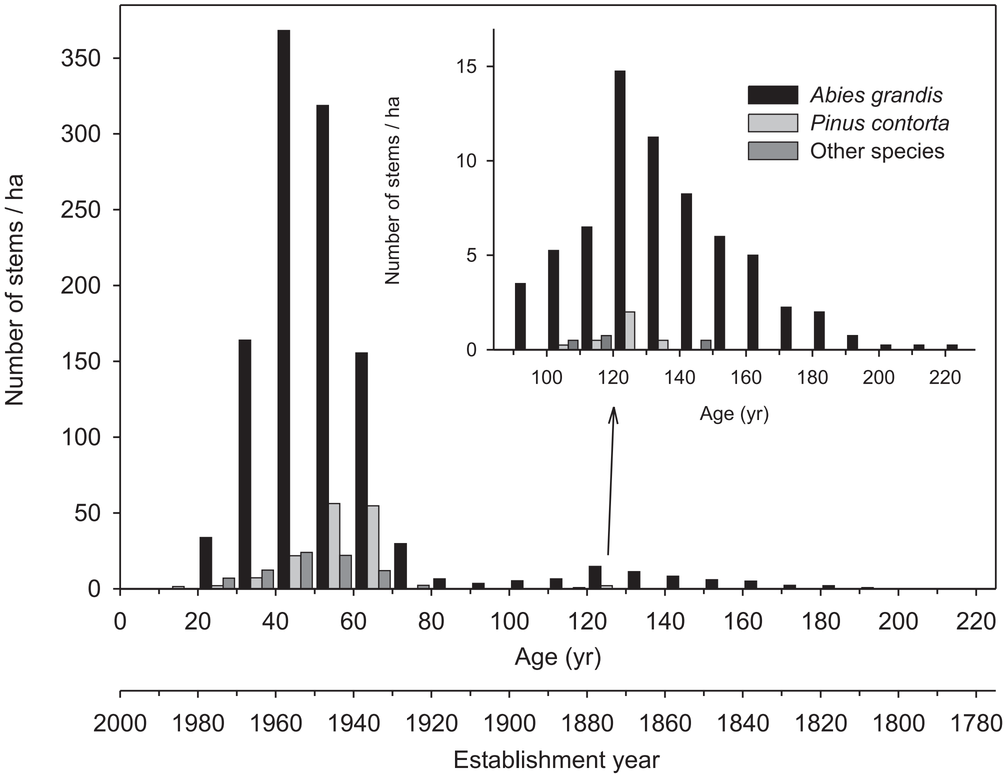


Table 1. Transmitted light and forest structure among encroachment classes.

	Open meadow (n = 24)		Young forest (n = 160)		Old forest (n = 25)	
Structural variable	Mean	SE	Mean	SE	Mean	SE
Transmitted light (%)	46.3	4.5	21.7	0.9	17.2	0.8
Stem density (stems/ha)						
Pinus contorta	17	10	180	17	28	11
Abies grandis	71	20	1268	63	1108	115
Other species	8	8	104	11	36	11
Total	96	28	1552	74	1172	121
Basal area (m^2/ha)						
Pinus contorta	0.2	0.1	5.8	0.7	2.1	1.7
Abies grandis	5.6	3.6	28.9	2.4	111.4	13.8
Other species	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

Note: n is the number of samples; n is reduced for transmitted light: open meadow (14), young forest (155), and old forest (24). Density and basal are based on trees ≥1.4 m tall. "Other species" are *Abies amabilis*, *Calocedrus decurrens*, *Castanopsis chrysophylla, Pinus monticola*, *Pseudotsuga menziesii*, *Taxus brevifolia*, *Tsuga heterophylla*, and *Tsuga mertensiana.*

tended to increase with forest age, but not significantly (Figs. 2*g* and 2*h*).

Germinant density of native species tended to be lowest in old forest, but differences were not significant among groups (Fig. 3*a*). Density of exotics was greatest in old forest (Fig. 3*b*); most germinants were *Lactuca muralis* (Table 2).

DCA revealed considerable overlap in seed bank composition among open meadow, young forest, and old forest samples. Each stage showed considerable variation along axis 1 (total gradient length of 5.45 SD unit) although meadow samples were largely restricted to the right half of axis 1 (higher scores) and old forest samples to the left half (lower scores) (Fig. 4*a*). Species with the highest scores on axis 1 were *Danthonia intermedia* Vasey, *Achillea millefolium*, and *Festuca idahoensis* — all meadow species (Fig. 4*b*; Table 2). Species with the lowest scores included the forest herbs, *Circaea alpina* L., *Campanula scouleri* Hook. ex A. DC., and *Galium triflorum* Michx., as well as the exotic ruderal, *Lactuca muralis* (common in old forests) (Fig. 4*b*).

Results of MRPP were consistent with DCA. There was 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 for-

Table 2. Frequency of occurrence (% of subplots) and abundance (mean cover or germinant density) of species in the ground vegetation and seed bank among the three encroachment classes.

			Vegetation						Seed bank					
			Frequency (%)			Cover (%)			Frequency (%)			Density (no./m^2)		
Species	Hab.	Origin	M	YF	OF	M	YF	OF	M	YF	OF	M	YF	OF
Graminoid														
Agrostis scabra	R	N	8	1		0.1	t		71	72	68	2042	1377	353
Carex pensylvanica	M	N	88	86	60	18.6	11.4	2.4	29	53	60	108	465	160
Unknown graminoids	—	—		4	4		t	t	25	8	16	29	8	16
Danthonia intermedia	M	N	54	5	4	0.9	0.1	t	17	1	4	20	2	5
Festuca idahoensis	M	N	92	31	24	18.9	1.9	1.5	4	3	8	5	5	9
Elymus glaucus	M	N	96	50	32	14.6	3.2	2.8	4	1	4	5	2	5
Luzula campestris	R	N	13	1	4	t	t	t	4	1	4	5	2	5
Stipa occidentalis	M	N	25	1		0.2	t		4			5		
Bromus vulgaris	F	N	46	74	84	0.8	3.7	3.0		2			3	
Melica subulata	F	N	25	45	68	1.2	1.0	1.5		1			1	
Bromus carinatus	M	N	75	20	28	3.9	0.9	0.5						
Agropyron repens	M	E	17	1		0.4	t							
Poa pratensis	M	E	17			0.1								
Herb														
Epilobium watsonii	R	N	4	8		t	t		25	33	40	98	124	113
Achillea millefolium	M	N	100	66	32	6.9	1.8	0.6	21	4		49	6	
Fragaria virginiana or *F. vesca*	M	N	96	92	60	6.3	4.4	1.1	17	16	20	20	38	24
Unknown dicots	—	—							17	16	24	236	31	47
Gnaphalium microcephalum	R	N							17	1	4	20	2	5
Lactuca muralis	R	E	13	43	80	0.9	1.0	5.0	8	19	64	15	108	382
Ranunculus uncinatus	—	N	17	12	32	0.1	t	0.1	4	20	36	39	68	75
Galium triflorum	F	N	17	63	88	0.3	0.8	3.9	4	13	24	5	25	57
Cirsium callilepis	M	N	92	40	28	3.9	0.8	0.2	4	4	4	5	6	5
Rumex acetosella	R	E		1	4		t	t	4	3	4	83	15	5
Hieracium albiflorum	F	N	29	81	40	0.2	1.1	0.4	4	1	4	15	2	5
Montia sibirica	R	N	4	2	28	0.6	t	0.9	4	1	8	5	1	19
Viola glabella	F	N	50	86	84	0.7	1.5	0.9	1			2		
Vicia americana	M	N	54	20	44	2.0	0.4	0.7	1			1		
Senecio sylvaticus	R	E								6	16		8	24
Campanula scouleri	F	N	8	61	48	0.3	2.0	1.7		6			12	
Arenaria macrophylla	F	N	58	79	80	0.3	1.1	0.8		6	4		7	5
Circaea alpina	F	N	8	26	88	0.1	0.7	5.1		5	16		13	19
Iris chrysophylla	M	N	33	69	40	0.8	2.1	0.4		1			2	
Asarum caudatum	F	N	4	36	44	0.3	1.6	1.7		1			1	
Unknown herb 1	—	—									8			9
Comandra umbellata	M	N	21	6	8	0.2	t	t			4			5
Erigeron aliceae	M	N	83	59	20	5.1	1.5	0.3						
Lupinus latifolius	M	N	75	33	4	6.5	0.9	t						
Lathyrus nevadensis	M	N	50	26	52	9.4	1.0	4.6						
Pteridium aquilinum	M	N	42	2		7.5	0.1							
Hieracium gracile	M	N	38	26	8	0.9	0.6	t						
Anemone oregana	F	N	33	58	80	0.2	0.6	0.6						
Galium oreganum	F	N	33	56	56	2.0	3.1	2.4						
Aster ledophyllus	M	N	33	9	4	0.9	0.1	0.1						
Osmorhiza chilensis	F	N	29	88	100	0.3	1.1	2.7						
Aster occidentalis	M	N	29	8		0.7	0.2							
Phlox diffusa	M	N	25	18	4	3.2	0.7	0.3						
Agoseris aurantiaca	M	N	25	8		0.2	0.1							
Anemone deltoidea	F	N	21	83	68	0.1	1.5	0.7						
Calochortus subalpinus	M	N	21	6		0.1	t							
Agoseris sp.	M	N	17	14	8	0.1	0.1	t						
Orthocarpus imbricatus	M	N	17	6		0.4	t							
Smilacina stellata	F	N	13	57	92	0.7	5.1	14.2						
Aster radulinus	M	N	13	13	16	0.3	0.4	0.5						
Anaphalis margaritacea	M	N	13	9		0.1	0.1							
Trillium ovatum	F	N	8	11	36	0.3	0.1	0.3						
Adenocaulon bicolor	F	N	4	64	56	t	1.9	1.5						
Rubus lasiococcus	F	N	4	44	24	0.1	1.3	0.2						

Table 2 (*concluded*).

			Vegetation						Seed bank					
			Frequency (%)			Cover (%)			Frequency (%)			Density (no./m^2)		
Species	Hab.	Origin	M	YF	OF	M	YF	OF	M	YF	OF	M	YF	OF
Actaea rubra	F	N	4	39	76	0.1	1.9	4.8						
Viola nuttallii	M	N	4	32	4	t	0.1	t						
Clintonia uniflora	F	N	4	16	12	t	0.4	0.3						
Anemone lyallii	F	N	4	16		t	t							
Lilium columbianum	—	N	4	12	8	t	0.1	t						
Trientalis latifolia	F	N	4	7	16	t	t	0.1						
Listera caurina or *L. cordata*	F	N		33			0.1							
Tiarella trifoliata	F	N		30	40		0.6	0.4						
Rubus ursinus	F	N		25	20		0.4	0.9						
Goodyera oblongifolia	F	N		6	12		t	0.1						
Disporum hookeri or *D. smithii*	F	N		1	12		t	0.1						
Shrub and Tree														
Abies grandis	F	N	4	46	4	0.1	0.8	t	4	3		5	4	
Symphoricarpos mollis	F	N		28	20		0.8	0.4						
Amelanchier alnifolia	F	N		11	12		0.1	0.1						
Rosa gymnocarpa	F	N		3	12		t	0.2						

Note: Open meadow, M (n = 24); young forest, YF (n = 160); and old forest, OF (n = 25). Codes for habitat affinity (Hab) are forest (F), meadow (M), and ruderal (R). N, native; E, exotic . Species that could not be classified are coded as "—". Species are listed if the frequency of occurrence was ≥10% in the vegetation or seed bank in at least one encroachment class. Within growth forms, species are arranged by descending frequency of occurrence in the meadow seed bank. Cover <0.1% is reported as "t" (trace).

est (A = 0.0472, p < 0.0001). However, for all tests, values of the A-statistic were very low, indicating that compositional differences were small.

Indicator species analysis (ISPAN) yielded only five taxa in the seed bank that showed positive associations with specific stages of encroachment (Table 3). Two meadow species and one ruderal were associated with open meadow, and two exotic ruderals were associated with old forest. However, maximum indicator values (a measure of the degree of association) were low for all but one species, *Lactuca muralis*.

Relationships between the seed bank and vegetation

Floristically, the seed bank and vegetation differed markedly. The vegetation was comprised of 113 taxa, 69 more than the seed bank. Of these, 40 were classified as meadow species, 59 as forest species, and 10 as ruderal species (4 remained unclassified; Table 2). Eleven (28%) of the meadow species were also present in the seed bank, as were 11 (20%) of the forest species. In contrast, all ruderals in the vegetation were also present in the seed bank.

In addition, species with high frequency in the seed bank were generally infrequent in the vegetation (Table 2). *Carex pensylvanica*, the dominant meadow sedge, was an exception, with high frequency in both the seed bank (51% of samples) and vegetation (83%). The most abundant species in the seed bank, *Agrostis scabra* Willd., a ruderal, was present in 71% of samples (57% of all germinants), but occurred in the vegetation in only 1% of subplots. Within individual subplots, similarity of species composition was extremely low. Sørensen's index, which can range from 0 to 1, averaged 0.05–0.08 among encroachment classes.

Only 13 of 44 species were present with sufficient frequency to test whether their presence in the seed bank was associated with presence in the vegetation. Six of these species showed significant associations (p < 0.0001–0.002): one meadow grass (*Danthonia intermedia*), three forest herbs (*Circaea alpina*, *Campanula scouleri*, and *Galium triflorum*), one ruderal herb (*Lactuca muralis*), and one unclassified herb (*Ranunculus uncinatus* D. Don ex G. Don).

Discussion

Density, richness, and composition of the seed bank

Ours is the first description of the soil seed bank in these montane meadow systems. Soils from both meadows and forests supported a well-developed and diverse community of viable seeds. Germinants occurred in 94% of samples with densities averaging >2300 seeds m^2, comparable in magnitude to those reported from other grasslands and coniferous forests in western North America (Major and Pyott 1966; Pratt et al. 1984; Kramer and Johnson 1987; Rice 1989; Harmon and Franklin 1995).

Because seed banks can show high spatial variability (e.g., Bigwood and Inouye 1988), we chose to maximize replication rather than to stratify samples by depth (e.g., litter vs. mineral soil). Thus, we do not attempt to quantify the relative contributions of transient versus persistent seeds (e.g., Thompson et al. 1997). The relative persistence of meadow species — the focus of this study — is instead inferred from the chronosequence of meadow and forest soils.

Ruderals dominated seed-bank samples in richness and especially in density, greatly exceeding the contributions of meadow and forest species. This is consistent with many grassland (Pratt et al. 1984; Rice 1989) and forest soils (Kellman 1970; Halpern et al. 1999; Bossuyt and Hermy 2003). Many of the common ruderal species at Bunchgrass possess plumed or comose seeds for long-distance dispersal (e.g., *Conyza canadensis* (L.) Cronq., *Epilobium watsonii* Barbey, *Gnaphalium microcephalum*, and *Senecio sylvaticus*) and are colonists of early seral forests throughout the region (Kellman 1970; Schoonmaker and McKee 1988; Halpern 1989; Halpern et al. 1999). However, dominance of the

Fig. 2. Mean (+1 SE) richness and density of germinants by functional type (habitat affinity) among the three stages of encroachment; *p* values are from ANOVA or Kruskal–Wallace (KW) tests. Differing letters above bars indicate significant differences in means (see Methods).

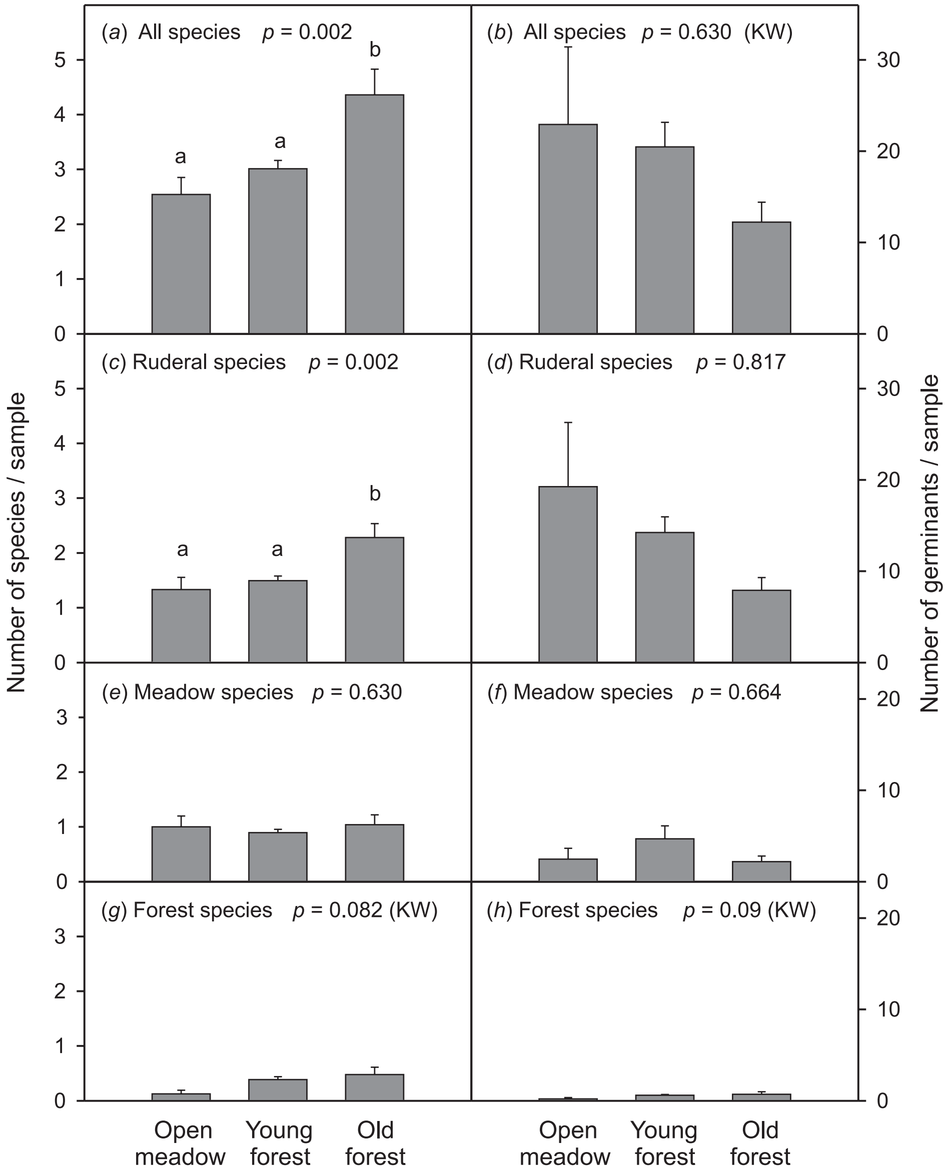


Fig. 3. Mean (+1 SE) density of native and exotic germinants among the three stages of encroachment; *p* values are from Kruskal–Wallace (KW) tests. Differing letters above bars indicate significant differences in means (see Methods).

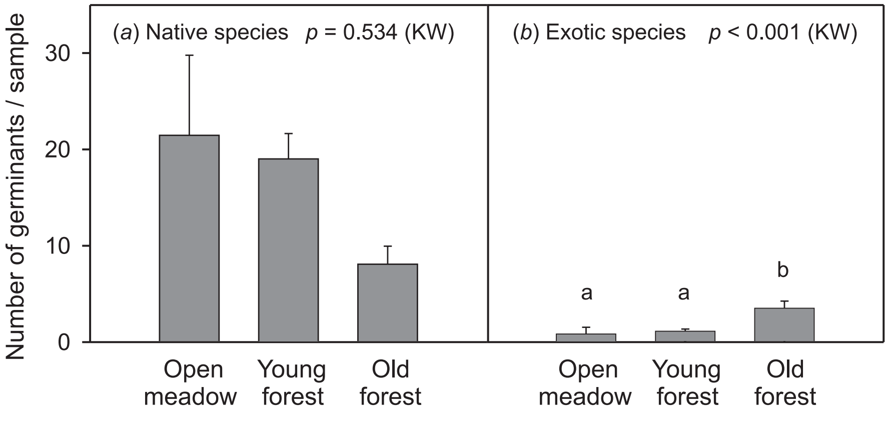
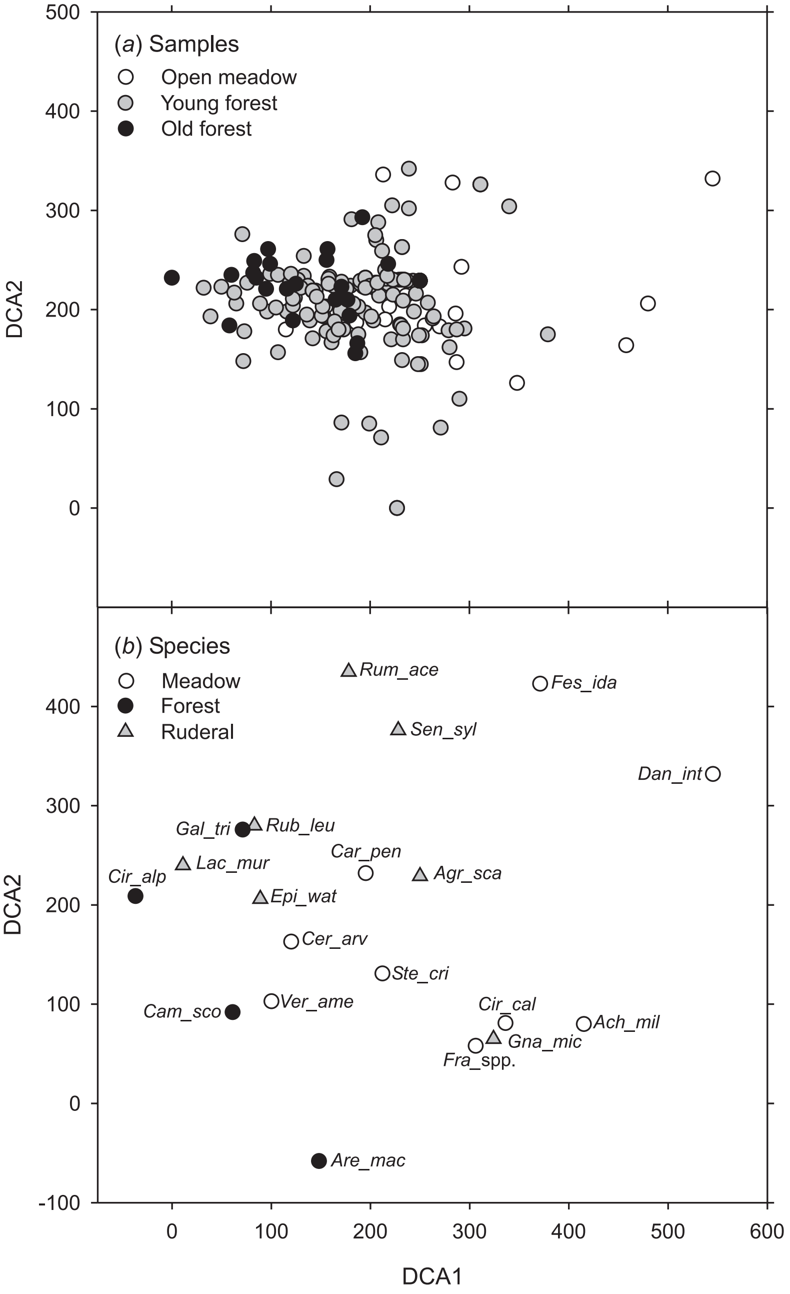


Fig. 4. DCA ordination of seed bank (*a*) samples and (*b*) species. Log-germinant density was used as the measure of species abundance. Ach_mil, *Achillea millefolium*; Agr_sca, *Agrostis scabra*; Are_mac, *Arenaria macrophylla*; Cam_sco, *Campanula scouleri*; Car_pen, *Carex pensylvanica*; Cer_arv, *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.



seed bank by *Agrostis scabra* was surprising. Although dispersal by wind is possible (e.g., Harmon and Franklin 1995), seeds of *A. scabra* do not possess traits for long-distance transport. The presence of *A. scabra* along roadsides or in adjacent clearcuts (Klinka et al. 1985) may have allowed for dispersal and accumulation in the seed bank.

More than 70% of the species comprising the meadow flora were absent from the seed bank, and the vast majority of meadow germinants were of a single species. Even common grass genera (*Elymus*, *Bromus*, and *Festuca*) — prolific seed producers and potential seed bankers (Strickler and Edgerton 1976; Pratt et al. 1984; Pitschel and Clinebell 1988) — were sparse in the germinant pool. Only two meadow species in the seed bank, *Achillea millefolium* and *Danthonia intermedia*, were significant indicators of meadow habitat, and only *Danthonia* showed spatial coherence with its distribution in the vegetation. For most meadow taxa, population persistence appears to occur pri-

Table 3. Seed bank species exhibiting significant associations ($p \leq 0.05$) with a particular stage of encroachment, based on indicator species analysis (ISPAN).

Species (habitat affinity)	Max group	IV_{max}	p
Achillea millefolium (meadow)	Meadow	19.3	0.004
Danthonia intermedia (meadow)	Meadow	13.2	0.008
Gnaphalium microcephalum (ruderal)	Meadow	13.2	0.010
Lactuca muralis (ruderal)	Old forest	50.0	0.001
Senecio sylvaticus (ruderal)	Old forest	12.3	0.046

Note: Only taxa present in ≥5 samples were considered. “Max group” is the stage of encroachment in which a species exhibited its maximum observed indicator value, IV_{max}; p is the proportion of randomized trials with an IV equal to or exceeding the observed IV.

marily through vegetative means (or recruitment from a transient seed bank), not through maintenance of persistent seeds (Rice 1989).

Forest herbs were also of minor importance in the seed bank, even in old forest. In most forest ecosystems, the characteristic understory species do not maintain viable seeds (Archibold 1989; Halpern et al. 1999; Bossuyt and Hermy 2001) and establishment from seed is generally infrequent (Bierzychudek 1982). Instead, most are clonal (Sobey and Barkhouse 1977; Antos and Zobel 1984) and rely on vegetative growth for persistence and spread. At Bunchgrass, however, seed dispersal and establishment have been integral in the gradual colonization of newly forming tree islands by forest herbs (Haugo and Halpern 2007), but establishment likely occurs without an intervening period of dormancy. Trends in richness and germinant density suggest a gradual accumulation of seeds as forests age, but at very low rates. Increases in richness of the ground vegetation were rapid by comparison (Haugo and Halpern 2007).

Changes in the seed bank with stage of encroachment

Despite the broad span of time represented by the chronosequence, the seed bank showed surprisingly small temporal variation. Density and richness of meadow taxa were consistently low and comparable among stages. For the few meadow species present in the seed bank, trends in frequency and density suggest that distributions are shaped by local input and short-distance dispersal, rather than long-term persistence. Few species showed declines in density among successive stages that would suggest a gradual senescence of viable seed (*cf*. Milberg 1995; Bakker et al. 1996; Davies and Waite 1998; Bossuyt and Hermy 2001). *Achillea millefolium* was an exception: seed density declined dramatically from meadow to young forest and seeds were absent in old forest. In contrast, seeds of *Carex pensylvanica* and *Fragaria* spp. were frequent and (or) abundant at each stage, which likely reflects continuous, local input — both species were present at high frequency in young and old forest (Table 2; see also Haugo and Halpern 2007). For other meadow species that were absent from the forest understory, low densities of seed in the soil may reflect proximity to propagule sources. Most patches of young and old forests at Bunchgrass either include small meadow remnants, or lie adjacent to larger meadow openings from which dispersal may occur (e.g., Dutoit and Alard 1995; Bisteau and Mahy 2005).

The density and diversity of seeds of ruderal species typically decrease during forest succession, reflecting the combined effects of reduced inputs (as ruderal species decline in abundance) and gradual loss of seeds to decay, predation, and germination (Oosting and Humphreys 1940; Livingston and Allessio 1968; Leck et al. 1989). However, ruderals play a minor role in meadow communities at these elevations in the Pacific Northwest (Halpern et al. 1984, Hemstrom et al. 1987) and in situ accumulation of seeds should be small. Thus, differences in the density of ruderal seeds in meadow and forest soils are likely to reflect differences in dispersal, not a gradual decay of a persistent seed bank. At Bunchgrass, these trends were driven by the spatial distribution and dispersal of *Agrostis scabra* and *Lactuca muralis*, which dominated the ruderal germinant pool. Seed density of *Agrostis* declined significantly from meadow to old forest, reflecting poorer dispersal from nearby clearcuts into forests where wind speeds are typically reduced (e.g., Willson and Crome 1989; Chen et al. 1995). In contrast, seeds of *Lactuca* increased markedly in old forest where it was locally abundant in the vegetation, flowering in profusion. *Lactuca* is one of the few exotics in this region that can establish and persist in shaded habitats (Clabby and Osborne 1997; Parendes and Jones 2000). Local input of seed explains its highly significant association (IV_{max}) with old-forest habitats and the strong spatial correspondence between the seed bank and vegetation. It was largely responsible for the counterintuitive result that richness of ruderals in the seed bank increased with forest age.

Implications for restoration

Conifer encroachment at Bunchgrass has been accompanied by dramatic changes in vegetation composition and structure. Successful restoration will require rejuvenation or reintroduction of many species that have experienced loss of vigor or abundance, or local extirpation. However, our results suggest that even with removal of the overstory, reestablishment of most species will not occur through a relictual seed bank. Similar constraints limit potential for restoration in other grasslands (Bakker and Berendse 1999; Bossuyt and Hermy 2003; Bisteau and Mahy 2005; Lett and Knapp 2005) and suggest that natural recovery would require dispersal of seeds into the target system (Dutoit and Alard 1995; Poschlod et al. 1998; Bakker and Berendse 1999). In our system, characterized by a patchy mosaic of forest and meadow, restoration efforts should target ecotonal areas or small tree islands to maximize the potential for dispersal (or vegetation spread of clonal species). In addition, soils in ecotonal areas are likely to retain properties of meadow soils (Griffiths et al. 2005) that are more conducive to germination and establishment of target species. Where the potential for natural dispersal is low, artificial seeding can be used to reintroduce species (e.g., McDonald 1993; Maret and Wilson 2000). However, this approach requires access to abundant sources of seed and consideration of the genetic and ecological consequences of introducing nonendemic genotypes (Lesica and Allendorf 1999; Jones 2003).

Dominance of the seed bank by ruderal species poses a challenge to restoration. Activities that expose or heat mineral soils will facilitate germination and growth of disturbance-dependent annuals and short-lived perennials (e.g., Schoonmaker and McKee 1988; Halpern 1989) that can compete with target species. Strategies that minimize soil disturbance (e.g., tree removal on snow or spring versus late-season burning) may reduce these impacts. However, disturbance may be necessary to induce germination of some meadow species. Competition from forest understory plants may also limit recruitment of meadow species. Although many shade-tolerant herbs are likely to decline after tree removal, some woody species (e.g., *Symphoricarpos mollis* and *Rubus ursinus*) are released and can dominate for many years after harvest (Halpern 1989). Where these woody species are initially abundant, attempts at restoration may produce shrub fields rather than graminoid- or herb-dominated communities.

Clearly, tree removal is a necessary precursor to meadow restoration. Whether fire is also needed remains an open question. Natural or anthropogenic burning may have contributed to the origin or maintenance of these systems (Burke 1979; Vale 1981). However, anecdotal evidence from Bunchgrass and nearby meadows suggests that under current conditions, prescribed burning may not be effective where conifers are already well established. In tree islands that were successfully killed by small experimental burns, *Abies* seedlings germinated quickly at high density, facilitated by abundant seed sources in adjacent forest and exposure of mineral soils by fire. Subsequent removal of seedlings is possible, but would be impractical to implement at larger spatial scales. Given the composition of the seed bank and the potential challenge of redirecting succession, the most effective and efficient strategy for maintaining open meadows in this landscape is one that targets tree removal during the initial stages of encroachment.

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