

# Vegetation responses to conifer encroachment in a western Cascade meadow: a chronosequence approach

Ryan D. Haugo and Charles B. Halpern

**Abstract:** Conifer invasion of mountain meadows is pervasive in western North America, but its consequences for plant composition and diversity have not been studied. We used a chronosequence approach to reconstruct temporal patterns of vegetation change in response to ~200 years of conifer encroachment of a dry, montane meadow in the western Cascade Range, Oregon. Tree age distributions, forest structure, light, and vegetation composition were determined for three hundred and fifty-six 10 m × 10 m samples representing a gradient from open meadow to old forest (>90 years). Nonmetric multidimensional scaling revealed strong turnover in species composition from open meadow to old forest. Ordination axes were highly correlated with light availability and density/basal area of encroaching grand fir, *Abies grandis* (Dougl. ex D. Don) Lindl., and lodgepole pine, *Pinus contorta* Dougl. ex Loud. Cover of meadow species declined steeply with establishment of *A. grandis*; richness declined more gradually and extirpations of meadow species were rare. Forest herbs colonized within two decades of tree establishment and within 60–80 years dominated the understory flora. In contrast with meadow species, changes in richness and cover of forest herbs were weakly related to changes in forest structure. Rapid replacement of meadow by forest species and long-term effects of trees on soils may limit potential for restoration of these unique habitats.

**Key words:** colonization, meadow dynamics, overstory–understory relationships, Pacific Northwest, species richness, tree invasion.

**Résumé :** L'invasion par les conifères des prairies montagneuses, est omniprésente dans l'ouest de l'Amérique du Nord, mais on en a jamais étudié les impacts sur la composition et la diversité végétale. Les auteurs utilisent une chronoséquence pour reconstruire les patrons temporels du changement de la végétation, en réaction à ~200 ans d'avancées des conifères, dans une prairie montagnarde sèche de l'ouest du Cascade Range, en Oregon. Les auteurs ont déterminé la distribution de l'âge des arbres, la structure forestière, la lumière et la composition de la végétation, sur 356 échantillons de 10 m × 10 m représentant un gradient allant de la prairie ouverte à la forêt surannée (<90 ans). L'ordination selon une échelle multidimensionnelle non-métrique (NMS) révèle un forte rotation dans la composition en espèces, de la prairie à la forêt surannée. Les axes d'ordination sont fortement corrélées avec la disponibilité de la lumière et la surface densité/basale du pin lodgepole et du sapin grand fir. La couverture par les espèces de prairie diminue rapidement avec l'établissement de l'*Abies*; la richesse décline plus graduellement et l'extirpation d'espèce de prairie est rare. En moins de deux décades d'établissement des arbres, les herbacées forestières s'installent et dominent le sous-étage en moins de 60–80 ans. Contrairement aux espèces de la prairie, les changements dans la richesse et la couverture des herbacées forestières montrent peu de relation avec la structure forestière. Le remplacement rapide des espèces de la prairie par les espèces forestières et l'effet à long terme des arbres sur le sol pourraient limiter le potentiel de restauration de ces habitats uniques.

**Mots-clés :** colonisation, dynamique des prairie, relation canopée-sous-étages, Pacific Northwest, richesse en espèces, invasion par les arbres.

[Traduit par la Rédaction]

## Introduction

Encroachment of woody species threatens the biological diversity of grasslands and other nonforested ecosystems in many regions of the world (Van Auken 2000). The causes of encroachment have been considered from many perspectives, including responses to changes in climate, land use, or

disturbance regime (e.g., Rochefort et al. 1994; Bond and Midgley 2000; Sturm et al. 2005). The consequences can be far-reaching and potentially irreversible, affecting soil ecosystem properties (Jackson et al. 2002; Griffiths et al. 2005), vegetation structure and productivity (Hobbs and Mooney 1986; Scholes and Archer 1997), and native plant diversity (Moore and Huffman 2004). In the Pacific Northwest, as in much of western North America, invasion of mountain meadows by conifers represents a recent, but widespread phenomenon triggered by changes in climate (Taylor 1995; Woodward et al. 1995; Rochefort and Peterson 1996; Miller and Halpern 1998), cessation of sheep grazing (Dunwiddie 1977; Vale 1981; Miller and Halpern 1998), and long-term suppression of wildfire (Arno and

Received 13 February 2007. Published on the NRC Research Press Web site at canjbot.nrc.ca on 8 June 2007.

**R.D. Haugo<sup>1</sup> and C.B. Halpern.** College of Forest Resources, P.O. Box 352100, University of Washington, Seattle, WA 98195-2100, USA.

<sup>1</sup>Corresponding author (e-mail: haugor@u.washington.edu).

Gruell 1986; Hadley 1999). In this region, montane meadows typically occur as small, isolated habitats with floras that are distinctly different from those of the surrounding forested landscape (Halpern et al. 1984; Franklin and Halpern 1999). Thus, conversion to forest can have direct impacts on local and regional patterns of diversity. Faced with gradual loss or degradation of these systems, natural resource managers have begun to experiment with prescribed fire as a strategy for their restoration and maintenance. Yet, little research has been devoted to the consequences of encroachment for biological diversity, to the rates at which meadow species are lost and forest species establish, or to how these changes may influence the potential for restoration. This is one of a series of retrospective and experimental studies that address these basic questions and challenges for management (Haugo 2006; Lang and Halpern 2007; C.B. Halpern, unpublished data, 2007).

Two types of processes accompany the transformation of grass- or forb-dominated meadows to those dominated by woody plants (trees in particular): loss of resident species adapted to open environments and colonization of understory species adapted to shade. Displacement of the former can occur through reductions in light, physical effects of litter accumulation, or changes in the chemical or biological properties of soils (Scholes and Archer 1997; Lett and Knapp 2003, 2005; Siemann and Rogers 2003; Griffiths et al. 2005). Positive feedbacks may develop between shrubs or trees and soil processes, ultimately leading to an alternative stable state (e.g., Archer 1990; Lett and Knapp 2003, 2005). Given the strong control of trees on the physical environment (Belsky et al. 1989; Amioti et al. 2000), declines in the abundance and diversity of meadow species should be closely tied to the density and duration of forest cover.

In contrast, colonization of forest understory species requires not only suitable environmental conditions but also successful dispersal (e.g., Brunet and von Oheimb 1998). Yet, dispersal distances are short for many forest herbs (Bierzuchdek 1982; Cain et al. 1998), potentially limiting rates of colonization (Matlack 1994; Butaye et al. 2002; Verheyen et al. 2003; Verheyen and Hermy 2004). Subsequent community development can be shaped by many factors including variation in resource availability, competition, and potential for clonal spread (Tappeiner and Alaback 1989; Lezberg et al. 1999). Thus, colonization and subsequent patterns of forest understory development should be less predictable and less responsive to changes in forest structure.

In this study, we explore these processes in a western Cascade meadow by reconstructing temporal changes in vegetation during nearly two centuries of encroachment of lodgepole pine, *Pinus contorta* Dougl. ex Loud., and grand fir, *Abies grandis* (Dougl. ex D. Don) Lindl. The study area provides an ideal setting for a chronosequence approach: it supports a large mosaic of grass- and forb-dominated meadow with forests of varying age that have established on similar topography and soils. We address the following questions. (i) How does the composition, abundance, and richness of meadow and forest understory species change during the transition from open meadow to old forest? How rapidly, and to what extent, are meadow

species lost from these systems? How quickly do forest species colonize and how does understory composition change in forests of increasing age? (ii) Do species within the same functional type (meadow or forest) show parallel trends in abundance? If not, can differences be explained by variation in life history traits (e.g., mode of dispersal)? (iii) Which attributes of forest structure (e.g., light, density, or basal area of trees) exhibit the strongest controls on vegetation, and do these attributes or the strength of relationships differ for meadow and forest species?

## Methods

### Study area

Bunchgrass Ridge (hereinafter Bunchgrass) forms a large (100 ha), gently sloping plateau in the Cascade Range of western Oregon (44°17'N, 121°57'W). It lies along the boundary of the geologically older and steeply dissected western Cascades and the younger, rolling terrain of the high Cascades (Franklin and Dyrness 1988). Elevations range from ~1300 to 1375 m; slopes rarely exceed 5% and generally face southward.

Bunchgrass supports a mosaic of dry meadow, areas of recent conifer encroachment (30–70 years), and older forest (>90 years). Meadows are dominated by graminoids (primarily *Festuca idahoensis* Elmer and *Carex pensylvanica* Lam.) and forbs (e.g., *Lupinus latifolius* Lindl. ex J.G. Agardh., *Erigeron aliceae* T.J. Howell, and *Phlox diffusa* Benth.). Forests are dominated by *A. grandis* in both the canopy and the subcanopy, but *P. contorta* commonly occurs as scattered individuals or cohorts that have invaded open meadow. Understories in older forests are dominated by herbs typical of rich, mesic sites in this region (e.g., *Smilacina stellata* (L.) Desf.), *Achlys triphylla* (Sm.) DC., *Galium oregonum* Britt., and *Anemone oregana* Gray; Hemstrom et al. 1987). Bunchgrass is surrounded by mature and old-growth forests, except for some stands that were clearcut and replanted in the 1970s and 1980s.

Soil profiles from areas of both open meadow and old forest indicate centuries of development beneath grassland vegetation (D.A. Lammers, personal communication, 2005). Soils are deep (>170 cm), fine to very fine sandy loams derived from andesitic basalt and deposits of tephra and contain large and highly variable amounts of glacially derived cobbles, stones, and boulders. They grade from Vitric Melanocryands in open meadow to Aquic Vitricryands in older forests (D.A. Lammers, unpublished data, 2005). Annual precipitation at Santiam Pass (1488 m elevation), the closest appropriate climate station 17 km to the north, averages ~216 cm, with 7.5% falling from June through August. Annual snowfall averages 1152 cm and winter snowpacks can exceed 2 m. Average minimum and maximum temperatures are –6.9 and 0.7 °C in January and 6.1 and 27.8 °C in July (Western Regional Climate Center; [www.wrcc.dri.edu/summary/climsmor.html](http://www.wrcc.dri.edu/summary/climsmor.html)).

### Disturbance history

Information on fire and grazing history are lacking for Bunchgrass. Fires at this elevation in the western Cascades are likely to be infrequent (>100 years; Teensma 1987) and episodic, driven by variation in climate and human activity

(Weisberg and Swanson 2003). Native Americans are thought to have used fire to maintain open meadow habitats throughout the Pacific Northwest (Boyd 1999). Forests adjacent to Bunchgrass, however, do not display any direct evidence of burning (e.g., fire scars) and archeological surveys have failed to produce artifacts from human use of the meadow prior to Euro-American settlement (E. Bergland, personal communication, 2004). Grazing by sheep is likely to have occurred during the early part of the twentieth century, synchronous with widespread grazing in the Cascades (Burke 1979; Johnson 1985; Rakestraw and Rakestraw 1991). However, data on the timing or intensity of local grazing are not present in US Forest Service archives (Johnson 1985; E. Bergland, personal communication, 2004).

### Sampling methods

Comparisons of historical (1946, 1959) and more recent (1990, 1997) aerial photographs of Bunchgrass were used to delineate potential study areas that had pronounced conifer encroachment during the twentieth century (Fig. 1). From a set of nine 1 ha (100 m × 100 m) experimental plots that comprise a larger restoration experiment at Bunchgrass, we selected four for intensive study prior to treatment (Fig. 1). Each plot included open meadow, recent encroachment, and older forest. Within each plot, we established a grid system to create a series of 10 m × 10 m subplots, the sampling units of this study (Fig. 1). Of the full set of subplots, 333 were selected; 23 additional subplots were established adjacent to two plots to increase representation of open meadow (Fig. 1). Analyses are based on a total of 356 subplots.

Within each subplot, we tagged, identified to species, and measured for diameter at breast height (DBH) all live stems  $\geq 1.4$  m tall. Dead trees  $\geq 5$  cm DBH were also identified to species and measured for DBH. Locations of all stems were mapped to the nearest 0.1 m (Fig. 1). We determined the ages of all live trees from increment cores or basal sections. Larger trees (mostly  $>10$  cm DBH) were cored as close to the ground as possible. Smaller trees were felled and a basal section was taken. Cores were mounted and all samples were sanded following standard dendrochronological methods (e.g., Stokes and Smiley 1968). Ring counts were made under 10–40 $\times$  magnification. For cores lacking pith, missing rings were estimated from a series of ring pattern templates (derived from complete cores with similar ring width patterns). Adjustments for age-to-sample height were based on age–height regressions developed from ring counts of basal sections of 30–40 seedlings per species. For trees with rotten or incomplete cores, age was estimated from diameter based on species-specific regression equations developed from the larger pool of aged cores and basal sections.

To estimate light availability, we took a digital hemispherical photograph at the center of each 10 m × 10 m subplot from a height of 1.65 m. Photographs were taken with a Nikon Coolpix 990 digital camera using an FC-E8 fisheye converter between 21 June and 4 August 2004 before 0800

or after 1800 or on uniformly overcast days to avoid direct sunlight. Total transmitted light or photosynthetic photon flux density (PPFD,  $\text{mol}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$ ) averaged over the year was calculated with Gap Light Analyzer 2.0 (Frazer et al. 1999) employing the standard overcast sky model.

Ground-layer vegetation was sampled between 5 July and 16 August 2004. Four 1 m<sup>2</sup> quadrats were established within the central 6 m × 6 m area of each subplot spaced 1 m apart along the northwest–southeast diagonal. Within each quadrat, we visually estimated the cover (%) of each vascular plant species; we then averaged these values to produce a subplot mean for each species. Nomenclature follows Hitchcock and Cronquist (1973).

### Chronosequence development and quantifying forest structure

To define stages in the transition from open meadow to old forest, we used a classification approach to group subplots by similarity in age structure. We used an agglomerative, hierarchical technique (Wishart 1969) implemented in PC-ORD version 4.0 (McCune and Mefford 1999). For each subplot (sample), we tallied the number of conifers in each of eleven 20-year age classes (e.g., see Taylor and Skinner 2003). We used relative Euclidean distance as the measure of dissimilarity and Ward's linkage method (Ward 1963). Subplots were grouped to the level of retaining 75% of information; this produced six "encroachment classes" with different age structures. Subplots without trees were omitted from the analysis but were assigned to an additional class (Class 0) representing open meadow. Evaluation of the full classification revealed 34 misclassified subplots (sensu McCune and Grace 2002). Nineteen subplots with only one or two trees were reassigned to Class 1, and 15 subplots with three or more trees  $>90$  years old were reassigned to Class 6. The final classification revealed a gradual increase in the mode and range of tree ages from Class 0 (open meadow) to Class 6 (old forest with overstory trees  $>90$  years old).

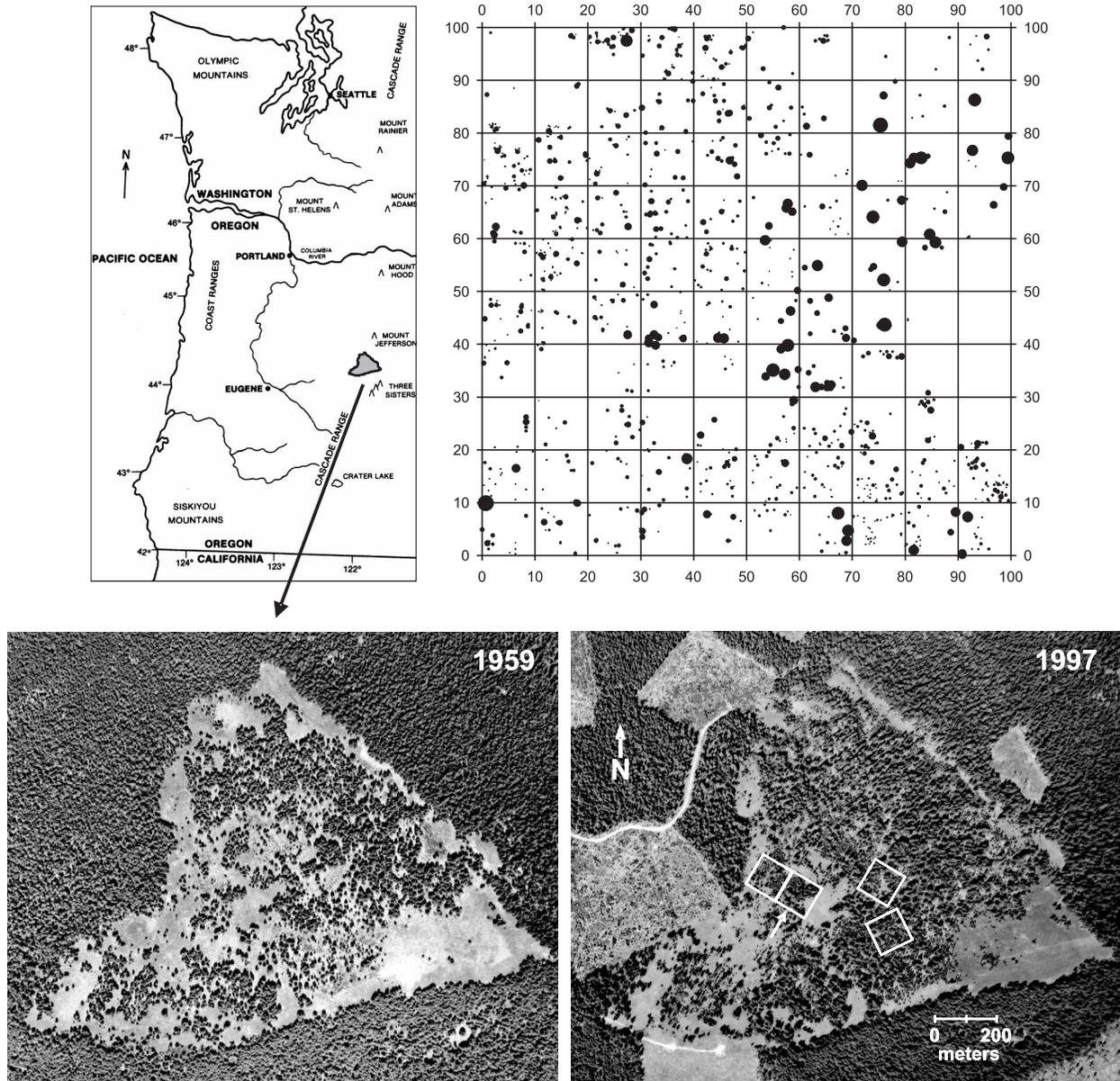
To quantify variation in forest structure, we computed the basal area ( $\text{m}^2\cdot\text{ha}^{-1}$ ) and density ( $\text{stems}\cdot\text{ha}^{-1}$ ) of live and dead stems of *A. grandis* and *P. contorta* in each subplot. Total basal area and density were not considered because they were highly correlated with values for *A. grandis*.

### Classification of species

Functional types are often used to generalize about species' performance (Smith et al. 1987). We classified ground-layer species by habitat affinity and growth form based on previous phytosociological studies (Halpern et al. 1984; Hemstrom et al. 1987) and regional floras (Hitchcock et al. 1969; Hitchcock and Cronquist 1973) (Table S1<sup>2</sup>). Habitat affinities included meadow ( $n = 43$  species), forest understory ( $n = 48$ ), or ruderal ( $n = 7$ ). Understory trees ( $n = 13$ ) and taxa that could not be assigned unambiguously to a group ( $n = 6$ ) were not classified. Although this classification may oversimplify the habitat distributions of some species, it captures the distinct associations of many species

<sup>2</sup>Supplementary data for this article are available on the journal Web site (canjbot.nrc.ca) or may be purchased from the Depository of Unpublished Data, Document Delivery, CISTI, National Research Council Canada, Building M-55, 1200 Montreal Road, Ottawa, ON K1A 0R6, Canada. DUD 5159. For more information on obtaining material refer to [cisti-icist.nrc-cnrc.gc.ca/irm/unpub\\_e.shtml](http://cisti-icist.nrc-cnrc.gc.ca/irm/unpub_e.shtml).

**Fig. 1.** Location of the study area, aerial photographs from 1959 and 1997, and a stem map of one of the four 1 ha plots (denoted by the arrow in the 1997 photograph). Subplots are 10 m × 10 m sections; additional subplots were established in open meadow west of the arrow (see Sampling methods section). Trees in the stem map are scaled to diameter; subplots with distinctly large stems were classified as old forest (Class 6) and those with smaller stems as young forest (Classes 2–5). Patches of old forest are apparent in the 1959 photograph; clearcuts appear adjacent to the study area in the 1997 photograph.



with native meadows, closed forests, or recently disturbed sites. Growth forms included sedge/rush ( $n = 3$  taxa), grass ( $n = 11$ ), herb (fern, suffrutescent forb, and subshrub;  $n = 68$ ), or tall shrub ( $n = 9$ ). Forest species were also classified by primary mode of dispersal (sensu Matlack 1994) and potential for clonal growth. Modes of dispersal were wind (including fern spores,  $n = 12$ ), ingested ( $n = 13$ ), adhesive ( $n = 4$ ), ant and (or) ballistic ( $n = 9$ ), or no obvious mechanism (none,  $n = 10$ ). Potential for clonal growth was coded as “no”, “yes”, or “strong” (Table S1).

#### Changes in species composition

We used nonmetric multidimensional scaling (NMS)

(Kruskal 1964) to portray changes in species composition during the transition from open meadow to old forest. NMS was performed on the full matrix of 356 subplots and 117 species using Sørensen’s distance measure. We used the “slow and thorough” autopilot of PC-ORD version 4.0 (McCune and Mefford 1999) conducting 40 runs that yielded one- to six-dimensional solutions. We selected a final two-dimensional solution with a stress of 18.57 by comparing final stress values of the best solutions at each dimensionality. A Monte Carlo test was then performed to compare stress of the final solution to values obtained from 50 runs of randomized data (McCune and Grace 2002). To simplify the graphical display of 356 subplots, we computed

a centroid ( $\pm 1$  SE) for each encroachment class based on subplot scores along the two NMS axes. We used Spearman rank correlations (Zar 1999) to identify forest structural attributes (including light) that showed strong correlations with composition (subplot scores on NMS axes). Correlations with axes were displayed as a biplot of “structural vectors” on the sample ordination, where  $r_{\text{NMS } 1} = \cos \theta$  and  $r_{\text{NMS } 2} = \sin \theta$ .

NMS was followed by multiresponse permutation procedures (MRPP) (Biondini et al. 1988) to test whether species composition differed among encroachment classes. MRPP is a nonparametric, Monte Carlo method that compares a weighted average within-group similarity with an expected average based on all possible partitions of the data for groups of the same size (McCune and Grace 2002). The method produces both a significance value ( $p$ ) and a measure of effect size ( $A$ , the chance-corrected within-group agreement). For consistency with NMS, we used a rank-transformed distance matrix based on Sørensen’s distance (PC-ORD version 4.0; McCune and Mefford 1999). An initial test included all encroachment classes; separate comparisons were then made between successive pairs of classes. To determine whether forest understory composition converged along the chronosequence, we compared values of mean similarity (1 minus Sørensen’s distance) of subplots within each encroachment class using only the pool of forest species.

#### Changes in cover and richness of meadow and forest species

For each subplot, we computed total (summed) cover, richness, and Shannon’s diversity index (Shannon and Weaver 1949) of species within each functional type (forest and meadow) and for growth forms within each group. Averages were then computed for each encroachment class and compared graphically to illustrate changes in the abundance and diversity of functional types during the transition from open meadow to old forest. Patterns of richness and diversity were similar; thus, we present only results for richness.

To test whether the species within the same functional type showed parallel trends in abundance, we plotted temporal trends in frequency (proportion of subplots) and average cover for a subset of the more common meadow and forest taxa. Species were selected if present in at least 50% of subplots in Class 0 (meadow species) or Class 6 (forest species).

#### Relationships between forest structure/light and plant functional types

We used multiple linear regression to explore relationships between forest structure/light and richness or abundance of functional types. Potential predictors in these models included total transmitted light (PPFD) and the density and basal area of live and dead stems of *A. grandis* and *P. contorta*. Although stem density and basal area may affect light transmission, they may also influence other aspects of forest environment, such as soil chemistry or nutrient availability. Models were created through stepwise addition/subtraction of predictors, with a probability of 0.05 to add and 0.10 to remove a variable (Neter et al. 1996). Model co-

efficients were standardized to allow direct comparison of the effects of predictors on response variables (Neter et al. 1996). Standard diagnostics were used to test the assumptions of normality and constant variance of residuals. PPFD, basal area, and density were square root transformed as a result. Regression analyses were conducted with SPSS version 13.0 (SPSS 2004).

## Results

### Conifer encroachment

Conifer encroachment occurred during two broad periods at Bunchgrass, with peaks in establishment in ca. 1870–1890 and 1950–1970 (Haugo 2006). Establishment during the more recent interval was distributed across numerous meadow openings (Fig. 1) and occurred at greater density than during the earlier interval. During both periods, *P. contorta* tended to establish before *A. grandis* in areas of open meadow (Haugo 2006).

Encroachment Classes 1–5 represented the transition from open meadow to young forest and displayed a clear progression of increasing mode and range of tree ages (Fig. 2). Class 6 represented the initial period of conifer invasion and exhibited a bimodal age structure (with peaks at 140 and 60 years), reflecting stratification of the canopy into distinct overstory and understory layers. The transition from Class 5 to 6, however, represented passage of considerably more time than that between more recent classes.

### Changes in light and forest structure

Light transmission and overstory structure changed markedly across the chronosequence. PPFD dropped steeply with initial establishment of trees (Class 0 to 1) (Fig. 3a). Subsequent forest development was characterized by rapid and abundant recruitment of *A. grandis* (Class 2) (Fig. 3b) followed by a gradual reduction in density and an increase in basal area (Classes 2–5) (Figs. 3b and 3c). The transition from Class 5 to 6 included a threefold increase in basal area of *A. grandis* reflecting presence of large-diameter (70–130+ cm) trees. *P. contorta* showed parallel trends in density and basal area with maxima in Classes 2–4.

PPFD had significant negative correlations with most measures of forest structure ( $r = -0.16$  to  $-0.55$ , all  $p < 0.001$ ). The strongest correlations were with density and basal area of live *A. grandis* ( $r = -0.55$  and  $-0.49$ , respectively).

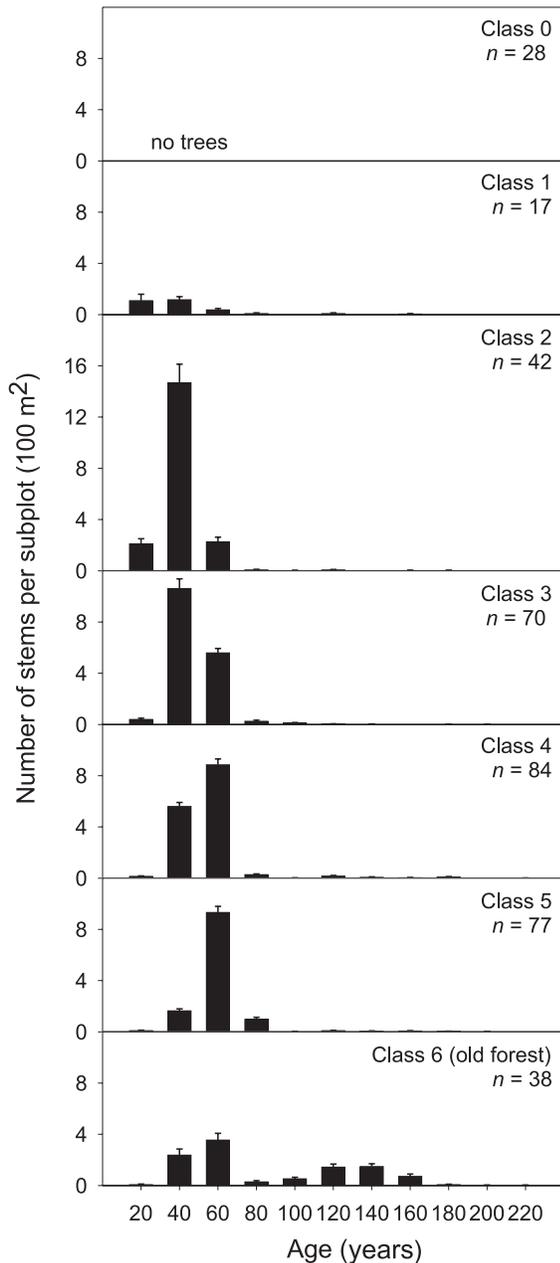
### Changes in species composition

In total, 117 vascular taxa were identified from the 356 subplots; these represented 94 genera and 38 families (see supplemental data in Table S1). Families with the greatest diversity of species included Compositae (14), Gramineae (11), and Rosaceae (8).

NMS ordination revealed a gradual shift in species composition from open meadow (Class 0, high scores on NMS 1) to old forest (Class 6, low scores on NMS 1) (Fig. 4a). Meadow and forest species showed clear separation along this axis (Fig. 4b); ruderal species were uncommon (except for *Lactuca muralis* (L.) Fresen. in Class 6) but were widely distributed across NMS 1.

MRPP indicated highly significant ( $A = 0.258$ ,  $p <$

**Fig. 2.** Age structures of trees ( $\geq 1.4$  m tall) in each of the seven encroachment classes: 0, open meadow; 2–5, young forest; 6, old forest. Ages are midpoints of 20-year age classes.

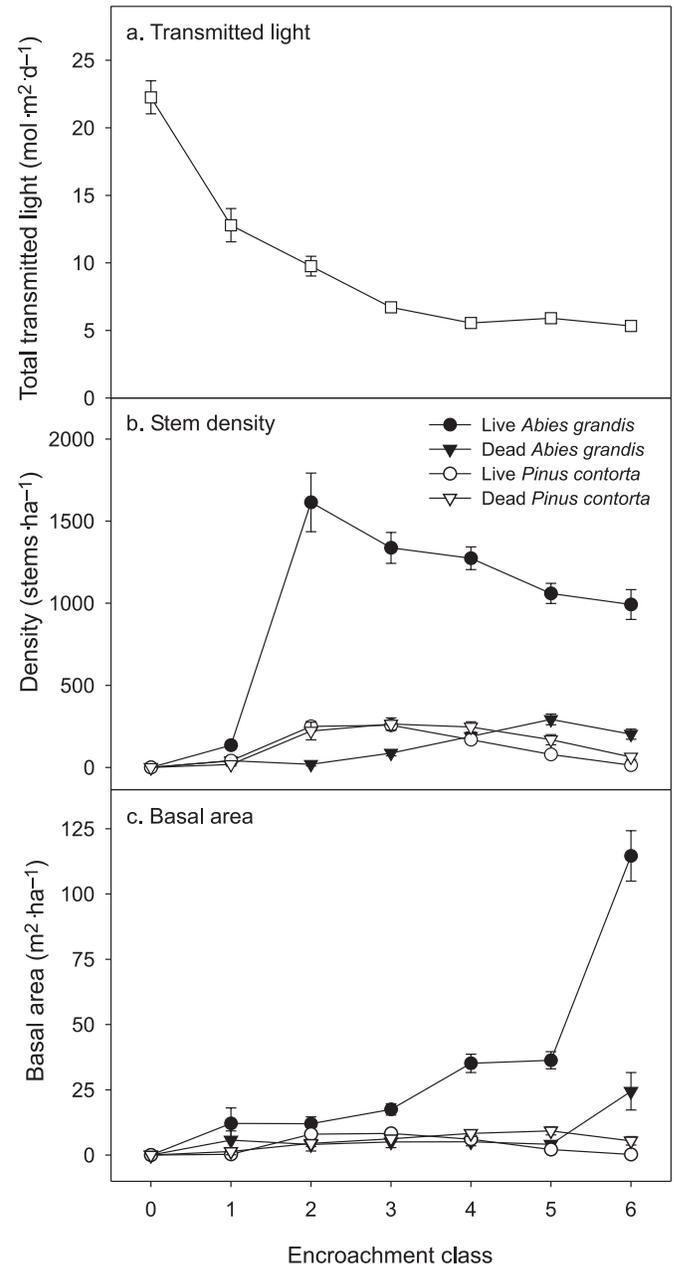


0.0001) differences in species composition among encroachment classes. Pairwise comparisons between successive classes indicated large compositional changes between Classes 0 (open meadow) and 1 (initial recruitment) ( $A = 0.104$ ) and between Classes 5 and 6 (old forest) ( $A = 0.088$ ). Effect sizes were significant but smaller for the remaining pairwise comparisons. Similarity of forest understorey species composition among subplots increased progressively from Class 0 (0.29) to Class 6 (0.75).

#### Changes in cover and richness of functional groups

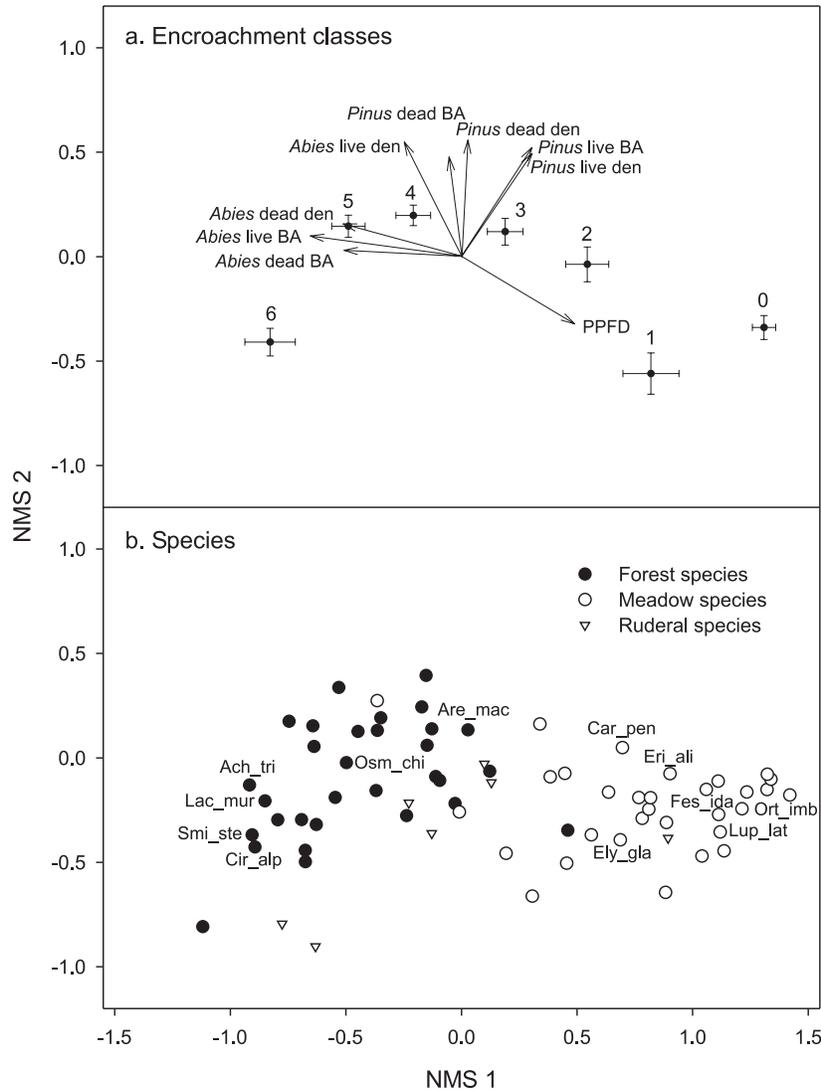
Meadow and forest species displayed contrasting trends in cover and richness (Fig. 5). Total cover of meadow species

**Fig. 3.** Changes in (a) transmitted light, (b) stem density, and (c) basal area among encroachment classes. Values are means  $\pm 1$  SE.



changed little in response to initial establishment of trees (cf. Classes 0 and 1), and meadow grasses actually increased in abundance (reflecting a marked increase in broad-leaved species) (Fig. 5a). Cover declined sharply in Class 2 (coincident with peak density of *A. grandis*) (Fig. 3b). Subsequent declines were more gradual, reflecting losses among all growth forms. Richness of meadow species declined more slowly than did cover, with losses of both grass and herbaceous species (Fig. 5b). Total cover of forest species (primarily herbs) increased slowly across the chronosequence to a maximum of ~50% in Class 6 (old forest) (Fig. 5c). In contrast, richness increased rapidly, surpassing that of meadow species in Class 3 and peaking in Class 5 (young forest) (Fig. 5d).

**Fig. 4.** NMS ordination of (a) subplots, represented by encroachment-class centroids ( $\pm 1$  SE), and (b) species, coded by functional type. Vectors portray direction and strength of Spearman rank correlations between forest structural variables or transmitted light (PPFD) and ordination axes. Codes (first three letters of genus and species) are shown for a subset of the common species: *Achlys triphylla*, *Arenaria macrophylla* Hook., *Carex pensylvanica*, *Circaea alpina* L., *Elymus glaucus* Buckl., *Erigeron aliceae*, *Festuca idahoensis*, *Lactuca muralis*, *Lupinus latifolius*, *Orthocarpus imbricatus* Torr ex S. Wats., *Osmorhiza chilensis* Hook. & Arn., and *Smilacina stellata*.



**Dynamics of individual species**

Trends in frequency and cover varied among the principal species comprising each functional group (Figs. 6 and 7). Two general trends emerged among meadow species. As expected, most species exhibited maximum cover in Class 0 (open meadow) and then declined across the chronosequence (left and middle panels, Fig. 6). Several taxa, however, showed greatest abundance in Class 1 (or 2) and then declined over time (right panels, Fig. 6). Among species present in  $\geq 50\%$  of open-meadow subplots, only *Orthocarpus imbricatus* Torr. ex S. Wats. exhibited local extirpation (absent from all subplots of Class 6) (Fig. 6). Four additional species were lost, but these were less common (present in 10%–50% of open meadow subplots).

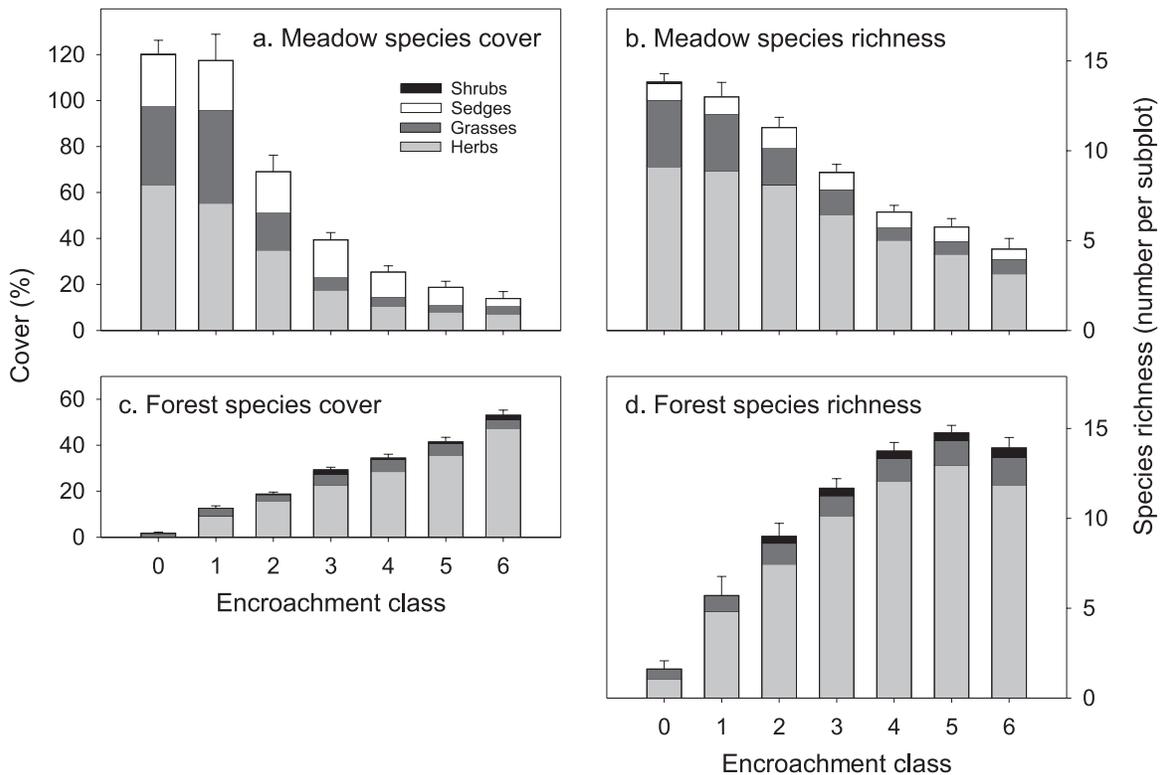
Forest species showed a diversity of abundance patterns, reflecting varying rates of colonization and growth (Fig. 7). Some species recruited rapidly, occupying 80% of Class 1

subplots (upper left panels, Fig. 7). Others established more slowly, achieving similarly high frequency in Class 3 or 4 (lower left panels, Fig. 7) and some as late as Class 6 (middle panels, Fig. 7). Changes in cover of forest species varied from unimodal to irregular. Cover of several species increased gradually or showed a distinctive increase in old forest (Class 6). However, others had no strong temporal trends (right panels, Fig. 7). There was little correspondence between rate of colonization (changes in frequency) and dispersal mechanism: species with similar trends in frequency often had different modes of dispersal, and species with similar modes of dispersal often had distinctly different trends in frequency (Fig. 7).

**Relationships between ground-layer vegetation, light, and forest structure**

NMS axes showed strong correlations with light availabil-

**Fig. 5.** Changes in total cover and richness of meadow and forest species by growth form among encroachment classes (0, open meadow; 2–5, young forest; 6, old forest). Values are means + 1 SE.



ity and overstory structure (Fig. 4a). NMS 1 was correlated with PPFd ( $r = 0.49$ ), basal area of live and dead *A. grandis* ( $r = -0.66$  and  $-0.51$ , respectively), and density of dead *A. grandis* ( $r = -0.51$ ) ( $p < 0.001$ ). NMS 2 was highly correlated with density of dead *P. contorta* ( $r = 0.56$ ), basal area of live *P. contorta* ( $r = 0.52$ ), and density of live *A. grandis* ( $r = 0.55$ ) ( $p < 0.001$ ). Viewed relative to the progression of encroachment classes in ordination space, structural vectors illustrate the gradual replacement of *P. contorta* by *A. grandis*: first in density, then in basal area (also see Figs. 3b and 3c).

Multiple regression models suggest stronger influences of forest structure on loss of meadow species than on colonization and growth of forest species. Models explained greater variation in cover and richness of meadow species ( $R^2 = 0.54$  and  $0.48$ ) than of forest species ( $R^2 = 0.34$  and  $0.42$ ) (all  $p < 0.001$ ) (Table 1). Transmitted light (PPFD) was highly significant in all models (positive correlation for meadow species, negative correlation for forest species) (Table 1). Three additional predictors were highly significant in meadow models: basal area of live *A. grandis* and density of dead *A. grandis* (negative correlations with cover and richness) and density of dead *P. contorta* (negative correlation with richness). Models for forest species had only one structural variable in common (negative correlations with basal area of live *P. contorta*).

## Discussion

Considerable research has been devoted to understanding the causes of conifer encroachment in western mountain meadows (e.g., Rochefort et al. 1994; Woodward et al. 1995; Miller and Halpern 1998), yet the consequences for

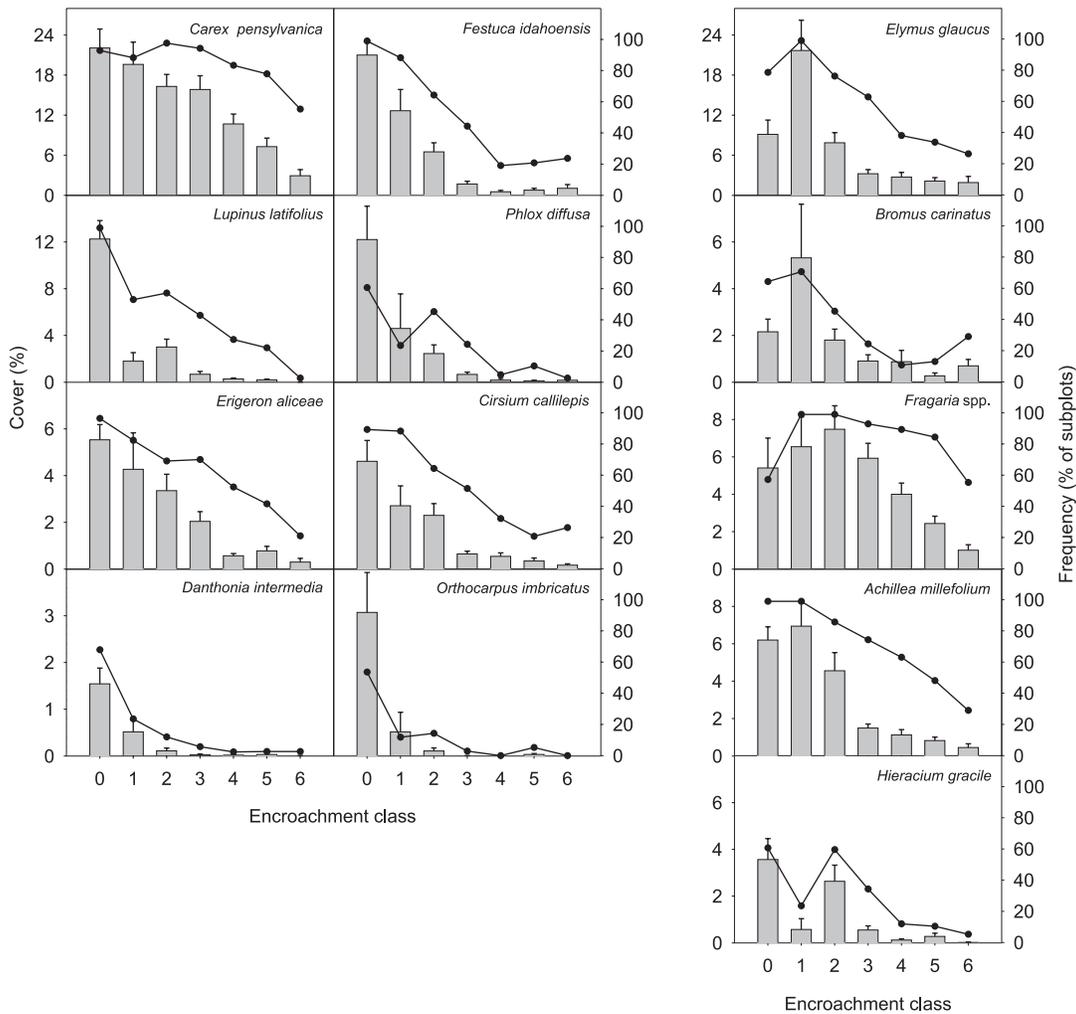
biological diversity have not been addressed. By combining fine-scale sampling of vegetation with detailed analysis of forest age structure, we have reconstructed nearly two centuries of vegetation change, from open meadow to old *A. grandis*-dominated forest. Two processes, driven or aided by the presence of conifers, contribute to these changes: suppression of the native meadow flora and colonization of meadow soils by forest herbs.

### Decline of meadow vegetation

Meadow communities at Bunchgrass were highly sensitive to conifer encroachment. Significant changes in composition were observed at the earliest stage of establishment, reflecting declines in dominant, as well as less frequent, but characteristic meadow species. Declines in cover were particularly dramatic when *A. grandis* reached peak density (Class 2). These changes are consistent with the responses of temperate grasslands to invasion of woody plants (Hobbs and Mooney 1986; Briggs et al. 2002). Not all species, however, showed negative responses during the earliest stages of encroachment. The most notable exceptions were broad-leaved grasses, *Elymus glaucus* Buckl. and *Bromus carinatus* Hook. & Arn., which doubled in abundance in Class 1, contributing to an overall increase in the cover of meadow grasses. These taxa may be more appropriately described as transitional in their habitat preference.

Despite significant declines in the cover and richness of meadow species, many taxa persisted in at least some forest locations; 24 of 43 meadow taxa were recorded in old forest (Class 6) and contributed an average of more than four species per subplot. Although most species were greatly re-

**Fig. 6.** Changes in cover (bars) and frequency (lines) among encroachment classes for common meadow taxa (present in  $\geq 50\%$  of open meadow (Class 0) subplots). Values are means + 1 SE. Note that scales on cover axes vary.

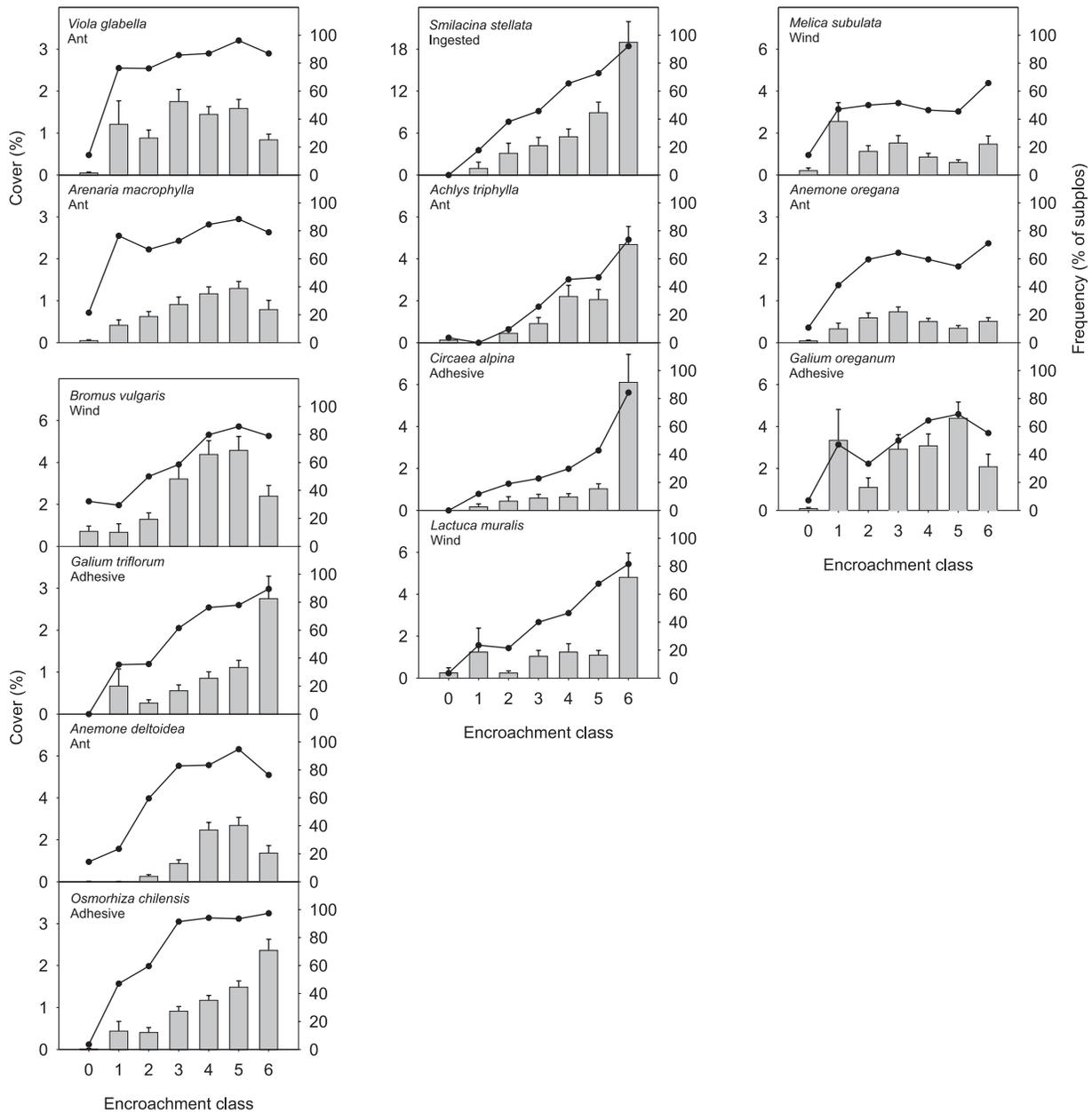


duced or absent from forest subplots, larger scale extirpations were uncommon. Moreover, several taxa (including the dominant sedge *Carex pensylvanica*) were present in  $\sim 50\%$  of old forest subplots, albeit at greatly reduced cover. Persistence of these open-habitat species may reflect the patchy nature of forest development at Bunchgrass that has left small areas of remnant meadow within larger stands of forest.

Several processes associated with tree encroachment may contribute to loss of meadow vegetation. In grassland systems, taller woody plants can reduce available light with substantial impacts to vegetation (Scholes and Archer 1997; Lett and Knapp 2003, 2005; Siemann and Rogers 2003). With initial establishment of conifers at Bunchgrass, PFD declined steeply (from  $\sim 22$  to  $13 \text{ mols}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$  from Class 0 to 1); this was synchronous with a large compositional change and a shift in dominance from grasses with filiform leaves (*Festuca idahoensis*) to broad leaves (*Elymus glaucus* and *Bromus carinatus*). Light was also a highly significant predictor in regression models for meadow species (Table 1). However, it is unlikely that shading is the sole mechanism by which conifers affect meadow composition and diversity. Similarly strong relationships were observed with other

measures of forest structure (basal area of live and density of dead *A. grandis*) that may be more indicative of changes in below-ground resources or environment. In previous studies of forest–meadow boundaries at Bunchgrass, Griffiths et al. (2005) documented strong gradients in litter depth, soil moisture, nitrogen availability, microbial activity, and the presence of ectomycorrhizal mats associated with tree roots. For many of these variables, transitional areas with recent encroachment were more similar to old forest than to meadow. Declines in meadow species may be a direct response to changes in litter or soil properties (e.g., Belsky et al. 1989; Facelli and Pickett 1991) or to competition for below-ground resources with newly established trees or forest understory plants (Callaway et al. 1991). Additionally, positive feedbacks can develop between trees and soils facilitating further recruitment and hastening the decline of meadow species (e.g., Li and Wilson 1998). Dramatic loss of cover of meadow species in Class 2 may illustrate this phenomenon: declines were relatively small at the onset of invasion when tree densities were low (Class 1) but were large when *A. grandis* recruited en masse several decades later facilitated by the initial cohort of *P. contorta* and *A. grandis*.

**Fig. 7.** Changes in cover (bars) and frequency (lines) among encroachment classes for common forest taxa (present in  $\geq 50\%$  of old forest (Class 6) subplots). Values are means + 1 SE. Primary mode of dispersal is listed below the name of each species. Note that scales on cover axes vary.



### Colonization of forest species

Colonization of meadow soils by forest understory species was synchronous with the establishment of trees. Increases in both the cover and the richness of forest understory species were rapid and continuous and within 60–80 years, forest species dominated the ground layer. Subplots representing progressively older classes of forest supported increasingly similar understories, suggesting convergence in species composition. However, two distinctive trends characterized the transition to old forest (Class 6, initiated nearly a century earlier than younger forest): richness of forest species declined and cover of several forest herbs increased markedly (e.g., *Achlyls triphylla* and *Smilacina stellata*). These trends are likely to be related: *A. triphylla* and *S. stel-*

*lata* can form large, contiguous patches in mature and late-seral forests (Antos and Zobel 1984), often to the exclusion of other species.

Changes in composition and increases in cover and richness of forest understory species were highly correlated with declines in transmitted light (PPFD). However, relationships with forest structural attributes differed for the primary tree species: cover and richness correlated positively with *A. grandis* and negatively with *P. contorta*. These contrasts reflect differences in canopy architecture and light attenuation as well as differences in shade tolerance (e.g., Minore 1979) that allow *A. grandis* to establish at considerably higher densities. In combination, however, light and forest structure explained only 34%–42% of the variation in

**Table 1.** Stepwise multiple regression models of richness and cover of meadow and forest species including standardized coefficients ( $\beta$ ) and  $p$  values of significant predictors.

Functional group/model	PPFD (mols·m <sup>-2</sup> ·day <sup>-1</sup> )	A. grandis, live			A. grandis, dead			P. contorta, live			P. contorta, dead		
		Density (stems·ha <sup>-1</sup> )	Basal area (m <sup>2</sup> ·ha <sup>-1</sup> )	Density (stems·ha <sup>-1</sup> )	Basal area (m <sup>2</sup> ·ha <sup>-1</sup> )	Density (stems·ha <sup>-1</sup> )	Basal area (m <sup>2</sup> ·ha <sup>-1</sup> )	Density (stems·ha <sup>-1</sup> )	Basal area (m <sup>2</sup> ·ha <sup>-1</sup> )	Density (stems·ha <sup>-1</sup> )	Basal area (m <sup>2</sup> ·ha <sup>-1</sup> )	Density (stems·ha <sup>-1</sup> )	Basal area (m <sup>2</sup> ·ha <sup>-1</sup> )
<b>Meadow species</b>													
Richness, adjusted $R^2 = 0.48, p < 0.001$	$\beta = 0.263$ $p < 0.001$	—	-0.298	-0.307	—	—	—	—	—	0.152	—	—	—
Cover, adjusted $R^2 = 0.54, p < 0.001$	$\beta = 0.470$ $p < 0.001$	—	-0.267	-0.184	—	—	—	—	—	0.005	—	—	—
	$p < 0.001$	—	<0.001	<0.001	—	—	—	—	—	—	—	—	—
<b>Forest species</b>													
Richness, adjusted $R^2 = 0.42, p < 0.001$	$\beta = -0.445$ $p < 0.001$	0.144	—	0.160	—	—	—	—	—	—	-0.317	—	—
Cover, adjusted $R^2 = 0.34, p < 0.001$	$\beta = -0.331$ $p < 0.001$	—	0.211	—	—	—	—	—	—	—	-0.326	—	-0.129
	$p < 0.001$	—	<0.001	—	—	—	—	—	—	—	<0.001	—	0.008

**Note:** Regression models are based on all subplots ( $n = 356$ ). All predictors were square root transformed. All variance inflation factors were <3.5 except where noted.  
\*Variance inflation factor = 4.3.

richness and cover of forest species, consistently less than that of meadow species. Residual variation may be explained, in part, by environmental factors that were not measured (e.g., litter depth or soil resource availability). It may also reflect the stochastic nature of dispersal and establishment; these are shaped by the species pool, dispersal traits, distances to seed sources, and the degree to which understory environments are suitable for germination. Evidence from analogous studies of forest herb migration into abandoned fields suggests that dispersal limitation, not environment, is the principal factor structuring community assembly (Brunet et al. 2000; Ehrlén and Eriksson 2000; Verheyen et al. 2003). For some herbaceous species at Bunchgrass, dispersal clearly was not limiting: frequency was as high in newly established forest (Class 1) as in old forest (Class 6). For most species, however, we could not distinguish dispersal from environmental limitation: frequency increased slowly with forest age, which may be indicative of either process. Interestingly, species that established at slower rates were not limited to those with more restrictive dispersal mechanisms (cf. Matlack 1994; Brunet and von Oheimb 1998). Instead, they displayed the full range of dispersal mechanisms: ant, adhesive, ingested, and wind. Proximity of old forest patches to areas of recent encroachment may have been sufficient to ensure abundant and rapid dispersal of most forest species.

**Implications for restoration and management**

Recent encroachment of conifers into mountain meadows of the western United States may constitute one phase of a cyclical process that includes periods of forest expansion, retraction, or stasis. At Bunchgrass, meadow soils underlie even the oldest patches of forest, strong evidence that non-forest vegetation has dominated this landscape for centuries or longer. Rapid conversion to forest, however, may signal a shift to an alternative stable state (e.g., Archer 1990; Briggs et al. 2002; Lett and Knapp 2003) triggered by a change in disturbance regime or climate and reinforced by positive feedbacks between trees and soils. Regardless of the cause(s) of encroachment, the desire to maintain open habitats for their biological diversity and other resource values has led federal land managers to experiment with tree removal and prescribed fire. However, restoration of meadow may be difficult once forest has established. In grasslands that have been transformed to shrubland or woodland in the absence of fire, reintroducing fire to restore grass or forb dominance is often unsuccessful (e.g., Laycock 1991; Heisler et al. 2004). Furthermore, woody species may transform soil properties so that even after they are removed, their residual effects may retard grassland recovery (Lett and Knapp 2003, 2005). Similar processes may limit the potential for restoration of montane meadows. In studies at Bunchgrass, soils in areas of recent encroachment exhibited chemical and biological properties distinctly different from those in adjacent meadows (Griffiths et al. 2005), in particular, the presence of mycorrhizal mats that facilitate survival and growth of conifer seedlings and thus favor persistence and gradual expansion of forest.

Even if trees are removed from meadows, there may be numerous additional impediments to restoration. Significant reductions in the abundance and vigor of meadow species

may limit their potential for vegetative recovery. In addition, few meadow species maintain viable seeds in the soil; instead, seed banks are dominated by early successional species (Lang and Halpern 2007). Thus, restoration activities that expose or heat mineral soils (e.g., tree removal or prescribed fire) can facilitate germination and growth of ruderal species that compete with those targeted for restoration. Forest shrubs or vines with the potential for clonal growth can also be released by overstory removal (Halpern 1989; Haeussler et al. 1990) and thus limit reestablishment of meadow species. Finally, mineral soils provide ideal sites for conifer germination. We have observed dense recruitment of *A. grandis* seedlings after experimental burning of tree islands at Bunchgrass and other meadows suggesting strong residual effects of trees on meadow soils. In combination, these observations suggest that there are barriers to restoration of dry, montane meadows where conifers have become well established. A more effective strategy for conservation of these systems is to remove or kill trees at an early stage before positive feedbacks lead to irreversible changes in community state.

## Acknowledgments

We thank Nicole Lang, Kyle Smith, James Freund, Jess Niederer, Jim Lutz, Janine Rice, Michael Frank, and Markus Koch for field assistance, Duane Lammers and Ted Dyrness for descriptions of soils, and Shelley Evans for taxonomic assistance. Joe Antos, Don McKenzie, and two anonymous reviewers provided helpful comments on earlier drafts of this manuscript. We appreciate the efforts of Fred Swanson (USFS-PNW), John Cissel (USDI-BLM), and staff of the USFS McKenzie River Ranger District and Willamette National Forest in facilitating field research at Bunchgrass Ridge. Funding was provided by the Joint Fire Science Program (agreement 1422RAH03-0021).

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