Tree age and tree species shape positive and negative interactions in a montane meadow

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Abstract: Few studies have considered how interactions between woody and herbaceous species change in direction or magnitude over time or with traits of the dominant woody species. We used a chronosequence approach to explore these interactions in a montane meadow in which *Pinus contorta* Dougl. ex Loud. and *Abies grandis* (Dougl. ex. D. Don) Lindl. have established gradually over a period of >70 years. Effects of individual trees (18–73 years old) were quantified by comparing plant community structure and composition under and adjacent to each tree. Trees generally exerted negative effects on cover and richness of resident meadow species and positive effects on colonizing forest herbs. Despite the average decline of meadow species under the canopy, cover was elevated (compared with adjacent meadow) under 33% of trees — most often under younger *Pinus*. Cover (but not richness) of meadow species declined with tree age, but the rate and magnitude of this decline did not differ under *Pinus* or *Abies*. In contrast, the cover and richness of forest herbs increased steeply with age under *Abies*, but not under *Pinus*. Our results illustrate the potential for complex and sometimes unpredictable interactions between woody and herbaceous species. A dynamic view of these relationships is critical for understanding or predicting the consequences of woody plant establishment in grassland and other herb-dominated ecosystems.

Key words: competition, facilitation, overstory-understory relationships, species' interactions, tree encroachment.

Résumé : Peu d'études ont porté sur la façon avec laquelle les interactions entre les espèces ligneuses et herbacées se modifient en direction et orientation avec le temps ou selon les caractères dominants des espèces ligneuses. Les auteurs ont utilisé une approche chronoséquentielle pour explorer ces interactions, dans une prairie montagnarde où le *Pinus contorta* Dougl. ex Loud. et l'*Abies grandis* (Dougl. ex. D. Don) Lindl. se sont graduellement établis au cours d'une durée > 70 ans. Ils ont quantifié les effets des arbres individuels (18–73 ans d'âge) en comparant la structure et la composition de la communauté sous et autour de chaque arbre. Les arbres exercent généralement une action négative sur la couverture et la richesse des espèces résidant en prairie et des effets positifs sur les herbes colonisant les forêts. En dépit d'un déclin moyen des espèces de prairie sous la canopée, la couverture demeure élevée (comparativement à la prairie adjacente) sous 33 % des arbres, le plus souvent de jeunes *Pinus*. La couverture (mais pas la richesse) par les espèces de prairie diminue avec l'âge des arbres, mais le taux et l'ordre de grandeur de ce déclin ne diffère pas entre les *Pinus* et les *Abies*. Par contre, la couverture et la richesse des herbes forestières augmentent rapidement avec l'âge sous les *Abies* mais pas sous les *Pinus*. Les résultats illustrent le potentiel d'interactions complexes et quelques fois imprévisibles qui existe entre les espèces ligneuses et herbacées. Une considération dynamique de ces relations apparaît nécessaire pour comprendre et prédire les conséquences de l'établissement de plantes ligneuses dans la prairie et autres écosystèmes dominés par des herbacées.

Mots-clés : compétition, assistance, relations étages supérieurs et sous-étage, interaction entre espèces, intrusion des arbres.

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Introduction

Interactions among plants can be positive, negative, or neutral (Clements 1929; Went 1942; Goldberg and Barton 1992; Callaway 1995). Although community structure is often viewed as the product of negative (competitive) interactions among plants (Tilman 1982; Grime 2001), the importance of positive (facilitative) interactions is becoming increasingly apparent (Bertness and Callaway 1994; Callaway 1995; Bruno et al. 2003; Brooker et al. 2008). This has led to a more complex model of community structure that incorporates both positive and negative interactions (Callaway and Walker 1997; Holmgren et al. 1997) that vary in importance along gradients of environmental stress or resource availability (Bertness and Callaway 1994; Callaway et al. 2002).

Interactions between plant species are particularly strong when there is a large asymmetry in size (e.g., trees vs. shrubs or herbs; Schwinning and Weiner 1998; Barnes and Archer 1999; Köchy and Wilson 2000). This asymmetry can have negative effects on subordinate species via competition for above- or below-ground resources (Goldberg and Barton 1992; Coomes and Grubb 2000), or positive effects via amelioration of environmental stress or enhanced resource availability (Pugnaire et al. 1996*a*; Tewksbury and Lloyd 2001). Negative effects of woody plants are well documented in grasslands and prairies where shrubs or trees can intercept or monopolize resources, change the quality or

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rate of litter input, and modify the chemical or biological properties of soils (Scholes and Archer 1997; Amiotti et al. 2000; Lett and Knapp 2003; Griffiths et al. 2005). Positive effects are more common in stressful environments, e.g., semi-arid grasslands and subalpine meadows, where trees or shrubs can moderate solar radiation, temperature, or wind, or improve soil moisture and nutrient availability (Callaway et al. 1991; Carlsson and Callaghan 1991; Schlesinger et al. 1996; Hibbard et al. 2001; Tewksbury and Lloyd 2001).

Despite an extensive literature devoted to the interactions among plant species, two questions have received limited attention. First, how do the magnitude or direction of effects of woody plants change with time (plant age)? Trees vary in their abilities to capture resources or modify the physical environment as they increase in size or age (Kellman and Kading 1992; Archer 1995; Köchy and Wilson 2000). Effects may be cumulative, reflecting gradual, but persistent changes in resource availability or environment (Pugnaire et al. 1996*b*; Griffiths et al. 2005). Second, is the nature of these interactions shaped by traits of the dominant woody species? Woody plants with different morphological or physiological traits (e.g., canopy architecture, water-use efficiency, or litter production) may differ in their abilities to preempt resources or to alter the physical environment for subordinate species (Belsky et al. 1989; Scholes and Archer 1997; Pugnaire et al. 2004). Thus, different woody species can affect different rates of change or different outcomes, depending on these traits. Understanding the temporal dynamics of these effects and the extent to which they vary among species is critical to anticipating and managing the effects of woody plant invasions in grasslands, a process that is occurring at a global scale (Van Auken 2000).

We pursue these questions in the current study of conifer encroachment of montane meadows in western Oregon. Long-term encroachment of these meadows by two native conifers, *Pinus contorta* Dougl. ex Loud. and *Abies grandis* (Dougl. ex. D. Don) Lindl., provides a model system for quantifying the temporal dynamics of tree–herb interactions and how they are influenced by tree species that differ in canopy architecture, foliage density, and other traits that affect resource availability (e.g., light) and environmental stress (e.g., temperature) (Scholes and Archer 1997; Pugnaire et al. 2004). *Pinus contorta* is intolerant of shade, maintains a sparse/open canopy, exhibits rapid juvenile growth, and is relatively short lived (Minore 1979; Lotan and Critchfield 1990). In contrast, *A. grandis* is shade tolerant, maintains a greater density of branches and needles, has slower juvenile growth, and is longer lived (Minore 1979; Foiles et al. 1990). In addition to these autecological differences, trees in this system can exert both negative and positive effects, displacing resident meadow species and facilitating recruitment of forest herbs (Haugo and Halpern 2007) leading to significant changes in community composition and structure. We explore these dynamics using a chronosequence approach, comparing effects of individual trees of both species and of varying age on plant functional group richness and cover, as well as species composition. We tested the following hypotheses:

1. Trees exert negative effects on meadow species (reducing richness and cover), but positive effects on forest herbs (facilitating increases in richness and cover).
2. The magnitude of these effects increases with time (tree age) leading to increasingly larger differences in community composition under the canopy and in adjacent meadow.
3. *Abies grandis* exerts stronger effects than does *Pinus contorta*, consistent with its ability to cast deeper and more complete shade.
4. Tree age and tree species explain a greater proportion of the variation in cover and richness of meadow species than of forest herbs. Declines in resident meadow species should show strong dependence on tree age or size, reflecting the degree or duration of above and belowground influences. In contrast, increases in forest herbs should be more variable or stochastic because establishment requires not only suitable environmental conditions, but successful dispersal.

Although we can only speculate about causal mechanisms (including both direct and indirect effects; Wootton 1994; Callaway and Walker 1997), our primary goal is to quantify patterns of vegetation change and how these vary in direction, rate, and magnitude under different tree species. This represents a first critical step in understanding the temporal dynamics of tree–herb interactions in this system.

Methods

Study area

The study area, Bunchgrass Ridge, occupies a large (100 ha), gently sloping plateau in the Cascade Range of western Oregon (44°17′N, 121°57′W) (Haugo and Halpern 2007). Elevations range from ca. 1300 to 1375 m a.s.l.; slopes rarely exceed 5% and generally face southward. The plateau supports a mosaic of meadows, individual trees and tree islands, and forest patches of varying age (Halpern et al. 2010). Meadows are composed of both graminoids (e.g., *Festuca idahoensis* Elmer and *Carex pensylvanica* Lam.) and forbs (*Fragaria* spp., *Lupinus latifolius* Lindl. ex J. Agardh., and *Erigeron aliceae* T.J. Howell) and are similar to other *Festuca*-dominated communities in the western Cascades (Franklin and Halpern 1999).

Factors contributing to the origin and historical maintenance of these montane meadows remain unclear. However, recent widespread encroachment by conifers represents a significant shift in ecosystem state — one variously attributed to cessation of sheep grazing, long-term suppression of fire, or changes in climate (Vale 1981; Rochefort et al. 1994; Miller and Halpern 1998; Takaoka and Swanson 2008). At Bunchgrass Ridge, soil profiles indicate the presence of grassland vegetation for many centuries or more (D.A. Lammers, personal communication, 2005) with no evidence of forest (e.g., decayed logs or fire-scarred trees) predating recent tree invasion. Soils are Vitric Melanocryands — deep, fine to very-fine-sandy loams derived from andesitic basalt and tephra deposits with varying amounts of glacially derived cobbles, stones, and boulders.

At Santiam Pass (1488 m a.s.l.), 17 km to the north of our study area, annual precipitation averages 216 cm. However, only 7.5% of this falls between June and August, resulting in frequent summer drought. Annual snowfall averages 1152 cm and winter snow pack can exceed 2 m, with snow cover often persisting into late May or June. 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).

Sampling design and methods

From a 10 ha area of meadow that has experienced recent (20th century) encroachment, we selected isolated individuals of *Pinus* ($n = 26$) and *Abies* ($n = 28$) that were >1.4 m tall. Tree selection was stratified by diameter (dbh) class to ensure a broad range of ages. All trees were at least two canopy diameters from the nearest neighbor. Each tree was measured for dbh, total height, height to live canopy, and canopy radius (measured to the northeast and southwest). Age was determined from an increment core taken as close to the ground as possible. Cores were mounted and sanded following standard dendrochronological methods (e.g., Stokes and Smiley 1968). Ring counts were made under 10–40× magnification. Adjustments for age-to-core height were based on age-height regressions developed from a destructive sample of 30–40 individuals per species (C.B. Halpern unpublished data.).

Ground vegetation was sampled along two transects starting at the base of each tree. To account for potential variation in composition due to differential shading, transects ran to the northeast (NE) and southwest (SW). Transects extended beyond the canopy drip-line into open meadow to a distance equal to the canopy radius of the tree. Transects thus consisted of two segments defined by the canopy drip-line: "under canopy" and "adjacent meadow" (a paired control). Each segment was sampled with equal numbers of 20 cm × 50 cm quadrats spaced 20 cm apart, oriented with the long axis perpendicular to the transect. Quadrats under the canopy began adjacent to the tree bole; quadrats in adjacent meadow began at the canopy drip-line. Quadrats were placed continuously under smaller trees when it was not possible to fit five quadrats with 20 cm spacing; for the smallest trees (nine *Pinus* and eight *Abies*), two to four quadrats were used. Within each quadrat, we visually estimated cover of each vascular plant species. Twenty "reference" transects were also established in areas of open meadow (a minimum of 20 m from the nearest tree) to test whether adjacent-meadow segments were affected by sample trees, thus compromising their ability to serve as paired controls for assessing tree effects (see below). Reference transects were 2 m long with five quadrats spaced 20 cm apart.

To confirm that physical environments differed under *Pinus* and *Abies*, we measured light availability, soil-surface (ground-surface) temperature, volumetric soil moisture, and soil pH under four individuals of each species. *Pinus* were 18–43 years old and 5.6–20.5 cm in diameter; *Abies* were 22–37 years old and 6.6–36.8 cm in diameter. Measurements were made along each transect, midway between the bole and canopy drip-line. Percentage of mid-day photosynthetically active radiation (PAR) transmitted through the canopy was measured between 1100 and 1400 h on 6 July (full sun, no clouds) with a LP-80 Ceptometer (Decagon Devices, Inc., Pullman, Washington); reference measurements (full sun) were taken adjacent to each tree. Soil-surface temperature was measured every 30 min for 2 weeks in July using temperature data loggers (Model DS1921G, iButton Thermochron; Maxim/Dallas Semiconductor Corp., Dallas, Texas). From these continuous measurements we selected two warm/sunny days (15–16 July) when maximum air temperatures averaged 33.8 °C to compare conditions beneath the tree species. Volumetric soil moisture (0–12 cm depth) was measured on 6 July using a Campbell Hydrosense TDR (Campbell Scientific, Inc., Logan, Utah). For analysis of pH, soil cores were taken to a depth of 10 cm (mineral soil; litter depth was minimal). pH was determined in a 2:1 suspension (10 mL deionized water, 5 g soil) using a PHM 85 pH meter (Radiometer Analytical, Lyon , France). For each of these variables, differences between tree species were assessed with *t*-tests. For light availability, soil moisture, and pH, transect values were first averaged for each tree ($n = 4$ per species). For soil temperature, separate tests were run for SW and NE transects ($n = 2$–4 per species).

Species classification

We identified a total of 88 vascular plant taxa (Appendix A, Table A1). We classified each taxon as characteristic of open meadow ($n = 39$) or forest understory ($n = 32$). Assignments were based on regional floras (Hitchcock et al. 1969; Hitchcock and Cronquist 1973) and phytosociological studies in the western Cascades (Halpern et al. 1984; Hemstrom et al. 1987). Tree seedlings and species not easily associated with either group remained unclassified ($n = 17$), although most of these contributed minimally to total plant cover. Although this classification may simplify the habitat breadth of some species, it captures the distinct associations of most taxa with either open meadow or closed-canopy forest.

Quantifying tree effects

To quantify tree effects on ground vegetation, we tallied the number and summed the cover of both meadow and forest species in each quadrat. For each tree we then computed mean values for quadrats representing under-canopy and adjacent-meadow segments. Means were also computed for each reference transect. To quantify the direction and magnitude of tree effects, we calculated for each variable the difference between under-canopy and adjacent-meadow segments. These difference values served as the basis for subsequent analyses of cover and richness. Finally we computed the compositional difference (or percent dissimilarity, PD) between under-canopy and adjacent-meadow segments using the quantitative form of Sørensen's community coefficient (Mueller-Dombois and Ellenberg 1974):

$$\mathrm{PD} = 100 \times \left\{ 1 - 2 \times \left[\frac{\sum \min(\mathrm{cov}_{\mathrm{ai}}, \mathrm{cov}_{\mathrm{bi}})}{\sum (\mathrm{cov}_{\mathrm{ai}} + \mathrm{cov}_{\mathrm{bi}})} \right] \right\}$$

where $\mathrm{cov}_{\mathrm{ai}}$ and $\mathrm{cov}_{\mathrm{bi}}$ are the mean cover of species "i" in under-canopy and adjacent-meadow segments, respectively. All species (meadow, forest, and unclassified) were included in calculations of PD.

We first tested whether adjacent-meadow segments could legitimately serve as paired controls for assessing tree effects (or alternatively, whether trees exerted significant influences beyond the canopy drip-line). We used a series of *t*-tests to compare mean richness and cover of adjacent-meadow segments to those of reference transects. Separate tests were run for segments associated with *Pinus* and *Abies*. Tests for forest species associated with *Abies* assumed un-equal variance (Zar 1999). To test whether species composition differed between adjacent-meadow segments and reference transects, we used multiresponse permutation procedures (MRPP; Biondini et al. 1988) with Sørensen's distance, as implemented in PC-ORD 5.0 (McCune and Mefford 2005); all three groups (reference and adjacent-meadow segments for *Pinus* and *Abies*) were analyzed together. MRPP provides both a significance value (p) based on a Monte Carlo method, and a measure of effect size (A, chance corrected within-group agreement).

To test whether trees exerted negative effects on meadow species and positive effects on forest herbs (hypothesis 1), we ran one-sided t-tests on the differences in cover and richness of under-canopy and adjacent-meadow segments, hypothesizing values <0 for meadow species and >0 for forest species. Separate tests were run for *Pinus* ($n = 26$) and *Abies* ($n = 28$).

We used general linear models to test the hypothesized effects of tree age (time) and tree species on the cover and richness of meadow and forest species (hypotheses 2 and 3). Response variables were the differences between under and adjacent-meadow segments. Tree age was treated as a continuous variable and tree species as a categorical (indicator) variable. A tree age × tree species interaction was also included in each model. Standard diagnostics were used to confirm the assumptions of normality and homogeneity of variance (Zar 1999). We considered tree height and diameter as potential predictors, but both were highly correlated with tree age and thus were not tested. Height to live canopy and canopy radius were also considered in preliminary models, but were not significant predictors and not included in final models. Coefficients of determination (R^2) for each model were compared to address our last hypothesis, that meadow species showed stronger relationships to tree age and tree species than did forest herbs. Analyses were conducted with SPSS 13.0 (SPSS 2004).

Results

Characteristics of sample trees

Sample trees ranged in age from 18 to 64 years for *Pinus* and 22 to 73 years for *Abies*. Diameter (dbh), height, height to live canopy, and mean canopy radius were highly correlated with age in both species (significant main effects of age from general linear models that included age, species, and an age × species interaction; range of p: < 0.001 to 0.05; Figs. 1*a*–1*d*). Diameter and height increased more steeply with age in *Abies* (significant age × species interactions; $p < 0.001$; Figs. 1*a* and 1*b*), and height to live canopy increased more steeply in *Pinus* (significant age × species interaction; $p < 0.001$; Fig. 1*c*). Increases in canopy radius with age were similar between species (non-significant age × species interaction; Fig. 1*c*).

Among the trees sampled, light availability and maximum soil-surface temperature were consistently lower under *Abies*. Only 3% of available PAR was transmitted through the canopy of *Abies* vs. 25% for *Pinus* ($t = –2.908$, df = 6, $p = 0.03$). Mean maximum soil-surface temperature was lower under *Abies*, but not significantly so owing to the small sample size (NE transects: 23.5 °C for *Abies* vs. 29.6 °C for *Pinus*; $t = 2.12$, df = 4, $p = 0.10$; SW transects: 32.2 °C for *Abies* vs. 44.3 °C for *Pinus*; $t = 1.62$, df = 4, $p = 0.18$). For comparison, the corresponding mean for reference transects was 47.8 °C. Soil moisture did not differ beneath *Abies* and *Pinus* (7.7 and 6.3%, $t = 1.59$, df = 6, $p = 0.16$) nor did pH (5.7 and 5.5, $t = 0.87$, df = 6, $p = 0.42$).

Effects of trees on adjacent-meadow segments

Trees exerted varying effects on adjacent-meadow segments (i.e., beyond the canopy drip-line), but these differed for *Pinus* and *Abies*. For *Pinus* (but not *Abies*), the cover of meadow species was depressed in adjacent meadow relative to reference transects (Fig. 2*a*). For *Abies* (but not *Pinus*), the richness of meadow species was elevated in adjacent meadow relative to reference transects (Fig. 2*c*). The magnitude of these effects, however, was small (<12% difference). *Abies* (but not *Pinus*) had large effects on forest species in adjacent meadow: species richness and cover were 7–10× greater than in reference transects (Figs. 2*b* and 2*d*). MRPP identified significant differences in species composition between adjacent-meadow segments and reference transects, however effect sizes were very small (*Pinus*: $A = 0.01$, $p = 0.05$; *Abies*: $A = 0.03$, $p < 0.01$).

Effects of trees under the canopy

Trees generally exerted negative effects on cover and richness of meadow species (i.e., smaller values under the canopy than in adjacent meadow) and positive effects on forest herbs (greater values under the canopy), consistent with hypothesis 1 (Table 1; Fig. 3) (for species' details see Appendix A, Table A1). However, the magnitude of these effects varied with tree species and tree age (see below). Counter to expectation, total cover of meadow species was significantly greater under *Pinus* than in adjacent meadow (Table 1). In addition, despite a general trend for trees to reduce the cover of meadow species, cover was elevated under 33% of trees (Fig. 3*a*). This positive effect was more frequent under *Pinus* (58% vs. 11% of *Abies*, $\chi^2 = 56.4$, $p < 0.001$) and more frequent under younger trees (77% of trees < 30 year old vs. 14% of trees > 60 year old, $\chi^2 = 11.6$, $p < 0.001$).

The hypothesized effects of tree age and tree species (hypotheses 2 and 3) were partially supported by our results. As predicted, we observed a significant decline in the cover of meadow species with tree age, but not a greater decline under *Abies* than under *Pinus* (Fig. 3*a*; Table 2). Moreover, neither tree age nor tree species affected the richness of meadow species (Fig. 3*c*; Table 2). For forest species, we observed significant interactions between tree age and tree species for both cover and richness: forest herbs showed minimal establishment under *Pinus*, but steep age-related increases in cover and richness under *Abies*, as predicted (Figs. 3*b* and 3*d*; Table 2). Consistent with hypothesis 2, trends among forest and meadow taxa led to increasingly larger differences in community composition (percent dissimilarity) with time under and adjacent to the canopy (Fig. 3*e*; Table 2).

Contrary to expectation, tree age and tree species did not explain a greater proportion of variation in the cover and richness of meadow species than of forest herbs (hypothesis 4). Coefficients of determination in cover models were similar for both plant groups ($R^2 = 0.54$ and 0.50, respectively;

Fig. 1. Relationships between tree age and (*a*) dbh, (*b*) total height, (*c*) canopy radius (mean of two radii), and (*d*) height to live canopy for *Pinus contorta* and *Abies grandis*. Separate regression lines are plotted where general linear models indicated a significant tree age × tree species interaction.

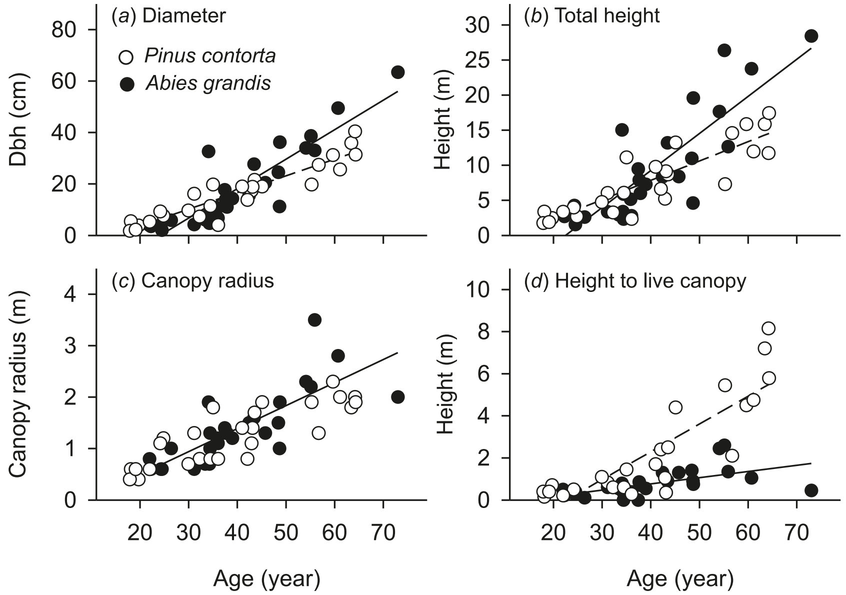


Fig. 2. Total cover (*a* and *b*) and mean richness per quadrat (*c* and *d*) of meadow and forest species in reference transects (n = 20) and in adjacent-meadow and under-canopy segments for *Pinus contorta* (n = 26) and *Abies grandis* (n = 28). Values are means (+1 SE). For each tree species, *t*-tests were used to compare adjacent-meadow segments to reference transects to assess tree effects beyond the canopy drip-line (under-canopy segments are included only for comparison); ns, not significant; *, $0.01 < p \leq 0.05$; **, $0.001 < p \leq 0.01$; and ***, $p \leq 0.001$.

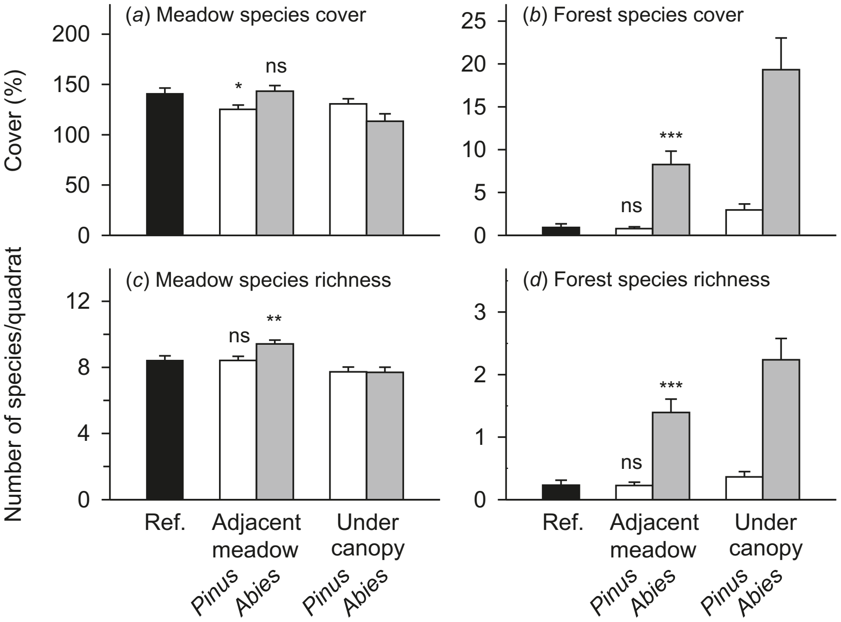


Table 2), and in richness models, they were considerably greater for forest than for meadow species (R^2 = 0.49 vs. 018, respectively; Table 2).

Discussion

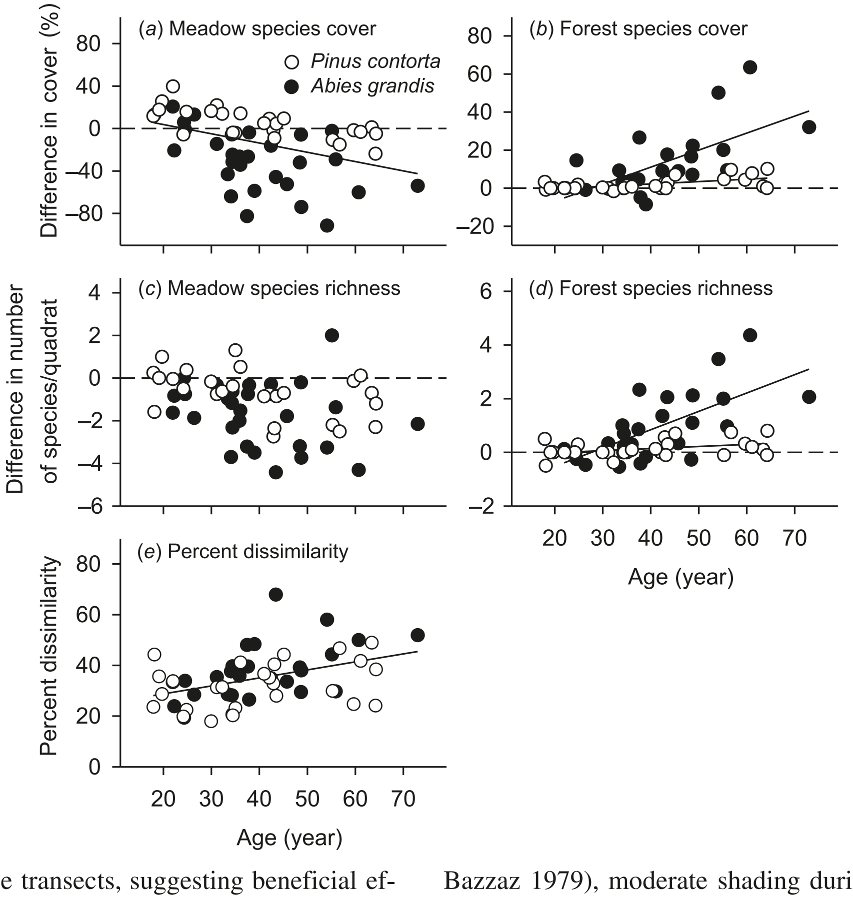
Ours is one of a handful of studies that explores the temporal dynamics of woody-herbaceous plant interactions (Pugnaire et al. 1996*b*; Tewksbury and Lloyd 2001; Reisman-Berman 2007). Decades of encroachment of meadows by conifers with differing traits provides an ideal system for exploring changes in the types and strengths of interactions between trees and herbaceous communities, and the extent to which these are shaped by the dominant woody species. As predicted, trees generally exerted negative effects on resident meadow species and positive effects on forest herbs. Effects were most apparent beneath the canopy, but for some community attributes, they extended beyond the drip-line into adjacent meadow. Most notably, for *Abies*, richness and cover of forest herbs were markedly greater in adjacent

Table 1. Effects of *Pinus contorta* and *Abies grandis* on the cover and richness (number of species/quadrat) of meadow and forest species.

	Pinus contorta				*Abies grandis*			
	Diff	df	*t*	*P*	Diff	df	*t*	*P*
Meadow species								
Cover (%)	5.2	25	1.90	0.035	–30.8	27	–5.62	**<0.001**
Richness	–0.7	25	–3.24	**0.002**	–1.7	27	–5.99	**<0.001**
Forest species								
Cover (%)	2.2	25	3.40	**0.018**	11.1	27	3.61	**<0.001**
Richness	0.1	25	2.20	**0.037**	0.8	27	3.64	**<0.001**

Note: Diff, mean difference between under-canopy and adjacent-meadow segments. For one-sided *t*-tests that support the predictions of hypothesis 1 (i.e., means significantly < 0 for meadow species or significantly > 0 for forest species), *p* values are in bold font.

Fig. 3. Relationships between tree age and the changes in ground vegetation beneath *Pinus contorta* and *Abies grandis*. Points represent the difference between under-canopy and adjacent-meadow segments in (*a*) total cover of meadow species, (*b*) total cover of forest species, (*c*) mean richness of meadow species, (*d*) mean richness of forest species, and (*e*) species composition. Difference in species composition is expressed as percent dissimilarity (the quantitative form of Sørensen's community coefficient). Separate regression lines are plotted where general linear models indicated a significant tree age × tree species interaction (Table 2). Tree age was not significant in the model for meadow species richness.



meadow than in reference transects, suggesting beneficial effects of shading beyond the canopy. However, this result also implies that effects beneath the canopy were greater than estimated because our difference measures used adjacent-meadow segments as paired controls.

Despite the general tendency for trees to reduce cover of meadow species, it was elevated under a surprisingly large proportion of trees. Prevalence of this positive effect under younger stems of the more open-canopied *Pinus* suggests that even for herbaceous species adapted to full sun (e.g., Bazzaz 1979), moderate shading during dry summer months may reduce physiological stress and thus benefit plant performance. Alternatively, increases in cover beneath the canopy may reflect a shift toward meadow species with greater foliage density or leaf area (e.g., Haugo and Halpern 2007), or changes in leaf orientation (from vertical to horizontal) in response to shading (McMillen and McClendon 1979). Under older trees and beneath *Abies*, however, more dramatic changes in physical and biotic environments may become detrimental to meadow species.

Table 2. Results of general linear models testing effects of tree age, tree species, and their interaction on the five measures of vegetation response.

	Meadow species		Forest species		
	Cover	Richness	Cover	Richness	PD
Adjusted R^2	0.54	0.18	0.50	0.49	0.22
Full model (p)	**<0.001**	**0.005**	**<0.001**	**<0.001**	**0.001**
Sources of variation					
Tree age	**<0.001**	0.152	**<0.001**	**<0.001**	**0.001**
Tree species	0.400	0.308	**0.006**	**0.005**	0.359
Tree age × tree species	0.188	0.925	**<0.001**	**<0.001**	0.116

Note: The cover and richness of meadow and forest species were analyzed as the differences between under-canopy and adjacent meadow segments (see Fig. 3). PD is the percent dissimilarity in species composition between under-canopy and adjacent-meadow segments. *P* values that denote a significant main effect or interaction are in bold font.

We predicted that the magnitude of tree effects would increase with tree age, reflecting increasing asymmetry in plant size and (or) cumulative effects on resource availability including changes in litter quality and the chemical and biological properties of soils (Scholes and Archer 1997; Amiotti et al. 2000; Köchy and Wilson 2000; Griffiths et al. 2005). The changes in cover of meadow species and in community composition supported this prediction. However, the trends in richness of meadow species did not, suggesting that the inhibitory effects of older trees were not sufficient to induce local extinctions. Extirpations of meadow species are more likely (but still uncommon) within larger, older (>90 year) patches of forest (Haugo and Halpern 2007).

For both meadow and forest species, temporal trends in richness and cover appeared linear over the range of tree ages considered (18–73 year). Because the size of quadrats (20 cm × 50 cm) limited our ability to assess effects of smaller trees, it is not clear at what ages *Pinus* or *Abies* begin to influence the herb layer (e.g., Köchy and Wilson 2000). A smaller sampling frame or a different measure of response would be needed to identify this threshold. Extrapolating to older trees is also difficult. Older individuals rarely occurred in isolation, but were part of larger tree islands or forest patches that established many decades earlier (Haugo and Halpern 2007; Halpern et al. 2010).

For a number of response variables, effects of tree age were highly contingent on tree species. Most notably, richness and cover of forest species showed a strong correlation with tree age under *Abies*, but not under *Pinus.* Although *Abies* may not establish as readily as *Pinus* in open-meadow habitats (Halpern et al. 2010), once established, it has a stronger effect on its surrounding environment, particularly light and temperature. Greater shade tolerance in *Abies* (Minore 1979) leads to a deeper canopy (Fig. 1*d*) and to greater branch and foliage density than in *Pinus*. *Abies*' greater ability to reduce light and temperature at the ground surface may facilitate colonization by forest herbs that require cooler, moister microsites to establish (e.g., Belsky et al. 1989; Pugnaire et al. 2004). Litter accumulation may also be greater beneath *Abies*, leading to more rapid changes in soil properties (Schlesinger et al. 1996; Griffiths et al. 2005) — changes that could promote germination and growth of forest species. For similar reasons, we anticipated stronger effects of *Abies* on meadow species. However, model results were not consistent with this expectation although trends in cover suggest consistently greater declines with time under *Abies* (Fig. 2*a*) in contrast to an overall positive effect under *Pinus* (Table 1).

In combination, tree age and species explained ca. 20%–50% of the variation in cover and richness of meadow and forest species. Counter to expectation, however, models for meadow species were not stronger than those for forest herbs. The strength of the richness model for forest species was particularly surprising given that colonization beneath isolated trees requires successful dispersal, as well as microclimatic and edaphic conditions conducive to germination and growth (Matlack 1994; Brunet and von Oheimb 1998; Fuller and del Moral 2003). Because forest herbs were uncommon in open-meadow environments (Fig. 2; Appendix, Table A1) and largely absent from the soil seed bank (Lang and Halpern 2007), dispersal must occur from adjacent forests or neighboring tree islands. However, dispersal distances are typically short for most forest herbs (Bierzychudek 1982; Cain et al. 1998). In this system, the proximity of older patches of forest (on the order of tens of metres) may ensure an abundance of seeds of most forest species, including those with more restrictive dispersal mechanisms (Haugo and Halpern 2007). Moreover, strong contrasts in the rates of accumulation of forest species beneath *Abies* and *Pinus* suggest that establishment is more limited by environmental conditions than by dispersal.

As in many grassland ecosystems, dense communities of forbs and graminoids can pose barriers to the germination and early survival of trees (Kunstler et al. 2006; Dickie et al. 2007). Once established, however, trees can grow rapidly, reducing light and temperature, changing litter quality, and modifying the physical, chemical, and biological properties of soils (Belsky et al. 1989; Amiotti et al. 2000; Griffiths et al. 2005). Experimental manipulations would be needed to identify the mechanisms — direct or indirect — by which trees exert positive or negative effects on herbaceous communities. *Abies* and *Pinus* differ in their abilities to modify their surroundings, with profound and predictable effects on some plant groups (e.g., facilitation of forest herbs by *Abies*, but not *Pinus*), but subtle, less intuitive effects on others (e.g., facilitation of meadow species by *Pinus*). Our study constitutes a first critical step in documenting the direction, strength, and timing of these interactions. It also has clear implications for the restoration and management of meadows that are experiencing encroachment. Prioritizing removal of *Abies*, particularly at an early age, will yield greater direct benefit than removing *Pinus*. Adopting a dynamic view of the interactions between trees and herbs is critical in systems in which the ecological consequences of woody plant invasions are potentially large, differ among the invading species, and unfold over decades or centuries.

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Appendix A

Appendix A, Table A1 appears on the following pages.

Table A1. Frequency (Freq, percentage of quadrats) and mean cover (Cov, %) of meadow, forest understory, and unclassified species in reference transects and under-canopy and adjacent-meadow segments of transects associated with *Pinus contorta* and *Abies grandis.*

				Pinus contorta (*n* = 26)				*Abies grandis* (*n* = 28)			
		Reference (*n* = 20)		Under		Adjacent		Under		Adjacent	
Species	Family	Freq	Cov	Freq	Cov	Freq	Cov	Freq	Cov	Freq	Cov
Meadow species											
Achillea millefolium	Compositae	80.8	10.8	83.6	13.4	82.3	11.7	71.7	8.2	9.0	11.6
Agoseris aurantiaca	Compositae	6.0	0.3	18.0	0.8	16.4	0.7	17.8	0.9	13.9	1.1
*Agropyron repens**	Gramineae	1.0	t								
Anaphalis margaritacea	Compositae	2.0	0.1					8.4	1.2	0.4	t
Aster ledophyllus	Compositae	6.5	0.7	1.0	1.2	8.8	0.6	14.6	1.4	16.6	1.9
Aster occidentalis	Compositae	8.5	1.1	1.8	0.2	4.3	0.5	10.5	1.5	15.5	1.9
Aster radulinus	Compositae	12.0	1.1	16.4	4.2	11.8	2.6	24.9	5.7	27.8	3.9
Bromus carinatus	Gramineae	68.5	9.1	41.1	4.3	59.3	6.1	50.4	4.8	62.4	6.7
Calochortus subalpinus	Liliaceae	18.0	0.4	12.6	0.2	25.8	0.6	6.3	0.1	8.7	0.1
Carex hoodii	Cyperaceae									0.9	t
Carex pensylvanica	Cyperaceae	95.0	22.1	95.0	24.0	92.5	20.9	68.9	12.4	77.9	14.2
Cerastium arvense	Caryophyllaceae							2.4	0.1	1.8	0.1
*Cerastium vulgatum**	Caryophyllaceae									3.1	0.4
Cirsium callilepis	Compositae	41.5	4.5	19.5	1.8	40.1	4.3	23.9	2.6	58.0	6.9
Comandra umbellata	Santalaceae	11.5	0.5	11.2	0.4	11.4	0.6	13.3	0.6	11.5	0.4
Danthonia intermedia	Gramineae	33.3	1.6	47.1	2.0	49.3	1.8	18.9	0.6	22.8	0.6
Elymus glaucus	Gramineae	51.8	9.3	29.1	3.6	34.8	5.1	48.9	7.0	62.5	10.4
Erigeron aliceae	Compositae	31.8	5.1	32.9	3.5	51.2	7.2	43.7	4.4	55.2	6.5
Erysimum asperimum	Cruciferae	1.0	0.1			0.9	t				
Festuca idahoensis	Gramineae	84.0	22.3	79.7	17.9	85.5	17.1	41.1	8.5	53.2	11.9
Festuca viridula	Gramineae	15.0	7.6	11.5	3.0	12.5	3.9	27.6	5.6	37.1	10.1
Fragaria vesca/F. virginiana	Rosaceae	61.0	15.6	46.1	9.1	53.6	8.7	79.8	14.9	92.9	19.9
Haplopappus greenei	Compositae					3.0	0.4				
Hieracium gracile	Compositae	33.8	4.7	52.0	8.2	50.9	8.0	28.7	3.5	40.3	5.4
Iris chrysophylla	Iridaceae	15.8	2.3	28.3	4.2	21.5	3.7	47.2	5.9	5.0	7.7
Lathyrus nevadensis	Leguminosae	9.0	1.0	8.3	2.6	11.8	2.8	32.1	7.9	3.0	5.9
Lomatium triternatum	Umbelliferae	1.0	t	5.1	0.2	4.1	0.1	1.2	0.1		
Lupinus latifolius	Leguminosae	66.0	7.9	54.9	4.4	72.6	7.5	28.9	2.6	53.7	5.2
Microsteris gracilis	Polemoniaceae	1.0	t			1.1	t	1.7	t	2.1	t
Orthocarpus imbricatus	Scrophulariaceae	3.0		1.1	t	9.1	0.2				
Penstemon procerus	Scrophulariaceae			1.3	0.2	1.8	0.1	1.0	0.1	2.6	0.3
Phlox diffusa	Polemoniaceae	29.0	6.3	61.1	17.8	61.9	14.4	5.1	0.7	14.8	2.1
*Poa pratensis**	Gramineae	6.0	0.5	0.3	t	5.9	0.4	5.5	0.2	8.2	0.6
Pteridium aquilinum	Polypodiaceae	5.0	1.4	7.6	1.6	6.0	0.6	9.7	2.6	10.3	2.7
Stellaria calycantha	Caryophyllaceae							1.8	0.2	0.6	t
Stipa occidentalis	Gramineae	1.0	t							0.5	t
Vaccinium caespitosum	Ericaceae	5.0	0.7					19.3	6.9	20.7	6.1
Vicia americana	Leguminosae	31.0	3.5	12.4	1.0	13.8	0.7	40.4	3.1	49.2	4.0

Table A1 (*continued*).

				Pinus contorta (*n* = 26)				*Abies grandis* (*n* = 28)			
		Reference (*n* = 20)		Under		Adjacent		Under		Adjacent	
Species	Family	Freq	Cov	Freq	Cov	Freq	Cov	Freq	Cov	Freq	Cov
Viola nuttallii	Violaceae	8.0	0.4	13.1	0.3	11.0	0.3	6.4	0.2	8.8	0.3
Forest understory species											
Acer circinatum	Aceraceae	1.0	t					0.6	t		
Achlys triphylla	Berberidaceae									0.5	t
Adenocaulon bicolor	Compositae							0.4	t		
Anemone deltoidea	Ranunculaceae			4.7	0.3			10.1	1.0	3.7	0.1
Anemone lyallii	Ranunculaceae							3.4	0.1	1.1	t
Anemone oregana	Ranunculaceae			8.6	0.8	11.3	0.7	14.2	0.6	11.4	0.7
Arenaria macrophylla	Caryophyllaceae	15.3	0.4	24.8	1.2	15.8	0.4	48.6	2.5	35.2	1.4
Asarum caudatum	Aristolochiaceae							5.8	0.6	4.3	0.3
Berberis nervosa	Berberidaceae			0.6	0.1			1.9	0.5		
Bromus vulgaris	Gramineae							2.3	0.2	0.9	t
Campanula scouleri	Campanulaceae			1.8	0.2			15.0	2.3	4.1	0.3
Chimaphila menziesii	Ericaceae							0.6	t		
Circaea alpina	Onagraceae							5.5	0.9	1.8	0.2
Galium oreganum	Rubiaceae			3.9	0.6			23.7	2.8	22.4	2.5
Galium triflorum	Rubiaceae					0.7	t	18.1	1.2	5.5	0.2
Goodyera oblongifolia	Orchidaceae							1.0	0.1		
Hieracium albiflorum	Compositae			2.8	0.2	1.0	0.1	11.3	0.8	4.9	0.3
Holodiscus discolor	Rosaceae							0.4	t		
*Lactuca muralis**	Compositae							3.8	0.4	1.0	0.1
Listera caurina/L. cordata	Orchidaceae							0.7	t		
Melica subulata	Gramineae	4.0	0.4	0.7				16.2	1.4	11.6	0.7
Osmorhiza chilensis	Umbelliferae			1.4	t			16.3	0.9	8.4	0.5
Rosa gymnocarpa	Rosaceae			0.6	0.1						
Rubus lasiococcus	Rosaceae							1.2	0.2	1.2	0.1
Rubus ursinus	Rosaceae							3.3	0.6	3.4	0.3
Smilacina stellata	Liliaceae			3.3	0.2	2.3	0.1	5.8	1.0		
Symphoricarpos mollis	Caprifoliaceae					0.7	t	3.6	0.4	2.2	0.1
Tiarella trifoliata	Saxifragaceae							3.8	0.4	1.3	0.1
Trientalis latifolia	Primulaceae							11.4	1.3	7.7	0.7
Trisetum canescens	Gramineae	1.0	0.1	1.0	0.2	0.5	t	7.0	0.3	13.0	0.6
Vaccinium membranaceum	Ericaceae										
Viola glabella	Violaceae	2.0	0.1	5.3	0.3	5.5	0.2	39.8	2.8	35.5	1.7
Unclassified species											
Abies grandis	Pinaceae			25.1	11.0	1.7	t	25.7	6.3	2.6	t
Abies procera	Pinaceae							0.5	t		
Amelanchier alnifolia	Rosaceae			6.4	1.4			1.3	0.1		
Epilobium angustifolium	Onagraceae							1.7	0.2	2.3	0.2

Table A1 (*concluded*).

				Pinus contorta (*n* = 26)				*Abies grandis* (*n* = 28)			
		Reference (*n* = 20)		Under		Adjacent		Under		Adjacent	
Species	Family	Freq	Cov	Freq	Cov	Freq	Cov	Freq	Cov	Freq	Cov
Epilobium watsonii	Onagraceae					0.7	t	1.2	t	4.0	0.7
Libocedrus decurrens	Cupressaceae							0.6	t		
Lilium columbianum	Liliaceae			3.9	0.2	2.4	0.1	4.5	0.3	7.0	0.4
Luzula campestris	Juncaceae	2.0	t	6.4	0.3	2.7	0.1	5.0	0.1	5.2	0.2
Montia perfoliata	Portulacaceae							0.4	t		
Montia sibirica	Portulacaceae							1.0	0.1		
Pinus contorta	Pinaceae			3.6	3.1	1.2	0.2	3.6	0.9		
Pseudotsuga menziesii	Pinaceae			2.8	0.1	0.7	t	5.1	0.8	0.9	0.4
Ranunculus uncinatus	Ranunculaceae							7.1	0.3	5.5	0.2
Rhamnus purshiana	Rhamnaceae			1.4	0.1			1.2	0.1		
*Rumex acetosella**	Polygonaceae	1.0	0.3	6.1	0.8	7.3	0.5	2.3	0.2	6.0	0.3
Satureja douglasii	Lamiaceae									1.8	0.2
*Tragapogon dubius**	Compositae	2.0	0.1								

Note: Numbers of transects are in parentheses; t, trace cover (<0.1%). Asterisks denote non-native species. Nomenclature follows Hitchcock and Cronquist (1973).