Conifer reinvasion of montane meadows following experimental tree removal and prescribed burning

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ABSTRACT

Tree invasion of mountain grasslands and meadows, pervasive throughout western North America, has become a management concern. Restoration of these systems requires tree removal and possibly prescribed burning; however, subsequent reinvasion by trees may compromise these efforts. In this study, we assess patterns of tree seedling establishment 8 years after tree removal (with and without burning) from 1-ha experimental plots in conifer-invaded meadows in the Oregon Cascades. We quantify variation in the timing, spatial distribution, and density of establishment of species with differing seral roles; compare effects of burning; and explore relationships with distance to and characteristics of adjacent, residual forests. Seedlings established continuously after tree removal, dominated by late-seral *Abies grandis* (cumulative plot densities of 116–460/ha). Early-seral *Pinus contorta* and *Pseudotsuga menziesii* were much less abundant (0–25 and 1–52/ha, respectively). Frequency (percentage of 5 × 5 m subplots) and density of seedlings did not differ between treatments (burned vs. unburned), nor did seedling growth rates (inferred from height-age relationships). Seedling spatial distributions and relationships with distance to adjacent forest varied both within and among plots. On average, however, seedlings were concentrated along edges. In the 5-m outer band of subplots, frequency averaged 37% and density, 682/ha, compared to 18% and 140/ha in the remaining cores of the plots. Density of *Abies* was significantly greater along more shaded southern edges (north-facing) than along more exposed northern edges (south-facing), but it declined steeply with distance from edge, especially for southern edges. Plot-level density of *Abies* seedlings was also correlated with basal area of *Abies* in the adjacent forest (but not with tree density or summed height). Strong relationships of seedlings with distance, exposure, and characteristics of adjacent forests suggest that conifer reinvasion can be minimized by targeting tree removal to maximize distances to residual trees. However, absence of a treatment effect suggests that burning—critical for reducing woody residues—does not increase the probability of seedling establishment, particularly in systems in which late-seral species are the principal colonists.

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1. Introduction

Woody-plant invasion of grasslands and meadows is a phenomenon of global relevance and of increasing concern to land managers (Archer et al., 1988; Scholes and Archer, 1997; Halpern et al., 2012). Recent invasions of systems that have long persisted in an open, herbaceous state suggest a shift in the balance between factors that inhibit woody-plant establishment (e.g., physical barriers to germination or periodic fires) and those that promote it (asymmetric competition, facilitation, or changes in soils). A variety of external factors may contribute to invasions, including changes in climate, land use, and disturbance regime (Vale, 1981; Rochefort et al., 1994; Scholes and Archer, 1997; Bond and Midgley, 2000; Norman and Taylor, 2005; Heyerdahl et al., 2006; Coop and Givnish, 2008). Moreover, once invasions are initiated, internal feedbacks (tree-tree or tree-soil interactions) can reinforce the shift to a woody state (Archer et al., 1988; D'Odorico et al., 2010; Ratajczak et al., 2011; Halpern et al., 2012). The consequences of these transitions can be profound, including fundamental changes to community structure, composition, and diversity (Scholes and Archer, 1997; Haugo and Halpern, 2007), as well as changes in nutrient cycles, water use, and carbon storage (Jackson et al., 2002; Lett and Knapp, 2003; Griffiths et al., 2005; Browning et al., 2008).

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In the Oregon Cascade Range, mountain meadows occur as small, often isolated habitats, with biotas distinctly different from those of the surrounding forest matrix (Franklin and Halpern, 1999). As such, they contribute disproportionately to local and regional biodiversity (Hickman, 1976; Franklin and Halpern, 1999). In some areas of the Cascade and Coast Ranges, meadow contraction has been estimated at ~50% since the 1940s (Dailey, 2007; Takaoka and Swanson, 2008; Zald, 2009). Concerned with the pace of habitat loss, federal land managers have implemented meadow restoration strategies that include tree removal and prescribed fire. However, the efficacy of these approaches is not well understood. Although burning may be necessary to consume residual woody fuels, its contribution as a disturbance process is poorly understood. First, it is unclear what role natural fire or anthropogenic burning played in the origin or maintenance of these high-elevation systems (Burke, 1979; Vale, 1981; Boyd, 1999). Second, grassland fires are typically low intensity events. However, the accumulation of woody fuels associated with conifer encroachment can lead to higher intensity fire, with adverse effects on soils and vegetation (Wan et al., 2001; Korb et al., 2004; Pyke et al., 2010), including greater risk of exotic invasion (D'Antonio, 2000) or reinvasion of pioneering conifers (e.g., *Pinus contorta* or *Pseudotsuga menziesii*) that germinate readily on disturbed or burned soils (Minore, 1979; Hermann and Lavender, 1990; Lotan and Critchfield, 1990).

The factors that promote tree invasions of natural grasslands should also be relevant to reinvasions that follow after tree removal or burning. Edge effects and species' traits are particularly relevant. Tree recruitment is often concentrated along edge environments where seed rain and habitat modification (canopy shading, root competition, and access to ectomycorrhizal symbionts) are greatest (Magee and Antos, 1992; Miller and Halpern, 1998; Dickie and Reich, 2005; Coop and Givnish, 2007; Rice, 2009). Effects can vary with exposure (aspect), characteristics of the edge (e.g., tree size or density, which relate both to seed production and shading), and the regeneration requirements of species (e.g., shade tolerance). By its nature, edge-establishment results in a gradual process of migration (e.g., Weltzin and McPherson, 1999; Dovčiak et al., 2008). However, tree recruitment can also occur far from the edge if seed is available, suitable germination sites exist, and seedling growth is sufficient to escape competition from herbaceous species. Such establishment events can lead to nucleation (localized clumping facilitated by initial recruits; Yarranton and Morrison, 1974) and accelerated invasion as seed sources become more widely distributed (Archer et al., 1988; Duarte et al., 2006; Boulant et al., 2008; Halpern et al., 2010). Whether edge-migration or nucleation dominates the invasion process may depend on the available species pool. If multiple tree species are present, differences in dispersal, physiological requirements, and growth rates can produce spatial or temporal asynchrony in species' establishment (Moore and Huffman, 2004) or allow for biotic interactions (facilitation) that promote more rapid invasion (Halpern et al., 2010).

In this study we examine patterns of conifer reestablishment 8 years after tree removal from experimental plots at Bunchgrass Ridge, a high-elevation meadow complex in the Oregon Cascade Range. Long-term encroachment by *P. contorta* and *Abies grandis*, culminating in a massive wave of invasion in the mid-late 1900s, had reduced meadow extent by >50% (Rice, 2009). The experiment, imposed on a mosaic of variously aged forests and meadows, tests (1) whether tree removal can reverse the effects of encroachment (including replacement of meadow by forest understory species; Haugo and Halpern, 2007, 2010) and (2) whether fire is also necessary (see early results in Halpern et al. (2012)). Here, we evaluate the potential for conifer reestablishment to compromise the effectiveness of these treatments. We assess the time course of early recruitment; variation in the abundance and spatial distributions of seedlings; and potential correlates of establishment, including species' traits, use of fire, and characteristics of residual forest edges. We pose the following hypotheses based on our understanding of species' life histories, treatment-induced changes in vegetation and soils, and the processes that structure natural invasions of these meadows:

Hypothesis 1. Temporal trends and species differences. (*H1a*) Seedling recruitment will decline with time since tree removal (or burning), paralleling trends in the availability of germination sites (cover of mineral soil). (*H1b*) Early-seral *P. contorta* (hereafter, *Pinus*) will tend to establish before, and with greater frequency and density, than late-seral *A. grandis* (hereafter, *Abies*). (*H1c*) Height growth will also be more rapid in *Pinus* than in *Abies*—patterns consistent with the seral roles and physiological traits of these species.

Hypothesis 2. Treatment differences. (*H2a*) Frequency and density of seedlings will be greater in burned than in unburned plots, reflecting greater availability of germination sites. (*H2b*) Seedling height growth will also be greater in burned plots, consistent with the greater reduction in cover of competing vegetation caused by fire.

Hypothesis 3. Relationships with distance to and characteristics of the adjacent forest. (*H3a*) Seedling density will decline with distance from residual forest edge. (*H3b*) For shade-intolerant *Pinus*, density will be greater along northern (N, more exposed) than along southern (S, more shaded) edges; for shade-tolerant *Abies*, the opposite pattern will occur. (*H3c*) Seedling density will correlate with characteristics of the adjacent forest (tree density, basal area, or height) that correlate with seed production or the intensity of edge effects.

2. Methods

2.1. Study area

Bunchgrass Ridge forms a gently sloping plateau at 1350 m elevation on the western slope of the High Cascades in Oregon (USA). The study area supports a mosaic of meadows (or grasslands) and coniferous forests of varying size, age, and structure, reflecting nearly two centuries of tree invasion (Halpern et al., 2010; Rice et al., 2012). Loss of meadow habitat was particularly rapid during the mid-late 1900s (>50% reduction in area; Rice, 2009). The remaining meadows support diverse communities of graminoids and forbs characteristic of mesic and dry-site meadows of this region (Franklin and Halpern, 1999; Haugo and Halpern, 2007). Forests are dominated by *A. grandis* and, to a lesser extent, *P. contorta*. Additional, less common species include *P. menziesii*, *Abies procera*, *Pinus monticola*, and *Tsuga mertensiana*.

Soils are deep (~1.7 m), fine to very fine sandy loams derived from andesitic basalt and tephra deposits with varying amounts of glacially derived rock. They grade from Vitric Melanocryands in open meadows to Aquic Vitricryands in older forests (Haugo and Halpern, 2007, 2010). Soil profiles indicate dominance of grassland vegetation for several centuries (possibly millennia), even in areas that currently support older forests (Haugo and Halpern, 2007). The climate is maritime, with cool, wet winters and warm, dry summers. At Santiam Pass (1488 m), 17 km to the north, temperatures average −7.0 °C (minimum) and 0.8 °C (maximum) in January, and 6.2 °C and 27.9 °C in July. Annual precipitation averages 220 cm but is highly seasonal, producing frequent

summer drought (data for 1948–1985; Western Regional Climate Center; available online). Annual snowfall averages 11.5 m, resulting in a deep snowpack that can persist into May or early June.

Fire is the primary form of disturbance in this region, but is relatively infrequent at this elevation (Morrison and Swanson, 1990; Weisberg and Swanson, 2003). There is no evidence of moderate- or high-intensity fire in the study area in the last two centuries (Halpern et al., 2010), although low-intensity fire may have been used by Native Americans to maintain meadow openings (Burke, 1979; Boyd, 1999). Grazing by sheep is likely to have occurred during the late 1800s and early 1900s (as in much of the Cascade Range; Elliot, 1946; Johnson, 1985), but grazing records specific to the study area are lacking. Roosevelt elk (*Cervus canadensis roosevelti*), which were historically abundant in western Oregon (Oregon Department of Fish and Wildlife, 2003), are common. Western pocket gophers (*Thomomys mazama*) are also common in adjacent meadow openings, creating soil mounds and winter castings (Jones et al., 2008; Case et al., 2013). They are known to feed on the roots or girdle the stems of conifer seedlings (Ferguson, 1999).

2.2. Site selection, experimental design, and treatment implementation

In 2002, aerial photographs (1946–1997) and field reconnaissance were used to delineate a 16-ha experimental area containing both past and recent conifer invasion (Fig. 1). Nine 1-ha (100 × 100 m) experimental plots were established in June 2003. Each plot contained a fine-scale mosaic of meadow openings and forest patches of varying age and structure (Haugo and Halpern, 2007; Halpern et al., 2010). Plots were randomly assigned to one of three treatments (n = 3): (1) control (C), no trees removed (not considered in this study); (2) unburned (UB), all trees removed and residual slash piled and burned leaving 90% of the ground surface unburned; and (3) burned (B), all trees removed and slash broadcast burned. Trees were removed in January–February 2006 on deep, compacted snow to minimize soil disturbance. Larger trees were cut with chainsaws and smaller trees with a mechanical faller. Rubber-tired and tracked skidders were used to yard tree boles to an off-site landing.

For the burned treatment (B), narrow fire lines, supplemented by a system of fire hoses, were constructed around the perimeter of each of plot. Slash was burned on 28 September 2006. Fine-fuel loadings (1- to 100-h) averaged 53–69 Mg/ha. Plots burned to completion within 2 h. Flame lengths averaged 1–2 m and consumption of fine fuels averaged 67–87%. For the unburned (UB) treatment, slash piles (2–4 m diameter × 1.8–2 m tall) were constructed by hand in June 2006. Piles were ignited on 2 November 2006 and burned to completion within two days (95–100% consumption).

2.3. Sampling methods

Prior to tree removal (summer 2003), a permanently marked grid was surveyed in each of the experimental plots to create a system of 10 × 10 m subunits. For this study we divided these into 5 × 5 m subplots, yielding a total of 400 subplots per plot. Following tree removal, distances to adjacent forest varied due to the adjacency of some plots (e.g., plots 2 and 3) and to the presence of natural meadow openings (Fig. 1). At least some residual trees were present within 20 m of all sides of three plots, but were lacking on one side of the other three plots (Table 1).

To quantify the frequency, density, and spatial distributions of conifer seedlings, we recorded the presence of all individuals ≥5 cm tall in each subplot. For each individual we recorded species, measured height (cm), and determined age from bud-scale scars. Post-treatment recruitment was distinguished from the relatively few residual seedlings based on age relative to timing of treatments. Dead seedlings comprised <4% of the total and were not analyzed further. Browsing by elk was minimal, thus no attempt was made to quantify the frequency or amount of damage.

To quantify the influence of adjacent forests (as sources of seed or shade), we established a 20-m-wide sampling band (occasionally 30 m when tree density was low) adjacent to each plot edge. Within each band we recorded the species and measured the diameter at breast height (dbh) of each tree ≥10 cm dbh.

2.4. Data summary and analysis

For each plot we computed the frequency (percentage of subplots) and density of seedlings of each species. We also characterized the structure of forests adjacent to each plot, including the

Fig. 1. Aerial photograph of Bunchgrass Ridge showing the locations of tree-removal plots (100 × 100 m) relative to adjacent forests and natural meadows. Plots outlined in black were broadcast burned (B); plots outlined in white were pile burned leaving 90% of the ground surface unburned (UB). Northern edges are denoted by "N". Plantations established in the 1970s and 1980s lie to the west, northwest, and northeast of the study site.

Table 1
Density, basal area, and summed height of the principal tree species bordering the experimental plots.

Plot	Treatment	Forest edges[a]	Abies grandis			Pinus contorta			Pseudotsuga menziesii		
			Density (trees/ha)	BA (m²/ha)	Height (m/ha)	Density (trees/ha)	BA (m²/ha)	Height (m/ha)	Density (trees/ha)	BA (m²/ha)	Height (m/ha)
2	Burned	3	234	8.8	4039	38	1.5	814	38	2.0	693
3	Unburned	3	164	8.7	3018	21	0.7	425	6	0.7	132
8	Burned	4	173	24.3	3898	1	<0.1	23	4	1.4	105
10	Unburned	4	391	38.3	8169	13	0.7	306	5	0.3	96
11	Burned	3	118	11.8	2428	1	0.5	71	12	1.8	248
13	Unburned	4	364	23.9	6942	18	0.8	386	13	6.3	431
Mean		3.5	241	193	4749	15	0.8	338	13	2.1	284

Note: Density, basal area (BA), and height are based on trees ⩾ 10 cm dbh. Height is the summed height of individuals expressed on a per-hectare basis (see Section 2.4). Additional species were present but uncommon.
[a] Number of plot edges with at least some trees within 20 m (see Fig. 1).

density, basal area, and summed height of each species (on a per hectare basis; Table 1). Tree height was estimated from diameter-height equations constructed prior to the experiment (C. B. Halpern, unpublished data).

To assess temporal trends (*H1a*) and species differences (*H1b*) in establishment we created cumulative establishment curves for the most common species (*Abies*, *Pinus*, and *P. menziesii*, hereafter *Pseudotsuga*). Separate curves were produced for frequency and density within each plot, then averaged for each treatment (*n* = 3). To compare growth rates among species (*H1c*), we used a linear model that included age, species, and the age × species interaction as main effects. A significant interaction was used as evidence of a difference in growth rate among species; species were then compared pairwise, similarly. Analyses were based on mean heights of individuals of a given age within each plot.

To determine whether seedling frequency and density were greater in burned than in unburned plots (*H2a*), we used two-sample *t*-tests. Tests were run for all seedlings combined and for *Abies* and *Pseudotsuga*, the only taxa with sufficient presence to assess statistically. For *Pseudotsuga*, data were log-transformed to attain homogeneity of variance. To test whether height growth was greater in burned than in unburned plots (*H2b*), we compared age–height relationships using a linear model that included age, treatment, and the age × treatment interaction as main effects (as for the comparison of species' growth rates). Separate models were run for *Abies*, *Pinus*, and *Pseudotsuga*. Analyses were conducted in R (R Development Core Team, 2012).

We developed a two-dimensional density map for each plot to visually display the spatial distribution and density of seedlings. To assess relationships between seedling density and distance from forest edge (*H3a*) we modeled mean density of *Abies* seedlings (5-m intervals) to a distance of 50 m from each edge of each plot. Two types of models were considered using the regression module of Sigmaplot 9.01 (Systat Software, 2004): linear ($y = y_0 + ax$) and one- or two- parameter exponential decay ($y = ae^{-bx}$ or $y = y_0 + ae^{-bx}$). We summarized results (including model form, significance, and adjusted R^2) by plot and edge type: northern (N, ranging from NW to NE), eastern (E, NE to SE), southern (S, SE to SW), and western (W, SW to NW) (Fig. 1).

We also tested whether *Abies* seedlings were more abundant along the S (vs. N) edges of plots (*H3b*). We used a series of paired *t*-tests (*n* = 6) to compare mean densities to distances of 10, 20, and 30 m from the edge. Finally, we used linear regression to test whether the mean density of *Abies* seedlings varied with the density, basal area, or summed height of *Abies* in the adjacent forest (*H3c*). Given the small sample size (*n* = 6), predictors were tested separately to avoid over-fitting models. Similar relationships were not tested for *Pinus* or *Pseudotsuga* because densities were too low in many plots.

3. Results

3.1. Temporal trends and species differences

Seedling recruitment did not decline with time as predicted (*H1a*) (Fig. 2). The apparent plateau in density 8 years after tree removal is likely due to the height threshold for recording seedlings. First-year seedlings were present in year 8 (2013), but most were <5 cm tall. Counter to prediction, *Pinus* did not establish before, or at greater frequency or density than did *Abies* (*H1b*) (Fig. 2). *Abies* occupied 12–27% of subplots with a density of 116–460 seedlings/ha (range of plot values), whereas *Pinus* occupied only 0–5% of subplots with a density of 0–25 seedlings/ha. Surprisingly, *Pseudotsuga* was as abundant as *Pinus* (0.3–5% of subplots and 1–52 seedlings/ha). As predicted, *Abies* grew significantly slower than did *Pinus* (*H1c*) or *Pseudotsuga* (significant species × age interactions: *P* < 0.001) (Fig. 3).

3.2. Treatment differences

Frequency and density of seedlings were no greater in burned than in unburned plots, counter to prediction (*H2a*) (Table 2). Only *Pseudotsuga* showed a trend toward more frequent establishment in burned plots (marginal significance; *P* = 0.09). Rates of height growth also did not conform to prediction (*H2b*). Growth, which varied considerably within and among plots, was no greater in the burned than in the unburned treatment for any of the species tested (non-significant treatment × age interactions) (Fig. 3).

3.3. Relationships with distance to and characteristics of adjacent forests

Relationships between seedling density and distance to forest edge were highly variable within and among plots (Fig. 4), partially supporting our hypothesis (*H3a*). Regressions for *Abies* were highly significant for eight of 21 edges tested—most often along the shaded, S edge of a plot (Table 3). Trends were best fit by an exponential decay model, capturing the high density of seedlings within 5 m of the edge (Fig. 4). Seedlings established in an average of 37% of these edge subplots (range of 13–67% among plots), but only in 18% of the remaining core (range of 11–24%). The contrast in seedling density was even greater: although edge subplots accounted for only 19% of the plot area, they contained an average of 48% of the seedlings (range of 10–72%), at an average density of 682/ha—nearly five times denser than the core subplots (140/ha).

Densities of *Abies* seedlings were significantly greater along the S than the N edges of plots, as predicted (*H3b*), but the magnitude of this effect declined with cumulative distance from the edge (Fig. 5). *Pinus* was too infrequent to test similarly (Table 2).
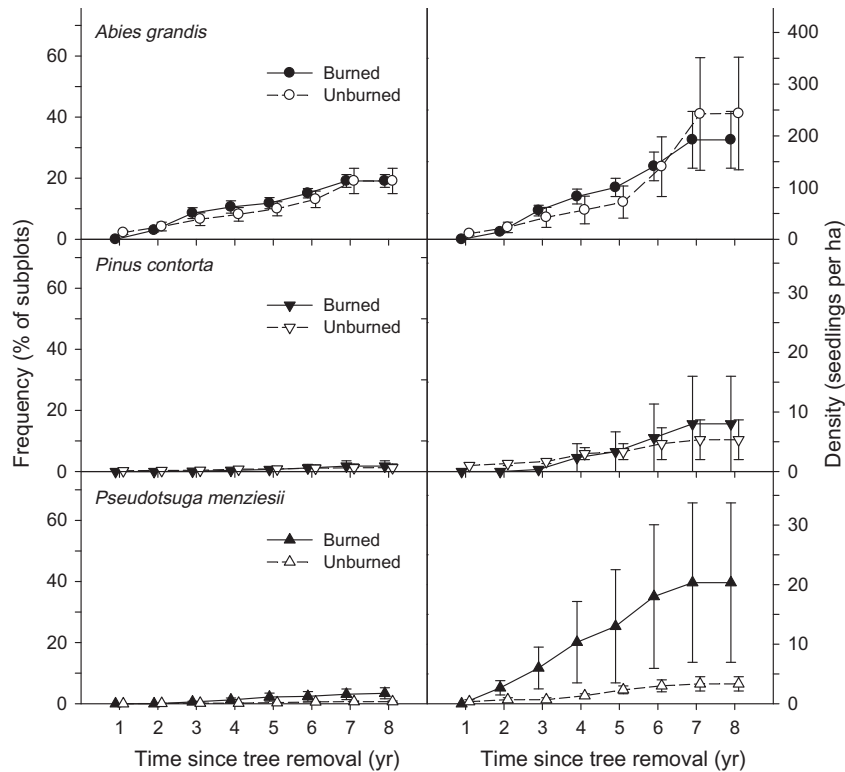
Fig. 2. Cumulative seedling frequency (percentage of subplots) and density of the principal species in burned and unburned treatments (closed and open symbols, respectively). Values are treatment means ± 1 SE. Note the change in density scales for *Pinus* and *Pseudotsuga* relative to *Abies*.

One measure of adjacent forest structure was a strong predictor of seedling density (*H3c*). For *Abies*, seedling density was highly correlated with basal area (Fig. 6), but not with density or summed height of mature trees (⩾ 10 cm dbh).

4. Discussion

Woody-plant invasions of grasslands and meadows can have dramatic consequences for species composition, diversity, and other ecosystem services (Scholes and Archer, 1997; Jackson et al., 2002; Haugo and Halpern, 2007; Ratajczak et al., 2012). Shrub or tree removal represents a first critical step toward restoration, but subsequent recolonization could compromise this goal. Rapid, post-treatment reestablishment of tree seedlings implies that the processes that once maintained these as open systems have changed, or that they have been altered by long-term tree presence. Additionally, disturbances associated with tree removal or disposal of woody residues (prescribed burning) might create conditions favorable for tree establishment. Our analyses provide insight into several of the factors hypothesized to influence the timing, intensity, or distribution of seedling reinvasion into grasslands targeted for restoration.

4.1. Temporal trends and species differences

We predicted that seedling recruitment would decline with time since disturbance (tree removal and burning; *H1a*) mirroring the availability of germination sites. However, trends in establishment offer no evidence of decline, suggesting that "safe sites" (Harper, 1977; Kunstler et al., 2007) are not limiting or have not decreased to date. Trends in cover of bare ground (exposed mineral soil) are consistent with this interpretation. In burned plots, it was initially elevated by consumption of fine litter, but was stable thereafter; in unburned plots it increased over time due to pocket gopher activity. Gopher mounds and winter castings

are common forms of soil disturbance in natural meadow openings (Jones et al., 2008; Case et al., 2013) and have become increasingly common after tree removal from the experimental plots (C. B. Halpern, unpublished data).

Despite continuous increases in seedling density, establishment was highly localized in many plots, suggesting that large portions of this system remain resistant to reinvasion. Preemption of space and competition for resources are among the processes that limit tree seedling establishment in natural grasslands (Magee and Antos, 1992; Peltzer, 2001; Kunstler et al., 2006; Picon-Cochard et al., 2006; Dickie et al., 2007; Haugo et al., 2013). Similar processes should be operating in this system because many of the same strong competitors are present (Halpern et al., 2012). Browsing by elk or predation by pocket gophers may also limit establishment (Graham and Kingery, 1990; Jenkins and Starkey, 1993; Ferguson, 1999) although it was not possible to quantify the importance of these factors in the current study.

We predicted that tree species would differ in their temporal patterns of colonization (*H1b*), consistent with their seral roles. Specifically, we expected that early-seral *Pinus*—characterized by shade intolerance, preference for disturbed (including burned) soils, and rapid growth—would precede establishment of *Abies*—characterized by greater shade tolerance, greater susceptibility to drought, and slower growth (Foiles et al., 1990; Lotan and Critchfield, 1990). However, we observed just the opposite trend: more frequent and dense establishment of *Abies*. Moreover, *Pseudotsuga* was as common as *Pinus*—a pronounced contrast to its near absence in the original invasion of these meadows (Halpern et al., 2010; Rice et al., 2012). Low density of *Pinus* is likely explained by limited seed availability—a consequence of its longevity and history of forest development on these sites. Although *Pinus* contributed significantly to the original invasions of Bunchgrass Ridge (Halpern et al., 2010), subsequent mortality of this relatively short-lived species (exacerbated, in part, by a recent bark-beetle outbreak) has left it with a sparse and patchy distribution in the sur-
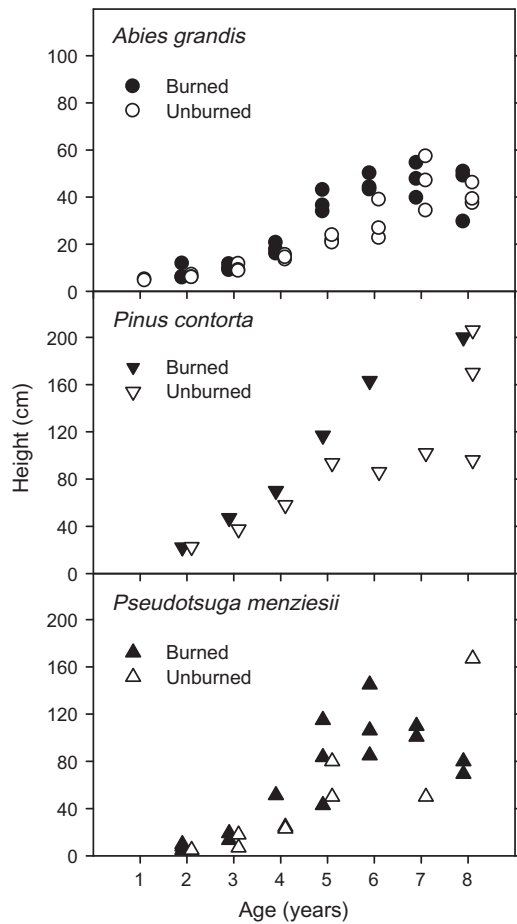
Fig. 3. Relationships between age and mean height for the principal seedling species in burned and unburned plots (closed and open symbols, respectively). Values are mean heights of individuals within a plot (maximum of three heights per age per treatment). Ages for burned and unburned plots are offset to reduce overlap. Note the change in height scales for *Pinus* and *Pseudotsuga* relative to *Abies*.

Pseudotsuga (Minore, 1979; Foiles et al., 1990; Lotan and Critch-field, 1990). An important implication of the slower growth of *Abies*, despite its greater abundance, is the resulting lag in its local influence on the recovering meadow, compared to faster-growing *Pinus*. In the longer term, however, *Abies* is likely to impose stronger effects—facilitating more rapid and intense clumping of future recruits (Rice et al., 2012) and colonization and growth of shade-tolerant forest herbs (Haugo and Halpern, 2010).

4.2. Treatment differences

We expected broadcast burning to enhance rates of seedling establishment (*H2a*). Despite greater reduction of plant cover and increased exposure of mineral soil (Halpern et al., 2012), cumulative seedling establishment was comparable between treatments. Among individual species, only *Pseudotsuga*—which establishes more readily on mineral substrates (Hermann and Lavender, 1990)—showed marginally greater frequency in burned plots. *Abies*, the principal invader, did not, consistent with its establishment across a broader range of edaphic and competitive environments (Antos and Shearer, 1980; Geier-Hayes, 1987; Foiles et al., 1990). Conifer reinvasion of this system thus appears to be driven, in large part, by differences in seed availability and the regeneration requirements of species and only minimally by effects of fire. Again, had treatments been applied earlier in the invasion process—when *Pinus* was more abundant—disturbance effects may have been more apparent, leading to greater and preferential establishment of *Pinus* in burned plots.

We also expected more rapid seedling growth in burned than in unburned plots (*H2b*), reflecting the characteristic flush in available nitrogen (N) (Prieto-Fernandez et al., 1993; Pietikainen and Fritze, 1995; Antos et al., 2003) and reduction in plant cover. However, we were unable to detect a difference in growth rate for any of the species tested. Several factors may have contributed to this result. First, although burning caused a large increase in available N, the effect was transient, limited to the first year (Halpern et al., 2012). Second, effects on plant cover were less dramatic and subsequent regrowth was comparable between treatments (Halpern et al., 2012; C.B. Halpern, unpublished data). Finally, we observed considerable variability within plots in the height of older seedlings, suggesting that the factors that influence early growth vary more at local scales than between treatments. This variation may be a legacy of the fine-grained mosaic of pre-treatment vegetation, which included small meadow openings, areas of recent invasion, and older (>130 year) forests (Haugo and Halpern, 2007).

4.3. Relationships with distance to and characteristics of adjacent forests

We expected seedling density to decline with distance from the forest edge (*H3a*) and to differ along edges with contrasting expo-

rounding forests (densities one to two orders of magnitude lower than those of *Abies*; Table 1). Had we conducted this experiment earlier in the invasion process, *Pinus* is likely to have been more common. These observations underscore a key point—the context, including timing, of restoration treatments can have a profound effect on the outcome, as shown in a variety of situations (Brudvig, 2011).

Although patterns of establishment among species ran counter to expectation, comparative growth rates were as predicted (*H1c*): markedly slower for late-seral *Abies* than for early-seral *Pinus* or

Table 2
Summary statistics and results of two-sample *t*-tests comparing frequency and density of recruitment in burned and unburned plots.

Species	Burned plots					Unburned plots					Frequency		Density	
	Frequency (% of subplots)		Density (seedlings/ha)			Frequency (% of subplots)		Density (seedlings/ha)						
	Plots[a]	Mean	(SE)	Mean	(SE)	Plots	Mean	(SE)	Mean	(SE)	t	P	t	P
Abies grandis	3	19.5	(2.3)	196.7	(54.6)	3	19.1	(4.1)	243.3	(108.9)	0.47	0.66	−0.25	0.82
Abies procera	1	0.3	(0.3)	1.3	(1.3)	1	1.1	(1.1)	6.0	(6.0)				
Pinus contorta	1	1.8	(1.8)	8.3	(8.3)	3	1.3	(0.8)	5.3	(3.3)				
Pinus monticola	0	–		–		2	0.2	(0.1)	0.7	(0.3)				
Pseudotsuga menziesii	3	3.8	(2.1)	22.3	(14.9)	3	0.7	(0.2)	3.3	(1.2)	2.23	0.09	1.89	0.14
All species pooled	3	21.1	(1.8)	228.7	(44.2)	3	20.4	(3.7)	258.7	(113.6)	0.09	0.93	−0.38	0.72

Note: *Abies procera*, *Pinus contorta*, and *Pinus monticola* were too sparse to test statistically. Data for *Pseudotsuga menziesii* were log-transformed prior to analysis to meet variance assumptions.
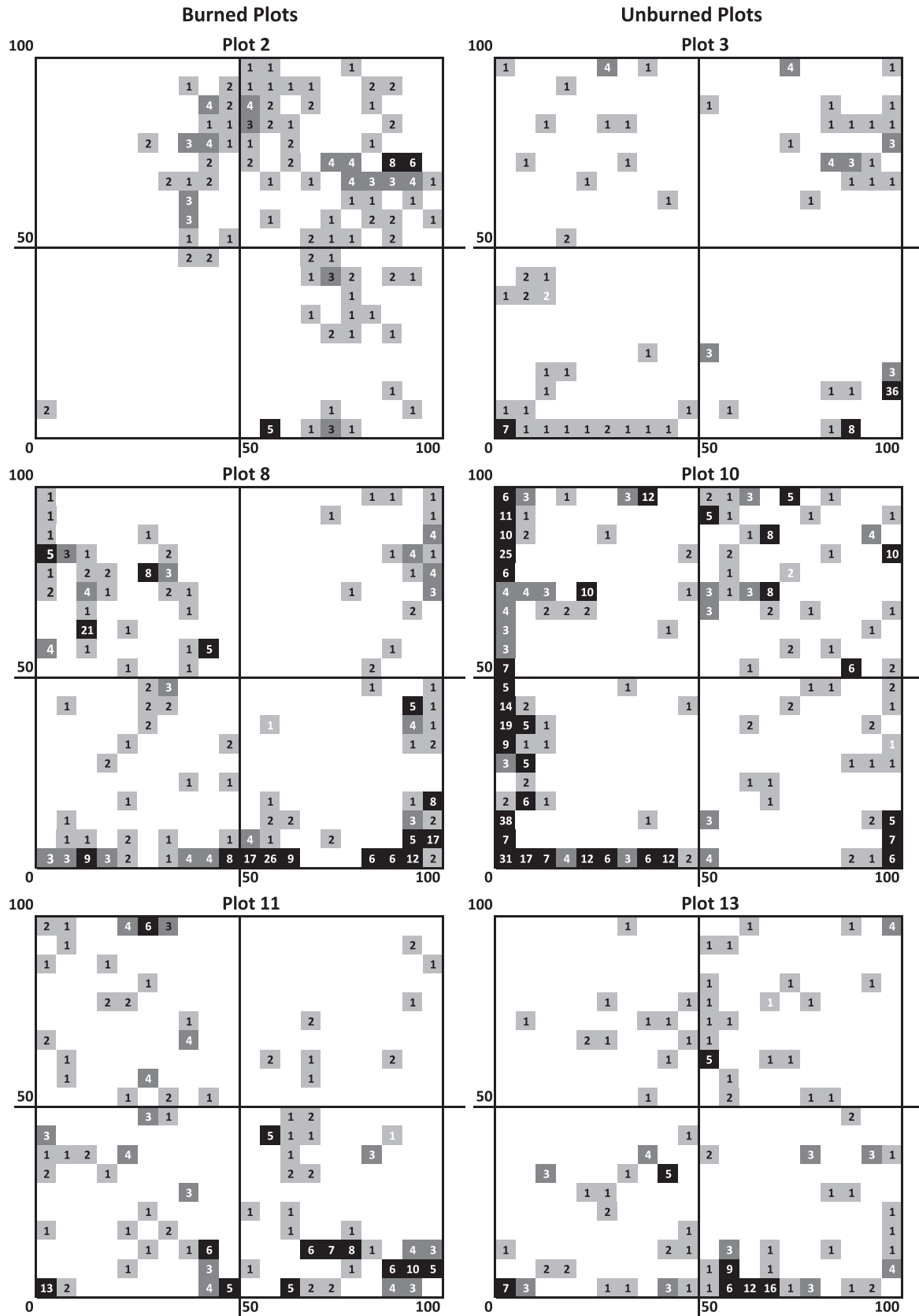[a] Number of experimental plots in a which a species was recorded (*n* = 3 per treatment).

Fig. 4. Maps of the distributions of all seedlings among the 400, 5 × 5 m subplots in each plot (1 ha). Shading corresponds to density: white = 0, light gray = 1–2, dark grey = 3–4, black = ⩾5 seedlings per subplot (i.e., numbers are seedling counts). The N edge of each of plot is at the top.

Table 3
Results of regression analyses (model form and adjusted R^2) relating decline in mean density of *Abies grandis* seedlings to distance from the plot edge (maximum of 50 m).

Plot	Treatment	N edge		S edge		E edge		W edge	
		Model	Adj R^2	Model	Adj R^2	Model	Adj R^2	Model	Adj R^2
2	Burned	–		–		Not tested		–	
3	Unburned	–		–		Decay²	0.90	Not tested	
8	Burned	–		Decay¹	0.97	–		–	
10	Unburned	–		Decay²	0.79	–		Decay²	0.99
11	Burned	Decay²	0.74	Decay¹	0.54	Not tested		–	
13	Unburned	–		Decay²	0.93	–		–	

Note: we tested models of two general forms: linear and one- or two-parameter exponential decay (Decay¹ and Decay², respectively). Dashes indicate non-significant relationships. Three edges were not tested due to the absence of adjacent forest (Table 1).
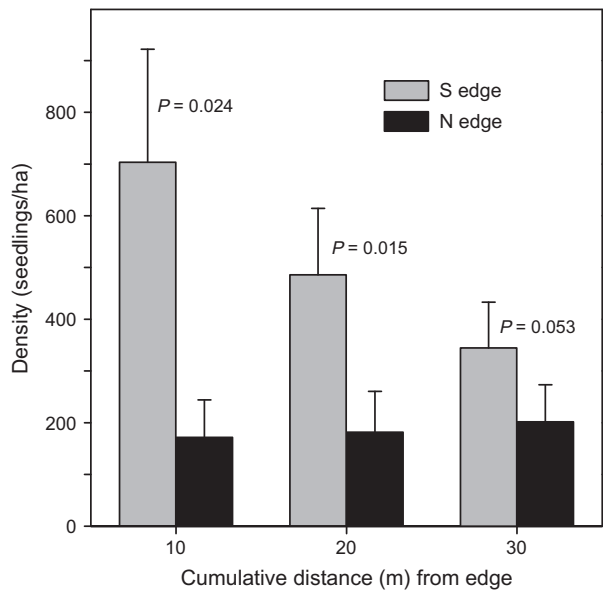

Fig. 5. Mean density (+1 SE) of *Abies grandis* seedlings along the S and N edges of plots. Densities are shown to distances of 10, 20, and 30 m from the plot edge. One-tailed *P* values test the hypothesized difference in density (S > N; *H3b*).
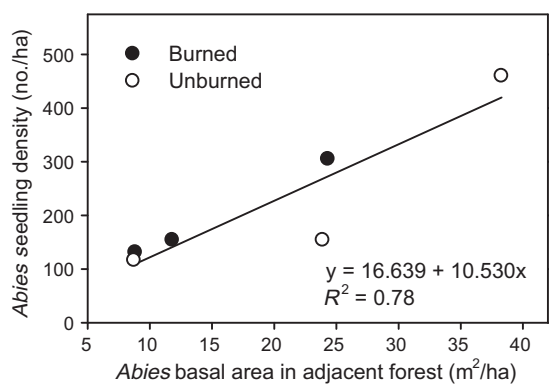

Fig. 6. Relationship between *Abies* seedling density and *Abies* basal area in the adjacent forest. Values are plot means, coded by treatment.

sures in a manner consistent with the physiological traits of *Pinus* and *Abies* (shade-intolerant and tolerant, respectively) (*H3b*). *Pinus* was too infrequent to assess statistically, but the density distribution of *Abies* was consistent with expectation, albeit not in all plots. Seedlings were concentrated within 5 m of the edge and density declined exponentially with distance for ~40% of the edges. This pattern is consistent with the dispersal kernels of wind-dispersed seeds (Franklin and Smith, 1974; Clark et al., 1999). However, for a shade-tolerant species it is also consistent with a model of

increasing exposure (solar radiation and temperature) with distance from the edge (Heithecker and Halpern, 2007). Additional support for this shading effect lies in the large differences in seedling density along S vs. N edges (an effect that diminished with distance from edge; Fig. 5), and in the more frequent decline in density with distance for S compared to N edges (67% vs. 17% of edges; Table 3).

We also hypothesized that seedling density would correlate with structural metrics that serve as proxies for seed production or dispersal (e.g., basal area or tree height) or for habitat modification near the edge (e.g., stand density) (*H3c*). For *Abies*, seedling density was strongly related to basal area. Fecundity is often a function of tree size or age (Clark et al., 1999; Greene and Johnson, 1999; Schurr et al., 2008), thus presence of large trees can have a disproportionate effect on the seed rain. These larger individuals (up to 160 cm dbh) also contributed to rapid infilling of meadows in the mid- to late 1900s (Halpern et al., 2010). In contrast, we found no relationship with stand density or cumulative tree height. Because modification of the edge environment appears limited to a short distance (<10 m), greater height or density of trees may have little affect on the probability of seedling establishment.

Despite the decline with distance and the strong association with shaded S edges, *Abies* established over substantial portions of the experimental plots—as far as 50 m from the nearest edge (the maximum possible in our plots). Moreover, density was often unrelated to distance or exposure, suggesting that establishment is regulated, in part, by local factors (seedbed conditions, residual woody debris, microtopography, gopher disturbance, and competing vegetation) that vary at fine spatial scales. Anecdotal observations suggest that *Abies* often established in concavities or adjacent to logs or stumps—microsites characterized by greater soil moisture or shade. We did not attempt to quantify the relative importance of these factors retrospectively because ground conditions and vegetation characteristics have changed dramatically over the time that seedlings have established (Halpern et al., 2012).

4.4. Management implications

Many factors can influence the success of meadow or grassland restoration following tree removal. However, maintenance of open conditions is key. Spatial and temporal patterns of seedling reinvasion in this experiment have important implications for the design of restoration treatments—including subsequent interventions—to minimize seed rain, seedling establishment, and the potential for established trees to accelerate the invasion process (Halpern et al., 2010; Rice et al., 2012; Zald et al., 2012). Recruitment was densest along forest edges, suggesting that tree removal should be configured to minimize edge effects and maximize distances to seed sources—approaches not used in this experiment (Fig. 1). Although restoration projects are likely to be spatially constrained by the small sizes, complex shapes, and topography of natural meadow openings, larger treatments that increase distance to forest edge would reduce the probability of reinvasion. Our results

also highlight the importance of tree size for seed production and seed rain. On balance, removing individual large trees is likely to reduce propagule pressure to a greater degree than removing many smaller trees. However, care must be taken because some individuals may predate historical invasions and removal would be inappropriate in the context of meadow restoration.

Broadcast burning—critical to reducing fuel accumulation and future fire hazard—does not appear to leave restoration sites more susceptible to seedling establishment, nor does it have a detectable influence on the growth of seedlings that do establish. Even the intense burn scars associated with pile burning (in our "unburned" treatment) were rarely colonized by tree seedlings (C. B. Halpern, unpublished data). Rapid healing of these scars appears aided by the soil tunneling and mounding activities of gophers (Halpern et al., 2012). That said, the absence of a significant burning effect in this experiment may reflect the historical and compositional context in which treatments were applied—in forests dominated by late-seral *Abies*. Use of fire in systems in which tree invasions are not as advanced, and in which *Pinus* or other early-seral species are more prevalent, could lead to a very different result.

We expected establishment to be restricted temporally to a narrow window of time after tree removal. However, we observed continuous recruitment, a trend that is likely to continue. Moreover, although most seedlings established along edges, scattered recruitment throughout plots creates strong potential for nucleation (facilitation and expansion), local seed production, and more rapid infilling of adjacent openings (Rice et al., 2012). Ongoing invasions of the surrounding meadow landscape and widespread (albeit sparse) recruitment into these tree-removal plots underscore the need for periodic intervention. Fortunately, removal of small trees can be done efficiently and economically with hand tools, eliminating the need for motorized equipment or subsequent burning of woody fuels; the latter is labor-intensive, contingent on weather, and often risky. Timing of re-entry may not be as critical in systems in which the dominant invader (here, *A. grandis*) is relatively slow growing. Still, growth that appears linear at first, may accelerate rapidly once seedlings escape the competitive environment of the ground layer. At that point, removal is more critical, because trees can begin to exert strong influences on the surrounding vegetation and soils (Griffiths et al., 2005; Haugo and Halpern, 2010). Earlier and more frequent cutting may be necessary in systems in which the dominant invaders are faster-growing species such as *Pinus* or *Pseudotsuga*. Ultimately, successful restoration of meadows and grasslands may hinge on management strategies that limit tree seed production, seed dispersal, and the length of time that established seedlings can inhibit or alter natural reassembly processes.

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