



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

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