Causes and Consequences of Conifer Invasion into Pacific Northwest Grasslands

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Abstract

Causes and Consequences of Conifer Invasion into Pacific Northwest Grasslands

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Forest Resources

Widespread invasion of conifers during the 20th century is threatening the biological diversity and ecosystem services sustained by grassland ecosystems throughout the Pacific Northwest. Understanding the causes and consequences of these invasions is essential to predicting future changes in these ecosystems. In this dissertation I present the results of field experiments, retrospective analyses, and long-term observations that explore this theme.

First, I examined how biotic relationships regulate conifer invasion. This study, conducted in low elevation prairies, involved experimental manipulations of above-ground competition, below-ground competition, and soil origin. I found that conifer establishment was strongly regulated by simultaneous positive and negative interactions between it and the recipient grassland community, but that the hierarchy of effects varied with life stage (germination, early survival, and seedling growth).

Second, I used a retrospective approach to demonstrate that the cumulative influences of invading conifers on resident grassland species can vary in direction and magnitude over time and with the traits of dominant conifer species. In a western Cascade meadow I quantified the effects of individual *Pinus contorta* and *Abies grandis* (18-73 years old) by comparing vegetation structure and composition under and adjacent to each tree. Although trees generally exerted negative effects on meadow species, cover was elevated under 33% of trees (mostly younger *Pinus*). Effects on forest herbs increased steeply with age under *Abies*, but not under *Pinus*.

Finally, I used three measurements over a 26-year period (1983-2009) to assess vegetation dynamics across forest-meadow boundaries representing diverse physical environments in the Cascade Range, Oregon. Over this period, declines in meadow species were greater in ecotones in which soil moisture was seasonally limiting. Forest understory species increased in montane, but not in subalpine ecotones (where depauperate forest understories limit potential for dispersal). The magnitude of change was not related to change in overstory structure, but to vegetation characteristics (overstory structure and ground vegetation) at initial measurement.

These studies contribute to an increased understanding of the biotic and abiotic factors that regulate conifer invasions of grassland ecosystems in the Pacific Northwest and the consequences of these invasions—both in time and space—for the resident vegetation.

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Chapter 1

A general overview of the causes and consequences of conifer invasion into Pacific Northwest grasslands

Although forests dominate the ecological character of the Pacific Northwest (PNW), grasslands contribute greatly to landscape-level biological diversity (Franklin and Dyrness 1988, Franklin and Halpern 1999). From the remnant prairies of the Puget Sound lowlands and Willamette Valley, to the mid- and high-elevation meadows of the Cascade, Olympic, and Coast Ranges, grasslands provide a range of important services including forage, wildlife habitat, carbon sequestration, natural fire breaks, cultural resources, and recreational opportunities. Globally, the ecological services and biological diversity sustained by grasslands are threatened by woody-plant invasions (Van Auken 2000). Within the PNW, prairies and meadows have experienced rapid encroachment by coniferous trees during the past century (Magee and Antos 1992, Rochefort and Peterson 1996, Miller and Halpern 1998, Haugo and Halpern 2007, Takaoka and Swanson 2008, Zald 2009). Woody-plant invasions can have significant negative consequences for grassland community structure and species composition (Scholes and Archer 1997, Haugo and Halpern 2007), and for ecosystem services such as nutrient cycling and carbon storage (Jackson et al. 2002, Browning et al. 2008). Despite widespread recognition of these processes, our understanding of the factors that regulate invasions and of their ecological consequences is still quite limited.

The causes of woody-plant invasion into grassland ecosystems are diverse and potentially complex. As grasslands are defined by the absence of woody plants, invasion results from a disruption the mechanisms that had previously inhibited woody plant establishment and /or growth. Retrospective studies of conifer invasion in the PNW have commonly focused on the role of extrinsic factors such fire suppression (including intentional burning by Native Americans), climate variation, and livestock grazing (Franklin et al. 1971, Vale 1981, Rochefort and Peterson 1996, Lepofsky et al. 2003, Heyerdahl et al. 2006, Takaoka and Swanson 2008). However, many factors, both abiotic and biotic, may regulate the timing and spatial pattern of invasion. For example, germination and growth of woody plants can be sensitive to fine-scale variation in microenvironment (Woodward et al. 1995, Miller and Halpern 1998, Lepofsky et al. 2003, Peters et al. 2006, Coop and Givnish 2008, Dovciak et al. 2008). Biotic interactions (both positive and negative) can also play an important role in regulating the establishment of invading woody plants (Rochefort et al. 1994, Davis et al. 1998, Li and Wilson 1998, Kunstler et al. 2006, Dickie et al. 2007, Halpern et al. 2010). Given these complex relationships, woody plant invasions of grasslands often defy simple characterization and can rarely be attributed to single causes.

The consequences of conifer invasion for grassland communities are also not well understood. Although trees are assumed to have substantial negative effects on the diversity, composition, and functioning of grasslands, only a handful of retrospective studies have quantified these effects (Hobbs and Mooney 1986, Briggs et al. 2002, Lett and Knapp 2003, 2005, Haugo and Halpern 2007). Moreover, to my knowledge, there have been no direct, long-term observations of the invasion process, or of its effects on grassland vegetation. Trees can impose dramatic changes in the physical and resource environments of grasslands. Effects can vary with size, density, or species identity and, given the longevity of these woody plants, accumulate over time (Kellman and Kading 1992, Belsky et al. 1993, Archer 1995, Köchy and Wilson 2000, Pugnaire et al. 2004). However, the nature of these relationships, and how they play out over time, has rarely been explored (Maestre and Cortina 2005, Reisman-Berman 2007).

The outcomes of interactions between woody and herbaceous species may also vary with the environmental or resource context in which they occur (Jones and Callaway 2007). This context dependency may be particularly evident in mountain landscapes with steep environmental gradients such as those in the PNW. Here, grasslands of varying types occupy diverse physical settings shaped by complex sets of abiotic controls (temperature, precipitation, snowpack, hydrology, and soil depth). Limited attention has been devoted to how this variation in vegetation and environmental context may affect the outcomes of recent invasions of these grasslands by conifers.

Scientists and land managers are placing increasing emphasis on the conservation, maintenance, and restoration of invaded grasslands across the world and within the PNW (Hoekstra et al. 2005, Thompson 2007). Understanding the causes and consequences of woody-plant invasions is essential to predicting and managing future changes in the biological diversity and ecosystem services of these critical habitats. In this dissertation, I explore the factors that regulate tree establishment in grasslands and the long-term consequences of tree invasions for biological diversity. I present three separate studies.

In the first I use experimental manipulations to examine the role which positive and negative biotic interactions play in regulating conifer establishment within prairie ecosystems (Chapter 2). My second study also focuses on the role of positive and negative biotic interactions. Here, I conduct a retrospective analysis of the influence that two species of invading conifers have on meadow vegetation (Chapter 3). My third and final study uses permanent plot measurements to assess long-term (multi-decadal) vegetation change across forest-meadow boundaries (Chapter 4). Within this study I investigate how vegetation changes are structured by ecotone structure and landscape context.

Note to the reader: Chapters 2 – 4 are each intended as a separate manuscript for publication. There is some variation in formatting among these chapters due to differing requirements among the intended publication outlets.

Chapter 2

Positive and negative biotic interactions regulate conifer invasion of prairie ecosystems

Summary

1. The interplay between positive and negative biotic interactions is recognized as an important driver of plant community dynamics, but is less well understood in the context of biological invasions.

2. I examined the influences of above-ground and below-ground interactions between an invading conifer (*Pseudotsuga menziesii*) and the resident vegetation of low-elevation prairie ecosystems in western Washington (USA). Few studies have assessed the relative importance of these interactions for different stages in the life histories of woody invaders (germination, early survival, and growth).

3. Using a fully factorial design, I experimentally tested the effects of shading, below-ground competition, and soil origin (prairie vs. forest) on seed germination, germinant and seedling survival, and seedling growth of *Pseudotsuga*.

4. Experimental treatments had strong effects on *Pseudotsuga* establishment. The relative importance of these effects, however, varied significantly with life stage. Shading had a positive (and primary) effect on germination and on the survival of germinants and transplanted seedlings. Below-ground competition had a negative (secondary) effect and forest soil had a positive (tertiary) effect. Among surviving seedlings, however, the negative influence of below-ground competition was the

primary influence on diameter and height growth, whereas shading had no influence on growth. Effects of soil origin on growth were small.

5. ***Synthesis***. My results indicate that simultaneous positive and negative interactions between an invading conifer and the recipient grassland community can have strong regulatory influences on invasion success. Furthermore, the nature and strength of these interactions differ among critical stages in the early establishment of the conifer. Efforts to predict long-term trends in woody-plant invasions and to develop effective management strategies must incorporate these complex and dynamic interactions.

Introduction

Plant community dynamics can be driven by a combination of positive (facilitative) and negative (competitive) interactions (Holmgren et al. 1997, Bruno et al. 2003, Lortie et al. 2004, Brooker et al. 2008, Maestre et al. 2009). The relative contributions of these interactions to community structure and assembly vary with environmental stress and resource availability (Bertness and Callaway 1994, Callaway et al. 2002, Butterfield 2009, Maestre et al. 2009), and with plant life stage (Miriti 2006, Schiffers and Tielborger 2006, Valiente-Banuet and Verdu 2008, Bullock 2009, Bustamante-Sanchez et al. 2010). The outcomes of biological invasions also depend on positive and negative interactions with the recipient community (Mitchell et al. 2006, Sax et al. 2007), but the interplay between these interactions is not well understood (Gilbert et al. 2009, Reinhart 2010).

Woody plant encroachment into grassland ecosystems provides a model system for exploring how positive and negative interactions influence invasion processes (e.g. Dickie et al. 2005, Kennedy and Sousa 2006, Kunstler et al. 2006, Dickie et al. 2007, Halpern et al. 2010). In many grasslands, mature, invading woody plants exhibit vigorous growth and resistance to common grassland stressors/disturbances (e.g. fire and drought; Scholes and Archer 1997, Miller and Halpern 1998, Bond 2008). Consequently, critical biotic interactions are not those that influence survival and growth of mature woody invaders, but those that affect establishment (seed germination, seedling survival and growth).

During the invasion process, woody plants may experience positive and negative interactions within the grassland mosaic (i.e., with both herbaceous species and pioneer woody invaders). Competition for above- and below-ground resources can limit establishment (Kolb and Robberecht 1996, Brown et al. 1998, Davis et al. 1998, Jurena and Archer 2003, Dickie et al. 2005, Bond 2008, Teste and Simard 2008), but facilitation can also occur via reduced abiotic stresses (temperature and wind) or enhanced soil resources (Belsky 1994, Scholes and Archer 1997, Hibbard et al. 2001, Tewksbury and Lloyd 2001, Siemann and Rogers 2003). Woody pioneers can modify soil biogeochemistry (Hibbard et al. 2001, Griffiths et al. 2005) and provide local access to ectomycorrhizae in soils otherwise dominated by arbuscular mycorrhizae (Dickie et al. 2005, Wiemken and Boller 2006, Dickie et al. 2010). These positive and negative interactions can occur simultaneously. For example, seedlings under mature trees or shrubs experience greater competition for soil resources and elevated rates of herbivory, while at the same time benefiting from reduced temperature and the presence of ectomycorrhizal fungi (Kennedy and Sousa 2006, Kunstler et al. 2006, Chaneton et al. 2010). The balance between positive and negative effects can vary at fine spatial scales and may be related to the size of the canopy or root system of the invader (Dickie et al. 2005, Teste and Simard 2008) or the availability of soil resources (Li and Wilson 1998, Holmgren et al. 2000).

Substantial progress has been made in understanding how positive and negative interactions can regulate the invasion of grasslands by woody plants, but several important questions remain unanswered. First, few studies of woody-plant invasions have explicitly considered the potential for biotic interactions to vary with plant developmental stage (e.g., Miriti 2006, Schiffers and Tielborger 2006). During woody-plant invasions does the nature of biotic interactions differ for germination, early survival, and growth? Dickie et al. (2007) found that the effects of herbaceous competition, resource addition, and distance to mature trees in Minnesota old fields and savannas were consistent among different developmental stages in *Quercus*. Whether these results can be generalized to other taxa or systems, however, has not been evaluated. Second, interactions involving root competition, soil biogeochemistry, light availability, and microclimatic conditions are widely recognized as key factors that influence the rate and success of woody-plant invasion (Scholes and Archer 1997, Davis et al. 1998, Dickie et al. 2005, Kennedy and Sousa 2006, Bond 2008). To my knowledge, however, no studies have directly compared the individual and interactive effects of these factors. Understanding the nature of these relationships is critical to predicting and managing future invasions.

Using field experiments in low-elevation prairies of western Washington, I quantified the individual and interactive effects of shading (e.g. above-ground competition), below-ground competition, and soil origin (prairie vs. forest) at critical stages in the early life history of the principal invading tree species, *Pseudotsuga menziesii* (Douglas-fir). *Pseudotsuga* is considered an early successional forest species (Franklin and Dyrness 1988), but in grasslands, it has been observed that shading can facilitate seedling establishment (Baumeister and Callaway 2006, Kennedy and Sousa 2006). I expected effects of shading, below-ground competition, and soil origin to vary with the life stage of *Pseudotsuga* because controls on germination, survival, and growth often differ (Gurevitch et al. 2006). I tested the following hypotheses:

1. Seed germination is promoted by shading, but is not influenced by below-ground competition or soil origin.
2. Seedling survival is promoted by shading and forest soil, but is inhibited by below-ground competition.
3. Seedling growth (height, diameter, and biomass) is promoted by shading and forest soil, but is inhibited by below-ground competition.

In addition to measuring plant performance, I quantified the physical environments (temperature, soil moisture, and soil chemistry) of these treatment combinations to gain insights into the resources for which *Pseudotsuga* competes and the role of environmental stress in regulating establishment.

Methods

Study Locations

This study was conducted in the south Puget Sound region in western Washington, USA, using remnants of the large grasslands that once occurred on glacial outwash plains (del Moral and Deardorff 1976). I replicated the experiments in three prairie preserves (sites): the 490-ha Black River-Mima Prairie Glacial Heritage Preserve (Glacial Heritage), the 28-ha Tenalquot Prairie and the 135-ha West Rocky Prairie. Sites are separated by up to 20 km. Soils at all sites are excessively drained, volcanic ash over gravelly outwash of the Spanaway-Nisqually complex with low available water-holding capacity (NRCS Web Soil Survey 2010). Annual precipitation at the Olympia climate station (ca. 15 km to the north) averages 129 cm with only 3% falling during June to August. Average minimum and maximum temperatures are 0 and 7°C in January and 10 and 25°C in August (Western Regional Climate Center 2010).

Historically, South Puget Sound prairies were dominated by the bunchgrass, *Festuca roemeri*, and other native species such as *Camassia quamash, Carex inops, Fragaria virginiana*, and *Luzula campestris* (Lang 1961). Agricultural, commercial and residential development along with fire suppression and invasion by exotic species have dramatically reduced the extent of these prairies and altered their species composition (Crawford and Hall 1997). In areas of remnant prairie, the current vegetation is dominated by exotic species, including *Agrostis tenuis, Anthoxanthum odoratum, Holcus lanatus, Hypochaeris radicata, Leucanthemum vulgare, Hypericum perforatum, Rumex acetosella* and *Cytisus scoparius* (Dunwiddie et al. 2006). Invasion of *Pseudotsuga* *menziesii* is widespread and ongoing, with over one-half of the original prairie converted to forest (Lang 1961). *Pseudotsuga* invasion is thought to reflect long-term suppression of fire (Lang 1961, Crawford and Hall 1997, Tveten 1997).

Experimental Design

I established 13 experimental blocks (five each at Glacial Heritage and Tenalquot, three at West Rocky) to account for variation among and within sites in vegetation, soils, and microenvironment. Blocks were established in areas of open grassland with no woody plants and >30 m from mature conifers. Each block contained eight 1 m x 3.25 m experimental units and one "control" (no manipulation). Each experimental unit contained 10 soil cores (see description of soil-origin treatments below) spaced 0.25 m apart. Cores were alternately assigned (five each) to the seed germination and seedling growth components of this experiment (see *Seed Germination* and *Seedling Growth*, below). A 1-m tall fence of 0.6 cm mesh hardware cloth was constructed around the perimeter of each block and buried to a depth of 7 cm to exclude small mammals. The control was placed adjacent to each block, but not fenced, allowing for granivory/herbivory. The eight experimental units per block were randomly assigned to one level of each of three factors: shading (shade or sun), neighbors (no neighbors or all neighbors), and soil origin (prairie or forest), resulting in a fully factorial design.

The shading treatment was designed to reproduce the level of photosynthetically active radiation (PAR) that a conifer seedling would receive beneath the herbaceous or tree canopy at these sites (>80% reduction in available light; R. Haugo, unpublished data). To approximate this reduction in light, 80% shade cloth (Frostproof Growers

Supply, Frostproof, FL) was installed over a series of 0.75 m tall hoops above each experimental unit. Poultry wire (which cast minimal shade) was placed over the unshaded units (sun) to prevent herbivory by ungulates.

The neighbor-removal treatment was used to assess effects of below-ground competition from herbaceous plants. In no-neighbor treatments, vegetation was killed with glyphosate in early May 2009 (following green-up), 2 wk prior to planting seeds and seedlings. Glyphosate is a non-selective herbicide that degrades within days and permits vegetation control with minimal soil disturbance. Subsequent herbaceous regrowth (which was minimal) was clipped at the ground surface and seedlings were pulled by hand. To isolate below-ground competition in the all-neighbors treatment, plastic mesh was used to hold herbaceous vegetation away from planted seeds and seedlings, which resulted in minimal competition for light (evaluated with the shading treatment).

The soil-origin treatment (prairie or forest) was used to test whether the influence of mature woody pioneers on soil biogeochemistry (e.g., pH, resource availability, and ectomycorrhizal inoculation) effects subsequent *Pseudotsuga* establishment. Soil cores, 10.5 cm diameter by 7 cm depth, were cut and removed using a golf course cup cutter (Par Aide Product Company, Lino Lakes, MN) leaving the above-ground vegetation and soil profile intact. Core depth was limited by an impenetrable layer of gravel, but it approximates the average rooting depth of the herbaceous vegetation (R. Haugo, personal observation). In units that received forest soil, the original prairie soil was removed and replaced with a soil core from a nearby *Pseudotsuga*-dominated stand (>50 yr old, same

Nisqually complex soils). In units that received prairie soil, soil cores were extracted, then set back in place (to control for effects of soil removal).

Pseudotsuga seeds and seedlings were planted May 18 - 23, 2009. June 2009 was unusually dry (13% of average precipitation), thus I conducted supplemental watering. On each of three dates, I applied a total of ~2 L of water to the 10 soil cores in each experimental unit. Following planting, I also used Sherman live-traps, baited with peanut butter and oats, to tally and remove small mammals from inside the blocks. No animals were captured over 40 trap-nights, suggesting that fences were effectively excluding rodents.

Seed Germination

I planted 10 *Pseudotsuga* seeds into each of five soil cores per experimental unit (450 seeds per block, 5,850 seeds in total). Moss was first removed from the soil surface so that seeds could be placed in contact with the mineral soil. Seeds were field-collected local ecotypes (PSME 05/seed zone 422) provided by the Washington Department of Natural Resources (WA DNR). They were cold-wet stratified for 45+ days (Boyd Johnson, WA DNR Webster Nursery, personal communication) and had a >90% test germination rate at the time of planting. Germination and survival were assessed monthly through November 2009.

Seedling Growth

Using the same seeds as in the germination experiment, seedlings were grown in plastic containers (2.5 cm diameter x 10.4 cm depth, Styroblock 310A, Beaver Plastics, Acheson, Alberta Canada) in a greenhouse at the University of Washington Botanic Gardens. Seedlings were grown in a mixture of peat and perlite (to minimize mycorrhizal infection) for 100 days and fertilized weekly with a 15-5-15 (N-P-K) fertilizer following WA DNR protocols (Boyd Johnson, WA DNR Webster Nursery, personal communication). Seedlings were hardened outdoors for 3 wk prior to outplanting.

One seedling was planted in the center of each of the five soil cores per experimental unit (45 seedlings per block, 585 seedlings in total). Seedlings that died within 2 wk (n = 59) were replaced. Survival was monitored monthly through November 2009. Seedling height and basal diameter were measured at planting and again in November 2009, after onset of winter dormancy. For a subset of surviving seedlings (one per experimental unit, if present, n = 51) I excavated the seedling in November 2009 to determine above- and below-ground biomass and assess ectomycorrhizal infection. Where multiple live seedlings were present, I selected the largest/most vigorous one. Root systems were washed and visually assessed for ectomycorrhizal infection (presence/absence) at 10-30x magnification. Shoots and roots were separated and weighed after drying at 60^{o}C for 7+ days.

Environmental Measurements

I recorded ground and air temperatures at hourly intervals during mid-summer (July 1-18, 2009) using ibutton thermochron data loggers (Maxim Integrated Products Inc., Dallas Semiconductor, Sunnyvale, CA). In each block, temperatures were measured at one location (associated with a prairie soil core) in each combination of shading and neighbor-removal treatments (*n* = 4; I assumed that soil origin would not affect temperature). Ground temperature was measured directly at the soil surface. Air temperature was measured at 30 cm above the ground, with ibuttons attached to posts and shaded from direct sun by a small, perforated plastic cup (Heithecker and Halpern 2006, 2007). Analyses focused on average daily maxima.

Soil moisture to a depth of 5 cm was measured monthly (June – October) using time-domain reflectometry. I used a HH2 portable moisture meter (Delta-T Devices, Cambridge, UK) connected to a TH_2O soil moisture probe (Dynamax Inc., Houston, TX). At each measurement I averaged three readings per unit. Analysis focused on measurements from July 2009 to coincide with temperature measurements and the period of peak mortality for *Pseudotsuga* germinants and seedlings.

Soil samples were collected at the end of the growing season (mid-October 2009) to assess pH and total available mineral nitrogen ($NH_4^+ + NO_3^-$). Samples were collected from each experimental unit in one block per site (*n* = 27). One soil core (systematically selected from the germination trials) was completely excavated to a depth of 7 cm and chilled in the field. Prior to analysis, each sample was passed through a 2 mm sieve. pH was measured in a 2:1 suspension (30 mL deionized water, 15 g soil) using an Oakton pH meter (Oakton Instruments, Vernon Hills, IL). Samples for total available N were extracted in 2M KCL within 72 hr of field collection, and analyzed at the University of Washington Analytical Services Center. Concentrations were corrected for gravimetric soil moisture content (Robertson et al. 1999).

Analysis

All statistical analyses were based on average responses within each experimental unit. Controls were used only to quantify background rates of germination and survival in the absence of experimental disturbance and where granivory/herbivory were not restricted; they were not included in statistical analyses. Response variables included measures of physical environment (mean maximum air and soil temperature, July soil moisture, total available mineral N, and pH) and measures of *Pseudotsuga* performance: germination rate; survival of germinants; and for transplanted seedlings, diameter and height growth (% of initial values), total biomass, and relative allocation of biomass to below- and above-ground structures (root:shoot ratio).

Analyses were conducted using univariate mixed-effects, permutational analysis of variance models (PERMANOVA; Anderson 2001, McArdle and Anderson 2001). A multivariate analysis would have been desirable to account for correlations among responses variables, but was not conducted because of differences in sample size and model terms (see below). I used Euclidean distances, thus the sums of squares and ‘pseudo-*F*’ values from these analyses are identical to those from traditional mixed-effect Analysis of Variance models (Anderson 2001, McArdle and Anderson 2001). The key advantage of PERMANOVA is that statistical significance of the pseudo-*F* statistic is determined from permutations of randomized real data, thus avoiding assumptions of normality and homogeneity of variances. For response variables in which the experimental design remained balanced, models included site (fixed effect); block nested within site (random effect); and shade, neighbor-removal, and soil origin treatments (fixed effects). Models included all treatment and site x treatment interactions. Significant main effects and interactions ($\alpha = 0.05$) were followed by post-hoc pairwise comparisons using Fisher's LSD (Zar 1999). All full models and pairwise comparisons were run with 9,999 iterations in the PERMANOVA+ add-on for PRIMER 6.0 (Anderson et al. 2008). I used partial R^2 values to compare the contributions of main effects and interactions to each full model (Zar 1999).

Where uneven survival yielded an unbalanced design, the analytical model was modified. No germinants survived in the no-shade treatment, thus for germinant survival, the shade treatment and its interactions were removed from the model. Similarly, no transplanted seedlings survived in the sun/all-neighbors treatment. Thus, for measures of seedling growth (diameter, height, and biomass), shade and neighbor-removal treatments were combined as a single factor with three levels: shade/no-neighbors, shade/all-neighbors, and sun/no-neighbors.

Results

Treatment Influences on the Physical Environment

Treatments had pronounced effects on the physical environment (Fig. 2.1, Table 2.1). Shading lowered maximum ground-surface temperatures (47.2 ^{o}C in sun vs. 30.4 ^{o}C in shade) but not air temperature (Table 2.1). Although the model for July soil moisture produced a significant shade x neighbor-removal interaction (Table 2.1), post-hoc comparisons indicated greater moisture in the shade in both neighbor-removal treatments and in the absence of neighbors in both shade treatments (Fig. 2.1, all $p < 0.01$).

Neighbors had a greater effect on soil moisture than did shade (41 vs. 27% of total variation). Total available mineral N was not affected by shading or soil origin (Fig. 2.1, Table 2.1), but was an order of magnitude greater in the absence of neighbors (105.7 vs. 12.4 mg/kg). Soil pH did not vary among treatments (Table 2.1).

I detected significant variation in physical environment among sites and significant interactions between site and treatment for air temperature (site x shade) and soil moisture (site x neighbor-removal) (Table 2.1). Glacial Heritage was warmer and drier than Tenalquot or West Rocky (all $p < 0.05$), although differences among sites were small compared to treatment effects. Site, block, and site x treatment terms explained only 9.0% of the total variation in soil moisture compared to 70% explained by the shade, neighbor-removal, and shade x neighbor-removal terms. In contrast, site was the primary influence on average daily maximum air temperature (30% of total variation).

Seed Germination

Only 0.3% of seeds germinated in the unmanipulated controls versus an average of 3.2% of seeds in manipulated blocks. As expected (hypothesis 1), germination was enhanced by shade (Table 2.2, Fig. 2.2a). Although PERMANOVA indicated significant site x shade and shade x neighbor-removal interactions, post-hoc tests confirmed that germination rates were greater in shade (6.0% vs. 0.4% in sun) at all sites and for all treatment combinations (range of p: 0.02 to <0.01). Counter to expectation, germination was also enhanced by neighbor-removal, but only in the shade (8.0% no neighbors vs. 3.7% all neighbors; $p = 0.05$). I also detected a significant neighbor-removal x soil interaction; germination did not differ between soils in the absence of neighbors, but

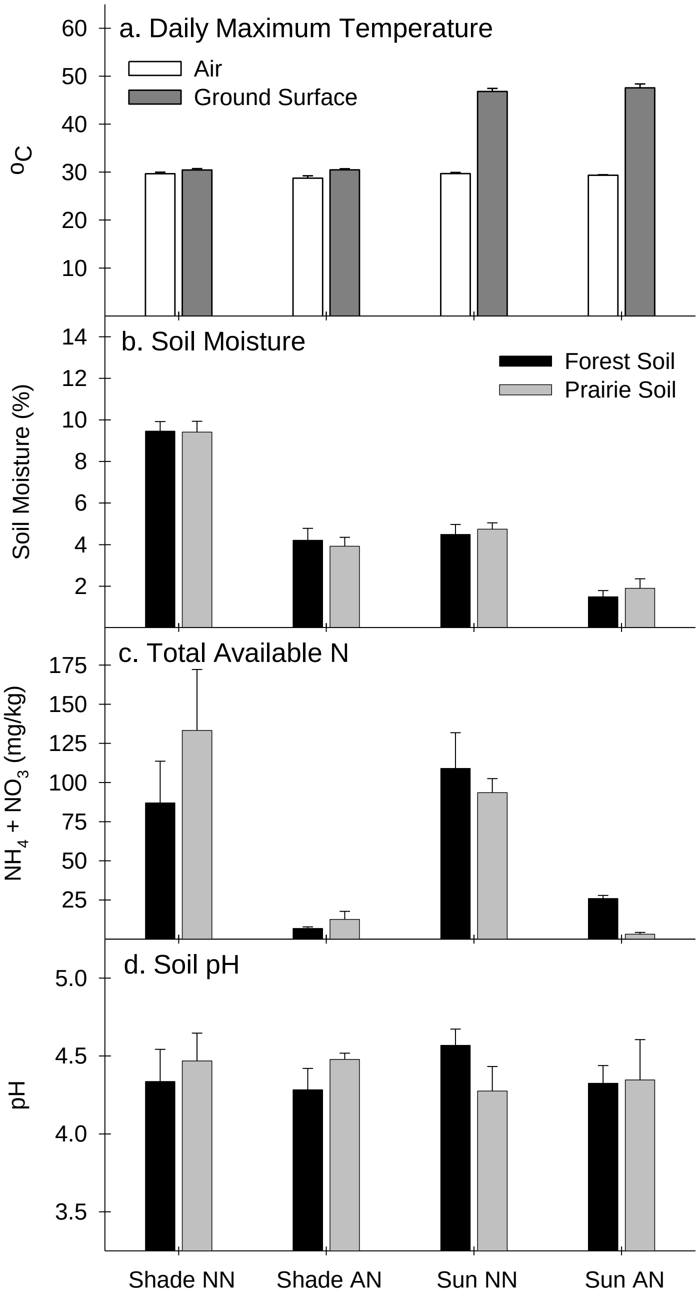

Figure 2.1. Environmental conditions among all treatment combinations: (a) mean daily maximum air and ground-surface temperatures for July 1–18, (b) July 2009 soil moisture, (c) total available nitrogen (NH_4^+ + NO_3^-, and (d) soil pH. Values are means (+1 SE). Neighbor-removal treatments are coded as NN (no-neighbors) and AN (all-neighbors). PERMANOVA results are in Table 2.1.

Table 2.1. Results (permuted P-values and partial R^2 values) of univariate PERMANOVA models testing the main and interaction effects of site; blocks (nested within sites); and the shade, neighbor-removal, and soil-origin treatments on daily maximum air and ground surface temperatures (July 1-18, 2009), soil moisture (July 2009), total available mineral nitrogen, and soil pH. Soil origin is excluded from models of temperature and soil moisture, which were only measured on prairie soil. Available N and pH were measured in one block per site. Significant effects (α = 0.05) are in bold font. Terms that are not included in a given model are blank for df, P, and R^2. Treatment means and SEs are presented in Fig. 2.1.

	Temp – Air			Temp – Ground			Soil Moisture			Mineral N			pH		
Main Effects	df	*P*	R^2	df	*P*	R^2	df	*P*	R^2	df	*P*	R^2	df	*P*	R^2
Site	2	**<0.01**	0.30	2	0.11	0.01	2	0.06	0.03	2	0.25	0.04	2	0.17	0.14
Block	10	0.54	0.11	10	0.14	0.01	10	**<0.01**	0.04						
Shade (Sh)	1	0.19	0.02	1	**<0.01**	0.80	1	**<0.01**	0.27	1	0.83	0.00	1	0.84	0.00
Neighbors (Ne)	1	0.13	0.03	1	0.31	0.00	1	**<0.01**	0.41	1	**0.01**	0.71	1	0.46	0.01
Soil (So)										1	0.74	0.00	1	0.84	0.00
Treatment Interactions															
Sh x Ne	1	0.52	0.01	1	0.89	0.00	1	**<0.01**	0.02	1	0.52	0.00	1	0.13	0.00
Sh x So										1	0.13	0.04	1	0.26	0.09
Ne x So										1	0.32	0.01	1	0.41	0.04
Sh x Ne x So										1	0.46	0.01	1	0.13	0.02
Site x Treatment Interactions	6	*b*	0.15	6		0.00	6	*c*	0.02	12	*a*	0.18	12	*a*	0.68
Residual	23			24			82			2			2		
Total	44			45			103			23			23		

a: The four-way site x treatment interaction was not included due to insufficient replication.

Significant (α = 0.05) Site x Treatment interactions:

b: Site x Shade

c: Site x Neighbors

was greater in forest soil in the presence of neighbors (3.6% forest vs. 0.9% prairie soil; $p = 0.05$). Germination also differed among sites with significantly lower rates at Glacial Heritage (0.3%) than Tenalquot (4.4%) or West Rocky (6.1%, Table 2.2). Site and treatments explained similar variation in seed germination: site and site x treatment terms explained 23% of total variation; shade, shade x neighbors, and neighbors x soil explained 20%.

Germinant and Seedling Survival

Survival of germinants and transplanted seedlings generally supported the predictions of hypothesis 2. Germinants survived only in shade treatments (Fig. 2.2b, Table 2.2) and survival was significantly greater in the absence of neighbors (60.8 vs. 19.2%). Survival also varied significantly among sites (25% at Glacial Heritage vs. 45-51% at West Rocky and Tenalquot, Table 2.2). Site and neighbor-removal explained comparable levels of variation (26 vs. 30%, respectively). Contrary to hypothesis 2, soil origin had no effect on germinant survival.

Transplanted seedlings failed to survive in the unmanipulated controls, whereas 36% of seedlings survived among manipulated blocks. As with germinants, both shading (70.0% shade vs. 12.3% sun) and neighbor-removal (57.4% no-neighbors vs. 24.3% all-neighbors) promoted survival of planted seedlings (Fig. 2.3a). Although survival varied among sites (significant site x shade and site x neighbor-removal interactions; Table 2.3), site explained only 10% of the variation in survival of transplanted seedlings (vs. 61% for shade, neighbor-removal, and their interaction).

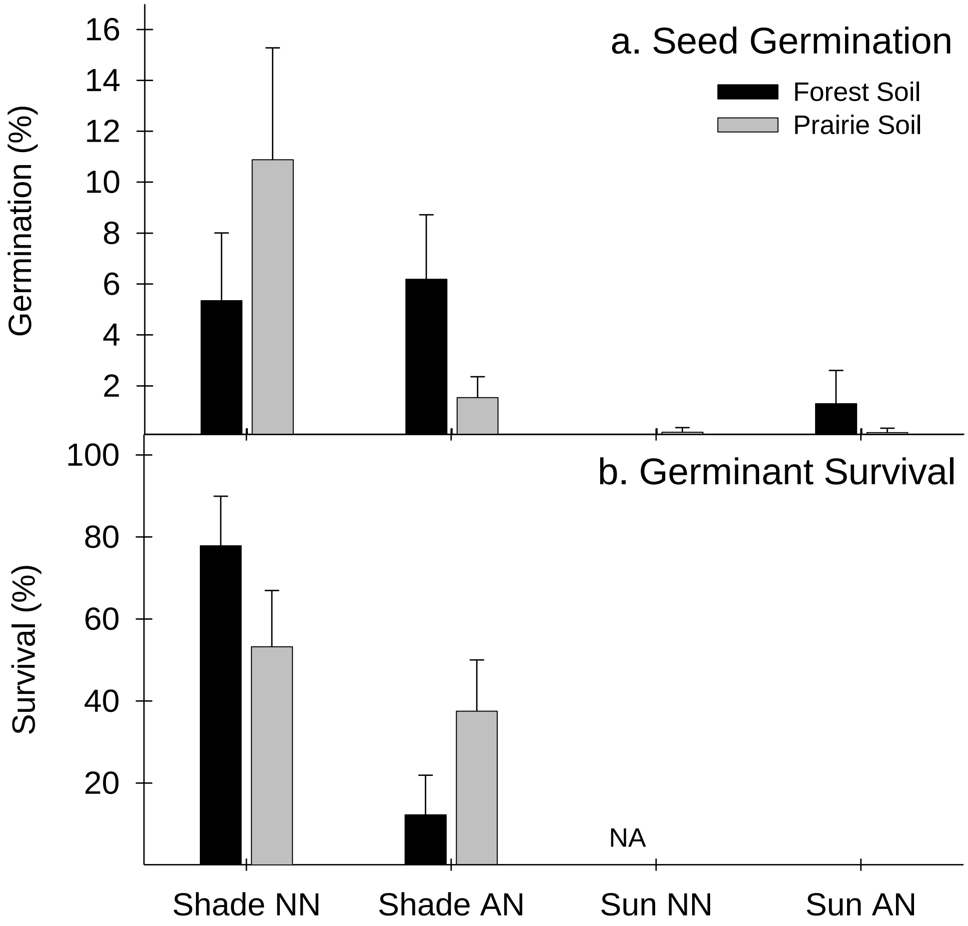

Figure 2.2. Mean (+1 SE) for (a) germination of *Pseudotsuga* seeds and (b) survival after one growing season for all treatment combinations. Neighbor-removal treatments are coded as NN (no-neighbors) and AN (all-neighbors). NA: There were no germinants in the sun/no-neighbors/conifer soil treatment. PERMANOVA results are in Table 2.2
.

Table 2.2. Results (permuted P-values and partial R^2 values) of univariate PERMANOVA models testing the main and interaction effects of site; blocks (nested within sites); and the shade, neighbor-removal, and soil-origin treatments on germination of *Pseudotsuga* seeds and survival of *Pseudotsuga* germinants. Significant effects (α = 0.05) are in bold font. Note: There were no surviving germinants in the sun treatments, thus the shade term was excluded from the germinant survival analysis. Treatment means and SEs are presented in Fig. 2.2.

	Germination			Germinant Survival		
Main Effects	df	*P*	R^2	df	*P*	R^2
Site	2	**0.02**	0.09	2	**0.06**	0.26
Block	10	0.42	0.07	8	0.60	0.21
Shade (Sh)	1	**<0.01**	0.14			
Neighbors (Ne)	1	0.09	0.02	1	**0.01**	0.30
Soil (So)	1	0.87	0.00	1	0.47	0.02
Treatment Interactions						
Sh x Ne	1	**0.04**	0.03			
Sh x So	1	0.65	0.00			
Ne x So	1	**0.04**	0.03	1	0.13	0.09
Sh x Ne x So	1	0.09	0.02			
Site x Treatment Interactions	14	*a*	0.14	4		0.13
Residual	70			9		
Total	103			26		

Significant (α = 0.05) Site x Treatment interactions:
a: Site x Shade

Seedling Growth

The hypothesized effects of shading, neighbor removal, and soil origin on seedling growth were partially supported by the results (hypothesis 3). In contrast to expectation, shading had no effect on seedling growth (Fig. 2.3; Table 2.3). As expected, however, neighbor-removal had a positive effect on all measures of growth. Diameter growth (Fig. 2.3b) and total biomass (Fig. 2.3d) were significantly greater in both no-neighbor treatments than in the all-neighbor treatment (p <0.01 to 0.02), and height growth (Fig. 2.3c) was greater in the shade/no-neighbor than in the shade/all-neighbor treatment ($p < 0.01$). I expected positive effects of forest soil on growth, but observed this effect only for diameter growth (Fig. 2.3b, Table 2.3).

Treatment effects on biomass allocation were not consistent among sites (significant site x treatment interaction; Fig. 2.3e, Table 2.3). At two sites, root:shoot ratio did not differ among treatments, but at Tenalquot, allocation to above-ground biomass was significantly greater in the shade/no-neighbors than in the shade/all-neighbor treatment (p=0.02; Table 2.3). Soil origin influenced biomass allocation in only one of three treatments (significant soil origin x treatment interaction; Fig. 2.3e, Table 2.3). In the shade/no-neighbor treatment, seedlings in forest soil had more aboveground biomass; soil origin had no effect in the remaining treatments.

The roots of nearly all destructively sampled seedlings displayed obvious signs of ectomycorrhizal infection: 100% of those in forest soil and 79% of those in prairie soil.

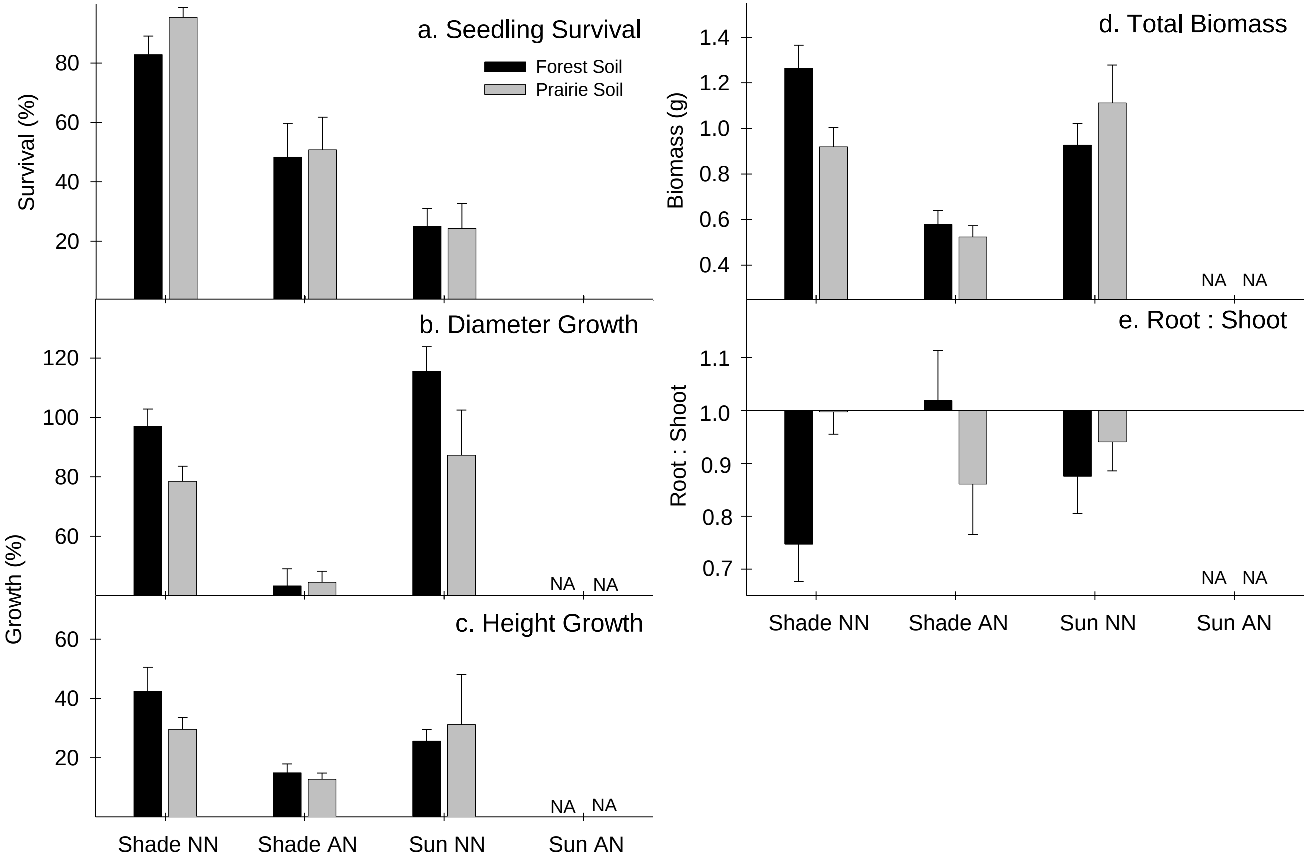

Figure 2.3: Mean (+1 SE) for (a) survival of planted *Pseudotsuga* seedlings, (b) percent diameter and (c) height growth of surviving seedlings after one growing season, (d) total (above + belowground) biomass, and (e) root:shoot biomass ratio for a subset of seedlings for all treatment combinations. Neighbor-removal treatments are coded as NN (no-neighbors) and AN (all-neighbors). NA: There were no surviving seedlings within sun/all-neighbors. PERMANOVA results are displayed in Table 2.3.

Table 2.3: Results (permuted p-values and partial R^2 values) of univariate PERMANOVA models testing the main and interaction effects of site; blocks (nested within sites); and the shade, neighbor-removal, and soil-origin treatments on the survival of planted *Pseudotsuga* seedlings, the height and diameter growth of surviving seedlings, and the total biomass (root + shoot) and the root: shoot ratio of seedlings. Significant effects ($\alpha = 0.05$) are in bold font. Note: There were no surviving seedlings in the sun/all-neighbors treatment; thus for all models except survival, the shade and neighbor-removal effects were assessed as a single, three-level "shade-neighbors" term. Treatment means and SEs are presented in Fig. 2.3.

	Seedling Survival			Diameter Growth			Height Growth			Total Biomass			Root: Shoot Ratio		
Main Effects	df	*P*	R^2	df	*P*	R^2	df	*P*	R^2	df	*P*	R^2	df	*P*	R^2
Site	2	0.20	0.01	2	0.07	0.05	2	0.26	0.06	2	0.48	0.02	2	0.22	0.04
Block	10	0.70	0.02	10	0.44	0.07	10	0.09	0.21	10	0.08	0.17	10	0.61	0.12
Shade (Sh)	1	**<0.01**	0.48												
Neighbors (Ne)	1	**<0.01**	0.12												
Soil (So)	1	0.36	0.00	1	**0.02**	0.04	1	0.72	0.00	1	0.25	0.01	1	0.15	0.03
Shade-Neighbors (ShNe)				2	**<0.01**	0.31	2	**0.01**	0.13	2	**<0.01**	0.20	2	0.86	0.00
Treatment Interactions															
Sh x Ne	1	0.09	0.01												
Sh x So	1	0.32	0.00												
Ne x So	1	0.91	0.00												
Sh x Ne x So	1	0.70	0.00												
ShNe x So				2	0.35	0.01	2	0.43	0.02	2	0.20	0.03	2	**0.03**	0.12
Site x Treatment Interactions	14	*a,b*	0.10	10		0.07	10		0.09	6		0.08	6	*c*	0.19
Residual	70			34			33			27			27		
Total	103			61			60			50			50		

Significant ($\alpha = 0.05$) Site x Treatment interactions:
a: Site x Shade
b:Site x Neighbors
c: Site x Shade-Neighbors

Discussion

Biotic Interactions are Important and Variable across Early Life Stages

The interplay between positive and negative biotic interactions during biological invasions is complex and often not well understood (Gilbert et al. 2009, Reinhart 2010). As predicted, I found simultaneous and, at times, opposing effects of shading, below-ground competition, and soil origin on measures of *Pseudotsuga* performance. Within each life stage, the relative importance of these effects was clearly hierarchical (*sensu* Baumeister and Callaway 2006) as reflected by effect size and proportion of variation explained (Table 2.4). Moreover, these relationships differed with plant life stage (germination, survival, and growth; Table 2.4). This contrasts sharply with previous studies of controls on tree invasion of grasslands, in which early life stages responded similarly to competition, resource addition, and other biotic factors (Baumeister and Callaway 2006, Dickie et al. 2007). Understanding how the importance of positive and negative interactions change with life stage is critical because the ultimate success of woody invaders depends not only on germination and survival, but on growth during the vulnerable seedling stage (Davis et al. 1998, Peltzer and Köchy 2001).

Shading had a positive (and primary) influence and below-ground competition had a negative (but secondary) influence on germination and survival. Although generally considered a shade-intolerant, early successional species (Minore 1979, Franklin and Dyrness 1988), *Pseudotsuga* establishment in grasslands can be promoted by shading through its effect on moisture availability (Baumeister and Callaway 2006, Kennedy and Sousa 2006). Similarly, my experimental manipulations suggest that

Table 2.4: Summary of treatment effects on the germination, survival, and growth of *Pseudotsuga* within prairie environments. Ranking of effects (based on effect size and portion of variation explained): 1 = primary, 2 = secondary, 3 = tertiary. ns = non-significant (α = 0.05) effect.

	Shade		Presence of neighbors		Forest soil		Interactions
Life Stage	Sign	Rank	Sign	Rank	Sign	Rank	
Germination	+	1	-	2-*a*	+	3-*b*	Yes
Survival - Germinants	+	1	-	2	ns		No
Survival - Seedlings	+	1	-	2-*c*	ns		Yes
Growth - Diameter	ns		-	1	+	2	No
Growth - Height	ns		-	1	ns		No
Growth - Biomass	ns		-	1	ns		No
Root : Shoot Ratio	ns		ns		-	1-*d*	Yes

a: Only in Shade and Prairie soil treatments
b: Only in all-neighbors treatments
c: Only at Glacial Heritage and Tenalquot study sites
d: Only in shade/no-neighbors treatments

soil moisture limits *Pseudotsuga* germination and survival through summer drought in these low-elevation grasslands. Shading and neighbor-removal increased mid-summer soil moisture availability and shading significantly reduced maximum soil-surface temperatures. Variation among sites further underscores the importance of drought stress: germination and germinant survival were substantially lower at Glacial Heritage, which was significantly warmer and drier.

In contrast to its effects on germination and survival, shade had no effect on growth (height, diameter, or biomass accumulation) or on biomass allocation of transplanted seedlings. In the absence of neighbors, similar growth in shade and no-shade treatments could reflect tradeoffs in resource availability and abiotic stress, with increases in light balanced by greater temperature and soil-moisture stress (Fig. 2.1). Seedling growth did respond negatively to competition for below-ground resources (Table 2.4), but the mechanistic basis of this effect is unclear because neighbor removals produced simultaneous increases in soil moisture and available N. Herbaceous communities may be strong competitors for one or both resources (Kolb and Robberecht 1996, Brown et al. 1998, Davis et al. 1998, Bond 2008). Patterns of above- and below-ground biomass allocation can be indicative of the resources that are most limiting for seedlings (e.g., Drew and Ferrell 1977, Tesch et al. 1993, Devine and Harrington 2009). However, in this study, allocation patterns in seedlings did not differ among treatments.

Soil origin had little or no influence on germination, survival, or height growth in *Pseudotsuga*. Seedlings did show greater diameter growth in forest than in native prairie soil, although the magnitude of the effect was small compared to that associated with below-ground competition (Table 2.4). However, the mechanism for this effect remains unclear. Although grown in soil-free media prior to transplanting, ectomycorrhizae were nearly ubiquitous in the destructively sampled seedlings and neither pH nor available nitrogen differed between forest and prairie soil. Peltzer (2001) conducted reciprocal soil transfers between prairie and forest habitats and also found that soil origin did not influence the survival or growth of transplanted shrubs. However, these results contrast with studies emphasizing the role of ectomycorrhizae in facilitating woody-plant invasions of grasslands (Dickie et al. 2005, Wiemken and Boller 2006, Dickie et al. 2007, Teste and Simard 2008, Dickie et al. 2010). One explanation for these differences may lie in the dispersal abilities of mycorrhizal fungi. Mycorrhizae of the *Quercus* species studied by Dickie et al. (2005, 2007) are poorly dispersed (I. Dickie, personal communication), whereas *Rhizopogon*, a common symbiont of *Pseudotsuga* in forest soils of the Pacific Northwest (Grubisha et al. 2002), is dispersed over long distances through small-mammal mycophagy (Jacobs and Luoma 2008).

Biotic Resistance and Facilitation of Conifer Invasion

Cumulative survival rates (combining germination, germinant survival, and seedling survival), indicate that under all experimental conditions an individual *Pseudotsuga* seed had a very low probability of becoming a two-year-old seedling (maximum of 4.4% when protected from mammalian herbivores). These survival rates are similar to those reported in other grassland systems (e.g., Coop and Givnish 2008). However, even low annual rates of establishment can lead to substantial accumulation of trees over time (Dovciak et al. 2005), particularly if the invading species have prolific seed production (e.g., *Pseudotsuga*; Hermann and Lavender 1990)**.**

I found intense resistance to *Pseudotsuga* establishment in these open prairie communities. No germinants or transplanted seedlings survived in the control or sun/all-neighbor treatment. Although periodic fire is assumed to be the primary barrier to *Pseudotsuga* invasion of these grasslands (Lang 1961, Crawford and Hall 1997, Tveten 1997), I have demonstrated that environmental stress and herbaceous competition can severely restrict establishment in the absence of fire. Nevertheless, mature conifers are found scattered throughout these prairies. Establishment is likely restricted to narrow windows of time (e.g., cool and wet summers) and/or to particular safe-sites (e.g., disturbed areas with limited herbaceous cover) (Agee and Dunwiddie 1984, Belsky and Blumenthal 1997, Dovciak et al. 2005, League and Veblen 2006).

Once established, trees can modify the surrounding microclimate, vegetation, and soils (Belsky et al. 1993, Scholes and Archer 1997, Hibbard et al. 2001, Haugo and Halpern 2010), increasing the likelihood of additional establishment, creating positive feedbacks that enhance rates of tree invasion (Li and Wilson 1998, Siemann and Rogers 2003, Halpern et al. 2010). The experimental treatments used in this study (shading, neighbor-removal, and forest-soil transfer) explore some of the mechanisms by which mature (pioneer) conifers mediate this process. In the shade/no-neighbor treatment, I observed high survival rates for both germinants (64%) and transplanted seedlings (88%) despite the unusually stressful conditions during the study period. Summer (June-August) 2009 was characterized by the third highest mean temperature and third lowest total precipitation of the past 30 years (Western Regional Climate Center 2010). The results of shading treatments suggest that pioneer conifers in these prairies can facilitate subsequent cohorts by ameliorating the biotic or abiotic conditions that limit germination or survival. However, this facilitation does not appear to involve modification of soil biogeochemical properties. In the longer term, ongoing invasions require the survival and growth of seedlings (Davis et al. 1998, Peltzer and Köchy 2001). The microhabitats in which trees are able to reach maturity are likely to be a subset of those in which they initially establish. Nevertheless, initial establishment is critical to tree invasion in many systems, and my results clearly demonstrate that pioneer trees could strongly facilitate subsequent establishment.

Conclusions

I found strong evidence that positive and negative biotic interactions regulate the establishment of *Pseudotsuga* in low-elevation prairies of western Washington. Studies of woody plant invasions of grassland ecosystems often focus on extrinsic controls, including disturbance (fire and grazing; Stohlgren and Bachand 1997, Hadley 1999, Briggs et al. 2002, Cote et al. 2004, Norman and Taylor 2005, Heyerdahl et al. 2006), climate, and seed availability (Franklin et al. 1971, League and Veblen 2006, Peters et al. 2006, Coop and Givnish 2008). Although these factors are clearly important in many situations, my results suggest that biotic interactions with the recipient community must also be considered (Mitchell et al. 2006, Sax et al. 2007). These are likely to be particularly important where natural disturbance regimes have been altered by land use or management practices. Global warming and atmospheric CO_2 enrichment will also influence the future distributions of grassland and forest biomes through the interactions of woody and herbaceous species (Davis et al. 2007, Bond 2008, Frelich and Reich 2010). Efforts to predict long-term trends in invasions and to develop effective grassland management strategies must account for the importance of biotic interactions in the establishment and survival of woody plants.

Chapter 3

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. I used a chronosequence approach to explore these interactions in a montane meadow in which *Pinus contorta* and *Abies grandis* 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 to 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* and *Abies*. In contrast, cover and richness of forest herbs increased steeply with age under *Abies*, but not under *Pinus*. My 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.

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 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. 1996a, 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 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 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. 1996b, 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).

I 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* and *Abies grandis*, 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. I 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. I 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 I can only speculate about causal mechanisms (including both direct and indirect effects; Wootton 1994, Callaway and Walker 1997), my 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^{o}17'N, 121^{o}57'W) (Haugo and Halpern 2007). Elevations range from ca. 1300 to 1375 m; 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 comprised of both graminoids (e.g., *Festuca idahoensis* and *Carex pensylvanica*) and forbs (*Fragaria* spp., *Lupinus latifolius*, and *Erigeron aliceae*) 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 (1,488 m elevation), 17 km to the north of the 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^{o}C in January and 6.1 and 27.8^{o}C in July (Western Regional Climate Center; http://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, I 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 10-40x 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 were thus comprised 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 x 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, I 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*, I 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 11:00 and 14:00 hours on 6 July (full sun, no clouds) with a LP-80 Ceptometer (Decagon Devices, Inc., Pullman, Wash.); reference measurements (full sun) were taken adjacent to each tree. Soil-surface temperature was measured every 30 minutes for two weeks in July using temperature data loggers (Model DS1921G, iButton Thermochron; Maxim/Dallas Semiconductor Corp., Dallas, Texas). From these continuous measurements I 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, Cedex, 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

I identified a total of 88 vascular plant taxa (Appendix A). I 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, I tallied the number and summed the cover of both meadow and forest species in each quadrat. For each tree I 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, I 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 I 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):

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

where cov_{ai} and cov_{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.

I 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). I 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 unequal variance (Zar 1999). To test whether species composition differed between adjacent-meadow segments and reference transects, I 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), I 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).

I 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 x 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). I 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 the last hypothesis, that meadow species showed stronger relationships to tree age and tree species than did forest herbs. Analyses were conducted with SPSS 17.0 (SPSS 2008).

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 x species interaction; range of *p:* < 0.001 to 0.05; Figs. 3.1a-d). Diameter and height increased more steeply with age in *Abies* (significant age x species interactions; $p < 0.001$; Figs. 3.1a,b), and height to live canopy increased more steeply in *Pinus* (significant age x species interaction; $p < 0.001$; Fig. 3.1c). Increases in canopy radius with age were similar between species (non-significant age x species interaction; Fig. 3.1c).

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 due to the small sample size (NE transects: 23.5 ^{o}C for *Abies* vs. 29.6 ^{o}C for *Pinus*; $t = 2.12$, $df = 4$, $p = 0.10$; SW transects: 32.2 ^{o}C for *Abies* vs. 44.3 ^{o}C for *Pinus*; $t = 1.62$, $df = 4$, $p = 0.18$). For comparison, the corresponding mean for reference transects was 47.8 ^{o}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*, cover of meadow species was depressed in adjacent meadow relative to reference transects (Fig. 3.2a). For *Abies*, richness of meadow species was elevated in adjacent meadow relative to reference

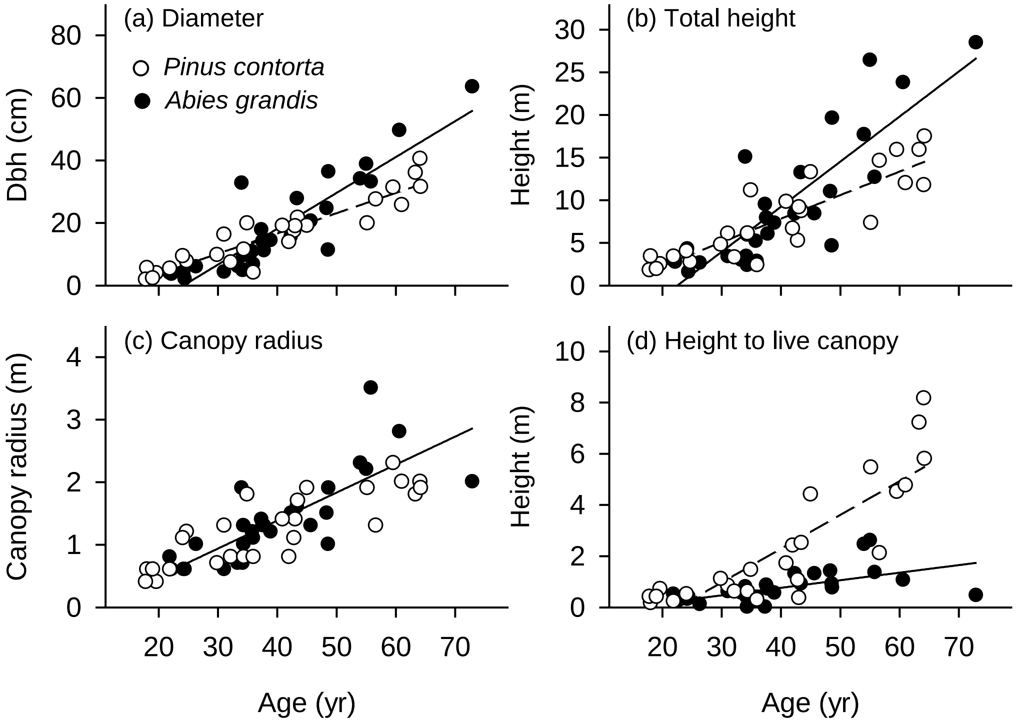

Figure 3.1. Relationships between tree age and (a) dbh, (b) total height, (c) canopy radius (mean of two radii), and (d) height to live canopy for *Pinus contorta* and *Abies grandis*. Separate regression lines are plotted where general linear models indicated a significant tree age x tree species interaction.

transects (Fig. 3.2c). 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 seven to ten times greater than in reference transects (Figs. 3.2b,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 3.1; Fig. 3.3) (for species' details see Appendix A). 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 3.1). In addition, despite a general trend for trees to reduce cover of meadow species, cover was elevated under 33% of trees (Fig. 3.3a). 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 yr old vs. 14% of trees >60 yr 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 the results. As predicted, I observed a significant decline in cover of meadow species with tree age, but not a greater decline under *Abies* than under *Pinus* (Fig. 3.3a, Table 3.2). Moreover, neither tree age nor tree species affected the richness of

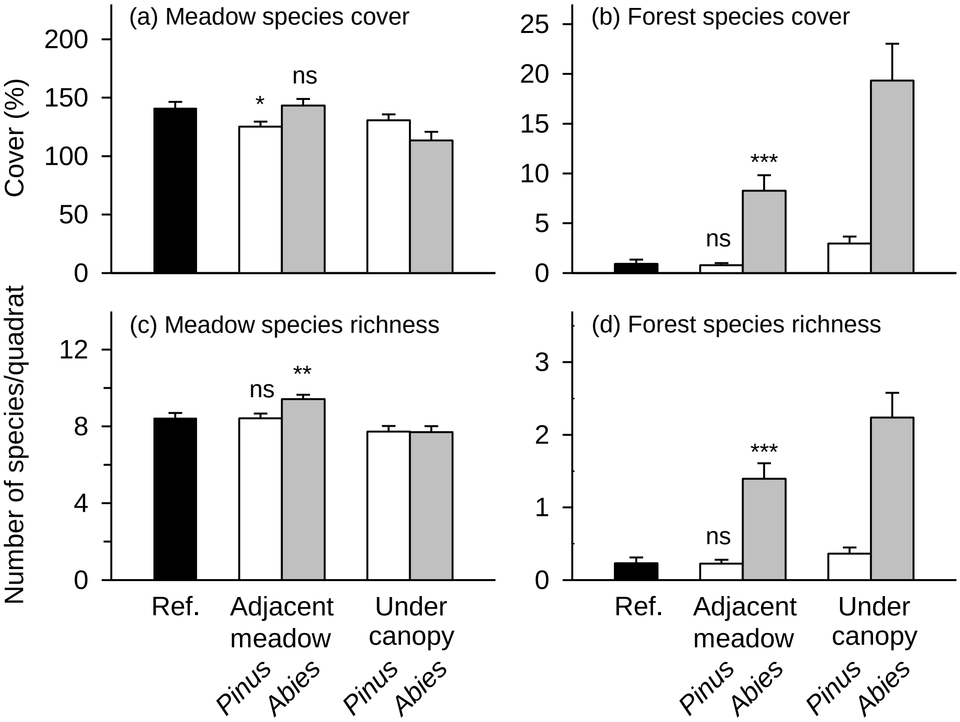

Figure 3.2. Total cover (a and b) and mean richness per quadrat (c and d) of meadow and forest species in reference transects (*n* = 20) and in adjacent-meadow and under-canopy segments for *Pinus contorta* (*n* = 26) and *Abies grandis* (*n* = 28). Values are means (+1 SE). For each tree species, *t*-tests 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). Statistical significance is coded as: ns = not significant, * = $0.01 < p \leq 0.05$, ** = $0.001 < p \leq 0.01$, and *** = $p \leq 0.001$.

Table 3.1: Effects of *Pinus contorta* and *Abies grandis* on 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 is the 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.

meadow species (Fig. 3.3c, Table 3.2). For forest species, I 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. 3.3b,d; Table 3.2). 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. 3.3e, Table 3.2).

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; Table 3.2), and in richness models, they were considerably greater for forest than for meadow species (R^2 = 0.49 vs. 018; Table 3.2).

Discussion

Ours is one of a handful of studies that explores the temporal dynamics of woody-herbaceous plant interactions (Pugnaire et al. 1996b, 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

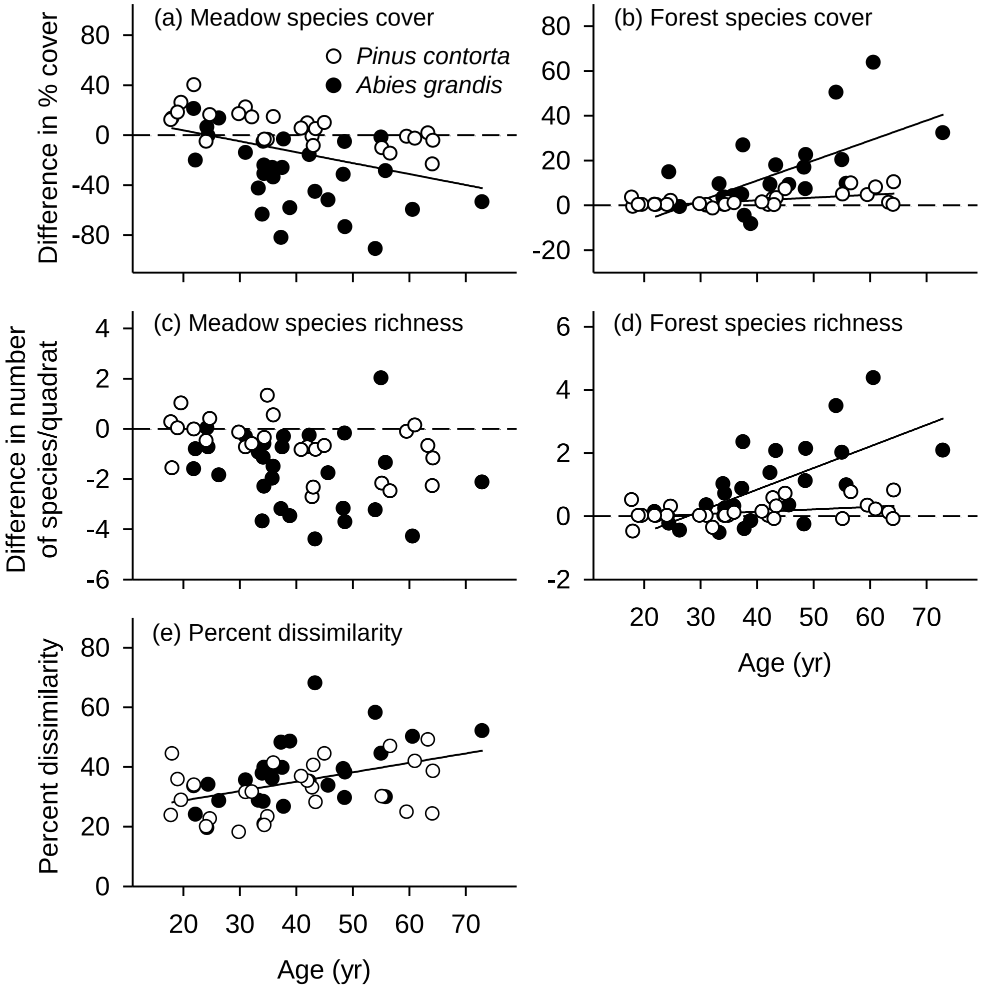

Figure 3.3: Relationships between tree age and changes in ground vegetation beneath *Pinus contorta* and *Abies grandis*. Points represent the difference between under-canopy and adjacent-meadow segments in (a) total cover of meadow species, (b) total cover of forest species, (c) mean richness of meadow 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 x tree species interaction (Table 3.2). Tree age was not significant in the model for meadow species richness.

Table 3.2. 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 x tree species	0.188	0.925	**<0.001**	**<0.001**	0.116

Note: Cover and richness of meadow and forest species were analyzed as the differences between under-canopy and adjacent meadow segments (see Fig. 3.3). PD is 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.

extended beyond the drip-line into adjacent meadow. Most notably, for *Abies*, richness and cover of forest herbs were markedly greater in adjacent 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 the 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.

I 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). Changes in cover of meadow species and in community composition supported this prediction. However, 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 yr) 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 yr). Because the size of quadrats (20 x 50 cm) limited my 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. 3.1d) 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, I 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. 3.2a) in contrast to an overall positive effect under *Pinus* (Table 3.1).

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. 3.2; Appendix A) 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 meters) 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*). This 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.

Chapter 4

Landscape context and tree influences shape the long-term dynamics of forest-meadow ecotones in the central Cascade Range, Oregon

Abstract

Questions: How have vegetation structure, composition, and diversity changed over 26 yr across forest-meadow boundaries in a diverse mountain landscape? To what extent are changes in ground-layer vegetation (herbs and shrubs) shaped by landscape context and the dynamics of tree invasion?

Location: Three Sisters Biosphere Reserve (1280-2000 m a.s.l), Cascade Range, Oregon, U.S.A.

Methods: Species abundance and tree structure were sampled in permanent transects across 20 forest-meadow boundaries in 1983, 1993, and 2009. I delineated forest, ecotone, and meadow habitats along each transect and examined changes in tree structure and ground-layer vegetation. I used NMDS, PCA, and multiple-regression models to elucidate the importance of initial tree structure, changes in tree structure, landscape context, and initial vegetation characteristics for changes in ground-layer vegetation in the ecotone.

Results: I observed significant (though variable) changes in structure, diversity, and composition in the ecotone, but little change in adjacent forest or meadow. I found no evidence that changes in ecotone ground-layer vegetation were driven by the direct effects of climate variation. Species diversity in the ecotones was not greater than in adjacent habitats, and declined over time as losses of meadow species exceeded gains in forest species. Declines were greater where soil moisture was seasonally limiting (montane slopes and subalpine early-snow melt sites). Forest understory species increased in montane sites but not in subalpine sites with typically depauperate forest understories. Changes in richness and cover of each plant group were related to its initial value and to initial, but not changes in, tree structure.

Conclusions: Tree influence in the ecotone has been highly variable. Future changes in vegetation are likely to be greatest where past tree invasion has progressed the furthest—where tree cover and continuity of cover are greatest. However, tree effects are context dependent, mediated by underlying gradients in resource availability and the landscape-scale patterns of species distribution. Some portions of the landscape are resistant to change (montane hydric meadows); others are more susceptible (subalpine, early-snowmelt sites). Understanding the nature of biotic interactions and the importance of environmental controls is critical to predicting future vegetation changes.

Introduction

Ecotones, the zones of transition between communities or ecosystems, are ubiquitous features of most biomes (Gosz 1991). They are critical landscape components that regulate the movements of organisms, materials, and energy (Fagan et al. 2003, Yarrow and Marin 2007), and can have profound influences on population and community dynamics (Fagan et al. 1999). Ecotones can be defined as vegetation zones across which compositional or structural change is abrupt relative to neighboring communities (Lloyd et al. 2000). They can reflect underlying gradients in environment, sharp contrasts in plant physiognomy (woody vs. herbaceous dominance), or disturbances that create edges (van der Maarel 1990, Wilson and Agnew 1992, Cadenasso et al. 2003). Ecotones are viewed as “tension zones”, sensitive to changes in climate or other extrinsic factors (van der Maarel 1990). Recent advances have been made in detecting and characterizing the spatial structure of ecotones (Fagan et al. 2003, Strayer et al. 2003, Yarrow and Marin 2007). However, major challenges remain in understanding why and how ecotones change over time and what these changes imply for other ecological attributes or functions (e.g., Fagan et al. 2003, Hufkens et al. 2009). Answers to these questions are fundamental to predicting future changes in vegetation at both local and landscape scales (Cadenasso et al. 2003, Strayer et al. 2003, Hufkens et al. 2009).

Among terrestrial systems, forest-grassland ecotones are among the most striking, dynamic, and widely studied (Archer 1995, Scholes and Archer 1997, Coop and Givnish 2008). Globally, grass- and forb-dominated ecosystems are experiencing encroachment by woodlands and forests (Van Auken 2000, Bowman et al. 2001, Norman and Taylor 2005, Coop and Givnish 2007), prompting concerns over the loss of biological diversity and ecosystem services (Van Auken 2000, Hoekstra et al. 2005). Given the time spans necessary to detect change, the ecological effects of encroachment are often inferred retrospectively (Jackson et al. 2002, Lett and Knapp 2003, Briggs et al. 2005, Haugo and Halpern 2007). Direct observations of these processes are rare.

Emphasis is often placed on the dynamics of ecotones where tree growth is limited by temperature (alpine or arctic treelines) or precipitation (lower arid treelines) (Scholes and Archer 1997, Allen and Breshears 1998, Danby and Hik 2007, Bond 2008, Batllori et al. 2009, Harsch et al. 2009). In the Pacific Northwest and other topographically complex mountain landscapes, however, natural boundaries between forest and grassland (or meadow) are shaped by a range of physical and historical factors—landform, soils, hydrology, and disturbance—in addition to climatic controls (Kuramoto and Bliss 1970, Franklin and Halpern 1999, Halpern et al. 2010). These ecotones could potentially undergo rapid change given the limited climatic constraint on tree development, and indeed, dramatic shifts in the boundaries between forests and meadows have occurred throughout the Pacific Northwest during the 20th century. Many studies have examined the patterns and causes of encroachment in this region (Franklin et al. 1971, Vale 1981, Woodward et al. 1995, Miller and Halpern 1998, Hadley 1999, Takaoka and Swanson 2008, Zald 2009). However, few studies explore community-level consequences of encroachment or how these changes are manifested across the landscape (but see Magee and Antos 1992, Haugo and Halpern 2007, Takaoka and Swanson 2008, Haugo and Halpern 2010).

Ecotones are often described as regions of elevated diversity arising from the blending of neighboring species' pools and unique environmental conditions (Ries et al. 2004, Camarero et al. 2006, Peterson and Reich 2008). Although theory predicts that ecotones should have greater species diversity than neighboring communities (Gosz 1991, Ries et al. 2004), this pattern is not always observed (Luczaj and Sadowska 1997, Lloyd et al. 2000). Where trees invade grasslands or meadows, several patterns of diversity are possible. If tree influences are moderate or spatially heterogeneous (partial or patchy shade), species with differing light requirements may coexist (meadow species adapted to full sun and forest species to deep shade; Haugo and Halpern 2007, Haugo and Halpern 2010). However, coexistence either requires stability of ecotone structure or periodic disturbance to reset the encroachment process. In the absence of stability or disturbance, strong asymmetric competition between trees and herbs (Peltzer and Köchy 2001) may cause extirpation of meadow species. Depending on the rate or density at which trees establish and the abilities of forest herbs to disperse to the ecotone, diversity may decrease if meadow species are lost faster than forest species can colonize.

The net effect of extirpation of meadow species and colonization by forest species may depend on factors such as: (1) the structural characteristics of the ecotone (i.e., spatial distribution, density, and sizes of trees); (2) the magnitude or rate of structural change within the ecotone; (3) the pool of available species (and their physiological and reproductive traits) in adjoining habitats; and (4) the ways in which each of these factors is shaped by landscape context. In the Pacific Northwest, context dependency (Jones and Callaway 2007) is likely to play a critical role in the outcomes of tree-herb interactions through the direct or indirect influences of physical factors that vary widely across the landscape (e.g., temperature, snowpack, hydrology, soil depth). Moreover, changes to the physical environment (e.g. climate warming) may alter species' interactions. Climate warming is anticipated to have particularly strong effects on the distribution and diversity of species in mountain environments (Cannone et al. 2007, Gonzalez et al. 2010, Lenoir et al. 2010). The ability to anticipate, adapt to, or manage for changes in biological diversity arising from gradual shifts in ecosystem state from meadow to forest requires an understanding of where on the landscape structural changes are most likely to occur or to have the greatest effect.

In this paper, I analyze long-term patterns of vegetation change across forest-meadow boundaries in the Three Sisters Biosphere Reserve/Wilderness Area (TSBR), a largely undisturbed mountain landscape in the central Cascade Range of Oregon. Data on vegetation structure and composition were collected over a 26-yr period (1983 – 2009) at 20 locations representing a diversity of physical environments and vegetation types. This is one of the longest and most extensive studies of vegetation change across forest-meadow boundaries in western North America. I address the following sets of questions, which explore patterns and correlates of vegetation change at a range of spatial scales.

1. How have vegetation structure, diversity, and composition changed across forest-meadow boundaries over 26 yr? Do the magnitude and direction of changes differ among forest, ecotone, and meadow habitats? How have the diversity and abundance of species with differing habitat preferences (meadow vs. forest understory species) and growth forms changed?
2. How are changes in the structure, diversity, and composition of ecotones related to landscape context?
3. To what extent are changes in the ground-layer vegetation driven by the dynamics of tree invasion? Do these relationships vary across the landscape?

Methods

Study area

The Three Sisters Biosphere Reserve is a federal wilderness area of nearly 100,000 ha in the Cascade Range of central Oregon, USA (Fig. 4.1). It encompasses two physiographic provinces, the Western and High Cascades. The former are older, more deeply dissected landforms, comprised of volcanic flows and pyroclastic deposits that originated during the Oligocene and Miocene epochs (Orr et al. 1992). Soils derive from basalts, andesites, and pyroclastic tuffs and breccias. The primary ridge crests average ~1500 m a.s.l. The High Cascades province lies to the east at higher elevations, dominated by younger (Quaternary) shield and composite volcanoes. Topography is comparatively gentle and rolling. Soils are deep and well drained, derived from recent deposits of pumice, ash, and cinders (Orr et al. 1992).

The climate is maritime, with cool, wet winters and warm, dry summers. Temperature and precipitation vary with elevation and topography, reflecting strong orographic effects. Within the study area, mean annual precipitation ranges from ~1700 to ~2700 mm and falls primarily as snow (Daly et al. 2008). Average maximum July temperature ranges from 19.4 to 22.8^{o}C and minimum January temperature ranges from -9.2 to -3.6^{o}C (Table 4.1; Daly et al. 2008).

TSBR has a diverse array of forested and non-forested communities whose structure and composition vary with elevation, topography, soils, and hydrology (Halpern et al. 1984). In the montane zone (typically <1600 m a.s.l.) forests are dominated by *Abies grandis, Pseudotsuga menziesii*, *Abies amabilis*, and *Pinus contorta*. Graminoid-, herb- and shrub-dominated meadows occur on south-facing slopes, in hydric basins, and on poorly drained flats. In the subalpine zone (~1600-2000 m a.s.l.) forests dominated by *Tsuga mertensiana* and *Abies lasiocarpa* are distributed among a mosaic of forb-, graminoid- and heath-dominated meadows (Halpern et al. 1984).

Fire is the primary agent of natural disturbance in this system, but is infrequent. Reconstructions of disturbance history suggest fire-return intervals of 100-150 yr in the montane zone (Teensma 1987, Cissel et al. 1999) but many hundreds of years in the subalpine (Halpern et al. 1984). Although aboriginal burning of meadows is likely to have occurred, primarily at lower elevations (Burke 1979, Boyd 1999), direct evidence is lacking in TSBR. None of the study locations has experienced recent fire. Sheep grazing was common in TSBR (and throughout the Cascade Range) between 1880 and 1910 (Rakestraw and Rakestraw 1991), but deteriorating range conditions resulted in closure of many areas between 1920 and 1938 (Rakestraw and Rakestraw 1991, Miller and Halpern 1998). Sheep last grazed in TSBR in 1947 (Johnson 1985).

Field measurements

In 1983, 21 transects were established across forest-meadow ecotones spanning a range of elevations, landforms, and vegetation types (Table 4.1, Fig. 4.1). These contributed to a broader study of the composition, environmental controls, and dynamics of major forest and meadow ecosystems in TSBR (Halpern et al. 1984, 1991). Transects are 2 m wide and range in length from 50 to 220 m (Table 4.1, Appendix B). Each originated in closed-canopy forest and extended into meadow, beyond any tree invasion.

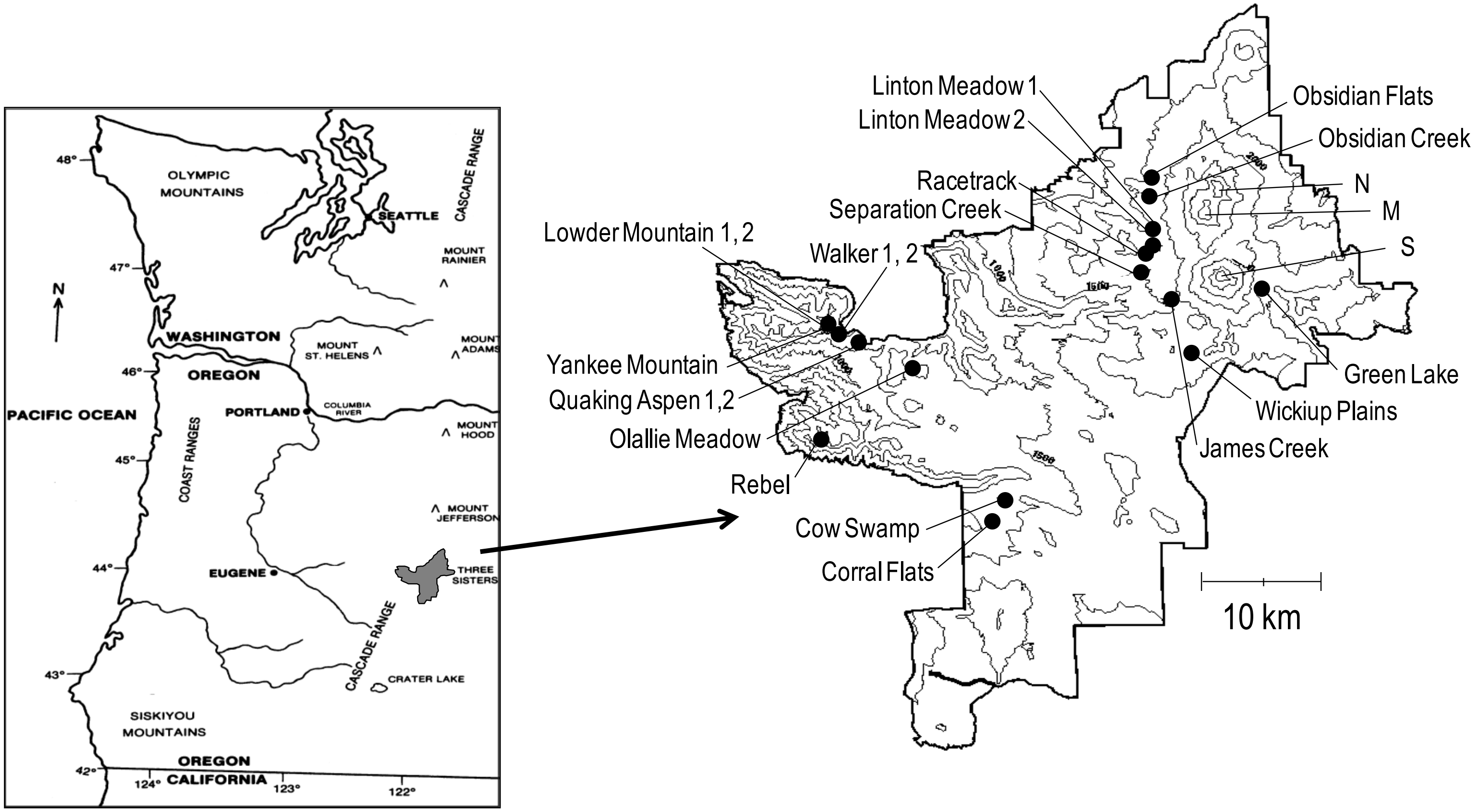

Figure 4.1. Location of permanent forest – meadow ecotone transects in the Three Sisters Biosphere Reserve. N, M, and S are the North, Middle and South Sisters respectively (~3,000 m volcanoes). Figure adopted from Miller and Halpern 1998.

Table 4.1. Landscape/environmental characteristics, transect length, and initial (1983) tree composition and structure in the ecotone at each transect in the Three Sisters Biosphere Reserve, Oregon. Temperature and precipitation are interpolated using Daly et al. (2008).

Physiographic province/Site	Site code	Annual precip. (mm)	July max. temp. (°C)	Jan min. temp. (°C)	Elev. (m)	Slope (%)	Aspect	Hyd.[a]	Trans. length (m)	Primary tree species[b]	Tree density (no./ha)	Tree basal area (m^2/ha)	Tree cover (%)	CV of tree cover (%)
Western Cascades														
Lowder Mountain 1	LW1	2154	21.0	-5.1	1668	5	Flat	M	76	Tm, Al	765	6.3	53.5	0.9
Lowder Mountain 2	LW2	2154	21.0	-5.1	1669	1	Flat	M	93	Tm, Al	608	15.7	37.9	1.2
Yankee Mountain	YM	2164	21.7	-4.2	1555	70	SSE	M	68	Ag, Pm	250	1.5	14.7	2.1
Olallie Meadow[c]	OM	2027	21.2	-4.6	1520	12	SSW	M	120	Ag, Pc	546	29.5	56.5	1.0
Walker 1	W1	2076	21.8	-3.9	1498	50	SSE	M	65	Ag	179	48.2	64.2	0.7
Walker 2	W2	2098	22.0	-3.7	1535	45	SSE	M	151	Ag	148	32.8	38.9	1.5
Rebel Rock	RR	1806	21.0	-4.1	1597	25	W	M	82	Tm, Ag, Al	928	12.6	44.5	1.2
Quaking Aspen 1	QA1	2029	22.3	-3.6	1280	5	NE	H	87	Al, Pe, Tm	1033	3.9	32.2	1.2
Quaking Aspen 2	QA2	2029	22.3	-3.6	1283	3	N	H	70	Al, Pe, Tm	2286	5.8	47.9	1.1

Table 4.1. Continued.

Physiographic province/Site	Site code	Annual precip. (mm)	July max. temp. (°C)	Jan min. temp. (°C)	Elev. (m)	Slope (%)	Aspect	Hyd.[a]	Trans. length (m)	Primary tree species[b]	Tree density (no./ha)	Tree basal area (m^2/ha)	Tree cover (%)	CV of tree cover (%)
High Cascades														
Corral Flat[c]	CF	1735	22.2	-5.0	1386	0	Flat	H	58	Pe, Pc	467	33.7	72.1	0.8
Cow Swamp	CS	1723	22.0	-4.8	1343	0	Flat	H	110	Pc	132	1.4	11.7	2.5
James Creek	JC	2683	21.0	-7.7	1832	27	SW	M	98	Tm, Al	917	19.3	41.3	1.0
Separation Creek	SC	2647	21.0	-6.9	1758	3	SE	H	75	Al	426	9.4	15.3	2.3
Wickiup Plains[c]	WP	2670	20.7	-7.9	1850	2	E	M	79	Tm	357	32.4	31.4	1.1
Green Lake[c]	GL	2544	19.5	-9.2	2000	0	Flat	H	220	Pc, Tm	9	0.0	4.0	2.1
Linton Meadow 1	LM1	2723	21.1	-7.0	1828	58	SW	M	60	Al	403	49.7	62.2	1.1
Linton Meadow 2[c]	LM2	2709	20.5	-7.3	1852	32	W	M	60	Tm	56	0.0	0.3	2.9
Racetrack Meadow	RM	2720	20.9	-7.0	1882	34	NE	M	100	Tm	3784	0.3	19.7	1.2
Obsidian Flat	OF	2696	20.8	-7.0	1869	15	WSW	M	60	Tm, Pa	286	0.8	14.0	1.7
Obsidian Creek	OC	2719	20.7	-7.0	1830	22	S	M	90	Al	3214	12.2	49.3	1.0

[a] Hydrological condition: M = mesic upland, H = hydric (seasonally high water table)

[b] Codes for tree species: Ag = *Abies grandis*, Al = *A. lasiocarpa*, Pa = *Pinus albicaulis*, Pc = *Pinus contorta*, Pe = *Picea engelmannii*, Pm = *Pseudotsuga menziesii*, Tm = *Tsuga mertensiana*

[c] Not sampled in 1993

In 1983 and 1993, all trees (>10 cm tall) and tree seedlings ($\leq$ 10 cm tall) were spatially mapped, measured for diameter (basal or breast height, depending on tree size), and aged using increment core samples or bud scar counts, facilitating reconstructions of tree invasion history (Miller and Halpern 1998). Canopy cover (%) of conifers > 10 cm tall (henceforth tree cover) and cover of each vascular plant species (including conifers $\leq$ 10 cm tall) were estimated in 1-m^2 quadrats placed on alternating sides of each transect (n = 39-108 quadrats per transect). In 2009, 26 yr after establishment, I recensused tree populations, recorded new tree recruitment (post-1993), and repeated all cover estimates. Of the original 21 transects, 16 were resampled in 1993 and 20 in 2009.

Habitat definitions

I delineated three habitats along each transect—forest, ecotone, and meadow—based on the presence, cover, and ages of trees (Appendix B). Forest was defined by the presence of trees that had established prior to 1900 (typically much earlier; Miller and Halpern 1998) and by continuous (occasionally patchy) canopy cover at initial measurement (1983). Meadow was defined as the terminal transect section where trees were either absent or present only as seedlings in 2009. In one instance (Obsidian Creek), I removed from the analysis a 10-m section of meadow habitat where a single, isolated tree island (>30m from the forest) interrupted otherwise contiguous open meadow habitat. Ecotone was defined as the intervening zone, comprised of former meadow into which conifers had established during the 20th century. Differences in the timing, intensity, and spatial pattern of tree invasion (Miller and Halpern 1998) have led to considerable variation in the cover, density, and distribution of trees (Appendix B, C).

Between 1983 and 2009, trees recruited past the endpoints of two transects (Rebel Rock and Ollalie Meadow) resulting in complete loss of meadow habitat.

Species classification

To facilitate analyses of community patterns among sites with distinctly different floras, I classified all species (excluding conifers) as associated with meadow (*n* = 197) or forest understory (*n* = 72). Assignments were based on previous phytosociological studies in TSBR (Halpern et al. 1984), regional floras (Hitchcock et al. 1969, Hitchcock and Cronquist 1973), and recent retrospective studies (Haugo and Halpern 2007, 2010). Although this approach simplifies the distributions of some species, it captures the distinct habitat associations of most. Conifers and other species which could not be classified as either meadow or forest (*n* = 23) were also included in analyses of species composition and total richness (see *Measures of Community Structure and Diversity* below). I also classified species by growth form according to the long-term protocols for these transects: grasses, sedges/rushes, herbs (including ferns), and shrubs (including sub-shrubs).

Climatic variation

To assess the potential influence of long-term trends or inter-annual variation in climate on vegetation change I examined climate records extending back to 1940. I selected four variables that affect plant phenology or productivity: mean annual and mean summer (June-August) temperature, total summer precipitation, and spring snowpack (snow water equivalent [SWE] on 1 April, a proxy for soil moisture availability early in the growing season). Temperature and precipitation data were from the closest meteorological station with long-term records (McKenzie Bridge, 450 m a.s.l.; U.S. Historical Climatological Network; http://cdiac.ornl.gov/epubs/ndp/ushcn/ushcn.html). Snowpack data were from the nearest SNOTEL site (McKenzie Pass, 1454 m a.s.l.; USDA Natural Resources Conservation Service; ftp://ftp-fc.sc.egov.usda.gov/OR/snow/snowcourse/or_data). For each variable I tested for a significant linear relationship with time for the full record (1940-2009) and for the period of study (1983-2009).

Measures of community structure and diversity

I computed average measures of community structure and diversity for each habitat at each transect and measurement period based on the quadrat-scale data. I focused on data at the quadrat scale (1 m^2) because the number of quadrats varied substantially among habitats and transects (Appendix B). Measures of tree structure included average conifer density (live stems >10 cm in height), basal area (m^2/ha), cover (summation of all tree species >10cm tall), and the coefficient of variation (CV) in tree cover among quadrats. The CV of tree cover was included to characterize the patchy nature of many ecotones. Tree variables were used as predictors in models of ground-layer vegetation change. For the ground-layer vegetation, response variables included total species richness (number of species per quadrat), richness and cover of meadow and forest species, cover of each growth form, and heterogeneity of species composition. Heterogeneity was expressed as the mean Bray-Curtis distance of all pairwise comparisons of species composition among quadrats within a habitat for each transect.

Comparing rates of change between sampling intervals

Prior to more comprehensive analyses of vegetation patterns, I tested whether rates of vegetation change were similar between sampling intervals (1983-1993 vs. 1993-2009). Comparable rates would support simpler analyses of change over the full study period using a larger sample size (20 transects, only 16 were sampled in 1993; Table 4.1). For each response variable x habitat combination, I computed an annualized change for each sampling interval (excluding compositional heterogeneity). I compared rates of change using paired *t*-tests ($n = 16$). Of 38 tests, I detected a significant difference ($P < 0.05$) in only two (change in richness of forest species in ecotone and in meadow habitats). Given the consistency of these results, I based all further analyses on changes over the 26-yr study period (1983-2009).

Temporal changes among forest, ecotone, and meadow habitats

To compare temporal changes in tree structure and ground-layer vegetation among habitats (question 1), I employed repeated measures Permutational Analysis of Variance (PERMANOVA; Anderson 2001, McArdle and Anderson 2001). I used PERMANOVA rather than ANOVA because the assumption of homogeneity of variance required for the latter was violated for many response variables. In PERMANOVA, significance tests are based on a "pseudo-*F* statistic" derived from permutations of randomized real data. Analyses used a blocked, split-plot design with transects as blocks, habitat (forest, ecotone, or meadow) as the main plot, and time (1983 or 2009) as the subplot. Models also included the time x transect and time x habitat interactions. For significant habitat effects or time x habitat interactions, post-hoc pairwise comparisons were made using Fisher's LSD (Zar 1999). Models were run with 9,999 iterations in the PERMANOVA+ (v.1.0.2) add-on for PRIMER 6.0 (Anderson et al. 2008).

To compare temporal changes in species composition among habitats (question 1), I used non-metric multidimensional scaling (NMDS; Kruskal 1964). Ordinations were based on the average species composition of each habitat at each sampling date, with rare species (those present in <5% of transects) removed and Bray-Curtis as the distance measure. Removing rare species minimizes the effect of different sample sizes among transects and habitats (e.g. species-area relationships). Large floristic differences among transects and habitats also reduces the effect of variable sample sizes. To prevent floristic differences among sites from masking temporal trends, sites (transects) were delineated into four landscape contexts (see below), which were analyzed separately using all transects and years for each context. To facilitate comparisons, I specified a two-dimensional solution for each ordination. Ordinations were initiated from random starting configurations for a maximum of 400 iterations and were rerun for a maximum of 40 times or until an instability criterion of 0.00001 was met (McCune and Grace 2002). Final solutions were rotated with principal components analysis (PCA; Hotelling 1933) to maximize the variation explained by the first axis. Final solutions had stress values ranging from 4.7 to 19.3. NMDS was implemented in R using the *metaMDS* function of the V*egan v1.11-0* package in R (version 2.10.0, R Development Core Team 2009).

Comparing changes among ecotones across the landscape

I developed a novel approach to compare patterns of change among ecotones across the landscape (questions 2 and 3). To define the environmental context of each site (transect), I conducted an ordination using the floristic data. This provided an indirect method of integrating the influences of multiple (and often complex) gradients in environment across the landscape. I ran NMDS (as described above) with each transect represented by the average species composition of its meadow habitat at initial sampling (thus minimizing effects of trees). For the two transects lacking meadow habitat (see *Habitat definitions*, above), I used the average composition of ecotone quadrats that lacked tree cover during the entire study period. The final two-dimensional solution had a stress value of 13.9. Based on qualitative comparisons, the first axis (NMDS 1) was primarily related to landform and hydrology and the second axis (NMDS 2) was primarily related to elevation (Fig 4.2).

To facilitate comparisons, results of NMDS were used to assign transects to one of four "landscape contexts" (Fig. 4.2a), which reflected differences in elevation, landform/topography, and hydrology, and were consistent with previous phytosociological studies in TSBR (Halpern et al. 1984). They were: (1) montane hydric basins: lower elevation basins supporting seasonally high water tables; (2) montane mesic slopes: lower elevation, south-facing slopes or benches; (3) subalpine early snowmelt: higher elevation benches and south-facing slopes with longer growing seasons; and (4) subalpine late snowmelt: higher elevation basins and north-facing slopes with shorter growing seasons. Each landscape context supported a distinct meadow flora (Fig. 4.2b).

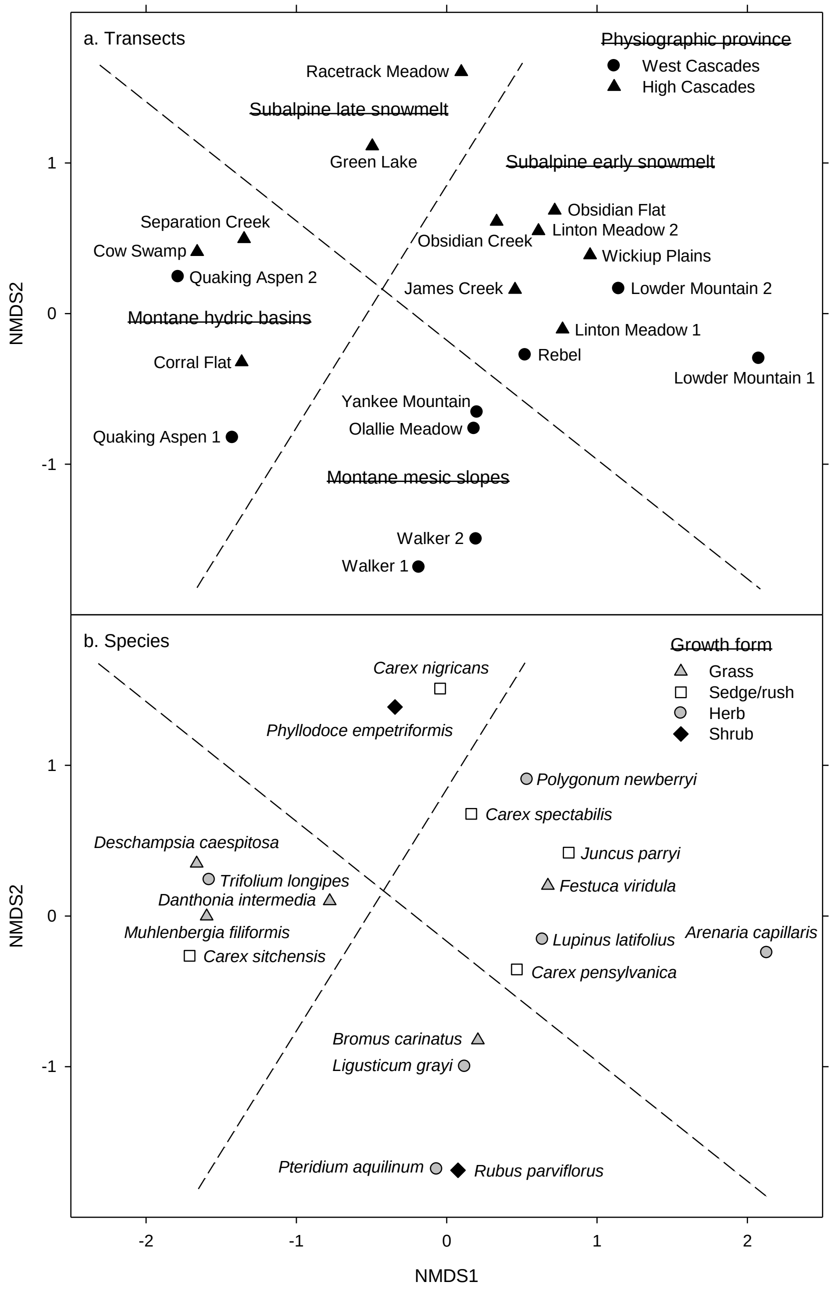

Figure 4.2. NMDS ordination illustrating (a) the landscape context of each transect and (b) characteristic meadow species coded by growth form. Transect values represent the average species composition of meadow habitats at initial sampling (1983) (see *Methods: Comparing changes among ecotones across the landscape*). The dashed lines separate the four landscape contexts delineated for subsequent analyses. Species selected based on average cover and frequency within each landscape context. See Table 4.1 for other site descriptors

The ordination scores were used in two ways to explore the importance of landscape context for changes in the ecotone (question 2). First, positions in ordination space served as a template for comparing changes in tree structure and ground-layer vegetation over the study period (1983 to 2009). For each response variable I produced a "bubble plot" quantifying the direction (positive or negative) and magnitude of change (1983-2009) at each site. Second, scores on NMDS1 and NMDS2 were used as explanatory variables quantifying the contributions of physical environment for regression models (see below).

Modeling the importance of landscape context and tree influence

I used multiple regression models to assess the relative contributions of landscape context (NMDS scores) and tree influence on changes in the ground-layer vegetation within ecotone habitats over the 26-yr study period (questions 2 and 3).

Tree influence was quantified by two types of variables. The first represented ecotone tree structure at the initial (1983) sampling: tree cover, CV of tree cover, tree density, and basal area. Because responses of ground-layer vegetation reflect the cumulative influences of trees over the study period (e.g., Pugnaire et al. 1996, Haugo and Halpern 2010), effects should be greater where tree cover, density, or basal area were initially greater. The second type of variable represented changes in tree structure (1983-2009): change in tree cover, change in CV of tree cover, change in tree density, and change in basal area. Effects should be greater where changes in structure are greater. To reduce the dimensionality of these eight structural variables I first ran a principal components analysis (PCA) using the function *prcomp* in R (version 2.10.0; R

Development Core Team 2009). The first principal component (PC1) explained 37% of the total variation and correlated positively with initial tree structure (tree cover, homogeneity of tree cover, and basal area; Table 4.2). PC2 explained 26% of the total variation and correlated negatively with measures of change in tree structure (change in density, change in basal area, and change in cover; Table 4.2).

I built multiple regression models for each measure of ground-layer vegetation change in the ecotone. Potential predictor variables were the scores on NMDS1 and NMDS2, the scores on PC1 and PC2, and the initial (1983) value of each vegetation response variable (initial vegetation). The latter were used to test whether the magnitude of change was correlated with the initial condition (e.g., if sites with greater richness declined more in richness). For each variable, I started with a "full" model; predictors were then removed in reverse order of strength (sums of squares) to minimize the Akaike Information Criterion (AIC; Akaike 1974). I used standard diagnostics to confirm normality and homogeneity of variance (Zar 1999). Models were developed in SPSS 17.0 (SPSS 2008).

Results

Climatic trends and inter-annual variation

In the long-term record (1940-2009) I detected small but significant increases in mean annual temperature (0.01 ^{o}C/yr; $R^2 = 0.105$, $p = 0.006$) and mean summer temperature (0.03 ^{o}C/yr; $R^2 = 0.312$, $p < 0.001$) (Fig. 4.3a), but no significant trends in summer precipitation or spring snowpack (SWE) (Fig. 4.3b). During the period of study

Table 4.2. Variation explained and variable loadings from principal components analysis (PCA) of tree structural characteristics within ecotone habitats. Variables included measures of initial (1983) structure and changes in structure over the study period (1983-2009). The first two components were used as predictors in multiple regression models (see Table 4.3).

	PC1	PC2
Variation explained:	0.37	0.26
Variable	Correlation	
Measures of initial structure		
Initial density	0.13	0.42
Initial basal area	0.44	-0.21
Initial cover	0.53	-0.04
Initial CV of cover	-0.54	0.04
Measures of change in structure		
Change in density	-0.13	-0.47
Change in basal area	0.24	-0.51
Change in cover	-0.11	-0.48
Change in CV of cover	0.35	0.26

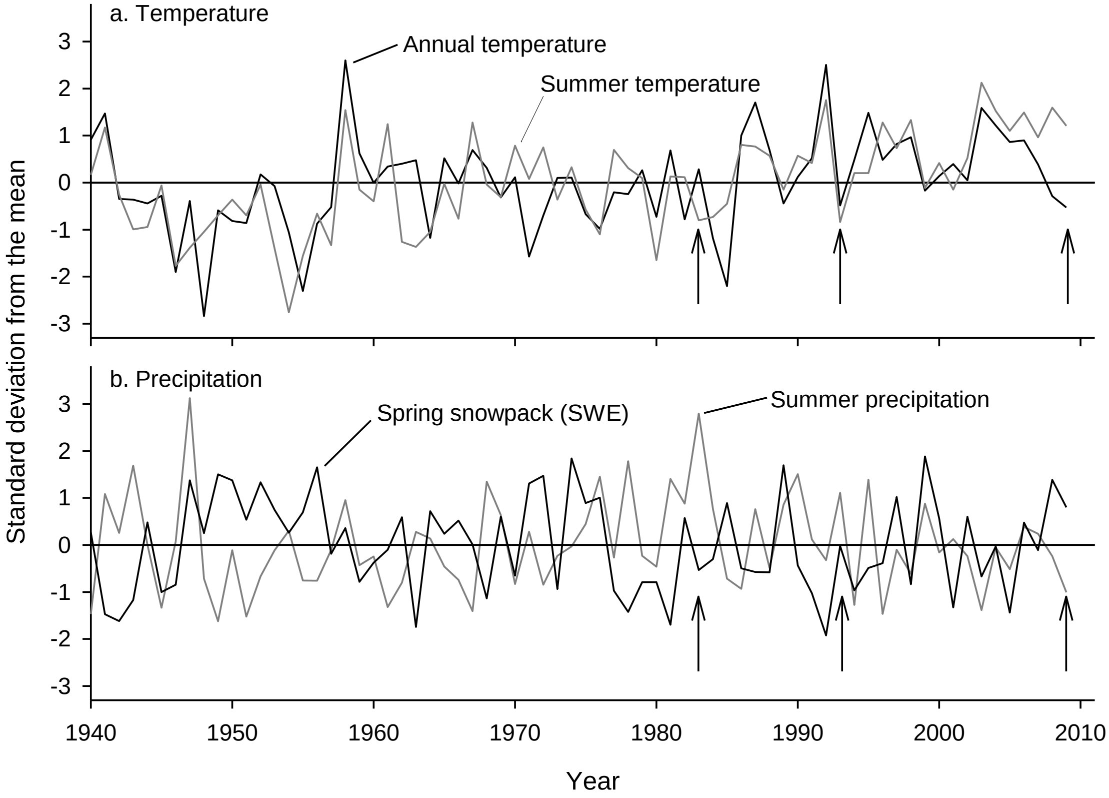

Figure 4.3. Climatic variation between 1940 and 2009 (expressed as standard deviations from the 1940 – 2009 mean). Temperature and summer precipitation data are from McKenzie Bridge, Oregon (450 m a.s.l.). Spring snowpack data are from McKenzie Pass, Oregon (1453 m a.s.l), expressed as snow water equivalent (SWE) on 1 April. The summer period for temperature and precipitation is June through August. Vertical arrows denote the vegetation sampling dates in 1983, 1993 and 2009.

(1983-2009), I detected a significant increase in summer temperature (0.064 ^{o}C/yr; R^2 = 0.354, p = 0.001), but no changes in mean annual temperature, precipitation or spring snowpack.

Among sampling years, 1983 and 1993 had relatively cool/wet summers, with average to below-average temperatures, above-average summer precipitation, and average spring snowpack (Fig. 4.3a, b). In contrast, 2009 had a warm, dry summer (Fig. 4.3a), but above-average snowpack (Fig. 4.3b).

Temporal changes in tree structure

In forest habitats, tree structure was stable over the study period (Fig. 4.4). In contrast, tree cover increased and heterogeneity of cover decreased within ecotones habitats (Fig. 4.4a, b), but tree density and basal area did not change (Fig. 4.4c, d). Cover and basal area remained greater in the forest whereas heterogeneity of cover remained greater in the ecotone over the entire study period.

Temporal changes in ground-layer vegetation among forest, ecotone, and meadow habitats

For most measures of vegetation structure and diversity, values in the ecotone were intermediate to those in the forest and meadow (Fig. 4.5). Exceptions included total richness (ecotone = meadow; Fig. 4.5a), compositional heterogeneity (ecotone = forest; Fig. 4.5b), sedge/rush cover (ecotone = forest; Fig. 4.5h), and shrub cover (similar in all habitats; Fig. 4.5j). Ecotones were also more dynamic than adjacent forests or meadows, which remained stable for most community attributes. In ecotones, total richness (Fig.

4.5a), richness of meadow species (Fig. 4.5c), and cover of grasses (Fig. 4.5g) declined, whereas richness of forest species (Fig. 4.5e) increased. Despite decreased heterogeneity of tree cover, heterogeneity of species composition remained unchanged in the ecotone (Fig. 4.5b).

Species composition in the ecotone was intermediate between forest and meadow at all sites (Fig. 4.6) except Green Lake (Fig. 4.6d), where tree structure was minimal in the ecotone (Table 4.1, Appendix B). Over time, ecotone composition trended toward forest, and forest composition diverged from ecotone and meadow. At some sites, compositional change was as large or larger in the forest than in the ecotone. In contrast, changes in meadows were consistently small and non-directional.

Changes among ecotones across the landscape

Increases in most measures of tree structure (basal area, cover, and homogeneity of cover) were generally greater where soil moisture was more limiting—on mesic slopes in the montane zone and earlier snowmelt sites in the subalpine zone (Fig. 4.7b-d). By comparison, tree density was generally stable (Fig. 4.7a). Landscape-scale trends in the ground-layer were more complex. With one exception (Corral Flat), declines in total richness were greatest in subalpine early snowmelt sites (Fig. 4.7e), which resulted from declines in the richness of meadow species (Fig. 4.7g). In contrast, increases in richness and cover of forest species were greater in montane than in subalpine sites (Fig. 4.7i, j). Changes in the heterogeneity of species composition were not related to landscape context. All growth-forms had highly variable changes in cover across the landscape except for grasses, which showed large declines in montane hydric basins (Fig. 4.7k).

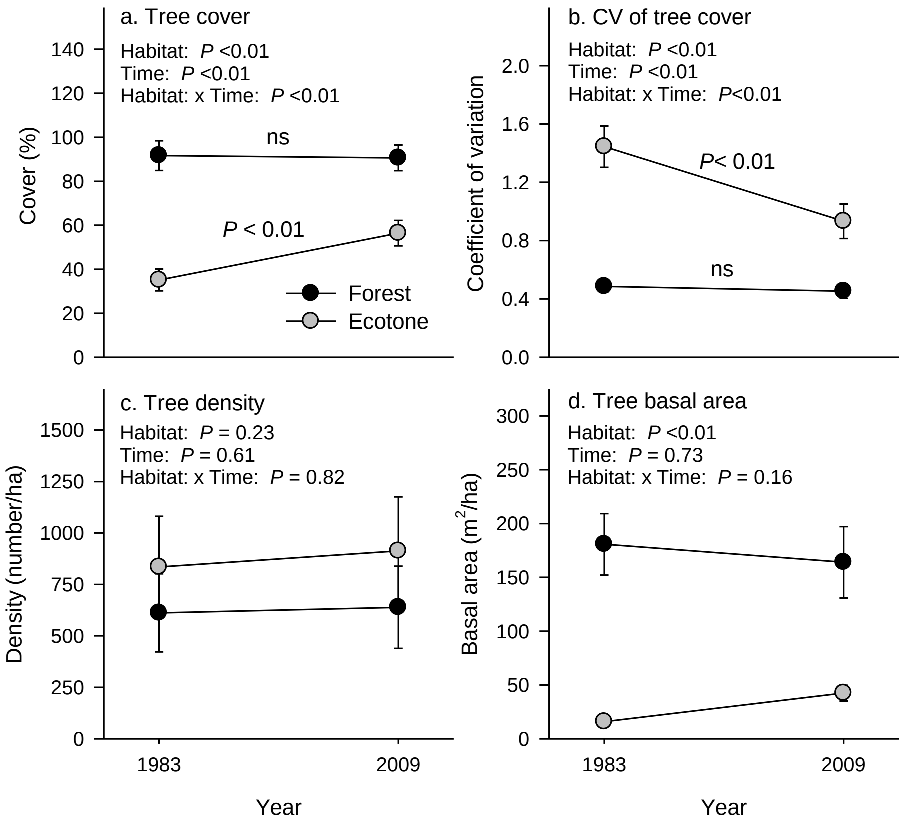

Figure 4.4. Changes in tree structure (mean ±1 SE) over the study period for forest and ecotone habitats. Statistical significance (*P*-values) for habitat, time, and habitat x time terms are from univariate repeated measures PERMANOVA models. For habitat x time interactions, post-hoc comparisons within each habitat were made using Fisher's LSD.

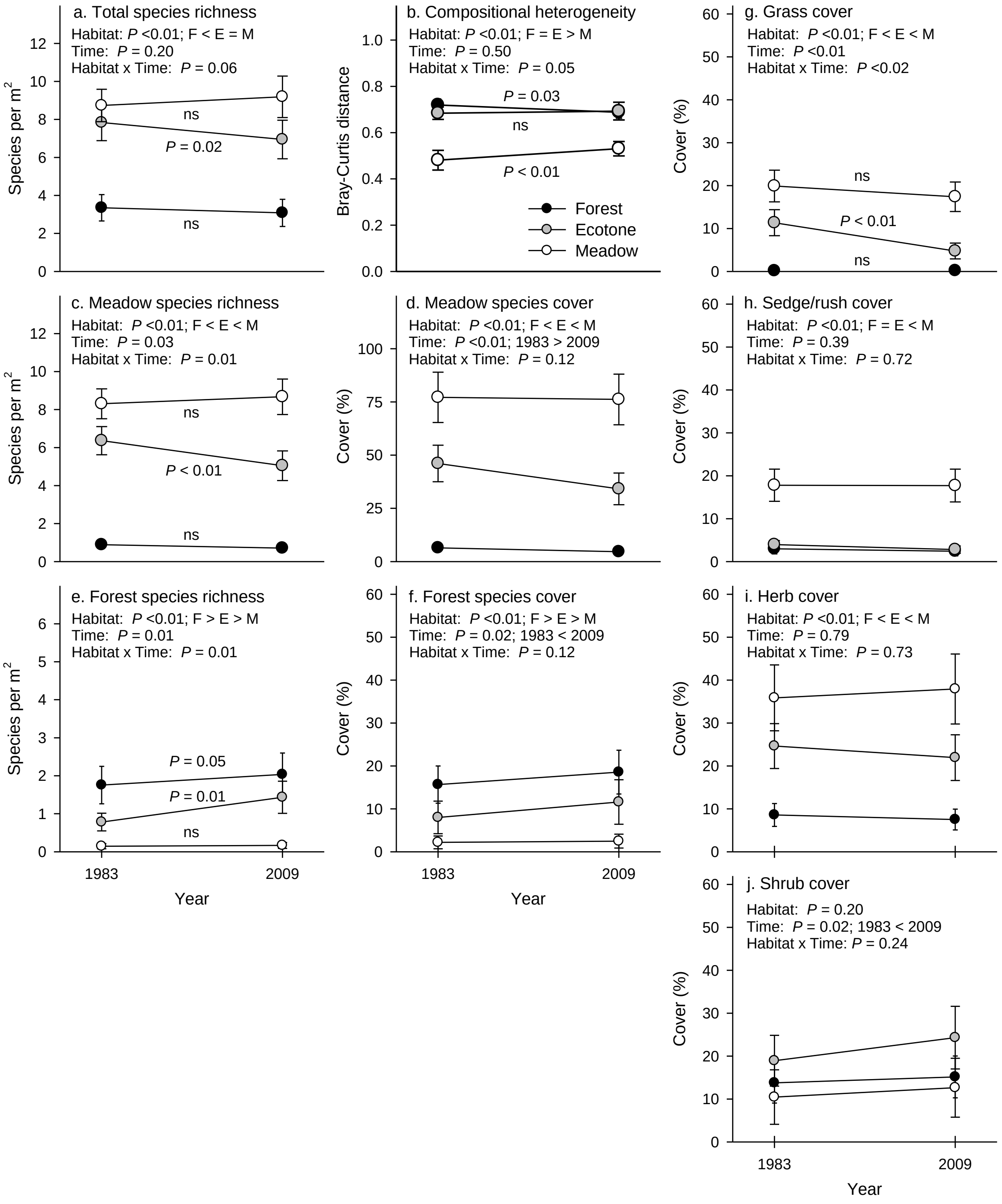

Figure 4.5 Changes in ground-layer vegetation (mean ±1 SE) over the study period for forest (F), ecotone (E), and meadow (M) habitats. Statistical significance (*P*-values) for habitat, time, and habitat x time terms are from univariate repeated measures PERMANOVA models. For main effects and significant habitat x time interactions, post-hoc comparisons within each habitat were made using Fisher's LSD.

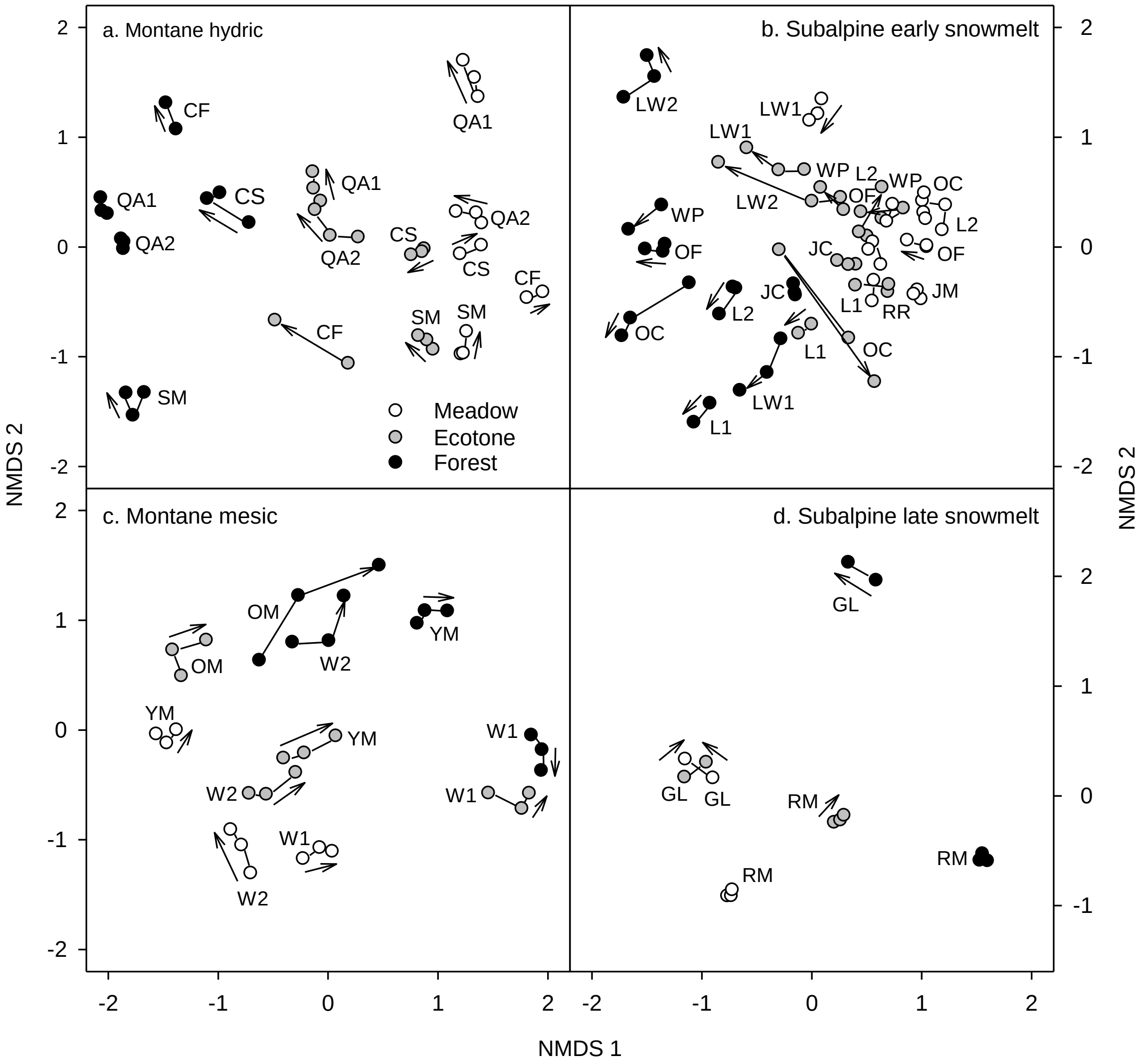

Figure 4.6 Temporal changes in species composition in forest, ecotone, and meadow habitats at each site as portrayed in NMDS space. Separate ordinations were run for each landscape context (Fig. 4.2a; see *Methods: Temporal changes among forest, ecotone, and meadow habitats*). Samples represent the average species composition of each habitat at each sampling date (1983, 1993, and 2009). Lines connect sampling dates and arrows indicate directions of change over time. Transect abbreviations are defined in Table 4.1. Note: CF, WP, LM2, OM, and GL do not have data from 1993.

Modeling the importance of landscape context, tree influence and initial vegetation values

Multiple regression models explained significant variation in nearly all (9 of 10) measures of vegetation change in the ecotones (R^2 of 0.30-0.81 for all plant groups; Table 4.3). Measures of landscape context were of varying importance in models of meadow and forest species response. NMDS1 (related to landform and hydrology) was a significant predictor of change in richness of meadow species and total species richness (Table 4.3). Declines were greater where moisture was more limiting (montane mesic slopes and subalpine early snowmelt sites). NMDS2 (related to elevation) significantly predicted greater declines in meadow species and increases in forest species at lower elevations (montane sites).

Initial tree structure (PC1) was significant (in 4 of 10 models, Table 4.3): sites with initially greater/more complete tree cover and basal area had larger declines in the cover and richness of meadow species (and thus total richness), and in the cover of most growth forms. In contrast, amount of change in tree structure over the study period (PC2) was not significant in any model.

Initial vegetation values were significant predictors of change in all regression models except compositional heterogeneity (Table 4.3). Cover or richness of meadow species and cover of non-woody growth forms declined more where initial values were greater. In contrast, cover or richness of forest species and cover of shrubs increased more where initial values were greater.

Table 4.3. Results of multiple regression models explaining changes in ground-layer vegetation within ecotones from 1983-2009. Results for each response variable include adjusted R^2 (variation explained) and level of significance (*P*) for the final model, and standardized coefficients (Coeff.) and significance (*P*) of predictors. Significant ($P<0.05$) and marginally significant ($0.05<P<0.1$) predictors are in bold font. Starting with a full model, final models were derived by sequential removal of predictors to minimize AIC. Predictors included two measures of landscape context (scores on NMDS1 and NMDS2; Fig. 4.2); initial tree structure (PC1 score; Table 4.2); change in tree structure over the study period (PC2 score; Table 4.2); and the value of the response variable at the initial sampling in 1983.

			NMDS1		NMDS2		PC1		PC2		Initial value	
Response variable	Adj. R^2	*P*	Coeff.	*P*	Coeff.	*P*	Coeff.	*P*	Coeff.	*P*	Coeff.	*P*
Compositional heterogeneity	0.14	0.108							-0.37	0.108		
Total species richness	0.43	0.007	-0.89	**0.005**			-0.45	**0.023**			-0.75	**0.014**
Meadow species												
Cover	0.46	0.002					-0.47	**0.012**			-0.55	**0.005**
Richness	0.53	0.003	-0.83	**0.004**	0.40	**0.037**	-0.49	**0.015**			-0.98	**0.002**
Forest species												
Cover	0.81	<0.001			-0.22	**0.090**					0.77	**<0.001**
Richness	0.61	<0.001			-0.53	**0.005**					0.41	**0.021**
Growth forms												
Grass cover	0.63	<0.001					-0.28	0.068			-0.81	**<0.001**
Sedge cover	0.41	0.004					-0.26	0.155			-0.64	**0.002**
Herb cover	0.35	0.044	-0.50	**0.064**	-0.36	0.149	-0.62	**0.012**	0.312	0.161	-0.68	**0.019**
Shrub cover	0.30	0.019					-0.28	0.166			0.54	**0.012**

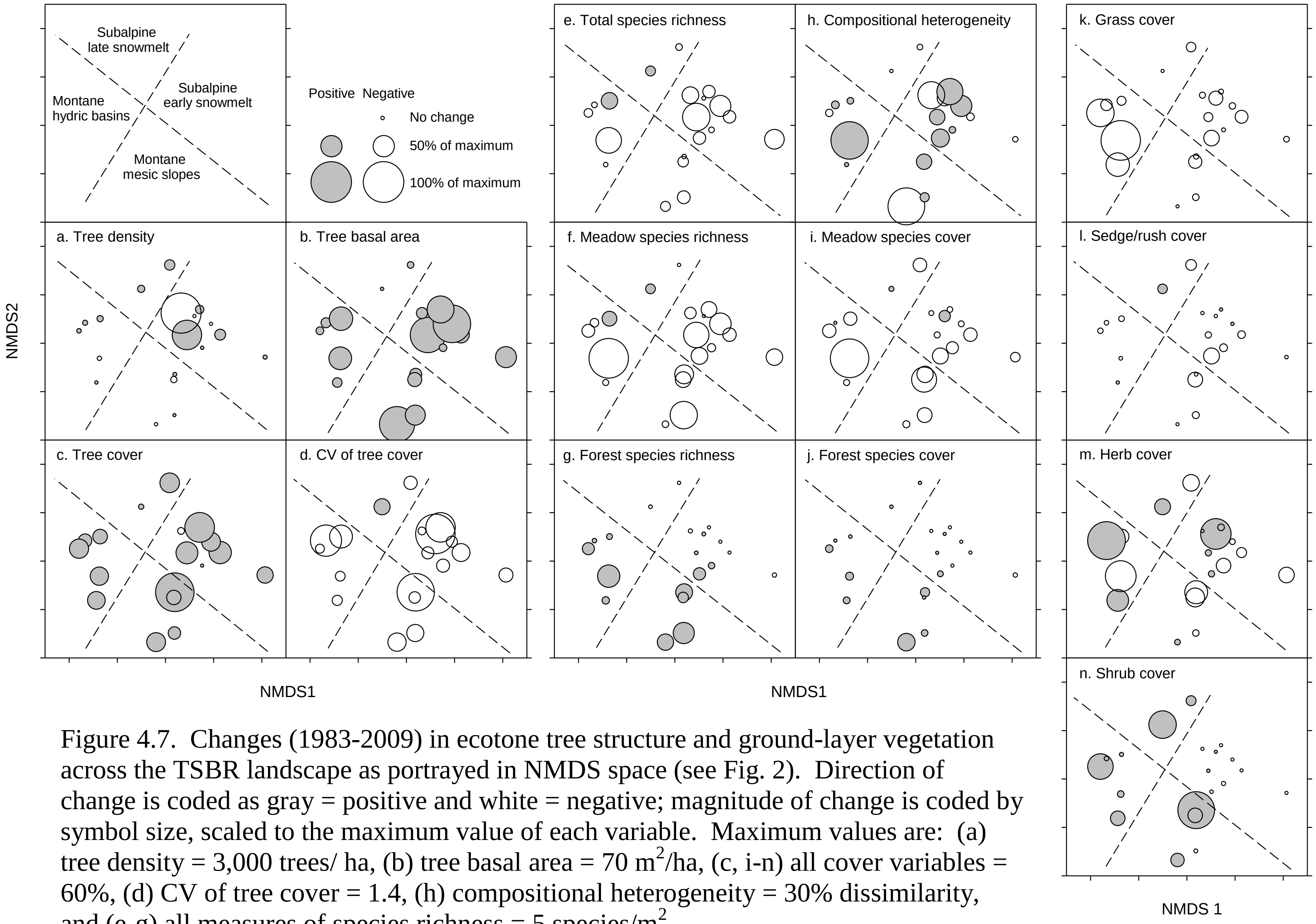

Figure 4.7. Changes (1983-2009) in ecotone tree structure and ground-layer vegetation across the TSBR landscape as portrayed in NMDS space (see Fig. 2). Direction of change is coded as gray = positive and white = negative; magnitude of change is coded by symbol size, scaled to the maximum value of each variable. Maximum values are: (a) tree density = 3,000 trees/ ha, (b) tree basal area = 70 m^2/ha, (c, i-n) all cover variables = 60%, (d) CV of tree cover = 1.4, (h) compositional heterogeneity = 30% dissimilarity, and (e-g) all measures of species richness = 5 species/m^2

Discussion

Forests have expanded into mountain meadows of the Pacific Northwest throughout most of the 20th century. In TSBR, patterns of conifer invasion have varied in time and space (Miller and Halpern 1998), giving rise to forest-meadow ecotones of diverse age, structure, and species composition. Despite this long history of tree invasion, however, these transitional zones remain structurally distinct from adjacent forests and dominated by a meadow flora. It is within these historical and structural contexts that I evaluate vegetation changes over the last quarter century.

The dynamics of forest-meadow ecotones

Ecotones are widely recognized as dynamic elements of the landscape, yet long-term measurements of vegetation change in them are rare (Cadenasso et al. 2003, Strayer et al. 2003, Hufkens et al. 2009). Using data collected from permanent transects over 26 years in TSBR I found significant changes in tree structure and shifts in the diversity and abundance of meadow and forest species. In contrast to earlier stages of invasion (Miller and Halpern 1998), recent changes in structure reflect the growth and canopy spread of established trees, not ongoing recruitment. During the same period, the structure, diversity and composition of adjacent forests and meadows remained stable. This contrast suggests a process of change in the ecotone (formerly meadow) driven by the cumulative influence of encroaching trees. It also provides evidence that climatic trends or inter-annual variation in climate were not directly responsible for these changes; direct effects of climate in the ecotone would also have been observed in the forest and meadow. Climate could have an indirect effect on ecotones manifested through tree growth. Any such effect, however, is subsumed in my assessment of tree influences (see below).

Patterns of species richness in the ecotone were counter to theoretical expectations of elevated species diversity within ecotones (Gosz 1991, Ries et al. 2004). Despite "blending" of species' pools from adjacent habitats, species richness was not elevated in the ecotone at the spatial scale of the sampling units (1 m^2 quadrats). At most sites, ecotones were dominated (in number and abundance) by meadow species and colonization of forest herbs was balanced, or outweighed, by concomitant loss of meadow taxa. However, trees may impose variation in microclimate or soils at larger spatial scales ($>1m^2$). For example, ecotones exhibited greater heterogeneity in species composition than meadows did, and this pattern persisted over the study period. This heterogeneity illustrates the potential for trees to enhance habitat diversity in these transitional zones (Peterson and Reich 2008).

The role of landscape context

It is important, but challenging, to identify the role of landscape context in shaping the dynamics of ecotones (Question 2). Most measures of community response varied considerably within and among landscape contexts (Fig. 4.7), and the proxies for landscape position were rarely significant predictors of vegetation change (Table 4.3). However, two important trends emerged. First, declines in meadow species (and overall richness) were greater in habitats with seasonally limiting soil moisture: montane mesic slopes and subalpine early snowmelt sites. The simplest explanation for this pattern may relate to how meadow species respond to differences in resource supply (in this case, soil moisture) under conditions of highly asymmetric competition with trees. Where soils are seasonally droughty, trees are at a competitive advantage due to greater lateral spread or depth of their root systems (Scholes and Archer 1997). Where soil moisture is not seasonally limiting (due to basin hydrology or late snowpack), competition for soil water is less relevant. Declines are more likely driven by competition for light (Tilman 1988) and thus be related to the structural characteristics of ecotones, not to landscape position.

Variation in the responses of forest herbs comprised the second important landscape trend: increases in richness and cover were largely limited to montane sites. This relationship to elevation reflects a simple, but striking aspect of the regional flora. Montane forests support a rich diversity of shade-tolerant species (total of 66 taxa, Appendix D) that can readily disperse into the ecotone (Haugo and Halpern 2007, 2010). Subalpine forests are depauperate by comparison. Only 37 forest understory species were identified in subalpine transects, and 22 of these taxa were found only at Rebel Rock (Appendix D). Deep and persistent snow packs, short growing seasons, and young, infertile soils contribute to poorly developed understories (Halpern et al. 1984, Franklin and Halpern 1999) and thus a limited source of plants that could colonize ecotones. When viewed in combination, these landscape-scale effects can lead to very low diversity in high-elevation, early-snowmelt sites.

The nature and strength of tree influences

I sought to examine the extent to which changes in ground-layer vegetation were driven by the recent dynamics of tree invasion (Question 3). Trees substantially alter their under canopy and near canopy environments—they create shade, moderate air and soil temperatures, affect snow accumulation, compete for soil resources, and alter litter inputs and nutrient cycles (Belsky et al. 1993, Scholes and Archer 1997, Coomes and Grubb 2000, Hibbard et al. 2001, Musselman et al. 2008). However, changes in tree structure (expressed by PC2 scores in my regression models) were not significant in any model of vegetation change. Instead, initial structure (expressed by PC1 scores) was a significant predictor in models for meadow species, with declines were more pronounced in ecotones in which tree structure was more developed at the time of initial sampling.

Several factors contribute to the limited importance of recent change in tree structure in models of vegetation response. First, these ecotones were still dominated by meadow vegetation at the beginning of the observations, indicating the potential for large vegetation changes due to tree influences. Second, vegetation responses to tree structure are cumulative, time-dependent processes (Pugnaire et al. 1996, Haugo and Halpern 2010). Thus, the magnitude of vegetation changes is the product of: (a) initial tree structure, (b) change in tree structure, and (c) the length of time over which tree influence is observed. Structural changes in these ecotones during the past 26 yr were small compared to initial conditions as trees have been present in these ecotones for as many as 50-100 yr prior to this study (Fig. 4.4). By comparison, the range of initial tree structure was large among sites (Table 4.1), reflecting diverse histories and intensities of invasion (Miller and Halpern 1998). As a result, vegetation change over the past three decades was more responsive to initial structure than to changes in structure.

Interestingly, initial cover and richness significantly predicted declines in meadow species that were proportional to their initial cover or richness, despite the presence of initial tree structure in these models. These relationships may reflect the simple statistical property that communities with greater richness or cover have "further to fall." However, they also highlight the presence of significant variation in the ecotone that is unrelated to tree structure, but critical for predicting future change.

In contrast to meadow species, forest species were not responsive to variation in tree structure. Although I anticipated greater dispersal and growth of forest species (increases in richness and cover) in ecotones with greater or more rapidly changing tree structure, neither predictor was significant. I attribute this lack of response to constraints on colonization in the subalpine zone. The abundance and diversity of herbs in these forests are low, limiting the potential for successful dispersal into the ecotone. Similar constraints do not exist in the montane zone where the dispersal of forest herbs can be very rapid following invasion (Haugo and Halpern 2007, 2010).

Conclusions

Long-term observations of forest-meadow ecotones in TSBR allow me to place recent changes into the broader historical context of forest expansion, and to consider what they imply for the future. Despite nearly a century of tree encroachment in this landscape (Miller and Halpern 1998), ecotones remain structurally distinct from adjacent forests and retain many elements of the meadow flora. Tree influences in the ecotone are highly variable across the landscape—legacies of historical invasion patterns (Miller and Halpern 1998) that continue to exert important controls on ground-layer vegetation. In contrast, recent changes in tree structure have been small and have played a comparatively minor role in shaping vegetation change. My analyses also highlight the importance of landscape context in mediating the outcomes of tree-herb interactions (both negative and positive), and the broader consequences of these interactions for biological diversity across the landscape. They indicate that some habitats are more resistant to change (e.g., montane hydric systems), and others are more susceptible (subalpine, early snowmelt sites).

This study has simple, but important, implications for the use of remote sensing in quantifying the extent or rate of forest expansion at landscape scales (e.g., Takaoka and Swanson 2008, Zald 2009). First, even in the absence of detectable changes in forest extent, changes in ground-layer vegetation within the ecotone can be significant. Second, estimates of the magnitude of change in forest extent may not capture important differences in biological responses that are contingent on landscape context. However, the combined application of remote sensing with ground-based statistical or qualitative models could provide a powerful tool for quantifying or predicting the community-level consequences of encroachment.

Future climate change may alter vegetation dynamics by influencing rates or patterns of tree establishment or growth in the ecotone. Predictions of warmer drier summers, warmer wetter winters (Mote and Salathe 2009), and shifts in the form of precipitation (snow to rain; Elsner et al. 2009), suggest the potential for increasing summer drought and longer growing seasons. These effects are likely to be manifested to varying degrees and in complex ways across the elevational, topographic, and edaphic gradients that define mountain landscapes (Daly et al. 2009). For example, in the montane zone, warmer drier summers may reduce rates of tree invasion and growth on mesic upland slopes, but enhance them in hydric basins, where waterlogged soils currently limit both the extent of invasion and associated changes in ground-layer vegetation (Miller and Halpern 1998). Similar "switches" may occur in early- vs. late-snowmelt sites in the subalpine zone in response to changing snowpack and growing-season length. Climate change also has the potential to elicit indirect or secondary effects in the form of increased frequency or intensity of insect outbreaks or wildfire (Littell et al. 2009), disturbances that can completely reset or reposition forest-meadow boundaries. Where invading trees are killed, ecotonal areas are likely to revert quite rapidly to dominance by meadow species.

To my knowledge, the permanent study sites in TSBR provide the first and only direct long-term measurements of recent vegetation response to 20th-century forest expansion in western North American meadows. Understanding the role of landscape context and the nature and diversity of tree influences within these transitional zones is a critical, yet challenging goal as we seek to anticipate or predict future changes in these and other mountain landscapes.

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Appendix A

Species at Bunchgrass Ridge, OR

Species observed in reference transects and under-canopy and adjacent-meadow segments of transects associated with *Pinus contorta* and *Abies grandis* at Bunchgrass Ridge, OR. Nomenclature follows Hitchcock and Cronquist (1973).

Appendix A. Species observed in reference transects and under-canopy and adjacent-meadow segments of transects associated with *Pinus contorta* and *Abies grandis* at Bunchgrass Ridge, OR. Species are grouped by habitat preference (meadow, forest, unclassified). Values are frequency species' (Freq, percentage of quadrats) and mean cover (Cov, %). t = trace cover (<0.1%). Asterisks denote non-native species.

		Reference (*n* = 20)		*Pinus contorta* (*n* = 26)				*Abies grandis* (*n* = 28)			
				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				

Appendix A. Continued.

		Reference (*n* = 20)		*Pinus contorta* (*n* = 26)				*Abies grandis* (*n* = 28)			
				Under		Adjacent		Under		Adjacent	
Species	Family	Freq	Cov	Freq	Cov	Freq	Cov	Freq	Cov	Freq	Cov
Meadow species											
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
Viola nuttallii	Violaceae	8.0	0.4	13.1	0.3	11.0	0.3	6.4	0.2	8.8	0.3
Forest 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		

Appendix A. Continued.

		Reference		*Pinus contorta* (*n* = 26)				*Abies grandis* (*n* = 28)			
		(*n* = 20)		Under		Adjacent		Under		Adjacent	
Species	Family	Freq	Cov	Freq	Cov	Freq	Cov	Freq	Cov	Freq	Cov
Forest Species											
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		

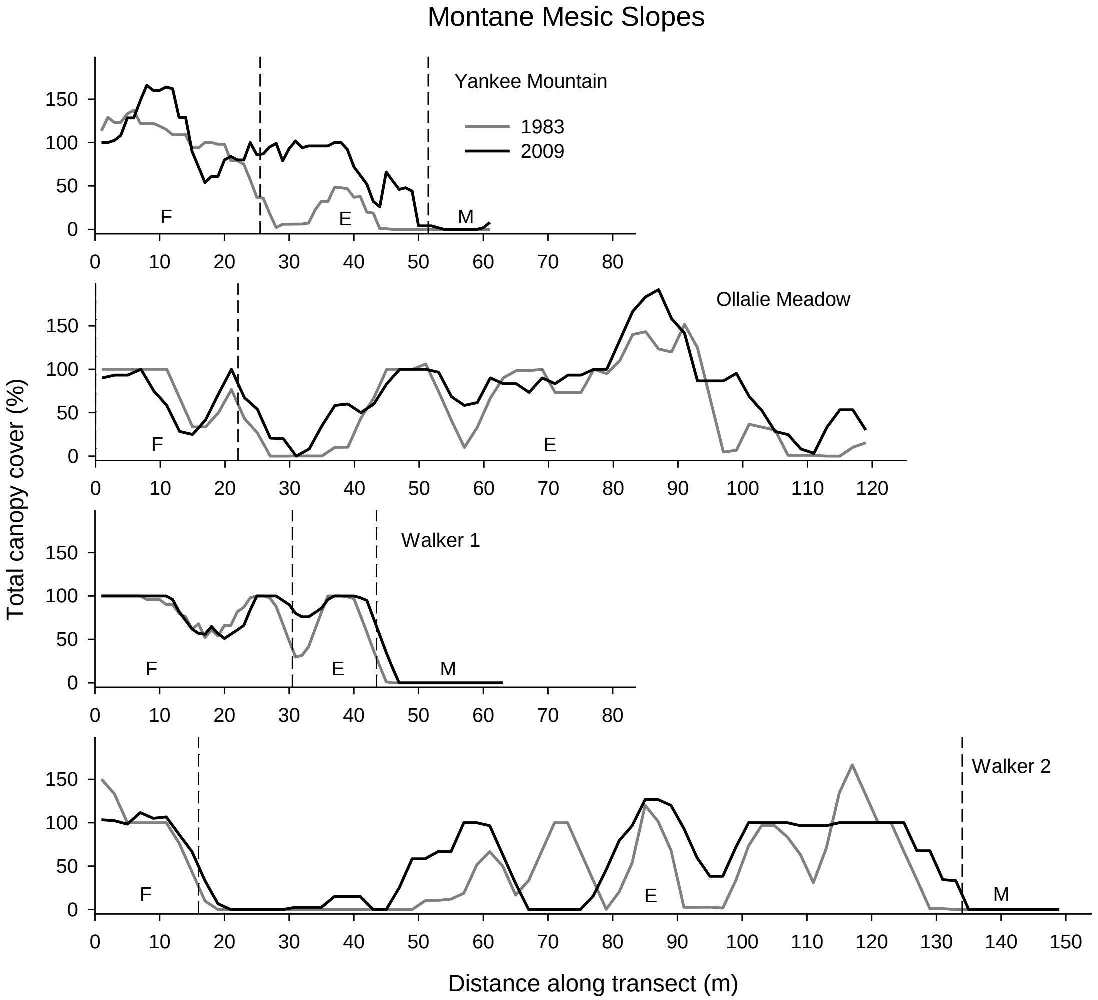
Appendix A. Continued.

		Reference		*Pinus contorta* (*n* = 26)				*Abies grandis* (*n* = 28)			
		(*n* = 20)		Under		Adjacent		Under		Adjacent	
Species	Family	Freq	Cov	Freq	Cov	Freq	Cov	Freq	Cov	Freq	Cov
Unclassified Species											
Amelanchier alnifolia	Rosaceae			6.4	1.4			1.3	0.1		
Epilobium angustifolium	Onagraceae							1.7	0.2	2.3	0.2
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								

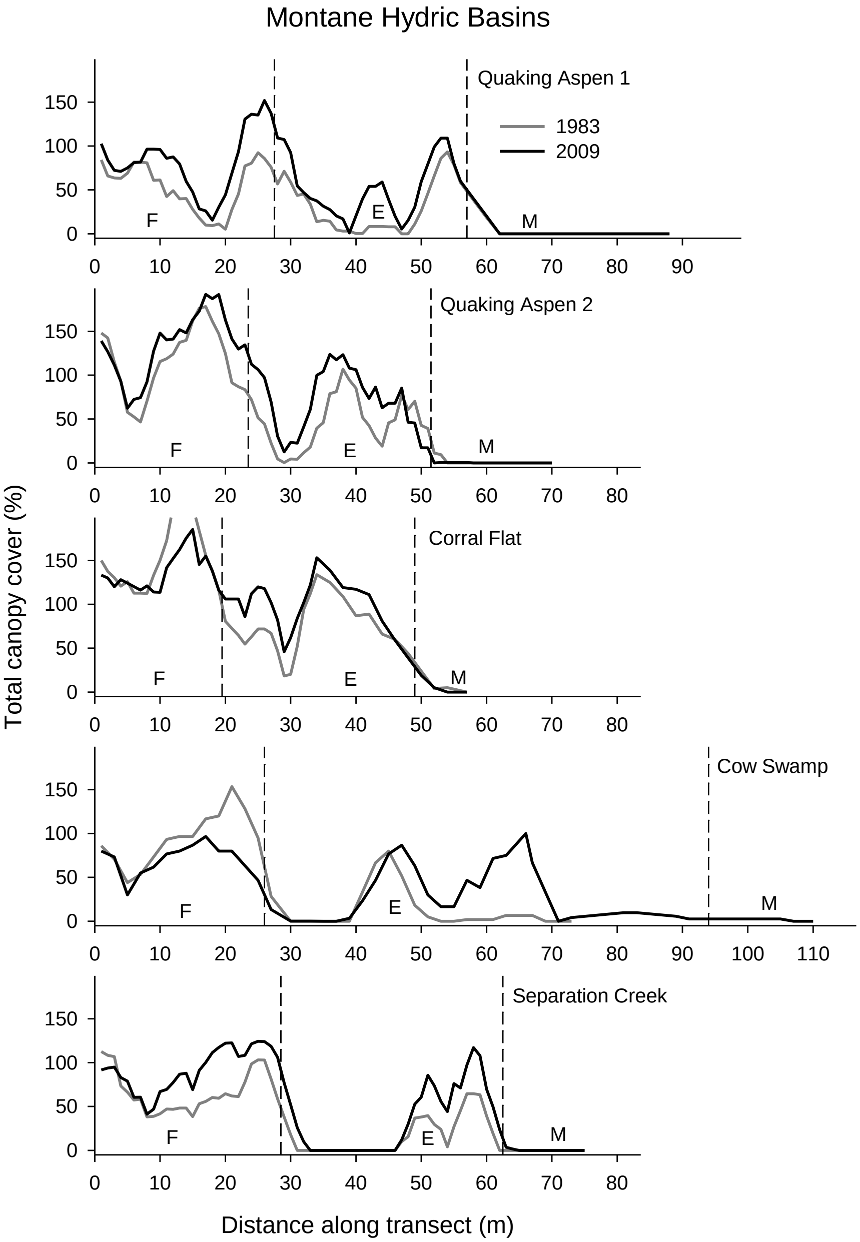
Appendix B

Tree canopy cover along TSBR forest-meadow ecotones

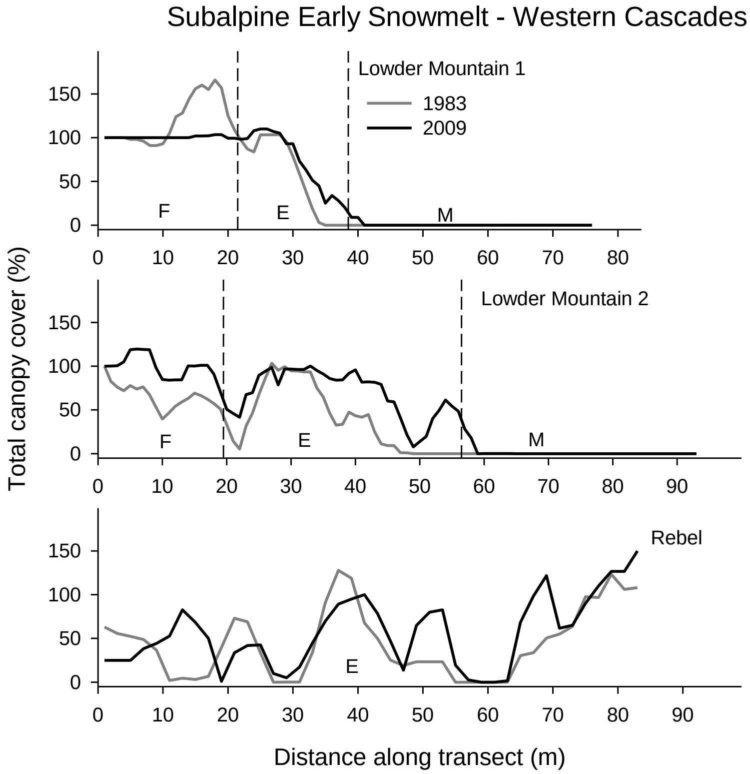
Changes in total canopy cover (summed cover of all conifer species) over the study period (1983-2009) for forest-meadow ecotone transects in the Three Sisters Biosphere Reserve (TSBR), Oregon. Values were smoothed as 3-m running averages. Gray lines represent 1983 values and black lines 2009 values. Habitats are delineated by vertical dashed lines and coded as F = forest, E = ecotone, and M = meadow. See *Chapter 4, Methods: Habitat definitions.*



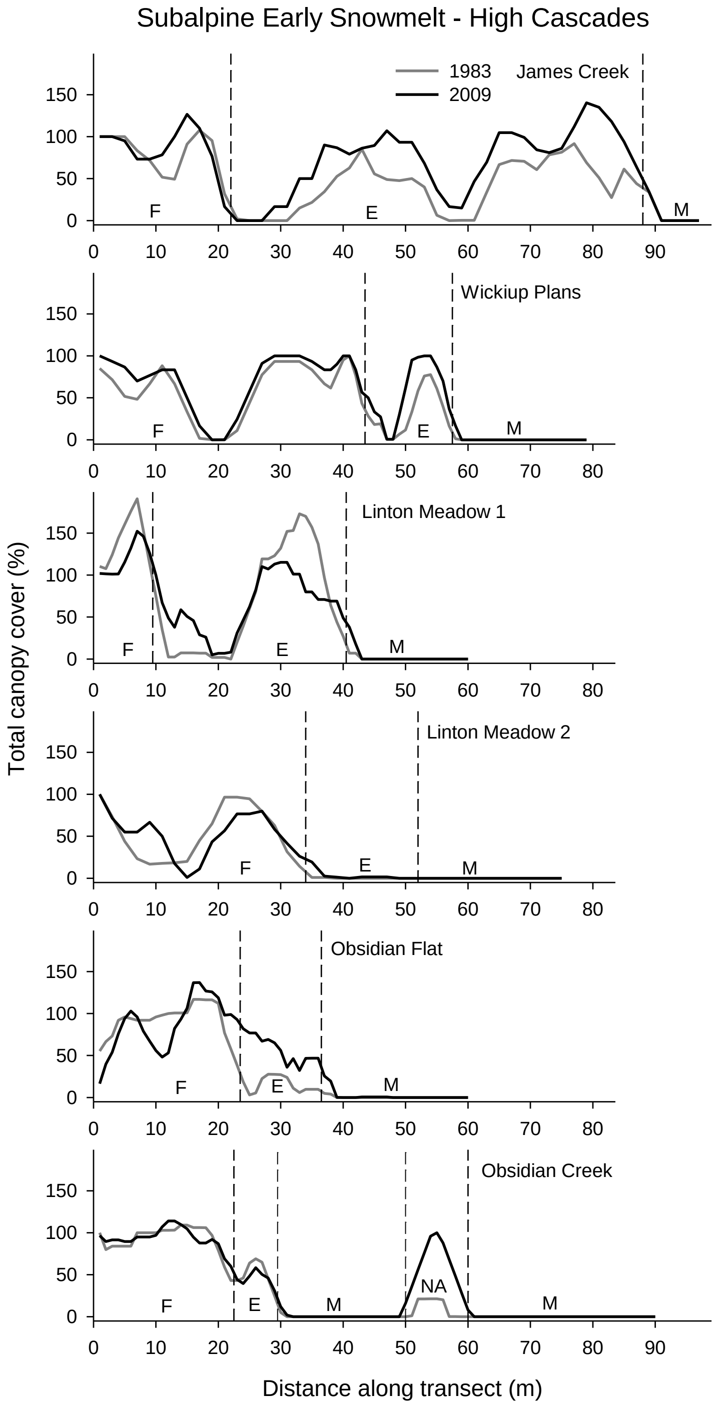
Appendix B.1. Changes in total canopy cover for transects located on montane mesic slopes (Western Cascades). Habitats are delineated by vertical dashed lines and coded as F = forest, E = ecotone, and M = meadow. Note: Ollalie Meadow did not contain meadow habitat as defined in this study (see *Methods: Habitat definitions*).



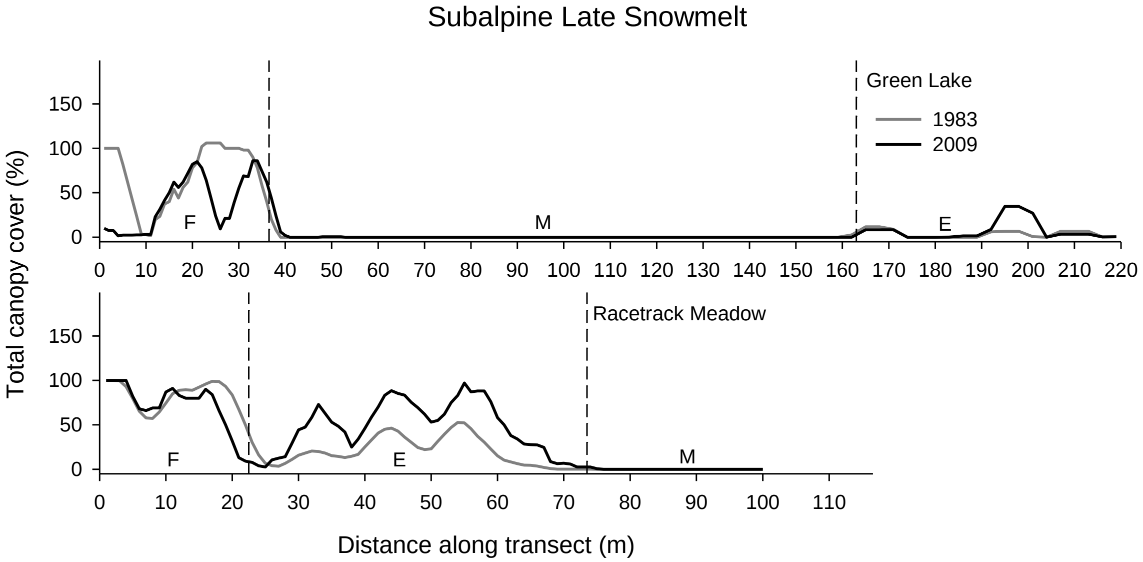
Appendix B.2. Changes in total canopy cover for transects located in montane hydric basins. Quaking Aspen 1 and 2 are in the Western Cascades; Separation Creek, Corral Flat, and Cow Swamp are in the High Cascades. Habitats are delineated by vertical dashed lines and coded as F = forest, E = ecotone, and M = meadow.



Appendix B.3. Changes in total canopy cover for transects located in subalpine sites with early snowmelt (Western Cascade sites). Habitats are delineated by vertical dashed lines and coded as F = forest, E = ecotone, and M = meadow. Note: Rebel did not contain forest or meadow habitat as defined in this study (see *Methods: Habitat definitions*).



Appendix B.4. Changes in total canopy cover for transects located in subalpine sites with early snowmelt (High Cascade sites). Habitats are delineated by vertical dashed lines and coded as F = forest, E = ecotone, and M = meadow. Note: At Obsidian Creek (d), NA (not analyzed) denotes a 10-m section of the transect where a single isolated tree island (>30m from forest) interrupted otherwise contiguous open meadow habitat. .

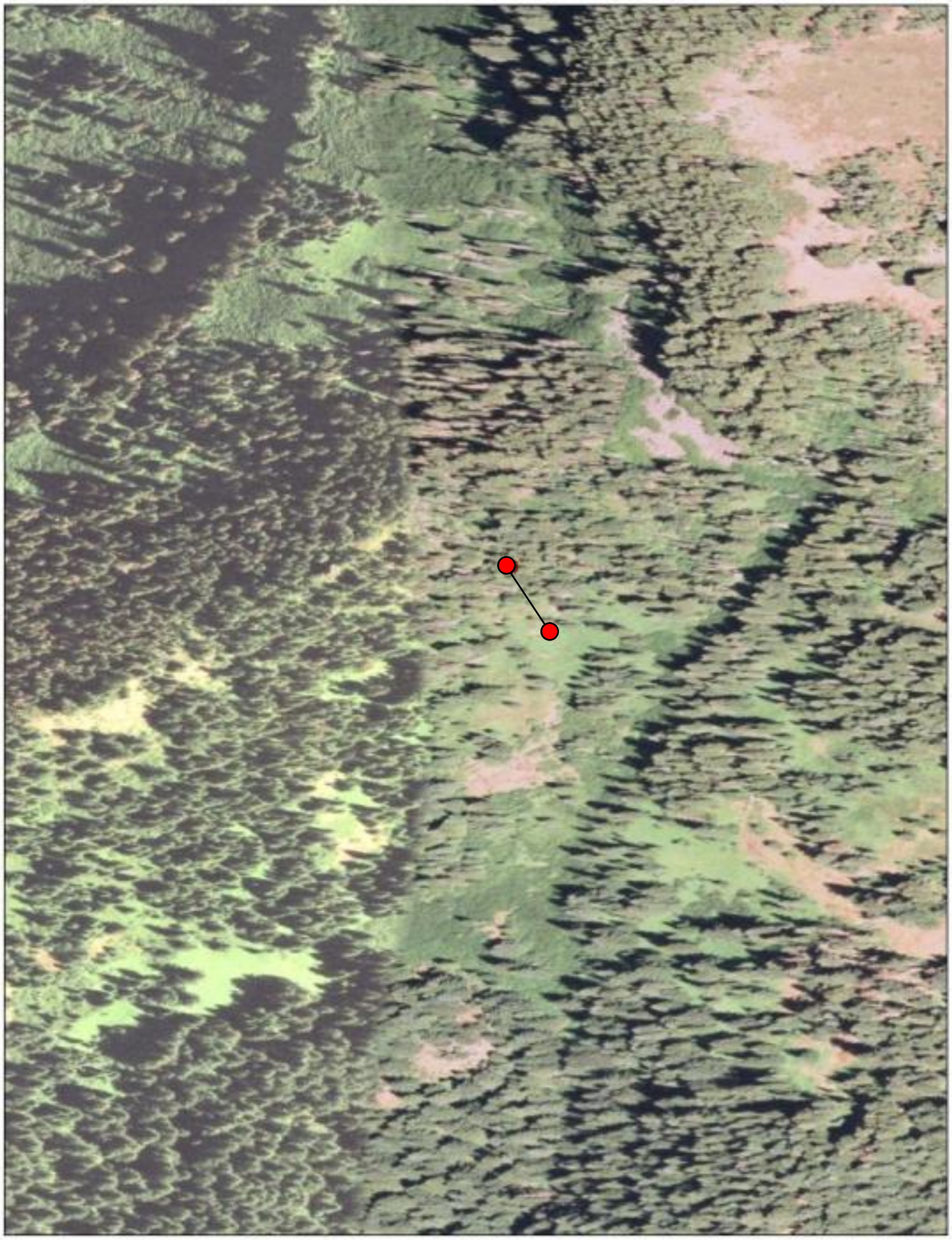


Appendix B.5. Changes in total canopy cover for transects located in subalpine sites with late snowmelt (High Cascades). Habitats are delineated by vertical dashed lines and coded as F = forest, E = ecotone, and M = meadow. Note: Reversed order of ecotone and meadow habitat at Green Lake represents an expanding patch of conifers in open meadow.

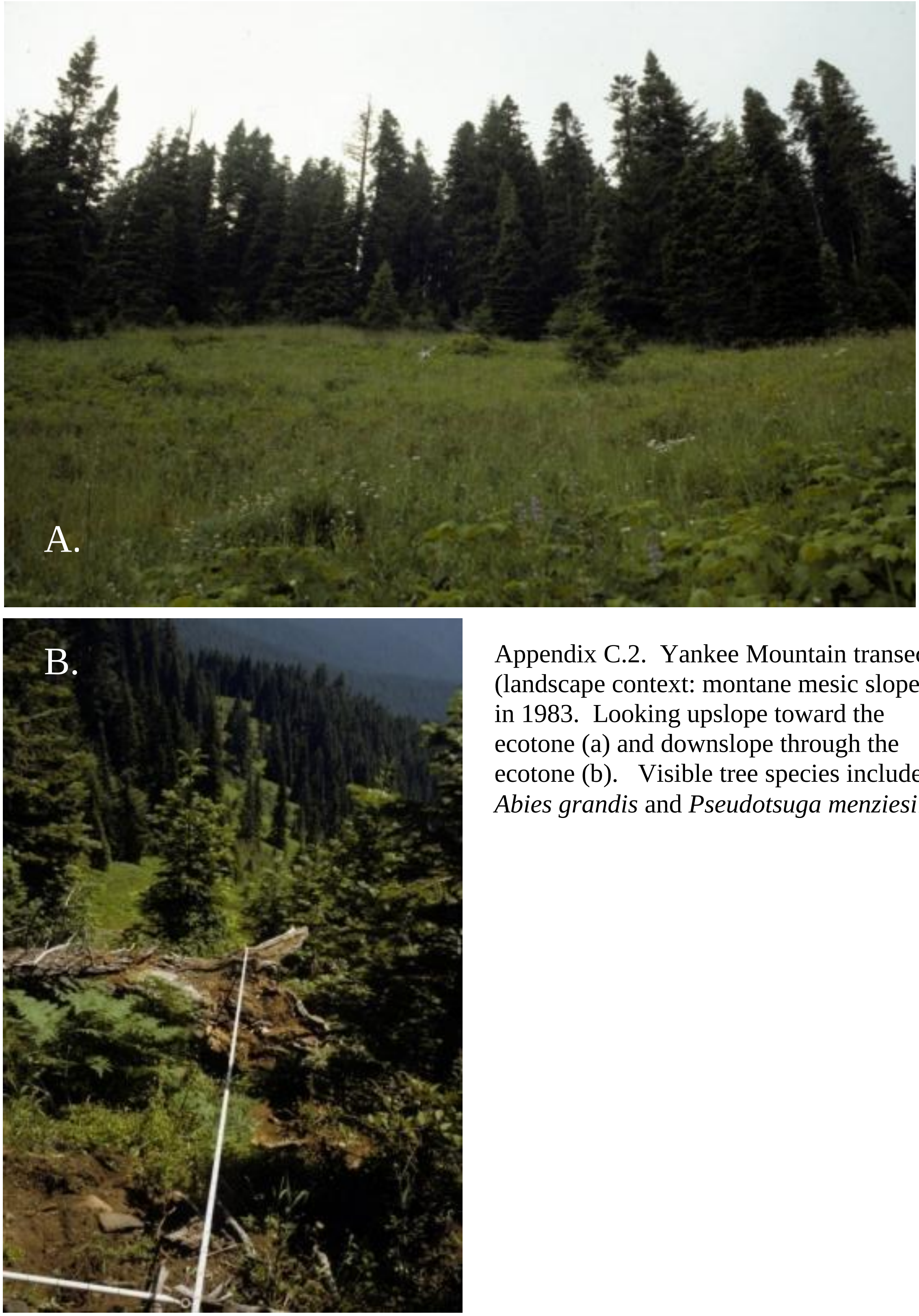
Appendix C

Photographs of TSBR forest-meadow ecotones

Aerial and ground-based photographs of the forest-meadow ecotone transects in the Three Sisters Biosphere Reserve (TSBR), Oregon. Aerial photographs (scale: 1:3500) were taken in 2006. Photographs are oriented N (top) to S (bottom). Transect end-points are indicated by red circles. Most ground-based photographs are from 1983 (as available) to illustrate ecotone structure at the beginning of the study. These are supplemented by more recent photographs (1993 and 2009).



Appendix C.1. Aerial photograph of the Yankee Mountain transect (landscape context: montane mesic slope) in 2006. The transect (68 m long) begins near a ridge top and extends downslope (upper left to lower right) through an ecotone with *Abies grandis* and *Pseudotsuga menziesii*.

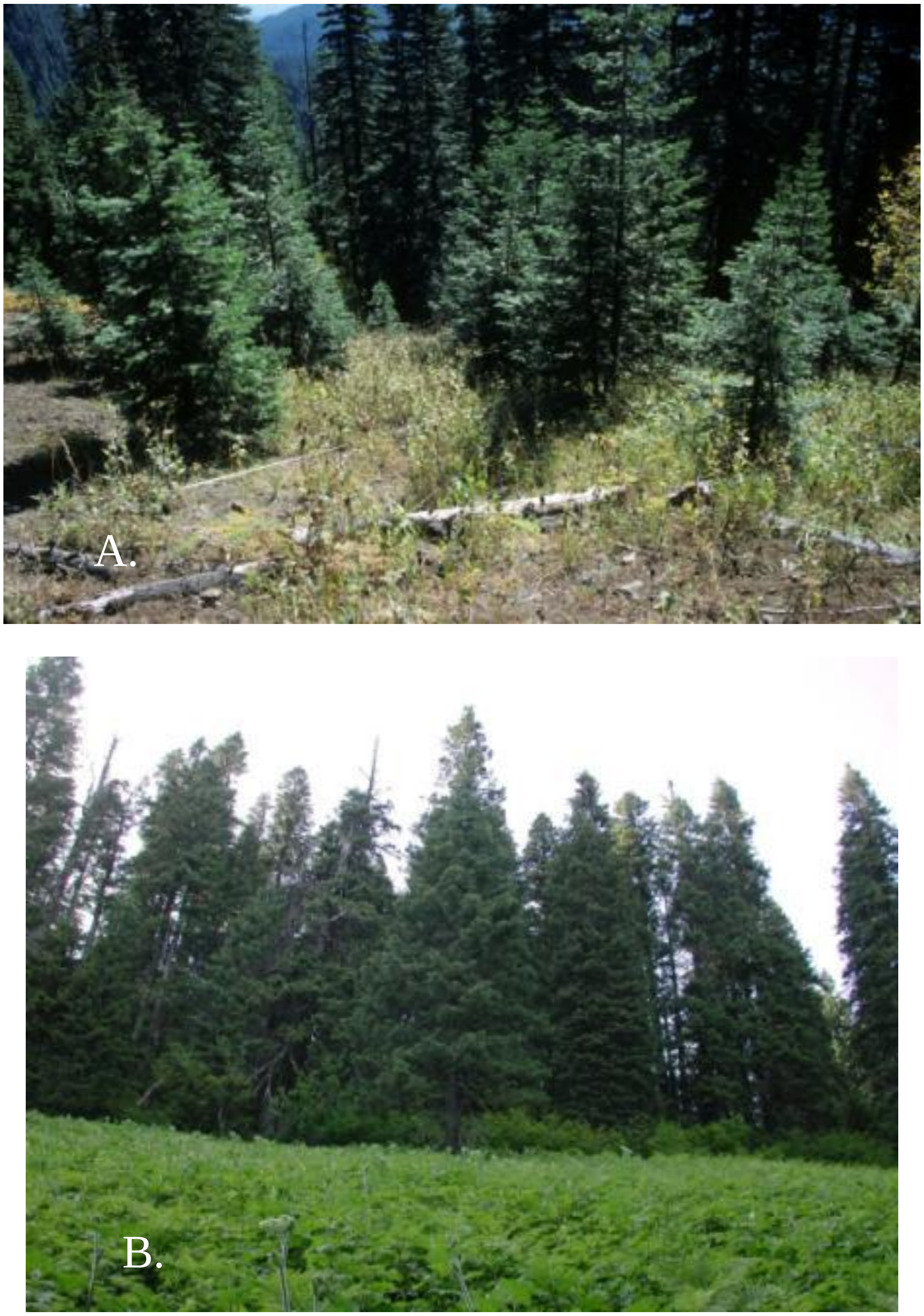


Appendix C.2. Yankee Mountain transect (landscape context: montane mesic slope) in 1983. Looking upslope toward the ecotone (a) and downslope through the ecotone (b). Visible tree species include *Abies grandis* and *Pseudotsuga menziesii*.

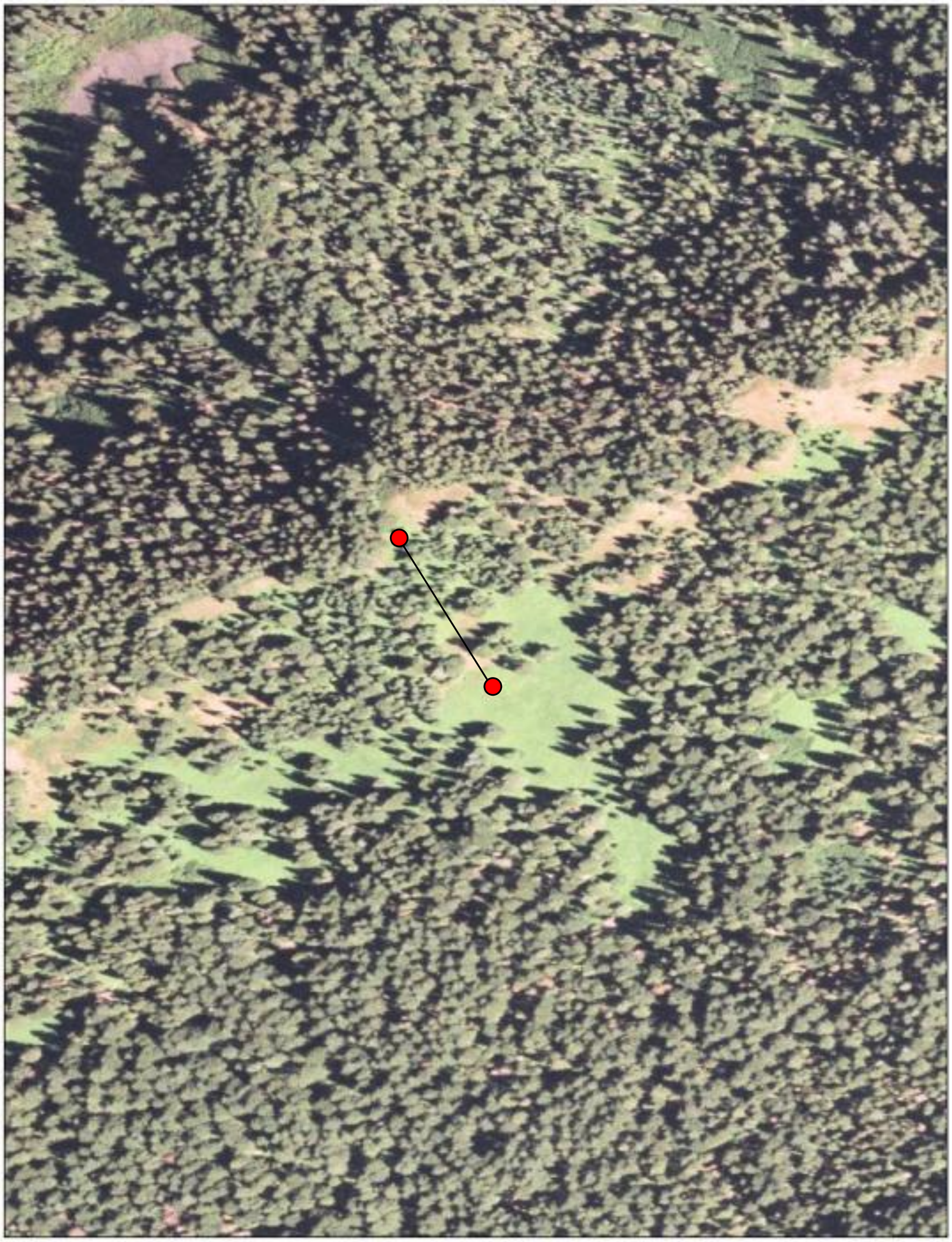
Appendix C.3. Aerial photograph of the Ollalie Meadow transect (landscape context: montane mesic slope) in 2006. The transect passes (120 m long; left to right) on level terrain from *Abies grandis* forest into dense ecotone with *Pinus contorta*, *Pseudotsuga menziesii*, and *Abies grandis*.

Appendix C.4. Ollalie Meadow transect (landscape context: montane mesic slope) in 1983. Looking along the ecotone to the forest. Visible tree species include *Pinus contorta* and *Pseudotsuga menziesii* (background) and *Abies grandis* (foreground); ground vegetation includes *Haplopappus greenei*, *Bromus carinatus*, and *Carex pensylvanica*.

Appendix C.5. Aerial photograph of the Walker 1 transect (landscape context: montane mesic slope) in 2006. The transect (65 m long) begins near a ridge top and extends downslope (upper left to lower right) through an ecotone with *Abies grandis* into *Rubus parviflorus-Pteridium aquilinum* meadow.



Appendix C.6. Walker 1 transect (landscape context: montane mesic slope). (a) Looking downslope along transect within the ecotone in 1993 (note tape running next to young *Abies grandis*). (b) Looking upslope toward the ecotone in 2009. Visible tree species include *Abies grandis* and *Pseudotsuga menziesii*. *Acer circinatum* is at the forest-meadow boundary; *Rubus parviflorus* and *Pteridium aquilinum* dominate the ground vegetation..

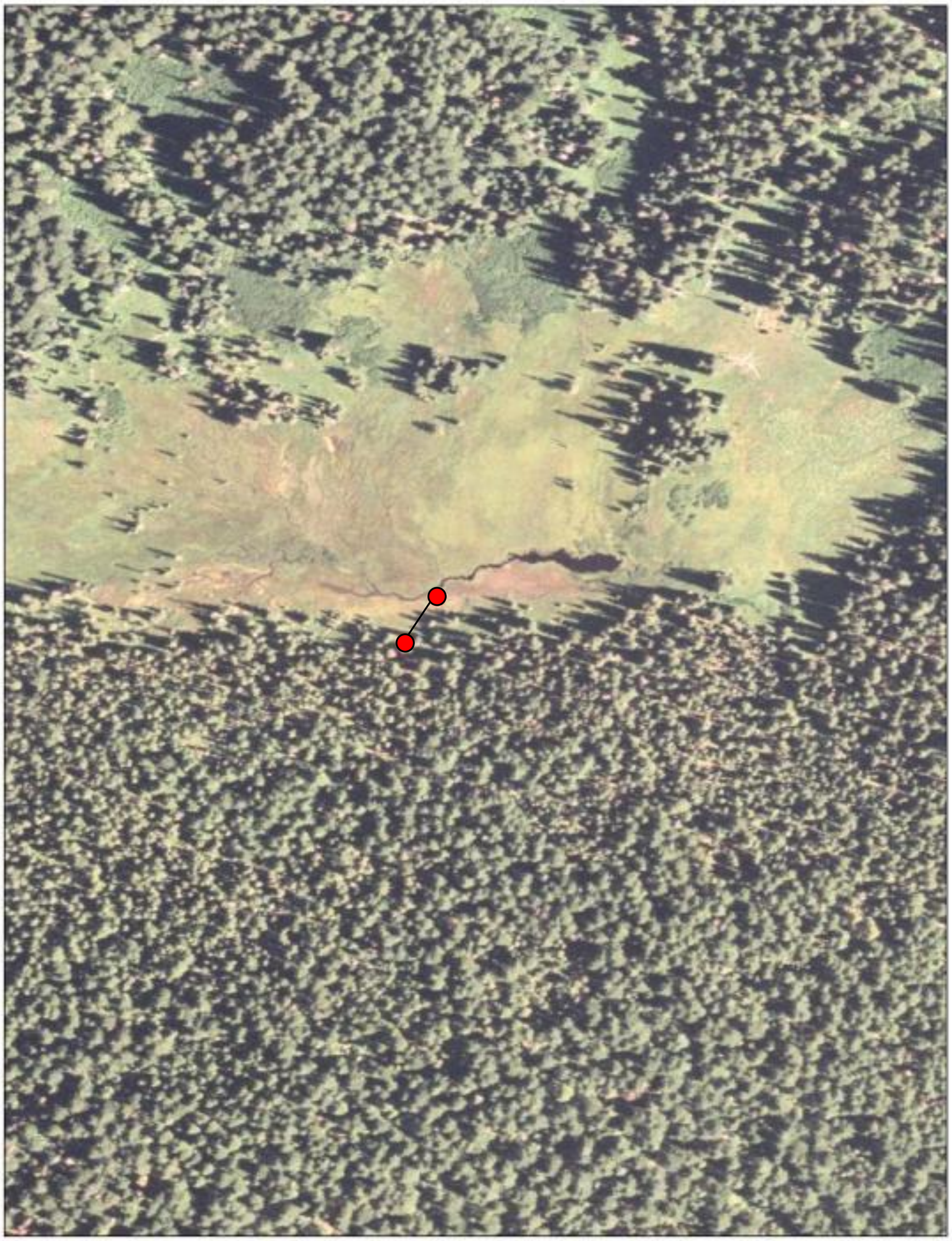


Appendix C.7. Aerial photograph of the Walker 2 transect (landscape context: montane mesic slope) in 2006. The transect (151 m long) begins near a ridge top and extends downslope (upper left to lower right) through a patchy ecotone with *Abies grandis* and *Pseudotsuga menziesii*.

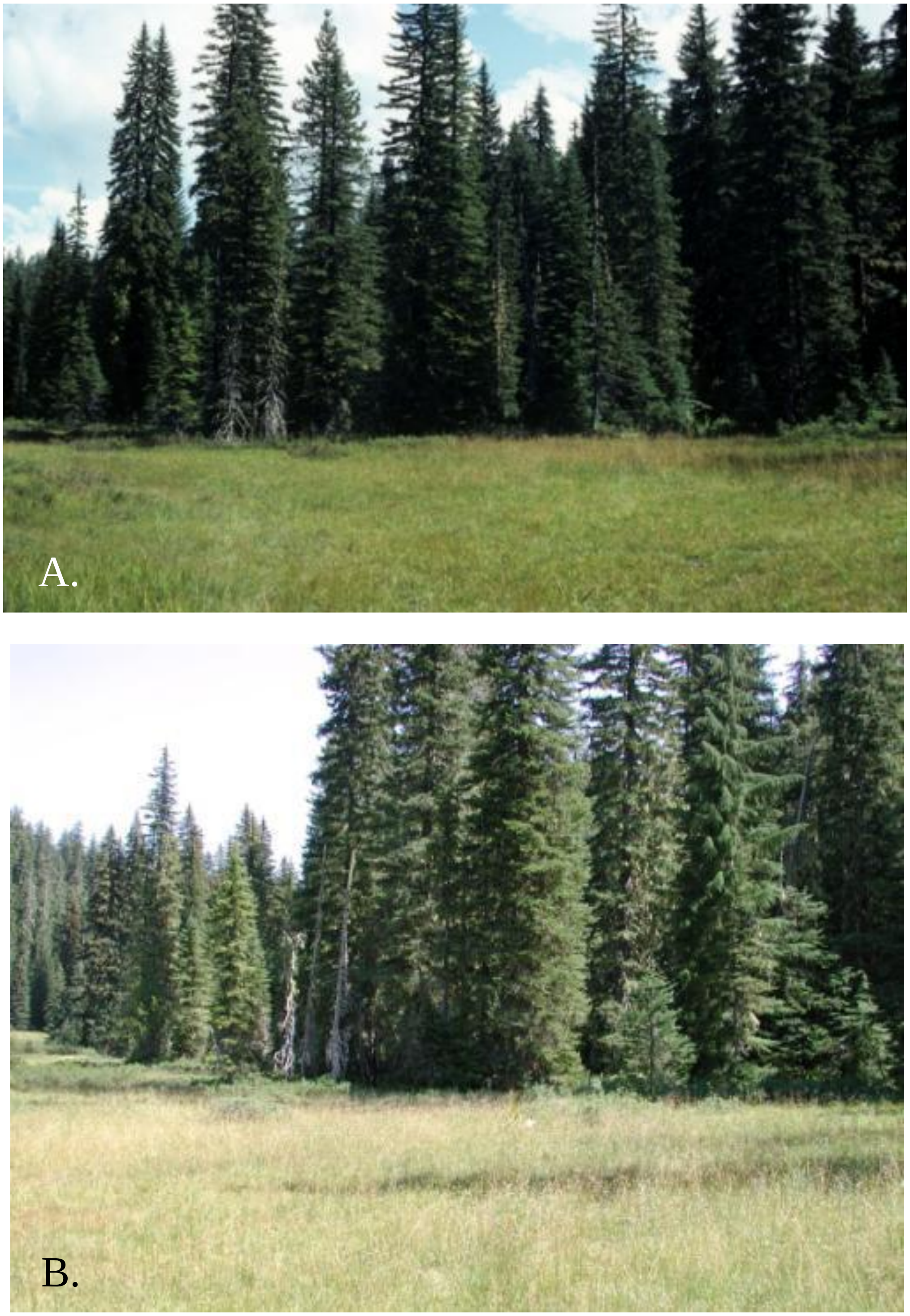
Appendix C.8. Walker 2 transect (landscape context: montane mesic slope). Looking upslope to the ecotone and forest in 1983 (a) and 2009 (b). Visible tree species include *Abies grandis* and *Pseudotsuga menziesii.*

Appendix C.9. Aerial photograph of the Quaking Aspen 1 transect (landscape context: montane hydric basin) in 2006. The transect (87 m long) begins in mixed forest of *Tsuga mertensiana*, *Abies amabilis*, *A. lasiocarpa*, and *Picea engelmannii* and extends across a sharp ecotone into hydric meadow.

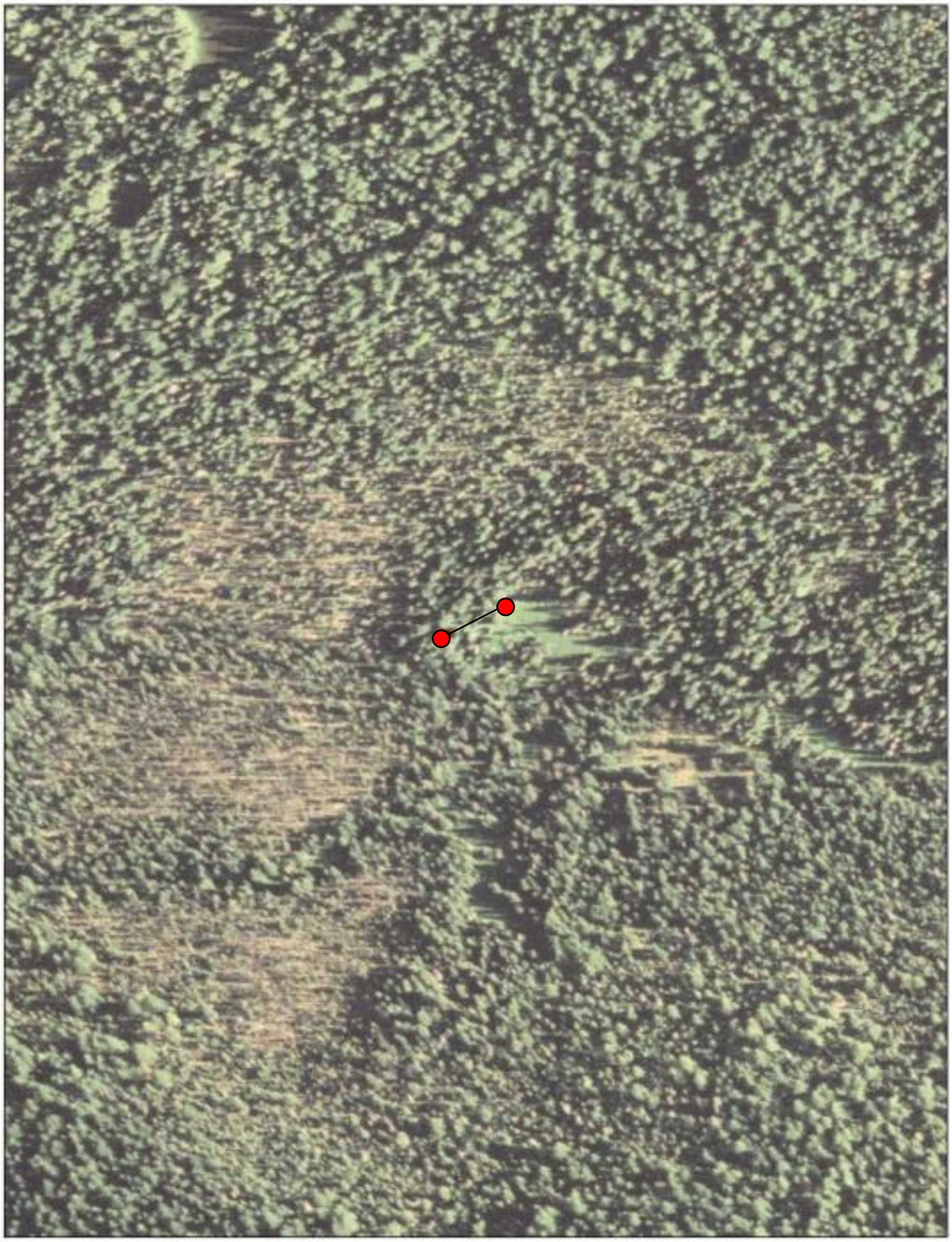
Appendix C.10. Quaking Aspen 1 (landscape context: montane hydric basin). Looking across the meadow to the ecotone and forest in (a) 1983 and (b) 2009. Visible tree species include *Abies lasiocarpa*, *Tsuga mertensiana*, and *Picea engelmannii*.



Appendix C.11. Aerial photograph of the Quaking Aspen 2 transect (landscape context: montane hydric basin) in 2006. The transect (70 m long) begins in mixed forest of *Tsuga mertensiana*, *Abies amabilis*, *A. lasiocarpa*, and *Picea engelmannii* and extends across a sharp ecotone into hydric meadow.

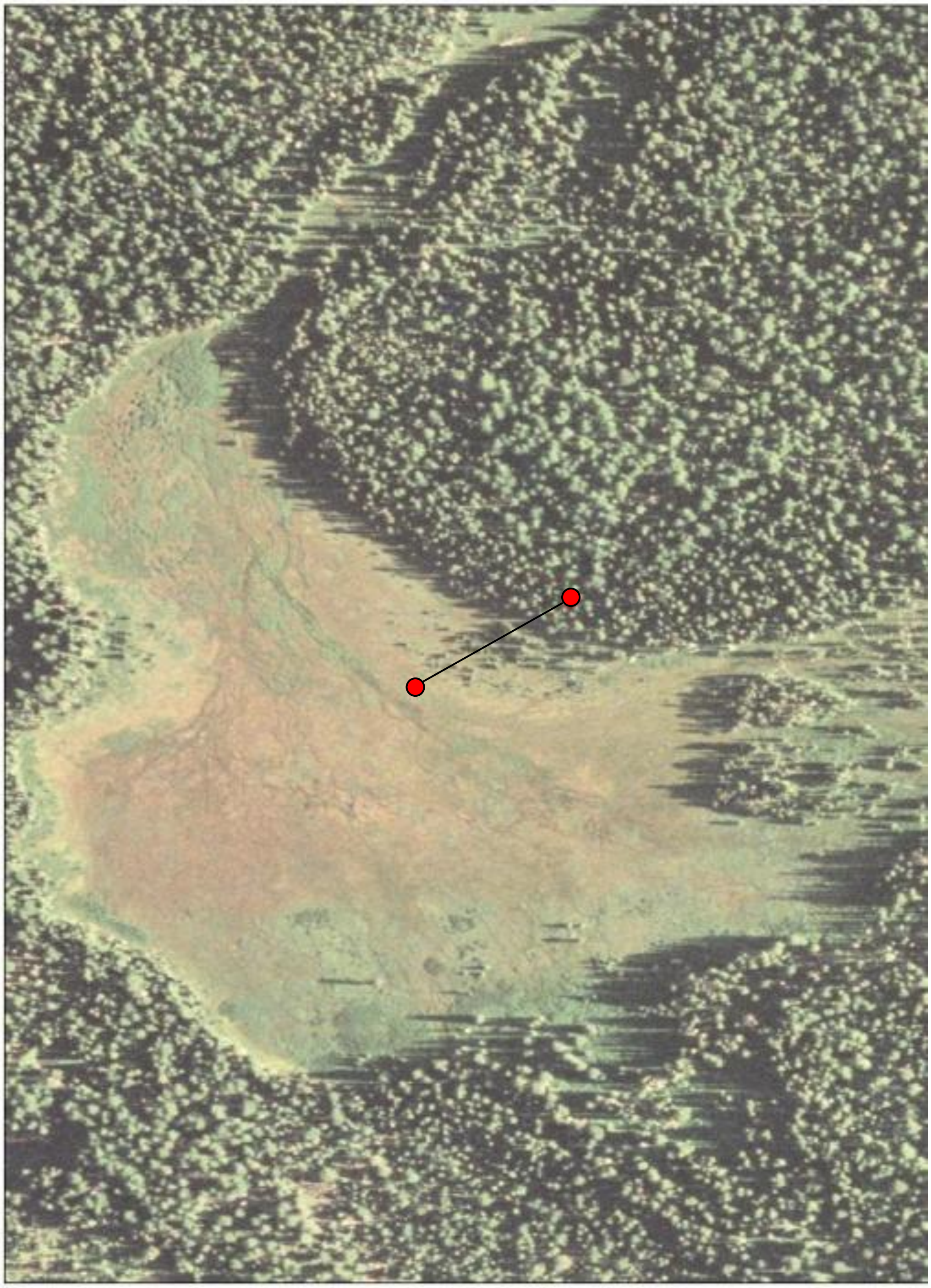


Appendix C.12. Quaking Aspen 2 (landscape context: montane hydric basin). Looking across the meadow to the ecotone and forest in (a) 1983 and (b) 2009. Visible tree species include *Abies lasiocarpa*, *Tsuga mertensiana*, and *Picea engelmannii*.



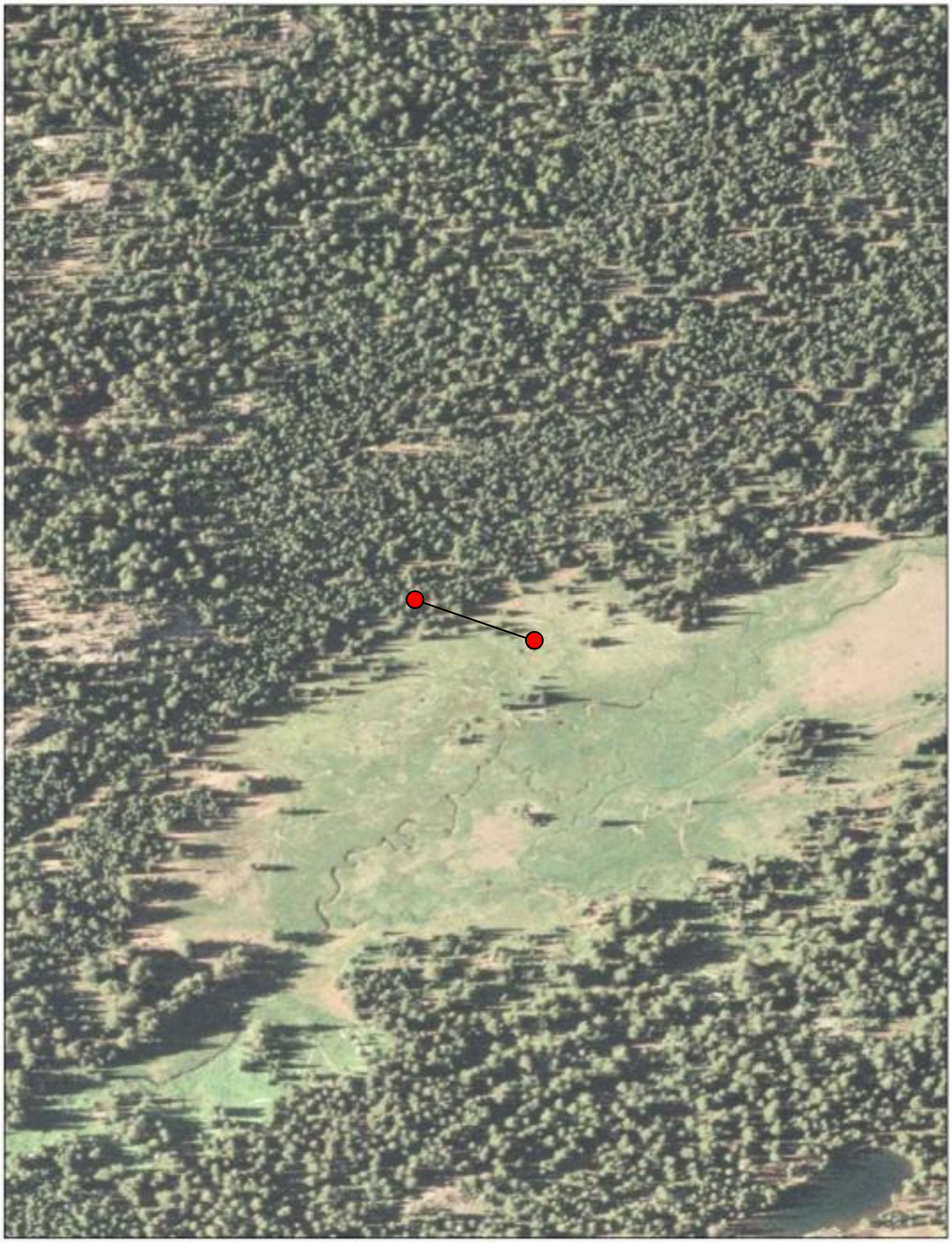
Appendix C.13. Aerial photograph of the Corral Flat transect (landscape context: montane hydric basin) in 2006. The transect (58 m long) begins in diverse forest of *Tsuga mertensiana*, *Picea engelmannii*, *Pseudotsuga menziesii*, *Abies lasiocarpa*, and *A. procera*, and extends (left to right) into hydric meadow invaded by *Picea engelmannii* and *Pinus contorta*.

Appendix C.14. Corral Flat transect (landscape context: montane hydric basin) in 1983. Looking from the transect end point in the meadow to the forest. Visible tree species include *Picea engelmannii* and *Pinus contorta* (ecotone and forest). Ground vegetation includes a diversity of graminoids and hydric-meadow forbs.



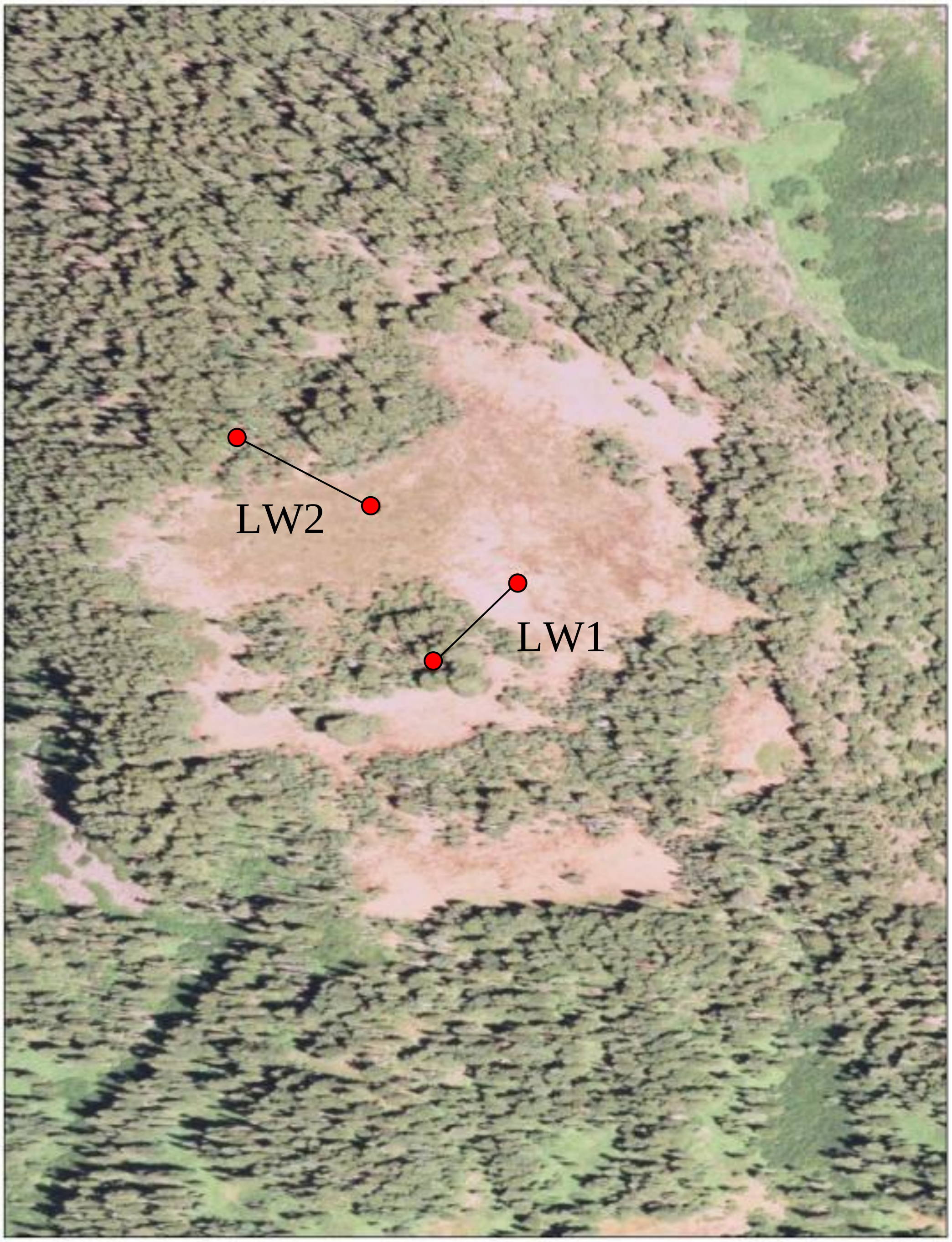
Appendix C.15. Aerial photograph of the Cow Swamp transect (landscape context: montane hydric basin) in 2006. The transect (110 m long) begins in mixed forest of *Picea engelmannii*, *Abies amabilis*, and *Pinus contorta* and extends across ecotone with *Pinus contorta* into hydric meadow.

Appendix C.16. Cow Swamp transect (landscape context: montane hydric basin) in 1983. Looking across the meadow to the ecotone and forest (note transect tape running through image). Visible tree species include *Picea engelmannii* (forest) and *Pinus contorta* (ecotone); ground vegetation is dominated by *Deschampsia caespitosa* and other hydric-meadow graminoids and forbs.



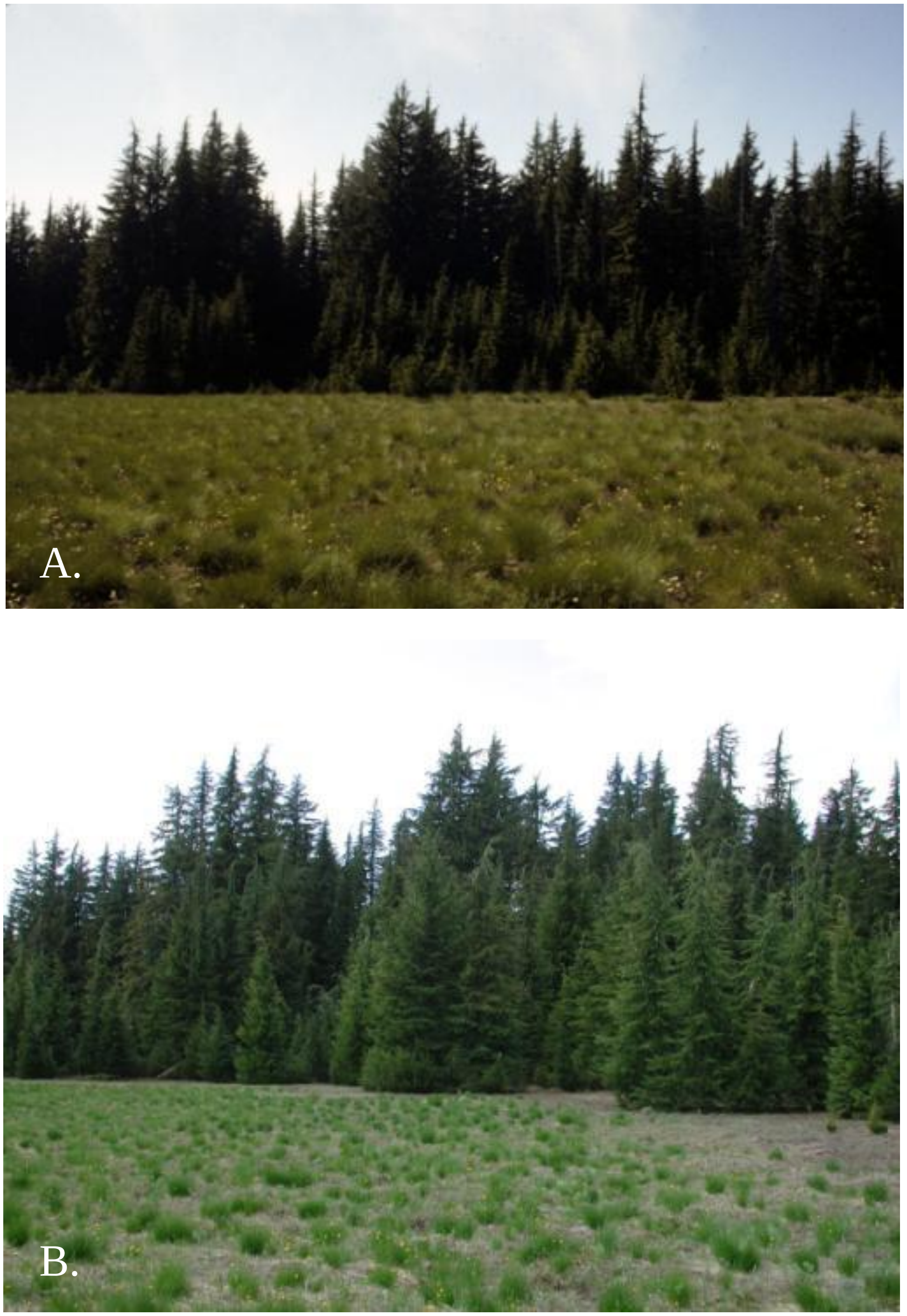
Appendix C.17. Aerial photograph of the Separation Creek transect (landscape context: montane hydric basin) in 2006. The transect (75 m long) begins in forest of *Tsuga mertensiana* and *Abies lasiocarpa* and extends across patchy ecotone into hydric meadow.

Appendix C.18. Separation Creek transect (landscape context: montane hydric basin). Looking across the meadow to the ecotone in (a) 1983 (note transect tape running across image) and (b) 2009. Visible tree species include *Abies lasiocarpa* and *Tsuga mertensiana*. Ground vegetation is dominated by *Deschampsia caespitosa*.



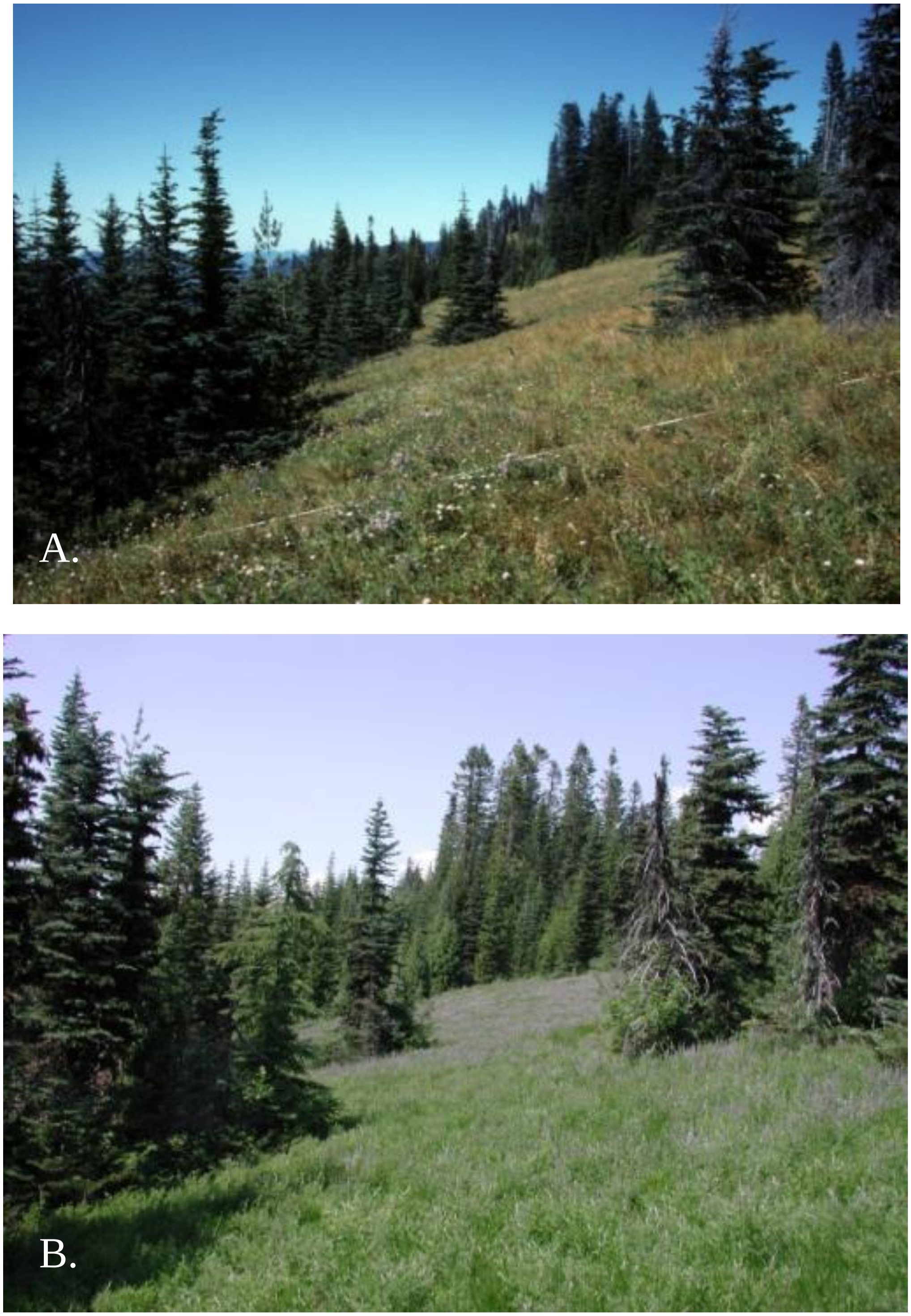
Appendix C.19. Aerial photograph of the Lowder Mountain 1 (LW1; 76 m long) and Lowder Mountain 2 (LW2; 93 m long) transects (landscape context: subalpine early snowmelt) in 2006. Transects begin in forests of *Tsuga mertensiana* and *Abies lasiocarpa* and extend across dense ecotones into meadows dominated by *Festuca viridula* (tan color at LW2) or *Arenaria capillaris* (lighter color at LW1).

Appendix C.20. Lowder Mountain 1 transect (landscape context: subalpine early snowmelt). Looking from the meadow to the ecotone and forest in (a) 1983 and (b) 2009. Note the sparse meadow vegetation in both transects. Visible tree species include *Tsuga mertensiana* in the forest (background) and *Tsuga mertensiana* and *Abies lasiocarpa* in the ecotone..



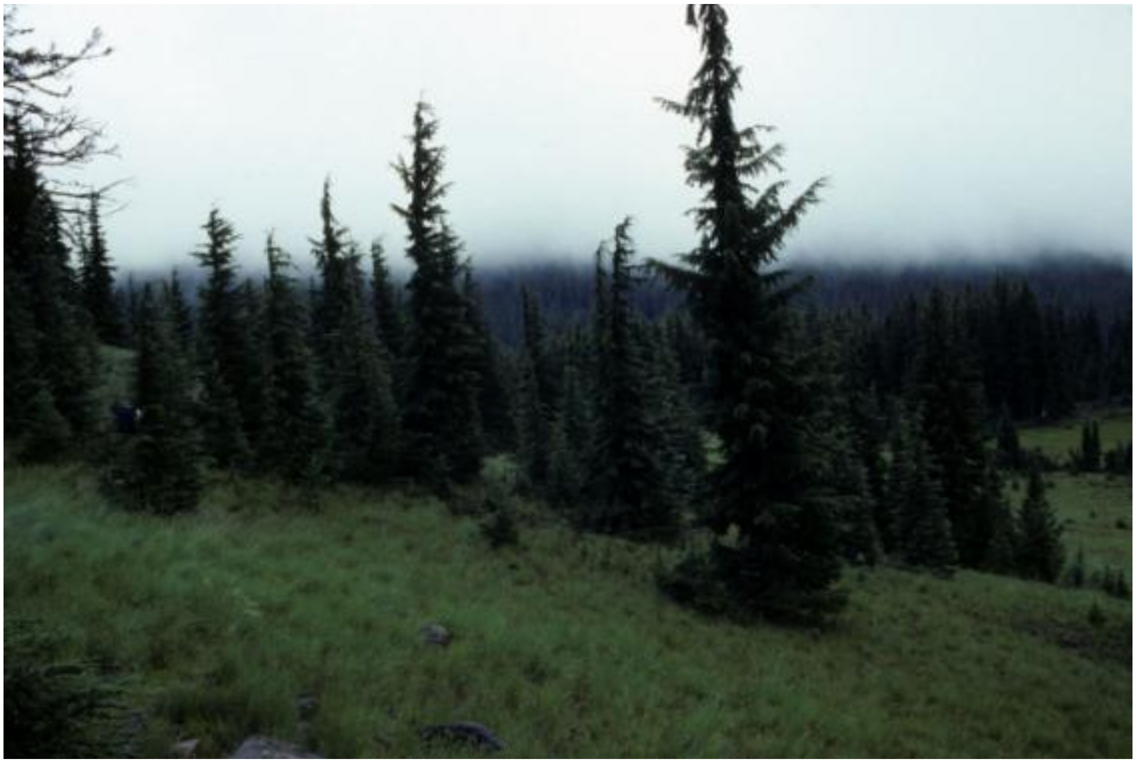
Appendix C.21. Lowder Mountain 2 transect (landscape context: subalpine early snowmelt). Looking from the meadow to the ecotone and forest in (a) 1983 and (b) 2009. *Tsuga mertensiana* dominates the forest (background) and ecotone. The principal meadow species is *Festuca viridula*. .

Appendix C.22. Aerial photograph of the Rebel Rock transect (landscape context: subalpine early snowmelt) in 2006. The transect (82 m long) extends (right to left) from a ridge top through a patchy ecotone dominated by *Tsuga mertensiana*, *Abies grandis*, and *A. lasiocarpa*.



Appendix C.23. Rebel transect (landscape context: subalpine early snowmelt). Looking across the ecotone in (a) 1993 and (b) 2009. Visible tree species (both up and downslope) include *Tsuga mertensiana, Abies grandis,* and *Abies lasiocarpa*; visible meadow species include *Festuca viridula* and *Lupinus latifolius* (in flower in 2009).

Appendix C.24. Aerial photograph of the James Creek transect (landscape context: subalpine early snowmelt) in 2006. The transect (98 m long) extends (upper right to lower left) from open forest of *Tsuga mertensiana* downslope across a patchy ecotone with *Tsuga mertensiana* and *Abies lasiocarpa*.

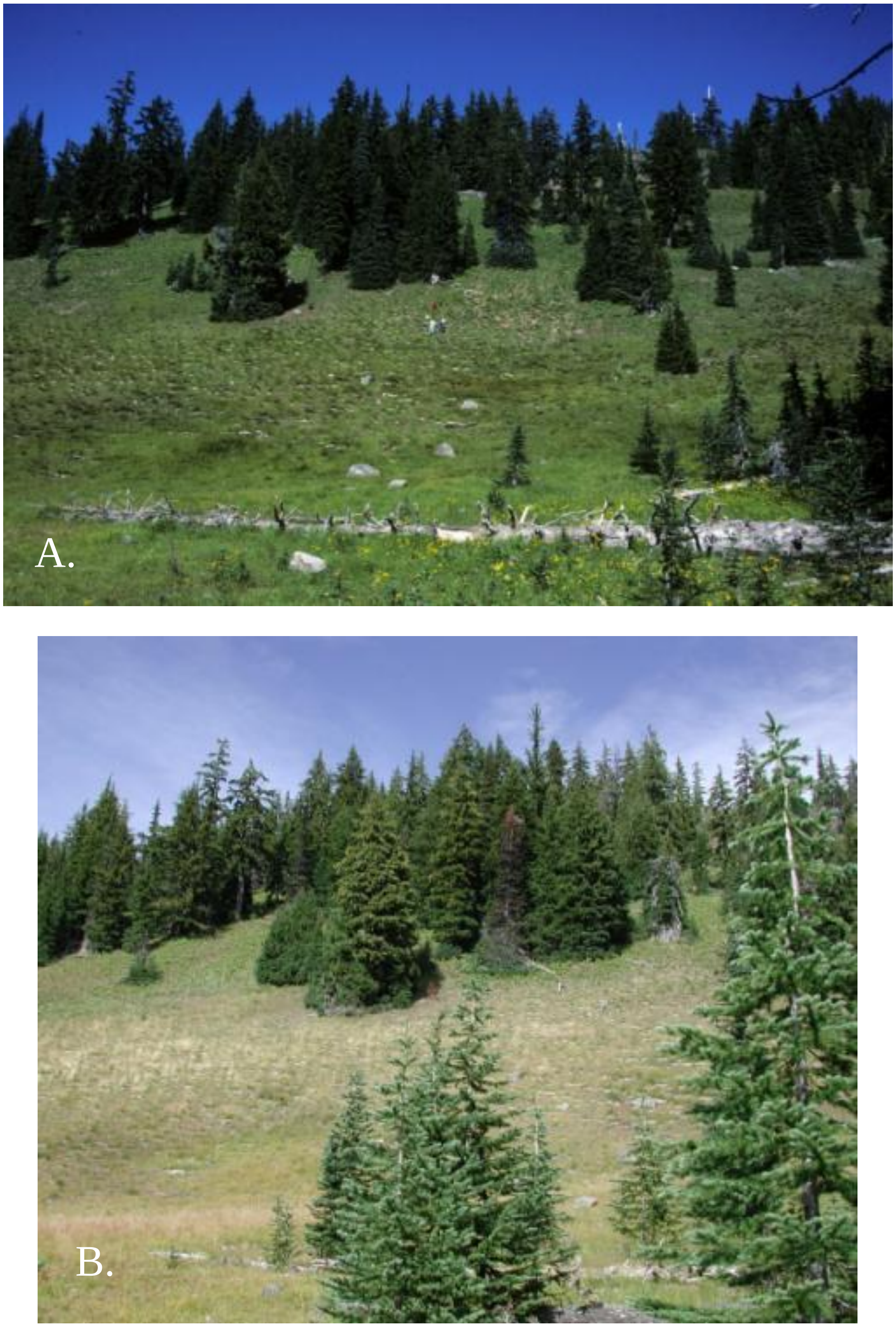


Appendix C.25. James Creek (landscape context: subalpine early snowmelt) in 1983 looking across the ecotone. Visible tree species include *Tsuga mertensiana* and *Abies lasiocarpa*. The principal meadow species is *Festuca viridula*.

Appendix C.26. Aerial photograph of the Wickiup Plains transect (landscape context: subalpine early snowmelt) in 2006. The transect (79 m) begins in *Tsuga mertensiana* forest and extends across ecotone into dry, graminoid-dominated meadow and pumice flat.

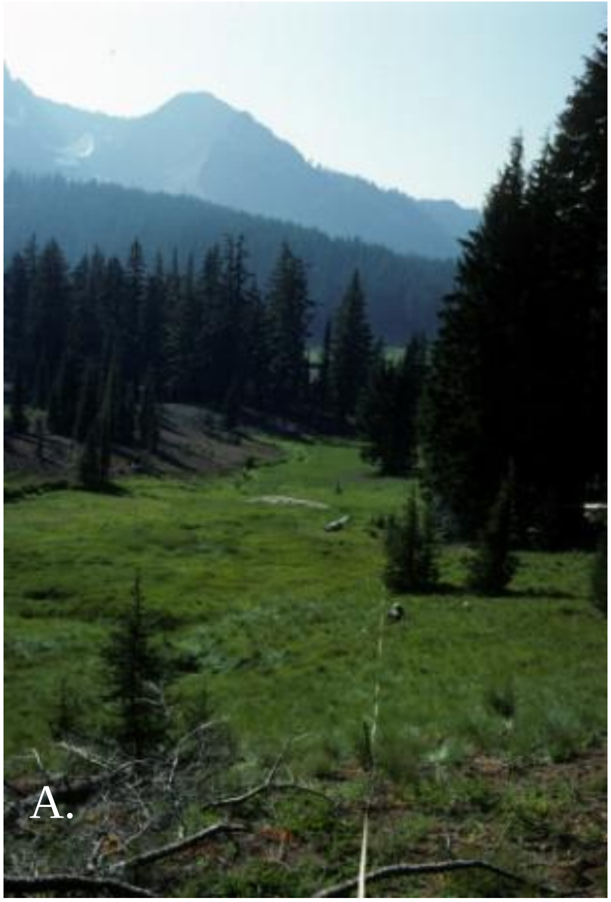
Appendix C.27. Wickiup Plains (landscape context: subalpine early snowmelt) in 1983 looking from the ecotone to meadow. Visible tree species in the ecotone is *Tsuga mertensiana*; graminoids including *Festuca viridula, Sitanion hystrix, Stipa occidentalis, and Juncus paryii*, dominate the ground vegetation.

Appendix C.28. Aerial photograph of the Linton Meadow 1 transect (landscape context: subalpine early snowmelt) in 2006. The transect (60 m long) runs downslope (upper right to lower left) from forest of *Tsuga mertensiana* and *Abies lasiocarpa* into meadow dominated by *Festuca viridula*.



Appendix C.29. Linton Meadow 1 transect (landscape context: subalpine early snowmelt). Looking upslope to the meadow, ecotone, and forest in (a) 1983 and (b) 2009. Visible tree species are *Tsuga mertensiana* and *Abies lasiocarpa*. Meadow is dominated by *Festuca viridula*. Transect passes beneath recently dead *A. lasiocarpa* (2009 photograph).

Appendix C.30. Aerial photograph of the Linton Meadow 2 transect (landscape context: subalpine early snowmelt) in 2006. The transect (60 m long) extends downslope (right to left) from open *Tsuga mertensiana* forest across a sharp ecotone into meadow dominated by *Festuca viridula* and *Carex spectabilis*.



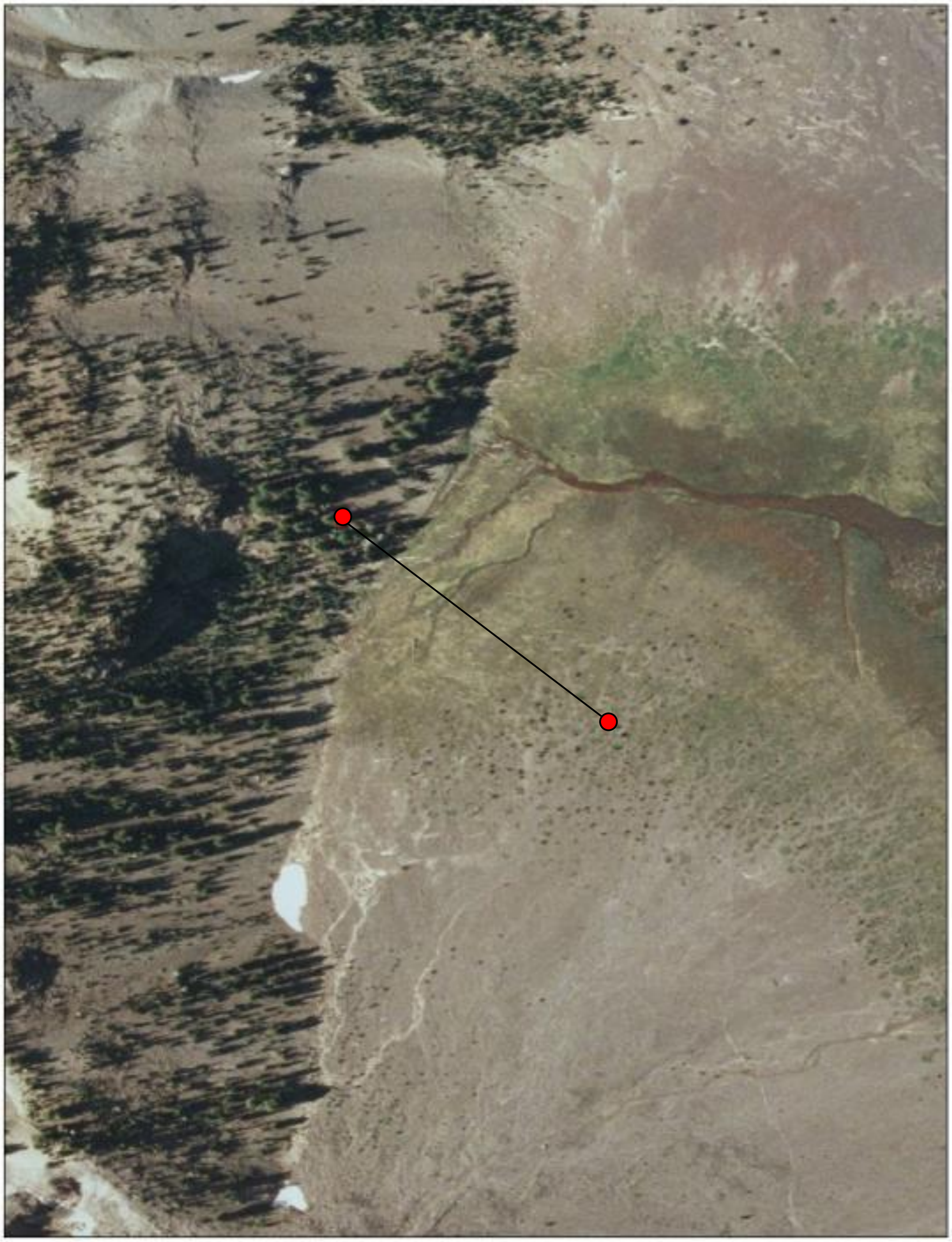
Appendix C.31. Linton Meadow 2 transect (landscape context: subalpine early snowmelt). (a) Looking downslope from the ecotone to the meadow in 1983. (b) Looking across the ecotone in 2009. Visible tree species is *Tsuga mertensiana* (forest and ecotone); ground vegetation is dominated by *Festuca viridula* and *Carex spectabliis* (lower on the slope).

Appendix C.32. Aerial photograph of the Obsidian Flat transect (landscape context: subalpine early snowmelt) in 2006. The transect (60 m long) extends (right to left) from open *Tsuga mertensiana* forest downslope into meadow dominated by *Festuca viridula*.

Appendix C.33. Obsidian Flat transect (landscape context: subalpine early snowmelt) in 2009. Looking from the meadow to ecotone and forest (note transect tape running across image). Visible tree species include *Tsuga mertensiana* (ecotone and forest); dead *T. mertensiana* and *Pinus albicaulis* are visible in the forest (center and right, respectively). Ground vegetation is dominated by *Festuca viridula*.

Appendix C.34. Aerial photograph of the Obsidian Creek transect (landscape context: subalpine early snowmelt) in 2006. The transect (90 m long) runs from hilltop forest of *Tsuga mertensiana* and *Abies lasiocarpa* downslope onto a graminoid-dominated flat.

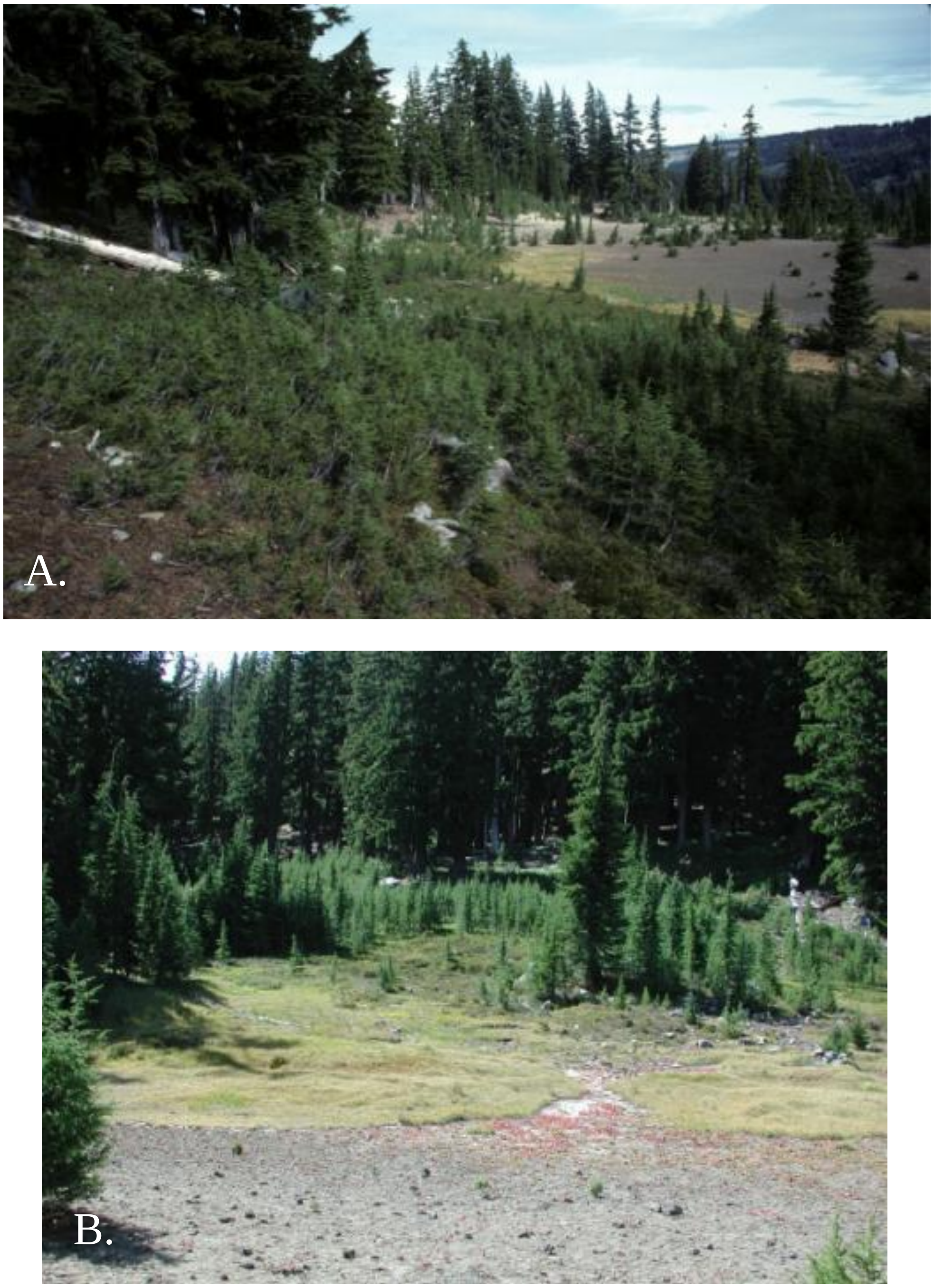
Appendix C.35. Obsidian Creek transect (landscape context: subalpine early snowmelt) in 2009. Looking across the ecotone. Visible tree species include *Tsuga mertensiana* and *Abies lasiocarpa*. Ground vegetation is dominated by *Festuca viridula* and *Carex spectabilis* (lower on the flat).



Appendix C.36. Aerial photograph of the Green Lake transect (landscape context: subalpine late snowmelt) in 2006. The transect (220 m long) runs from open *Pinus albicaulis* forest on the slope onto a broad meadow flat.

Appendix C.37. Green Lake transect (landscape context: subalpine late snowmelt) in 1983. Looking down the transect across the meadow; small *Pinus contorta* are scattered in the background.

Appendix C.38. Aerial photograph of the Racetrack transect (landscape context: subalpine late snowmelt) in 2006. The transect (100 m long) runs downslope (left to right) from *Tsuga mertensiana* forest into a heath-dominated and sedge-dominated late snowlie basin.



Appendix C.39. Image of Racetrack (landscape context: subalpine late snowmelt). (a) Looking through dense establishment of *Tsuga mertensiana* in the ecotone in 1993. (b) Looking upslope at ecotone and forest from the meadow in 2009. Visible tree species is *Tsuga mertensiana* (forest and ecotone). Bare pumice soils are visible in the foreground. A dense carpet of *Carex nigricans* extends to the base of the slope giving way to a heath-dominated (*Phyllodoce empetriformis*) community within which invasion is most dense.

Appendix D

Species along TSBR forest-meadow ecotones

Species observed within permanent forest-meadow transects in the Three Sisters Biosphere Reserve (TSBR), Oregon during 1983, 1993, and/or 2009. Nomenclature follows Hitchcock and Cronquist (1973).

Appendix D.1. Species observed in montane forest-meadow ecotone transects in the Three Sisters Biosphere Reserve, Oregon. Species are grouped by habitat preference (meadow, forest, and unclassified) and growth form (grasses, sedges/rushes, herbs, and shrubs). Tree species were not classified. "X" indicates presence in a transect at one or more sampling dates (1983, 1993, or 2009). Asterisks denote non-native species. YM = Yankee Mountain, OM = Ollalie Meadow, W1 = Walker 1, W2 = Walker 2, QA1 = Quaking Aspen 1, QA2 = Quaking Aspen 2, CF = Corral Flat, CS = Cow Swamp, SC = Separation Creek. See Chapter 3, Table 1 for more details.

	Mesic Slopes				**Hydric Basins**				
Species	**YM**	**OM**	**W1**	**W2**	**QA1**	**QA2**	**CF**	**CS**	**SC**
Forest Species									
Grasses									
Bromus vulgaris	X	X	X	X				X	
Festuca occidentalis	X			X		X	X		
Melica subulata	X		X	X			X		
Trisetum canescens	X	X							
Trisetum cernuum	X				X	X	X		
Sedges / Rushes									
Luzula hitchcockii									X
Luzula parviflora	X	X							
Herbs									
Achlys triphylla		X	X	X			X	X	
Actea rubra		X	X						
Adenocaulon bicolor			X	X					
Anemone deltoidea	X	X	X	X	X	X	X	X	
Anemone lyallii	X		X	X			X	X	
Anemone oregana		X							
Arenaria macrophylla	X	X	X	X		X			
Arnica mollis						X			
Asarum caudatum			X						
Blechnum spicant					X				
Campanula scouleri	X		X	X			X		
Circaea alpina		X							
Clintonia uniflora				X	X	X	X	X	
Disporum species		X	X	X	X	X			

Appendix D.1. Continued.

	Mesic Slopes				Hydric Basins				
Species	**YM**	**OM**	**W1**	**W2**	**QA1**	**QA2**	**CF**	**CS**	**SC**
Forest Species									
Herbs									
Galium oreganum	X	X		X					
Galium triflorum	X	X	X	X		X			
Goodyera oblongifolia		X	X	X					
Habenaria unalascensis	X								
Hieracium albiflorum	X	X		X		X	X	X	
*Lactuca muralis**		X	X	X					
Linnaea borealis							X		
Listera caurina		X					X	X	
Listera cordata						X			
Mianthemum dilatatum		X							
Mitella breweri		X			X	X			X
Mitella trifida	X	X	X	X					
Osmorhiza chilensis	X	X	X	X		X	X	X	
Osmorhiza occidentalis	X	X	X	X					
Pedicularis racemosa						X	X	X	X
Polystichum munitum	X			X					
Pyrola picta	X	X	X	X					
Pyrola secunda				X	X	X	X	X	X
Smilacina racemosa	X	X	X						
Smilacina stellata	X	X	X	X	X	X	X	X	
Tellima grandiflora	X								
Tiarella trifoliata							X	X	
Trientalis latifolia			X	X				X	
Trillium ovatum	X		X	X			X	X	
Viola glabella		X		X	X	X	X	X	
Viola orbiculata					X	X	X	X	X

Appendix D.1. Continued.

	Mesic Slopes				Hydric Basins				
Species	**YM**	**OM**	**W1**	**W2**	**QA1**	**QA2**	**CF**	**CS**	**SC**
Forest Species									
Herbs									
Xerophyllum tenax				X	X	X	X	X	
Shrubs									
Acer circinatum	X		X						
Berberis nervosa								X	
Chimaphila menziesii	X	X	X	X			X		
Chimaphila umbellata		X					X		
Cornus canadensis					X	X	X	X	
Cornus nuttallii								X	
Corylus cornuta	X								
Gaultheria ovatifolia					X	X		X	
Holodiscus discolor	X								
Pachistima myrsinites	X	X							
Rhododendron albiflorum					X				
Rhododendron macrophyllum					X				
Rosa gymnocarpa	X			X					
Rubus lasiococcus	X	X			X	X	X	X	X
Rubus ursinus						X			
Symphoricarpos mollis	X			X					
Vaccinium alaskaense / V. ovalifolium		X			X	X		X	
Vaccinium membranaceum	X	X		X	X	X	X	X	X
Vaccinium scoparium								X	X
Whipplea modesta						X			
Meadow Species									
Grasses									
Agrostis exarata					X				
Agrostis scabra	X					X	X	X	
Agrostis tenuis							X		

Appendix D.1. Continued.

	Mesic Slopes				Hydric Basins				
Species	**YM**	**OM**	**W1**	**W2**	**QA1**	**QA2**	**CF**	**CS**	**SC**
Meadow Species									
Grasses									
Agrostis thurberiana									X
Agrostis variabilis									X
Bromus carinatus	X	X	X	X		X	X		
Calamagrostis canadensis					X	X			
Calamagrostis inexpansa						X		X	X
Cinna latifolia					X				
Danthonia californica		X				X		X	
Danthonia intermedia		X				X	X	X	X
Deschampsia atropurpurea					X	X			X
Deschampsia caespitosa					X	X	X	X	X
Elymus glaucus	X	X	X	X	X	X	X	X	
Festuca idahoensis				X					
Festuca viridula	X	X		X					
Glyceria elata					X				
Hordeum brachyantherum							X		
Koeleria cristata									X
Muhlenbergia filiformis						X	X	X	X
*Poa pratensis**							X		
Stipa occidentalis	X	X		X					
Trisetum spicatum									X
Sedges / Rushes									
Carex buxbaumii								X	
Carex eurycarpa								X	
Carex halliana									X
Carex hoodii		X	X	X					
Carex jonesii							X		
Carex lenticularis					X				

Appendix D.1. Continued.

	Mesic Slopes				Hydric Basins				
Species	**YM**	**OM**	**W1**	**W2**	**QA1**	**QA2**	**CF**	**CS**	**SC**
Meadow Species									
Sedges / Rushes									
Carex limnophila							X		
Carex luzulina					X	X	X	X	
Carex mertensii					X				
Carex microptera									X
Carex muricata						X			
Carex nigricans									X
Carex pachystachya		X			X				
Carex pensylvanica	X	X	X	X			X		X
Carex rossii						X			
Carex rostrata						X			
Carex sitchensis					X	X		X	
Carex spectabilis									X
Eleocharis pauciflora						X		X	
Juncus balticus						X		X	
Juncus mertensianus							X		X
Juncus parryi									X
Scirpus congdonii					X	X	X	X	
Herbs									
Achillea millefolium	X						X		
Aconitum columbianum					X				
Agoseris aurantiaca		X		X			X		
Anaphalis margaritacea	X	X							
Angelica arguta	X	X	X		X				
Antennaria umbrinella									X
Aquilegia formosa	X			X			X		
Aspidotis densa	X								
Aster alpigenus						X		X	X

Appendix D.1. Continued.

	Mesic Slopes				Hydric Basins				
Species	**YM**	**OM**	**W1**	**W2**	**QA1**	**QA2**	**CF**	**CS**	**SC**
Meadow Species									
Herbs									
Aster foliaceus	X	X			X	X	X	X	
Aster ledophyllus	X	X		X					
Aster occidentalis		X						X	
Calochortus subalpinus		X		X					
Caltha biflora					X	X		X	
Castilleja hispida	X								
Castilleja miniata							X	X	
Cerastium vulgatum							X		
Cheilanthes gracillima	X								
Cirsium callilepes	X	X	X	X					
Collinsia parviflora	X								
Cryptantha affinis				X					
Cuscuta species								X	
Delphinium menziesii		X		X					
Dodecatheon jeffreyi					X	X	X	X	
Drosera anglica						X			
Drosera rotundifolia						X			
Epilobium alpinum						X	X		X
Epilobium glandulosum					X	X			X
Epilobium species	X			X	X	X			X
Epilobium watsonii					X	X			
Equisetum arvense					X				
Erigeron aliceae	X	X	X	X		X			
Eriogonum nudum	X			X					
Eriophyllum lanatum	X								
Erysimum arenicola	X			X					
Fragaria species		X		X	X	X	X	X	

Appendix D.1. Continued.

Species	Mesic Slopes				Hydric Basins				
	YM	OM	W1	W2	QA1	QA2	CF	CS	SC
Meadow Species									
Herbs									
Galium bifolium	X		X	X					
Galium trifidum					X	X	X	X	
Gentiana simplex							X		
Geum macrophyllum					X		X		
Gilia aggregata	X	X		X					
Gilia capitata	X								
Habenaria dilatata					X	X			
Heracleum lanatum					X				
Hieracium gracile	X	X							X
Hieracium scouleri	X	X		X					
Hydrophyllum capitatum	X								
Hydrophyllum occidentale			X	X					
Hypericum anagalloides					X	X	X	X	X
Iris chrysophylla	X			X					
Lathyrus nevadensis	X	X	X	X			X	X	
Ligusticum grayi	X	X	X	X	X	X	X	X	X
Linanthus bicolor	X			X					
Luetkea pectinata									X
Lupinus latifolius		X		X					X
Mertensia species					X				
Microseris alpestris		X							
Microseris boreale					X	X		X	
Microseris nutans	X								
Microsteris gracilis	X	X		X					
Mimulus guttatus					X		X		
Mimulus moschatus	X		X	X			X		X
Mimulus primuloides						X			

Appendix D.1. Continued.

	Mesic Slopes				Hydric Basins				
Species	**YM**	**OM**	**W1**	**W2**	**QA1**	**QA2**	**CF**	**CS**	**SC**
Meadow Species									
Herbs									
Montia parvifolia	X								
Montia sibirica	X	X	X	X					
Montia spathulata									X
Myosotis laxa			X						
Nemophila parviflora	X								
Orthocarpus imbricatus	X	X		X					
Pedicularis bracteosa					X	X			
Pedicularis groenlandica								X	
Penstemon procerus									X
Perideridia gairdneri							X		
Phacelia heterophylla	X	X	X	X					
Polemonium carneum	X	X							
Polygonum bistortoides					X		X		
Polygonum douglasii	X	X	X	X					
Polygonum minimum	X	X		X					
Polygonum phytolaccaefolium	X		X						
Potentilla drummondii	X		X		X	X	X	X	
Potentilla flabellifolia									X
Potentilla glandulosa	X	X		X		X			
Prunella vulgaris							X		
Pteridium aquilinum	X		X	X					
Ranunculus alismaefolius									X
Ranunculus flammula								X	
Ranunculus gormanii					X	X	X	X	
Rudbeckia occidentalis		X	X	X	X	X			
Sanicula graveolens	X			X					
Sedum spathulifolium	X								

Appendix D.1. Continued.

	Mesic Slopes				Hydric Basins				
Species	**YM**	**OM**	**W1**	**W2**	**QA1**	**QA2**	**CF**	**CS**	**SC**
Meadow Species									
Herbs									
Senecio triangularis					X	X	X	X	X
Sidalcea cusickii							X		
Sisyrinchium douglasii						X	X		
Spiranthes romanzoffiana						X	X	X	X
Spraguea umbellata									X
Stachys cooleyae		X	X	X	X				
Stellaria crispa		X			X				
Thalictrum occidentale	X				X				
Tofieldia glutinosa					X	X		X	
Trifolium longipes						X	X	X	X
Valeriana sitchensis					X	X	X		
Veratrum viride					X				X
Veronica americana					X				
Veronica scutellata							X	X	
Veronica serpyllifolia							X		X
Veronica wormskjoldii					X	X	X		X
Vicia americana	X	X	X	X			X	X	
Viola macloskeyi					X	X		X	X
Viola nuttallii		X					X		
Shrubs									
Betula glandulosa								X	
Haplopappus greenei		X							
Kalmia microphylla						X			
Kalmia occidentalis					X	X		X	
Phyllodoce empetriformis					X	X			
Rosa pisocarpa								X	
Rubus parviflorus	X		X	X					

Appendix D.1. Continued.

	Mesic Slopes				Hydric Basins				
Species	**YM**	**OM**	**W1**	**W2**	**QA1**	**QA2**	**CF**	**CS**	**SC**
Meadow Species									
Shrubs									
Spiraea densiflora					X	X		X	
Spiraea douglasii					X	X		X	
Vaccinium caespitosum					X	X		X	X
Vaccinium occidentale					X	X		X	
Unclassified species									
Sedges / Rushes									
Carex deweyana			X						
Luzula campestris	X	X			X	X	X		
Herbs									
Cystopteris fragilis	X								
Lilium columbianum	X		X						
Lycopodium sitchense					X				
*Rumex acetosella**	X	X		X					
*Taraxacum officinale**							X		
Viola adunca						X	X		
Shrubs									
Acer glabrum	X		X	X					
Alnus sinuata					X				
Amelanchier alnifolia	X	X					X	X	
Castanopsis chrysophylla						X			
Crataegus douglasii					X				
Lonicera ciliosa						X		X	
Rhanmnus purshiana	X			X		X			
Ribes lacustre				X					
Ribes lobbii	X	X		X					
Ribes sanguineum	X			X					
Ribes viscosissimum	X			X					

Appendix D.1. Continued.

	Mesic Slopes				Hydric Basins				
Species	**YM**	**OM**	**W1**	**W2**	**QA1**	**QA2**	**CF**	**CS**	**SC**
Unclassified species									
Shrubs									
Sambucus racemosa	X								
Sorbus sitchensis	X	X		X		X	X		
Trees Species									
Abies amabilis	X				X	X	X	X	X
Abies grandis	X	X	X	X		X	X		
Abies lasiocarpa	X	X			X	X	X		X
Abies procera							X		
Calocedrus decurrens		X							
Picea engelmannii		X			X	X	X	X	X
Pinus contorta		X					X	X	
Pinus monticola						X	X		X
Prunus emarginata						X			
Pseudotsuga menziesii	X	X		X			X		
Tsuga heterophylla						X	X		
Tsuga mertensiana					X	X	X		X

* exotic species

Appendix D.2. Species observed in subalpine forest-meadow ecotone transects in the Three Sisters Biosphere Reserve, Oregon. Species are grouped by habitat preference (meadow, forest, and unclassified) and growth form (grasses, sedges/rushes, herbs, and shrubs). Tree species were not classified. "X" indicates presence in a transect at one or more sampling dates (1983, 1993, or 2009). Asterisks denote non-native species. LW1 = Lowder Mountain 1, LW2 = Lowder Mountain 2, RR = Rebel, JC = James Creek, WP = Wickiup Plain, LM1 = Linton Meadow 1, LM2 = Linton Meadow 2, OF = Obsidian Flat, OC = Obsidian Creek, GL = Green Lake, RM = Racetrack Meadow. See Chapter 3, Table 1 for more details.

	Early Snowmelt									**Late Snowmelt**	
Species	**LW1**	**LW2**	**RR**	**JC**	**WP**	**LM1**	**LM2**	**OF**	**OC**	**GL**	**RM**
Forest Species											
Grasses											
Festuca occidentalis			X								
Trisetum canescens			X								
Trisetum cernuum			X								
Sedges / Rushes											
Luzula hitchcockii	X			X	X	X	X	X	X	X	X
Luzula parviflora	X									X	X
Herbs											
Anemone deltoidea			X								
Anemone oregana			X								
Arenaria macrophylla			X								
Arnica latifolia			X								
Arnica mollis										X	
Campanula scouleri			X								
Circaea alpina			X								
Corallorhiza species			X								
Galium oreganum			X								
Galium triflorum			X								
Goodyera oblongifolia			X								
Hieracium albiflorum	X		X			X					
Hypopitys monotropa	X										X
Listera caurina			X				X				X

Appendix D.2. Continued.

	Early Snowmelt									Late Snowmelt	
Species	**LW1**	**LW2**	**RR**	**JC**	**WP**	**LM1**	**LM2**	**OF**	**OC**	**GL**	**RM**
Forest Species											
Herbs											
Mitella breweri							X				X
Mitella trifida			X								
Monotropa hypopitys											X
Osmorhiza chilensis			X								
Osmorhiza occidentalis							X				
Pedicularis racemosa	X		X			X					
Pyrola picta			X								
Pyrola secunda						X	X				
Senecio cymbalarioides										X	
Smilacina racemosa			X								
Smilacina stellata			X								
Trillium ovatum			X								
Viola glabella			X								
Viola orbiculata	X										
Xerophyllum tenax			X								
Chimaphila umbellata			X								
Rubus lasiococcus	X		X	X		X	X		X		X
Vaccinium membranaceum			X			X	X		X		X
Vaccinium scoparium				X						X	X
Meadow Species											
Grasses											
Agrostis humilis				X							
Agrostis variabilis				X	X					X	X
Bromus carinatus			X								
Danthonia intermedia		X	X	X				X	X		
Deschampsia atropurpurea										X	X

Appendix D.2. Continued.

	Early Snowmelt									Late Snowmelt	
Species	**LW1**	**LW2**	**RR**	**JC**	**WP**	**LM1**	**LM2**	**OF**	**OC**	**GL**	**RM**
Meadow Species											
Deschampsia caespitosa									X	X	
Elymus glaucus			X			X					
Festuca viridula	X	X	X	X	X	X	X	X	X		
Phleum alpinum										X	
Sitanion hystrix				X	X	X		X	X	X	
Stipa occidentalis	X	X	X	X	X	X	X	X	X	X	
Sedges / Rushes											
Carex breweri					X						
Carex luzulina										X	
Carex microptera				X						X	
Carex nigricans							X		X	X	X
Carex pachystachya					X				X		
Carex pensylvanica	X	X	X	X		X		X	X		
Carex praeceptorum										X	
Carex rossii					X			X	X	X	
Carex scopulorum										X	
Carex spectabilis							X		X	X	X
Eleocharis pauciflora										X	
Juncus drummondii									X		
Juncus mertensianus										X	
Juncus parryi	X	X		X	X			X		X	X
Herbs											
Agoseris aurantiaca			X			X				X	X
Antennaria alpina										X	
Antennaria umbrinella								X			X
Arabis drummondii					X						

Appendix D.2. Continued.

	Early Snowmelt									Late Snowmelt	
Species	**LW1**	**LW2**	**RR**	**JC**	**WP**	**LM1**	**LM2**	**OF**	**OC**	**GL**	**RM**
Meadow Species											
Herbs											
Arabis holboellii			X								
Arenaria capillaris	X	X									
Aster alpigenus								X		X	X
Aster foliaceus			X	X		X	X	X		X	
Aster ledophyllus	X		X	X		X	X	X	X	X	
Calochortus subalpinus	X	X	X	X		X	X	X	X		
Castilleja arachnoidea					X			X	X		
Castilleja miniata											X
Cirsium callilepes			X								
Delphinium menziesii			X								
Dicentra formosa			X								
Epilobium alpinum										X	
Epilobium angustifolium			X			X					
Epilobium species					X		X				X
Epilobium watsonii			X				X				
Erigeron aliceae			X								
Eriogonum pyrolaefolium								X	X		X
Eriogonum umbellatum				X	X	X	X	X	X	X	
Erysimum arenicola			X								
Hieracium cynoglossoides			X								
Hieracium gracile				X	X		X	X	X	X	X
Lewisia pygmaea										X	
Ligusticum grayi	X		X							X	X
Lomatium martindalei				X		X				X	
Luetkea pectinata					X					X	X
Lupinus latifolius	X	X	X	X	X	X	X	X	X		X

Appendix D.2. Continued.

	Early Snowmelt									Late Snowmelt	
Species	**LW1**	**LW2**	**RR**	**JC**	**WP**	**LM1**	**LM2**	**OF**	**OC**	**GL**	**RM**
Meadow Species											
Herbs											
Lupinus lepidus										X	
Microseris alpestris	X	X		X	X	X	X	X	X		X
Microseris nutans			X								
Microsteris gracilis			X								
Montia sibirica			X								
Nemophila parviflora			X								
Orogenia fusiformis			X								
Pedicularis attolens										X	
Penstemon cardwellii			X								
Penstemon procerus					X					X	
Phacelia heterophylla			X								
Polygonum douglasii			X								
Polygonum minimum			X								
Polygonum newberryi				X	X	X	X	X	X	X	X
Polygonum phytolaccaefolium			X								
Potentilla flabellifolia											X
Pteridium aquilinum						X					
Ranunculus alismaefolius									X		
Senecio triangularis							X			X	
Spraguea umbellata	X			X	X		X	X	X	X	X
Stellaria obtusa										X	
Tofieldia glutinosa										X	
Valeriana sitchensis			X				X				
Veratrum californicum	X		X						X		
Veronica wormskjoldii										X	
Viola nuttallii			X	X		X		X			

Appendix D.2. Continued.

	Early Snowmelt									**Late Snowmelt**	
Species	**LW1**	**LW2**	**RR**	**JC**	**WP**	**LM1**	**LM2**	**OF**	**OC**	**GL**	**RM**
Meadow Species											
Shrubs											
Arctostaphylos nevadensis										X	
Cassiope mertensiana										X	X
Gaultheria humifusa										X	
Kalmia microphylla										X	
Phyllodoce empetriformis										X	X
Salix commutata										X	
Vaccinium caespitosum											X
Vaccinium occidentale										X	
Unclassified Species											
Sedges / Rushes											
Carex deweyana							X				
Luzula campestris	X	X									X
Herbs											
Erythronium grandiflorum		X	X								
Lycopodium sitchense										X	
Polemonium pulcherrimum						X					
Rumex acetosella	X										
Shrubs											
Acer glabrum			X								
Amelanchier alnifolia		X									
Ribes viscosissimum			X								
Sambucus racemosa			X				X				
Sorbus sitchensis	X		X			X				X	X

Appendix D.2. Continued.

	Early Snowmelt									Late Snowmelt	
Species	**LW1**	**LW2**	**RR**	**JC**	**WP**	**LM1**	**LM2**	**OF**	**OC**	**GL**	**RM**
Unclassified Species											
Shrubs											
Trees Species											
Abies amabilis	X	X	X				X	X			X
Abies grandis			X								
Abies lasiocarpa	X	X	X	X	X	X		X	X		
Abies procera			X								
Pinus albicaulis						X		X		X	
Pinus contorta				X						X	
Pinus monticola			X								
Pseudotsuga menziesii			X								
Tsuga mertensiana	X	X	X	X	X	X	X	X	X	X	X

VITA

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