Arctic and Alpine Research, Vol. 28, No. 1, 1996, pp. 52–59

Temporal and Spatial Distribution of Trees in Subalpine Meadows of Mount Rainier National Park, Washington, U.S.A.

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Abstract

Tree establishment patterns vary considerably at different locations in the subalpine zone of Mount Rainier National Park, with substantial temporal variation in regeneration of subalpine fir (*Abies lasiocarpa*). Recruitment in subalpine meadows has been continuous on the west side of Mount Rainier since about 1930, but has occurred in short, discrete periods on the east side. Variation in snowpack from west to east on the mountain has a substantial impact on climatic factors that limit tree establishment. Warm, dry summer climate facilitates tree establishment on the west side where snowpacks are generally very high; cool, wet summer climate enhances tree establishment on the east side where snowpacks are lower. Density of tree establishment is significantly greater in heath-shrub (ericaceous) vegetation than in other vegetation types. Within heath-shrub vegetation types, tree establishment is highest at lower elevations, on topographic convexities, and in plant communities dominated by *Phyllodoce empetriformis.* Survival of subalpine fir seedlings during the first 3 yr after germination is significantly greater in heath-shrub vegetation than other vegetation types. If the climate becomes warmer and drier during the next century, continued rapid regeneration of trees can be expected in subalpine meadows on the west side of Mount Rainier National Park. This may result in displacement of wildflower meadows that are an attraction for park visitors. A better understanding of climatic and environmental limitations on tree establishment will assist resource managers in developing sound management strategies for subalpine ecosystems.

Introduction

Visitors to the subalpine region of Mount Rainier National Park, in the early 20th century viewed a different landscape from that present today (Fig. 1). The ecotone between forest and meadow vegetation was more clearly defined and helped to establish the reputation of the park for spectacular summer floral displays in subalpine meadows. In fact, nearly half of the 2 million people who visit the park annually go to view wildflowers in the meadows (Johnson et al., 1991). The possibility that recent increases in tree establishment are related to climatic patterns (e.g., Rochefort et al., 1994) is relevant for understanding how subalpine ecosystems respond to climatic change and for resource managers responsible for managing these areas.

Tree establishment in subalpine meadows is frequently associated with changes in climatic patterns or human activity (Dunwiddie, 1977; Vale, 1981; Rochefort et al., 1994). Increases in tree establishment have been documented during summers with above average temperatures (Franklin et al., 1971; Henderson, 1974; Kearney, 1982; Agee and Smith, 1984), after termination of grazing (Dunwiddie, 1977; Vale, 1981), and following fire (which could be related to both climate and human activity; Agee and Smith, 1984; Little et al., 1994). Distribution of tree establishment across the landscape is influenced by vegetation type (Brink, 1959; Fonda and Bliss, 1969; Arno, 1970; Kuramoto and Bliss, 1970; Franklin et al., 1971; Henderson, 1974), topographic relief (Brink, 1959; Douglas, 1972; Lowery, 1972), microsite features (e.g. soils, woody debris; Agee and Smith, 1984; Woodward et al., 1995), and the source of ecotone perturbation. The source of ecotone perturbation may be the predominant influence on spatial distribution within a discrete site. Disturbances that create a meadow (or forest opening) often affect spatial distribution of regeneration within the area. For example, regeneration following a large fire or long periods of grazing typically occurs along the forest edge, gradually moving into an open meadow (Dunwiddie, 1977; Agee and Smith, 1984; Little et al., 1994). Tree establishment, within an existing meadow, following climate change is generally widespread within the meadow or landscape unit and controlled primarily by topography or vegetation type (Brink, 1959; Franklin et al., 1971; Douglas, 1972; Kearney, 1982).

In Mount Rainier National Park, the subalpine zone is characterized by a mosaic of tree clumps and open, herbaceous meadows. Depth and duration of snowpack are the predominant factors maintaining the meadows (Henderson, 1974) while meadow creation may have resulted from glacier recession or infrequent fires (Henderson, 1974). As a result, temporal variation in climatic factors that affect snowpack has the potential to influence spatial distribution of subalpine vegetation.

Tree establishment in the subalpine meadows of Mount Rainier National Park, resulting in an "altered" natural and cultural landscape for park visitors, has been a source of concern for park resource managers since the early 1960s. There are two chief questions relevant for the management of subalpine ecosystems and for park policy: (1) will increasing tree regeneration eventually displace flowers in the subalpine meadow, and (2) should the park preserve "natural" processes (allow tree regeneration) or a particular resource condition (open meadows with

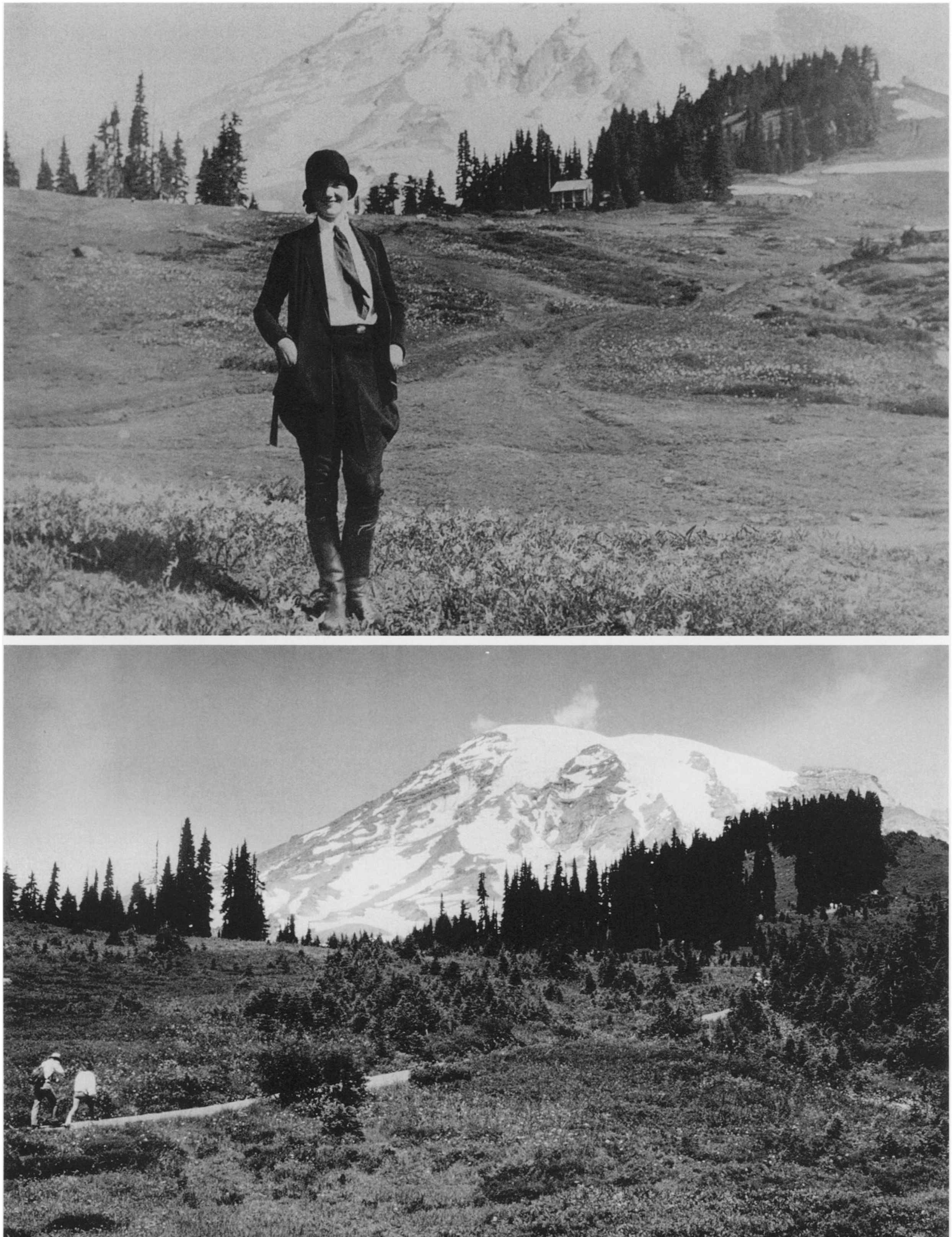

FIGURE 1. Photographs of the Paradise area of Mount Rainier National Park taken in 1929 (upper) and 1992 (lower). Note the prominence of recent tree establishment.

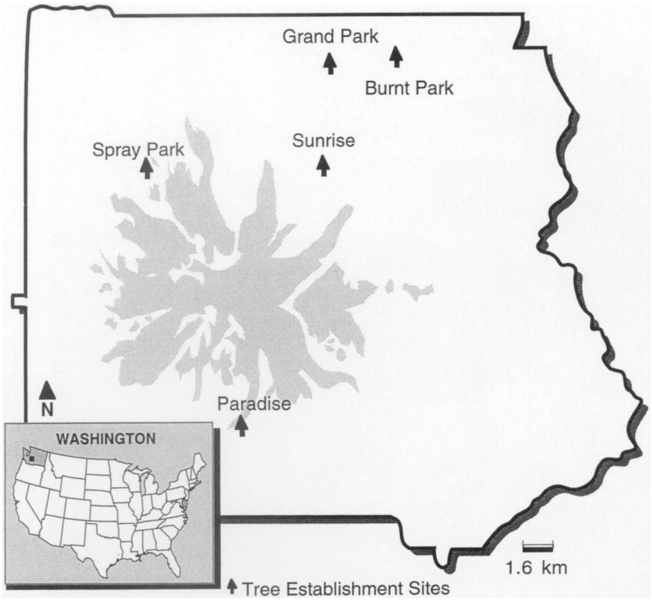

FIGURE 2. Location of study sites within Mount Rainier National Park.

flowers, which are valued by visitors)? Studies conducted in the 1960s demonstrated that most tree establishment had occurred during a warm, dry period from 1915 to 1940 (Franklin et al., 1966; Franklin et al., 1971). The National Park Service then embarked on a tree removal program in the Paradise area of Mount Rainier National Park, targeting areas where trees obscured scenic vistas or appeared to be displacing wildflowers. Although the tree removal program was terminated in 1979, the debate concerning preservation of natural processes, historic scenes, and cultural landscapes is becoming more prominent among resource managers and the public.

The subalpine ecosystem of Mount Rainier National Park has clearly been affected by both climate and human activities during the 20th century. In this study, we investigated tree establishment patterns at five locations in the subalpine zone of Mount Rainier National Park, representing variation in geographic location, climate, vegetation type, and landscape position. Specifically, we wanted to determine (1) whether tree establishment periods vary among subalpine meadows within the park, (2) whether factors limiting tree establishment vary over space and time, and (3) what might we expect the meadows to look like, with respect to trees, in the future. Increased understanding of current tree establishment patterns and local factors affecting tree establishment will improve our predictions of the future composition of the subalpine zone. This information can then be used to develop scientifically-based resource management decisions in response to potential climatic change and increasing demands for human use of park resources.

Methods

STUDY AREA

Study sites were located in five subalpine meadows within Mount Rainier National Park (Fig. 2). The park is located on the western slope of the Cascade Range, 100 km southeast of the Seattle-Tacoma metropolitan area. It encompasses 95,389 ha and extends from low elevation, old growth forest (530 m) through subalpine and alpine communities to the summit of Mount Rainier at 4400 m. Climate is temperate maritime with cool, wet winters and mild, dry summers. Most of the annual precipitation falls as snow between October and May. Limited climatic data indicate that precipitation generally is higher on the west side of the park, and increases with elevation up to about 3000 m.

Subalpine parkland covers approximately 23% of the park. Meadow vegetation of this zone can be described by five broad vegetation types (Henderson, 1974): (1) heath-shrub types dominated by one or two ericaceous species, including *Phyllodoce empetriformis, P. glanduliflora, Cassiope mertensiana,* and *Vaccinium deliciosum,* (2) lush herbaceous vegetation dominated by tall perennials including *Valeriana sitchensis, Lupinus latifolius,* and *Veratrum viride,* (3) low herbaceous vegetation dominated by *Potentilla flabellifolia* and *Antennaria lanata,* often with lesser amounts of *Carex nigricans,* (4) wet sedge types in low, wet areas dominated by *C. nigricans, C. spectablis, Aster alpigenus,* and *Antennaria lanata,* and (5) dry grass vegetation found on well-drained sites common on the east side of the park, dominated by *Festuca viridula* and *Lupinus latifolius.* The dominant tree species in the subalpine zone are *Abies lasiocarpa, Tsuga mertensiana,* and *Chamaecyparis nootkatensis. Pinus albicaulis* and *Picea engelmannii* are present on drier sites on the east side of the park.

Human activities have had limited influence on the subalpine ecosystem of Mount Rainier National Park. Grazing by sheep and cattle occurred in several areas on the east side of the park in the early 1890s prior to the establishment of the Pacific Forest Reserve in 1893. Once the reserve was created, it became illegal for stock to graze on federal lands, but it still continued to some extent due to lack of enforcement (Martinson, 1966). After the establishment of the park in 1899, grazing was limited to cattle in two areas during 1917–1919, use of milk cows in Paradise (1905–1910), and sheep for 2 yr (1931–1932) on the east boundary (McIntyre, 1952). Plant removal and soil erosion was so great from these practices that a survey completed in 1944 recommended that no additional grazing permits be issued in the event of a war emergency (Stagner, 1944). More recent influences on subalpine ecosystems include tree removals from the Paradise region of the park, as well as increased recreational use of this area (Rochefort and Gibbons, 1993; Rochefort and Peterson, 1993).

FIELD METHODS

Study sites were established in five subalpine meadows of Mount Rainier National Park in 1991: Spray Park, Paradise, Sunrise, Grand Park, and Burnt Park (Fig. 2). Sites were selected based on geographic location and weather patterns within the park. Paradise and Sunrise were selected because they were surveyed in the 1960s and we wanted to see if more recent periods of establishment had occurred since that time (Franklin et al., 1966; Franklin et al., 1971). The three additional meadows were chosen to expand the geographic scope of the Franklin study and to describe variation in patterns of establishment within the park. We concentrated on west versus east (rainshadow) sides of the park because weather patterns (precipitation and temperature) and vegetation vary significantly between the two sides. Two to five strip transects were established randomly within the predominant vegetation types of each meadow (Table 1). Strip transects were used to estimate tree density because visual observation indicated that tree density decreased with distance from clumps of large trees (trees approximately 20—30 m tall and 200 yr old). Transects were established in areas where there were no visible signs of fire (fire scars or charred trunks) or human use (tree cutting or bare ground) and in sites that had no recorded

TABLE 1

Description of study sites

Study site	Number of transects	Elevation (m)	Vegetation type[a]	Number of *Abies lasiocarpa* (number aged)
West-side meadows				
Spray Park	2	1770–1830	Heath-shrub	161 (83)
Paradise	5	1650–1900	Heath-shrub	661 (302)
			Low herbaceous	
			Lush herbaceous	
			Dry grass	
East-side meadows				
Sunrise	2	1950–2010	Low herbaceous	25 (25)
			Dry grass	
Grand Park	2	1700–1720	Heath-shrub	110 (51)
			Low herbaceous	
Burnt Park	3	1700–1770	Lush herbaceous	177 (98)
			Dry grass	

[a] See text for description of vegetation types.

history of grazing, tree cutting or development. Strip transects were 3 m wide and extended 60 m from the outer edge of mature tree clumps. Transects were divided into 3 m × 5 m blocks for ease in tallying trees. Within each block, tree species were identified, tree height and basal diameter were recorded, and every other tree was sampled for age determination. Seedlings and saplings (<5 cm basal diameter) were collected for age determination by cutting below the root collar. Seedlings were aged by counting terminal bud scars, and saplings were aged by counting rings on sanded basal disks; both counts were conducted under a dissecting microscope. Seedlings were generally trees with a basal diameter less than 2 mm, height less than 12 cm, and less than 15 yr old. Larger trees were sampled by collecting a core close to the root collar. Cores were finely sanded and annual rings counted under a dissecting microscope. Only tree cores that included the center of the tree were included for aging. All trees were aged by two individuals, and discrepancies were resolved by additional counts.

Analysis of our 1991 data revealed that more trees established in heath-shrub vegetation types than other vegetation types surveyed. Therefore, we wanted to look more closely at seedling survival patterns among vegetation types. *Abies lasiocarpa* seedlings germinating in 1992 were monitored for 3 yr to determine if survival rates of seedlings germinating in heath-shrub vegetation (*Phyllodoce empetriformis, P. glanduliflora, Cassiope mertensiana*) were significantly different from those germinating in other vegetation types. Eleven paired sites were established at the Paradise study site. In each site, 20 to 50 seedlings were tagged and monitored for survival from July 1992 until October 1994.

Surveys of heath-shrub communities were conducted in 1992 to determine if tree establishment within them is random with respect to landscape position and other environmental parameters. Forty-five circular plots (12.6 m^2) were randomly established in heath-shrub vegetation at the Paradise study site (1640 to 1920 m elevation). Random sample points were selected by placing a grid over a vegetation map of the Paradise meadow (approximately 390 ha). A random number generator was used to select coordinates for potential plots; all random locations falling within mapped ericaceous vegetation types were sampled. Within each plot, all trees were counted, identified to species, and height measured. Dominant plant association, slope, aspect, topography (convex, flat, concave), and landscape position (ridge, midslope, bench, valley bottom) were recorded. Vegetation was classified into one of four plant community types based on the dominant species: (1) *Phyllodoce empetriformis/Vaccinium deliciosum*, (2) *P. empetriformis/Lupinus latifolius*, (3) *P. empetriformis/Cassiope mertensiana*, (4) *P. empetriformis*.

DATA ANALYSIS

Tree establishment and climatic data were summarized by 5-yr intervals for the 1930–1990 time period. Five-year periods were used to examine these relationships because successful tree establishment depends on climatic factors during at least 3 yr after germination (Cui and Smith, 1991; Jakubos and Romme, 1993). In addition, we recognized that germination dates could be miscalculated by several years due to missing rings and the difficulty recognizing terminal bud scale scars (Henderson, 1974; Little et al., 1994; Miller, 1995). Data analysis focused on the 1930–1990 period, for which climatic data was nearly complete.

Stepwise multiple regression was used to examine the relationship between climate and tree establishment. Numbers of trees established were summed for each period, and climatic variables were averaged. Counts of tree establishment were transformed using a square root transformation to stabilize the variance. Climatic variables included monthly average temperature (May through October) and total precipitation (May through September) (Paradise Ranger Station, Mount Rainier National Park database), and monthly Palmer Drought Severity Index (PDSI) (state of Washington Division 4 data from the National Climatic Data Center database). Spring PDSI was the average value for May-June, while summer PDSI was the average value for July–August. The effect of snowpack on tree establishment was investigated by using snow depth at Paradise on 15 May (Paradise Ranger Station, Mount Rainier National Park database). Data missing from these records were previously estimated by Little (1992) using standard techniques (Paulhus and Kohler, 1952; MacDonald, 1957). Selection of climate variables for analysis was based on the assumption that seed germination and survival of seedlings are most influenced by growing season length, temperature, and precipitation. Relationships with winter weather were not examined because snow generally covers seedlings from November through May.

Tree density by vegetation type was compared using data from all established strip transects. Blocks along each transect were numbered from 1 to 12 indicating their distance from mature trees. The number of blocks sampled in each vegetation type was then tallied by distance class. A chi-square analysis was performed to determine if the sampling distribution among vegetation types was homogeneous with respect to distance from a tree clump (seed source). Tree density for each 3 m × 5 m subplot was tallied and categorized by vegetation type. Data were transformed using the log $(x + 1)$ transformation (Zar, 1984) because the variances were positively skewed. Analysis of variance was then used to compare tree densities within four vegetation types: heath-shrub, lush herbaceous, low herbaceous, and dry grass. The wet sedge vegetation type did not have a large enough sample size to include in the analysis. Following rejection of the null hypothesis of equal mean tree densities among the four vegetation types, multiple comparisons were made using the Tukey HSD test ($p = 0.05$).

Seedling survival was analyzed by performing a paired *t*-test comparing percent survival of seedlings inside and outside heather at annual intervals. Mean differences between 11 paired

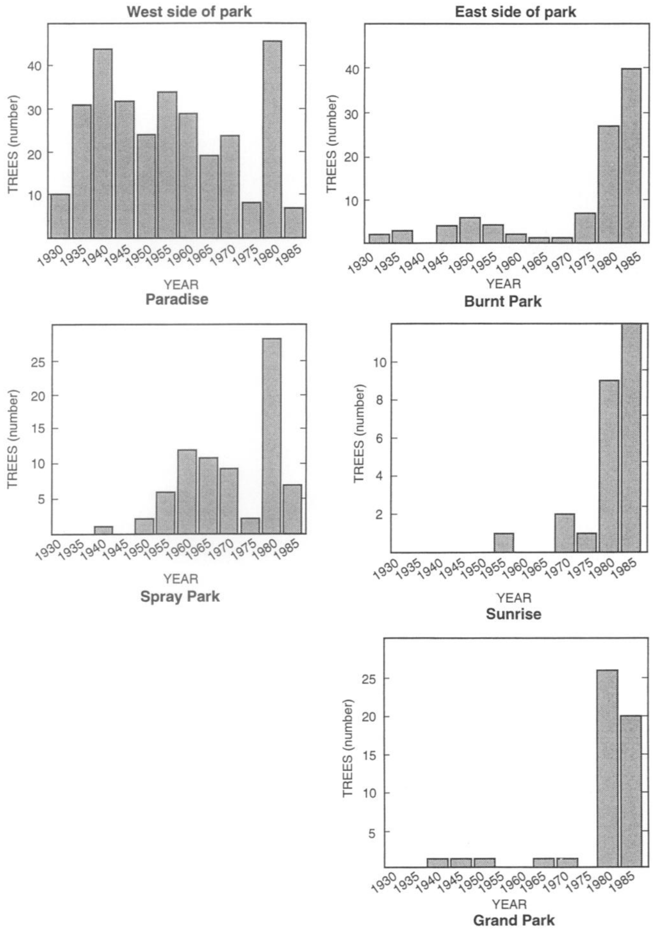

FIGURE 3. Histograms of Abies lasiocarpa *establishment in five subalpine meadows of Mount Rainier National Park.*

plots were used for analysis in 1992 and 1993, but only 9 pairs were used in 1994 due to removal of tags by animals that summer.

Discriminant analysis was used to identify important factors associated with successful tree establishment in heather communities. Predictor variables were categorized using a binary dependent variable (i.e., "0" if no *A. lasiocarpa* were observed in the plots, "1" if one or more *A. lasiocarpa* were observed). Prediction potential of the classification criteria was evaluated using a cross-validation (jackknife) procedure (SAS, 1988). Discriminant coefficients were examined to identify the direction of the relationship between predictor variables and the dependent variable. Class means were then compared with an ANOVA to identify significant differences.

Results

GEOGRAPHIC DISTRIBUTION AND CLIMATIC INFLUENCES

Four tree species were inventoried at the study sites: *Abies lasiocarpa, Picea engelmannii, Pinus albicaulis,* and *Tsuga mertensiana.* The vast majority of trees were *A. lasiocarpa*; sample sizes of other species were too small to examine differences between species. All species were aggregated for vegetation type analysis, but only *A. lasiocarpa* individuals were used for the remaining analyses.

Histograms of tree establishment by 5-yr intervals (Fig. 3) indicate that periods of peak establishment (greater than 10% of all establishment in a meadow) varied between study sites. Paradise meadows exhibited continuous recruitment between 1930 and 1990, with peaks in establishment during three periods: 1935–1950, 1955–1960, and 1980–1985. Spray Park also had long periods of tree recruitment: 1960–1975 and 1980–1985. Meadows on the east side of the park were characterized by shorter periods of establishment than Paradise or Spray Park. All three meadows had establishment peaks during the 1980–1990 period. Additional establishment occurred at Burnt Park from 1945 to 1980.

TABLE 2

Summary of multiple regression between square-root transformed number of trees established and climatic variables. The sign of the regression coefficient is listed as positive (+) or negative (−). Adjusted r^2 *of the regression model is listed for each study site.*

Study site	Climatic variable, *p* value	Adjusted r^2
West-side meadows		
Spray Park	Summer PDSI (−), 0.005	0.51
Paradise	May precipitation (+), 0.036	0.76
	June precipitation (+), <0.001	
	July temperature (+), 0.019	
East-side meadows		
Sunrise	July temperature (−). 0.001	0.62
Grand Park	July precipitation (+), 0.063	0.69
	July temperature (−), 0.014	
	August PDSI (−), 0.005	
Burnt Park	July temperature (−), 0.002	0.60
	October temperature (+), 0.069	

Results of regression analysis also show variation among study sites and climatic factors associated with tree establishment (Table 2). May and June precipitation and July temperatures were positively correlated with establishment at the Paradise meadows. Summer PDSI is negatively correlated with tree establishment at Spray Park. July temperature is negatively correlated with establishment at Burnt Park, while October temperature was positively correlated. Cool, wet July conditions are correlated with establishment at Grand Park as indicated by a positive correlation between July precipitation and establishment and a negative correlation between July temperature and establishment. In addition, August PDSI is negatively correlated with tree establishment. Tree establishment at Sunrise is negatively correlated with July temperature as was establishment in Burnt and Grand Parks.

VEGETATION TYPE

Homogeneity of sample plot distribution with respect to distance from seed source is not significantly different among vegetation types ($\chi^2 = 8.74$, df = 15, $p = 0.89$). ANOVA indicates that tree density is significantly different among vegetation types (F = 9.29, df = 139, $p < 0.001$). Multiple comparisons (Tukey HSD) reveal that density of tree establishment in heath-shrub communities was significantly greater than density of establishment in the other three vegetation types surveyed (Fig. 4).

SEEDLING SURVIVAL

Seedling survival is significantly different between trees that established within heather communities and those that es-

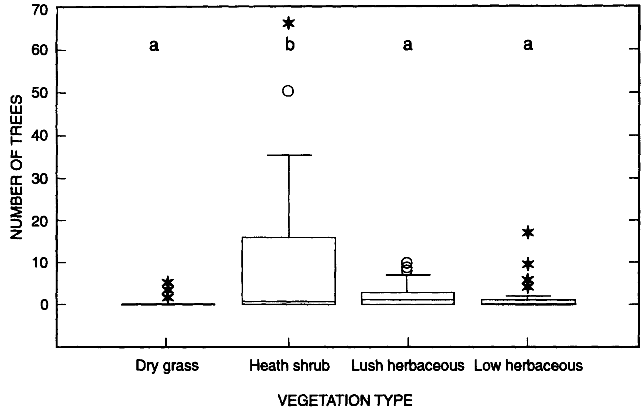

FIGURE 4. Boxplot illustrating density of tree establishment within four vegetation types. Values within the box represent 50% of the quadrats surveyed, the horizontal line in the box illustrates the median, and outliers are illustrated by asterisks and circles. Vegetation types with different lower case letters are statistically different at the p *= 0.001 level.*

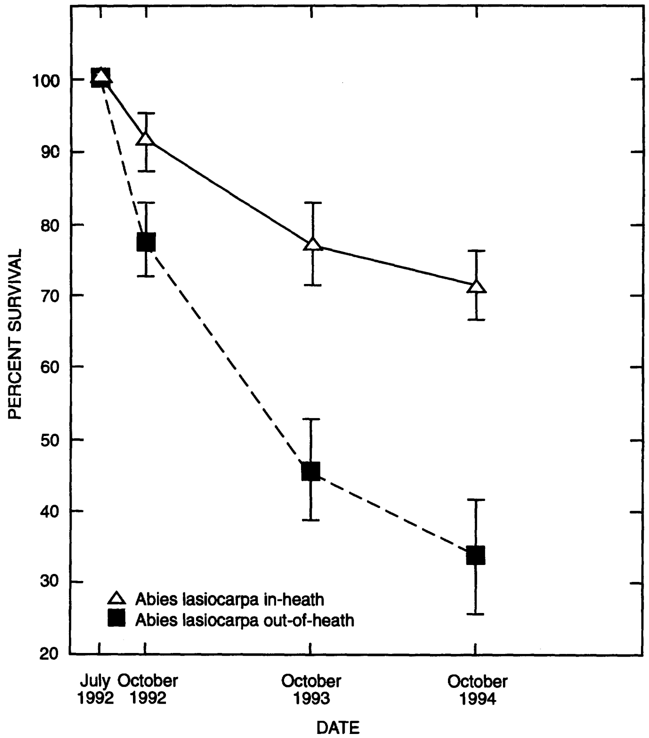

FIGURE 5. Mean survival and standard error of Abies lasiocarpa *seedlings in heath and other vegetation types.*

tablished in other vegetation types (Fig. 5). *T*-value and associated probabilities for each year are: October 1992, $t = 2.19$, $p = 0.053$; October 1993, $t = 3.65$, $p = 0.004$; and October 1994, $t = 4.48$, $p = 0.002$. Seedling survival was lower for trees germinating outside heather communities than within and survival continued to decrease for both sites during the 3 yr of the study.

LANDSCAPE POSITION

Surveys of tree establishment in heath-shrub communities documented 287 trees in 28 of the 45 plots; 17 plots had no trees. Three tree species were inventoried: *Abies lasiocarpa* ($n = 243$), *T. mertensiana* ($n = 42$), and *Chameacyparis nootkatensis* ($n = 2$). Discriminant analysis indicates that topographic position, elevation, and the dominant meadow species are the most important factors influencing tree establishment in heather communities. More trees are established on convex surfaces than on concave surfaces. Tree establishment is negatively associated with elevation. Tree density is greatest in *Phyllodoce empetriformis/Vaccinium deliciosum* communities followed by *P. empetriformis/Lupinus latifolius, P. empetriformis/Cassiope mertensiana,* and *P. empetriformis.* Examination of class means indicates that means are significantly different for topographic position ($p = 0.008$), elevation ($p = 0.004$), and dominant meadow plants ($p = 0.019$). Classification cross-validation indicates the model has a predictive capability of 67%.

Discussion

The response of subalpine tree establishment to climate at Mount Rainier National Park varies spatially and temporally. In general, recruitment in subalpine meadows has been fairly continuous on the west side of the park, but has occurred in short, discrete periods since 1930 on the east side. This pattern corroborates the findings of other recent studies (Little et al., 1994; Miller, 1995) and suggests that local climatic variation is an important factor in tree establishment.

Subalpine meadows on the west side of the park are generally wetter than those on the east side and have deeper snowpack of longer duration. Increased precipitation in May and June, in Paradise, may be important for seedling survival by ensuring adequate soil moisture (Evans and Fonda, 1990) and by increasing the length of the growing season through increased snow melt by rain-on-snow events. Higher temperatures in July, in Paradise, are necessary to complete snow melt and enhance germination and growth. The most significant climate variable enhancing tree establishment in Spray Park was the negative coefficient for summer Palmer Drought Severity Index. Although both higher July temperatures and negative PDSI coefficients both reflect dry summer conditions, the difference in indicator variable between parks may result from slightly different site characteristics. Spray Park receives similar amounts of snow as Paradise, but snow melt is generally slower due to a more northerly aspect and undulating topography with many snowbanks protected from insolation resulting in slightly wetter conditions than Paradise. Although PDSI values during successful periods of establishment were negative, they were generally between 0 and -0.5, indicating moderately low soil moisture but not droughty conditions stressful to seedling survival (Palmer, 1965). The significance of higher July temperatures and mild summer droughts in the regression model indicates that warm summers are important for tree establishment at sites that generally experience cool, short summers (Brink, 1959; Franklin et al., 1971; Douglas, 1972; Kearney, 1982; Agee and Smith, 1984; Woodward et al., 1995).

In east side subalpine meadows, hot and dry summers may prevent tree establishment. East side meadows generally receive less snow, and snowpack melts earlier than on the west side (Hamann, 1972; Henderson, 1974). Vegetation types are dominated by *Festuca viridula, Potentilla flabellifolia,* and *Antennaria lanata,* growing on well-drained soils with high pumice content (Ahlstrand, 1973; Henderson, 1974). The dominant plant species are deciduous perennials, indicating early season conditions characterized by high insolation and fluctuations in soil temperature. Wet July conditions are probably important because they ameliorate potentially high soil temperatures and low soil moisture which would be lethal to young seedlings (Baig, 1972; Ballard, 1972; Douglas, 1972). Cool, mild early season conditions followed by a long growing season (as indicated by high October temperatures in Burnt Park) appear to provide optimal conditions for subalpine tree establishment in meadows on the east side of Mount Rainier.

Tree establishment is influenced locally by vegetation type, topographic variation, and landscape position. Most trees are established in heath-shrub communities, potentially reflecting: longer growing season due to topographic convexities (Brink, 1959; Arno, 1970; Brooke et al., 1970), moderate soil temperature and moisture conditions in summer due to shading by evergreen foliage or woody stems (Baig, 1970; Ballard, 1970; Douglas, 1972; Weisberg and Baker, 1995), potential ectomycorrhizal infection from ericaceous species (Cui and Smith, 1991), and favorable retention and germination of dispersed seeds. Amelioration of site conditions, through control of soil moisture and temperature, is especially critical during the first 2 to 3 yr after germination (Day, 1964; Knapp and Smith, 1982; Soll, 1994).

Cui and Smith (1991) monitored mortality of *A. lasiocarpa* seedlings in shaded and unshaded sites for 3 yr following germination in the Medicine Bow Mountains, Wyoming. They found that seedling survival was greater on shaded microsites and that most mortality occurred during the first year on both sites; seedlings died at a lower rate during the second year. Our results follow a similar trend, with seedling survival significantly higher in heather (shaded) sites than in other vegetation types. Dominant vegetation on the nonheather sites includes *Lupinus latifolius, Carex spectablis,* and *Valeriana sitchensis,* all deciduous species which allow relatively high radiation at the soil surface during germination of *A. lasiocarpa* seeds. Unlike the pattern found by Cui and Smith (1991), highest mortality at Mount Rainier National Park occurred during the second year after germination which may reflect generally milder summer conditions than occur in the Medicine Bow Mountains.

Soll (1994) studied germination and first-year seedling survival of *A. lasiocarpa* in the Olympic Mountains, Washington. He found that although seed germination was lowest in ericaceous (*Vaccinium*) communities (lichen > rush > sedge > *Vaccinium*), percentage seedling survival was greatest in ericaceous communities. Mortality during the third year after germination (an extremely dry year) was high but significantly less in ericaceous communities than in other plant associations where soil conditions were drier (Soll, pers. comm.). Although our third year of monitoring coincided with Soll's, we did not observe a similar large increase in mortality, probably because the Olympic Mountain sites have much lower precipitation than the Mount Rainier region.

Tree establishment within heath-shrub vegetation types at Mount Rainier National Park is generally greater on topographic convexities, at lower elevations, and in communities dominated by *Phyllodoce empetriformis* (rather than *Cassiope mertensiana*). These patterns of tree establishment are especially prominent at the Paradise study site, for which we have the most observations. Tree densities are greatest in the lower meadows (1600–1750 m) and on convex surfaces; trees are rarely seen in *C. mertensiana* communities. Convex surfaces generally melt out faster and provide warmer, drier microsites and a longer effective growing season. *Phyllodoce* communities, especially those dominated by *P. empetriformis,* tend to occupy sites with warmer soils than other heather communities (Edwards, 1980). In addition, *A. lasiocarpa* is more tolerant of warm, dry microsites than are associated subalpine tree species (Day, 1964). Unfortunately we do not have microenvironmental data to confirm apparent relationships between characteristics of the physical and biotic environment. However, our results corroborate Henderson's (1974) successional interpretation that *Phyllodoce/Vaccinium* communities are frequently a seral stage to subalpine forests.

Conclusions

Interpreting patterns of tree establishment at different levels—local and park-wide—provides a more complete understanding of the dynamics of subalpine meadows of Mount Rainier National Park. Density of tree establishment is generally greatest in heath-shrub communities where slightly elevated ground surfaces provide a longer growing season, and shade moderates soil temperature and moisture. The conditions provided by heath-shrub communities are most beneficial to seedling establishment on the west side of the park where cool summer temperatures and short growing seasons (snow-free period) limit regeneration. Relatively warm, dry summers encourage regeneration and heath-shrub communities modify extreme conditions. In contrast, tree establishment on the east side of the park is limited by high soil temperatures and low soil moisture; regeneration is encouraged by cool, wet summers. These patterns suggest that regeneration is most successful under "mesic" conditions, when limiting factors are ameliorated by the appropriate climatic conditions. Similar patterns of regeneration have been found for other subalpine ecosystems of the Pacific Northwest (Agee and Smith, 1984; Little et al., 1994; Miller, 1995; Woodward et al., 1995).

A warmer, drier climate during the 20th century (compared to the Little Ice Age) has favored tree establishment in meadows on the west side of Mount Rainier National Park, while limiting tree establishment on the east side. If these warmer climatic conditions persist, or if the climate becomes even warmer as predicted for the next century (e.g., Mitchell et al., 1990), we can expect continued rapid regeneration of *Abies lasiocarpa* on the west side of the park, with additional displacement of subalpine meadows by trees.

Acknowledgments

We thank Ann Bell, Brendan Brokes, Chris Chappell, Eric Dolven, Bob Gendron, Shane Gibbons, Taylor Gibbons, David Larson, Pat Milliren, Bill Moe, and Kathryn Uziel for assistance with field surveys and Darcy Horner, Bob Gendron, David Larson, Eric Miller, Bill Moe, and Herb Vogel for assistance with tree sample preparation and aging. We also thank Dr. Loveday Conquest for statistical advice, Beth Rochefort for developing the graphics, and Steve Gibbons, Charlie Halpern, Peter Weisberg, Andrea Woodward, and an anonymous reviewer for helpful comments on the manuscript. This research was supported by Mount Rainier National Park and the US National Park Service Global Climate Change Program.

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Ms submitted June 1995