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Spruce and Fir Regeneration and Climate in the Forest-Tundra Ecotone of Rocky Mountain National Park, Colorado, U.S.A.

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Abstract

As an ecological boundary zone, the forest-tundra ecotone is a valuable location to study the initial response of vegetation to global climate change. The purpose of this study is to predict the potential response of the forest-tundra ecotone in Rocky Mountain National Park to future climate change using data on historical episodes of establishment in patch forest openings of the forest-tundra ecotone. We hypothesized that recent seedling establishment in patch forest openings of the forest-tundra ecotone, not balanced by mortality, was triggered by a warm, but wet period following the end of the Little Ice Age ca. A.D. 1850. At four sampling locations distributed throughout the Park, we determined dates of establishment among patch forest trees using increment cores and basal disks. We studied the relationship between establishment dates in relation to historical climate records using *t*-tests and logistic regression. In Rocky Mountain National Park, tree invasion in patch forest openings is episodic in nature, concentrated between 1951–1964, and is not balanced by mortality, suggesting more than a short-term change in the ecotone. On the basis of the climate record, *t*-tests, and logistic models, we concluded that both high temperatures and high snow depths must occur simultaneously for several years in order to generate climatic conditions suitable for tree establishment. The historic climate record indicates that a warmer and wetter period occurred during the 1950s and 1960s, but climate data are unavailable before 1880. According to proxy climate records, it appears that the regional climate of the southern Rocky Mountain region has been both warmer and wetter since the end of the Little Ice Age (ca. A.D. 1350–1850). We conclude that these climatic conditions may be related to the tree invasion we observed in patch forest openings of Rocky Mountain National Park.

Introduction

The North American forest-tundra ecotone, as the ecological gradient between alpine tundra and closed canopy forest, has responded to climatic changes in the past (Andrews et al., 1975; Fall, 1988; Lloyd and Graumlich, 1993) and may respond to predicted temperature changes in the next few decades. Changes in the extent and area of the forest-tundra ecotone and alpine vegetation, as well as changes in fire regime and alterations of forest structure may occur due to future climate variation (Romme and Turner, 1991). These changes may have serious implications for both wildlife and plant species diversity on public lands. Rocky Mountain National Park contains 367 km² of forest-tundra ecotone (Baker et al., 1995). Potential changes in climate and resulting changes in vegetation would alter the ecological composition of Rocky Mountain National Park.

Broadly speaking, temperature is the primary factor controlling the elevation of treeline (Daubenmire, 1954; Tranquillini, 1979). The 10°C mean July isotherm is considered to be the lower temperature limit below which trees are unable to maintain a positive carbon balance (Griggs, 1946; Daubenmire, 1954; LaMarche and Mooney, 1967). However, alpine treeline does not follow the 10°C isotherm exactly (Tranquillini, 1979), suggesting that there are a variety of other factors, in addition to temperature, controlling the position and form of treeline. Among these are snow depth and duration, wind, and physical damage asso-

ciated with microenvironmental conditions. However, like temperature, all of these factors are climatically induced, and may be approximated using meteorological data.

While recent seedling establishment above treeline has been noted in only a few regions (Daly and Shankman, 1985), seedling establishment in the subalpine zone, just below treeline, has been extensively described in Northern Europe (Hustich, 1958; Kullman, 1986, 1987, 1992), New Zealand (Wardle and Coleman, 1992), Canada (Brink, 1959; Kearney, 1981), Washington and Oregon (Franklin et al., 1971; Little and Peterson, 1994; Woodward et al., 1995; Rochefort and Peterson, 1996), Wyoming (Dunwiddie, 1977), and California (Vale, 1987; Taylor, 1995). Although changes in fire regime and grazing pressure have been proposed as explanations for widespread seedling establishment in some regions, climate change has become the primary explanation for this phenomenon (Rochefort et al., 1994).

In Rocky Mountain National Park, both widespread seedling establishment in patch forest openings and significant leader growth of krummholz trees have been observed (Weisberg, 1994; Weisberg and Baker 1995a, 1995b). Establishment and leader growth appear to be in excess of seedling and leader mortality, suggesting a potential for change in the ecotone. Though these patterns are broadly consistent with current ideas regarding forest-tundra ecotone expansion and climate change, the timing and causes of recent establishment and leader growth remain

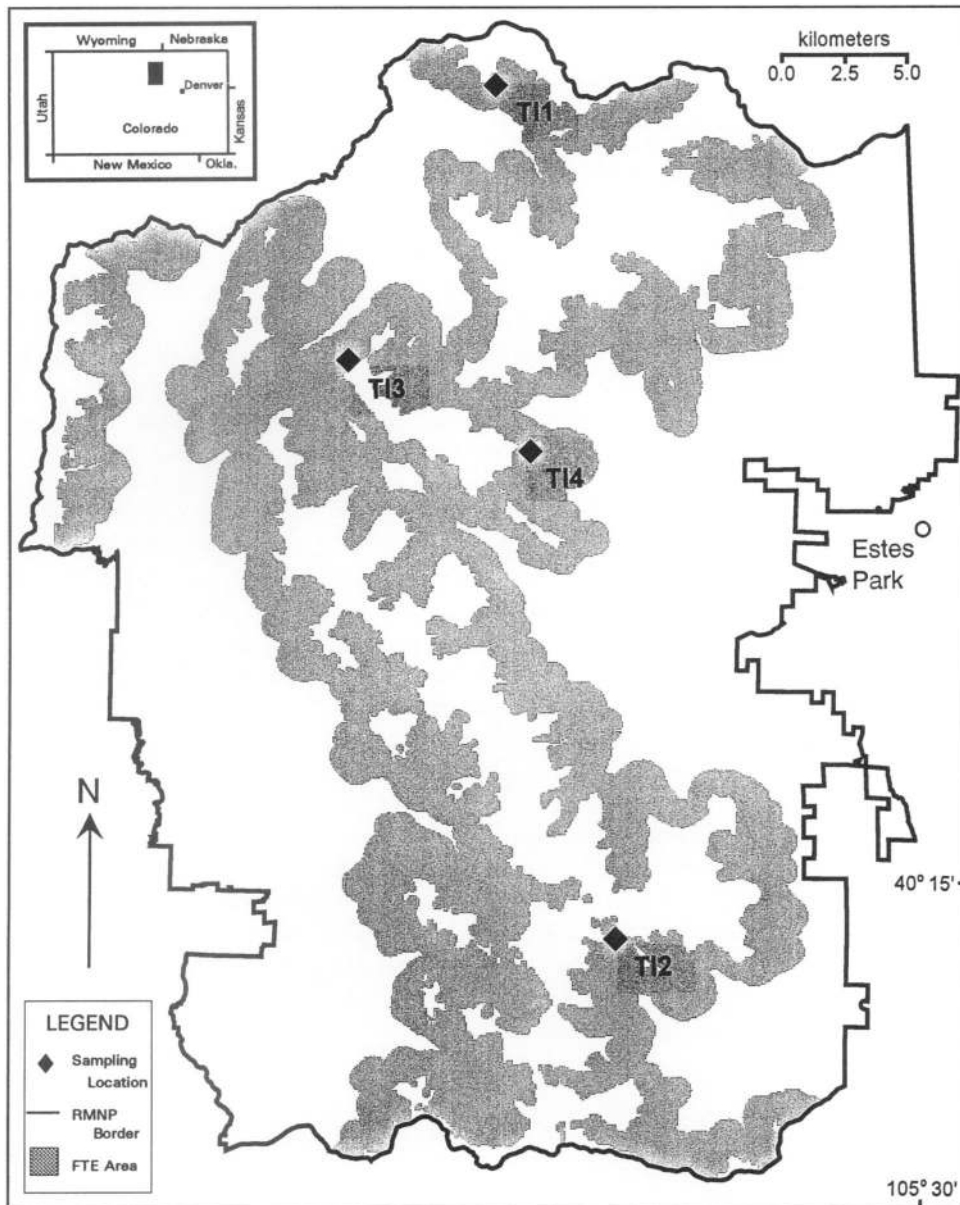


FIGURE 1. The four sampling locations in Rocky Mountain National Park, Colorado.

unclear, as Weisberg's work focused on spatial rather than temporal variation in the ecotone.

We hypothesized that recent seedling establishment in patch forest openings of the forest-tundra ecotone, not balanced by mortality, was triggered by a warm, but wet period following the end of the Little Ice Age ca. A.D. 1850. By investigating recent changes in regeneration of spruce-fir forest in the forest-tundra ecotone of Rocky Mountain National Park, we use historical patterns of vegetation change to predict the potential response of the forest-tundra ecotone to future climate change.

Study Area

The study area includes four sampling locations within the forest-tundra ecotone of Rocky Mountain National Park, Colorado (Fig. 1). Baker et al. (1995) divided the ecotone into four ecological zones based on the physical structure of the forest: closed forest, patch forest, krummholz, and tundra zones. The patch forest zone consists of patches of symmetrical trees interspersed with herbaceous or shrubby openings (Weisberg, 1994).

It is in these openings that Weisberg (1994) observed widespread seedling establishment in the Park.

The climate of the Colorado Front Range is predominantly continental, with most precipitation occurring as snow in winter (Barry, 1973). A second precipitation maximum, generated by localized convective activity and the Mexican Monsoon, occurs in summer. Forest vegetation in the forest-tundra ecotone of Rocky Mountain National Park consists primarily of coniferous forest dominated by *Picea engelmannii* Parry and *Abies lasiocarpa* (Hook.) Nutt. with occasional stands of *Pinus flexilis* James occurring only in the most xeric sites (Peet, 1981). The study area is almost completely underlain with Silver Plume granite, gneiss, and biotite schist (Braddock and Cole, 1990).

Methods

SAMPLING DESIGN

A subset of four sampling locations (T11-T14) was chosen from Weisberg's sample of 36 based on the abundance of tree regeneration in the patch forest openings (Weisberg, 1994) (Fig.

1). Sampling locations range in elevation from 3414–3511 m. Slopes were moderate, ranging from 7 to 22°. Aspects were variable, ranging from 111 to 335°. In each of the four patch forest sampling locations we placed three belt transects at the same elevation across the slope. Each belt transect was located within a representative patch forest opening containing at least 150 invading trees. Invading trees are less than half the height of the tallest trees in the surrounding patches. We used a belt transect of variable length and width in order to include at least 150 trees in each. General characteristics such as elevation, slope, aspect, understory species, moisture level, and an ocular estimate of percent cover of rock, bare ground, and shrubs were measured and recorded for every belt transect. In addition, we looked for evidence of recent fire on the surface of the soil (e.g., charcoal), and on surrounding trees (e.g., fire scars), in and around each belt transect.

Within each belt transect, we tallied all live and dead trees by species and by 13 height classes (from less than 10 cm to greater than 400 cm) to determine tree density and percent mortality. To develop an age structure for the patch forest opening trees and determine any microenvironmental characteristics associated with age, 25 trees from each belt transect (for a total of 75 trees per sampling location) were randomly chosen to sample more intensively. Tree species, height, and percent and type of damage (i.e., snow, wind, snow mold, or none) were recorded for each tree sampled. Percent damage was used to determine whether these trees have established successfully or whether they represent only an ephemeral change in the ecotone. To estimate the microenvironment of each tree, we recorded the microtopographic position of each tree (low, medium, or high) and its relative exposure (protected or exposed). In addition, we recorded, by ocular estimate, the immediate habitat of each tree as hydric, mesic, or xeric (scale of 1 to 3), and any shrub species located within a 0.5 m radius of the tree bole. The species identity of associated shrubs may be indicative of the local moisture regime and, along with other microenvironmental variables, may be related to the successful establishment of individuals (Weisberg, 1994). A basal disk or core was collected from each of the 25 trees sampled from each transect and brought back to the laboratory where they were mounted, sanded, and aged. We also examined a 1.0-m-wide transect along the centerline of each belt transect to search for very young live and dead "seedlings." These seedlings were also brought back to the laboratory, mounted, sanded, and aged in the laboratory.

Dates of tree establishment were determined from the basal disks and cores collected from patch forest sites. All cores and basal disks were processed in the laboratory according to standard dendrochronological procedures (Stokes and Smiley, 1968). A binocular scope was used to count annual rings. Cross dating was not performed due to the young age of the trees. Disks were sliced into 6 to 10 sections, 5 mm wide, which were all counted. The highest ring count was accepted as the age of the tree. Estimated year of establishment was determined for samples without pith (43 of 297) by geometrically estimating the number of rings required to reach the pith. Tree ages were not compiled into classes for analysis because most samples had the pith present, and aggregating the data into classes would remove much of the resolution in climatic variables. However, samples were grouped into age classes for figures to simplify graphical presentation.

CLIMATE DATA

Monthly precipitation and temperature records are available from Estes Park, Colorado, just outside the park; however the

climate station was moved several times during the early part of its record, and data from this station are unreliable (Doesken, pers. comm., 1996). Monthly temperature records were instead taken from Fort Collins, Colorado (NOAA, Climatological Data, Colorado), approximately 45 km northeast of Rocky Mountain National Park at an elevation of 1525 m. These temperature records were highly correlated with Estes Park records ($r > 0.69$, $P < 0.000$ for all seasonal and annual temperatures). Monthly temperature records were compiled into seasonal averages to reduce the number of variables necessary for analysis of years of successful seedling establishment. Precipitation data from Fort Collins were not used in the analysis, because precipitation is locally variable, and there is considerable distance and difference in elevation between the Fort Collins climate station and the sampling locations. A 5-yr running mean of annual temperature was compiled for 5-yr periods following each year of potential establishment. Successful establishment of subalpine fir trees may be dependent on the climate for at least 2 yr following establishment (Cui and Smith, 1991). Monthly snow depth data for February–May from the Natural Resource Conservation Service SNOWTEL monitoring station in Wild Basin were also used. Missing data were estimated from a calculated regression relationship between the Wild Basin station and the nearby Hidden Valley station (Dunne and Leopold, 1978). Monthly snow depths were summed to form a relative index of snow depth for February–May. This index was also compiled into a running mean for the 5 yr following years of potential establishment of invading trees.

STATISTICAL ANALYSIS

Histograms of tree ages by species for each site were constructed in order to determine whether establishment was episodic or regular throughout the Park, and whether temporal patterns in tree establishment could be related to the microenvironmental conditions present at each site. Finally, climatic conditions were related to years of successful tree establishment using *t*-tests and where possible, logistic regression (Hosmer and Lemeshow, 1989). Because tree establishment that has occurred during the last 5 yr is difficult to detect due to small seedling sizes, and because recently established trees may not necessarily represent successful regeneration over time, only trees that established before 1990 were included in this part of the analysis. In order to determine which climatic factors were associated with tree regeneration *t*-tests were performed.

Logistic regression was chosen as a statistical technique over classical regression in order to eliminate the influence of years with a high rate of establishment on the regression equation. Six models with binary dependent variables (1 = at least one tree established, 0 = no trees established) were developed. These models were derived from two subsets of available climatic data; a long-term record (1882–1989) which includes only temperature, and a short-term record (1936–1989) which includes both temperature and snow depth variables. Snow depth data were only available for the short-term record. For both periods of record, we generated three models, each with a different response variable; pooled spruce and fir, spruce alone, and fir alone.

To choose climatic variables to enter each model, we used the significance of univariate *t*-tests comparing variable values during years of establishment with values during years of no establishment. Significant variables ($P < 0.10$) were then tested for multicollinearity using correlation analysis. Because some of the independent variables for predicting long-term fir establish-

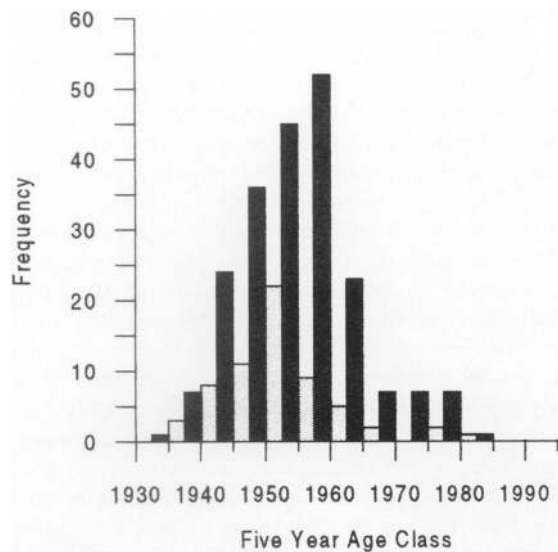


FIGURE 2. Frequency of Engelmann spruce (dark bars) and subalpine fir (light bars) establishment in five year age classes at all sites combined. Bars represent age classes starting after the date below each pair of spruce and fir bars (e.g. "1940" = 1940–1944).

ment were correlated ($r > 0.5$), and the logistic regression procedure assumes no major correlations between the predictors, we performed a principal components analysis with varimax rotation (Jackson, 1991) to generate uncorrelated principal components suitable for entry into the logistic model. The models included the raw variables or components that proved significant according to the t -tests. To evaluate all logistic models, we used the chi-square goodness of fit statistic, the classification accuracy of each equation, and the $-2 \log$ likelihood statistic recommended by Hosmer and Lemeshow (1989).

Results

ESTABLISHMENT

Mean years of establishment varied slightly between spruce and fir ($t = 4.75$, $P < 0.001$) and among sites ($F = 11.278$, $P < 0.001$). Firs established earlier than spruces by 5.88 yr on average (95% CI: 3.5–8.3). For all sites combined, fir establishment began in the late 1930s, peaked between 1949–1955, and then declined, with only one fir tree establishing after 1980 (Fig. 2). Spruce establishment also began in the late 1930s, but peaked slightly later, between 1955 and 1963. For all species at all sampling locations, establishment was highest between 1951–1964, when 51.3% of the sampled trees regenerated. We recorded no establishment prior to 1935.

All four sampling locations showed a generally synchronous peak in establishment between 1950 and 1965, although there are some species-specific differences (Fig. 3). Sampling locations TI1 and TI4 had younger trees than the other two sites. At TI4, this was due to the large proportion of firs, which are younger overall than the spruce. When spruce ages alone are compared between sites, only the mean age at TI1 (37.1 yr) was significantly different from the mean age at other sampling locations (31.9) ($t = 4.51$, $P < 0.001$).

Small seedling establishment (those sampled along the centerline of each transect) was low at all sampling locations except TI2, but species composition did vary by sampling location. TI1 and TI3 were dominated by spruce seedlings while TI2 and TI4

were dominated by fir seedlings. Dates of seedling establishment were difficult to determine due to the extremely small size of the disks. In addition, recently established seedlings, less than 5 yr of age, do not necessarily represent successful establishment in the ecotone. For those seedlings which were dated, ages ranged from 1 to 15 with a mean of 6.91 ($n = 11$).

MICROENVIRONMENT

The microenvironment at each of the four sampling locations is different, especially with respect to moisture-related variables. Trees at TI1 were predominantly located in mesic locations, trees at TI2 and TI3 were predominantly located in moderate conditions, and trees at TI4 were located in xeric conditions. Within a 0.5 m radius of tree boles, *Vaccinium* spp. were the most common shrubs at all sampling locations except TI1 where *Salix brachycarpa* Nutt. was most common. The presence of *S. brachycarpa* may also be indicative of the mesic nature of this site. *Juniperus communis* L. was only present at TI4, and represents a drier environment (Peet, 1981).

DAMAGE

Neither damage nor mortality appeared to affect the long term survival of invading trees. Though evidence of mortality of very young trees may have decayed over time, we were only interested in the long-term survival of individuals, and thus only recorded mortality of well-established trees. Damage to seedlings from snow, snow mold, wind, and competition from other trees and understory plants was common at all four sites, but overall mortality was low. There was some evidence of spruce mortality (10.22% of total spruce tallied) and fir mortality (17.39% of total fir tallied) at TI3 (Table 1). Damage by snow and wind were the most common forms of damage, occurring on 16 and 38% of the trees, respectively. However, snow mold and needle desiccation caused the highest average percentage of damage per tree (36 and 65%, respectively). There were no significant differences in type or severity of damage between the four sites. We did not find any damage due to elk herbivory, elk trampling, or fire.

CLIMATE EFFECTS

T -tests for evaluating univariate relationships between tree establishment and climatic variables indicated that both temperature and snow depth variables differ between years of successful tree establishment and years without tree establishment (Table 2). The data for the short-term record (1936–1989), which included both temperature and snow depth variables, indicated that summer temperature and spring temperature were cooler during years of establishment ($P < 0.10$), and running mean snow depth were higher during the 5 yr following successful establishment ($P < 0.10$). For fir alone, total snow depth and April snow depth also proved significantly different during years of establishment when compared to years with no establishment ($P < 0.10$). For both variables, snow depths were higher during years of establishment than during years with no establishment.

In contrast to the short-term record, the long-term record (1882–1989), which included only temperature variables, suggested that in general, warmer temperatures are related to years of tree establishment (Table 3). For all three models, summer temperature, fall temperature, and running mean annual temperature were significantly different between years of establishment and years of no establishment ($P < 0.10$). Winter temperature

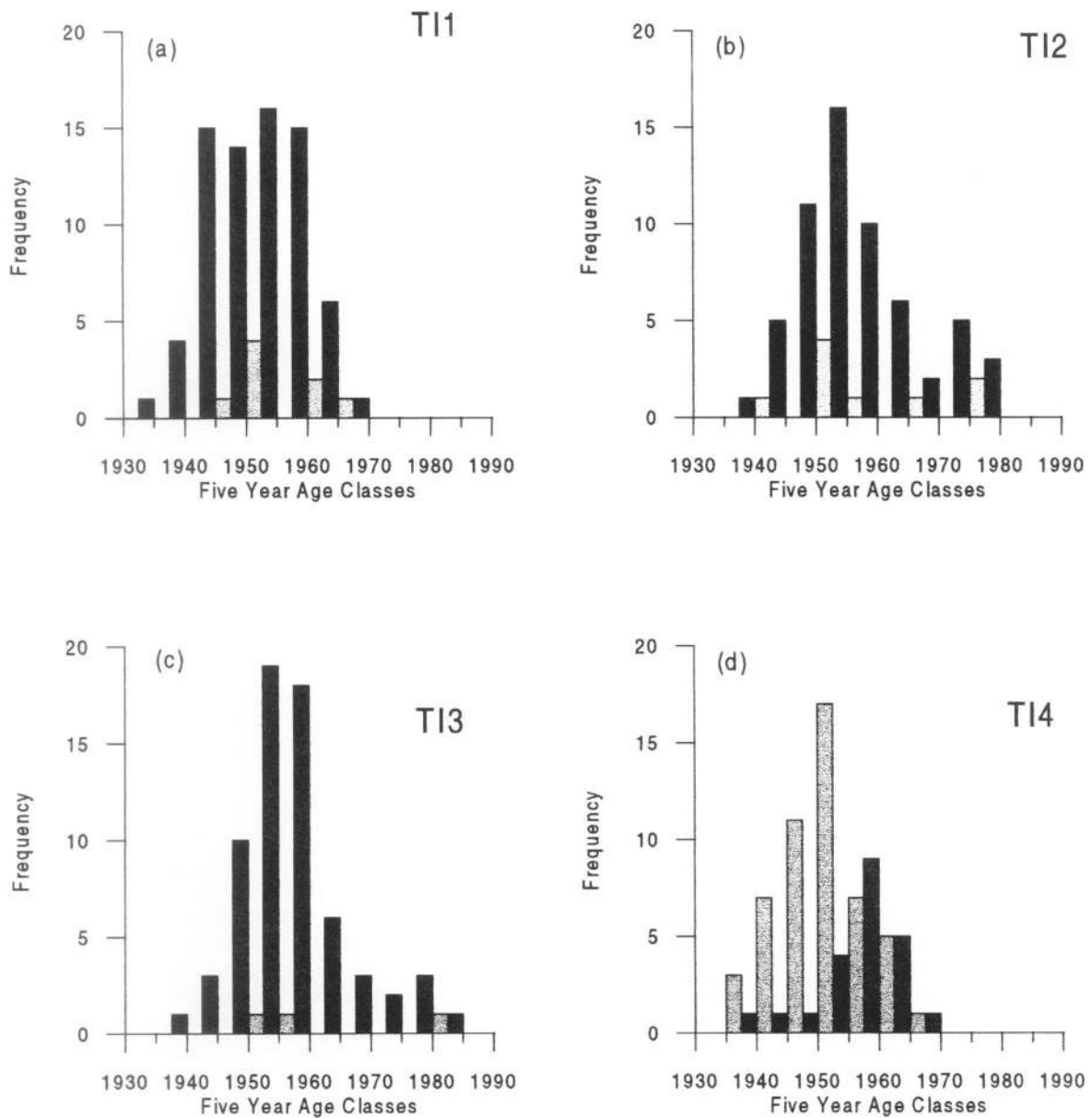


FIGURE 3. Frequency of Engelmann spruce (dark bars) and subalpine fir (light bars) establishment over time at the four sampling locations (T11-T14). Bars represent age classes starting after the date below each pair of spruce and fir bars (e.g. "1940" = 1940-1944).

TABLE 1
Sampling location characteristics^a

SL	Spruce density (no./ha)	Fir density (no./ha)	% Mortality spruce	% Mortality fir	Mean % damage	%cov rock	%cov bg	%cov forb	%cov Jun. spp.	%cov Vacc. spp.	%cov Salix spp.	Mean moist.
T11	1100	20	0.58	0.00	11	1	1	48	0	20	30	1.26
T12	2300	340	1.96	5.19	15.20	45	10	10	0	25	10	2.17
T13	800	40	10.22	17.39	23.56	25	30	3	0	40	2	1.96
T14	900	2070	6.71	6.57	20.87	35	1	13	1	50	0	2.00

^a SL refers to sampling location, %cov rock to percent cover rock, %cov bg to percent cover bare ground, %cov forb to percent cover by forbs, %cov Jun. spp. to percent cover by *Juniperus communis*, %cov Vacc. spp. to percent cover by *Vaccinium* spp., %cov Salix spp. to percent cover by *Salix* spp., and mean moist. to mean moisture on a scale from 1-3, where 1 is hydric and 3 is xeric.

TABLE 2

T-tests for difference between years of tree establishment and years of no tree establishment, 1936–1989^a

Variable	N	P-value		
		(spruce & fir)	P-value (spruce)	P-value (fir)
Spring temp.	53	0.004*	0.004*	0.061*
Summer temp.	54	0.066*	0.022*	0.055*
Fall temp.	54	0.157	0.225	0.561
Winter temp.	53	0.551	0.594	0.514
Running mean annual temp.	54	0.001*	0.108	0.000*
Total snow depth (Feb.–May)	39	0.241	0.796	0.083*
Feb. snow depth	42	0.600	0.893	0.133
March snow depth	51	0.903	0.442	0.112
April snow depth	54	0.708	0.375	0.042*
May snow depth	53	0.503	0.453	0.312
Running mean total snow depth	54	0.001*	0.001*	0.000*

^a Asterisks indicate significant at the $P < 0.10$ level.

was only significantly different for pooled establishment and spruce establishment ($P < 0.10$). Spring temperature was not significantly different for any of the dependent variables ($P > 0.10$).

Significant climatic variables, as well as elk numbers, were plotted against time and compared to the frequency of tree establishment (Fig. 4). Elk population estimates, taken from the winter range (Stevens, 1980), were lowest during the peak of tree establishment (1950–1965), but were both low and high during periods with no establishment (pre-1937 and post-1981) (Fig. 4a). Running mean annual temperature has been increasing since at least 1910 (Fig. 4b). But, there is no distinct relationship apparent between this variable and the frequency of establishment. Running mean annual snow depth broadly mirrors the histogram of tree establishment (Fig. 4c). However, the period of record may be too short to determine if this relationship has held over time as suggested by our hypothesis. Finally, March, April, and total snow depth are highly variable on an annual basis, making it difficult to observe any relationships between tree establishment and these snow depth variables (Fig. 4d).

LOGISTIC REGRESSION ANALYSIS

Of the short-term models, only the model predicting fir establishment has good fit and classifies well. Models predicting short-term spruce establishment and pooled (spruce and fir) establishment did not have good fit or classification, partly due to severely unequal group sizes for the dependent variable, and are not included here. For the short-term fir model, there was multicollinearity ($r > 0.6$), between the predictors. We used principal components analysis with varimax rotation to derive uncorrelated predictors (Table 4). Principal component 1 represents both April and total snow depth, principal component 2 represents running mean annual temperature, principal component 3 represents summer temperature, principal component 4 represents spring temperature, and principal component 5 represents running mean snow depth. Due to low loadings, principal component 6 is uninterpretable. All components were entered into the logistic model (Table 5). However, only components 2 and 5, representing running mean annual temperature and running mean snow depth, respectively, were significant ($P < 0.01$). The log likelihood for the model, ($-2 \log \text{likelihood} = 40.024$) is much lower than the log likelihood for the constant only model

TABLE 3

T-tests for difference between years of tree establishment and years of no tree establishment, 1882–1989^a

Variable	N	P-value		
		(spruce & fir)	P-value (fir)	P-value (spruce)
Spring temp.	104	0.200	0.676	0.286
Summer temp.	104	0.000*	0.035*	0.001*
Fall temp.	105	0.000*	0.008*	0.000*
Winter temp.	102	0.011*	0.134	0.026*
Running mean annual temp.	108	0.000*	0.010*	0.000*

^a Asterisks indicate significant at the $P < 0.10$ level.

($-2 \log \text{likelihood} = 69.31$), indicating a good fit. Similarly, the chi-square goodness of fit, indicating the significance of the model over a model with only the constant, was high ($\chi^2 = 29.291$, $df = 6$, $P = 0.0001$). Finally, the model was able to distinguish both classes of the dependent variable (82.0% concordance).

Principal component 2, representing running mean annual temperature for 5 yr after each recorded year, has a negative coefficient, indicating that cooler temperatures, at least during the short-term record, are associated with fir regeneration. Principal component 5, representing running mean annual snow depth, has a positive coefficient, indicating that high snow depths for at least 5 yr after establishment may also be important for successful regeneration. This, and the results of the *t*-tests, indicate that low temperatures and deep snow, relative to the rest of the short-term record, were associated with successful fir regeneration.

Two logistic regression models derived from the long-term record of temperature variables had good fit and good classification. Based on the univariate *t*-tests (Table 3), summer temperature, fall temperature, winter temperature, and running mean annual temperature were entered into the model for pooled establishment as well as the model for spruce establishment. Since there was low correlation among the predictors ($r < 0.6$), principal components were not extracted for these models. The pooled establishment model (Table 6) had high log likelihood ($-2 \log \text{likelihood} = 93.543$), but lower log likelihood than for the constant only model ($-2 \log \text{likelihood} = 138.815$). The model was, as a result, highly significant according to the chi-square goodness of fit ($\chi^2 = 45.273$, $df = 4$, $P < 0.0001$). Concordance was also good for both classes of the dependent variable (78.2%). Despite the goodness of fit and classification, only running mean annual temperature and fall temperature appeared significant in the model ($P < 0.05$). The coefficients for both running mean annual temperature and fall temperature are positive, indicating that high temperatures, relative to the rest of the period of record, were associated with tree establishment. These results are also supported by the long term record *t*-tests (Table 3), which suggest that warmer temperatures relative to the rest of the record are associated with tree establishment.

The model predicting spruce establishment (Table 7) also had high log likelihood ($-2 \log \text{likelihood} = 94.383$), but distinctly less than that of the constant only model ($-2 \log \text{likelihood} = 136.420$). Again the model was significant compared to the constant only model ($\chi^2 = 42.073$, $df = 4$, $P < 0.0001$). This model had reasonably good predictive power (75.3% concordance). Like the pooled establishment model, the spruce model included running mean annual temperature and fall temperature, as the only significant predictors ($P < 0.05$). Running mean

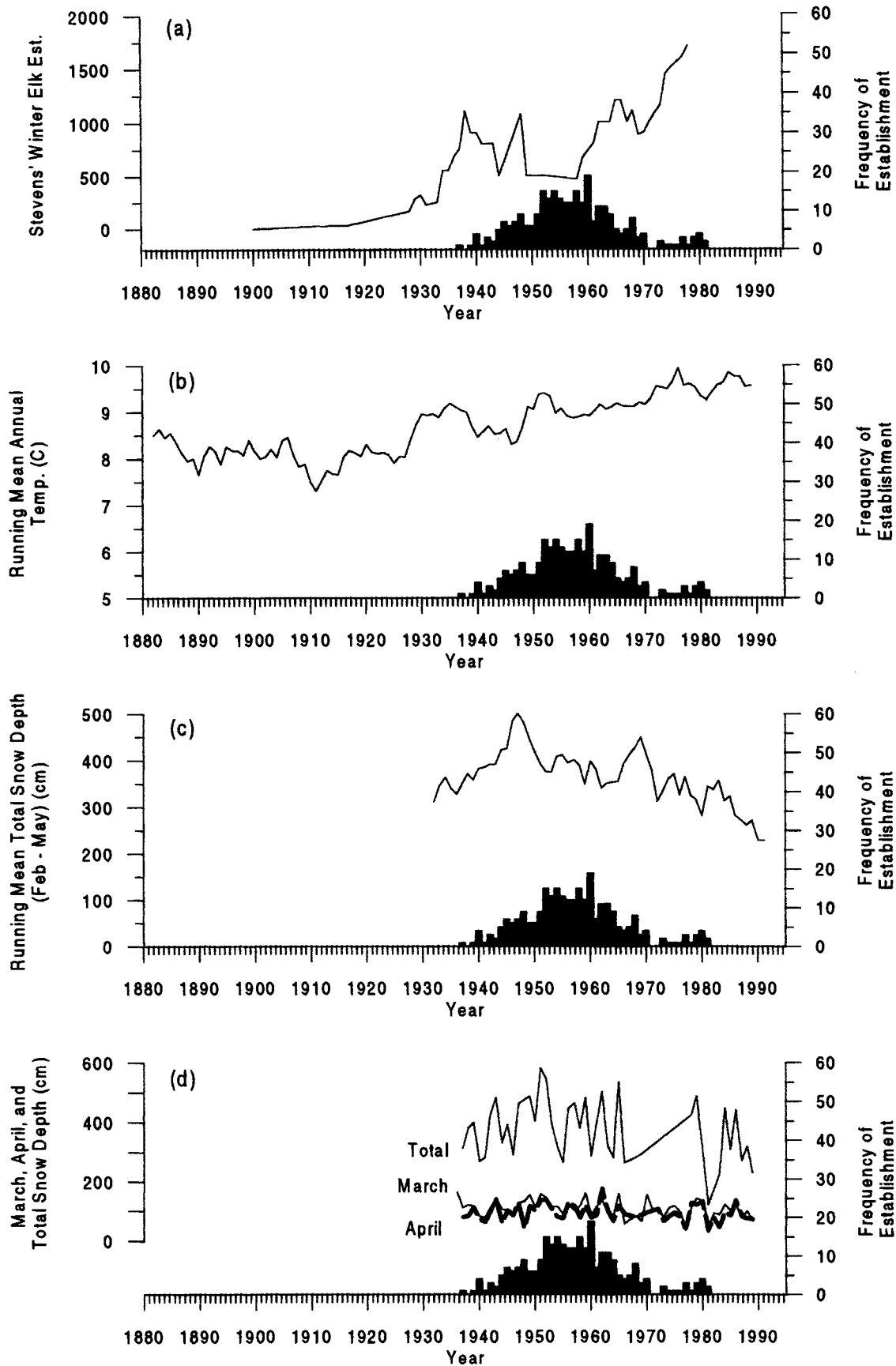


FIGURE 4. Estimate of elk counted in winter range (Stevens, 1980), 5-yr running mean annual temperature, running mean of total snow depth, March, April, and total snow depth each plotted against pooled frequency of Engelmann spruce and subalpine fir establishment recorded for each year.

TABLE 4

Varimax-rotated loadings for climatic predictors (short-term fir model)^a

Variable	Component					
	1	2	3	4	5	6
April snow depth	0.963	-0.523	-0.034	-0.183	0.003	-0.188
Total annual snow depth	0.941	-0.007	-0.157	-0.207	0.052	0.212
Running mean annual temp.	-0.037	0.933	0.127	0.123	-0.312	0.002
Summer temp.	-0.124	0.126	0.956	0.142	-0.185	-0.007
Spring temp.	-0.317	0.136	0.160	0.912	-0.155	-0.003
Running mean snow depth	0.030	-0.398	-0.235	-0.170	0.870	0.004

^a Loadings in bold are the highest loadings for each variable.

annual temperature and fall temperature have positive coefficients, indicating that warmer temperatures relative to the rest of the record are associated with years of successful tree regeneration. The similarity of the two long-term models can be explained by the heavy influence of spruce establishment on the pooled model.

Discussion

TREE INVASION IN ROCKY MOUNTAIN NATIONAL PARK

Tree establishment in patch forest openings of Rocky Mountain National Park occurred nearly synchronously across four widely separated sites in differing environments, suggesting that some Park-wide phenomenon influenced establishment. Trees in patch forest openings are experiencing little mortality (Table 1), and though damage from wind and snow is significant (Table 1), many trees have survived several decades. This strongly suggests that the tree invasion into patch forest openings represents more than an ephemeral change in the ecotone. Establishment in openings peaked between 1951 and 1964 but was virtually nonexistent before 1930 and after 1980 (Fig. 2). Stand destructive fires, domestic livestock grazing, and changing climate conditions have all been proposed to explain this phenomenon both in the Rockies and elsewhere in North America (Vale, 1987; Little and Peterson, 1994; Rochefort et al., 1994).

POTENTIAL EXPLANATIONS FOR TREE INVASION

The period of intense establishment in patch forest openings of Rocky Mountain National Park was probably not the result

of delayed succession following an episode of stand destructive fires. If this was the case, evidence of fire in the subalpine zone should still be present as charcoal or as fire scars on older trees. Despite efforts to detect past fires, no charcoal or fire scar evidence was found at any of the four sampling locations. Furthermore, stand destructive fires would have had to occur synchronously at small disjunct sites in order to produce the patchy nature of establishment observed in this study. Though fires have occurred in the forest-tundra ecotone of Rocky Mountain National Park, their frequency and extent is limited by late spring snows, frequent summer showers, and discontinuous fuels (Clagg, 1975). Only 4% of the forest-tundra ecotone of Rocky Mountain National Park has been burned over the last century (Baker et al., 1995).

Grazing pressure may be a likely explanation in other subalpine zones, but seems unlikely in Rocky Mountain National Park. Grazing pressure from domestic livestock has not occurred in the subalpine zone of Rocky Mountain National Park for at least 80 yr, and probably did not significantly affect the forest-tundra ecotone (Hess, 1993). However, recent densities of native elk have been high enough to cause damage to willow and aspen communities in the elk's winter range (Braun et al., 1991; Hess, 1993; Baker et al., in press). It is possible that grazing pressure from elk was high enough to influence coniferous seedling establishment in the forest-tundra ecotone (Fig. 4a). Elk populations reached a high in 1942, just prior to the implementation of an elk control program (Hess, 1993). Reduced pressure following this intense period of grazing could have allowed for the successful seedling establishment observed during the early 1950s and 1960s. This pattern was observed in the Sierra Nevada by Vale (1987) and in the Colorado Rockies by Baker

TABLE 5

Logistic regression classification table and equation for short-term fir establishment model (1936-1989)

Classification		Percent correct	
No establishment (0)		80.00	
Establishment (1)		84.00	
Overall		82.00	
Variable	B	S.E.	Significance
PC 1	0.7191	0.4443	0.1055
PC 2	-1.8406	0.5847	0.0016
PC 3	-0.4956	0.3865	0.1997
PC 4	-0.2742	0.4696	0.5593
PC 5	1.6770	0.6376	0.0085
PC 6	-0.0469	0.3684	0.8988
Constant	-0.1124	0.4101	0.7840

TABLE 6

Logistic regression classification table and equation for long-term pooled establishment model (1882-1989)

Classification		Percent correct	
No establishment (0)		80.36	
Establishment (1)		75.56	
Overall		78.22	
Variable	B	S.E.	Significance
Summer temp.	0.048	0.197	0.807
Winter temp.	0.086	0.087	0.323
Running mean			
annual temp.	1.080	0.305	0.000
Fall temp.	0.347	14.758	0.000
Constant	-74.210	14.758	0.000

TABLE 7

Logistic regression classification table and equation for long-term spruce establishment model (1882–1989)

Classification		Percent correct	
No establishment (0)		78.33	
Establishment (1)		70.73	
Overall		75.25	
Variable	B	S.E.	Significance
Summer temp.	-0.114	0.199	0.567
Fall temp.	0.362	0.156	0.020
Winter temp.	0.053	0.086	0.541
Running mean temp.	1.212	0.321	0.000
Constant	-69.601	14.402	0.000

(1991). However, tree establishment did occur during the late 1970s and early 1980s when the elk population began to increase far beyond previously recorded levels, making elk numbers an unlikely explanation for the observed changes in regeneration among patch forest trees.

CLIMATE AS AN EXPLANATION FOR TREE INVASION

While some researchers have argued that recent tree invasion may be the result of variations in fire or grazing pressure, my data suggest that there is a strong relationship between climatic variation and tree establishment. The short-term record indicates that cool summer, spring, and running mean annual temperatures are related to years of tree establishment (Tables 2, 5, 6). This conclusion is drawn relative to years of no tree establishment, which for the short-term record, occur mostly in the 1980s when temperatures were the highest on record (Fig. 4b). For the long-term record, most years with an absence of tree establishment occurred early in the record, prior to the 1930s, when temperatures were much lower than during the period of intense establishment (1930s–1960s). The long-term record suggests that as temperature increased, it became more likely that trees established (Tables 3, 6). However, the absence of establishment in the early 1970s and late 1980s, when temperatures reached their highest values, is not consistent with this conclusion. It is possible that temperatures simply became too high to allow for successful establishment.

The short-term record, the long-term record, univariate *t*-tests (Tables 2, 3), and logistic models (Table 5, 6), suggest that it is more likely that both high temperatures and high snow depths must occur in order to generate climatic conditions suitable for tree establishment. The high temperatures in the early 1970s and late 1980s were accompanied by unusually low snow depths, possibly resulting in the absence of establishment observed for this period (Fig. 4b, 4c). In the 1950s, during the peak in establishment, both temperature and snow depth were high. The importance of snow depth in determining suitable climatic conditions for tree establishment is also supported by both the temporal and spatial patterns of establishment at different sampling locations. The broad curve in establishment at T11 (Fig. 3a), the most mesic sampling location, suggests that moist sites mitigate climatic conditions, and, as a result, allow establishment to occur in a wider range of climatic conditions. Previous work also suggests that widespread seedling establishment in patch forest openings in Rocky Mountain National Park may be related to soil moisture conditions as indicated by certain shrub species and by snow beds (Weisberg, 1994).

Although it appears that both temperature and snow depth are important for predicting when trees establish, it is difficult to interpret the absence of trees in the early part of the long-term record (pre-1936). It is possible that temperature alone was too cold to allow for successful establishment. However, it is also possible that snow depths were too low to promote regeneration. Without accurate precipitation data, it is impossible to determine which of these factors contributed to the absence of regeneration during this period. It should also be noted that because establishment occurred as a single pulse, there is only one event which can be compared to climate variables. This makes the effective sample size equal to one. It also introduces a problem with temporal autocorrelation which may affect any tests associated with the coefficients derived from the logistic regression.

Other studies of subalpine meadow invasion in North America have suggested that changing climatic conditions may be connected to new patterns of tree establishment (Table 8). Above average summer temperatures (Kearney, 1981; Taylor, 1995) and wet summers (Jakubos and Romme, 1993; Little and Peterson, 1994) have been associated with coniferous tree establishment in other regions. These may be consistent with the conclusions discussed here. However, establishment in North America has also been associated with diminished snow cover (Brink, 1959), dry springs and cool summers (Little and Peterson, 1994), and low April snowpack (Taylor, 1995), which are inconsistent with our results. Differences in both periods of establishment and climatic conditions associated with establishment may be the result of differing regional climates as well as differences in establishing species' adaptations (Woodward et al., 1995).

Despite the conclusions drawn here, the question remains whether the temporal pattern of tree establishment in Rocky Mountain National Park is indicative of a response to a larger scale climatic trend or simply to a unique climatic period occurring in the 1940s to 1960s. In North America, periods of seedling establishment have occurred most frequently following A.D. 1890, with the most significant establishment occurring between A.D. 1920 and 1950 (Rochefort et al., 1994). In the Northern Hemisphere, a general trend towards cooler periods, known as the Little Ice Age, occurred between approximately A.D. 1350 and 1850 (Jones et al., 1982; Grove, 1988). Some researchers have suggested that recent periods of tree invasion in the subalpine zone may be the result of a warming and drying trend following the cessation of the Little Ice Age ca. A.D. 1850 (Franklin et al., 1971; Kearney, 1982; Earle, 1993; Rochefort et al., 1994). Indeed, mean global temperatures have increased since the end of the nineteenth century by approximately $0.45 \pm 0.15^\circ\text{C}$ (Houghton et al., 1990), and may have been highest between 1877 and 1906 for the period 1602–1961 (Fritts and Lough, 1985).

In southwestern Colorado and the Northern Great Plains, the Little Ice Age may have been characterized by a cool, dry climatic regime (Petersen, 1994; Fritz et al., 1994; Meko et al., 1995). Veblen's climate reconstruction based on trees just south of Rocky Mountain National Park, indicates a cool period in the mid 1600s and a gradual decline in growing season temperature from about 1700 to 1910 (Veblen, pers. comm., 1996). Finally, Hansen-Bristow et al. (1988) identified a cool period with temperatures well below normal from 1835 to 1900. If this climatic pattern also occurred in Rocky Mountain National Park, then the absence of establishment before the 1930s might be explained by a cool, dry climate, a conclusion consistent with the models generated here, and consistent with temporal timberline patterns

TABLE 8

Previous studies of tree invasion in subalpine meadows in North America

Citation	Location	Species	Years of establ.	Climatic conditions	Analytical technique
Brink (1959)	Garibaldi National Park, British Columbia	<i>Abies lasiocarpa</i> <i>Tsuga mertensiana</i>	1919–1939	Diminished snow cover	None
Franklin et al. (1971)	Cascade Range, Washington and Oregon	<i>Abies lasiocarpa</i> , <i>Tsuga mertensiana</i> , <i>Larix lyalli</i>	1923–1944	None mentioned	Graphing
Kearney (1981)	Jasper National Park, Canada	<i>Abies lasiocarpa</i> , <i>Picea engelmanni</i> , <i>Pinus contorta</i>	1965–1973 1940–1950	Above ave. mean summer temperature	Chi-square contingency tables
Agee and Smith (1984)	Olympic Mountains, Washington	<i>Abies lasiocarpa</i> , <i>Tsuga mertensiana</i>	1920–1945	Normal to wet years	ANOVA
Jakubos and Romme (1993)	Yellowstone National Park, Wyoming	<i>Pinus contorta</i>	1865–present	Warm, wet summers	Stepwise multiple regression
Little and Peterson (1994)	Cascades, Washington	<i>Abies lasiocarpa</i>	1950–1990	Warm, dry springs and cool, wet summers	Multiple and logistic regression
Taylor (1995)	Lassen National Park, California	<i>Tsuga mertensiana</i>	1895–1910 1910–1930 1955–1972 1988–1990	Warm summers, low April snow pack	Correlation coefficients (Kruskall Wallis H-test)
Rocheftort and Peterson (1996)	Mt. Rainier National Park, Washington	<i>Abies lasiocarpa</i>	1980–1990	Spatially variable	Stepwise multiple regression
Woodward et al. (1995)	Olympic Mountains, Washington	<i>Abies lasiocarpa</i> , <i>Tsuga mertensiana</i>	1921–1945 1956–1985	Spatially variable	Correlation coefficients (Pearson)

observed in the White Mountains of California (LaMarche and Mooney, 1967).

The 1950s to 1960s, which were relatively wetter and warmer than the Little Ice Age, may have initiated the coniferous tree establishment in patch forest openings that we observed. Precipitation generally increased following the end of the Little Ice Age in the middle 1800s (Petersen, 1994). The period from 1941 to 1970 in the Rockies had wetter summers than any other period since the end of the Little Ice Age (Bradley, 1976).

If predictions about future climate change are correct, warmer temperatures may create conditions conducive to further tree establishment in patch forest openings. However, it is possible that the absence of tree establishment that we observed in the 1970s and 1980s is the result of temperatures too high for successful tree establishment. If this were the case, we would expect to observe regeneration at higher elevations in the ecotone. Instead, establishment may depend on both temperature and moisture conditions, where there may be an optimal temperature range for establishment, given a certain moisture regime, above or below which, establishment will not occur in its present spatial pattern.

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