Spruce-fir growth form changes in the forest-tundra ecotone of Rocky Mountain National Park, Colorado, USA

Amy E. Hessl and William L. Baker

Tree regeneration has traditionally been used as a measure of the response of treeline to climate. Changes in growth form of krummholz trees may also indicate whether treeline is responding to changes in climate. The purpose of this study was to determine whether krummholz trees in the forest-tundra ecotone of Rocky Mountain National Park, Colorado have experienced significant vertical stem growth, in the absence of mortality, and if this growth occurred in response to recent changes in climate. We sampled and dated Engelmann spruce and subalpine fir krummholz leaders stratified by height class at three sampling locations to determine the dates leaders initiated growth above mean snow depth. At one sampling location, 215 additional leaders were sampled to construct an age structure of leader release dates. Dates of leader release taken from the age structure were compared with seasonal temperatures, seasonal precipitation, winter snow depths, and annual runoff using t-tests. Dates of leader release were also compared to proxy climate records for the southern Rocky Mountain region. Based on historical photos as well as the data presented here, both spruce and fir krummholz trees experienced significant height growth as early as the 1850’s and continued to grow vertically, at least through the 1970’s. This vertical stem growth occurred in the absence of significant mortality. Running mean annual temperature and May snow depth are both positively associated with years of leader release, suggesting that a warmer, wetter climate, possibly following the end of the Little Ice Age ca 1850, may have induced these changes in the ecotone.

If current rates of CO₂ emissions continue, the mean global temperature may rise 1.8°C by the year 2030 (Houghton et al 1990). A rise in mean temperature could initiate changes in vegetation distributions on a global scale (Gates 1993). However, vegetation may respond in a species-specific manner, making predictions about vegetation change difficult (Hustich 1958). In order to detect early manifestations of the effects of this rise in temperature, studies should focus on vegetation types most likely to exhibit a response to varying climate. It has been argued that vegetation changes due to climate variation can best be measured at the limit of a species’ range (Griggs 1938). As the elevational limit of tree growth, the alpine forest-tundra ecotone (FTE) may be especially sensitive to changes in climate (Romme and Turner 1991). Dendrochronological research has shown that some portions of the North American FTE have responded to climatic changes in the past (Andrews et al 1975, Fall 1988, Lloyd and Graumlich 1993), indicating that the FTE may respond to projected temperature changes in the next few decades.

Though much research has focused on the dynamic relationship between treeline and climate, several re-
searchers have suggested that treeline is relatively stable and therefore resistant to short-term changes in climate making it a poor place to study climate change (Ives 1978, Hansen-Bristow and Ives 1985, Slatyer and Noble 1992). Once trees are established only a series of highly unfavourable years or a severe disturbance might lead to a retreat of treeline (Slatyer and Noble 1992). The supposed absence of seedlings above treeline is also cited, indicating that current treeline may be a relict which established during a different climate (Hansen-Bristow and Ives 1985). Other researchers have observed seedling establishment above the treeline, suggesting that the FTE may be changing under current conditions (Daly and Shankman 1985).

While regeneration is one aspect of the relationship between treeline and climate, phenotypic adaptation, or changes in growth form, may be an important measure of the influence of climate on treeline (Payette et al. 1985, Kullman 1986, Payette et al. 1989, Lavore and Payette 1994). While regeneration may occur under consistently beneficial growing conditions, changes in growth form may be triggered by milder changes which occur more frequently. For example, vertical stem growth above mean snow depth may be indicative of more suitable growing conditions (Payette et al. 1989). Kullman (1986, 1990, 1991) suggested that tree limit populations in Sweden responded to warming following the Little Ice Age by accelerated height growth of old, established, but stunted individuals. Vertical stem growth alone could lead to a shift from krummholz to forest, resulting in a structural and, perhaps, a functional change in the ecotone.

In Rocky Mountain National Park, Weisberg and Baker (1995a) observed that krummholz leaders are actually growing faster than seedlings in krummholz openings, and may develop into tree growth forms in time. A historical photo taken in the 1930s also indicates that krummholz trees have experienced significant height growth in the last 65 yr, changing the appearance and possibly the ecological dynamics of the ecotone (Fig. 1). Structural changes, due to phenotypic changes in trees, have been shown to affect snowdrift patterns and regeneration in the ecotone (Earle 1993). Regeneration may not be successful until significant vertical growth occurs, creating a suitable microenvironment for seedling establishment and survival. To fully understand the FTE, changes in growth form must be understood. Our objectives were to 1) determine when changes in growth form have occurred in the FTE in the last century, 2) determine what may have triggered growth releases, and 3) develop a statistical model to predict future changes in the ecotone. We have hypothesized that krummholz leaders (flags) are experiencing significant vertical height growth (above mean snow depth), not balanced by stem mortality, and this growth was triggered by a warm, but wet period following the end of the Little Ice Age ca 1850 A.D.

Methods

Study area

The climate of the southern Rocky Mountains is predominantly continental (Barry 1973). Most precipitation occurs as snow during the winter, however, a second precipitation maximum, known as the Mexican Monsoon, occurs in summer. Forest vegetation in the FTE of Rocky Mountain National Park is primarily composed of coniferous forest dominated by *Pinus engelmannii* Parry and *Abies lasiocarpa* (Hook) Nutt with occasional stands of *Pinus flexilis* James occurring only on dry slopes and ridges (Peet 1981). The geology of the study area is almost completely composed of Silver Plume granite, gneiss and biotite schist (Bradock and Cole 1990).

Field methods

A subset of 3 sampling locations was chosen from Weisberg's sample of 36 sites based on the presence of...
seedling regeneration and vertical leader growth in the krummholz zone (Weisberg and Baker 1995a) (Fig 2). Krummholz patches often have leaders growing above the height of mean snow depth, sometimes called "supranival" leaders (Lavoie and Payette 1994) (Fig 3). While krummholz patches often look stable and unchanging, leaders appear to have developed over a relatively short time period, with obvious points of
release. At each sampling location, we identified an area of krummholz patches with representative leaders and established a belt transect of variable length and width perpendicular to the slope. Transects were designed to include at least ten patches of krummholz trees.

In every belt transect, general characteristics such as elevation, slope, aspect, understory species, moisture level (scalar index 1–7), and ocular estimates of percent cover of rock, bare ground, and shrubs were measured and recorded. These variables were used to characterize the microenvironment of the transect. In addition, we looked for evidence of fire on the surface of the soil (e.g., charcoal), and on surrounding trees (e.g., fire scars). In each transect to determine whether fires had recently occurred in the area. We tallied all live and dead leaders by species and by three height classes (<1.0 m, 1.0–2.0 m, and >3.0 m). Live leaders were identified as any stem growing above mean snow depth that is at least 30% above the height of mean snow depth at that location. Mean snow depth was identified by either the average height of the krummholz “skirt” or by the lower edge of ice particle abrasion on exposed stems. Dead leaders were tallied if they were standing or if they were downed and obviously part of the patch.

In each krummholz patch, we randomly selected at least three leaders from every height class to date the initiation of leader growth above mean snow depth. Because a limited sample could be processed, we stratified the sampling by height class so that different periods of release would not be missed. Between 94 and 121 cores were taken from each of the krummholz transects to determine the timing of release. Leader cores or disks were taken just above the height of mean snow depth or at an obvious release point near mean snow depth in order to date the year of growth release. Though multiple points of release above mean snow depth are visible on some fir leaders, these cores were not included in the analysis because of a limited sample size. Basal cores were taken as close to the ground as possible. If the base was rotten, the core was taken no more than 15 cm above the ground. One core or disk was taken from each tree at the base and from a leader chosen from that tree. The largest base in each patch was also cored to approximate patch and stand age.

For each leader sampled, we recorded the total leader height, height to the release point on each leader, diameter of the tree base, diameter of the leader base, position of the leader within a patch (windward, middle or leeward) and level of exposure (protected or exposed) relative to other leaders.

At one sampling location, TL3, we established an additional belt transect in order to generate a complete age structure of leaders. This sampling location was chosen because it was within the scope of the re-photograph of the Medicine Bow curve (Fig 1). At this sampling location, we sampled every supranival leader (n = 215) within a representative 150 × 50 m belt transect. We also recorded the species, height, and diameter of each leader, as well as exposure (protected or exposed) and patch position (windward, middle, or leeward).

All cores and basal disks were processed in the laboratory according to standard dendrochronological procedures (Stokes and Smiley 1968). Cores were mounted to prevent damage and sanded to enhance visual identification of annual rings. Disks were sliced into 6–10 sections 2–4 mm wide, which were all mounted and sanded. The disk with the highest ring count was then used as the age of the leader. Rings from both cores and disks were counted under a binocular microscope.

Climate data

Temperature, precipitation, snow depth, and runoff data are available from several locations near the Park. However, many of these climatic records are short or cover different time periods. Monthly temperature records are available from Fort Collins, Colorado (NOAA, Climatological Data) for the period 1882–1995. These temperature records were highly correlated with Estes Park records (r > 0.69, p < 0.001 for all seasonal and annual temperatures). Precipitation from Fort Collins was not used in the analysis because precipitation is locally variable, and because Fort Collins precipitation was not correlated with snow-depth data for the Park. Instead, we used monthly snow-depth records for February–May from the Wild Basin SNOWTEL site within the Park (Natural Resource Conservation Service) for the years 1936–1995. Snow-depth is recorded on or around the first day of the month. Missing values were estimated from another SNOWTEL site at Hidden Valley using a regression equation based on overlapping years between the two sites (Dunne and Leopold 1978). Because the snow-depth record is short (1936–1995), we also developed a longer snow-depth record based on Longs Peak precipitation data (1895–1944). We used a regression equa-

Fig 3 Example of the krummholz leaders sampled
tion to reconstruct May snow-depth from 1895–1936 based on the overlapping eight years of Longs Peak precipitation and Wild Basin snow-depth. Finally, we compiled total annual runoff information for 1888–1994 from a station at Lyons, Colorado (US Geological Survey) ca 25 km from the Park. Where possible, climate records were compiled into seasonal averages to compare with years of successful growth releases.

**Data analysis**

Based on the samples taken from krummholz leaders, we determined that the leader growth “released” (grew above the height of mean snow depth) Histograms of stem age for each krummholz transect were constructed to determine whether stem growth above mean snow depth is episodic or regular. Using the age structure data, we used univariate t-tests to determine if climatic variables were associated with years of successful growth releases. Statistically significant variables were forced into a logistic regression equation predicting years of establishment based on climatic variables (Hosmer and Lemeshow 1989). We also placed leaders from the age-class structure as well as the climate data into five-year classes because of the difficulty in determining the exact point of release, as well as dating errors due to missing or false rings present in the cores. With these data, we determined correlation coefficients between climatic variables and frequency of leader release. Because the absence of leader releases after 1970 may be an artifact of our sampling design, all statistical analysis relating leader release dates to climatic variables was limited to the climatic record up to 1970 only.

### Results

#### Height class data

Sampling locations differed in terms of moisture-related variables and physical variables (Table 1). Elevations ranged from 3432 m to 3511 m and slopes ranged from 12 to 16 degrees. Sampling location 3 was the most mesic with a dense cover of *Salix* spp. (*S. planifolia* Pursh and *S. brachycarpa* Nutt.) and *Vaccinium* spp. (*V. scoparium* Leiberg and *V. caespitosum* Michx.) Sampling location 1 was also mesic, but contained a higher percentage of rock cover than the other sites. Sampling location 2 was the most xeric site, as indicated by the presence of *Juniperus communis* L. and only a small percent cover of *Salix* spp. No evidence of fire was observed at any of the sampling locations.

Over all size classes and all sampling locations, krummholz leader release dates ranged from 1879–1976 A.D. However, dates were dependent on size class (p < 0.001), where the shorter height classes contained younger leaders and taller height classes contained older leaders (leaders < 1 m had a mean age of 36.6 yr, leaders between 1 and 2 m had a mean age of 51.1 yr, and leaders > 2 m had a mean age of 71.1 yr) (Fig 4).

The pattern of leader releases also differed by sampling location (Fig. 5). SL 2 experienced a greater frequency of leader releases before the 1930’s than the other two sampling locations. Leader release at SL 2 was characterized by an earlier period of fir leader releases with very few spruce releases.

Leader age is significantly related to two of the microenvironmental variables we measured: patch position (F = 7.559, p = 0.001) and exposure (F = 24.776, p < 0.001). These variables were designed to measure the same basic condition, and results were consistent between the two variables. For patch position, the oldest leaders were located in the middle or leeward end of the patch. Similarly, the oldest leaders were not exposed.

The age of bases and the age of leaders were only weakly associated. In general, older bases hosted older leaders (r = 0.3275, p = 0.006). Similarly, the diameter of the base is only broadly related to the age of associated leaders (r = 0.2706, p = 0.002). Base ages ranged from 27 to 259 yr. All three sampling locations contained at least one base older than 220 yr.

Diameter of the base and of the leaders, as well as the heights of leaders and leader releases varied, indicating that the physiological status of the tree is unrelated to the leader release phenomenon. Basal

### Table 1 Sampling location characteristics

<table>
<thead>
<tr>
<th>SL #</th>
<th>Elev (m)</th>
<th>Slope (°)</th>
<th>Aspect (°)</th>
<th>Moist (1–7)</th>
<th>% cov rock</th>
<th>% cov Vacc spp</th>
<th>% cov <em>Salix</em> spp</th>
<th>% cov Junip spp</th>
<th>% cov <em>Ribes</em> spp</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>3511</td>
<td>16</td>
<td>246</td>
<td>4</td>
<td>50</td>
<td>10</td>
<td>10</td>
<td>25</td>
<td>0</td>
</tr>
<tr>
<td>2</td>
<td>3432</td>
<td>12</td>
<td>152</td>
<td>5</td>
<td>30</td>
<td>15</td>
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</tr>
<tr>
<td>3</td>
<td>3505</td>
<td>16</td>
<td>336</td>
<td>3</td>
<td>5</td>
<td>5</td>
<td>40</td>
<td>40</td>
<td>0</td>
</tr>
</tbody>
</table>

*SL #* refers to sampling location, *Elev* refers to elevation, *Moist* refers to moisture on a scale of 1–7 where 1 is mesic and 7 xeric, *% cov rock* refers to percent cover of rock, *% cov Vacc spp* refers to percent cover by *Vaccinium* spp., *% cov *Salix* spp* refers to percent cover by *Salix* spp., *% cov Junip spp* refers to percent cover by *Juniperus communis*, and *% cov *Ribes* spp* refers to percent cover by *Ribes* spp.
diameters ranged from 4.0 to 42.0 cm with a mean of 16.0 cm, while leader diameters ranged from 3.0 to 18.1 cm with a mean of 7.9 cm. Height of leader release was also variable, ranging from 18.0 to 155.0 cm with a mean of 79.1 cm. Finally, leaders themselves ranged in height from 26.0 to 486.0 cm with a mean of 190.9 cm.

Based on leader tallies, leader mortality was not significant overall, and did not differ dramatically between sampling location or species. Fir leader mortality was greatest at sampling location 2, but did not exceed 10% at any sampling location. Similarly, spruce leader mortality was greatest at sampling location 1, but did not exceed 7% at any sampling location. Over all sampling locations, fir mortality averaged 9%, while spruce mortality averaged only 3%.

**Age structure data**

The age structure of leader release dates at sampling location 3 indicates a major spike in frequency of fir leader releases between 1920 and 1925 and a broader peak for spruce leaders ranging from 1905 to 1955 (Fig. 5d). This broader peak in spruce leader release dates can be broken down into two spikes separated by a gap between 1935 and 1945, when only seven leaders released. The oldest leader releases recorded were a few spruces dating to the 1850’s and 1860’s. Fir leaders did not, in general, initiate growth until ca 1895. Though the age of leaders at all three sampling locations was dependent on patch position and exposure, this was not the case for the leaders sampled for the age structure (p > 0.10).
Though two climate variables, running mean annual temperature and May snow depth, were significantly different between years of leader release and years of no release, these variables proved to be only poor predictors in a logistic model. Running mean annual temperature and May snow depth were both significantly greater during years of pooled (spruce and fir) release than during years with no release \( (p < 0.10) \). These variables were also significantly greater during years of fir release than during years with no fir leader releases \( (p < 0.10) \) (Table 2, Fig 6). No variables were significantly different for spruce release alone. The two logistic models predicting pooled leader release and fir leader release based on running mean annual temperature and May snow depth classified poorly \( (<4\% \text{ correct classification of years without leader release}) \) and were not significant over the constant only model \( (p > 0.10) \). Thus the details of these models are omitted.

Correlation coefficients for five-year classes of climate variables and five-year age classes of leaders yielded only weak results. Summer precipitation from Longs Peak was positively correlated with pooled leader release \( (r = 0.602, p = 0.065) \). However, this correlation is only based on ten cases (50 yr) (Table 3, Fig 6). Similarly, spruce leader release was positively correlated with winter precipitation based on ten cases \( (r = 0.603, p = 0.020) \). Fir release was positively correlated with summer precipitation from Longs Peak, based on ten cases \( (r = 0.6024, p = 0.065) \). None of the other variables (seasonal temperature, monthly snow depths or annual runoff) with longer periods of record were significantly correlated with leader releases \( (p > 0.10) \).
Discussion

Based on historical photos as well as the data presented here, both spruce and fir krummholz trees in Rocky Mountain National Park experienced significant height growth as early as 1850 and continued to grow vertically at least into the 1970's (Figs 1, 4, 5). The frequency of leaders growing above the height of mean snow depth continued to increase until the 1930's, when the most intense period of leader release occurred. Though leaders may have continued to release until the present day, our sampling strategy may not have identified these younger leaders due to their small size and the resulting difficulty of identifying them in the field.

Significant leader growth has been observed among krummholz trees before (Vale 1987, Kullman 1987, 1990, 1991, Petersen 1988, Earle 1993, Payette et al 1994), suggesting that these stunted trees may have the potential to develop into patch forest trees (Weisberg 1994). However, our research represents one of only a few quantitative studies, and contains the largest sample of leader dates for any study in the western USA.

Autoecological processes, fire, and climate change have all been proposed as possible explanations for the proliferation of leader releases among krummholz trees. Earle (1993) suggested that release dates may be dependent on both autoecological factors (species-specific factors) as well as the structure of the surrounding forest. Though our results indicate that patch position and exposure are related to the age of leaders, these variables only account for a small amount of the variability (<16%) in leader age and were not significant variables for the age-structure data. The dates of leader release were only broadly related to either the age of the base or the size of the base, indicating that the timing of release is probably not dependent on the developmental status of the tree, but is instead tied to some larger-scale, external phenomenon. Furthermore, because our sampling locations were widely separated, occurred on different slopes and aspects, but had similar release dates (Table 1, Fig. 5), we suggest that autoecological or local environmental factors may only partially explain the timing of release. Though SL 2 experienced a higher frequency of releases between 1875 and 1920 (Fig 4b), the temporal extent of leader releases was consistent with other sampling locations. The early peak in leader release observed at this sampling location may be due to species-specific differences in sensitivity to climate change. Subalpine meadows dominated by fir invasion tended to experience slightly earlier periods of establishment than meadows dominated by spruce invasion (Hessl and Baker unpubl.)

Though fires do occasionally occur in the FTE, no evidence of fire was observed at any of our sampling locations. Furthermore, it is unlikely that the krummholz patches we sampled represent post-fire regeneration. As basal dates vary in age between 27 and 259 yr, while leader release dates were concentrated in the last 90 yr, this indicates that krummholz patches regenerated at different times, but leader releases occurred within a single period. Finally, because release dates were relatively coincident throughout the Park, fires would have had to burn a large portion of the FTE in order to produce the observed pattern of krummholz releases.

As a regionally synchronous phenomenon, climate change has been proposed by many researchers to explain both vertical height growth (Vale 1987, Kullman 1990, 1991, Earle 1993) and leader mortality among krummholz trees (Kullman 1987, Payette et al 1994). Kullman (1987) observed a decline in populations of Pinus sylvestris in response to previous periods of cooling during the Little Ice Age, suggesting that changes in phenotype may be indicative of climate change within the last century. Payette et al (1994) also concluded that stem decline of a black spruce clone in Quebec may have been the result of cold spells or decreasing snow pack during the Little Ice Age. Though we did not record stem decline, we did observe an absence of leader releases before the 1850's. Unfortunately, climate records for the Park are temporally limited and do not cover the period before the leaders released.

Though we did not observe evidence of tree decline during the Little Ice Age, we did observe patterns in vertical height growth among stunted individuals which were associated with climatic variables (temperature, snow depth, and precipitation). All of these variables were positively associated with the timing of releases, suggesting that, in general, a warmer, wetter climate may be related to the vertical height growth observed among these krummholz trees (Tables 2, 3, Fig 6). This is consistent with our hypothesis that warmer and wetter conditions following the end of the Little Ice Age ca 1850, may be related to the vertical height growth of krummholz trees in the FTE. Though our results show an absence of leader release dates in the last 15 yr, when temperatures have been highest, this may be a sampling artifact. The absence of leader releases may also be related to low snow depths in recent years (Fig 5b).

Table 2 T-tests for difference between years of leader release and years of no release (1882–1970). Only variables with p < 0.10 reported

<table>
<thead>
<tr>
<th>Variable</th>
<th>N</th>
<th>P-value spruce and fir</th>
<th>P-value spruce</th>
<th>P-value fir</th>
</tr>
</thead>
<tbody>
<tr>
<td>Running mean annual temp (Ft Collins)</td>
<td>89</td>
<td>0.039</td>
<td>-</td>
<td>0.084</td>
</tr>
<tr>
<td>May snow depth (calculated from Wild Basin snow depth and Longs Peak precip)</td>
<td>76</td>
<td>0.068</td>
<td>-</td>
<td>0.071</td>
</tr>
</tbody>
</table>
Several researchers, in the USA and in Europe, have observed that climatic variables may be associated with the timing of leader release. Kullman (1990, 1991) observed that altitudinal tree-limits in Sweden may have changed as a result of vertical height growth among stunted trees in response to warming following the Little Ice Age. Vale (1987) used rephotography to gauge changes in alpine and subalpine vegetation in the Sierra Nevada. He observed that krummholz stands of whitebark pine have not changed in aerial extent, but that in some areas these trees have experienced increased upright growth. Vale also attributes the change...
in vertical growth of krummholz trees to warmer temperatures between 1910 and 1930 and generally warmer temperatures since the late 1800's.

Similarly, in the southern Rockies, Earle (1993) concluded that growth from krummholz to symmetrical tree form occurred in the Medicine Bow Mountains, ca 120 km north of Rocky Mountain National Park, following the end of the Little Ice Age ca 1850. Earle identified two periods of release based on a small sample, (1827–1935 and 1936–1971, n = 22). Though his release dates differ slightly from ours, his research is consistent with our conclusions that rapidly changing climatic conditions could be the cause of growth form changes in Rocky Mountain National Park. Petersen (1988) also related changes in Engelmann spruce and subalpine fir growth form in the La Plata Mountains of southern Colorado to a wetter and warmer period following the end of the Little Ice Age, though his results are also based on a small sample size.

Climate variables associated with the period of release did not prove strongly significant in this analysis, and there are several possible explanations for this. First, it was difficult to identify the exact location of release on leader stems in the field. Though many stems had an obvious point of release just above mean snow depth, some leader release points were more obscure. This may have created significant error in dating releases, even within 5-yr classes. Second, though many types of climate data are available in the region, many of these records are short, and do not overlap in time with other variables. The climate data do not include records before 1880, the period before most leaders initiated, making it difficult to isolate the effects of climate. Third, other climatic variables in addition to temperature and precipitation variables may be related to leader growth. Wind scouring and ice particle abrasion are important components of the FTE environment (Tranquillini 1979, Baug and Tranquillini 1980, Holtmeier 1985, Hadley and Smith 1986), yet wind data are seldom available, especially for earlier periods.

We examined proxy climate records to supplement the available historical climate record. These proxy climate records indicate that a general trend towards cooler periods, known as the Little Ice Age, occurred between ca 1350 and 1850 A.D. in the northern hemisphere (Jones et al 1982, Grove 1988). Since the 1850's, mean global temperatures have increased by ca 0.45 ± 0.15°C (Houghton et al 1990). In the western US and the Northern Great Plains, the Little Ice Age may have been characterized by a cool, dry climatic regime, relative to current conditions (Fritz et al 1994, Petersen 1994, Meko et al 1995, Brunstein 1996). In the southern Rockies, Brunstein (1996) suggests that frost-rings, ring widths, glacial advances, and historical data point to an extended cool period beginning in 1816 and ending in the 1850's. Climate reconstructions based on tree-rings from a sampling area just south of the Park indicate that this region of the southern Rockies may have experienced cool temperatures in the mid-1600's and a gradual decline in growing season temperature from ca 1700 to 1910 (Veblen pers. comm), Hansen-Bristow et al (1988) identified a significantly cool period 1835 to 1900. Reconstructed flow for the Colorado River at Lees Ferry, Arizona indicate flows below the long-term mean from ca 1750 to 1900, followed by peak flows above the long-term mean between ca 1900 and 1950. If this climate pattern was also true for Rocky Mountain National Park, then the scarcity of leader releases before the 1850's, and especially before the 1900's, might be explained by a cool, dry climate, and the proliferation of leader releases since the 1900's could be related to both increased moisture and increased temperature, consistent with our original hypothesis.

The proliferation of leader releases that we observed has occurred in the absence of significant mortality (<10% in most cases). Furthermore, these leaders have persisted for several decades of variable climate. This vertical stem growth among krummholz trees therefore represents a directional change in the structure of the ecotone from krummholz in the late 1800's to near patch forest tree height at present. Because the timing of leader releases coincided with a warmer and wetter climate, leader growth may continue if the regional climate remains warm and wet. Future predictions of global temperature for the next few decades indicate temperatures may continue to rise, though information about precipitation is equivocal (Houghton et al 1990). Given that current patch forest trees may have been krummholz trees and that current krummholz trees appear to be in transition between krummholz and patch forest, increasing temperatures, in combination with increased moisture, may produce further structural changes in the ecotone.

These structural changes may be associated with the pattern of tree invasion we observed in patch forest openings. As krummholz and patch forest trees grow up, subalpine meadows or openings may become suitable locations for seedling establishment due to changes in microenvironment, given the right climatic condi-

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**Table 3** Correlation coefficients between frequency of leaders and climatic variables in five year classes

<table>
<thead>
<tr>
<th>Variable</th>
<th>N</th>
<th>Corr coeff</th>
<th>P-value spruce and fir</th>
<th>P-value spruce</th>
<th>P-value fir</th>
</tr>
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<tr>
<td>Summer precip (Longs Peak)</td>
<td>10</td>
<td>0.602</td>
<td>0.065</td>
<td>0.020</td>
<td>0.065</td>
</tr>
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tions. This process may ultimately "fill in" patch forest openings, leading to closed forest at higher elevations (Weisburg and Baker 1995a) Whether the current tree-limit will move up in elevation as a result of changing climatic conditions is still unknown. Little tree establishment has been observed above current tree-limit, making it difficult to identify the conditions necessary for regeneration and tree-limit migration (Weisburg and Baker 1995b).

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