Quaking aspen (*Populus tremuloides* Michx.) at treeline: a century of change in the San Juan Mountains, Colorado, USA

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ABSTRACT

During a repeat photography study quaking aspen (*Populus tremuloides* Michx.) was observed invading conifer stands at treeline in the San Juan Mountains of south-western Colorado. Aspen tree core samples were collected from nine plots ranging in elevation from 3192 to 3547 m, and estimated dates of establishment of aspen were grouped into 10-year intervals for analysis. Estimated periods of establishment were compared with century-long climate data records to derive any correlations with aspen invasion. Other disturbance agents, such as fire and livestock grazing were also considered. Quantitative analysis of climate variables suggests that decreased mean spring precipitation and increased mean summer maximum temperature provide optimal conditions for aspen establishment. Episodes of invasion were non-synchronous, but all occurred after 1900, and are likely from seed germination, considered unusual in aspen. Different climate variables explain stand initiation from seed and subsequent peak establishment from vegetative reproduction. Long-term climate records indicate a general warming since the beginning of the 20th century and explain the continued invasion and persistence of aspen at treeline, resulting from asexual reproduction. Short-term climate records identify anomalously cool, moist years that explain rarely observed sexual reproduction in aspen.

Keywords


INTRODUCTION

Quaking aspen (*Populus tremuloides* Michx.) is not a likely candidate for invasion into treeline areas. In the Rocky Mountains, aspen reproduction from seed is rare (DeByle & Winokur, 1985; McDonough, 1985; Kay, 1993; Mitton & Grant, 1996; Romme *et al.*, 1997), as it requires unique environmental conditions. Widespread quaking aspen germination from seeds may not have occurred in the western USA since the last glaciation around 10,000 years ago (McDonough, 1985). Aspen commonly regenerates through vegetative reproduction, or asexual root suckering (Sheppard, 1990; Quinn & Wu, 2001). Disturbances, such as fire, often trigger root suckering that allows for rapid regeneration (Jones & DeByle, 1985; Sheppard, 1990) and can occasionally lead to sexual regeneration (Romme *et al.*, 1997). Under certain conditions aspen can perpetuate itself without a major disturbance, but it is more common as a seral post-fire invader (Betters & Woods, 1981; Mueggler, 1989; Peet, 2000).

Changes in the distribution of subalpine trees within the forest-tundra ecotone throughout western North America have been attributed to climate change (Rochefort *et al.*, 1994). Studies throughout the northern hemisphere have documented tree regeneration, growth-form changes, and elevational adjustments within the ecotone in response to the climatic warming of the first half of the twentieth century (Kearney, 1982; Kuliman, 1986a,b, 1991, 1993; Taylor, 1995; Hesl & Baker, 1997a,b). Tree invasion of montane and subalpine meadows has also occurred as a result of decreased livestock grazing (Vale, 1981; Butler, 1986). Conifers have been the focus of research in western North America at treeline, as deciduous trees are uncommon. A rare quaking aspen (*P. tremuloides* Michx.) stand has been observed at treeline (3600 m) in the Colorado Front Range (Mitton & Grant, 1996), but other research is lacking.

Aspen is the predominant deciduous tree in the Rocky Mountain uplands northward of southern Arizona and New Mexico (Peet, 2000), and is commonly found below treeline.
between 2370 and 3330 m in the San Juan Mountains (Romme
et al., 1999). Although aspen accounts for only c. 5% of forest
cover in the Rocky Mountains, it offers important habitat for
wildlife (Suzuki et al., 1999), provides high biodiversity (Kay,
1997), and is valued for its aesthetic qualities. Intentional fire
suppression, along with removal of fuels by domestic cattle and
sheep grazing are thought to have reduced fire in aspen,
possibly threatening its continued existence (Brown & DeByle,
1987, 1989). Conifers, such as Engelmann spruce (Picea
eengelmannii [Parry] Engelm.) and subalpine fir (Abies
lasiocarpa [Hook] Nutt) may successionally replace aspen
stands (Mueggler, 1985; Crawford et al., 1998). Conversely,
Romme et al. (2001) suggest that there is no evidence
indicating widespread aspen replacement by conifers in the
San Juan Mountains. Thus, the successional status of aspen
forests remains uncertain.

Repeat photography and dendrochronology are tools that
have been widely used to resolve controversies regarding
landscape change (Rogers et al., 1984; Kipfmueller & Swetnam,
2001). Notable repeat photography studies have been
conducted in the high country of Yosemite National Park (Vale &
Vale, 1994), Yellowstone National Park (Meagher & Houston,
1998), the Colorado Front Range (Veblen & Lorenz, 1991), the
western slope of the Colorado Rocky Mountains, including
scenes in the northern San Juans (Manier & Laven, 2002), and
the state of Colorado (Noel & Fielder, 2001). Moreover,
Petersen (1988) examined treeline environments using four
repeat photos in the La Plata Mountains, a sub-range of the
San Juans. Such studies typically analyse landscapes and their
changing environment over a temporal scale of c. 100 years.
Tree rings analysed during dendrochronological studies also
provide an excellent natural archive of ecological variation,
which can be used to reconstruct ecosystem changes spanning
centuries (Kipfmueller & Swetnam, 2001). For instance,
Romme et al. (2001) conducted aspen dendrochronology
work at middle elevations in the western San Juan National
Forest to examine disturbance regimes and landscape patch
dynamics.

We studied the invasion of quaking aspen into treeline areas
in the San Juan Mountains of Colorado and the potential
causes. We hypothesized that the quaking aspen found
invading at treeline were the result of germination from seed,
de spite the accepted rarity of such occurrences, and that
changing climatic conditions were the catalyst for such events.
Furthermore, we hypothesized the invasion is an increase in
the elevational range of aspen, so that aspen is not decreasing
in abundance across the landscape. Examining recent altitu-
dinal migrations in quaking aspen distribution is essential for
not only determining treeline dynamics, but for understanding
the species’ response to long-term climate change.

STUDY AREA
The San Juan Mountains of south-western Colorado encom-
pass c. 31,080 km² and form part of the southern boundary of
the Southern Rocky Mountain Physiographic Province
(Thornbury, 1965). The mountains are chiefly composed of
Tertiary volcanic rocks, but in the northern and western parts
of the mountains and locally elsewhere, bodies of older, highly
metamorphosed, sedimentary, and Precambrian rock are
exposed (Larsen & Cross, 1956).

Although a detailed climatic study of the San Juans has not
been published, data are obtainable from weather stations
throughout the region (Colorado Climate Center). Data from
Telluride, Silverton, and Lake City were selected based upon
their high elevation (2667, 2871, and 2710 m, respectively),
long history (since 1901, 1907, and 1906, respectively) and
proximity to study sites. Data from these three stations were
averaged to produce an estimated regional average. Mean
annual temperature for the three is 3.2 °C with an average high
of 12.4 °C and an average low of −5.9 °C. There are an average
of 254 days when the minimum temperature is below 0 °C,
indicating a mean of 111 frost-free days during the summer.
The San Juans experience a summer rainy season that is
typically initiated in July due to an influx of monsoonal air
from the Gulf of Mexico and Gulf of California (Mitchell,
1976; Keen, 1996). Winter storms fueled by intrusions of
Pacific air (Mitchell, 1976) begin blanketing higher elevations
in snow by mid-November and generally cease in early May
(Keen, 1996). The mean annual precipitation for the region is
50.83 cm. However, temperature and precipitation values
could vary considerably from the three stations as a result of
an increase in elevation. At high elevations air temperatures are
suppressed by strong winds (Villalba et al., 1994) and preci-
pitation varies based upon location with respect to the
Continental Divide.

Higher elevations (2580–3550 m) of the San Juan Moun-
tains support subalpine forests of Engelmann spruce and
subalpine fir interspersed with aspen groves and meadows.
Dominant subalpine meadow species include Thurber’s fescue
(Festuca thurberi) and Parry’s oatgrass (Danthonia parryi).
Treeline areas of the San Juan Mountains have been subject to
sheep grazing since the middle- to late-1800s (Dubois, 1903).
Sheep most often are grazed in high-elevation meadows, but
do sometimes use forests. Many of our study sites are on very
steep slopes and did not contain evidence of recent sheep
grazing.

METHODS
To obtain early photographs of treeline in the San Juan
Mountains we systematically searched the US Geological
Survey Photographic Library, the Colorado Historical Society,
and the Western History Collection at the Denver Public
Library (Table 1). Nineteen photographs were located and
rephotographed, but only three are used and reproduced in
this study (see Elliott, 2003 for other photographs). Once in
the field, we located and rephotographed the original photos
using topographic maps and field notes that usually accom-
panned the original photos. If adequate original notes were not
available, we found the general location using landforms
displayed in the photograph and the exact photo point using
large boulders and other identifiable objects in the foreground. This is a trial-and-error process of repeated moves with the camera, until the scene best matches the original (Gruell, 1980; Rogers, 1982). We took all the pictures in the summer of 2002 with a digital camera. For each site (Fig. 1) we completed a field form, noting the date, time, direction of view, aspect of slope, and the current vegetation. We systematically scanned the photos and recorded visible changes in the stand structure and type of vegetation by comparing the original photo to the present-day scene. Other obvious ecological changes, such as invasions, were noted as well. Furthermore, we used a global positioning system to record the geographic coordinates of each photo point.

After discovering from two of the rephotos that aspen had apparently invaded into established conifer stands near treeline (Figs 2 and 3), we focused additional research on aspen. By automobile and on foot, using binoculars and observation from high points, we searched the San Juans for stands visually similar to those in Figs 2 and 3, containing aspen among or adjacent to conifers at treeline. These types of stands occurred only on southerly-facing slopes; northerly-facing slopes lack aspen near treeline (Fig. 4). More than 15 stands were located, but many were on precipitous slopes. However, we were able to access and sample the two stands in Figs 2 and 3 plus six other stands in the San Juans (Fig. 1). One additional stand, c. 20 km northeast of Leadville, Colorado near Fremont Pass was sampled for comparison with the San Juan sites.

The stands were sampled using rectangular plots of varying sizes (75–200 m²) because stem density and stem size varied (Taylor, 1995). Plots were placed in a representative portion of the stand and the diameter at breast height (dbh) of all aspen rooted within the plot (> 2 cm) was measured. A core was removed from as close to the base as possible with an increment borer to date tree origin. Aspen saplings (< 2.0 cm dbh) were cut off at ground level and a basal disk was removed. Basal disks (n = 57) are 14% of the total aspen collection (n = 400). An average of three coniferous trees (Engelmann spruce and subalpine fir) were also cored (total n = 31), but one stand lacked conifers (Table 2). The elevation, geographic coordinates, and slope aspect of each plot were recorded (Table 2).

All cores and basal disks were mounted and sanded in the laboratory according to standard dendrochronological procedures (Stokes & Smiley, 1968). Annual rings were counted using a binocular microscope. Cross-dating was not used due

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**Table 1** Historical photographs retaken during the Summer of 2002. The elevation and slope aspect refer to the photo point.

<table>
<thead>
<tr>
<th>Photo number</th>
<th>Original photographer</th>
<th>Original number</th>
<th>Original year</th>
<th>Elevation (m)</th>
<th>Slope aspect (°)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Unknown</td>
<td>Unknown</td>
<td>1902</td>
<td>3268</td>
<td>275 W</td>
</tr>
<tr>
<td>2</td>
<td>W.H. Jackson</td>
<td>546</td>
<td>1875</td>
<td>3228</td>
<td>305 NW</td>
</tr>
<tr>
<td>3</td>
<td>C.W. Cross</td>
<td>1016</td>
<td>1909</td>
<td>3654</td>
<td>230 SW</td>
</tr>
</tbody>
</table>

Source: United States Geological Survey Photographic Library, Denver, CO.

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**Figure 1** Study area in the San Juan Mountains, Colorado. Triangles represent the weather stations used to calculate a regional mean. Photo points are circles and aspen stands are crosses. Note that 1 and 2 represent both simultaneously. One additional aspen stand about 20 km northeast of Leadville, Colorado CUTM 39828 Easting, 4357338 Northing is not shown on the map.
to the young age of the trees (e.g. Hessl & Baker, 1997a). Of the 400 aspen sampled, 81% (324 trees) were successfully aged, while 12% had rotten centres, and 7% consisted of chalk-white cores that did not provide identifiable annual rings (Table 2). All conifers sampled (n = 31) were successfully aged. Basal disks of aspen were sliced into two to four sections, 5 mm wide, which were all counted (Hessl & Baker, 1997a,b). The oldest date reached was accepted as the age of the tree. Ages of core samples that did not contain the pith (156 of 324) were estimated based upon the width and perpendicular distance between the earliest 10 annual rings (Norton et al., 1987). To reflect the imprecision of dating, ages were grouped into 10-year classes for analysis. Mean climatic data from Telluride, Silverton, and Lake City were used to identify past changes in temperature and precipitation that may have facilitated tree establishment. A single station in a complex mountain environment cannot be relied upon to be representative of the entire region (Villalba et al., 1994). We calculated nine summary statistics, grouped into the same 10-year intervals used to summarize tree ages (Fig. 5). In preparation for regression analysis, scatter plots of each climate variable and pooled aspen establishment were examined to see if these variables had a linear relationship or if transformations were needed. Pearson’s correlation was used to measure the individual relationships. Best subsets multiple regression (Rawlings, 1988) was used to identify the best combination of predictors of aspen establishment among the climate variables. However, available climate data are limited; although snow melt data and other data might be useful, these data are unavailable.

**RESULTS**

**Age structure**

The aspen plots ranged in elevation from 3192 to 3547 m and were predominantly located on slopes with a southerly aspect (Table 2). Aspen stands near treeline have the appearance of an invasion, since they typically are uniformly small trees within or adjacent to taller conifers (Figs 2 and 3).
Aspen invasion at treeline is not synchronous among the nine plots (Fig. 6). Aspen did not establish before 1900 in any of the stands, and only 6% of the trees originated before 1921 (Fig. 6). Moreover, only three stands (1, 5, 7) contain aspen dating before 1921 (Fig. 6). These three stands have similar structural configurations with aspen intermixed among older conifers (Table 2), but do not exhibit any distinctive environmental characteristics within the plot suggesting an alternate origin. In plots 1 and 7, peak establishment dates precede peaks in all other plots and stands are generally dominated by older aspen. Plot 5 is unique because it experienced a peak in establishment between 1951 and 1940 with 17 trees, more than double the total aspen established during the same period in any other stand (Fig. 6). As a whole, however, aspen trees presently at treeline became established mostly between 1971 and 1980 (26%), followed by 1961 and 1970 (21%). Five of the nine (56%) plots had peak establishment during this period (Fig. 6). The distribution of estimated origin years within each stand varies considerably among the plots sampled, but all are uneven-aged (Betters & Woods, 1981) (Fig. 6).

The Engelmann spruce and subalpine fir sampled often predate aspen stand invasion, but not always. Estimated dates of establishment range from before 1800 to between 1971 and 1980 (Fig. 6). Most conifers originated between 1951 and 1970, but 19% became established before 1900 (Fig. 6). Conifers predated aspen in 67% of the plots, but aspen preceded conifer establishment in one stand (plot 6) and coincided with it in another (plot 3) (Fig. 6). The three oldest aspen stands (1, 5, and 7) have the consistently oldest conifers, while conifers are not much older than aspen in the younger aspen plots, with the exception of plot 9 (Fig. 6).

Climate effects

Pooled dates of aspen establishment at treeline for all nine stands were plotted against mean temperature and precipitation data (Fig. 5). Two possible patterns are visible. First, the decade of 1951–60 precedes the most abundant period (1961–80) of aspen establishment. During 1951–60, three of five temperature plots reach a 100-year peak, and precipitation values reach some of their lowest means of the century (Fig. 5); immediately after this, every temperature variable significantly decreases and half of the precipitation values notably increase (Fig. 5). Second, the high aspen establishment during 1961–80

Figure 3 Photo site 2. View is to the northwest looking up into Boren’s Gulch in the La Plata Mountains. The original photo (a) was taken by W.H. Jackson in 1875. Source: United States Geological Survey Photographic Library, Denver, CO. Note the aspen invasion in the middle of the recent photograph (b) and subsequent conifer growth within the aspen.
appears to coincide with both high mean summer maximum temperature and low mean spring precipitation (Fig. 5).

Visual scatter plot analysis showed that certain transformations were needed. A log transformation was performed on mean spring precipitation to linearize the relationship with pooled aspen establishment. Three other independent variables (mean summer minimum and maximum temperature and mean summer precipitation) were log transformed to linearize their relationships with pooled aspen establishment. Pearson’s correlation was used to determine the strength of relationship, and we obtained coefficients ranging in absolute value from 0.069 to 0.663 (Table 3). Mild correlations ($r = 0.400–0.700$)

**Table 2** Sampled aspen plots. Plot locations are given in Fig. 1

<table>
<thead>
<tr>
<th>Plot</th>
<th>Elevation (m)</th>
<th>Aspect (°)</th>
<th>Plot size (m²)</th>
<th>Aspen and conifer stand configuration</th>
<th>Number of aspen dated</th>
<th>Number of conifers dated</th>
<th>Number of rotten cores</th>
<th>Number of uncountable cores</th>
<th>Total trees sampled</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>3547</td>
<td>130 SE</td>
<td>200</td>
<td>Intermixed</td>
<td>29</td>
<td>4</td>
<td>8</td>
<td>8</td>
<td>49</td>
</tr>
<tr>
<td>2</td>
<td>3192</td>
<td>125 SE</td>
<td>86</td>
<td>Individual</td>
<td>36</td>
<td>5</td>
<td>4</td>
<td>0</td>
<td>45</td>
</tr>
<tr>
<td>3</td>
<td>3192</td>
<td>175 S</td>
<td>126</td>
<td>Individual</td>
<td>32</td>
<td>1</td>
<td>8</td>
<td>6</td>
<td>47</td>
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<tr>
<td>4</td>
<td>3431</td>
<td>135 SE</td>
<td>150</td>
<td>Individual</td>
<td>41</td>
<td>5</td>
<td>3</td>
<td>1</td>
<td>50</td>
</tr>
<tr>
<td>5</td>
<td>3452</td>
<td>160 S</td>
<td>120</td>
<td>Intermixed</td>
<td>31</td>
<td>5</td>
<td>11</td>
<td>3</td>
<td>50</td>
</tr>
<tr>
<td>6</td>
<td>3339</td>
<td>125 SE</td>
<td>185</td>
<td>Intermixed</td>
<td>34</td>
<td>3</td>
<td>8</td>
<td>5</td>
<td>50</td>
</tr>
<tr>
<td>7</td>
<td>3447</td>
<td>215 SW</td>
<td>180</td>
<td>Intermixed</td>
<td>40</td>
<td>4</td>
<td>4</td>
<td>2</td>
<td>50</td>
</tr>
<tr>
<td>8</td>
<td>3447</td>
<td>110 E</td>
<td>75</td>
<td>Individual</td>
<td>38</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>40</td>
</tr>
<tr>
<td>9</td>
<td>3483</td>
<td>240 SW</td>
<td>90</td>
<td>Intermixed</td>
<td>43</td>
<td>4</td>
<td>2</td>
<td>1</td>
<td>50</td>
</tr>
<tr>
<td>Mean</td>
<td>3392</td>
<td>157 SE</td>
<td>135</td>
<td>Intermixed</td>
<td>36</td>
<td>3</td>
<td>5.4</td>
<td>3</td>
<td>47.9</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td></td>
<td>324</td>
<td></td>
<td>31</td>
<td>49</td>
<td>27</td>
<td>431</td>
<td>431</td>
</tr>
</tbody>
</table>

**Figure 4** Photo site 3. View is toward the southwest from the south-western spur of Bent Peak. The original photo (a) is from C.W. Cross in 1909. Source: United States Geological Survey Photographic Library, Denver, CO. In the recent photo (b) note the lack of aspen on a northeast-facing slope.
suggest that high pooled aspen establishment is favored by low mean spring and summer precipitation and high mean summer maximum temperature (Table 3).

Best subsets regression generated a three variable model (mean spring, mean annual, and mean summer precipitation) with an $R^2_{adj}$ value of 0.549. This was the simplest model with $R^2_{adj}$ near its maximum (Rawlings, 1988). The model suggests that both mean spring and summer precipitation are negatively correlated with pooled aspen establishment, but that mean annual precipitation is positively correlated (Pooled aspen establishment = $211–326 \times$ mean spring precipitation $+ 3.87 \times$ mean annual precipitation $– 31.5 \times$ mean summer precipitation). Overall, both correlation and regression analysis suggest that low spring and summer precipitation lead to increased aspen establishment at treeline, which is amplified during years with abundant snowfall and warm summers.

**DISCUSSION**

Aspen stands were found to be regenerating and increasing in density in the San Juan Mountains (Figs 2 and 3). This is consistent with another study (Manier & Laven, 2001, 2002). Conversely, many researchers argue that aspen is decreasing in abundance across the landscape due to the initiation of fire suppression policies since Euro-American settlement (Brown & DeByle, 1987; Mueggler, 1989; Bartos et al., 1994; Kay, 1997). However, our repeat photos indicate continued aspen regeneration, denser, taller aspen stands, and aspen invasion into grasslands (Figs 2 and 3).

There are several reasons that we think aspen invasion at treeline occurred as the result of germination from seed. First, in the sampled plots there were no standing aspen that originated before A.D. 1900 (Fig. 6), nor were there any large downed trees within the stand that could have provided the
necessary root suckers. Aspen can live much longer than 100 years, with the oldest recorded ones surpassing 200 years (Betters & Woods, 1981; Mueggler, 1989). Moreover, other aspen stands were either absent from the mountainside or were a few hundred metres downslope. Asexual root suckering upslope this distance is unlikely. More likely, aspen invaded up onto these slopes by episodes of sexual reproduction beginning shortly after A.D. 1900.

Episodes of aspen sexual reproduction have been observed following intense fires and periods of favourable weather conditions in Yellowstone National Park (Kay, 1993; Romme et al., 1997) and in the Chiricahua Mountains of south-eastern Arizona (Quinn & Wu, 2001). Despite the rarity of regeneration from seed described in the literature, sexual reproduction may be a more general trait than has been previously recognized (Kay, 1993; Quinn & Wu, 2001). The aforementioned studies suggest that severe disturbance events

![Figure 6](image-url) Estimated year of establishment of quaking aspen (*Populus tremuloides* Michx.) and conifers. Plot locations are given in Fig. 1.

Table 3 Pearson's correlation coefficients ($r$) between pooled aspen establishment at treeline and climatic variables in 10-year classes. Pooled aspen establishment is the dependent variable ($y$) and the listed climate variables are independent variables ($x$).

<table>
<thead>
<tr>
<th>Climate variable</th>
<th>$n$</th>
<th>$r$</th>
<th>P-value</th>
<th>Transformation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean annual temperature</td>
<td>10</td>
<td>0.133</td>
<td>0.715</td>
<td></td>
</tr>
<tr>
<td>Mean spring temperature</td>
<td>10</td>
<td>−0.091</td>
<td>0.802</td>
<td></td>
</tr>
<tr>
<td>Mean summer temperature</td>
<td>10</td>
<td>0.279</td>
<td>0.436</td>
<td></td>
</tr>
<tr>
<td>Mean summer minimum temperature</td>
<td>10</td>
<td>−0.069</td>
<td>0.850</td>
<td>log $y$</td>
</tr>
<tr>
<td>Mean summer maximum temperature</td>
<td>10</td>
<td>0.584</td>
<td>0.076</td>
<td>log $y$</td>
</tr>
<tr>
<td>Mean annual precipitation</td>
<td>10</td>
<td>−0.389</td>
<td>0.267</td>
<td></td>
</tr>
<tr>
<td>Mean spring precipitation</td>
<td>10</td>
<td>−0.663</td>
<td>0.036</td>
<td>log $x$</td>
</tr>
<tr>
<td>Mean summer precipitation</td>
<td>10</td>
<td>−0.425</td>
<td>0.220</td>
<td>log $y$</td>
</tr>
<tr>
<td>Mean May precipitation</td>
<td>10</td>
<td>−0.333</td>
<td>0.347</td>
<td></td>
</tr>
</tbody>
</table>
paired with specific meteorological conditions allow for aspen seed germination spanning a latitudinal range from near the USA–Mexican border to the Central Rocky Mountains.

**Disturbance events**

In the subalpine forests of Colorado, fire has historically been the most important form of natural disturbance (Veblen et al., 1994; Peet, 2000). These fires are characteristically infrequent, but typically stand-replacing, resulting in extensive exposure of bare mineral soil that facilitates new stand development (Baker & Veblen, 1990; Veblen et al., 1991, 1994; Peet, 2000; Kulakowski & Veblen, 2002). No estimates are available for fire frequency in the subalpine forests of the San Juans, but the fire rotation in northern Colorado is estimated to be c. 350 years (Buechling, 2003). Aspen typically flowers in the spring and produces variable amounts of seeds from year-to-year, but these typically fail to germinate due to competition from other vegetation or from inadequate exposure to sunlight (Mitton & Grant, 1996; Romme et al., 1997, 1999). However, crown fires promote stand development from seed due to the creation of bare mineral soil devoid of plant-to-plant competition and from destruction of the canopy allowing necessary solar radiation to penetrate the forest floor.

This scenario may not fit quaking aspen at treeline in the San Juans because conifers were already established prior to aspen invasion in two-thirds of the plots sampled (Fig. 6). Fires that burn across variable topography, as in treeline environments, can result in a mosaic of heavily-burned areas where bare mineral soil is exposed interspersed with patches that burned as surface fire (Quinn & Wu, 2001; Buechling, 2003). The conifers sampled could have been within the areas that experienced surface fire conditions. However, there was no visible evidence in aspen plots in the field or in the photos suggesting such stand-replacing fires occurred. Moreover, it is unlikely that the conifers would have been spared if indeed a fire did recently burn through. The intermixed stand configuration of plots 1, 5, 6, 7, and 9 (Table 2), also visible in Figure 2, could not have arisen from crown fire. If fire were the explanation, it is unclear why surface fires would have led to aspen appearing after 1900 in established conifer stands when no earlier aspen were found (Fig. 6). A more likely explanation than fire history is a climate change.

**Climate**

Recent altitudinal migrations in subalpine tree distribution can be compared with climatic records to allow for an examination of relationships between the two at a finer resolution (Rochefort et al., 1994). In the San Juans, invasion was limited to southerly-facing slopes with aspects between 110° East and 240° Southwest. We rephotographed six scenes at treeline with northerly-facing aspects ranging from 300° Northwest to 55° Northeast and discovered no aspen present (e.g. Fig. 4). If climate was not influential, then why is aspen invasion at treeline absent on northern slopes in the San Juan Mountains? Kay (1993) observed that most stands produced from seed occurred on south-facing to east-facing slopes in the Greater
mountain hemlock (both spruce and birch in Sweden, Taylor (1995) studied America and Europe have linked tree invasion at treeline to
Mountains, then the lack of aspen germination before 1900 this early twentieth century precipitation, primarily in the
(1994) attributed forest expansion visible in his rephotos to
with this warming was the second wettest period of the past
1994; Mann et al. c. data suggest unprecedented warming since c. A.D. 1900 (Fritts et al., 1979; Bradley, 1980; Fritts & Lough, 1985; Petersen, 1994; Mann et al., 1998, 1999; Briffa et al., 2001). Coinciding with this warming was the second wettest period of the past millennium (1905–28) (D’Arrigo & Jacoby, 1991). Petersen (1994) attributed forest expansion visible in his rephotos to this early twentieth century precipitation, primarily in the form of snow. If these trends are true for the San Juan Mountains, then the lack of aspen germination before 1900 might be a result of cooler, drier conditions, whereas post-1900 establishment could be linked to both an increase in temperature and precipitation. Other studies in both North America and Europe have linked tree invasion at treeline to post-Little Ice Age warming. Kullman (1986a, 1989) observed both spruce and birch in Sweden, Taylor (1995) studied mountain hemlock (Tsuga mertensiana [Bong.] Carr.) in Lassen Volcanic National Park, California, Woodward et al. (1995) researched mountain hemlock and subalpine fir in the Olympic Mountains, Washington, and Hessl & Baker (1997a) documented spruce and fir invasion in Rocky Mountain National Park, Colorado.

After the beginning of aspen invasion in the early 1900s, can shorter-term climatic fluctuations explain variation in the initiation of sampled stands (Fig. 6)? The establishment of stands 1, 5, 6, and 7 (1900–30) coincides with a very moist period (Bradley, 1976; D’Arrigo & Jacoby, 1991) and relatively cool temperatures compared with the rest of the twentieth century (Bradley, 1980; Fritts & Lough, 1985). These short-term climatic conditions (Fig. 5) are consistent with aspen seeds needing continuing moist soil and cooler temperatures to germinate and survive during the first several years (McDonough, 1985; Kay, 1993; Romme et al., 1997, 1999; Quinn & Wu, 2001).

However, initiation of the other five stands (1931–70) does not appear superficially to match this climate pattern. The 1930s were very warm, the 1940s were wet, and there was a severe drought during some years between 1950 and 1970 (Bradley, 1976, 1980; Grissino-Mayer, 1996; Cook et al., 1999). However, annual climate data between 1931 and 1970 reveals anomalously cool, wet years (Fig. 7). These years are 1938, 1941, 1947, 1952, 1964, and 1965 based upon temperature and precipitation values (Fig. 7). Despite below average precipitation in 1952, it was the coldest year since 1939 and the only relatively cool year with near-mean precipitation totals during the 1950s (Fig. 7). These years are the years that would be consistent with climatic conditions known to enable aspen to sexually reproduce and initiate stand development in plots 2, 3, 4, 8, and 9.

Different climate variables might explain stand initiation from seed and subsequent peak establishment from vegetative reproduction. Initial seed germination was probably facilitated by localized cool, moist conditions, whereas later peaks in establishment could be the result of asexual reproduction in response to warmer, drier conditions. The period of peak regeneration often occurred 10–30 years after the earliest tree established in each stand (Fig. 6), suggesting vegetative reproduction. Overall, the period of peak aspen regeneration occurred between 1961 and 1980 when 47% of the sampled trees originated (Fig. 6). Furthermore, the sampled conifers demonstrate a peak in establishment from 1951 to 1970, which corresponds with similar studies of subalpine coniferous trees in the Canadian Rockies (Kearney, 1982), Olympic Mountains, Washington (Woodward et al., 1995), and in Rocky Mountain National Park (Hessl & Baker, 1997a). These studies attributed tree invasion to various climatic variables, including some that we used in our analysis (e.g. mean summer minimum temperature, mean spring temperature, and mean summer precipitation), but not mean spring precipitation and mean maximum summer temperature. Despite the lack of similar results, peak aspen establishment appears to be favoured by warm and dry climatic conditions and is most likely the result of enhanced asexual reproduction.

There have not been other dendrochronological studies of aspen at treeline in the western USA for comparison, but we cannot find evidence to support any other phenomena besides climate. Baker et al. (1997) discovered that climatic fluctuations had only weak, if any, correlation to aspen cohort regeneration in the elk winter range (<2800 m) in Rocky Mountain National Park and that ungulate browsing was the controlling factor. However, Romme et al. (2001) state that ungulate browsing is of minimal importance in the San Juan National Forest and surrounding area. Ungulate grazing effects are diminished in the San Juan Mountains because of the relatively high mean elevation, therefore preventing easily accessible winter range habitat. Also, if they occurred, fires did not leave visible evidence, but we cannot exclude fire from having a role in aspen invasion. However, if fire was influential, climate still needs to have been favourable after such events.

Overall, the relative warming trend since the late 1800s explains the general invasion at treeline. If a continually warming climate is indeed what our future holds, then we would expect conditions to remain conducive for aspen regeneration at treeline through enhanced root suckering. Moreover, possible alternate disturbance regimes created by a warming climate with increased fire frequency or severity would appear favourable to expansion at higher elevations. Ultimately, the fate of quaking aspen establishment will depend upon the temporal sequence of both temperature
and precipitation regimes, where cooler, moist conditions favour regeneration from seed and a warmer, drier climate promotes vegetative reproduction.

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REFERENCES


Colorado Climate Center. Atmospheric Science Department. Colorado State University. Fort Collins, Colorado. (URL: http://ccc.atmos.colostate.edu/mlfy_form.html)


**BIOSKETCHES**

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