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Disturbance and climatic influences on age structure of ponderosa pine at the pine/grassland ecotone, Colorado Front Range

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Abstract. In the Colorado Front Range, disturbances and climatic variation influence stand structure of ponderosa pine (*Pinus ponderosa*) along the lower timberline ecotone. Over the past 100 years there has been a shift to a greater density and extent of ponderosa pine at the forest-grassland boundaries. Ponderosa pine regeneration at lower timberline appears to be influenced by fires in the 1860s and decreased grazing pressure in the 1970s–1980s. Climatic variation may also have influenced age structure, even though analyses of age structure at a 10-year class scale prevented the detection of climatic influences occurring at a finer scale. These changes in disturbance regimes, possibly together with moister springs/early summers, created favourable conditions for the increase in density and extent of ponderosa pine at lower timberline ecotone.

Key words. Dendrochronology, timberline, fire, grazing.

INTRODUCTION

Stand-scale patterns of seedling establishment may be interpreted from age structure analysis together with past records of disturbance, climate, and other factors related to site history (Lorimer, 1985). Yet since static age structure indicates only survival, to identify pulses of establishment we must assume that age structure is shaped mainly by recruitment rather than by episodes of mortality. In this study, dendrochronological techniques were used to develop long records ($\approx$300 years) of disturbance history, climatic variation and tree establishment for different habitat types along lower timberline in the Colorado Front Range.

Lower timberline refers to the lower elevational limit of forest cover, often controlled by water availability and other climatic factors (Wardle, 1974). During the last 10,000 years in the Rocky Mountains, climatic variations affected the ecotone from the plains grasslands to the coniferous forest (Daubenmire, 1943; MacDonald, 1989). On a shorter temporal scale, many forest-grassland ecotones in the western United States appear unstable, experiencing tree invasion since the mid-1800s. For example, ponderosa pines (*Pinus ponderosa*) have invaded the prairies while junipers (*Juniperus monosperma*) have spread in both the Southwest and the Great Basin (Foster, 1917; Johnsen, 1962; Burkhardt & Tisdale, 1976; White, 1985) (nomenclature follows Marr, 1965). World-wide, several pine species are invasive and indeed may be considered serious weeds in places where they have been introduced due to impacts on watersheds, grazing lands and protected areas (Richardson *et al.*, 1994; Rejmanek & Richardson, 1996). Besides Northern Hemisphere cases, Southern Hemisphere pine invasions are well documented in Argentina, Australia, Chile, Madagascar, Malawi, New Zealand, South Africa, and Uruguay (Richardson *et al.*, 1994).

Climatic variability is an important factor affecting regeneration dynamics and successional processes in forest communities (Prentice, 1992). Such climatic impacts may be especially important at ecotonal limits, and ecotones may provide early detection of climatic change (Solomon, 1986; di Castri *et al.*, 1988; Dryer *et al.*, 1988; Hansen *et al.*, 1992; Noble, 1993). In addition, the extent of climate induced vegetation change is likely to be indirectly affected by varying degrees of disturbance (Overpeck *et al.*, 1990; Peet, 1981; Johnson & Larsen, 1991; Sirois & Payette, 1991; Veblen & Lorenz, 1991; Neilson, 1993). Although mature ponderosa pine display a wide ecological tolerance due to long tap roots, frequent droughts in spring and/or competition for water with grasses may limit ponderosa pine establishment in lower timberline forests (White, 1985). In addition, low temperatures can restrict ponderosa pine seedling establishment due to direct damage to tissue, freezing of soil, and through frost heaving (Schubert, 1974).

In addition to climatic factors, pine regeneration at lower timberline appears to be increased by altered disturbance regimes that reduce competition with ground cover. Many ecosystems world-wide contain pine species which have been affected by fire suppression (Richardson & Bond, 1991). In western North America frequent natural or human-initiated fires may limit tree invasion into grasslands by killing tree seedlings (Buell & Buell, 1959; Johannessen *et al.*, 1971; Bragg & Hulbert, 1976). Conversely, cessation of periodic

fires results in increases in the density and distribution of particular conifer species (Kilgore & Sando, 1975; Burkhardt & Tisdale, 1976; Parsons & DeBenedetti, 1979; Romme, 1982; Vale, 1982; Savage, 1989). In western United States, previous studies have related increases in ponderosa pine densities primarily to fire suppression during this century (Gruell, 1983; Covington & Moore, 1994; Savage *et al.*, 1996; Covington *et al.*, 1997) and to changes in grazing history (Marr, 1961; Bahre, 1993). In the Colorado Front Range, fire suppression appears to correspond well with the timing of tree invasions (Peet, 1981; Veblen & Lorenz, 1986; Veblen & Lorenz, 1991; Goldblum & Veblen, 1992; Mast *et al.*, 1997).

The nearly ubiquitous charcoal found in the soils of the southern Rocky Mountain Front Range forests suggests wide-spread importance of fire as a stand-initiating disturbance (Peet, 1981; Veblen, 1986). Ponderosa pine woodlands, with ample flammable grasses and forbs, burned frequently (every 5–12 years) in the Rocky Mountains in the past due to a combination of lightning fires and aboriginal-set fires for at least 8000 years (Weaver, 1951; Husted, 1965; Benedict, 1974; Arno, 1980; Dieterich, 1980; Goldblum & Veblen, 1992). Then when the Euro-American settlers and prospectors arrived in a given area, as they did in Boulder County in 1858, the frequency of wildfires dramatically increased (Veblen & Lorenz, 1986; Goldblum & Veblen, 1992). Finally, fire suppression policies implemented since the 1920s in the Colorado Front Range resulted in reduced frequency and extent of wildfires (Gruell, 1980; Veblen & Lorenz, 1986; Peet, 1988).

In addition to fire, overpopulations of mule deer (*Odocoileus hemionus*) and elk (*Cervus canadensis*) are special problems in Rocky Mountain National Park and the mountain parks of Boulder County. This population build-up is usually attributed to a combination of protection from hunting during most of the twentieth century and the decimation of predator populations. Mule deer and elk often cause severe damage or even kill ponderosa pines by browsing on terminal shoots of small trees and by rubbing their antlers against the bark (Heidmann, 1972; Heidmann *et al.*, 1982).

Moderate livestock grazing may change forest structure and facilitate tree invasion by exposing bare mineral soil and reducing competition from grasses (Rummel, 1951). However, intense grazing may prevent widespread tree invasion due to trampling and direct herbivory on seedlings and saplings (Dunwiddle, 1977; Richardson *et al.*, 1994). Due to a lack of precise historical data, the role of grazing on forest structure in the Colorado Front Range is speculative.

In this study, we examined the possible influences of climatic variation and disturbance on changes in ponderosa pine stand structure along the lower timberline ecotone in the Colorado Front Range. We hypothesize that the rate and timing of tree invasion is influenced by climatic variation. Specifically, moist springs and early summers are hypothesized to result in greater tree seedling establishment rates. To test this hypothesis, we compared tree population age structures to the instrumental record of climatic variation and the tree-ring record. Given the confounding and co-occurring changes in disturbance history and climate, it is not possible to prove that climate causes tree invasions. Hence, the goal of this research is to determine if the timing of tree establishment is consistent with the hypothesis that establishment depends on climatically favourable conditions.

STUDY AREA

This study was conducted in the montane zone (1800–2600 m) in Rocky Mountain National Park and Boulder County on the eastern slope of the Colorado Front Range. The Colorado Front Range, a north–south orientated massif creating the easternmost range of the Rocky Mountains, extends from near Canon City northward to 150 km south from the Wyoming border (Chronic & Chronic, 1972). The bedrock is comprised of a core of acidic Precambrian intrusives, penetrated by acidic Tertiary plutons (Thornbury, 1965; Ives, 1980). In the lower montane forest, although ustolls also occur on south-facing slopes, cryoboralf soils dominate with typically rocky, thin, immature, and slightly acidic soil characteristics (Johnson & Cline, 1965; Peet, 1981).

According to climatological records from Estes Park at *c.* 2100 m elevation and near the sampling sites in Rocky Mountain National Park (Fig. 1), mean annual precipitation is 540 mm, with January being the driest month and May the wettest month. The mean July daily temperature maximum is 25 °C, while the mean daily temperature minimum is −10 °C in January. According to climatological data from the City of Boulder at 1800 m elevation and near the Boulder County sample sites, mean annual precipitation is 395 mm, with January being the driest month and May the wettest month. July mean daily temperature maximum is 31 °C, while the mean daily temperature minimum is −8 °C in January. Extremely windy conditions, not uncommon throughout the Colorado Front Range, may also influence tree establishment along the lower timberline ecotone.

The lower montane zone in the Colorado Front Range (from *c.* 1800 and 2600 m) is characterized by ponderosa pine on south-facing slopes, with Douglas-fir (*Pseudotsuga menziesii*) and ponderosa pine on north-facing slopes. Rocky mountain juniper (*Juniperus scopulorum*) is also present in the drier, open sites on the south-facing slopes. South-facing slopes have a lower tree density and higher herbaceous density than adjacent cooler and moister north-facing slopes. Common understory species in the lower timberline forests include common juniper (*Juniperus communis*), wax currant (*Ribes cereum*), waxflower (*Jamesia americana*), kinnikinnik (*Arctostaphylos uva-ursi*), spike fescue (*Leucopoa kingii*), blue grama grass (*Bouteloua gracilis*), and buffalo grass (*Buchloe dactyloides*) (Marr, 1965). Yucca (*Yucca glauca*) and prickly pear cacti (*Opuntia rafinesquei*) are also common on south-facing slopes. Along the plains grassland region up to *c.* 1750 m, common grasses include grama grasses (*Bouteloua* species), little bluestem (*Andropogon scoparius*), needle grasses (*Stipa* spp.), the introduced cheatgrass (*Bromus tectorum*), and wheatgrasses (*Agropyron* spp.) (Weber, 1976).

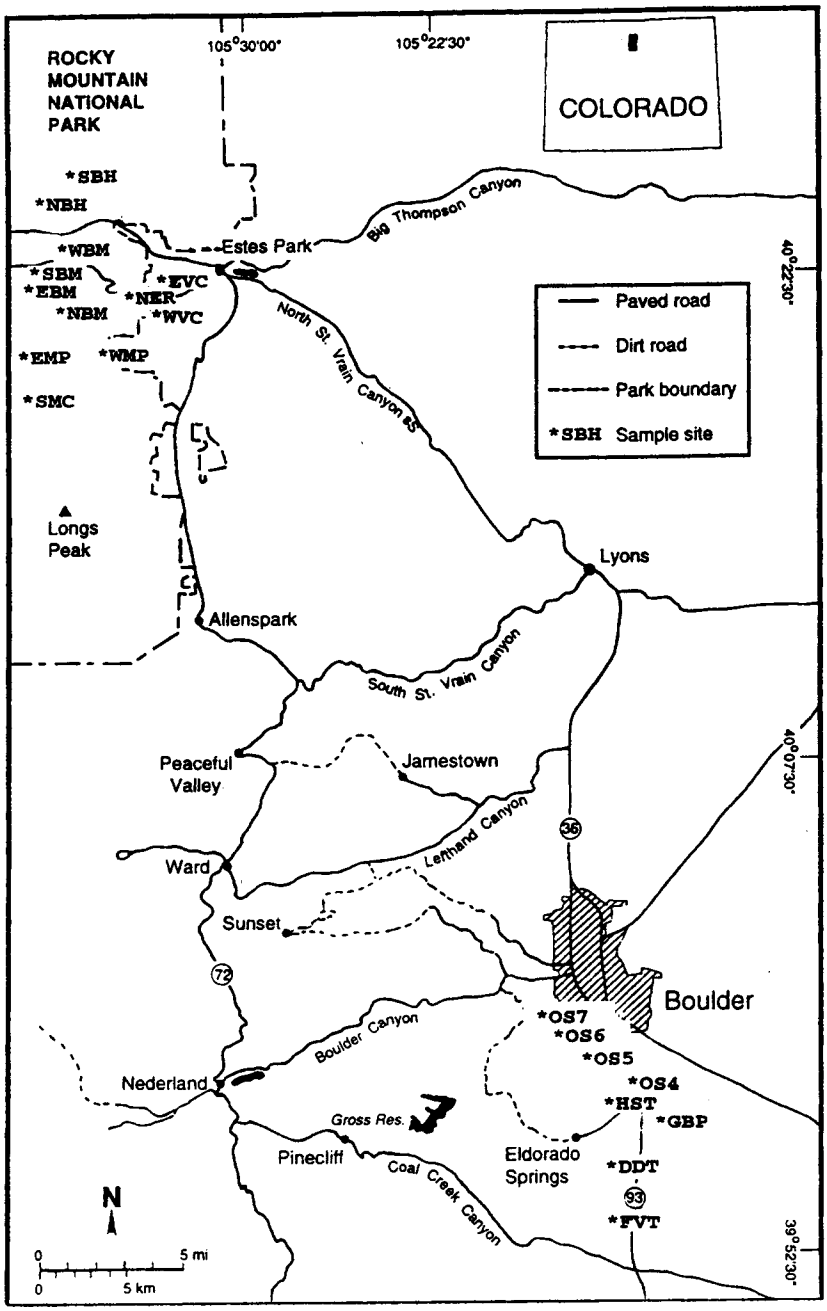


FIG. 1. Map of study sites in the Colorado Front Range.

Study sites

This study was conducted in two distinct types of lower timberline ecotonal habitats on the eastern slope of the Colorado Front Range: (1) the intermontane basins in Rocky Mountain National Park near Estes Park, Colorado, and (2) the plains grasslands near Boulder, Colorado (Table 1, Fig. 1).

The Rocky Mountain National Park intermontane basin sites, located at higher elevations (c. 2100 m), consist of trees on slopes and meadows along valley bottoms. The lower timberline ecotone probably results from environmental factors such as cold-air drainage (caused by temperature inversions) and variations in soil texture and drainage. Ponderosa pine dominates on south-, east- and west-facing slopes around these sites, whereas Douglas-fir and lodgepole pine dominate the cooler, moister north-facing slopes. Rocky Mountain National Park, established in 1915, currently manages these lands by suppressing fires and prohibiting all livestock grazing. Cattle grazing started in the ponderosa pine-meadow areas near Estes Park in 1860, with over 1400 cattle reported in the area by 1874 (Carothers, 1951; Peet, 1981). From 1915 to 1930, park managers

TABLE 1. Permanent plot site information.

Site	Location	Plot size	Aspect	Core numbers
Rocky Mountain National Park				
SBH	South Bighorn	40 × 55 m	S	42
SBM	S. Beaver Meadows	40 × 140 m	S	48
SMC	S. Mill Creek	40 × 120 m	S	50
NBH	North Big Horn	30 × 30 m	N	56
NBM	N. Beaver Meadows	20 × 25 m	N	69
NER	N. Entrance Rd.	35 × 25 m	N	71
EBM	East Beaver Meadows	40 × 50 m	E	52
EMP	E. Moraine Park	40 × 70 m	E	60
EVC	E. Visitors Center	120 × 50 m	E	39
WBM	West Beaver Meadows	40 × 60 m	W	41
WMP	W. Moraine Park	40 × 200 m	W	38
WVC	W. Visitors Center	100 × 65 m	W	49
Boulder City Open Space				
DDT	Doudy Draw Trail	100 × 150 m	r/t	47
FVT	Flatirons Vista	50 × 75 m	r/t	43
GBP	Greenbelt Plateau	50 × 50 m	r/t	50
HST	Homestead Trail	40 × 280 m	r/t	49
OS4	Open Space #4	150 × 50 m	r/t	7
OS5	Open Space #5	150 × 50 m	r/t	19
OS6	Open Space #6	150 × 50 m	r/t	78
OS7	Open Space #7	150 × 50 m	r/t	116

Aspect: S, south-facing slope; N, north-facing slope; E, east-facing slope; W, west-facing slope; r/t, ridgetop.

gradually eliminated cattle from the park, although deer and elk populations are currently large (Hess, 1993). Twelve permanent plots were located in Rocky Mountain National Park intermontane basins, with three sites per major aspect (Table 1, Fig. 1).

At the Boulder lower elevation ecotone sites (starting at *c.* 1800 m), trees occur along sandstone ridges and mesa tops where coarse-textured soils may give deep-rooted trees an advantage over grasses in competition for soil moisture (Schubert, 1974). Grasses dominate the slopes and valley bottoms where soil derived from shale bedrock holds more water in the upper soil horizon, favouring grasses over trees. The lower timberline appears to be mainly determined by the ability of ponderosa pines to tolerate water stress. Since the purchase of these sites by the Boulder City Open Space in the early 1970s, moderate levels of cattle grazing have been permitted in some areas but fires are suppressed. A total of eight permanent plots were located on mesas, with a transect series of four permanent plots located on one of the mesas (Table 1, Fig. 1). Three of the sites (HST, OS6, and OS7) have experienced no grazing since the early 1970s, whereas grazing still occurs at the remaining five sites in both spring and fall.

METHODS

Field methods

Field data collected in 1992 and 1993 allowed analysis of climatic variation, disturbance history, tree population age structure, and approximate dates of tree establishment. Sampling included cores for tree ageing, harvested seedlings, and fire-scar wedges, plus the species and diameter for every tree (> 4 cm d.b.h.), sapling (< 4 cm d.b.h., > 30 cm tall) and seedling (< 30 cm tall). Diameter was measured at breast height (d.b.h.; at 1.4 m) for trees and saplings, and at ground height (dgh) for seedlings. For sites OS6 and OS7, sampling of seedlings was not conducted due to time and resource limitations (> 1000 seedlings per site).

In each of the twenty permanent plots, all trees > 4 cm d.b.h. were cored and identified with numbered tags. In addition, there are re-bar stakes at plot boundaries. Each plot contains 40–60 cored trees, with the size of the plots depending on tree species richness (Table 1). This study included a total of 1115 trees, all cored at ≈40 cm above the ground for later analysis. Basal disks cut from ≈10–20 randomly selected seedlings next to each of the twenty sites allowed estimates of the number of years needed to reach coring height.

Cores from the oldest trees in the permanent plots permitted the construction of five tree-ring chronologies (see below for methods), one chronology for each of the four aspects in intermontane basins at Rocky Mountain National Park plus one chronology for the Boulder mesa top sites. In addition, removal of non-destructive wedge samples from selected fire-scarred trees in or adjacent to plots allowed for fire-history dating (McBride & Laven, 1976). Wedges were cut with a two-person hand saw because of the prohibition of chain saw use at these sites.

Analyses of the instrumental climate record

The instrumental climate record (1910–91) from a weather station in Estes Park, Colorado (less than 10 km from the

study plots) provided data for comparison with the four tree-ring chronologies from Rocky Mountain National Park. The instrumental climate record (1893–1986) from Boulder, Colorado (less than 10 km from the sites) was compared with the chronology created from Boulder sites. Climate data analyses included summaries of monthly means, monthly maximums, monthly minimums, two-and three-month averages, and annual means.

Climatic conditions are reflected in the growth response of ponderosa pine. Ponderosa pine at elevations below 2800 m show a relatively strong positive growth response to both current spring and summer precipitation (April through August), as well as to late summer and fall precipitation (August through October) of the previous year (Graybill, 1989). April through June are critical months for ponderosa pine seedling survival, since drought or temperature extremes during this period may kill seedlings (White, 1985; Graybill, 1989). For this reason, water balance calculations were made, which consisted of a combined April through June period for both precipitation and temperature values. Water balance values are obtained by subtracting potential evapotranspiration (based partially on temperature) from precipitation (Thornthwaite & Mather, 1957).

Dendroecological analyses

Age structure

Tree cores were processed using the procedures of Stokes & Smiley (1968). Tree ages at coring height were determined and periods of growth suppression and release (250% change in mean ring width between consecutive groups of five rings) were identified. Total tree age was estimated by adding the estimated number of years required to reach coring height to tree age at coring height. For Rocky Mountain National Park, height to age regressions calculated from harvested seedlings of each species were used to estimate the number of years required for seedlings to reach coring height and to estimate the ages of non-harvested seedlings (Table 2). At the Boulder sites, harvested seedlings included only those at the 40 cm coring height (hence there was no need for an age to size regression analysis); in addition counting of whorls was used to determine ages of non-harvested seedlings (from a previous study, Linhart unpublished). To allow for possible error in estimating seedling ages, tree ages were grouped into 10-year age classes.

Tree-ring chronologies

Five tree-ring chronologies were constructed using the fifteen oldest trees from each of the four major aspects in Rocky Mountain National Park sites and from the Boulder mesa top sites. Visual crossdating of these cores (Stokes & Smiley, 1968) allowed for later comparison with the results. Ring widths were measured to the nearest 0.01 mm with a computer compatible incremental measuring machine and the TRIMS computer program (Madera Software 1986). Ring-width series were crossdated visually by identifying marker years and also quantitatively with the tree-ring program COFECHA (Holmes, 1983).

The tree-ring program ARSTAN (Cook & Holmes, 1992) was used to standardize tree-ring series and to develop mean chronologies. Standardization of each series reduced variances among cores by transforming ring widths into dimensionless index values before averaging ring-width series to produce mean chronologies. For this study, the ring-width series are double detrended by fitting them first to a negative exponential or straight line and then to a cubic spline function. This type of standardization removes or reduces the tree's 'growth trend' (i.e. the tendency for rings to become narrower towards the bark due to the geometry of tree growth). The resulting chronology reflects mainly the influence of climatic variation on ring width (Fritts, 1976; Cook, 1985).

Fire history

Fire-scar dating from the wedge samples provided fire history information for the permanent plots, following standard methods including crossdating (Arno & Sneck, 1977; Romme, 1982; McBride, 1983). Wedges were mounted and sanded with successively finer grades of sand paper following the procedures of Stokes & Smiley (1968). Annual rings on the wedges were counted under stereomicroscopes. Visually crossdating with marker years was used as a dating control for the fire scar samples.

RESULTS AND DISCUSSION

Climatic variation in the Colorado Front Range

Instrumental record

The instrumental records from Estes Park and Boulder indicate relatively dry conditions occurred during the critical establishment months of April, May and June in the late 1920s–early 1930s and the mid-1950s (plus the 1980s for Estes Park) (Fig. 2). A combination of relatively drier conditions and above average temperatures in April, May and June in the 1950s created drought conditions as shown by Thornthwaite water balance values (Fig. 3). These drier conditions in the late 1920s–early 1930s and mid–1950s may have been detrimental to seedling survival. In contrast, the instrumental record shows relatively high spring precipitation for many years in the 1970s, creating possibly favourable conditions for seedling establishment.

Dendroclimatic records

Relevant statistics for the five chronologies are listed in Table 3. Comparison of all five chronologies indicate certain periods of below- or above-average growth appear in most or all locations, suggesting influences on tree growth by climate. In the Rocky Mountain National Park sites, slower growth occurs in the early 1820s, the late 1840s, and the mid-1950s (also a period of below average growth in the Boulder sites). Common periods of above average growth in all Rocky Mountain National Park sites sampled are the mid-1860s to the mid-1870s 1941–45 and 1980s, with the latter two are also periods of above average growth in the Boulder sites.

TABLE 2. Mean number of years needed to reach coring height: for Rocky Mountain National Park sites based on age to height regressions ($n = 10$, 95% confidence interval) with standard error and r^2 in parentheses; for Boulder sites based on seedlings cut at coring height ($n = 10$) with range of ages at coring height in parentheses.

	Species				
Site	Ponderosa	Douglas-fir	Lodgepole	Juniper	E spruce
RMNP (Mean years to coring height (SE; r^2))					
SBH	15(4.8;.62)	26(3.6;.93)	–	–	–
SBM	10(2.4;.72)	–	–	–	–
SMC	11(0.9;.73)	–	–	–	–
NBH	20(0.5;.91)	21(2.0;.83)	41(7.8;.53)	–	4(2.6;.87)
NBM	27(2.4;.50)	38(7.8;.82)	27(8.9;.41)	–	–
NER	43(7.8;.52)	27(4.7; n/a)	13(3.4; n/a)		–
EBM	26(5.1;.68)	–	–	–	–
EMP	37(5.1;.73)	22(3.7;.91)	–	32(3.5;.69)	–
EVC	20(1.5;.64)	–	–	–	–
WBM	18(3.0;.74)	–	–	–	–
WMP	7(2.3;.80)	–	–	–	–
WVC	32(5.0;.61)	–	–	–	–
BCOS (Mean years to coring height (range))					
DDT	5(4–6)	–	–	–	–
FVT	6(4–8)	–	–	–	–
GBP	6(4–9)	–	–	–	–
HST	7(4–9)	–	–	–	–
OS4	6(5–9)	–	–	–	–
OS5	6(5–8)	–	–	–	–
OS6	7(4–10)	–	–	–	–
OS7	10(8–11)	–	–	–	–

When comparing these periods of below or above average growth with the instrumental climate records, certain trends in spring/early summer precipitation and temperature emerge. For instance, both the Rocky Mountain National Park chronologies and the Estes Park's weather station records show drier spring and early summer conditions in the late 1920s to early 1930s and mid-1950s, with above average moisture levels in spring and early summer in the early 1940s (also reported by Graybill, 1989). In addition, the chronology from Boulder sites and the Boulder weather station records both show favourable growing conditions in the late 1960s, the late 1970s to early 1980s, that in turn also coincides with increased seedling establishment (Figs 4 and 5).

Patterns of tree establishment

Age structure was compared to disturbance history. For sites in Rocky Mountain National Park, fire-scars exist in eight of the twelve sites, with the most recent fire scar dated at 1900 and the oldest fire scar dated at 1798 (Table 4). Five of the eight plots experienced fire in the 1860s, following drought conditions in the 1850s. Rocky Mountain National Park sites clearly show major pulses of tree establishment following the mid-19th century fires, while the Boulder sites show tree invasion following fire suppression in the 20th century (Fig. 5). In addition, a huge pulse of seedling establishment followed a release from more intensive grazing at the Boulder sites in the 1970s (Fig. 5).

In Rocky Mountain National Park sites, ponderosa pines, which are relatively shade-intolerant, dominate at south-, east- and west-facing slopes, with few seedlings in the understory (Fig. 5). At most sites on these three aspects, broadly even-aged cohorts became established primarily in the 1860s and 1870s. This time period corresponds with above average growth in tree-ring chronologies, indicating favourable growth conditions. These dates also correspond to above average growth detected in Colorado Front Range chronologies by Graybill (1989).

Comparisons by aspect type at Rocky Mountain National Park (Fig. 5) indicate that south-facing slopes show mature ponderosa pines and few if any mature Douglas-firs, with peak pine establishment in the late 1800s (mainly due to fire). On the east-facing slopes ponderosa pine became established mainly from 1860 to 1890 due to a postfire pulse in establishment, with almost no establishment since the 1950s. Similarly, a pulse in seedling establishment on west-facing slopes from 1860 to 1870 corresponds to fire scars as well as to a period of release in the tree-ring chronology.

In contrast, the north-facing slopes support the more shade-tolerant and moisture-demanding Douglas-fir and lodgepole pine (Fig. 5). Ponderosa pines are codominants only at one site (NER), whereas at the other two sites ponderosa pines appear as remnants representing the oldest trees with little or no recent seedling establishment. Douglas-firs comprise almost an all-age distribution, whereas lodgepole pines established in even-aged cohorts corresponding to fire dates. Ponderosa pine seedlings appear to require some gap (such as a tree death) or spot fire to establish successfully. Unless a stand-initiating disturbance such as fire occurs, ponderosa pine at these sites may eventually be completely replaced by Douglas-fir and lodgepole pine. At

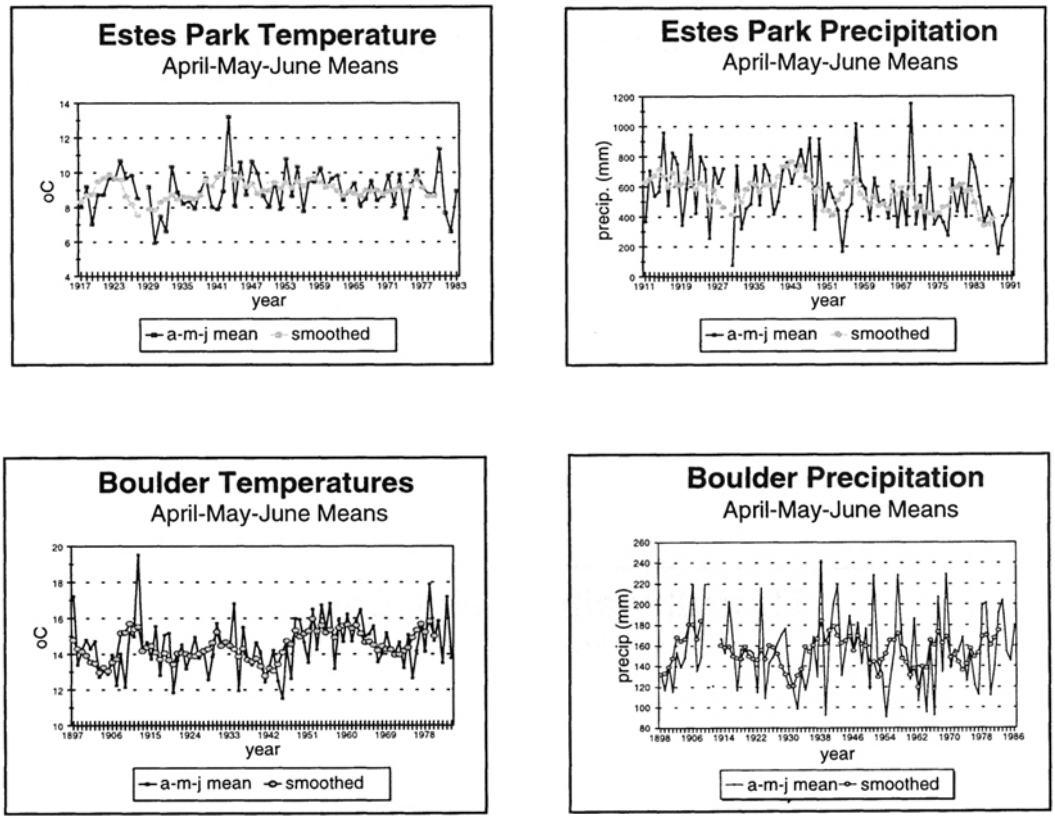
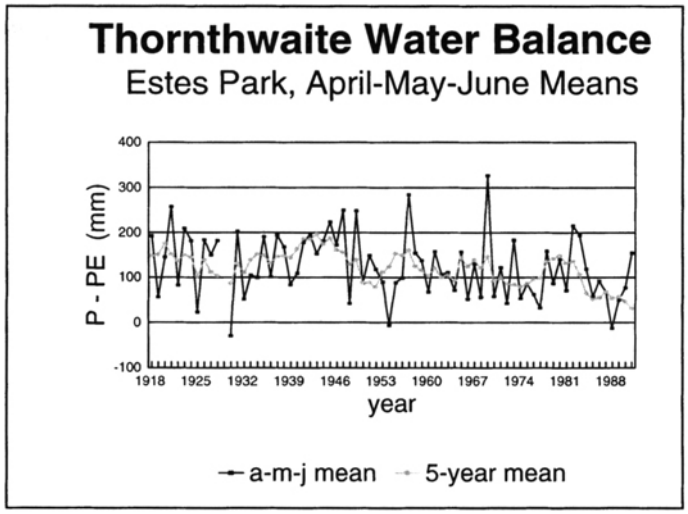


FIG. 2. Estes Park and Boulder instrumental April-May-June mean temperature and precipitation data, by yearly mean and 5-year smoothed mean.

TABLE 3. Dendrochronological information on the cubic spline fit tree-ring chronologies for four main aspect types at Rocky Mountain National Park and for mesa tops at Boulder sites.

	Chronology				
Characteristic	South	North	East	West	Mesa
Number of dated series	10	10	10	10	14
Chronology length	1775–1992	1749–1992	1674–1991	1800–1991	1907–92
Years of Master Series	218	244	318	192	86
Total dated rings checked	1543	1193	1556	1672	1028
Series intercorrelation	0.521	0.579	0.637	0.466	0.536
Average mean sensitivity	0.379	0.276	0.380	0.425	0.344

NER, ponderosa pine exhibit a broadly even-aged age structure, with establishment dating from 1870 to 1890, representing a period of favourable climate following fire. Overall, the peak establishment period for all trees in the three north-facing sites occurred during the late 1800s through 1910, with additional seedling establishment in the 1960–80s. In addition, north-facing sites contained higher tree densities than the other three aspect types, as indicated by the much smaller plot sizes needed to obtain the minimum number of sample trees (Table 1) and the greater basal area (Table 5). Similarly, greater seedling suppression at north-facing sites may stem from higher basal areas (average 38.23 m^2/ha for north-facing slopes *v.* 5.59 m^2/ha basal area for Boulder mesa-top sites) (Table 5). Ponderosa pines along ecotonal boundaries on Boulder sites (Fig. 5, a composite of these mesa top sites combined due to very similar age structures) exhibit a significantly different age structure distribution than the trees in higher elevation Rocky Mountain National Park intermontane basins. The first major difference is the lack of trees over 90 years old in Boulder, possibly attributable to frequent low-intensity fires typical of the Colorado Front Range in the mid- to late-1800s. Second, ponderosa pine is the only tree species in the Boulder sites. Third, there appears to be more continuous tree establishment, except during the 1960s at some sites. Fourth, Boulder sites have large numbers of



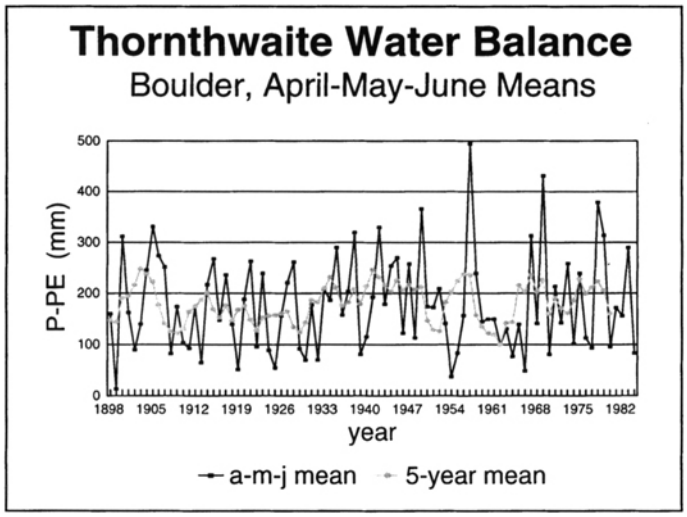


FIG. 3. Estes Park and Boulder Thornthwaite water balance calculations (based on precipitation minus potential evapotranspiration) for April-May-June means and April-May-June 5-year smoothed mean.

seedlings recently established. Finally, on the Boulder sites, ponderosa pines grew to coring height (40 cm) within 5–10 years, *v.* an average of 22 years (7–43 years depending on the site) in Rocky Mountain National Park sites (Table 2).

The abundant number of ponderosa pines that established in the 1970s and 1980s may be explained by a combination of factors, including (1) favourable moisture and temperature conditions, (2) a decrease in cattle grazing of pine seedlings, and/or (3) an absence of thinning. First, in terms of climate, the tree-ring chronology indicates 1968–71 and 1983–91 as favourable years for ponderosa pines, while the instrumental record shows high spring/early summer moisture levels for 1967–69 and many years in the 1970s and 1980s. Conversely, the apparent paucity of ponderosa seedling establishment during the 1950s and 1960s may be related to the drier conditions and above average temperatures in spring and early summer during the critical establishment months from 1953 to 1956 and 1959–66.

The second explanation for the increase in establishment may be a reduction from more intensive to moderate levels of cattle grazing, producing small openings free from perennial bunch-grasses without high amounts of pine seedling herbivory or trampling. This moderate level of grazing combined with continued fire suppression favours seedling establishment. A third reason reflects an age structure before thinning. Few of the ponderosa pine seedlings now established will survive to maturity, especially at sites like OS6 that has almost 1000 seedlings in a 50×150 m area. Hence, the current age structure in these plots may represent a negative exponential distribution, to be expected at sites where the seedlings have not yet been thinned by competition and herbivory.

Possible reasons for variations in age structure between

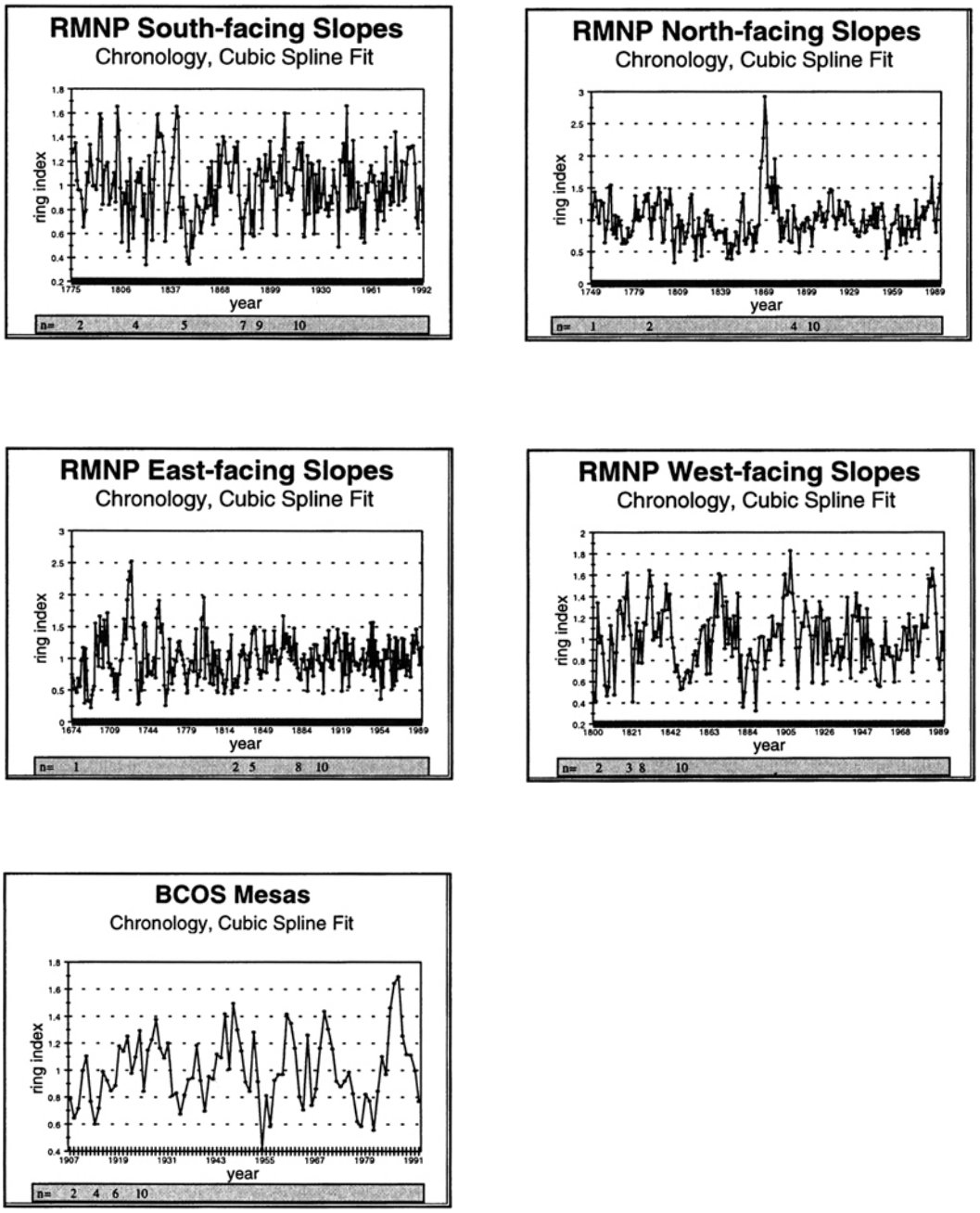


FIG. 4. Cubic spline fit tree-ring chronologies for 4 main aspect types at Rocky Mountain National Park and for mesa tops at Boulder (n = number of cores included for each time period in the chronology).

Rocky Mountain National Park sites as compared to Boulder sites include differences in disturbance histories, climate, elevation, and aspect. First, the Rocky Mountain National Park intermontane basins sites have a different disturbance history than the Boulder mesa top sites. Currently there is no cattle grazing in the National Park; however, elk and deer damage and kill younger trees by rubbing their antlers on trees and browsing. The majority of the Boulder sites have moderate levels of cattle grazing that may facilitate ponderosa pine establishment in some cases, but cattle can also damage them by trampling and grazing. In addition to different grazing/browsing regimes, Rocky Mountain National Park sites clearly show major pulses of tree establishment following the mid-19th century fires due to gap creation. In the Boulder sites, ponderosa pine invaded grasslands partially due to fire suppression in the 20th century allowing seedling survival.

In terms of climatic and associated factors, Rocky Mountain National Park sites are located ≈300 m higher and farther north and west than Boulder sites. Snow melt

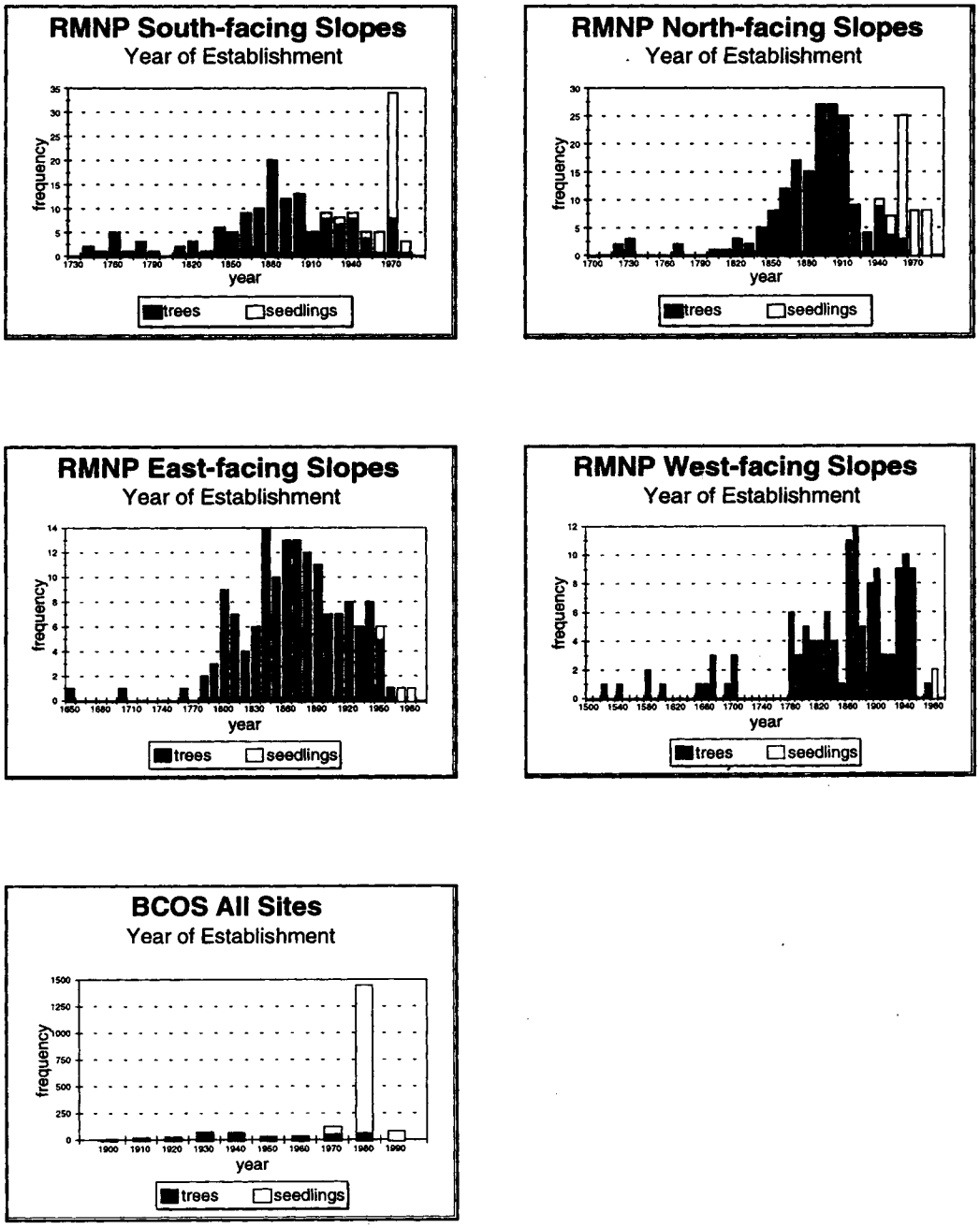


FIG. 5. Age structure by aspect for Rocky Mountain National Park sites and for Boulder mesa top sites.

is generally later for the Rocky Mountain National Park sites, with frost-heaving and late spring storms common in this area. In contrast, heat stress and drought appear to be more common limiting factors at lower elevation sites. Hence, since ponderosa pine regeneration requires a combination of factors, such as good seed year, favourable seedbed conditions, and subsequent drought-free and fire-free period (Schubert, 1974; Peet, 1981), tree invasions into grassland may be influenced by both climate and disturbance history.

Although we could identify some time periods of tree establishment during years of above average spring moisture, we could not rule out other explanations for the pulses in tree establishment. Increases in ponderosa pine establishment in the 1870s–1890s and in the 1970s–1980s do correspond with periods of above average precipitation, but also correspond with postfire or postgrazing periods. Age structures show too many inconsistencies to support a purely climatic interpretation. For example, two of the three east-facing sites (EMP and EVC) in Rocky Mountain

TABLE 4. Fire history at sites in Rocky Mountain National Park, based on crossdated fire-scar wedges.

Site	1st fire year	2nd fire year
SBH1	1867	–
MCT1	1860	–
BMT1	1798	1845
NBH1	1842	1860
NBM1	1900	–
EMP1	1851	–
EBM1	1860	1884
WBM1	1860	–

TABLE 5. Basal area (m^2/ha) by site.

Location	Plot	Basal area (m^2/ha)
RMNP South Aspect	SBH	17.84
	SBM	36.14
	SMC	10.21
RMNP North Aspect	NBH	44.96
	NBM	34.44
	NER	35.30
RMNP East Aspect	EBM	17.09
	EMP	8.14
	EVC	8.59
RMNP West Aspect	WBM	20.53
	WMP	5.34
	WVC	6.59
BCOS Mesa-top	DDT	1.30
	FVT	3.27
	GBP	4.20
	HST	3.19
	OS4	1.26
	OS5	4.25
	OS6	12.90
	OS7	14.37

National Park show peak establishment during the late 1940s dry period and no pulse of establishment in the wetter 1970s and 1980s. It is possible to identify some periods of establishment that correspond generally with periods of above average precipitation, but the data cannot be used to demonstrate a close relationship between them because of the confounding effects of variable disturbance regimes and the some ambiguities in dating. Specifically, the estimates of total tree ages have errors of about 5 years, while many of the climatically distinct periods only last a few years. Consequently, age data combined into 10-year classes are too coarse for the highly variable climatic conditions documented by the instrumental climate records.

CONCLUSIONS

Age structures of lower ecotone forests along the Colorado Front Range are strongly linked to changes in disturbance regimes. Frequent burning in the mid-1800s may have kept these areas free from invading pine seedlings, while lack of fires in the 1900s allowed tree seedlings time to establish at the ecotonal boundaries. These fires created favourable establishment conditions for ponderosa pine seedlings, that in turn produced even-aged cohorts at many sites. Stands in the Colorado Front Range often show release within 2–12 years after a fire (Goldblum & Veblen, 1992) that would correspond with the releases and establishment seen in the late 1860–1880s in many plots. In addition, moderate levels of cattle grazing produced small openings free from perennial bunch-grasses without high amounts of pine seedling herbivory or trampling. This moderate level of grazing combined with continued fire suppression favours ponderosa pine seedling establishment. Finally, climatic variation may also have influenced age structure, even though it was not possible to conclusively demonstrate such an influence. In particular, analyses of age structures at 10-year class scales prevented the detection of climatic influences occurring at a finer scale. Overall, with respect to climate change affecting ecotones, other factors such as altered disturbance regimes may have significant influence such that climatic change alone is not the sole driver of ecotone change.

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