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Climatic variability and episodic *Pinus ponderosa* establishment along the forest-grassland ecotones of Colorado

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Abstract

The primary objective of this study was the detection of possible climatic influences on the recent (i.e., past c. 40 years) establishment of ponderosa pine (*Pinus ponderosa*) at or near forest-grassland ecotones in the northern Front Range of Colorado. Germination dates were precisely determined for >500 juvenile ponderosa pine collected in six widely dispersed sample areas. All sites sampled were open areas lacking an overstory tree cover but located near seed sources. To evaluate the effects of recent climatic variation on recruitment and survival patterns, three types of climate data were used: (1) instrumental climate records from nearby local weather stations; (2) a multivariate index of El Niño/Southern Oscillation (ENSO); and (3) a regional, ponderosa pine tree-ring index sensitive to moisture variation. There is a strong association between episodic recruitment of ponderosa pine and years in which spring and fall moisture availability is high in the instrumental climate record. During the past 40 years, tree establishment was highly episodic and concentrated mainly in four years—1973, 1979, 1983, and 1990. These years are also associated with large-scale warming of sea-surface temperatures in the eastern tropical Pacific (i.e., El Niño events). These years of abundant seedling establishment also coincide with years of above average radial growth in mature ponderosa pine. Thus, at open sites suitable for the survival of shade-intolerant ponderosa pine, successful establishment of seedlings is highly episodic depending on local moisture availability related to broad-scale climatic variation. This study demonstrates the climatic sensitivity of ponderosa pine recruitment at low elevation sites along forest-grassland ecotones in the northern Colorado Front Range.

Keywords: *Pinus ponderosa*; Ecotone; Forest-grassland; Climate; Synchronous; Recruitment; Establishment; El Niño; La Niña

1. Introduction

Shifts in forest-grassland ecotones associated with tree invasions in the western United States have long been the source of much interest among ecologists and land mangers (Foster, 1917; Johnsen, 1962; Burkhardt and Tisdale, 1976). Occurring at the extreme limits of tolerance for certain plant species, ecotones are areas of transition believed to be particularly sensitive to climatic changes (Neilson, 1986). Shifts in forest-grassland ecotones also often appear to be affected by changes in disturbance regimes such as altered fire frequency and herbivory. For example, variations in densities of ponderosa pine (*Pinus ponderosa*) in open woodland areas and along forest-grassland ecotones have been attributed to effects of grazing (Pearson, 1942; Madany and West, 1983), fire suppression (Covington and Moore, 1994; Arno et al., 1997), and climatic variation (Savage et al., 1996), either acting alone or in combination. In long-term retrospective studies, for example, based on reconstructions from tree-ring evidence, it is often difficult to distinguish effects of variations in fire from more direct influences of climatic variation on tree recruitment. This is both due to the fragmentary nature of tree-ring evidence subject to decay or destruction by subsequent fires, and to the difficulty of obtaining annual resolution of germination dates from samples of large trees (see Savage et al., 1996). In the current study, we focus on a relatively short time period (the past 40 years) to try to determine if the establishment of ponderosa pine along forest-grassland ecotones in the northern Colorado Front Range has been episodic, and if so, any relationship with annual-scale climatic variation.

Studies in the southwest have related episodic seedling establishment of ponderosa pine to variability in seed

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production, climatic variation, and fire-related availability of suitable sites (Schubert, 1974; White, 1985). Pulses of ponderosa pine establishment in the southwest have been related to the coincidence of abundant seed crops followed by favorable temperatures and precipitation for seedling survival (Schubert, 1974). For example, a widespread recruitment event in 1919 in Arizona has been related to an unusually favorable combination of climatic conditions following a year of abundant seed production (Pearson, 1923). Based on annually precise reconstruction of germination dates determined by felling mature trees, Savage et al. (1996) related abundant tree seedling establishment and recruitment to warm, wet conditions in May and well-distributed moisture throughout the year.

In the Colorado Front Range, episodic establishment of ponderosa pine has been interpreted from tree population age structures and attributed both to open sites becoming available after severe fire and/or logging for this shade-intolerant species and to climatic variation (Veblen and Lorenz, 1986; Mast et al., 1997; Kaufmann et al., 2000; Ehle and Baker, 2003). These age structure studies were conducted in areas of mature trees (e.g., >100 years old) where precise determination of germination dates of large trees is rarely achieved with an increment core due to the time required for seedlings to reach the height at which the tree can be cored and/or the difficulty of intercepting the first annual ring right at the root/shoot boundary. Furthermore, seedling survival in this shade-intolerant species is limited by light availability and other understory conditions that change with stand development and canopy tree mortality, thus confounding any statistical association of tree ages with climatic variation. For example, in the only previous study of ponderosa pine in the Front Range that attempts to quantitatively relate tree ages to instrumental climatic records, the precision in determining germination dates was on the order of 5–10 years (Mast et al., 1998). In the absence of destructive sampling to determine germination dates, annual resolution is not obtained, and consequently linkage of tree establishment to annual-scale climatic variation is difficult or impossible. In the current study, we focused on relatively small and young (<40 years old) ponderosa pines that could be easily harvested for precise determination of germination dates. The objective of this study was to determine if during the past 40 years there has been a detectable annual-scale influence of climatic variation on ponderosa pine establishment along forest-grassland ecotones at low elevations in the northern Front Range. Forest-grassland ecotones were chosen for study to assure that tree recruitment would not be limited by light attenuation associated with the development of older forests. Site locations at ecotones also assured that distance to seed source would not limit seed availability. Sites were chosen to minimize any differences in land use or management practices such as fire suppression or grazing. Sites were dispersed across a wide range (a north–south distance of c. 65 km) so that if annual-scale patterns in tree establishment were synchronous, the most likely explanation would be regional climatic variation. Because previous research has shown that ponderosa pine tree growth and fire occurrence in these environments are sensitive to seasonal moisture variations associated with El Niño/Southern Oscillation (ENSO), we attempted to relate variation in ponderosa pine establishment to both local climatic records and an index of ENSO (Wolter, 2004). To evaluate the frequency of years climatically suitable for ponderosa pine establishment over the past c. 300 years, we compared recruitment years to a regional tree-ring index of ponderosa pine.

2. Methods

2.1. Study area

The Colorado Front Range is the easternmost range of the Rocky Mountains, extending north to south ~150 km from the Wyoming border paralleling the Great Plains. The climate is typical of high elevation, continental regions with strong temperature contrast between summer and winter (Greenland et al., 1985). In winter, synoptic scale climate is dominated by westerly flow aloft from the Pacific. Uplift caused by the Rocky Mountains results in precipitation on the western slopes primarily in the form of snow. In spring and autumn, occasional eastern upslope conditions develop, pulling moist air from the Gulf of Mexico, creating heavy precipitation along the eastern slopes of the Front Range and adjacent plains. Summer precipitation is mostly from convective storms associated with the North American monsoon. The Boulder climate station (Table 1) at 1671 m elevation has a mean annual precipitation of 403 mm (1893–2003). Precipitation typically peaks in May. The July mean daily temperature maximum is 31 °C, and the January mean daily temperature minimum is −8 °C in January for the Boulder station.

ENSO events have been shown to have a significant influence on seasonal temperature and precipitation along the

Table 1
Description of weather stations along the lower montane foothills of the northern Front Range of Colorado

Station	Location	Elevation (m)	Record duration	Annual mean
Temperature (°C)				
Evergreen	39°38′N/105°19′W	2134	1961 to present	22.60
Denver (Stapleton)	39°46′N/104°52′W	1611	1927 to present	26.30
Fort Collins	40°37′N/105°08′W	1525	1937 to present	25.60
Precipitation (mm)				
Evergreen	39°38′N/105°19′W	2134	1961 to present	401.30
Boulder	40°00′N/105°16′W	1671	1948 to present	403.20
Waterdale	40°26′N/105°13′W	1594	1948 to present	347.03

Colorado Front Range (Veblen et al., 2000; Donnegan, 2000). Below average winter–spring precipitation and above average fall and spring temperatures are associated with La Niña events. Conversely, above average spring precipitation and below average temperatures are associated with El Niño events. These patterns imply that moister conditions associated with El Niño events could be conducive to years of ponderosa pine recruitment.

In the northern Front Range the vegetation of the montane zone (c. 1700–2700 m) ranges from open park-like stands of ponderosa pine at the plains-grassland ecotone to dense stands mixed with Douglas-fir (*Pseudotsuga menziesii*) in more mesic sites and on north-facing slopes. The lower elevations of the ponderosa pine woodlands form the ecotone with the plains-grasslands, but grassy meadows are commonly found throughout the lower part of the montane zone. In the upper part of the montane zone, topographic position becomes increasingly important with dense stands of ponderosa pine-Douglas-fir on north-facing slopes and more open ponderosa pine woodlands characteristic of south-facing slopes.

Grazing occurred in the lower montane zone beginning in the mid 19th century along with the arrival of Euro-American settlers. However, at the sites sampled (Table 2) on lands purchased for preservation of open space, livestock grazing ceased by the 1970s. Browsing by ungulate species such as elk and deer is still an apparent factor on these landscapes today. Additionally, fire suppression policies have been in effect on these lands since the 1920s.

2.2. Field sampling procedures

Tree-ages were sampled in the lower montane zone (~1888–2408 m) on the eastern slope of the northern Front Range at six locations along a c. 65 km north–south line from near Lyons (40°13′) to Evergreen (39°41′) (Fig. 1). During spring 2003, 10 plots were located according to criteria given below on six

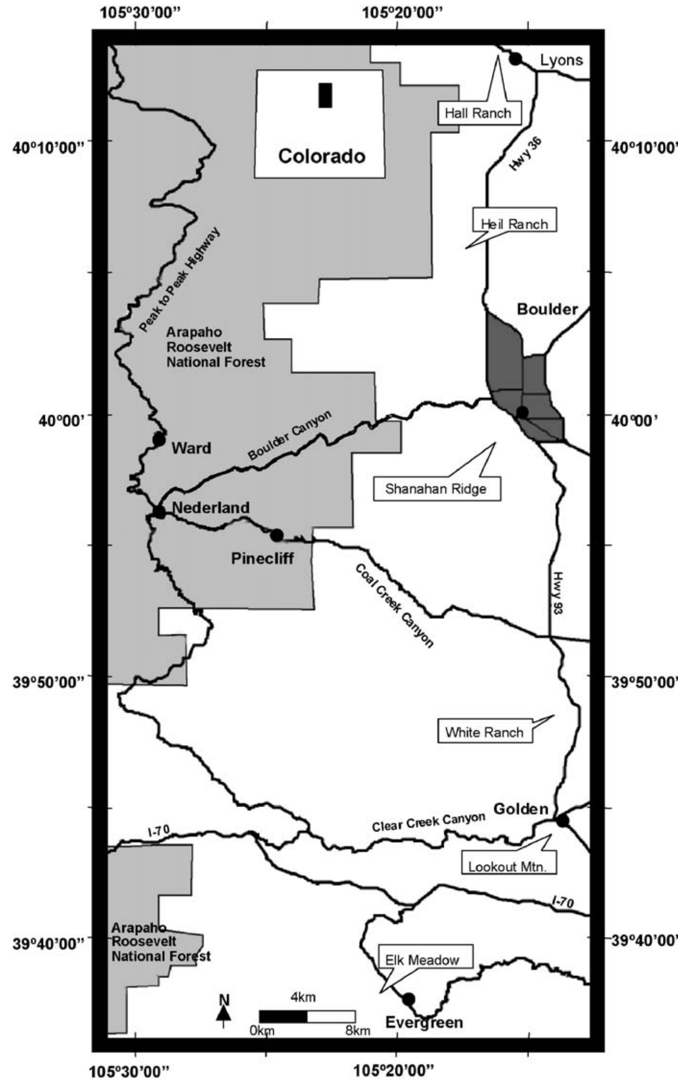

Fig. 1. Map showing all six study sites sampled along the lower montane foothills of the northern Front Range of Colorado.

Table 2
Sample site descriptions and biological variable comparison

Location	Site	Latitude	Longitude	Altitude (m)	Aspect	Slope (%)	Plot Size (m)	Density (stems/sq m)	*n*
Hall Ranch (Boulder Co. Parks and OS)	Hall01	40°13.01′N	105°19.54′W	1974	15/N	10	10 × 8	0.70	48
Heil Ranch (Boulder Co. Parks and OS)	Heil01	40°8.81′N	105°19.02′W	1984	12/N	8	10 × 20	0.25	47
	Heil02	40°8.81′N	105°19.02′W	1986	150/SSE	13	10 × 20	0.31	52
Shanahan Ridge (City of Boulder Mtn. Parks)	Shan01	39°57.73′N	105°16.46′W	1889	40/NE	12	10 × 30	0.19	54
	Shan02	39°57.73′N	105°16.46′W	1888	20/N	12	10 × 10	0.52	48
White Ranch (Jefferson Co. Open Space)	White01	39°49.07′N	105°16.67′W	2255	355/N	7	10 × 6	1.13	52
Lookout Mountain (Jefferson Co. Open Space)	Look01	39°43.74′N	105°14.87′W	2305	160/SSE	9	5 × 2	6.00	59
	Look02	39°43.74′N	105°14.87′W	2302	143/SSE	9	4 × 9	1.83	48
Elk Meadow (Jefferson Co. Open Space)	Elk01	39°40.33′N	105°22.31′W	2407	100/E	10	9 × 12	0.47	50
	Elk02	39°40.33′N	105°22.31′W	2408	110/E	8	10 × 20	0.29	49
Total (*n*)									507

properties owned by Boulder County Open Space, City of Boulder Open Space and Mountain Parks, and Jefferson County Open Space (Fig. 1).

All areas chosen for sampling contained abundant juvenile (<3 m tall) ponderosa pine along ecotones between grasslands and ponderosa pine forests. Areas chosen for sampling intentionally covered a wide range of aspects and slope steepness (Table 2). To reduce the chances of conflating climatic influences on tree regeneration with other factors that could trigger tree establishment, sites were located at least 10 m away from evidence of any disturbance (i.e., roads, trails, tree fall, water courses). Sites were not selected if they showed any evidence of logging, recent fire, or geomorphic disturbances that would have exposed bare substrate.

Within each subjectively determined homogeneous area, one to two rectangular plots of 10–300 m^2 were randomly located. More than one plot was included in study sites that had larger populations (i.e., >200) of juvenile ponderosa pine. Plots were in areas of grassland being invaded by juvenile ponderosa pine. Each plot was within c. 20 m of the forest edge with mature trees that would be potential seed sources. Plot size varied according to tree seedling density so that a minimum of 50 individuals were included in each plot.

In each plot, all juvenile ponderosa pine (<200 cm tall) were cut with a handsaw. A spade was used to excavate around each juvenile so that a 10 cm long section could be cut from 5 cm below to 5 cm above the root collar. Seedlings that were small enough to be uprooted were pulled up and later cross-sectioned in the lab.

2.3. Sample processing

Germination dates were determined by successively cutting cross-sections to reveal the root–shoot boundary, and determining the pith date in the shoot portion of the section (Telewski and Lynch, 1990; Telewski, 1993). The pith is present in the shoot (trunk portion of the tree) but not in the root. Cross-sections were repeatedly cut from the root upwards into the stem until the pith appeared. Each cross-section was finely sanded (up to 600 grit) and examined under a microscope. For most samples, the root–shoot boundary was at or just above the root collar. Narrow ring patterns, injuries and other scars were also observed and recorded.

After the root–shoot boundary was identified on a cross-section, the germination date of each cross-section was determined by counting rings from the outermost ring (2003) to the pith. Marker rings from a regional ponderosa pine tree-ring chronology (Veblen et al., 2000) were used to aid detection of possible false or missing rings. However, records were too short to allow quantitative crossdating.

2.4. Analytical methods

After graphically identifying years of above average tree establishment, Superposed Epoch Analysis (SEA; Grissino-Mayer, 1995) was used to determine if the following three climate indicators departed significantly from their long-term means during recruitment events: (1) regional climate records from three nearby climate stations; (2) a Multivariate El Niño/Southern Oscillation Index (MEI; Wolter, 2004); and (3) a regional tree-ring index from ponderosa pine in the Northern Colorado Front Range (Veblen et al., 2000).

A regional instrumental record of temperature and climate was developed for a 40-year time period (1963–2002) for the lower montane zone of the northern Colorado Front Range. Data sets of mean monthly temperature and precipitation were obtained from five meteorological stations (National Climatic Data Center, Asheville, N. Carolina, unpublished data). To determine whether these stations would be suitable for use in the assemblage of a regional climate data set, we tested for common variances and homogeneous temporal trends using the Homogeneity of Meteorologic Data (HOM) component of the Dendrochronology Program Library (DPL) (Holmes, 1997). Three temperature (Evergreen, Denver, and Fort Collins) and three precipitation (Evergreen, Boulder, and Waterdale) stations were selected as having similar temporal trends and similar variances (Table 1). All stations were within or near the forest-grassland ecotones of northern Colorado and had a consistent record of data from at least 1961 to the present. By including only stations with similar trends and variances in temperature and precipitation, it was feasible to compute averages for each parameter that are indices of climatic variation over the entire region studied.

Precipitation and temperature records were used to create an aridity index by using the formula $1.2P/(T + 10)$ (De Martonne, 1926), where P is monthly precipitation in mm and T the monthly temperature in °C. Monthly aridity averages were calculated and organized in 2, 3, 4, 6, 8, and 12 seasonal groupings representing late winter, early winter, spring run-off, germination, summer survival, and fall survival periods for seasonal analysis. Years of abundant tree recruitment versus no recruitment were determined from visual inspection of frequency distributions of tree establishment dates, and means of aridity indices for those years were compared by independent sample t-tests.

Wolter's (2004) Multivariate El Niño/Southern Oscillation Index (MEI) was used to investigate relationships between ENSO events and ponderosa pine recruitment. Negative values of the MEI indicate the cold ocean water ENSO phase (La Niña), and positive MEI values indicate the warm ocean water ENSO phase (El Niño). A 40-year period (1963–2002) of two bi-monthly MEIs (January–February and February–March) were calculated to examine the relationship between ENSO and ponderosa pine recruitment. These seasons were chosen because previous research has shown that climate in Colorado is strongly associated with variations in ENSO indicators from the tropical Pacific during these months (Diaz and Kiladis, 1992; Donnegan, 2000).

Mean climatic parameters and MEI were compared for recruitment years and non-recruitment years. Superposed epoch analysis (SEA; Grissino-Mayer, 1995) was used to test the null hypothesis that there is no relationship between occurrence of recruitment years and climatic conditions in the years preceding, during, and after recruitment years. Mean values of climatic variables were calculated for 8-year windows including the year of recruitment. These mean values were compared to variation in the complete record by performing Monte Carlo simulations that randomly pick years, calculate expected means, and provide 95% bootstrap confidence intervals (Grissino-Mayer, 1995). In each case, the number of randomly selected years equals the number of actual recruitment years. Results are described as percentage departures from the mean values determined by the random selection of non-recruitment years.

To assess the frequency over the past several centuries of climatic conditions suitable for ponderosa pine establishment, we compared tree-ring indices during known establishment events with a 300-year ponderosa pine chronology (Veblen et al., 2000). This regional ponderosa pine chronology (1696–1996) was developed from eight ponderosa pine ring-width chronologies at sites spread across the Front Range and is an indicator of variation in moisture availability, especially during the spring of the year of ring growth (Veblen et al., 2000). An average tree-ring index for years of known establishment was

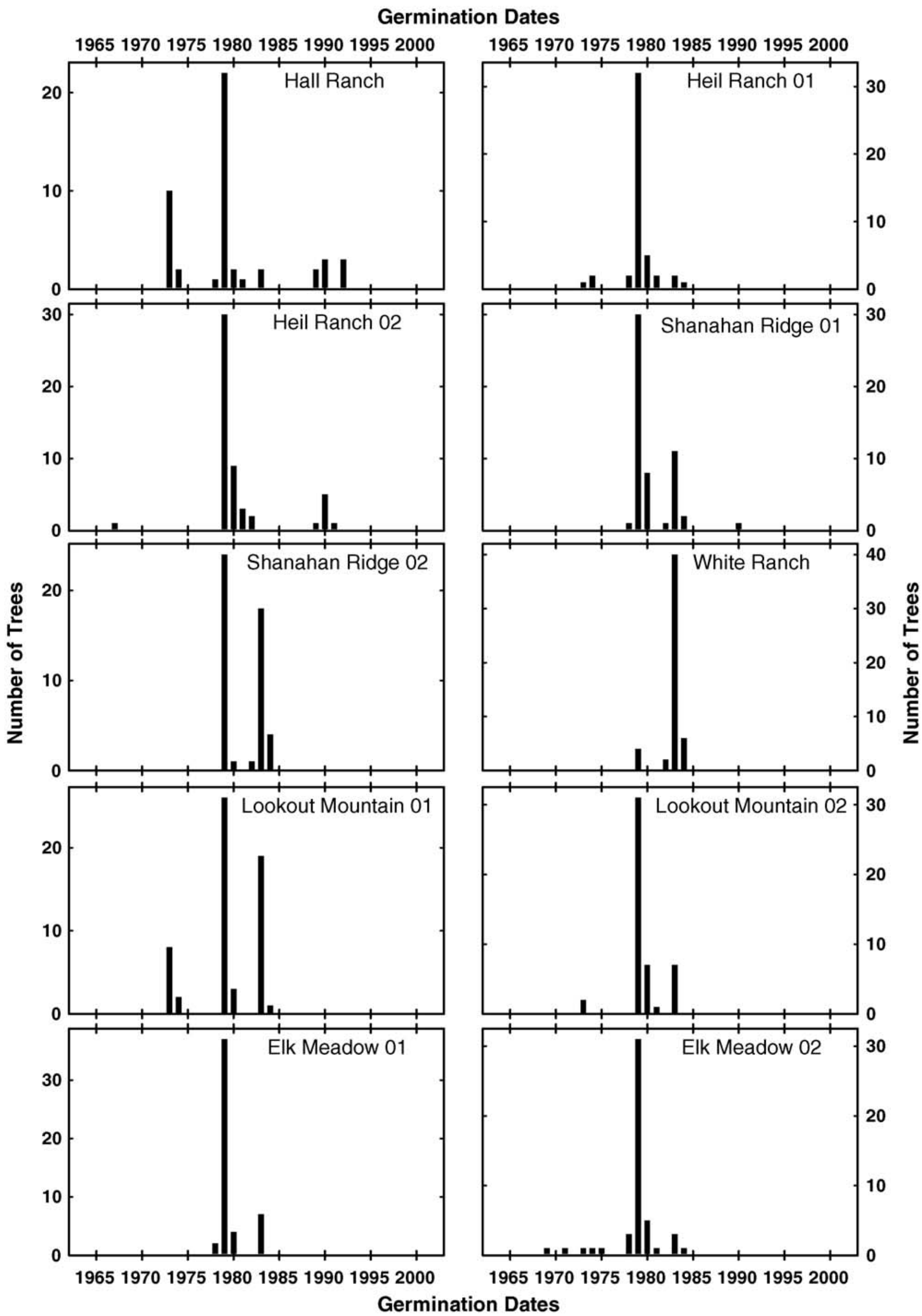

Fig. 2. Age frequency distributions of *Pinus Ponderosa* from all sample sites. A total of 507 saplings and seedlings were sampled and dated from six locations yielding 10 sites along the lower montane foothills of the northern Front Range of Colorado.

computed, and then compared to the ranked values of tree-ring indices to determine how often this threshold value was exceeded.

3. Results

3.1. Tree establishment dates

Germination dates were determined for 507 ponderosa pine seedling and sapling cross-sections. The youngest sample age was 1992 while the oldest was 1967. In each plot, there were no years of abundant establishment that were not also years of abundant establishment in at least several other plots (Fig. 2). This strongly implies that regional climate is the major determinant of these recruitment events and justifies compositing the 10 sites into a single regional record for further analysis (Fig. 3A). The most common germination date was 1979 (53% of samples), while the second most abundant date of germination was 1983 (21% of samples) (Fig. 3A).

Due to the difficulty of crossdating short records, it is uncertain if some of the smaller peaks in establishment represent 2- or 3-year episodes of recruitment, or were 1-year dating errors (Fig. 3A). For instance while 1980 is the third most frequent germination date, it is directly adjacent to 1979, the year of the largest number of seedling establishments, and it is likely that many of these dates were actually 1979. Another example of a potentially erroneous date is 1984, which is the fourth most frequent germination date but is adjacent to the 1983 pulse (second highest). Because the years 1973 and 1990 were isolated from the two main establishment pulses (1979 and 1983), it is highly likely that they were valid establishment pulses. Thus, a set of four years of abundant tree establishment (1973, 1979, 1983, and 1990) was identified and used in the climatic analyses. A set of the seven top years of establishment was also used in the climatic analyses to account for the possibility that these were valid establishment dates. The analyses based on the set of seven years showed the same patterns as those based on the four recruitment years (League, 2004), and consequently are not presented here.

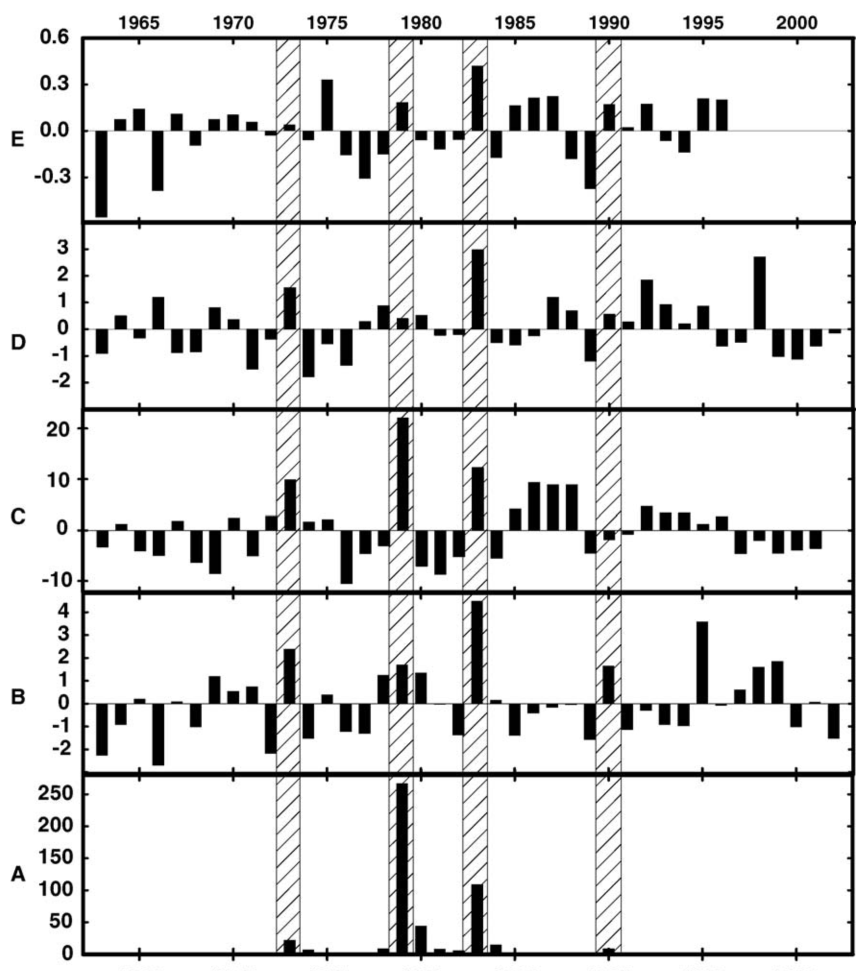

Fig. 3. (A) Composite frequency distribution of ponderosa pine establishment dates taken from all sampling locations along the lower montane foothills of the northern Front Range of Colorado. De Martonne's aridity index for (B) March–May (spring preceding seedling establishment) and (C) November–February (fall and winter following seedling establishment). High aridity index values indicate more moisture availability; (D) January–February Multivariate El Niño/Southern Oscillation Index (MEI). High MEI values equal El Niño conditions; and (E) Tree-ring index. Higher tree-ring index values equal more spring moisture availability. Cross-hatched areas are aligned with the four years of episodic establishment and corresponding indices.

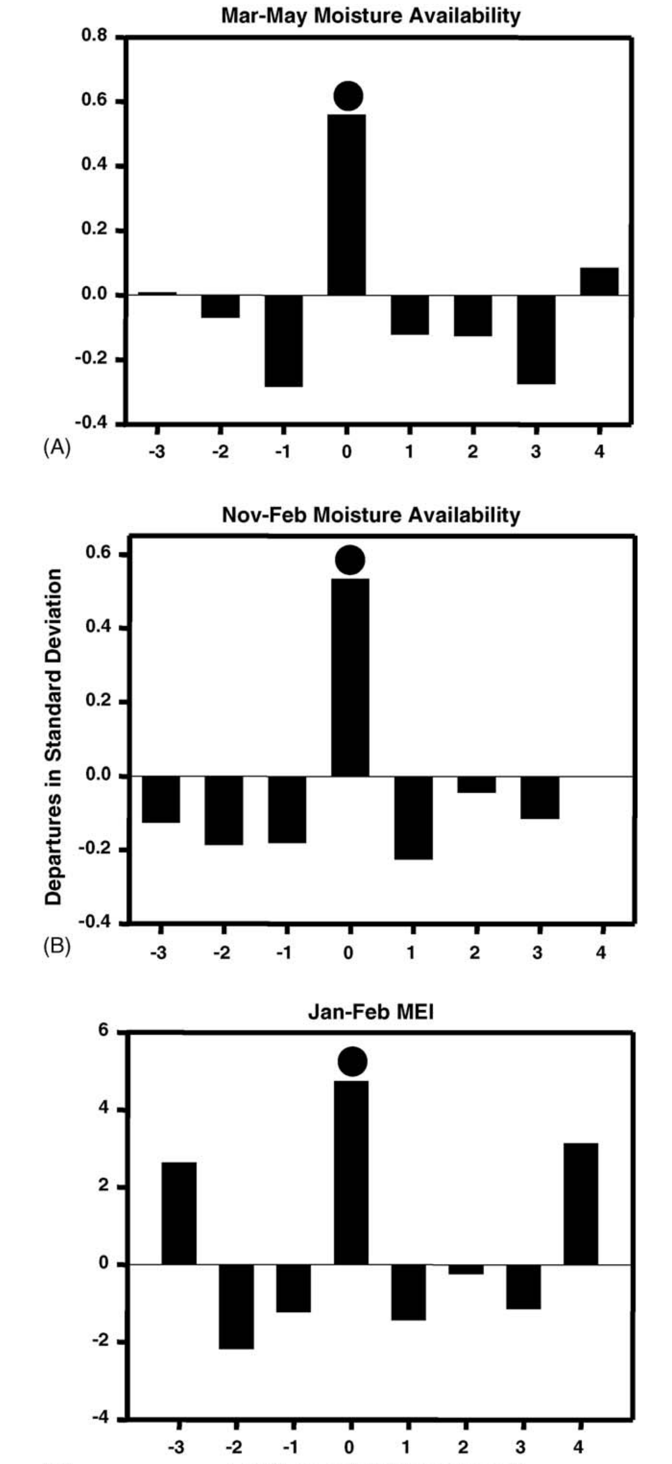

Fig. 4. Superposed epoch analysis (Grissino-Mayer, 1995) of (A) March–May; (B) February–November seasonal aridity index; and (C) January–February Multivariate El Niño/Southern Oscillation Index (MEI) (Wolter, 2004) departures from the mean prior to and following regeneration events of *Pinus ponderosa* along the lower montane foothills of the northern Front Range of Colorado. Year zero represents the recruitment event year with the bar indicating the departure from average moisture availability (A and B) and MEI (C) for all years. High MEI values equal El Nino conditions. Negative and positive years indicate lag years before and after recruitment year. Recruitment record includes the four years of major episodic recruitment (1973, 1979, 1983, 1990). Circle symbols above bars indicate significant values at $\geq$95% confidence interval.

3.2. Relationships to climatic indices

Regional records of climatic variables were grouped into seasonal sets of 2, 3, 4, 6, 8, 12 month combinations and compared with both the four recruitment years and non-recruitment years (years of zero establishment; League, 2004) but only the most consistent patterns are presented here. The most consistent patterns graphically relating tree recruitment to moisture availability were spring (March–May) and the following fall/winter season (November–February) (Fig. 3B and C). The four episodes of peak establishment of ponderosa pine in 1973, 1979, 1983, and 1990 were all years of above average March–May moisture availability. November–February moisture availability was above average, or in one case (1990) near average. The two peak years of establishment, 1979 and 1983, were the years of peak November–February and March–May moisture availability, respectively, during the period 1963–2002. The three years of highest November–February moisture availability were all establishment peaks. Overall, years of recruitment were distinguished from non-recruitment years by above average moisture availability during spring and above or near average moisture availability during the following fall/winter seasons. Non-recruitment years exhibited below average moisture availability in one or both of these seasons (Fig. 3B and C).

SEA indicates that seedling establishment coincides with above average March–May and November–February moisture availability immediately preceding and following seedling establishment, respectively (Fig. 4A and B). However, the small number of years available for statistical analysis is cause for caution in interpretation of these results. SEA also shows that the four recruitment years coincide with above average January–February MEI (Fig. 4C). Above average MEI values indicate the warm (El Niño) phase, which is associated with greater moisture availability and lower temperatures during spring.

A regional ponderosa pine tree-ring chronology (Veblen et al., 2000) was used to assess how frequently the moisture conditions associated with the four recruitment years occur over longer time periods. For comparison of moisture availability during the four years of recruitment, we simply ranked tree-ring indices over the past 300 years. A tree-ring index of 1.0 is the expected ring width, and values greater than 1.0 indicate above average moisture availability. Tree-ring indices from the regional ponderosa pine chronology for the four years of abundant seedling establishment ranged from 1.05 (1979) to 1.43 (1983) and averaged 1.21. Over the 300 year (1696–1996) record of the chronology, the tree-ring indices for the four recruitment years were ranked 3rd, 51st, 56th, and 120th over the years from 1696 to 1996. The average tree-ring index of 1.21 for the four recruitment years corresponded to a rank of 41 for this 300-year period.

4. Discussion

Germination dates of the c. 500 ponderosa pine from six scattered sites along the forest-grassland ecotones indicate that successful establishment during the past c. 40 years occurred in four episodes centered on the years 1973, 1979, 1983, and 1990. The high percentages of trees established during these four years, and in the case of 1973 and 1990 their separation from other peaks by at least several years, indicate that in spite of potential dating errors these were the central years in establishment peaks. More than 80% of the 507 dated juveniles established during those four years. More than 98% of the population established in the four peak years and the two years to each side of a peak. Due to the difficulty of crossdating all of the short time series, it is uncertain if the apparent tree establishments in the years to either side of one of the four establishment peaks were accurately enumerated. However, we believe they were inaccurate because the establishment years other than the four identified peaks were not characterized by above average moisture availability as in the case of the four peak years. Over the 1967–1992 span of germination dates determined in this study, there were no years other than the four peaks (± 1 year) in which more than eight ponderosa pine established. Indeed, between 1967 and 1992, there were 24 years in which ≤ 1 seedling established.

The highly episodic and synchronous nature of ponderosa pine across the six sample areas is unlikely to have resulted from synchronous disturbance events (e.g., changes in fire or grazing regimes). Instead, they were most parsimoniously explained by the coincidence of abundant seed production of ponderosa pine with climatically suitable conditions. Seed availability of ponderosa pine is highly variable, and periods of several consecutive years were common in which seed production is low or nil at individual sites and in regional populations (Krannitz and Duralia, 2004). Although records of seed production were not available for the sample sites, multiyear studies of ponderosa pine seed production elsewhere have documented population-wide crop failures. Weather variation during the 24–27 months from seed cone initiation to maturity has been shown to affect cone production (Krannitz and Duralia, 2004). For example, in a 23-year study in California, above average cone crops were associated with above average temperatures in April and May 2 years earlier (Maguire, 1956). However, in the current study there were no statistically significant relationships of peak establishment years with temperature and precipitation conditions 2 years earlier (League, 2004).

We interpret the four episodes of peak establishment of ponderosa pine in 1973, 1979, 1983, and 1990 to have been periods of adequate seed production that coincided with suitable climatic conditions for seedling establishment and survival. These were all years of above average March–May moisture availability resulting in favorable conditions for initial seedling establishment. November–February moisture availability was above average, or in one case (1990) near average. The two peak years of establishment, 1979 and 1983, were the years of peak November–February and March–May moisture availability, respectively, during the 1963–2002 period. The three years of highest November–February moisture availability were all establishment peaks. The small number of peak establishment years mandates caution in the interpretation of these patterns, but tentatively we suggest that abundant establishment and survival of ponderosa pine seedlings depends on above average March–May moisture availability followed by lack of drought in the following November–May period. Because establishment peaks must be years in which seed production and favorable weather coincide, not every year of favorable weather will result in an establishment peak. For example, 1995 was a year of high March–May moisture availability and near average November–February moisture availability (i.e., similar to 1990) but no seedlings dated from 1995. Alternatively, our method of selecting sites based on 1–3 m tall juveniles may have reduced the chances of sampling such young and small seedlings.

Variations in spring climate in the Colorado Front Range have a statistically significant association with ENSO activity patterns (Veblen et al., 2000; Donnegan, 2000). The current research shows that peaks of establishment of ponderosa pine along forest-grassland ecotones in northern Colorado are associated El Niño conditions in the eastern tropical Pacific. Wetter, cooler conditions in the spring and fall in the Front Range are associated with El Niño conditions (Donnegan, 2000) and are favorable for establishment and survival of ponderosa pine.

As a potential indicator of the frequency of years climatic conditions suitable for ponderosa pine establishment over the past c. 300 years we used a regional tree-ring index of ponderosa pine growth. Using the average tree-ring index for the four recent episodes of establishment, similarly favorable conditions occurred 40 times during the period from 1696 to 1996. This is only a crude indicator of conditions suitable for establishment because the radial growth of ponderosa pine is primarily determined by spring, not fall, moisture availability. Nevertheless, these results suggest that any individual year over the past three centuries had less than a 14% chance of meeting the climatic requirements for ponderosa pine establishment. When the dependence of successful recruitment on episodic cone production is considered, it is evident that conditions for ponderosa pine establishment occur relatively infrequently, perhaps with an annual probability of 10% or less. Although the probability of any individual year being suitable for establishment is quite low, obviously the probability of such years occurring during the multi-century life spans of mature trees is high.

In the current study, by destructively sampling small trees and determining the dates of initial growth rings at root/shoot boundaries it was possible to identify a relatively small number of episodes of ponderosa pine establishment during the past c. 40 years along forest-grassland ecotones in the northern Colorado Front Range. These recruitment episodes appear to be dependent on infrequent favorable spring and fall/winter moisture conditions. In addition to dependence on favorable moisture conditions for establishment, a relatively long period free of fire is required for the survival of the ponderosa pine seedlings. The areas sampled in this study were generally in the lower montane zone where formerly there was a significant incidence of low-severity fires affecting grasslands and adjacent ponderosa pine woodlands (Veblen et al., 2000;

Sherriff, 2004). Prior to fire exclusion in the early 20th century, low-severity fires may have occurred with sufficient frequency to prevent the survival of most of the ponderosa pine that may have established during moist years. This interpretation is consistent both with the decline in fire occurrence since the late 1800s as documented by tree rings and with the comparison of modern and historical photographs showing tree invasions of grasslands in this general habitat (Veblen et al., 2000; Veblen and Lorenz, 1991). Currently, these tree invasions are interpreted primarily as a consequence of fire suppression (e.g., Winiger Ridge Project, 1999; Sugarloaf Fuel Reduction Project, 2004), but the current study shows that although protection from fire may be required for sustained tree invasions, the pace and timing of such tree invasions is highly dependent on climatic variation. The role of climatic variation and its influence on episodic establishment of ponderosa pine needs to be considered in any interpretations of reference landscape conditions as well as management plans in the context of ecological restoration.

We stress that the current findings pertain to forest-grassland ecotones in the lower montane zone. In the upper montane zone, the importance of more severe fires historically was much greater and the role of climatic variation in determining the success of post-fire tree establishment has not been systematically examined, especially at an annual resolution. Because most stands in this higher elevation developed after the occurrence of 19th century fires in the northern Front Range and now consist of large trees (Veblen and Lorenz, 1986; Veblen et al., 2000; Sherriff, 2004; Ehle and Baker, 2003), it is much more difficult to precisely determine tree germination dates. At increasing elevation in the Front Range, moisture stress declines and it is possible that establishment of ponderosa pine is less sensitive to annual climatic variation. Or alternatively, even at higher elevations the dependence of tree establishment on infrequent moist years may continue. To evaluate these two alternatives will require future research based on precise dating of tree germination to determine the effects of climatic variation on ponderosa pine establishment at an annual resolution.

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