THE ROLE OF RECENT CLIMATIC VARIABILITY

ON EPISODIC *PINUS PONDEROSA*

RECRUITMENT PATTERNS ALONG THE

FOREST-GRASSLAND ECOTONE OF

NORTHERN COLORADO

By

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B.S., Montreat College, 1999

A thesis submitted to the Faculty of the Graduate School

of the University of Colorado for the degree of

Masters of Arts

Department of Geography

2004

This thesis entitled:

**The Role of Recent Climatic Variability on Episodic *Pinus ponderosa*
Recruitment Patterns Along the Forest-grassland Ecotone of Northern
Colorado**

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find that both the content and the form meet acceptable presentation
standards of scholarly work in the above mentioned discipline

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The Role of Recent Climatic Variability on Episodic *Pinus ponderosa* Recruitment Patterns Along the Forest-grassland Ecotone of Northern Colorado

Thesis directed by Professor Thomas T. Veblen

The primary objective of this study was the detection of climatic influences on the recent establishment of ponderosa pine at or near the forest-grassland ecotone in the northern Front Range of Colorado. The study was motivated by the observation of an abundance of similarly-sized (i.e. less than 3m tall) ponderosa pine and that these abundant populations of juvenile trees may represent one or a few cohorts of similarly aged individuals across a large area. These questions were examined by precisely determining the germination dates of > 500 juvenile ponderosa pine at an annual resolution and relating dates of regeneration pulses to climatic variables. To evaluate the effects of recent climatic variation, on recruitment and survival patterns, 3 types of climate data were used: (1) instrumental climate records from nearby local stations, (2) Multivariate El Niño/Southern Oscillation Index (3) local tree-ring index from ponderosa pine in the Northern Colorado Front Range. Based on a regional sample of regeneration dates, a strong association between climatic variation and episodic recruitment of ponderosa pine exists. The strongest association exists during years in which spring and fall moisture availability is coincidently high. The four years in which recruitment was observed during the past forty years includes 1973, 1979, 1983, and 1990. Additionally, This research indicates that recent years of episodic recruitment occurring along the forest-grassland ecotone in northern Colorado are strongly correlated with large scale warming of sea-surface temperatures in the eastern Pacific, along with other ENSO identifying factors. Furthermore, analysis of a tree-ring width index from a local ponderosa pine chronology proved that in instances where regional episodic recruitment occurred, strong responses in radial growth of adult ponderosa pines transpired simultaneously.

ACKNOWLEDGEMENTS

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Introduction

Shifts in forest-grassland ecotones associated with pine invasions in the western U.S. have long been the source of much interest among ecologists and land managers (Foster 1917; Johnsen 1962; Burkhardt and Tisdale 1976; Mast *et al.* 1997). Occurring at the extreme limits of tolerance for plant species, ecotones are areas of transition where spatial controls of species distribution are evident, and are also areas believed to be particularly sensitive to climatic changes (Neilson 1993; Mast et al., 1998). The focus of the present study is on the lower montane zone of the Colorado Front Range where the ecotone between grasslands and ponderosa pine (*Pinus ponderosa*) woodlands is believed to be sensitive to changes in disturbance regimes (e.g. fire and grazing) as well as climatic variation (White 1985; Savage, 1996; Mast et al. 1998). The primary objective of the present study is the detection of climatic influences on the recent establishment of ponderosa pine at or near the forest-grassland ecotone in the northern Front Range of Colorado.

The present study was motivated by the observation of an abundance of similarly-sized (i.e. less than 3m tall) ponderosa pine at widely dispersed sites near the forest/grassland ecotone in the northern Front Range (mainly Boulder and Jefferson Counties). It was conjectured that these abundant populations of juvenile trees may represent one or a few cohorts of similarly aged individuals across a large area. Consequently, it was natural to pose the question: Are there one or a few cohorts of young ponderosa pine in the

forest/grassland ecotone that have established synchronously over a large area in response to favorable climatic conditions or some other regional environmental change? Thus, the current study was designed to address the following specific questions for the lower montane zone of the northern Front Range: 1) Can distinct pulses of ponderosa pine establishment be identified at temporal scales of one or a few years? 2) If these are distinct pulses of establishment, are they synchronous across dispersed sites? 3) Is there an association of pulses of ponderosa pine establishment with particular climatic conditions? These questions were examined by precisely determining the germination dates of > 500 juvenile ponderosa pine occurring at widely dispersed lower montane (1800m- 2400m) sites and relating dates of regeneration pulses to climatic variables.

Current State of Knowledge

Regeneration and forest dynamics have been studied in many ponderosa pine ecosystems in the western U.S., but the most influential work in the context of forest management has been developed in the southwestern United States (Pearson, 1923; Schubert, 1974; White, 1985). Many of these studies use classic dendrochronological methods for their investigations. One major assumption and limitation of forest studies using traditional dendrochronological methods is the difficulty in detecting the precise year of germination. Identifying the exact date of germination of trees would be helpful in elucidating, at finer scales, the role of historical factors in forest development. Most studies of aging trees give a general estimate based on

annual ring counts on increment cores taken at ~ 30 cm above ground, or at an angle toward the tree base. Recently, a methodology was proposed to achieve annual resolution of germination through analysis of the anatomical characteristics of the pith region on cross-sections taken at the base of a tree (Telewski & Lynch 1990; Telewski 1993). Accurate evaluation of germination dates would allow an assessment of the influence of seasonal to interannual temperature and precipitation factors, and a determination of the ecological requirements for ponderosa pine germination (Savage 1996).

Several regional, local, and micro-site factors can negatively affect Ponderosa pine regeneration, including but not limited to, regional drought, local water availability, seed crop production, fire, browsing and trampling by cattle and ungulates, sunlight intensities, and substrate composition, (Pearson 1923; Larson & Schubert 1969; Harrington & Kelsey 1979). In addition, the depth of litter and duff layers is a significant deterrent, considering that it has little moisture capacity and high susceptibility to temperature extremes (Schubert 1974).

Successful establishment of ponderosa pine in some habitats is thought to be periodic (White 1985). In the southern Front Range of Colorado, stand-age reconstructions have been interpreted as evidence that open sites believed to be suitable for ponderosa pine establishment may remain uncolonized by ponderosa pine for decades (Kaufman et al. 2000). Irregularity of successful recruitment in ponderosa forests can be attributed to the species characteristics that require the synergy of several factors for a

suitable regeneration year. Studies in the southwest indicate that conditions necessary for germination and establishment of ponderosa pine include timing of precipitation, seed crop, and seasonal temperature changes. Schubert (1974) documents the coincidence of a good seed supply with timely temperature and precipitation patterns. Specifically, Ponderosa pine seeds appear to need continually moist conditions for at least 7 days at temperatures >13 C° to germinate. In addition, regeneration of Ponderosa appears to be intermittent due to the uncommon occurrences of these types of scenarios, thereby suggesting the importance of climatic influence on ponderosa stand initiations (Schubert 1974; White 1985). Building upon observations made by Pearson in 1923, Savage and others (1996) found that a major regional recruitment period of ponderosa pine had occurred in 1919. By using precise aging techniques, Savage *et al.* found that a unique combination of climatic factors had supported this large episode of recruitment. These conditions included a warm and wet May with an above average, well-distributed water supply throughout the year. In Colorado pulses of regeneration have been identified in the late 19th and 20th centuries (Mast *et al.* 1998) but due to a lack of precision in dating procedures only a suggested link could be made between above average spring moisture and ponderosa pine recruitment. While the warm (El Niño) phase of the El Niño Southern Oscillation (ENSO) is associated with greater moisture availability during the spring for the Colorado Front Range (Veblen *et al.* 2000; Donnegan 2000), and has direct links affecting regional fire regimes in these

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areas, no quantitative evidence exists linking episodic recruitment of ponderosa pine during ENSO events.

Ponderosa pine is not a seed banking species and therefore is reliant upon annual seed production for reliable regeneration. Seed production has been found to be cyclic with trees producing crops every 2-5 years as found in the Black Hills of South Dakota (Boldt 1974). Correlating recurring seed crop production and climatic influences has been difficult and has shown inconsistent periodicity (Keyes 2000). Above average temperatures during cone formation has been correlated with good seed crops (Daubenmire 1960) however, the overall affects of climate variation on seed crop production are not well understood. In addition, predation of seeds and cones by insects, rodents, and birds has shown to significantly decrease viable seed, thus directly affecting pine tree recruitment success (Keyes 2000; Larson 1961; Larson et al. 1969).

Generally ponderosa pine seedlings are relatively shade intolerant and require canopy-opening disturbances such as fire, logging or gap caused by tree death to become established (Mast et al. 1997; Stein 1998). Recruitment pulses may occur on open sites during optimal climatic conditions where moisture thresholds that usually limit recruitment are surmounted. Seedlings quickly develop a long taproot that enables them to reach moisture even on sites that have low moisture availability. While drought overall is the apparent controlling factor for maintaining ecotonal boundaries between forest and

grasslands (Barton 1992), studies have shown that spring and fall drought is a major limiting factor to survival of ponderosa pine seedlings.

The presence and absence of fire also plays a major role in ponderosa pine regeneration. Abundant charcoal found in the soils of the Front Range of Colorado forest suggests the widespread importance of fire in forest and grassland dynamics (Peet 1981). Along the Colorado Front Range, ample flammable grasses and herbaceous species in and around ponderosa pine woodlands have burned frequently. Typically, these fires maintain grasslands and prevent pine seedling encroachment into grasslands (Goldblum & Veblen, 1992). During the period of Euro-American settlers and prospectors in the 1850s, the frequency of wildfires increased dramatically until the 1920s, when fire suppression policies resulted in significant decreases in fire frequency (Veblen & Lorenz, 1986; Veblen *et al.* 2000). Climatic conditions favorable to fire were a major cause of increased fire spread during the second half of the 19th century in the Colorado Front Range (Goldblum & Veblen 1992; Veblen et al. 2000, Donnegan 2000). The lack of fire in the region during the 20th century is a major contributor to the encroachment and increased densities of pine seedlings in the region (Figure 1) (Mast *et al.* 1998).
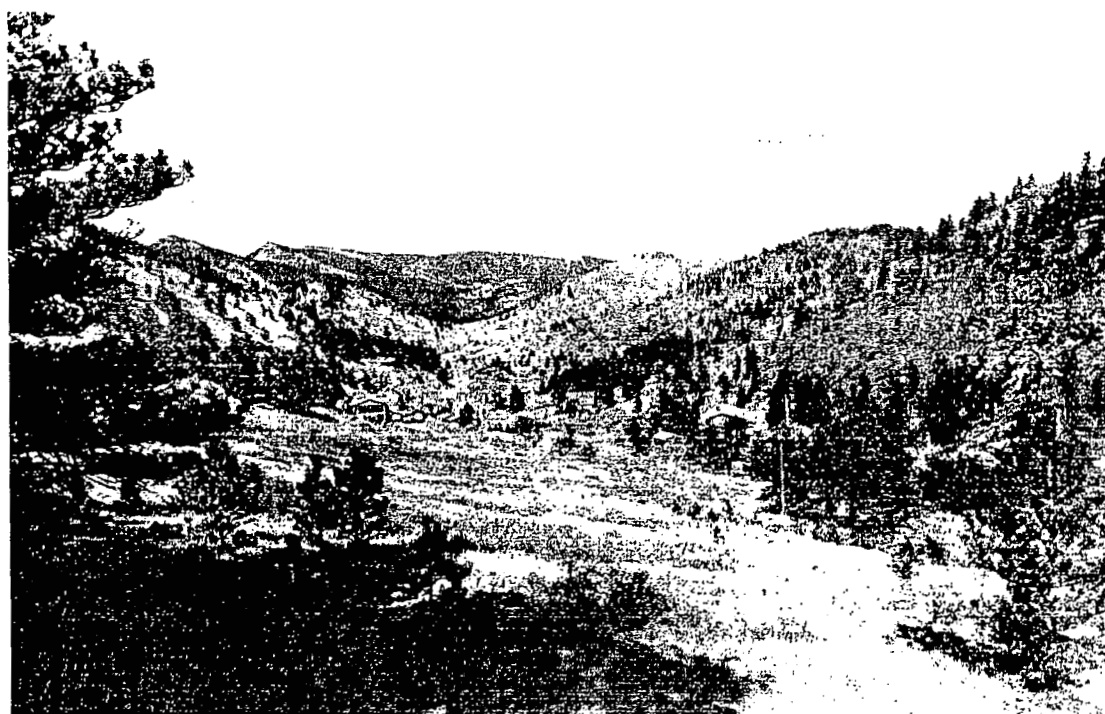
Figure 1 Red Hill Valley northwest of Boulder. The above photo was taken in 1899 while the matching photo was produced in 1984 (Veblen, & Lorenz 1991). This pair of photos shows increasing abundance of ponderosa pine over the course of 85 years during the past century. Sparse groups and open woodlands have become dense forest.

In addition to fire, land use practices such as cattle grazing on private lands or dense ungulate populations as a result of protection from hunting pressures in management areas can have important effects on pine seedling regeneration. While light to moderate grazing can actually promote regeneration by exposing bare mineral soils and reducing competition from herbaceous species, intense grazing by cattle and/or ungulates may prevent widespread tree invasions due to trampling and direct herbivory on seedlings and saplings (Rummel 1951). Inversely, the cessation of grazing could possibly lead to a great potential for ponderosa pine regeneration.

Invasions of ponderosa pine into ecotonal grassland regions can also be attributed to light and moisture availability. These factors have been studied as a product of topographic orientation (aspect) in GIS modeling applications (Mast et al. 1997). In Boulder County, research has indicated greater tree invasion on north-facing slopes than on south-facing slopes (Mast et al., 1997). Preference of tree invasions on north aspects is believed to be attributed to greater water availability than on the warmer and drier south facing slopes. In addition, soil depth and texture have direct impacts on water availability. Ponderosa pine is almost always found in thin or rocky soils where competition from grasses and forbs for water recourses is much less than in deep fine textured soils where herbaceous vegetation can form dense sod that inhibits tree regeneration (Peet 1981).

These are the primary factors that are believed to affect ponderosa pine regeneration in and along the Front Range of northern Colorado. With

the identification of the timing of germination of ponderosa pine, it may be possible to identify climatic conditions suitable for regeneration in the lower montane zone of northern Colorado. This knowledge is essential for providing a better understanding of the role of climatic, historical, and site-specific influences on ponderosa pine-grassland ecotones in northern Colorado.

Methods

Study Area

The Colorado Front Range is the easternmost range of the Rocky Mountains, extending north to south ~150km from the Wyoming border paralleling Great Plains. The majority of this land mass is composed of a core of acidic Precambrian intrusive rocks, which frequently contain intrusions of acidic Tertiary plutons (Madole 1973). Toward the east at elevations below ~2400 m, outside the mineralized belt, are a series of narrow sedimentary formations forming cuestas and hogbacks. Soil types found in the lower montane zone commonly are cryboralfs, while ustolls are found on south-facing slopes. Generally, the soils of the Colorado Front Range are rocky, thin, immature, coarse, and slightly acidic (Peet 1981). Trees are located along mesas and sandstone ridge tops where coarsely textured soils may give deep-rooted trees a competitive advantage over grasses for competition of soil moisture (Schubert 1974).

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 is influenced by the North American

monsoon where convective storms develop, occasionally providing brief but substantial amounts of precipitation. There is a gradual decrease in the influence of the monsoon pattern as you move from south to north along the Front Range. In a given year increases in precipitation typically yield decreases in temperature. The study area's mean annual precipitation is 395 mm, with January being the driest month and May the wettest. The July mean daily temperature maximum is 31°C while the mean daily temperature minimum is minus 8 °C in January (data from Boulder, C.O. station).

ENSO events have been shown to have a significant influence on seasonal temperature and precipitation along the Colorado Front Range (Veblen et al. 2000; Donnegan 2000). Precipitation is often below average during winter through spring during La Niña events while El Niño tends to increase precipitation to above average during the same period. Temperatures during La Niña events during fall and spring tend to be above average, while below average temperatures occur during El Niño events. These types of patterns imply that El Niño events could be conducive to years of ponderosa pine recruitment.

Vegetation along the lower-montane region varies along elevational gradients and can be found in several structural states, from open park like stands of ponderosa pine near the forested-grassland ecotone and on south-facing xeric sites where rocky mountain juniper (*Juniperus scopulorum*) are frequently present, to more dense stands on north-facing mesic slopes where forest typically is mixed with Douglas-fir (*Pseudotsuga menziesii*). Generally,

south-facing slopes have a lower tree density and higher herbaceous concentration than adjacent cooler and moister north-facing slopes. The forested-grassland ecotone, also referred to as the lower tree-line, appears to be a product of ponderosa pine's ability to tolerate water stress. At the higher elevations limber pine (*Pinus flexilis*), aspen (*Populus tremuloides*), and lodgepole pine (*Pinus contorta*) co-exist with Ponderosa pine and Douglas fir. Mixed within the forest are open meadows which are found through the region from valley bottoms and on hill slopes. Common understory species in the lower timberline forests include shrubs: common juniper (*Juniperus communis*), wax currant (*Ribes cereum*), mountain mahogany (*Cercocarpus montanus*), antelope bitterbrush (*Purshia Tridentata*), Threeleaf Sumac (*Rhus trilobata*); yucca (*Yucca glauca*); herbaceous: waxflower (*Jamesia communis*), kinnikinnik (*Arctostaphylos uva-ursi*), prickley pear cacti (*Opuntia rafinesquei*); grasses: spike fescue (*Leucopoa kingii*), blue grama grass (*Bouteloua species*), little bluestem (*Andropogon scoparius*), needle grass (*Stipa species*), cheatgrass (*Bromus tectorum*), buffalo grass (*Buchloe dactyloides*).

Native Americans settled and hunted along and in the Front Range for at least several thousand years prior to the first settlement by Euro-American settlers in the late 1850's (Buccholtz 1983). Evidence suggests that Native-Americans intentionally set fires in the Front Range of Colorado for hunting purposes and in times of warfare (Stewart 1942). During the late 1850s, gold rush prospecting attracted a large number of Euro-American settlers to the

region. There are numerous reports of early settlers intentionally setting fires during the second half of the 19th century (Fosset 1893; Stewart 1942). Fire frequencies during this time dramatically increased (Goldblum & Veblen, 1992) but by the 1920s fire suppression polices across the region had reduced the frequency and extent of wildfires. Fire exclusion in the lower montane forest of Colorado have resulted in increased tree densities inside of forests and has promoted the invasion of trees into grasslands along the forest-grassland ecotone (Mast et al. 1997).

The shade-intolerant ponderosa pines in Rocky Mountain Forest are adapted to and directly benefit from wildfire. Along the lower montane Colorado Front Range crown fire and surface fire have played a major role in shaping the historic ponderosa pine forests (Veblen & Lorenz 1986; Brown *et al.* 1999; Kaufmann *et al.* 2000; Ehle & Baker 2001). Ample grasses and forbs have offered a fine fuel base for fires that burn frequently from a combination of lightning, aboriginal, and Euro-American ignition sources. Ubiquitous charcoal found through the Colorado Front Range forest adds to the evidence of the widespread importance of fire as an ecological disturbance (Peet 1981).

Grazing became an integral part of life in the 19th century in the region and livestock numbers are believed to have peaked in the 1890s to early 1900s (Marr 1961), and most of the area has not been grazed since the 1960s. Selective logging of ponderosa pine and Douglas-fir was widespread

from the late 1850s to early 1900s but, following subsequent logging, has been minor (Veblen & Lorenz 1991).

Study Sites

Recruitment sampling took place in the lower montane zone (~1888-2408m) on the eastern slope of the northern Colorado Front Range foothills at locations found along a ~35km north-south line from near Lyons (40° 13') to Evergreen (39° 40') (Figure. 2). During the spring of 2003, a total of 10 sampling plots were located on 6 properties owned by Boulder County Open Space, City of Boulder Open Space and Mountain Parks, and Jefferson County Open Space. (Figure. 2; Table 1.).

Location	Size in Hectares	Previous Uses	Year Park Established
Hall Ranch			
Boulder Co. Parks and OS	1298	Cattle Ranch	1993
Heil Ranch			
Boulder Co. Parks and OS	1992	Cattle Ranch	1993
Shanahan Ridge			
City of Boulder Mountain parks	2732	Cattle Ranch	1972
White Ranch			
Jefferson Co. Open Space	1762	Cattle Ranch	1969
Lookout Mountain			
Jefferson Co. Open Space	45	Private Residence	1968
Elk Meadow			
Jefferson Co. Open Space	507	Cattle Ranch	1977

Table 1 Descriptions and previous land use histories as well as date of preservation for each research location. Site locations can be seen on Figure 2
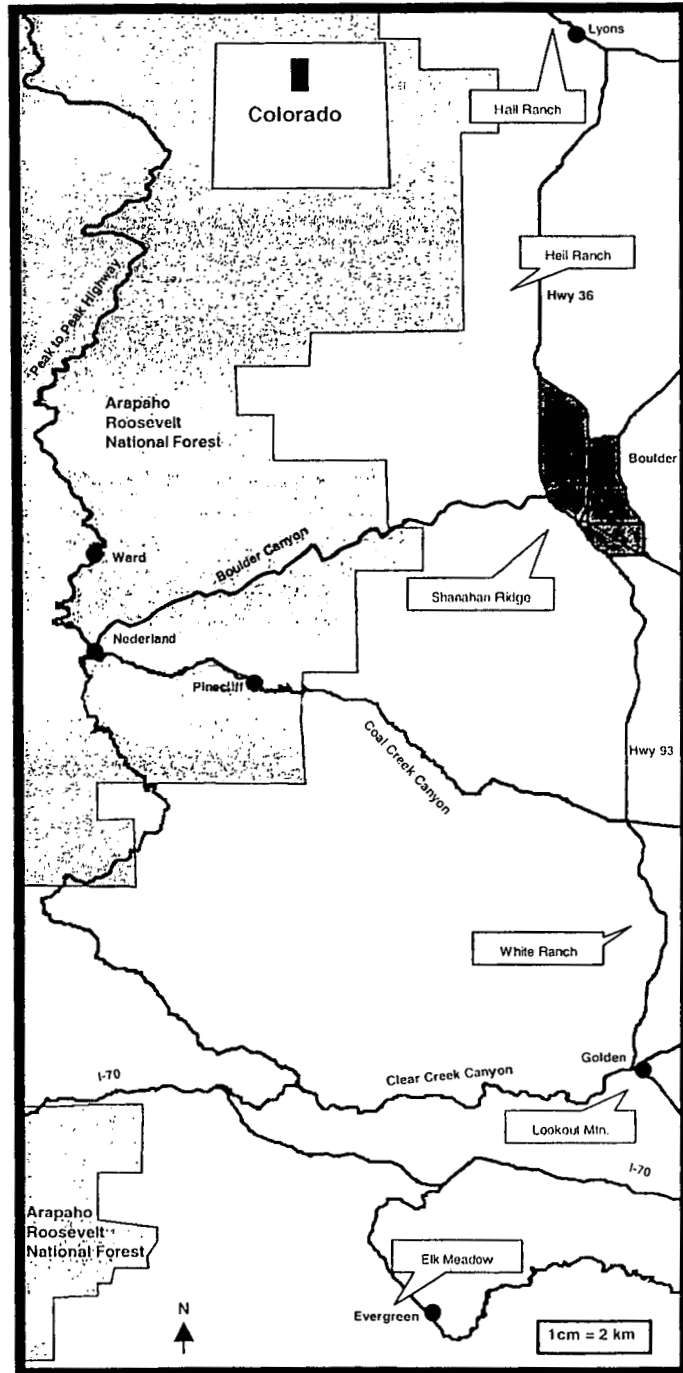
Figure 2 Map of study sites in the northern Colorado Front Range

Grazing occurred in most of these areas beginning in the mid 19th century along with the arrival of Euro-American settlers, but by the 1970s due to the purchase and preservation of open spaces along the rapidly developing Front Range communities grazing had nearly ceased (Table 1). However, grazing 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 while controlled burning and forest thinning prescriptions have become more abundant in the past century.

Field Methods

The goal of field sampling was to generate an extensive sample of juvenile trees (i.e. less than 3 m tall and presumably less than 40 years old) that have characteristics to permit determination of their exact ages (i.e. germination dates). Areas in which spatial patterns imply a recent tree invasion of forest-grassland ecotone were preferentially selected for sampling. Areas chosen covered a wide range of aspects and slope steepness within the forest-grassland ecotone. Areas were sampled with a clear bias towards younger stands that were believed to be the result of synchronous regeneration (Figure 3).

Figure 3 The typical signature of a pulse of ponderosa pine recruitment that is frequently observed along the lower montane Front Range foothills of Northern Colorado.

To maximize the chance of detecting climatic influences on tree regeneration, sites chosen where located in undisturbed locations, or at least 10m from any disturbed area (i.e. roads, trails, tree fall, water courses). Additionally, logged areas, floodplains, eroded areas, areas of evidence of recent fire, areas of recent forest management, and areas of general human activities were avoided. Within each subjectively determined homogeneous area, one to two plots 10-300m^2 were randomly located. Plot size varied according to tree seedling density so that a minimum of 50 individuals were

included in each plot. In each plot all saplings and seedlings (<200cm tall) were cut down using handsaws 5 cm below and above the root collar (total sample lenght 10cm) by excavating around each stem with small garden spades to allow for exact determination of regeneration dates in the lab. Seedlings that were small enough to be uprooted were pulled up and cross-sectioned in the lab. Other data collected for each cross-section included: seedling/sapling height, percent overstory canopy, distance from seed source, percent of rock visible around stems, and average soil depth.

Sampled areas were in and along forest-grassland ecotone boundaries and in open stands of Ponderosa pine. For descriptive purposes, a qualitative site description of forest stand characteristics was completed which included visual measurements of percent canopy overstory and quantitative measurements of distances of sample plots from nearest adult seed bearing individuals. Distance from seed source was measured by taking the average distance of the five nearest trees. This measurement represented the distance from seed source or the average distance from potential parent trees (>20cm dbh). Additionally, to examine the minimum time that sites have had viable seed sources, adjacent stands were aged using standard dendrochronology methods. For this we cored 10 of the oldest trees that were nearby sampling plots. The criteria used for selecting the oldest individual trees were: tree size, presence of large diameter branches, a large round crown, and thick orange bark with large fissures. Trees were cored as close to the base as possible to achieve the most

accurate estimate of the individual trees. Other information recorded for each tree included core height, estimated rings to center, diameter at breast height (dbh), initial growth patterns, suppressions, releases, and the approximate age of the tree.

Additional site information relevant to Ponderosa Pine regeneration included observations on site substrate conditions. To inspect the amount of rock contained on-site, an estimate of visible rock around each stem was calculated by erecting a 1m x 1m collapsible wire plot around each seedling/sapling and visually estimating the percent amount of rock for each specimen. Additionally the average soil depth (to a maximum depth of 20 cm) was calculated by inserting a long metal probe 3 times in the soil surrounding each stem. The average of the three measurements was recorded for each tree (Table 2).

Location	Site	Latitude	Longitude	Altitude (m)	Aspect	Slope	Plot Size (m)	Density (stems/sq m)	n	% Overstory	Avg. Seed Source Distance (m)	Height (cm)	Avg. % Rock	Avg. soil depth (cm)
Hall Ranch	Hall01	40° 13.01'N	105° 19.54'W	1974	15/N	10%	10x8	0.70	48	0	25	121	0.5	8
Boulder Co. Parks and OS														
Heil Ranch	Heil01	40° 8.81'N	105° 19.02'W	1984	12/N	8%	10x20	0.25	47	0	19.2	215	19	8
Boulder Co. Parks and OS	Heil02	40° 8.81'N	105° 19.02'W	1986	150/SSE	13%	10x20	0.31	52	10	11.8	66	21	6
Shanahan Ridge	Shan01	39° 57.73'N	105° 16.46'W	1889	40/NE	12%	10x30	0.19	54	0	55.8	187	0.3	>20
City of Boulder Mountain parks	Shan02	39° 57.73'N	105° 16.46'W	1888	20N	12%	10x10	0.52	48	0	21.6	173	0	>20
White Ranch	White01	39° 49.07'N	105° 16.67'W	2255	355N	7%	10x6	1.13	52	0	13.2	64	0	>20
Jefferson Co. Open Space														
Lookout Mountain	Look01	39° 43.74'N	105° 14.87'W	2305	160/SSE	9%	5x2	6.00	59	20	10.6	86	0	>20
Jefferson Co. Open Space	Look02	39° 43.74'N	105° 14.87'W	2302	143/SSE	9%	4x9	1.83	48	15	10.2	112	10	5
Elk Meadow	Elk01	39° 40.33'N	105° 22.31'W	2407	100/E	10%	9x12	0.47	50	10	16.8	105	3	8
Jefferson Co. Open Space	Elk02	39° 40.33'N	105° 22.31'W	2408	110/E	8%	10x20	0.29	49	15	14	69	12	10
Averages & Totals				2139.8		9.8%		1.17	507	7	19.8	119.8	6.6	≥12.5

Table 2 Sample site descriptions and biological variable comparisons. Number of juveniles sampled is given by n. Data are from all study areas.

Sample processing

Determining the total age of each seedling/sapling sample required careful laboratory processing of the root collar to acquire a cross section of the root and aerial portion of the stem. This portion of the stem is critical in determining the location of the pith for discovery of the exact year of germination. The pith and primary vascular bundles are contained within the sheath created by the vascular cambium of the stem. The vascular cambium is the tissue that forms around the pith forming an annual growth ring in the stem *but not in the root*. This distinct boundary between the two is known as the "root-shoot boundary" and contains a full record of annual rings which was used to determine the total age of a specimen (Telewski, 1993). Cross sections were cut and finely sanded (up to 600 grit) and examined under microscopes repeatedly until determination of the root shoot boundary was expressed in each sample. For most samples, the root shoot boundary could be found at or just above the root collar. Narrow ring patterns, injures and other scars where also observed and recorded.

After all cross-sections had been processed to identify the root-shoot boundary, the most confident germination date was assigned for each sample by counting all annual rings to pith. All samples were dated to an annual resolution, although some difficulties existed due to missing, extremely narrow, or false rings. These difficulties are believed to have caused dating errors within 1 year plus or minus the actual germination date. Regardless of

these errors, pulses of recruitment were very apparent in the data across all sites.

Tree core samples were processed according to standard dendrochronological techniques (Stokes and Smiley 1968). All tree core samples were mounted, sanded using consecutively finer sandpaper (up to 600 grit), and dated to the earliest ring date. Marker rings where derived from previous studies done in ponderosa pine on the Northern Colorado Front Range lower montane aided in visually cross-dating samples (Veblen *et al.* 2000).

For cores that did not reach pith, Duncan's (1989) method was used to estimate rings to the center of the tree. This method averages the width of the 5 innermost tree-rings and the curvature of these rings. Additionally, tree-ring suppressions, releases, patterns and anomalies were observed and recorded.

Climate Data Analysis Methods

To evaluate the effects of recent local and regional climatic variation, on Ponderosa Pine recruitment and survival, 3 types of climate data were used: (1) instrumental climate records from nearby local stations, (2) Multivariate El Niño/Southern Oscillation Index (Wolter, 2004), (3) local tree-ring index from ponderosa pine in the Northern Colorado Front Range (Veblen *et al.* 2000).

Instrumental Record

Local instrumental records of temperature and climate were developed for a 40 year time period (1963-2002) for the Northern Colorado Front Range lower montane forest (Table 3). Data sets of mean monthly temperature and precipitation were obtained from 5 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, 2 tests of homogeneity where computed: (1) a Mann-Kendall test of randomness of annual ratios from a homogeneous series; and (2) a scattergram of cumulative differences in temperature or precipitation over time approximating a straight line. These two procedures were preformed with the HOM program in the Dendrochronology Program Library (DPL) (Holmes 1994). According to these criteria, 3 temperature (Evergreen, Denver, and Fort Collins) and 3 precipitation (Evergreen, Boulder, and Waterdale) stations were selected. All stations were within or nearby the forest-grassland ecotone of Northern Colorado.

Weather Station Information					
Station	Location	Elevation (m)	Record duration	Estimated monthly values	Annual Mean
Temperature (°C)					
Evergreen	39°38'N / 105°19'W	2134	1961-to-present	1.6	22.60
Denver (Stapleton)	39°46'N / 104°52'W	1611	1927-to-present	0.1	26.30
Fort Collins	40°37'N / 105°08'W	1525	1937-to-present	0.0	25.60
Precipitation (mm)					
Evergreen	39°38'N / 105°19'W	2134	1961-to-present	3.3	401.30
Boulder	40°00'N / 105°16'W	1671	1948-to-present	3.1	403.20
Waterdale	40°26'N / 105°13'W	1594	1948-to-present	1.0	347.03

Table 3 Description of temperature and precipitation weather stations included in regional records for northern Colorado Front Range.

The MET program in DPL (Holmes 1994) was used to estimate monthly mean missing values from individual stations and to calculate a single regional record for precipitation and temperature. The regional record is created by averaging all values from stations. 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 is monthly temperature in °C. Monthly aridity averages, precipitation and temperature departures from the mean 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, fall survival periods for seasonal analysis (Table 4).

Table 4 Organization scheme for seasonal climate analysis. (Data from Boulder, Denver, Evergreen, Fort Collins, and Waterdale stations.

SHORT	MEDIUM	LONG
2, 3, and 4 month combinations	6 month combinations	8 and 12 month combinations

Early Winter — November-December(2)

Late Winter — January-February(2)

Spring — March-April(2) & March-May(3)

Germination — May-June(2)

Summer — July-August(2)

Fall — September-October(2)

Early-Late Winter — November-February(4)

MidWinter Spring — January-April(4)

Spring-Germination — March-June(4)

Summer — May-August(4)

Summer-Fall — July-October(4)

Spring-Germination-Summer — March-August(6)

Germination-Summer-Fall — May-October(6)

Spring-Germination-Summer-Fall — March-October(8)

Calendar Year — January-December(12)

To statistically determine if moisture availability averages during years of tree recruitment were significantly different from years in which no recruitment occurred, an independent samples t-test was conducted. Aridity index values during years of recruitment were compared against years of non-recruitment. Years of recruitment included 2 groups of years as determined from initial inspection of frequency distributions of tree establishment dates (see below): (1) the four years which could be clearly identified as pulses of Ponderosa Pine recruitment. (2) the seven years of most abundant recruitment which included the four clearly defined pulses as well as consecutive years which potentially resulted from erroneously dating the germination dates of some trees. These tests confirmed that the means of aridity indices during recruitment years and years when no regeneration occurred are significantly different from one another at the 95% confidence interval. All statistics for this procedure where done in SPSS statistic software package.

ENSO Data

The multivariate El Niño/Southern Oscillation Index (MEI) (Wolter, 2004) was used to investigate relationships between the El Niño/Southern Oscillation (ENSO) events and ponderosa pine recruitment. MEI is based on six main observed variables of the tropical pacific. These six variables are: (1) sea-level pressure, (2) zonal and (3) meridional components of the surface wind, (4) sea surface temperature, (5) surface air temperature, and (6) total cloudiness fraction of the sky. MEI is calculated as the first unrotated

principal component of all six observed fields combined and is computed separately for each of twelve sliding bi-monthly seasons. Negative values of the MEI represent the cold ENSO phase, a.k.a. La Niña, while positive MEI values represent the warm ENSO phase (El Niño). A forty year period (1963-2002) of 2 bi-monthly MEIs (January/February & February/March) were calculated to examine the relationship between ENSO and ponderosa pine recruitment. These seasons where chosen because previous research has shown that climate in Colorado is strongly associated variations in ENSO indicators from the tropical Pacific during these months (Donnegan 2000; Diaz & Kiladis 1992).

Relationships of recruitment to climatic variation

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 11 year windows including the year of recruitment. Mean values of climatic parameters preceding, during, and following recruitment years 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.

Tree-ring Indices Data

To permit determination of possible recruitment-climate relationships over a multi-century period, a regional tree-ring record of climatic variability was used (Veblen, et al. 2000). This regional ponderosa pine chronology is an indicator of variation in moisture availability, especially during the spring of the year of ring growth. The regional chronology was developed from eight ponderosa pine ring-width chronologies. Seven were developed from data in the International Tree-Ring Data Bank of the National Oceanic and Atmospheric Administration (NOAA) for the time span 1550-1988, and an eighth chronology was developed to extend the chronology to1996. We analyzed a 300 year period of the chronology from 1996 to 1696. A ranking of tree-ring index values was assigned for years of ponderosa pine recruitment. Years of recruitment included both the 4 years of believed recruitment and the top 7 years that recruitment had occurred. For determining a threshold value for regeneration using the tree-ring index, values during recruitment years were averaged and a percentile was computed.

Results

Tree establishment dates

A total of 507 ponderosa pine seedling and sapling cross-sections were confidently dated to within 1 year of the germination date. For all age frequency distributions (Figure 4), ages include germination dates of all seedlings and saplings successfully dated. The youngest sample age was 1992 while the oldest was 1967. The most common germination date was 1979 (53% of samples), while the second most abundant date of germination was 1983 (21% of samples) (Table 5). 1979 and 1983 are present across all study locations and appear to be obvious dates of episodic regeneration due to the abundance and frequency of seedlings/ saplings across all study sites (Figure 4). Similar trends in recruitment were found across study sites and justified combining the 10 study plots into a single record of regional recruitment (Figure 5)

Germination Date	Count	% of Total
1979	267	52.6
1983	109	21.5
1980	44	8.6
1973	22	4.3
1984	15	3
1990	9	1.7
1978	9	1.7

Table 5 Seven most abundant years of recruitment with sample sizes and percent of total, respectively.
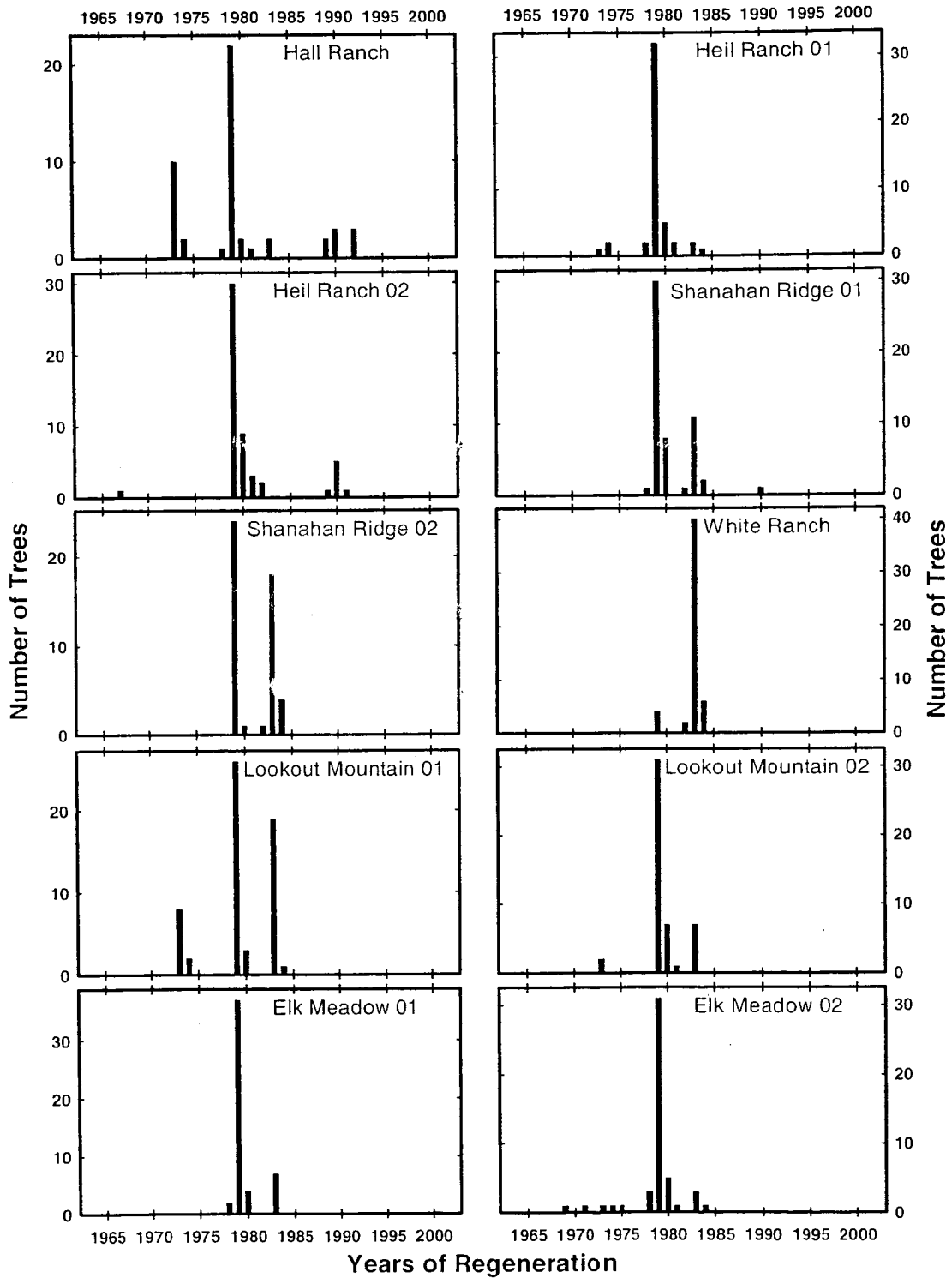
Years of Regeneration

Figure 4 Age Frequency distributions of *Pinus Ponderosa* from all sample sites. A total of 582 saplings and seedlings were extracted from 10 sample sites at 6 locations in the lower montane Northern Colorado Front Range foothills.
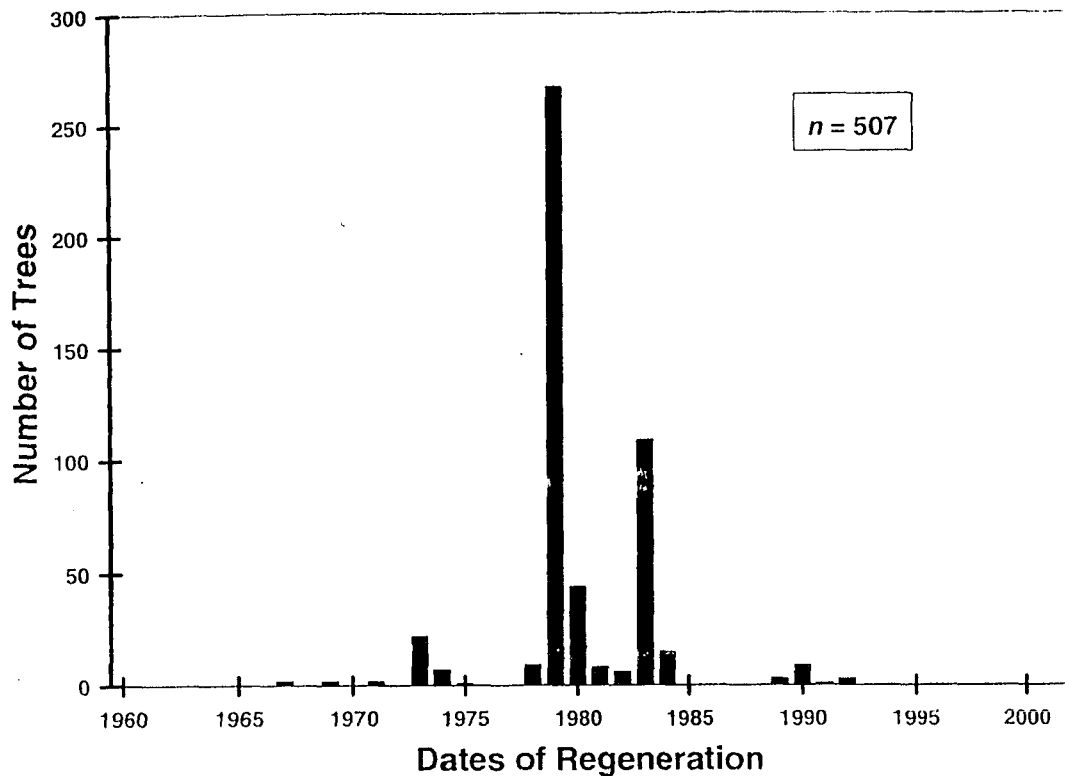
Figure 5 Composite age frequency of recruitment dates of ponderosa pine taken from all sampling locations along the lower montane Front Range foothills of Northern Colorado.

Due to the difficulty in determining total ages of samples, some germination date errors were expected. The majority of errors are believed to be 1 year ± the actual year of recruitment. For instance while 1980 is the third highest tally age it is directly adjacent to 1979, the year of the largest number of recruitment dates, and it is likely that many of these dates are actually 1979. Another example of a probable erroneous date can be seen in 1984, which is the 4th highest tally but is adjacent to the 1983 pulse (2nd highest tally). However, there are two years that are isolated from the two main pulses (1973 and 1990) that appear to be separate pulses of

establishment. It is plausible that 1973 which is present in 4 out of 6 study locations (Hall Ranch, Heil Ranch, Lookout Mtn. Preserve, and Elk Meadow) accounting for 4.3% of the total sample and 1990 which is present in 3 out of 6 study locations (Hall Ranch, Heil Ranch, and Shanahan Ridge) accounting for 1.7% of the total sample, are genuine dates of establishment since they are present in a majority of locations and are not consecutive with the two main pulses of establishment. Thus, a set of four years of abundant tree establishment (1973, 1979, 1983, and 1990) was identified and used in the climatic analyses. The set of all seven years of establishment was also used in the climatic analyses, even though it is not certain if the three additional years were years of actual establishment or were the result of erroneous dates. The potentially erroneous dates, apparently limited to $\pm$ 1 year, resulted from severe growth suppressions, missing and false rings, or simply exceptionally narrow or fuzzy ring boundaries especially near the pith in smaller seedlings. Extremely fine sanding and high magnification in some cases did not permit visual detection of rings and ring boundaries that could exist. These anomalies made cross dating nearly impossible in some samples although narrow rings found in 2001 and 1999 where fairly consistent in most cross-sections. Regardless of these errors four years of clear establishment pulses could be identified and this set of four years is the primary objective of the climatic analyses. Climatic analyses of the set of seven years are also included to account for the possibility that those additional three years were also years of tree establishment.

Instrumental climate record and tree recruitment patterns

Regional records of climatic variables were grouped into seasonal sets of 2, 3, 4, 6, 8, 12 month combinations (Table 4) and compared with both recruitment years and non-recruitment years. Years of recruitment include (1) the four years which could be clearly identified as pulses of recruitment and (2) the seven most abundant years of recruitment which included the four clearly defined pulses as well as consecutive years which potentially resulted from erroneously dating the germination dates of some trees. Non-recruitment years were the years in which no recruitment was detected. Results show that several seasonal combinations of aridity and precipitation consistently exhibit significant positive associations to years of above-average moisture availability during years of recruitment. The most consistent pattern relating tree recruitment patterns to climatic factors is seen in the spring season (March-May) and during the following fall/winter winter season (November-February) (Figure 6, 7a, & 7b). During recruitment years above-average moisture availability occurred during both spring and fall seasons. Superposed epoch analysis (SEA) results indicated a strong significant association of spring and fall above-average precipitation and moisture availability and seedling recruitment (Figure 8a, b, 9a, b, c, d) (Table 6.). Additionally, SEA trended towards significantly below-average temperatures during years of establishment (Figure 10a, b). Years of non-recruitment did not yield significant results for any climatic variables (Table 6). However, the level of significance found from these results should be interpreted with some

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caution due to the low number of event years used for the analysis and the potential for autocorrelation between spring and the following fall/winter period.

Favorable spring climatic conditions for ponderosa recruitment also existed in other years, notably: 1970, 1995, 1998, and 1999. Although these years show considerable above-average moisture availability early in the year, they do not during the following fall/winter season (Figure 11). Thus, years of recruitment are distinguished from non-recruitment years by above average moisture availability during both spring and the following fall/winter seasons. Non-recruitment years that exhibited above-average moisture availability during spring experienced below-average moisture availability during the fall/winter seasons. This points to the significance that both spring and fall moisture significantly impact the recruitment and survival patterns of ponderosa pine and the successful establishment of a seedling cohort that is able to survive into the following growing seasons.
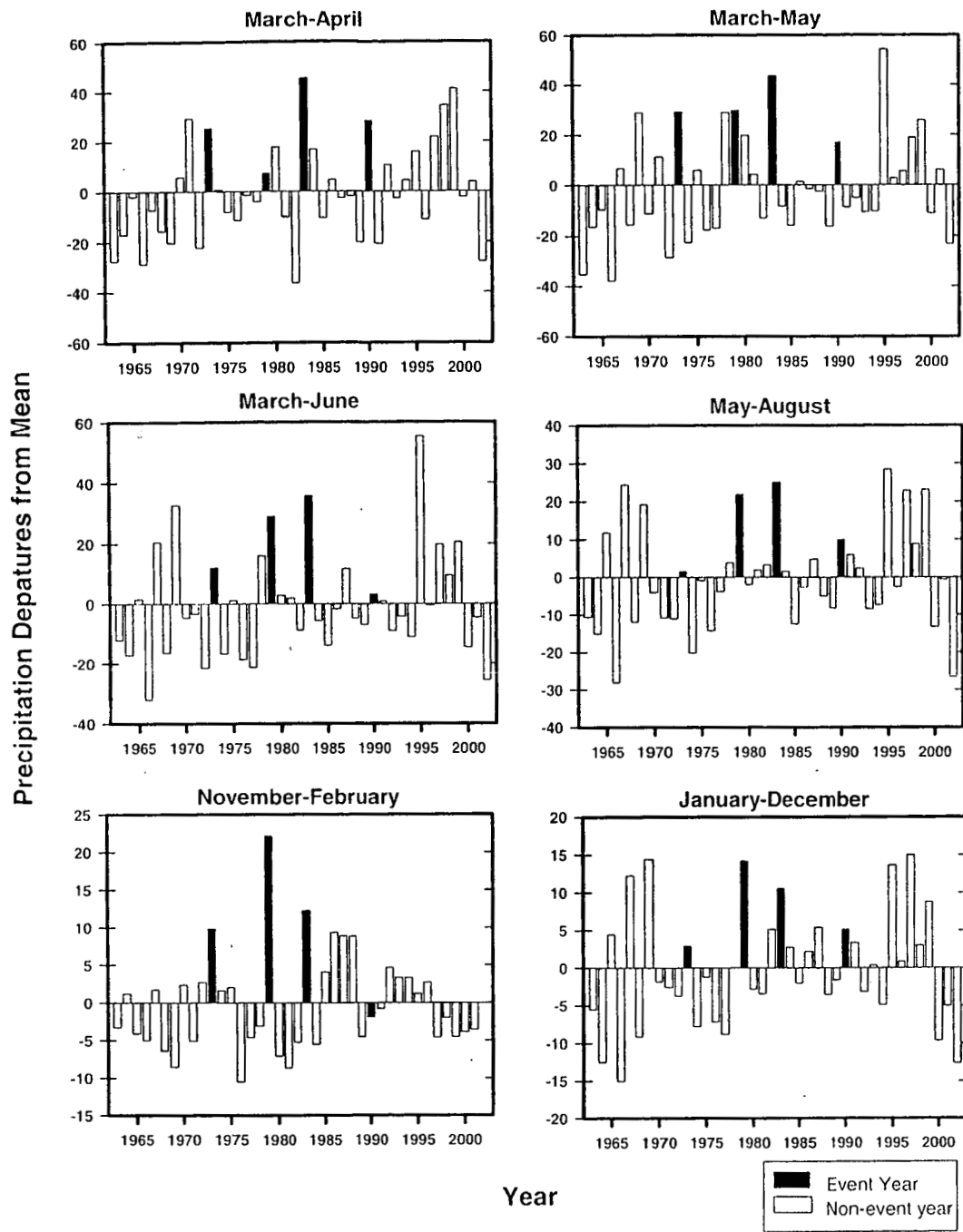
Figure 6 Regional precipitation departures from the mean of monthly combinations for the interval 1963-2002 for *Pinus ponderosa* in the lower montane zone of the northern Front Range of Colorado. Black bars indicate event years (the four years of major episodic recruitment, 1972, 1979, 1983, 1990) while white bars represent non-event years.
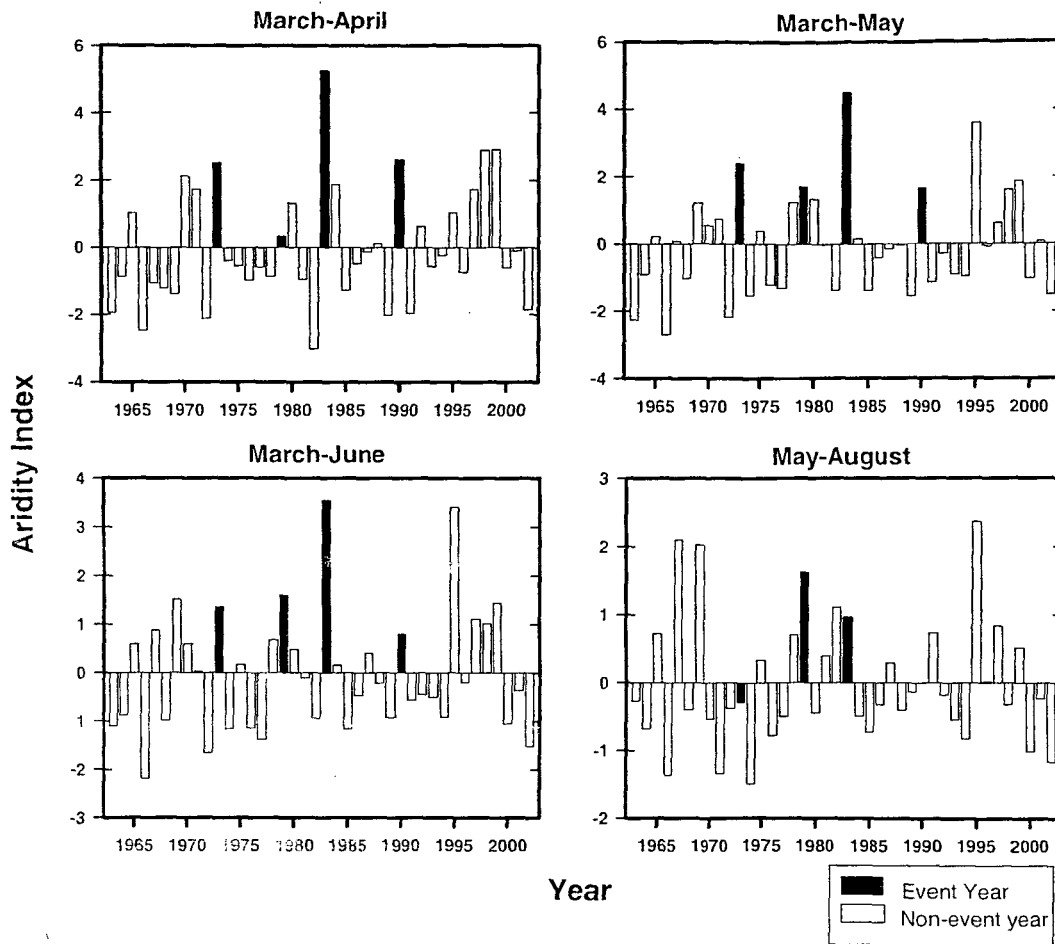
Figure 7a De Martonne's (1926) regional aridity index for the interval 1963-2002 for specific seasons for *Pinus ponderosa* in the lower montane zone of the northern Front Range of Colorado. . Black bars indicate event years (the four years of major episodic recruitment, 1972, 1979, 1983, 1990) while white bars represent non-event years.

Fig 7b De Martonne's (1926) regional aridity index for the interval 1963-2002 for specific seasons for *Pinus ponderosa* in the lower montane zone of the northern Front Range of Colorado. Black bars indicate event years (the four years of major episodic recruitment, 1972, 1979, 1983, 1990) while white bars represent non-event years.
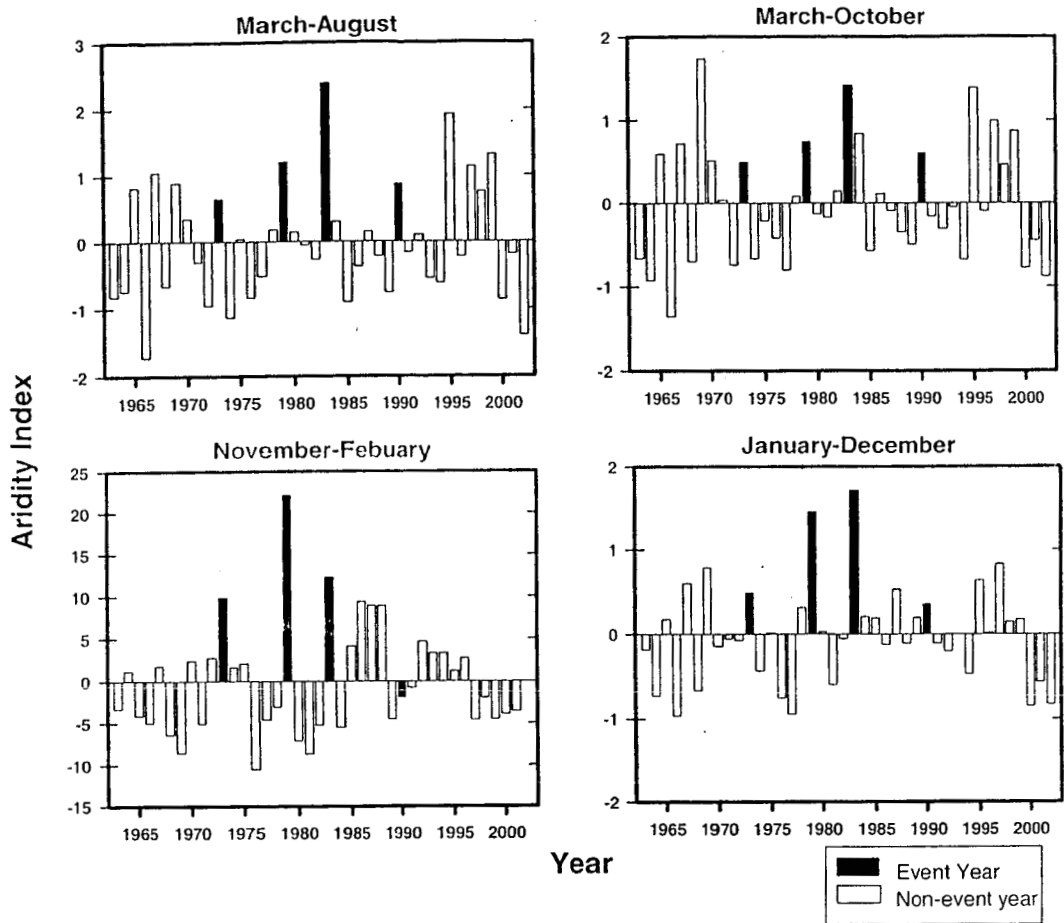
Four Recruitment Years

Figure 8a Superposed epoch analysis (Grissino-Mayer 1995) of seasonal precipitation departures from the mean prior to and following regeneration events for *Pinus ponderosa* in the lower montane zone of the northern Front Range of Colorado. Year zero represents the recruitment event year with the bar indicating the departure from average moisture availability for all years. Negative and positive years indicate lag years before and after recruitment year. Recruitment record includes the 4 years of major episodic recruitment (1973, 1979, 1983, 1990). Circle symbols above bars indicate significant values at ≥ 95% confidence interval.
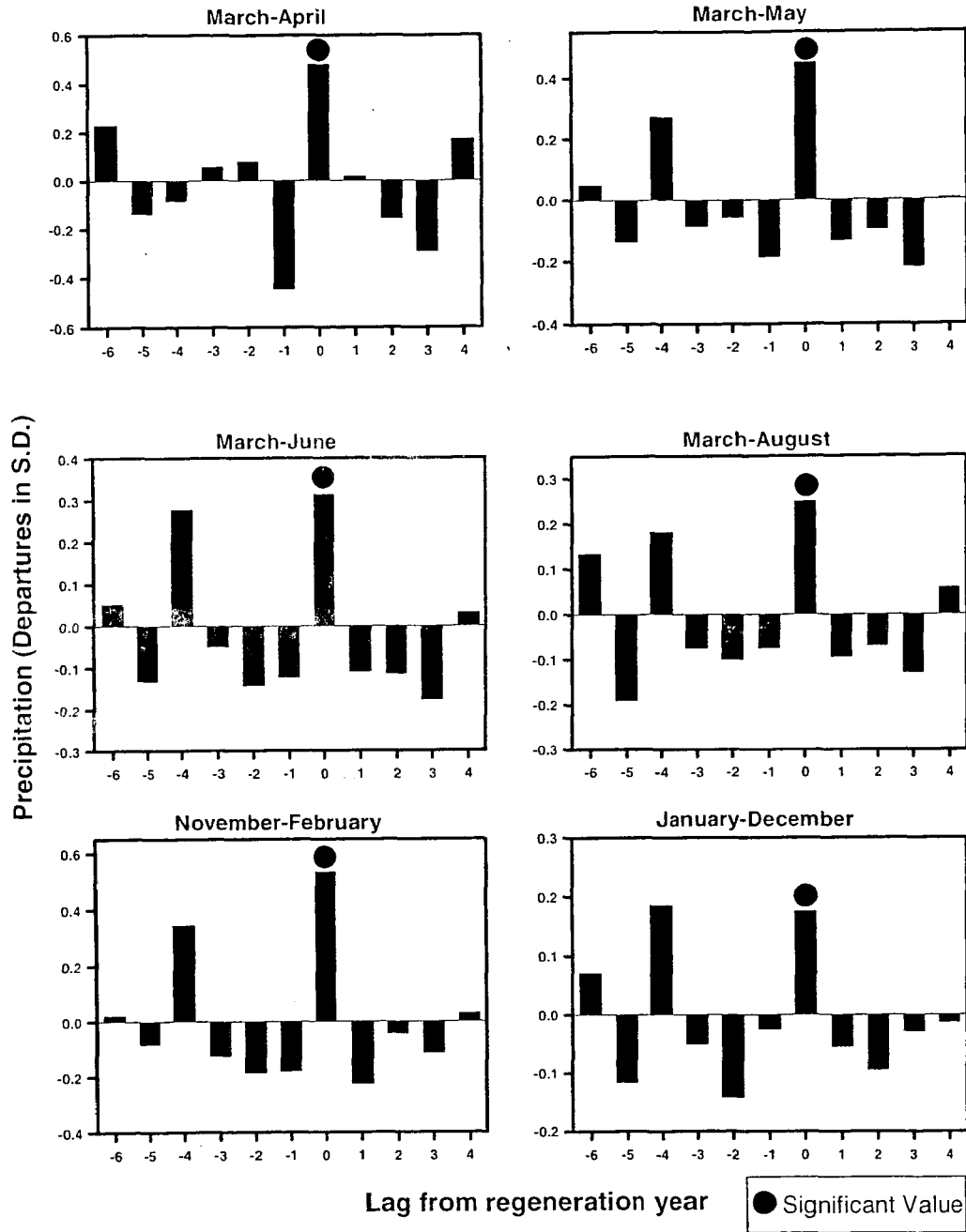
Seven Recruitment Years

Figure 8b. Superposed epoch analysis (Grissino-Mayer 1995) of seasonal precipitation departures from the mean prior to and following regeneration events for *Pinus ponderosa* in the lower montane zone of the northern Front Range of Colorado. Year zero represents the recruitment event year with the bar indicating the departure from average moisture availability for all years. Negative and positive years indicate lag years before and after recruitment year. Recruitment record includes the 7 top years of recorded recruitment (1973, 1978, 1979, 1980, 1983, 1984, 1990). Circle symbols above bars indicate significant values at ≥ 95% confidence interval.

Figure 9a Superposed epoch analysis (Grissino-Mayer 1995) of seasonal aridity index departures from the mean prior to and following regeneration events for *Pinus ponderosa* in the lower montane zone of the northern Front Range of Colorado. Year zero represents the recruitment event year with the bar indicating the departure from average moisture availability for all years. Negative and positive years indicate lag years before and after recruitment year. Recruitment record includes the 4 years of major episodic recruitment (1973, 1979, 1983, 1990). Circle symbols above bars indicate significant values at ≥ 95% confidence interval.
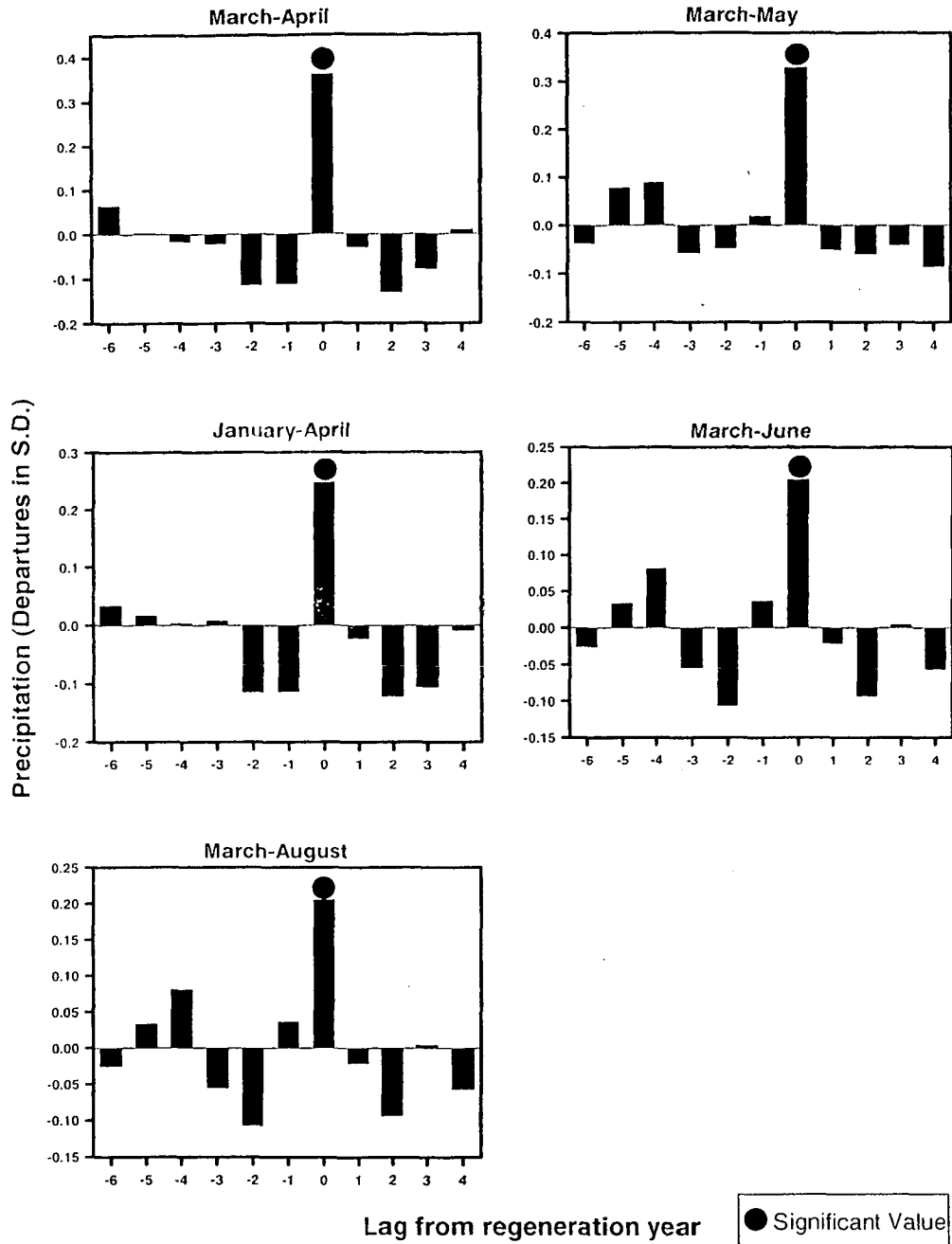
Four Recruitment Years

Figure 9b Superposed epoch analysis (Grissino-Mayer 1995) of seasonal aridity index departures from the mean prior to and following regeneration events for *Pinus ponderosa* in the lower montane zone of the northern Front Range of Colorado. Year zero represents the recruitment event year with the bar indicating the departure from average moisture availability for all years. Negative and positive years indicate lag years before and after recruitment year. Recruitment record includes the 4 years of major episodic recruitment (1973, 1979, 1983, 1990). Circle symbols above bars indicate significant values at ≥ 95% confidence interval.
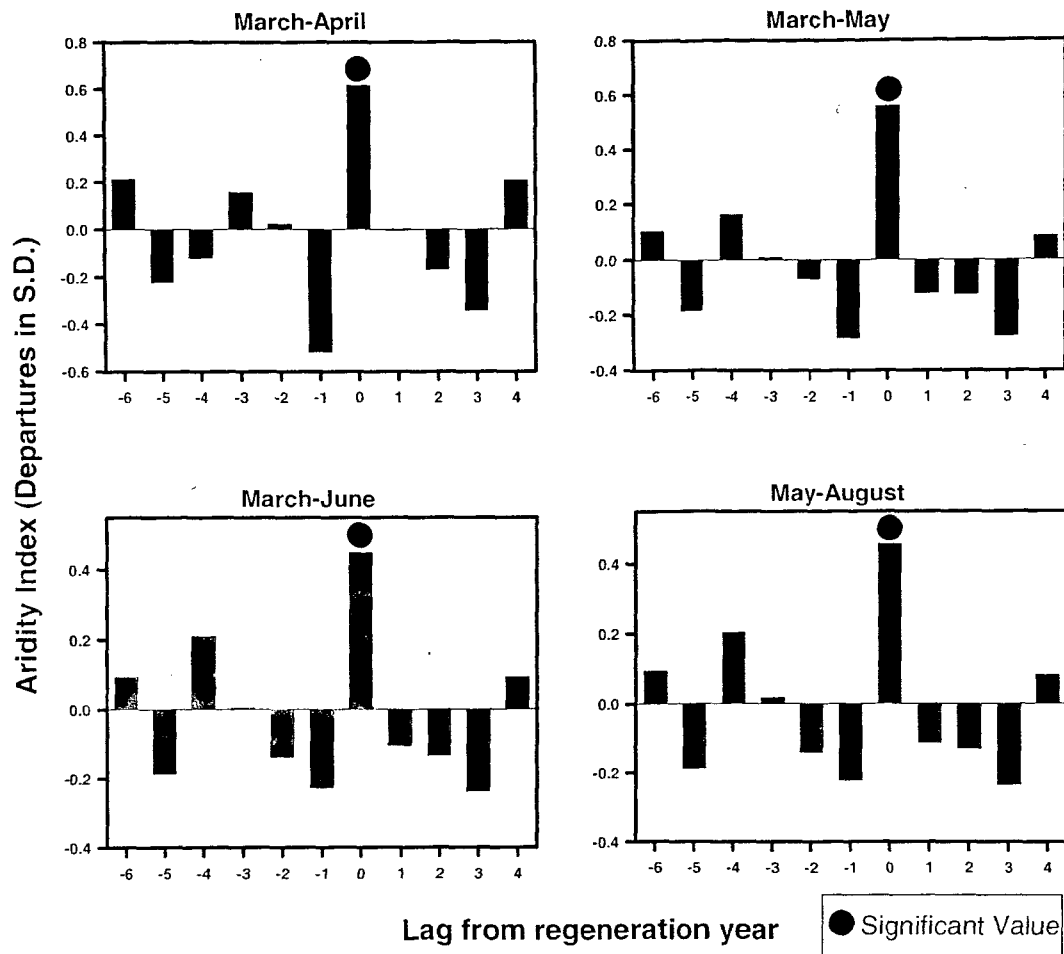
Seven Recruitment Years

Figure 9c Superposed epoch analysis (Grissino-Mayer 1995) of seasonal aridity index departures from the mean prior to and following regeneration events for *Pinus ponderosa* in the lower montane zone of the northern Front Range of Colorado. Year zero represents the recruitment event year with the bar indicating the departure from average moisture availability for all years. Negative and positive years indicate lag years before and after recruitment year. Recruitment record includes the 7 most abundant years of recorded recruitment (1973, 1978, 1979, 1980, 1983, 1984, 1990). Circle symbols above bars indicate significant values at ≥ 95% confidence interval.
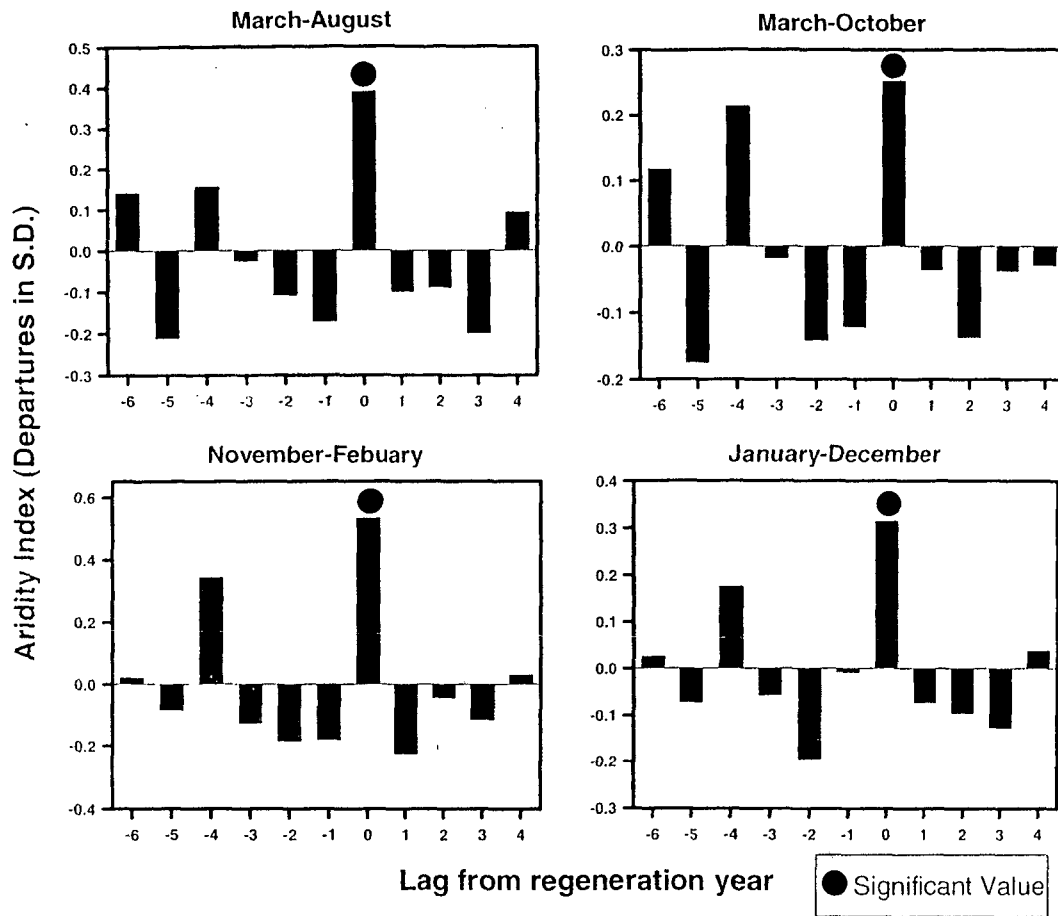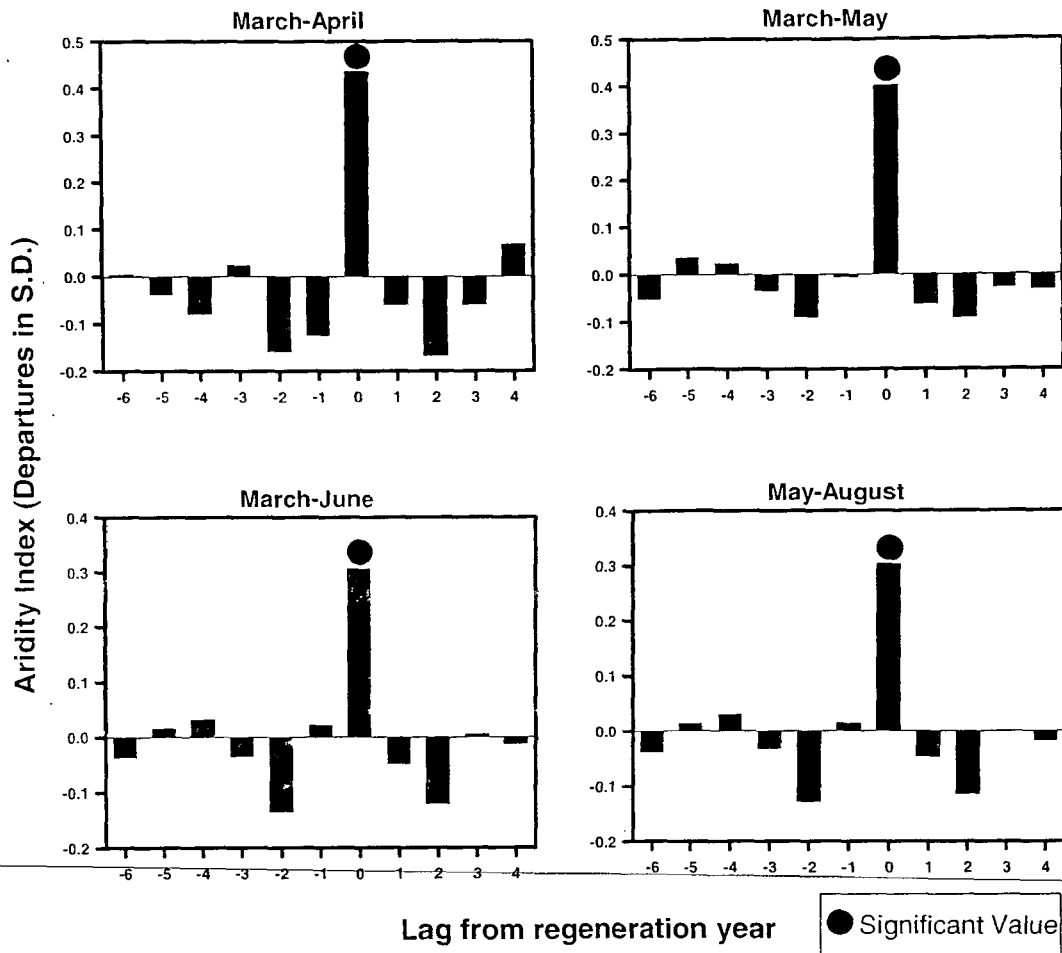
Seven Recruitment Years

Figure 9d Superposed epoch analysis (Grissino-Mayer 1995) of seasonal aridity index departures from the mean prior to and following regeneration events for *Pinus ponderosa* in the lower montane zone of the northern Front Range of Colorado. Year zero represents the recruitment event year with the bar indicating the departure from average moisture availability for all years. Negative and positive years indicate lag years before and after recruitment year. Recruitment record includes the 7 most abundant years of recorded recruitment (1973, 1978, 1979, 1980, 1983, 1984, 1990). Circle symbols above bars indicate significant values at ≥ 95% confidence interval.

Four Recruitment Years

Figure 10a Superposed epoch analysis (Grissino-Mayer 1995) of seasonal temperature departures from the mean prior to and following regeneration events for *Pinus ponderosa* in the lower montane northern Front Range of Colorado Year zero represents the recruitment event year with the bar indicating the departure from average moisture availability for all years. Negative and positive years indicate lag years before and after recruitment year. Recruitment record includes the 4 years of major episodic recruitment (1973, 1979, 1983, 1990). Circle symbols above bars indicate significant values at ≥ 95% confidence interval.
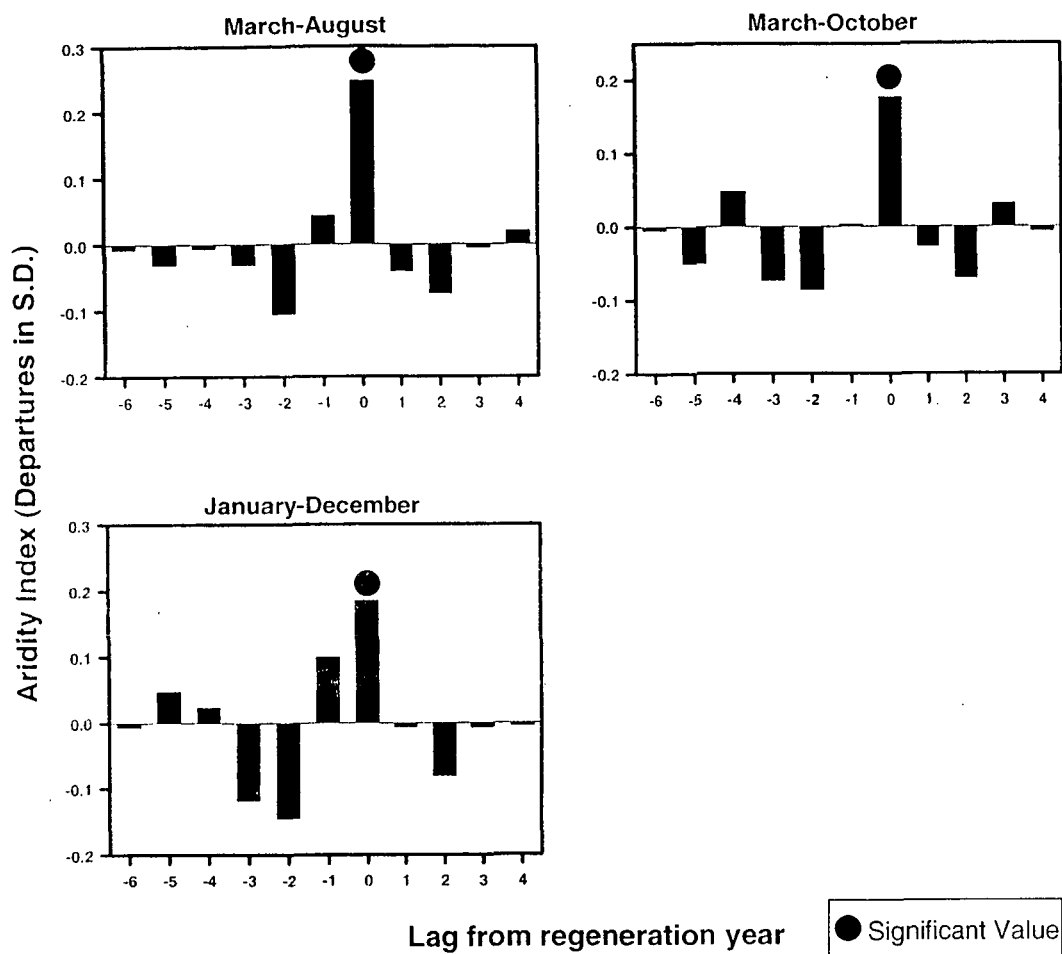
Seven Recruitment Years
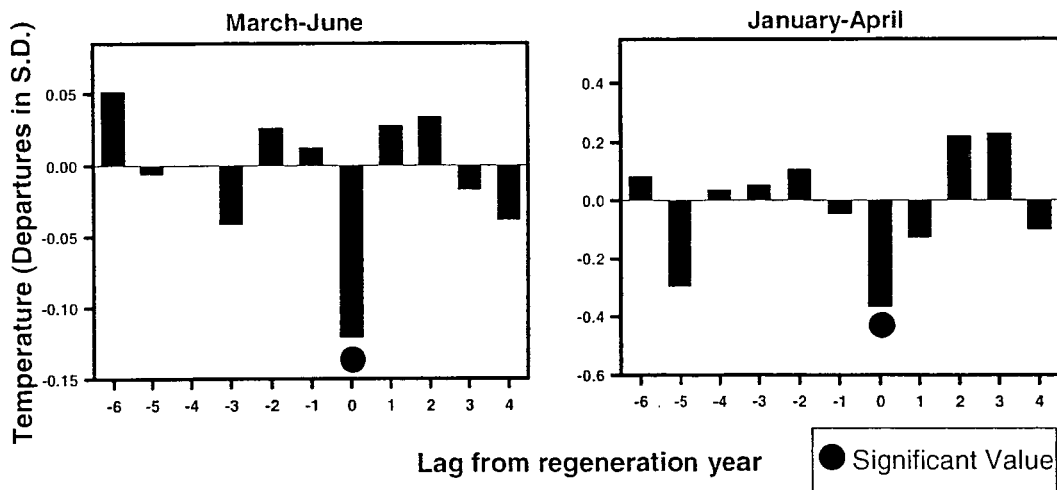
Figure 10b Superposed epoch analysis (Grissino-Mayer 1995) of seasonal temperature departures from the mean prior to and following regeneration events for *Pinus ponderosa* in the lower montane northern Front Range of Colorado. Year zero represents the recruitment event year with the bar indicating the departure from average moisture availability for all years. Negative and positive years indicate lag years before and after recruitment year. Recruitment record includes the 7 most abundant years of recorded recruitment (1973, 1978, 1979, 1980, 1983, 1984, 1990). Circle symbols above bars indicate significant values at ≥ 95% confidence interval
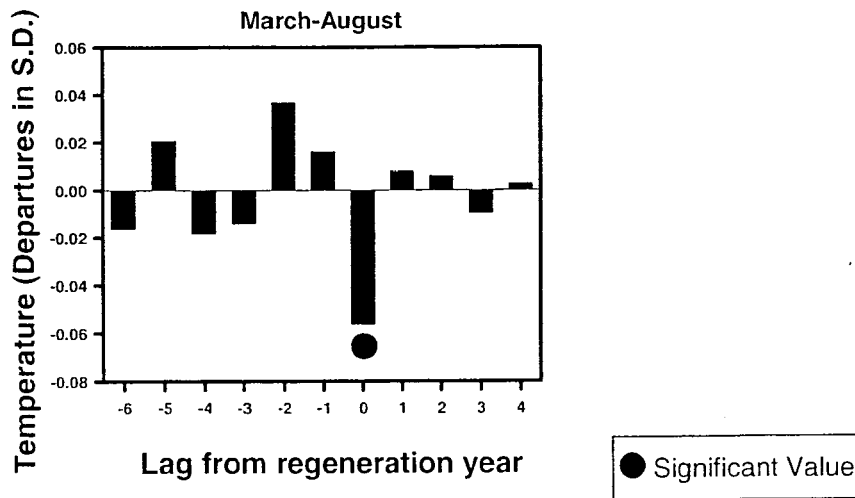
Month Combination	4 events	% Departure @ ≥ 95 % Confidence Interval	7 events	% Departure @ ≥ 95 % Confidence Interval	21 non events	% Departure @ ≥ 95 % Confidence Interval
Aridity						
January-Febuary(2)	1.86	--	2.27	--	2.24	--
March-April(2)	6.58	61%	5.77	43%	3.80	--
May-June(2)	4.17	--	3.79	--	2.79	--
July-August(2)	2.11	--	1.92	--	1.92	--
September-October(2)	1.40	--	1.83	--	1.81	--
March-May(3)	6.50	56%	5.79	40%	3.57	--
January-April(4)	4.22	--	4.02	--	3.02	--
March-June(4)	5.37	45%	4.78	31%	3.29	--
May-August(4)	3.14	46%	2.86	30%	2.36	--
July-October(4)	1.75	--	1.88	--	1.86	--
November-February(4)	2.72	55%	3.38	--	2.17	--
May-October(6)	2.56	--	2.51	--	2.17	--
March-August(6)	4.28	39%	3.83	25%	2.84	--
March-October(8)	3.56	25%	3.33	18%	2.58	--
January-December(12)	3.63	32%	3.28	19%	2.46	--
Precipitation (mm)						
January-Febuary(2)	9.21	--	12.52	--	15.50	--
March-April(2)	74.55	48%	67.53	36%	46.89	--
May-June(2)	77.06	--	70.72	--	57.41	--
July-August(2)	52.32	--	48.41	--	48.88	--
September-October(2)	27.18	--	31.53	--	33.74	--
March-May(3)	15.03	45%	20.37	33%	17.06	--
January-April(4)	86.23	--	79.19	25%	50.57	--
March-June(4)	75.80	31%	69.12	21%	52.15	--
May-August(4)	64.69	--	59.56	--	53.15	--
July-October(4)	39.75	--	39.97	--	41.31	--
November-February(4)	41.88	55%	40.02	--	31.19	--
May-October(6)	52.19	--	50.22	--	46.68	--
March-August(6)	67.98	25%	62.22	15%	51.06	--
March-October(8)	57.78	--	54.55	--	46.73	--
January-December(12)	46.57	18%	43.07	--	36.79	--
Temperature (°C)						
January-Febuary(2)	-1.40	--	-1.73	--	-0.60	--
March-April(2)	4.28	--	4.48	--	5.38	--
May-June(2)	14.19	--	14.59	--	15.40	--
July-August(2)	20.17	--	20.42	--	20.55	--
September-October(2)	13.12	--	12.59	--	12.22	--
March-May(3)	-1.16	--	-1.19	-12%	0.21	--
January-April(4)	1.44	--	1.37	-37%	2.39	--
March-June(4)	6.49	--	6.81	--	7.91	--
May-August(4)	9.23	--	9.53	--	10.39	--
July-October(4)	17.18	--	17.50	--	17.98	--
November-February(4)	12.94	--	13.02	--	13.39	--
May-October(6)	16.65	--	16.51	--	16.38	--
March-August(6)	15.83	-6%	15.87	--	16.06	--
March-October(8)	12.88	--	13.16	--	13.78	--
January-December(12)	8.31	--	8.44	--	8.98	--

Table 6 Seasonal means for the 4 years of major episodic recruitment (4 events), the 7 most abundant years of recruitment (7 events), and the 21 years that no recruitment was detected (21 events). Percent departures from the mean are only presented if found statistically significant (≥ 95 % Confidence Interval) using superposed epoch analysis (Grissino-Mayer 1995) and are comparisons of event years to non-event years. For example: March-April aridity during the 4 years of major episodic recruitment is 61% higher (more moisture) than during years of no recruitment.

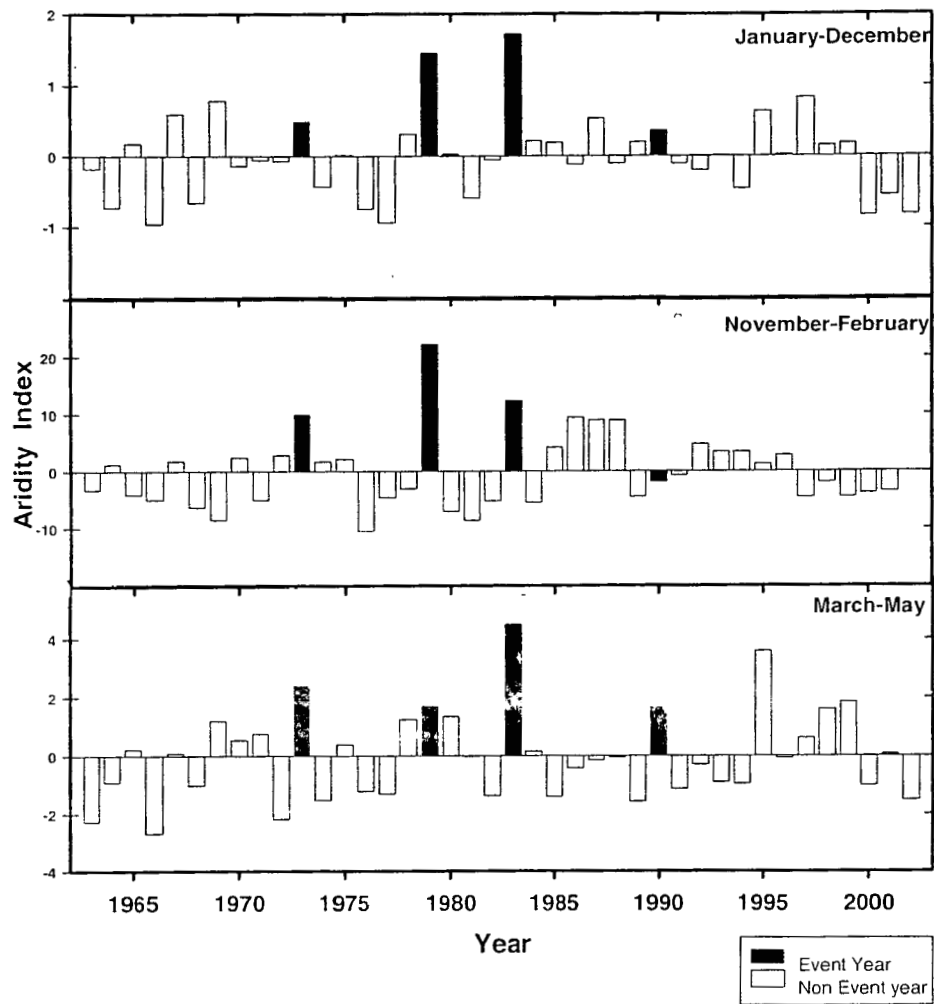**Figure 11** Seasonal aridity index for March-May, November-February, and January-December. Although spring moisture is an important factor during years of ponderosa recruitment, fall drought as well as moisture thought the entire calendar year plays an important role in creating the necessary conditions for recruitment. Notice high values during non-recruitment years in spring generally do not continue into Fall/Winter.

ENSO and tree recruitment patterns

Multivariate El Niño/ Southern Oscillation Index (MEI) was used to investigate responses of seedling recruitment to ENSO activity. Influences on ponderosa pine recruitment by MEI values during both bi-monthly seasons, January-February and February-March, were shown statistically significant (Figure 12a, b).

Four Recruitment Years

Figure 12a. Superposed epoch analysis (Grissino-Mayer 1995) of Multivariate El Niño/Southern Oscillation Index (MEI) (Wolter, 2004) prior to and following regeneration events for *Pinus Ponderosa* in the lower montane zone of the northern Front Range of Colorado. Year zero represents the recruitment event year with the bar indicating the departures from average MEI for all years. Negative and positive years indicate lag years before and after recruitment year. High MEI values equal El Nino conditions. Recruitment record includes the 4 years of major episodic recruitment (1973, 1979, 1983, 1990). Circle symbols above bars indicate significant values at ≥ 95% confidence interval.
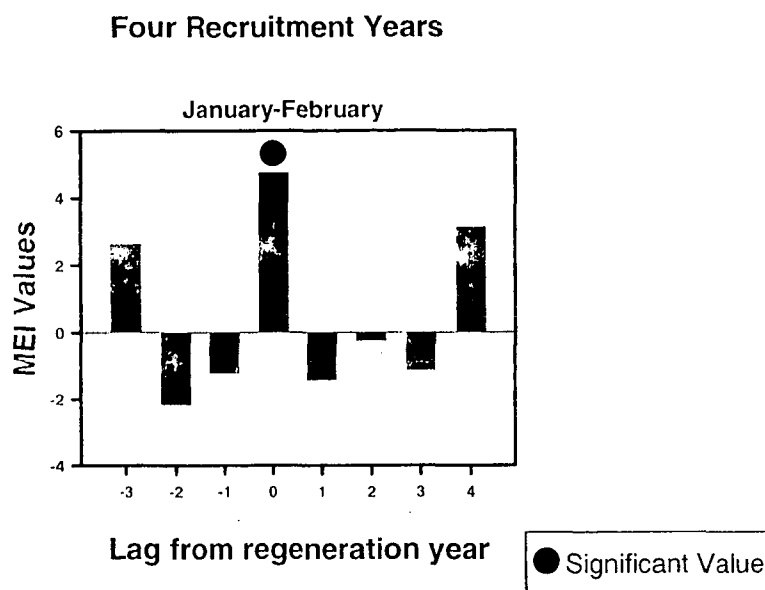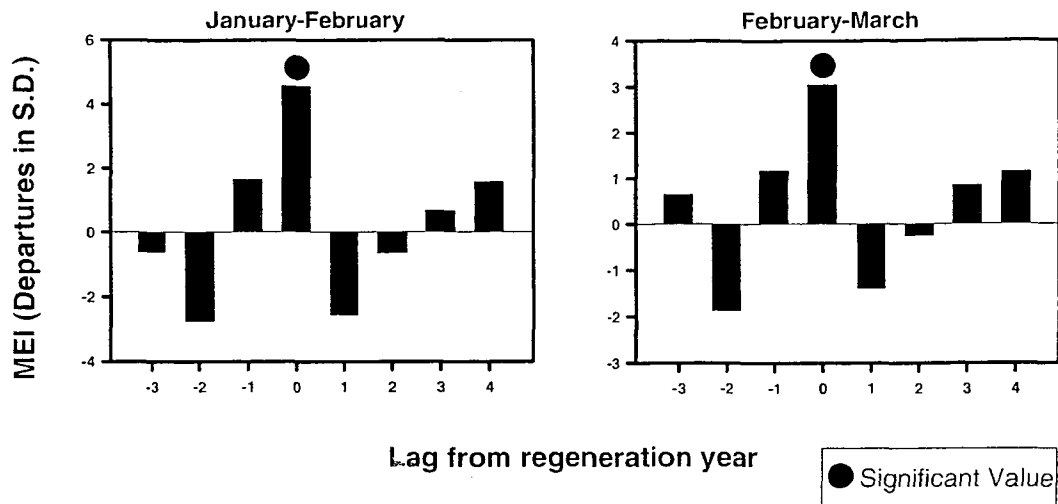
Seven Recruitment Years

Figure 12b Superposed epoch analysis (Grissino-Mayer 1995) of Multivariate El Niño/Southern Oscillation Index (MEI) (Wolter, 2004) prior to and following regeneration events for *Pinus Ponderosa* in the lower montane zone of the northern Front Range of Colorado. Year zero represents the recruitment event year with the bar indicating the departure from average MEI for all years. Negative and positive years indicate lag years before and after recruitment year. High MEI departures equal El Nino conditions. Recruitment record includes the 7 most abundant years of recorded recruitment (1973, 1978, 1979, 1980, 1983, 1984, 1990). Circle symbols above bars indicate significant values at ≥ 95% confidence interval.

In both cases significant above average MEI values were associated with years of recruitment using SEA. Above average MEI values indicate the warm (El Niño) phase which is associated with greater moisture availability and lower temperatures during spring, while below average ENSO activity indicates the cold (La Niña) phase of ENSO which is associated with below average moisture availability and warmer temperatures. In this case years of recruitment coincided with years of El Niño events.

Tree-ring index and tree recruitment patterns

A regional ponderosa pine tree-ring chronology was used to investigate potential climate relationships and recruitment episodes over a

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multi-century period. The local chronology used for this comparison showed that growth of ponderosa pine was positively correlated with spring-summer (March-August) precipitation and negatively correlated with spring-summer temperatures (Veblen *et al.* 2000). Since tree-ring widths of ponderosa pine can be used as a proxy for moisture availability, the analysis of climate influences on years of recruitment can be extended over several centuries. We comprised a simple ranking of tree-ring index values was assigned for years of ponderosa recruitment for the past 300 years (Table 7). For the 4 years of major episodic recruitment the lowest rank was 120th (1973) while, the highest was 3rd (1983). The average value for these years was 1.214, which was within the top 13.6 percentile (rank 41st) of the entire chronology. Lower tree-ring index values where found for the seven most abundant years that recruitment was recorded.

Year	Value	Rank
4 recruitment years		
1979	1.194	51th
1983	1.429	3rd
1973	1.052	120th
1990	1.182	56th
Mean	**1.214**	
Rank	→	**41st (13.6%)**
7 recruitment years		
1979	1.194	51th
1983	1.429	3rd
1980	0.951	178th
1973	1.052	120th
1984	0.838	245th
1990	1.182	56th
1978	0.86	238th
Mean	**1.108**	
Percentile	→	**93rd (31.0%)**

Table 7 Ranking and percentiles of tree-ring width index values for the past 300 years (1996-1696) for the four years of believed recruitment and the top 7 years that recruitment was observed. Tree-ring index values derived from a local chronology. Based on these data mean values from years of recruitment are rank 41st and 93rd and are within the 13.6 and 31.0 top percentile, respectively, of the total 300 years that the chronology represents.

Local and micro-site factors and tree recruitment patterns

Grazing and disturbance history play an important in role in the structure and dynamics of forest including direct influences on ponderosa pine seedling recruitment. Although study areas contained no nearby field signs of recent fire or grazing we cannot confidently say that the episodes of recruitment presented in this study had not been affected by these variables. Additionally study locations covered several aspects, slopes and substrate conditions. However, all study locations showed similar recruitment patterns validating that the primary influence on these episodes of regeneration is

climate. Viable seed sources from nearby parent trees were typically located in close proximity to establishment pulses (Table 2). While only four pulses were detected in this study, ages of the oldest parent tress elucidated that a viable seed source had been available to areas where recruitment had occurred for at least the past 150 years.

Discussion and Conclusion

The influence of recent climatic variation on ponderosa pine recruitment patterns is apparent along the forest-grassland ecotone in northern Colorado. Based on a regional sample of c. 500 regeneration dates, a strong association between climatic variation and episodic recruitment of ponderosa pine exists. The strongest association exists during years in which spring and fall moisture availability is coincidently high. The four years in which recruitment was observed during the past forty years includes 1973, 1979, 1983, and 1990. During these years, above-average precipitation, below-average temperatures, and overall above-average moisture availability, during spring and fall, coincided with years of ponderosa pine recruitment. These findings are consistent with conclusions from the southwestern U.S. which have shown that episodic pulses of regeneration and survival coincide with above average spring (Savage, 1996) and fall (Larson, 1961) moisture availability. Cool and wet conditions in spring and fall appear to facilitate the successful germination of seeds and promote survival of seedlings. However, years in which only spring moisture was abundant do not necessarily result in

the establishment and survival of ponderosa seedlings. Additionally, this evidence suggests the importance of snowpack in the lower elevations during spring melting periods and in fall for insulation against temporary cold temperature spells and resistance to drought. Furthermore, ponderosa pine seedlings seem to need an overall well-balanced availability of moisture throughout the entire year to avoid mortality to either drought or competition from herbaceous species. Although data were not available, a viable seed crop coinciding with advantageous climatic conditions is necessary for episodes of regeneration to occur. Thus, years in which climate is suitable for regeneration do not always result in tree establishment if seed is absent.

Variations in spring climate seem to have a strong association with ENSO activity patterns. Above-average spring moisture availability, which is critical to ponderosa pine germination success, is strongly associated with years in which the warm El Niño phase of ENSO occur. This research indicates that recent years of episodic recruitment occurring along the forest-grassland ecotone in northern Colorado are strongly correlated with large scale warming of sea-surface temperatures in the eastern Pacific, along with other ENSO identifying factors. This evidence broadens the notion that not only are local climatic patterns responsible for episodes of recruitment, but that large scale climatic influences also significantly impact ponderosa pine regeneration patterns along the Front Range of Colorado. Since ENSO activity is only correlated with years of above-average spring moisture and

does not typically affect fall precipitation, it appears that ENSO alone cannot explain years in which recruitment occurred.

In addition to the instrumental record the analysis of a tree-ring width index from a local ponderosa pine chronology proved that in instances where regional episodic recruitment occurred, strong responses in radial growth of adult ponderosa pines transpired simultaneously. Radial growth responses in ponderosa pines from this chronology are indicators of spring and early summer moisture availability. The average value for years in which ponderosa recruitment occurred ranked 41st, thus providing a potential threshold value that can by used to model previous years in which moisture was suitable enough for germination. If this interpretation is correct, 40 years out of the last 300 years have been suitable for germination (Table 8).

Year	Ring-Width Value	Year	Ring-Width Value	Year	Ring-Width Value
1995	1.219	1907	1.386	1828	1.317
1987	1.233	1904	1.261	1803	1.285
1986	1.223	1903	1.303	1792	1.270
1983	1.429	1897	1.294	1787	1.293
1975	1.340	1894	1.236	1761	1.545
1949	1.238	1878	1.311	1754	1.307
1947	1.389	1869	1.336	1749	1.336
1941	1.306	1858	1.274	1734	1.261
1928	1.221	1843	1.453	1726	1.265
1926	1.392	1839	1.308	1720	1.352
1923	1.302	1838	1.355	1719	1.221
1921	1.257	1836	1.231	1714	1.370
1909	1.232	1835	1.339	1705	1.312
				1697	1.281

Table 8 Dates and tree-ring width index values (n=40) from a local chronology that exceed the threshold (1.214) determined by averaging all tree-ring width index values for years that recruitment occurred (1973, 1979, 1983, 1990). The years listed indicate years in which spring moisture may had been suitable enough for germination of ponderosa pines in Colorado within the past 300 years (1996-1696).

However, this interpretation is limited since tree-ring index values tend to indicate only spring and early summer moisture availability and do not imply the survival of germinated seedlings through the fall of following winter period. Regardless, the view that episodic recruitment is exceptionally rare may not be valid for the Colorado Front Range since 40 out of the last 300 years have shown potential for successful germination. A synthesis of instrumental climate records, ENSO activity, and tree-ring index values in comparison with recruitment dates is seen in Figure 13.
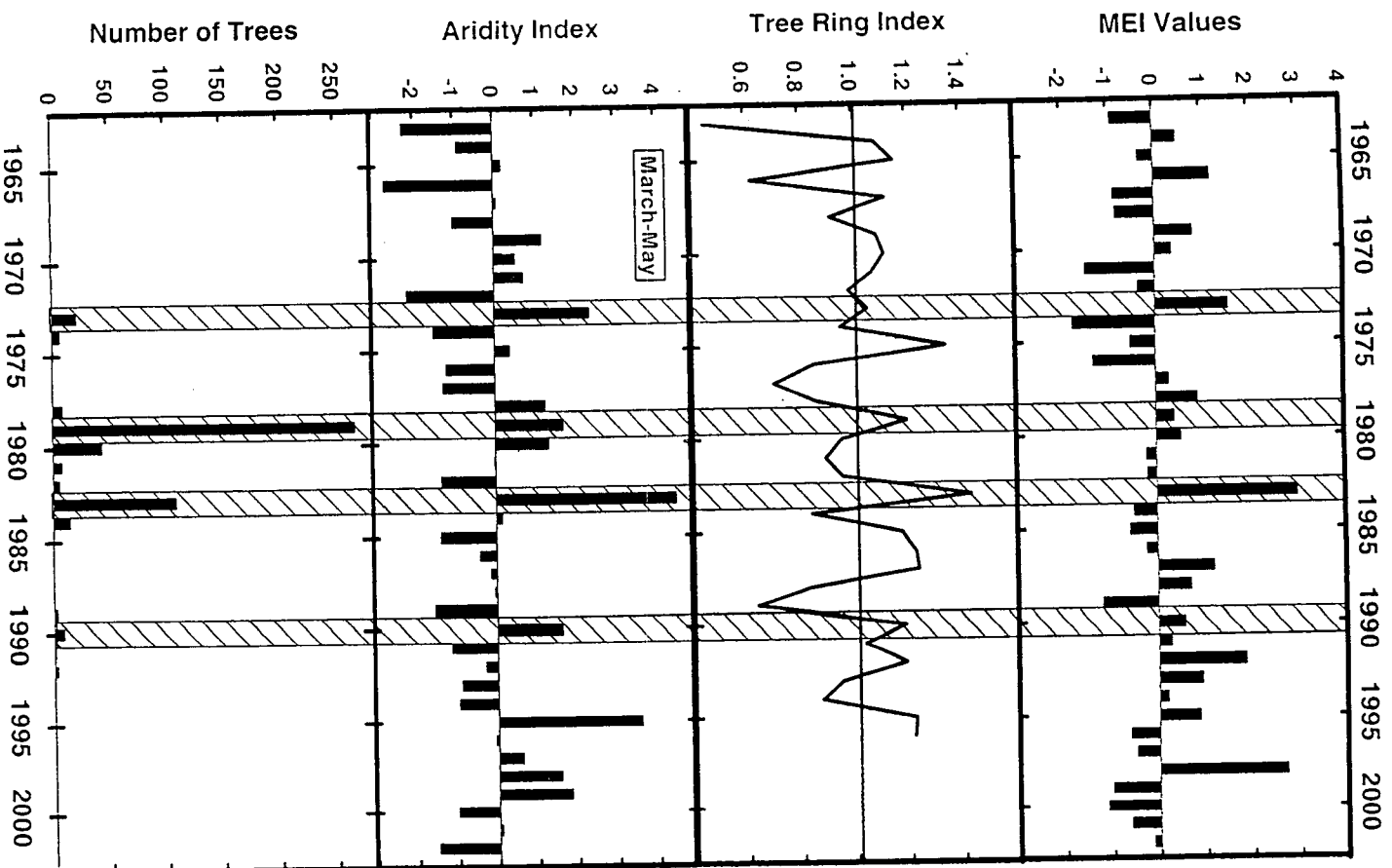
Figure. 13 (From top to bottom) Multivariate ENSO index (MEI) (January-February), tree-ring index from local chronologies (line equals mean), De Martonne's aridity index (March-May), and composite age-frequency distributions of *Pinus ponderosa* plotted. Highlighted cross-hatched areas are aligned with the four years of major episodic with corresponding Indices.

Variations in tree demography have often been related to disturbance history such as grazing or fire (Kaufman *et al.* 2000; Bahre 1993), to climate variation (Savage 1996; Brubaker 1986), or a combination of both (Villalba and Veblen 1997; Mast *et al.* 1998). This study, however, uses several lines of evidence to show that recent tree recruitment patterns along the forest-grassland ecotone are primarily influenced by variations in climate. Across all study sites there are variations in land histories and in local site characteristics such as substrate conditions, and grazing history, yet our results show synchronous ponderosa pine recruitment age structures across sites which could only be explained as a climatic response.

By using precise aging techniques to achieve annual tree age resolution in comparison with climatic data, studies of tree establishment at ecotonal boundaries proved to be an excellent opportunity for testing climate-tree recruitment hypothesis. While determining the age of tree populations to an annual resolution can be extremely time consuming, such information is essential for reconstruction of the details of stand development and possible relationships with regional climatic variations, thus providing directly useful information to land managers and scientist alike.

Literature Cited

Baker, W.L., and D. Ehle. 2001. Uncertainty in surface-fire history: the case of ponderosa pine forest in the Western United States. Canadian Journal of Forest Research 31 (7): 1205-1226.

Bahre, C.J. 1993. Historic vegetation change, mesquite increase and climate in southeastern Arizona. Journal of Biogeography, 20: 489-504

Barton, A. M. 1992. Factors controlling lower elevational limits of plants: responses of pones to drought in the Chiricahua Mountains, AZ. In: Folliott, P.F., Gottfried, G.J., Bennett, D.A., technical coordinators. Ecology and management of oak and associated woodlands: perspectives in the southwestern United States and northern Mexico: Proceedings; 1992 Apr. 27-30; Sierra Vista, AZ. Gen. Tech. Rep. RM-218. Fort Collins, CO: USDA, FS, RMFRES: 191-194.

Boldt, C.E. and V. L. Van Deusen. 1974. Silviculture of ponderosa pine in the Black Hills: the status of our knowledge. Res. Pap. RM-124. Fort Collins, CO: USDA, FS, RMES. 45 p.

Bormann, F.H. and G.E. Likens. 1979. Pattern and process in a forested ecosystem. New York: Springer-Verlang.

Brown, P.M., M.R. Kaufmann, and W.D. Shepperd. 1999. Long-term, landscape patterns of past fire events in a montane ponderosa pine forest of central Colorado. Landscape Ecology 4(6): 513-532.

Brubaker, L.B. 1986. Responses of tree populations to climate change. Vegetatio, 67 119-130.

Buccholtz, C.W. 1983. Rocky Mountain National park: a history. Colorado Associated University Press, Boulder, Colorado, USA.

Burkhardt , J.W., Tisdale, E.W. 1976. Causes of juniper invasion in southwestern Idaho. Ecology. 57, 472-484.

Daniels LD, Veblen T.T. 2003. Regional and local effects of disturbance and climate on altitudinal treelines in northern Patagonia. Journal of Vegetation Science, 14(5): 733-742

Daubenmire, R. 1960. A seven-year study of cone production as related to xylem layers and temperature in Pinus Ponderosa. The American Midland Naturalist. 64(1):187-193.

De Martonne, E. 1926. Ine nouvelle fonction climatologique: l'indice d'aridite. Meteorologie. 2, 449-458.

Diaz, H.F. and G.N. Kiladis. 1992. Atmospheric teleconnections associated with extreme phases of the Southern Oscillation. Pages 7-28 in H.F. Diaz and V. Markgraf, editors. El Nino: Historical and Paleoclimatic Aspects of the Southern Oscillation. Camridge University Press, Cambridge, U.K.

Donnegan, J. A. 2000. Climatic and human influences on fore regimes in Pike national Forest. Ph.D. thesis, University of Colorado, Boulder, Colorado, U.S.A.

Duncan, R.P. 1989. An evaluation of errors in the tree age estimates based on increment cores in Kahikatea, New Zealand Natural Sciences, 16, pp. 31.

Fosset, F. 1880. Colorado: its gold and silver mines, fars and stock ranges, and health and pleasure resorts. C.G. Crawford, New York, New York, USA.

Foster, J.H. 1917. The spread of timbered areas in central Texas. Journal of Forestry. 15, 442-445.

Goldblum, D. & Veblen, T.T. 1992 Fire history of a ponderosa pine/Douglas-fir forest in the Colorado Front Range. Physical Geography (13): 133-148.

Greenland, D., Burbank, J. Key, J., Klinger, L., Moorhouse, J., Oaks, S. & Shankman, D. 1985. The bioclimates of the Colorado Front Range. Mount. Res. Development. 5: 251-262.

Grissino-Mayer, H.D. 1995. Tree-ring reconstruction of climate and fire history at El malpais National Monument, Arizona, Tucson. 407pp.

Harrington, M.G. & R.G. Kelsey. 1979. Influence of some environmental factors on initial establishment and growth of ponderosa seedlings. Forest Service Research Paper INT-330, U.S. Department of Agriculture, Fort Collins, Colorado.

Johnsen, T.N. 1962. One-seed juniper invasion of northern Arizona grasslands. Ecological Monographs. 32, 187-206.

Kaufmann, M.R., C.M. Regan, & P.M. Brown. 2000. Heterogeneity in ponderosa/pine Douglas-fir forest: age and size structure in unlogged and logged landscapes of central Colorado. Canadian Journal of Forest Research 30: 698-711.

Keyes, C.R. 2000. Natural regeneration of ponderosa pine: Pest Management strategies for seed predators. The Forestry Chronicle 76(4): 623-626.

Larson, M.M. 1961. Seed size, germination dates, and survival relationships of ponderosa pine in the Southwest. Research Note No. 66. Fort Collins, CO: USDA, FS< RMFREP. 4p.

Larson, M.M. & G.H. Schubert. 1969. Root competition between ponderosa pine and grass. Forest Service Research Paper RM-54, U.S. Department of Agriculture, Fort Collins, Colorado.

Madole, R.F. 1973. Environmental history and land use recommendations for Boulder County, Colorado. Institute of Artic and Alpine Research Occasional Paper No. 8.

Marr, J.W. 1961. Ecosystems of the east slope of the Front Range of Colorado. University of Colorado Studies Series in Biology 8.

Mast, J.N., T.T. Veblen and M.E. Hodgson. 1997. Tree invasion within a pine/grassland ecotone: an approach with historic aerial photography and GIS modeling. Forestry Ecology and Management, (93): 181-194.

Neilson, R.P. 1986. High-resolution climatic analysis and southwest biogeography. Science, 232: 27-34.

Ogden, J. 1985. Past, present and future: Studies on the population dynamics of some long-lived trees. Pp. 3-16 in J. White (eds.), Studies in Plant Demography: A Festschrift for John Harper. London: Academic Press.

Pearson, G.A. 1923. Natural reproduction of western yellow pine in the Southwest. Forest Service bulletin, number 1105, U.S. Department of Agriculture, Washington, D.C.

Peet, R.K. 1981. Forest vegetation of the Colorado Front Range: composition and dynamics. Vegetatio (45): 3-75.

Pickett, S.T.A. and P.S. White. 1985. Patch Dynamics: A synthesis. Pp. 371-384 in S.T.A. Pickett and P.S. White (eds.), The ecology of natural disturbance and patch dynamics. New York: Academic Press.

Risser, P.G., and R.T.T. Forman. 1983. landscape Ecology: directions and approaches. Champaign: Illinois natural history Survey, Special Publication 2.

Rummell, R. 1951. Some effects of livestock grazing on ponderosa pine forest and range in central Washington, Ecology, (62): 594-607.

Sauer, C.O. 1925. The morphology of landscape. Pp. 315-350 in J. Leighly (ed.), Land and life. 1963. Berkeley: University of California Press.

Savage, M., P.M. Brown and J. Feddema. 1996. The role of climate in a pine forest regeneration pulse in the southwestern United States. Ecoscience 3(3): 310-318.

Schubert, G.H. 1974. Silviculture of southwestern ponderosa pine: The status of our knowledge. Forest Service Research Paper RM-123, U.S. Department of Agriculture, Fort Collins, Colorado.

Stein, S.J. 1988. Explanations of the imbalanced age structure and scattered distribution of ponderosa pine within a high-elevation mixed conifer forest. Forest Ecology and Management. 25: 139-153.

Stewart, O.C. 1942. Culture element distributions: XVIII Ute-Southern Paiute. University of California Anthropological Records 6:231-356.

Telewski, F.W. 1957. Instructions and tables for computing evapotranspiration and the water balance. Drexel Inst. Tech. Publicat. Climatol. 10(3), New Jersey.

Telewski, F.W. & A.M. Lynch. 1990. Measuring growth and development of stems. Pages 505-555 in J.P. Lassoie & T.M. Hinckley (ed.). Techniques and Approaches in Forest Tree Ecophysiology. CRC Press, Boca Raton.

Thornthwaite, C.W. & Mather, J.R. 1993. Determining the germination date of woody plants: A proposed method for locating the root/shoot interface. Tree Ring Bulletin, 53: 13-16.

Veblen, T.T., and D.C. Lorenz. 1986. Anthropogenic disturbance and recovery patterns in montane forests, Colorado Front Range. Physical Geography 7(1):1-24.

Veblen, T.T., and D.C. Lorenz. 1991. The Colorado Front Range: a century of ecological change. University of Utah Press, Salt Lake City, Utah, USA.

Veblen, T.T., T. Kitzberger, and J. Donnegan. 2000. Climatic and human influences on fire regimes in Ponderosa pine forests in the Colorado Front Range. Ecological Applications, 10(4): 1178-1195

Villalba, R. and T.T. Veblen. 1997. Regional patterns of tree population age structures in northern Patagonia: climatic and disturbance influences. Journal of Ecology 85:113-124.

Watt, A.S. 1923. On the ecology of British beechwoods with special reference to their regeneration. Journal of Ecology 11: 1-48.

White, A.S. 1985. Presettlement regeneration patterns in a southwestern ponderosa pine stand. Ecology, 66: 589-594.

Wolter, Klaus 2004. Multivariate ENSO Index (MEI) NOAA-CIRES Climate Diagnostics Center, Document maintained by Klaus Wolter (Klaus.Wolter@noaa.gov), Updated: Mar 3, 2004, http://www.cdc.noaa.gov/~kew/MEI/mei.html