

The role of climate in a pine forest regeneration pulse in the southwestern United States¹

Melissa SAVAGE, Department of Geography, University of California, Los Angeles 90095-1524, U.S.A., e-mail:

savage@geog.ucla.edu

Peter M. BROWN, Rocky Mountain Tree-Ring Laboratory, Fort Collins, Colorado 80526, U.S.A.

Johannes FEDDEMA, Department of Geography, University of California, Los Angeles 90095-1524, U.S.A.

Abstract: The role of historical influences in patterning forest landscapes was explored in a case study of forest structure change in the American Southwest. A group of ponderosa pine trees was destructively sampled and year of germination identified in order to assess the strength and nature of the climate signal in influencing ponderosa pine germination in this century. A novel methodology for estimating year of germination in woody species by identifying the root-shoot boundary appears to be promising. Both rare seasonal and interannual climatic factors and a unique set of circumstances associated with anthropogenic disturbances played a role in shaping a germination pulse early in the 20th century. A cohort originating in 1919 captured available space and, barring major disturbance, will dominate forest structure at the site for centuries. Such rare germination events support the view that forest communities are essentially dynamic and non-equilibrium over the long-term.

Keywords: regeneration, forest structure, climate, anthropogenic disturbances, regional processes, *Pinus ponderosa*.

Résumé: Le rôle des facteurs historiques influençant les paysages forestiers a été analysé à l'aide d'une étude de cas se rapportant aux changements de la structure d'une forêt du Sud-Ouest américain. Des pins ponderosa (*Pinus ponderosa*) ont été tronçonnés et l'année de germination déterminée afin d'évaluer la nature et l'importance du signal climatique ayant favorisé leur germination au cours du vingtième siècle. Nous avons utilisé une nouvelle technique pour la détermination de l'année de germination des espèces ligneuses en identifiant le contact tige-racine. Ajoutés à un ensemble particulier de perturbations d'origine anthropique, des facteurs climatiques saisonniers de faible fréquence ainsi que des facteurs climatiques interannuels ont provoqué une germination massive des pins au début de ce siècle. Une cohorte d'arbres établis en 1919 a occupé tout l'espace disponible et, à moins d'une perturbation d'importance, dominera éventuellement le peuplement au cours des siècles à venir. De tels événements rares confortent l'idée que les communautés forestières sont dynamiques et n'atteignent pas un état d'équilibre à long terme.

Mots-clés: régénération, structure de la forêt, climat, perturbations anthropiques, processus régionaux, *Pinus ponderosa*.

Introduction

Ecologists have often stressed the role of local, deterministic processes, such as competition and the influence of the physical environment, in explanations of vegetation community structure. Ricklefs (1987), however, suggests that recent studies of community dynamics lend support to the view that historical and regional-scale processes may be important in influencing the structure of communities. May (1986) points to a growing awareness of the dynamic nature of landscapes and the importance of historical accidents in the assembly of communities. An emphasis on the role of history and chance in shaping ecosystems has been most appreciated thus far in the literature on ecological disturbance (Veblen, 1979; Sousa, 1984; Pickett & White, 1985).

The structure of ponderosa pine forests in the American Southwest has changed conspicuously over historical time. Open, park-like forests of a century ago now have dense stands of trees, a directional change ascribed to abundant regeneration shortly after the turn of the century (Covington & Moore, 1994). The proximate cause of this trend has been the subject of controversy. Some authors propose that regional climatic trends, such as wet decades or droughts (Hastings & Turner, 1965; Swetnam, 1993), or single anomalous climate years (Schubert, 1974) may override

local processes in long-term vegetation dynamics. But novel anthropogenic disturbances were intensive during this period, particularly in the decades before and after 1900. Severe grazing by domestic livestock, primarily sheep, and the cessation of the historical regime of episodic surface fires, are also cited as primary agents in forest structure shifts in the Southwest (Bahre, 1993).

Identification of the timing of germination of forest trees can be a window of opportunity for evaluating hypotheses of forest dynamics. Literature on southwestern ponderosa pine forest development is substantial, and one year in particular, 1919, has become famous as an "*annus mirabilis*" of reproduction for the entire region. Schubert (1974) estimates that the cohort covered over a million ha of the Colorado Plateau. Many authors cite this cohort as the major component of forest density increase in the Southwest (Arnold, 1950; Rummell, 1951; Cooper, 1960). Pearson (1923) suggests that 1919 was an "epoch-making" year for reproduction due to an excellent seed year in 1918 and high summer precipitation in 1919. Yet some researchers report other years of strong regeneration in northern Arizona: in 1903, 1909, 1923, and 1928 (Cooper, 1960); in 1910, 1914, and 1929 (Eagan, 1949; Arnold, 1950); in 1913 (Schubert, 1974); and 1910 and 1914 (Pearson, 1923).

Identifying the date of germination of trees would be

¹Rec. 1995-09-12; acc. 1996-02-12.

helpful in elucidating the role of historical factors in forest development. This has generally been lacking because of the difficulty of detecting precise year of germination. Most methods of aging trees give a general estimate based on crossdating tree ring series on increment cores taken at ≈ 30 cm above the ground, or at an angle towards the tree base. Recently, a methodology was proposed to identify the year of germination through an analysis of the anatomical characteristics of the pith region on cross-sections taken at the base of the tree (Telewski & Lynch, 1990; Telewski, in press). Accurate germination dates would allow an assessment of the influence of seasonal to interannual temperature and precipitation factors from instrumental records, and a determination of the autecological requirements for species' germination.

The objectives of this research are *i*) to reconstruct dates of establishment of a group of ponderosa pine in northern Arizona, and *ii*) to investigate the strength and nature of the climate signal in influencing ponderosa pine regeneration in this group in this century. We investigate the hypothesis that a single year of excellent germination, 1919, produced a cohort, and that germination of this species requires rare, favorable climate conditions. In addition, we evaluate the viability of a method for absolute determination of tree age, which, if robust, could increase our ability to understand mechanisms that control tree establishment. The documented germination event of 1919 enables us to test the method's accuracy in identifying year of germination.

PONDEROSA PINE REGENERATION

A large number of local ecological factors can negatively effect ponderosa pine regeneration, including drought, seed predation, browsing by rodents and ungulates, sunscald, frost heaving, trampling, fire, damping-off disease, and competition, particularly with grasses (Pearson, 1923; Larson & Schubert, 1969; Harrington & Kelsey, 1979). The presence of a deep layer of organic litter is a particular deterrent, since it has little moisture and high temperature amplitude (Schubert, 1974).

Extensive study of the conditions necessary for germination and establishment of ponderosa pine suggests a critical influence of the timing of precipitation and seasonal temperature changes. Regeneration appears to be intermittent because successful germination and establishment require a series of years with specific precipitation and temperature parameters which tend to be rare (Schubert, 1974; White, 1985). Maguire (1956), based on correlation of 23 years of California cone crop yields with temperature data, suggests that specific climate conditions in that location are required in two of three consecutive years, *i*) the critical temperature year *ii*) the flower or conelet year, and *iii*) the mature cone year. In the critical temperature year, above average temperatures in April/May allow differentiation of cells in newly formed terminal buds that leads to flowering in the following year. During the year in which conelets form, temperatures cannot drop below -4°C in June. No particular conditions are required for the cones to mature in late summer of the third year.

For successful establishment, abundance and timing of

precipitation is critical beginning the following year, when seeds germinate. Seeds do not usually germinate until the growing season following maturation (Pearson, 1923). The earlier in the summer seeds germinate, the more likely the seedlings are to establish. Drought in that spring and summer is a major cause of seedling mortality (Larson, 1963; Rietveld & Heidmann, 1976). Germination is delayed until summer, when soil temperatures reach 13°C and summer rains begin (Schubert, 1974). Failure of regeneration is often due not to poor germination but to high mortality in the 2 or 3 years following germination, either because of drought in the fall of germination year, or in spring and summer of the following years, and because of early frosts (Pearson, 1923).

REGIONAL REGENERATION

Historical studies indicate that regeneration has been episodic in the Southwest, producing pulses of establishment (Schubert, 1974; White, 1985; Biondi, Myers & Avery, 1994). Dendrochronological analyses reveal that ponderosa pine establishment there is historically episodic and infrequent. Even-aged cohorts which reflect synchronous regeneration events in past centuries at the stand level have been found in the nearby White Mountains (Cooper, 1960) and Chuska Mountains (Savage, 1991), and on the Pearson Natural Area itself (White, 1985). Pearson's (1910; 1923; 1950) observations over several decades near Flagstaff that years of successful germination are scarce and years of high seedling mortality are common, confirm these historical reconstructions.

Pine regeneration on the Colorado Plateau, and in much of the Southwest, was characterized by foresters in the early part of this century as acutely inadequate. Lieberg, Rixon & Dodwell (1904) document an almost complete cessation of reproduction in the region for the last two decades of the nineteenth and first decade of the twentieth century.

Pearson is primarily responsible for the claim that a large proportion of the ponderosa pine trees on the Colorado Plateau originated as a cohort in 1919. He began research at the study site in 1908 and documented in some detail not only the abundance of seed crops, but also climate conditions month by month, and the fate of ponderosa pine seedlings (Pearson, 1910; 1923; 1933; 1936). In the second decade of the century, some years had good seed crops, but poor germination, while others, such as 1910 and 1914, had adequate germination but suffered losses to drought or frost.

However, an abundant 1918 seed crop over a wide region was followed by an anomalously warm and wet year in 1919. In the latter part of May 1919, rain fell almost daily for two weeks, giving seedlings the advantage of an unusually early start in the growing season. By 1920, there was an average of over 150 000 first-year seedlings/ha, and by September of 1921, 19 000/ha remained (Pearson, 1923). A series of repeat photographs taken at the Pearson Natural Area over nearly a century confirm regeneration in the early decades of the century. Three of these photographs are published in Covington & Moore (1994), with the earliest, taken in 1909, showing a landscape devoid of visible seedlings and saplings. In the latter two, from 1949 and 1990, a massive increase in density is conspicuous.

Methods

STUDY AREA

Research was conducted in a monospecific group of ponderosa pine in the Gustav A. Pearson Natural Area, 15 km northwest of Flagstaff, Arizona ($35^{\circ} 16' N$, $111^{\circ} 44' W$). The terrain is slightly rolling, at an elevation of 2255 m above sea level. Soils are formed of montmorillonitic clay-loams derived from late Tertiary lava flows (Biondi, Myers & Avery, 1994).

Climate patterns are typical of the region, with cold, wet winters, early summer and fall droughts, and mild summers with frequent convective thunderstorms. The climate station at the site has reported average monthly temperature and precipitation data since 1909. There appear to be several secular climate trends in both temperature and precipitation in the region over the past century. The instrumental climate record indicates a slow decline from a precipitation maximum around 1915 (Sellers, 1960). This century (Grissino-Mayer, in press), and particularly the early decades (Granger, 1984), have been identified as anomalously warm. Secular trends early in the century, both warmer and wetter than normal and lasting several decades, provided benign conditions for ponderosa pine germination.

At the same time, the regional forest suffered from profound anthropogenic disturbances. A historical regime of low-intensity surface fires was responsible for the open, park-like nature of the presettlement regional forest (White, 1985; Swetnam 1990). Fire frequency, reconstructed from a fire scarred tree-ring record in a ponderosa pine stand 6 km from the study site, averaged every 2.2 years in the early part of the 1800s (Dieterich, 1980). Patchy, light fires thin stands by killing seedlings and saplings. Burning the dry litter layer, on the other hand, provides a favorable mineral seedbed for germination (White, 1985), and improves soil characteristics for seedling survival, by increasing nitrogen and raising pH (Harrington & Kelsey, 1979).

Toward the end of the 1800s, escalating livestock numbers eliminated the fine fuels that supported surface fires, and fire frequency plummeted (Dieterich, 1980; Swetnam, 1990). Fires have been suppressed in the region since then, at first indirectly by intense domestic grazing, and later by active fire management. Seedling mortality from surface fires was virtually eliminated as grass fuels were drastically reduced. Managed protection from fires became effective on the Pearson Natural Area from about 1908, when it became an experimental forest, although there is some evidence that in the early 1950s a light fire burned a small area before being extinguished.

Domestic grazing by sheep and cattle on the meadows beneath ponderosa pine forests began in the Flagstaff area around the late 1870s, with construction of the railroad (Cooper, 1961). Impacts on young trees from trampling and browsing were most severe around the turn of the century. But grazing can also improve seedbed conditions for pine germination; the mineral and organic soil is churned by hooves, and urine and feces from livestock provide a nutrient pulse (Savage, 1991). While chronic, intense grazing is detrimental to pine regeneration, light grazing, and especially the cessation of intense grazing, can have a

beneficial effect on germination of woody species (Cooper, 1960). When livestock herds dwindled after World War I, the release from grazing presented an exceptional opportunity for ponderosa pine germination in enhanced seedbed conditions (Pearson, 1923; Arnold, 1950).

An unusual opportunity to investigate the factors that influence pine germination prevails at the Pearson Natural Area, because of long instrumental climate records at the site and long-term vegetation studies. Pearson chose the site because it had never been harvested. Unofficial establishment of the reserve in 1908 initiated systematic inventories of the vegetation. Protection of seedlings from livestock grazing began with fence construction around 1910 (Olberding, Fort Valley Experimental Forest historian, pers. comm., 1995). While analysis of regeneration patterns, here as elsewhere in the Southwest, is confounded by the synchronous occurrence of anthropogenic disturbance and climatic fluctuations, this site has offered semi-controlled conditions since 1908. However, although little grazing and no harvesting has occurred here since protection began, the historic fire regime was much altered as fire is almost completely excluded.

DENDROCHRONOLOGICAL ANALYSIS

In 1989, all trees in a $32\text{ m} \times 40\text{ m}$ plot, except the largest 9, were destructively sampled. The dense group was slated to be thinned to preserve nearby buildings from fire. Basal sections were cut with a chainsaw from 212 trees. The nine trees not sampled (37, 25, 26, 77, 80, 24, 41, 28, 26 cm d.b.h.), were assumed to have germinated before the turn of the century, and were not included in this analysis. Sample trees were sawn 15 cm below and 15 cm above the ground surface in an attempt to ensure the sampling of the earliest pith rings, and thus the capture of the germination year, in the case of a shift in ground surface.

Following Telewski (1993), we sought to determine the year of germination of the trees by locating the boundary between the root and the shoot, and by determining the pith date at that location. Pith and the primary vascular bundles lie within the sheath formed by the vascular cambium in the stem. The vascular cambium produces a growth ring around the pith in the stem, but not in the root and this marks the boundary between the two, and can therefore be used to determine the germination year. Analysis, then, entailed the identification of stem tissue with a pith and root tissue without a pith. Germination year applies to the length of stem from the root/shoot interface to the top of the first year's growth.

Traditional methods of estimating germination year are usually approximate; tree age is determined by using a ring count or crossdated age from an increment core added to a mean age of seedlings to coring height. Identification of the root-shoot boundary is a novel technique to date tree germination, and similar methods have been applied thus far only for dating seedling germination (Baker, 1990). The far greater accuracy of this method of aging allows a more accurate reconstruction of the timing of tree establishment. A description of the physiological basis for the methodology is presented in Telewski (1993).

Samples sawn from each tree consisted of full disk cross sections, varying from 4 to 7 disks per tree but generally

5, taken from near the base of the stems and root collars of individual trees. Cross-sections were finely surfaced with sandpaper of 320 to 500 grit to reveal cell structure in the ring series, and examined under a microscope. All ring series were dendrochronologically crossdated using variations in patterns seen in ring widths, latewood widths, and false rings. Because of difficulties in distinguishing near-pith rings on most of the sections, all cross sections had two dates recorded: the last dated ring for which we were confident of the crossdating, and an estimated date for the pith. Scars and other injuries were also observed and recorded by year.

After all sections from an individual tree were crossdated, the youngest or most confident pith date on any section of a tree was then assigned as the germination year for the tree. In general, dating error appeared to be within one to two years for successfully dated samples. If the last dates and the pith dates for all sections of a tree were 6 or more years apart, no germination date was assignable for that tree and it was not included in the final germination date tally. A histogram of the number of trees germinating in each year since 1909 was created.

CLIMATIC ANALYSIS

To evaluate possible links between local climate conditions and ponderosa pine germination, we used a daily water balance model. We attempted to establish links between moisture and temperature conditions, cone development and maturation, and germination and survival of seedlings. Climate data used were from the Fort Valley climate station at the Pearson Natural Area, which has a continuous record of daily temperature and precipitation from 1912 to 1993 (data obtained from the National Climate Data Center). The water budget model is a modification of the Thornthwaite model (Thornthwaite, 1948; Thornthwaite & Mather, 1955; Willmott, 1977; Mather, 1978). It includes a standard Soil Conservation Service (US SCS) (1972) runoff model that separates precipitation into a portion of direct overland runoff and a portion that infiltrates into the soil layer and becomes part of the water budget. The model also incorporates snowfall as a component (Willmott, 1985), since seedling survival may be affected by the presence of snow. When the average daily temperature falls below -1.0°C , precipitation is assumed to fall as snow. When the average daily temperature remains below -1.0°C , snow is allowed to accumulate on the ground surface, and does not become a part of the water budget until it melts. To calculate the effective precipitation, or that which infiltrates the soil, the total rainfall or snowmelt was estimated on each day, and the combined water input was run through the SCS model to separate overland runoff. Soil moisture loss to actual evapotranspiration (AE) is regulated by a simple function which allows the soil moisture layer to release 100% of the water demand until soil moisture is reduced to 70% of field capacity, and is then reduced linearly until soil moisture is zero (Mather, 1978).

Inputs to the model are daily minimum and maximum temperatures and daily values of precipitation from January 1, 1912 through December 31, 1993. Missing data were sparse, and those missing before January 1951 were interpo-

lated from values at Williams, Arizona and Grand Canyon Headquarters, Arizona. Temperature data from these two locations were first adjusted by the difference in the long-term monthly mean temperature between these stations and Fort Valley and then averaged for the two locations. Missing precipitation data were generated by averaging recorded daily observations at Williams or Grand Canyon. After January 1951, long-term adjusted values of temperature and raw values of precipitation from Pulliam Airport, Flagstaff were directly substituted for missing values.

Additional model input requirements were the latitude of Fort Valley, used to calculate day length (Willmott, 1977), estimates of soil field capacity, and the SCS curve numbers based on local soil conditions. Local soils are comprised primarily of silty clays or silty clay loams, with a maximum depth of 76 cm (Covington & Moore, 1994). We estimated a maximum field capacity of 140 mm and an average of 120 mm. Determining the SCS curve numbers for runoff estimates was also based on local soil and vegetation properties. The soils were classified as SCS type D soils, clays with poor drainage and infiltration rates. Runoff curves were assigned values of 60, 78 and 90 for the three different antecedent 5-day precipitation totals. May through September was considered the growing season when calculating the five-day antecedent precipitation conditions (US SCS, 1972; Mather, 1978).

A water budget was run on a daily basis for the entire length of record. Advantages of a daily, rather than monthly basis, include a more accurate assessment of water available for plant transpiration (AE), and improved assessments of plant water stress (deficit). In addition to daily input values of minimum temperature (Tmin), maximum temperature (Tmax), and precipitation (P), calculated data consisted of daily estimates of average temperature (Tav), effective precipitation (eP: that portion of precipitation that infiltrates the ground), direct overland runoff (dro), snow melt (melt), snow depth (snow), potential evapotranspiration (PE: based on the Thornthwaite method), soil moisture depth (soil), actual evapotranspiration (AE), deficit (def) and surplus water (sur), and combined water runoff (ro: sum of surplus and direct overland runoff). When aggregated to monthly averages or totals, monthly moisture index values were also obtained (Im; see Willmott & Feddema, 1992), as well as the number of days when temperatures fell below freezing (< 0) and lower than -15°C (< 15). Similar counts were also kept where these temperature thresholds were reached without a calculated snow cover of at least 0.5 mm water equivalent ($< 0\text{ns}$ and $< 15\text{ns}$), and finally the lowest minimum temperature recorded for the month (minT).

Water budget output data were used to test hypotheses relating cone production and germination to climate variation (Maguire, 1956; Schubert, 1970). (A cautionary note: While we assume, with Maguire, that cone crop equals seed crop, this may not always be the case.) Proposed explanations for regeneration success include: *i*) normal or above normal temperatures in the spring two years prior to the mature cone crop (3 years prior to germination year); *ii*) June temperatures above -3.9°C in the year prior to the crop year; *iii*) very wet conditions and simultaneous warm temperatures (one week over 12.8°C) in the spring of the germination

year; iv) a warm and wet period early enough in the germination year to allow seedlings to be well established before the fall frosts; v) favorable moisture conditions in the summer of the germination year so that seedlings do not experience water deficit; and vi) a mild winter following germination season to protect the seedlings from extreme frost. For each year of the instrumental record, each of 11 conditions proposed as important to regeneration by Maguire (1956) or Schubert (1970) was tested (Table I). While each condition is assigned an equal weight in our analysis, some of these conditions are probably more important than others in fostering germination.

TABLE I. Climatic criteria used to select climatic situations hypothesized to produce good ponderosa pine regeneration

Condition number	Years prior to germination	Month	Variable tested	Condition
1	-3	5	Temp.	Above normal
2	-3	6	Temp.	Above normal
3	-2	6	Tmin	> -4°C
4	0	5	AE	> 1 SD above normal
5	0	5	Surplus	> 0 mm
6	0	5	Tmin	> -4°C
7	0	6	AE	> 1 SD above normal
8	0	6	Tmin	> -4°C
9	0	7	Deficit	< 0.5 SD below normal
10	0	7	Tmin	> -4°C
11	0	8	Deficit	< 0.5 SD below normal

Tmin: minimum temperature, AE: actual evapotranspiration, SD = standard deviation.

We had three goals in using the water budget model: *i*) evaluating the conditions that may have led to germination in 1919, *ii*) testing hypotheses proposed by Maguire (1956) and Schubert (1970) relating climate to successful cone production and germination, and *iii*) identifying other potential periods in the climate record when conditions were optimal for germination. Caution should be used in assessing the results of this analysis, since Maguire's study was conducted on ponderosa pine growing not in north-central Arizona, but rather in California.

Results

DENDROCHRONOLOGICAL ANALYSIS

A total of 166 trees (78%) were confidently crossdated to within one to five years of germination date (Figure 1). The most common estimated germination date was 1919 (44%). All other germination dates were near 1919. Since pith dates on these trees were often one to several years from the last certain dates, many of these germination dates may also be from 1919. The year 1920, for example, was the second most common germination date and it is likely that many of these actually date to 1919 but were underestimated due to indistinct near-pith rings. If the error in dating was ± 1 year, then 71%, and if ± 3 years, then 97%, of the germination dates could fall in 1919. Some of the dates prior to 1919, however, may be attributable to years in which Pearson observed some germination, 1914 for example.

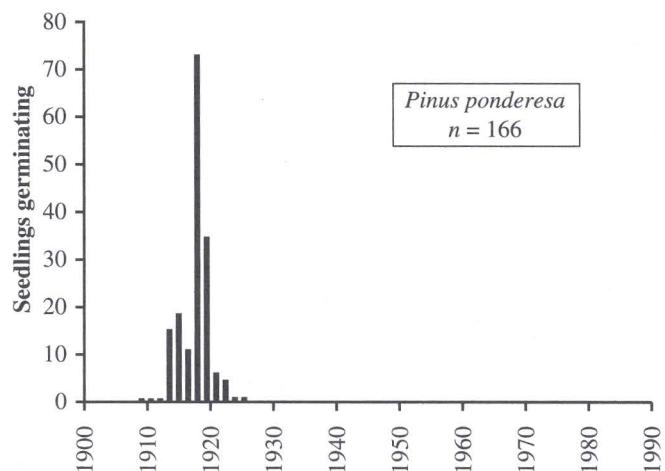


FIGURE 1. Frequency of germination dates of ponderosa pine in sample plot at the Pearson Natural Area, Flagstaff, Arizona.

Total stand density was extremely high, 1727 stems/ha. This is very dense compared to a presettlement abundance of perhaps 48-60 trees/ha (Covington & Moore, 1994), and clearly reflects long-term protection from fire in addition to a germination pulse. Many trees were small in diameter although about 70 years old; mean diameter was 13.2 cm (standard deviation 4.2 cm; range 4.5 to 25.0 cm).

Outside of the pith area, crossdating was generally straightforward. Many narrow rings were consistent among all trees (1925, 1932, 1948, 1951, 1956, 1958, 1963, 1974, 1977, 1981, 1985). Other useful ring characteristics were common, including thin latewood (1932, 1953, 1956, 1974, and 1985), false rings (1948, 1951, 1963, 1971), and a fire scar (1952).

Abundant synchronous establishment at the site, however, caused severe growth suppression, and ring anomalies presented difficulties in dating some trees. Many small diameter trees had very suppressed outside rings, usually beginning around 1966 or 1968. Some sections could not be crossdated owing to missing or distorted rings created by reaction wood or light latewood bands. Crossdating in the pith area of some trees was difficult because of narrow rings, false rings, light latewood, small rings, reaction wood, or injuries. Even with very finely sanded surfaces and high magnification, visual separation of tissue structure from parenchyma cells formed by apical meristem and the earliest xylem cells formed by vascular cambium at the base of the stem was difficult. Having several sections extend below to above the root collar on each tree for comparison helped to determine probable pith dates.

Determination of precise germination dates was also difficult due to abnormal ring patterns or injuries in the earliest years of a tree's life. Injuries were common in the first few rings of many sampled trees. These injuries may have resulted from rodents, frosts, fire, wind, or other factors. On the other hand, injuries or fire scars well outside of the pith area were often beneficial in identifying ring boundaries. Often, a discolored area caused by resin extended from the pith to the site of the injury, and made ring boundaries more distinct than in normal sapwood areas.

The methodology for identification of germination date proposed by Telewski (1993) appears to be promising. The technique may be used with greater success in cases where there is minimal growth suppression in early years. The method is labor intensive, both in terms of data collection, preparation, and analysis, which in general, will limit sample sizes.

CLIMATIC ANALYSIS

Analysis of climatic factors suggests that optimal conditions for ponderosa pine germination are not common. Average values and variance statistics for the monthly aggregated water budget values indicate considerable variability in climate values over 82 years (Table II).

The year 1919 was clearly unusual in the instrumental record. It was one of the wettest on record, and the winter that followed was notably mild with extensive snow cover. Table II presents general climate factors that we assumed to be biologically significant, primarily related to measures of surplus water and warmth, and particularly in spring, a critical season for germination. It is evident that while 1919 was not always the top ranked or record year, it was usually among the best years in every category (Table III). In 1919, an unusual coincidence of climatic factors led to an extremely favorable climatic year measured by year round water supply and optimal spring temperatures, as reflected in AE. The winter of 1919-1920 had very mild temperatures and ample snow to protect seedlings from winter stress. Water stored in the snow pack also helped continue surplus moisture conditions for seedlings in the spring of 1920. The following year, 1921, was exceptionally wet, with high actual evapotranspiration, reflecting abundant biologically available moisture. A cold snap in late spring of 1921 probably deterred germination in that year, but moist conditions

would have fostered the growth of established seedlings.

Other years had favorable climatic conditions, but not consistently so. Some years had record conditions but only for one or two variables (Table III). While most of the growing season was climatically optimal in 1921, 1951, and 1965 for example, the combination of spring conditions, either high temperatures and AE, and surplus water conditions were not steadily favorable.

The only other year to match 1919 in germination year climate criteria proposed by Maguire (1956) and Schubert (1970) was 1992. It emerged as the only year on record, besides 1919, in which the last 8 of the proposed conditions for germination were met (Table IV). These criteria all relate to conditions within the germination year, and exclude those prior to germination year. Only 1919 and 1992 share a moist, warm May reflected by conditions 4-6 (Table IV). As described by Pearson (1923) this early onset of spring is the primary factor that allows ponderosa pine to germinate early enough to be robust in the ensuing winter frosts and the next spring's drought. Based on the correlation of our climate criteria with known germination in 1919, 1992 is the only other climate year in the record when successful germination was predicted by the model. While our sampling of the vegetation was completed in 1989, there is anecdotal data that germination was abundant in 1992 (Covington, pers. comm., 1995).

Late spring conditions appear to play an important role in ponderosa pine germination. Schubert (1970) suggests that seeds must be continuously wet, implying surplus surface water, but germination will not occur unless temperatures are warm. This special case may only be possible in late May and early June, prior to the typical spring drought. The presence in the entire record of only one year with a June

TABLE II. Mean monthly values of water budget variables estimated from daily observations, Fort Valley, AZ, 1912-1993 (see text for explanation of variable names. Balances may not match due to rounding error)

Month	Tmin	Tmax	Tav	P	eP	dro	melt	snow	PE	soil	AE	def	sur	ro	Im	< 0	< 15	< 0ns	< 15ns	minT
January	-11.0	5.1	-3.0	56	39	2	22	30	2	104	2	0	23	25	0.89	31	6	7	0	-17.3
February	-9.7	6.4	-1.6	55	57	3	32	35	4	114	4	0	47	50	0.76	28	4	9	0	-16.7
March	-7.8	8.8	0.5	58	73	2	45	24	12	117	12	0	62	64	0.68	30	2	16	0	-15.7
April	-4.9	13.7	4.4	37	48	1	22	6	30	110	30	0	30	31	0.10	27	0	24	0	-12.1
May	-2.0	18.9	8.4	21	23	0	3	0	57	88	53	4	5	5	-0.60	23	0	22	0	-7.7
June	1.7	24.9	13.3	15	15	0	0	0	86	49	51	35	0	0	-0.83	10	0	10	0	-4.1
July	7.2	26.7	16.9	75	74	1	0	0	109	36	60	49	0	1	-0.33	1	0	1	0	1.3
August	6.9	25.1	16.0	84	83	1	0	0	98	53	70	28	3	4	-0.18	1	0	1	0	1.6
September	2.6	22.7	12.6	48	46	1	0	0	70	55	48	22	2	4	-0.39	7	0	7	0	-3.6
October	-2.9	17.1	7.1	40	37	2	1	0	39	58	26	13	3	4	-0.20	24	0	24	0	-10.2
November	-7.7	10.6	1.4	36	29	1	8	3	13	69	9	4	4	6	0.19	29	2	23	1	-15.3
December	-10.4	6.2	-2.1	52	36	1	16	13	3	88	3	1	14	16	0.66	31	5	14	1	-16.9
Annual	-3.2	15.5	6.2	577	560	15	149	9	523	78	368	156	193	210	0.09	242	19	158	2	-17.3
Standard deviations for the same variables																				
January	1.7	2.2	1.5	46	32	7	19	33	2	25	2	0	30	34	0.21	1	4	9	1	0.9
February	2.1	2.4	1.9	41	41	9	30	43	3	15	3	0	42	47	0.45	1	3	9	1	1.5
March	1.9	2.5	1.9	45	40	7	38	41	7	5	7	0	39	42	0.44	1	2	10	0	2.1
April	1.5	2.5	1.6	31	42	3	37	31	8	7	8	0	40	41	0.54	2	0	5	0	2.7
May	1.5	2.2	1.4	22	26	0	15	2	8	15	7	5	16	16	0.37	5	0	5	0	2.4
June	1.8	0.9	1.4	19	18	2	0	0	8	15	13	14	0	2	0.21	6	0	6	0	1.8
July	1.5	1.6	1.0	41	39	3	0	0	6	17	19	19	3	5	0.33	2	0	2	0	2.6
August	1.7	1.3	0.9	41	39	4	0	0	5	21	16	17	9	12	0.35	2	0	2	0	2.8
September	1.7	1.7	1.1	44	41	6	0	0	6	24	15	15	11	15	0.45	5	0	5	0	2.6
October	1.5	2.4	1.4	38	33	7	4	1	7	27	10	11	9	15	0.55	4	0	4	0	3.2
November	1.7	2.3	1.5	32	26	6	10	6	5	31	4	4	11	15	0.67	2	2	6	1	2.2
December	1.7	2.4	1.6	40	32	4	17	16	3	30	2	1	28	29	0.58	1	4	9	2	0.9

TABLE III. Ranking of years ($n = 82$) for biologically significant climate variables including annual actual evaporation (AE), annual precipitation, May actual evapotranspiration, May surplus, May minimum temperature, and summer season (June/July/August) deficit. Values in parentheses are total values in mm for AE, precipitation and surplus, and $^{\circ}\text{C}$ for temperature

Rank	Annual AE	Annual prec.	May AE	May surplus	May min. T	Summer deficit
1	1967 (493)	1965 (947)	1934 (70)	1973 (128)	1992 (-2.8)	1967 (16)
2	1921 (489)	1919 (814)	1919 (66)	1992 (33)	1925 (-3.3)	1965 (23)
3	1990 (472)	1941 (792)	1958 (65)	1926 (27)	1924 (-3.3)	1955 (29)
4	1919 (469)	1992 (745)	1940 (64)	1915 (26)	1934 (-3.9)	1919 (33)
5	1931 (466)	1940 (732)	1984 (63)	1960 (21)	1919 (-3.9)	1921 (45)
6	1927 (439)	1936 (724)	1925 (63)	1965 (18)	1939 (-4.4)	1937 (50)
7	1965 (436)	1982 (721)	1931 (62)	1933 (17)	1926 (-4.4)	1930 (53)
8	1981 (429)	1993 (720)	1928 (62)	1921 (17)	1923 (-4.4)	1992 (58)
9	1930 (429)	1990 (719)	1992 (61)	1957 (16)	1952 (-5.0)	1957 (63)
10	1934 (428)	1937 (717)	1976 (61)	1976 (15)	1947 (-5.0)	1975 (63)
other	#11 1992 (426)	#11 1967 (712)	#41 1990 (53)	#11 1919 (14)	#12 1921 (-5.6)	#14 1991 (69)
	#17 1951 (414)	#13 1951 (704)	#44 1967 (52)	#13 1951 (9)	#32 1990 (-6.7)	#25 1951 (95)
			#58 1921 (49)		#72 1967 (-10.6)	
			#65 1965 (46)		#81 1965 (-13.9)	

water surplus (1955) implies that June, no matter how warm, is almost always too dry. The climate model predicts that of the 82 years in the record, only 18 had surplus water in late May, but under two conditions: *i*) when it was cold, and the snow pack extended late in the season, or *ii*) when it was warm, but there was ample rainfall. Of these 18 years, only two, 1919 and 1992, fit the latter case of wet, warm spring conditions (Table IV). Years that seemed favorable in many other respects usually had problematic spring seasons. In 1965, for example, a year that ranked first in annual precipitation, one of the coldest May temperatures on record occurred (Table III).

Analysis of the climate record did not find evidence that temperature conditions alone bear upon cone crop success (conditions 1-3) (Table IV) and does not support Maguire's (1956) suggestion that a series of warm years produces successful seed crops. Maguire reported data from California, however, and temperature requirements for ponderosa pine germination there, differ significantly from the Southwest (Schubert, 1970). This also suggests that there is not only a quantitative difference in temperature requirements, but a difference in temperature pattern as well. A modification of our criteria might reveal climate factors that influence successful seed crops.

Years before and after 1919 had a variety of shortcomings that may have deterred germination. Unfavorable spring season conditions included extreme cold (1915) and the lack of any moisture surplus in May (1916, 1917, 1918, 1920, 1921, 1922, 1923), factors which appear to be crucial for germination. This makes it likely that germination dates

of trees identified for the years near 1919 by the dendroecological analysis result from dating error based on anomalous rings. While there may have been some successful germination in 1910 or 1914, the vast majority of germination dates probably were from 1919.

Discussion

Age structure of the ponderosa pine group at the Pearson Natural Area reflects a remarkable temporal coherence in germination. A vast majority of the trees there originated in one year or within a few years in the second decade of the century. This study lends support to the hypothesis that 1919 was a unique year for germination in southwestern ponderosa pine forests. An analysis of climatic patterns also clearly suggests that temperature and precipitation anomalies played a fundamental role in the establishment of the cohort. These results offer evidence that confirm the view that regeneration of ponderosa pine in the American southwest is strongly episodic, and that the basis of those pulses is at least partly climatic control. An analysis of climate variables in this century specifically predicts that ponderosa pine requires a warm and wet last few weeks of May, together with an above-average, well-distributed water supply throughout the year. Benign climate conditions, especially warm and wet springs, which would support germination, were very rare in this century. Still, this analysis must be considered preliminary until more data on the specific physiological germination requirements of north central Arizona ponderosa pine are available.

Human disturbance cannot be ruled out, however, as a significant agent in this germination pulse. Intensive livestock grazing, together with drought, at the end of the 1800s created a lack of germination that offered favorable seedbed conditions in the early 1900s. The precipitous decline in domestic grazing in the region after World War I created a release for woody species, exacerbated by the virtual elimination of fire on the site. Under the historical pre-settlement regime of frequent surface fires, much of this germination pulse would have been eliminated. Similar levels of grazing conditions and fire exclusion prevailed throughout the Colorado Plateau. The almost unique circumstance presented

TABLE IV. Years meeting 7 or more of the 11 specific climate conditions proposed for successful regeneration of ponderosa pine (see Table III). 1 = conditions met in that year; 0 = conditions not met in that year

Year	Total	Conditions										
		1	2	3	4	5	6	7	8	9	10	11
1919	9	0	1	0	1	1	1	1	1	1	1	1
1921	8	0	1	1	1	0	0	1	1	1	1	1
1922	7	1	1	1	1	0	0	1	1	0	1	0
1931	9	1	1	1	0	0	1	1	1	1	1	1
1992	10	1	1	0	1	1	1	1	1	1	1	1

by timing of intense anthropogenic pressures are critical to an interpretation of the origin of this anomalous germination pulse. Only comparative studies at multiple sites throughout the region will enable us to explore the extent to which anthropogenic disturbances or extreme climatic events explain forest shifts. Biological controls, such as insects, disease and seed predation, can also be significant factors in constraining regeneration.

A water budget analysis of climatic factors proved a successful method for assessing the impacts of climate on plant regeneration, since it takes water storage into account and thereby focuses on those variables that specifically indicate plant water stress (AE and deficit). The distribution of these variables can be significantly different from those of local variables of temperature and precipitation. For example, while June 1919 surprisingly had no rainfall at all, soil moisture was abundant enough to support large numbers of seedlings.

The optimal combination of temperature and precipitation factors that prevailed in 1919 on the Pearson Natural Area was not repeated for 73 years. One interpretation of the regenerational history of the site is that the existence of the cohort effectively inhibited germination and masked any further regeneration response to climate signals. Density remains extremely high even now.

The methodology for identifying date of germination proposed by Telewski & Lynch (1990) and Telewski (1993) has promise. In this case, on-site observations by Pearson of seedlings in a specific year in the past facilitated an evaluation of the methodology. Over three-quarters of the sampled trees were successfully crossdated. Nearly half of these were identified to the single most probable year, nearly three-quarters to within + one year, and nearly all to within + three years. Both crossdating and determination of germination date would have a higher proportion of success if unusual conditions of growth suppression had not prevailed at the site. Moreover, these trees were about 70 years old, and aging younger trees should produce more confident results.

Community structure is the result of complex interactions of local-scale processes, such as competitive interaction and succession, and regional-scale processes, such as disturbance and climatic patterns. Swetnam (1993), in examining the effects of climate on vegetation communities as mediated through fire, suggests that regional climate events can overwhelm patterns governed by local, more stochastic factors. Identification of regional scale events with long-term consequences for community structure lends support to the view that communities are essentially dynamic and non-equilibrium over the long-term and large areas. The development of a regional-historical perspective is most likely to gain support through the exploration of natural experiments and unique historical circumstances such as this regeneration pulse. The regeneration history of this group of ponderosa pine on the Pearson Natural Area in this century suggests that the imprint of such an event on forest structure will be seen for centuries. Correlation of age structure, disturbance history, and climate reconstructions at a regional scale will further clarify the role of anomalous historical events.

Acknowledgments

We thank T. Swetnam and T. Caprio for initial analysis and advice, the USDA Forest Service, Rocky Mountain Forest and Range Experiment Station for permission to conduct research on the Gustav A. Pearson Natural Area, and D. Goldblum for field assistance. Dendrochronological analysis was conducted at the Tree-Ring Laboratory at the Rocky Mountain Forest and Range Experiment Station, Ft. Collins, Colorado, through CA28-C3-738.

Literature cited

Arnold, J. F., 1950. Changes in ponderosa pine bunchgrass ranges in northern Arizona resulting from pine regeneration and grazing. *Journal of Forestry*, 48: 118-126.

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

Baker, W. L., 1990. Climatic and hydrologic effects on the regeneration of *Populus angustifolia* James along the Animas River, Colorado. *Journal of Biogeography*, 17: 59-73.

Biondi, F., D. E. Myers & C. C. Avery, 1994. Geostatically modeling stem size and increment in an old-growth forest. *Canadian Journal of Forest Research*, 24: 1354-1368.

Carter, D. B. & J. R. Mather, 1966. Climatic Classification for Environmental Biology. *Publications in Climatology*, 19: 305-395.

Cooper, C. F., 1960. Changes in vegetation, structure, and growth of southwestern pine forest since white settlement. *Ecological Monographs*, 30: 129-164.

Cooper, C. F., 1961. The ecology of fire. *Scientific American*, 204: 150-160.

Covington, W. W. & M. M. Moore, 1994. Southwestern ponderosa forest structure. *Journal of Forestry*, 92: 39-47.

Dieterich, J. M., 1980. Chimney Springs Forest Fire History. *Forest Service Research Paper RM-220*, U.S. Department of Agriculture, Fort Collins, Colorado.

Egan, J. A., 1949. Forestry above the Mogollon Rim. *Journal of Forestry*, 47: 14-17.

Foiles, M. W. & J. D. Curtis, 1965. Natural regeneration of ponderosa pine on scarified group cuttings in central Idaho. *Journal of Forestry*, 63: 530-535.

Granger, E. O., 1984. Twentieth-century climate anomaly patterns over the southwestern United States. *Physical Geography*, 5: 164-185.

Grissino-Mayer, H. D., in press. A 2219 year annual reconstruction of precipitation for northwestern New Mexico, USA. Pages 17-21 in J. S. Dean, D. M. Meko & T. W. Swetnam (ed.) *Proceedings, International Conference on Tree-Rings, Environment, and Humanity*, Tucson, Arizona.

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

Hastings, J. R. & R. M. Turner, 1965. *The Changing Mile: An Ecological Study of Vegetation Change with Time in the Lower Mile of an Arid and Semiarid Region*. University of Arizona Press, Tucson, Arizona.

Larson, M. M., 1963. Initial root development of ponderosa pine seedlings as related to germination date and size of seed. *Forest Science*, 9: 456-60.

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.

Lieberg, J. B., T. F. Rixon, & A. Dodwell, 1904. Forest conditions in the San Francisco Mountains Forest Reserve, Arizona. U. S. Geological Survey Professional Paper 22, Washington, D.C.

Maguire, W. P., 1956. Are ponderosa pine cone crops predictable? *Journal of Forestry*, 54: 778-779.

Mather, J. R., 1978. The Climatic Water Budget in Environmental Analysis. Lexington Books, Lexington.

May, R. M., 1986. Species interactions in ecology. *Science*, 231: 1451-1452.

Pearson, G. A., 1910. Reproduction of western yellow pine in the southwest. Forest Service Circular 174, U.S. Department of Agriculture, Washington, D.C.

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.

Pearson, G. A., 1933. A twenty-year record of changes in an Arizona pine forest. *Ecology*, 14: 272-285.

Pearson, G. A., 1936. Some observations on the reaction of pine seedlings to light. *Ecology*, 17: 270-276.

Pickett, S. T. A. & P. S. White, 1985. Patch dynamics: A synthesis. Pages 371-384 in S. T. A. Pickett & P. S. White (ed.). *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press, New York.

Ricklefs, R. E., 1987. Community diversity: Relative roles of local and regional processes. *Science*, 235: 167-171.

Rietveld, W. J. & L. J. Heidmann, 1976. Direct seeding ponderosa pine on recent burns in Arizona. Forest Service Research Note RM-312, U.S. Department of Agriculture, Fort Collins, Colorado.

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

Savage, M., 1991. Structural dynamics of a southwestern pine forest under chronic human influence. *Annals of the Association of American Geographers*, 81: 271-289.

Schubert, G. H., 1970. Ponderosa pine regeneration problems in the Southwest. Pages 1-4 in R. K. Hermann (ed.). *Regeneration of Ponderosa Pine*. School of Forestry Paper 601. Oregon State University, Corvallis, Oregon.

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.

Sellers, W. D., 1960. Precipitation trends in Arizona and western New Mexico. Pages 81-94 in *Proceedings of the 28th Western Snow Conference*. Colorado State University, Fort Collins, Colorado.

Sousa, W. P., 1984. The role of natural disturbance in natural communities. *Annual Review of Ecology and Systematics*, 15: 353-91.

Swetnam, T. W., 1990. Fire-southern oscillation relations in the southwestern United States. *Science*, 249: 1017-1020.

Swetnam, T. W., 1993. Fire history and climate change in giant sequoia groves. *Science*, 262: 885-889.

Telewski, F. W., 1993. Determining the germination date of woody plants: A proposed method for locating the root/shoot interface. *Tree Ring Bulletin*, 53: 13-16.

Telewski, F. W. & A. M. Lynch, 1990. Measuring growth and development of stems. Pages 503-555 in J. P. Lassoie & T. M. Hinckley (ed.). *Techniques and Approaches in Forest Tree Ecophysiology*. CRC Press, Boca Raton.

Thornthwaite, C. W., 1948. An approach toward a rational classification of climate. *Geographical Review*, 38: 55-94.

Thornthwaite, C. W. & J. R. Mather, 1955. The water balance. *Publications in Climatology*, Volume 8, Number 1.

United States Soil Conservation Service, 1972. *National Engineering Handbook*, Section 4. United States Department of Agriculture, Washington D.C.

Veblen, T. T., 1979. Structure and dynamics of *Nothofagus* forests near timberline in south-central Chile. *Ecology*, 60: 937-402.

Weaver, H., 1964. Fire and management problems in ponderosa pine. *Tall Timbers Ecology Conference*, 7: 127-149.

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

Willmott, C. J., 1977. WATBUG: A FORTRAN IV algorithm for calculating the climatic water budget. *Publications in Climatology*, Volume 50, no. 1.

Willmott, C. J. & J. J. Feddema, 1992. A more rational climatic moisture index. *The Professional Geographer*, 44: 84-88.