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Population Maintenance of *Pinus pungens* Lam. (Table Mountain Pine) After a Century Without Fire

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ABSTRACT: A Table Mountain pine (*Pinus pungens* Lam.) population on an extremely xeric site in western North Carolina recruited new individuals during each of the 12 decades between 1877 and 1996, despite the absence of fire since 1889. Censuses of the population in 1976, 1986, and 1996 showed that the number of pines > 10 years of age increased by 11% during the two decades. However, the number of pines in the 0-to-9-year age class declined by 92% during the same period. Germination rates of seeds extracted from serotinous cones that had matured during 1967–1977 and 1986–1996 declined with seed age at a rate of 2.6 percentage points per year. However, germination rates were higher for seeds that matured during the period 1967–1977 than for those that matured during 1986–1996 (average of 32% and 18%, respectively). The lower germination rates and smaller 0-to-9-year age class in 1996 may have resulted from a 54-month drought that occurred during 1984–1989, which reduced annual radial growth of trees by 20–30%. However, during the seven years preceding the 1996 study, there were no significant droughts, yet recruitment of seedlings did not increase. At this xeric site, precipitation and temperature are more important than fire and competition in maintenance of *P. pungens*.

Index terms: fire, climate change, demography, southern Appalachian Mountains, succession

INTRODUCTION

In eastern North America, plant community succession often halts at an early stage of development on extremely xeric sites (Abrams and Orwig 1995). Such sites often harbor endemic plant species that cannot survive competition on more mesic sites (Baskin and Baskin 1988). Factors influencing plant demography on xeric sites are often climatic (e.g., precipitation) rather than biotic (e.g., competition) (Barden 1977). Consequently, long-term demographic shifts in natality or mortality in long-lived plant species on xeric sites may indicate biological effects of gradual climatic change in eastern North America (Iverson and Prasad 1998).

Table Mountain pine (*Pinus pungens* Lam.) is an endemic species that is common on xeric sites in the central and southern Appalachian Mountains (Zobel 1969). It overlaps in elevation with two other "hard pines" (section *Diploxylon*, Mirov 1967), *P. virginiana* Miller and *P. rigida* Miller, but it is often more abundant at higher elevations than these congeners (Whittaker 1956). *Pinus pungens* tolerates drought better than *P. virginiana* and *P. rigida*, but its seed germination rate is reduced much more by high temperature (> 30°C) than are the germination rates of the other pine

species (Zobel 1969). *Pinus pungens* sheds its pollen about 2 weeks earlier than sympatric pine species, but freezing during meiosis can cause pollen inviability, which may partly explain why *P. pungens* is absent from areas where late spring frosts are frequent (Zobel 1969).

On most sites, regeneration of *Pinus pungens* requires fire of medium-high intensity to open the forest overstory and reduce organic litter (Williams and Johnson 1992, Waldrop and Brose 1999). However, in 1976, I discovered a population of *P. pungens* that, despite the absence of fire since 1889, had recruited surviving members during each of the 10 decades from 1877 to 1976 (Barden 1977). It appeared that plant community development at this extremely xeric site, a granitic outcrop near Brevard, North Carolina, was arrested at the "pine stage" of succession because of moisture limitation in the shallow soil. In 1986 and 1996 I recensused the stand to determine whether the population had continued to maintain itself without fire.

Although cones of *Pinus pungens* remain attached to the tree after they mature, some release seeds spontaneously within two years of maturity, while others remain closed with stored viable seeds (serotinous cones) for more than a decade (McIn-

tyre 1929, Sargent 1965, Zobel 1969). In 1977 and 1996 I tested viability of seeds stored in serotinous cones (Barden 1979), and in 1996 I measured radial growth of pines growing in shallow, well-drained soil where annual growth increments tend to be sensitive to climate variations (Stokes and Smiley 1968). The motivation for the seed and growth studies in 1996 was to investigate effects of an extreme drought during the 1980s on tree growth and seed viability, which may help explain differences in demography observed in 1976 and 1996.

STUDY AREA AND CLIMATE

Looking Glass Rock, an oblong 2.0-km x 0.5-km granitic dome 1209 m in elevation at its highest point, is located in Pisgah National Forest, 10 km northwest of Brevard, North Carolina, USA (82° 23' 5" North, 35° 10' 25" West; Figure 1). A cap of deep soil on top of the dome supports an oak-hickory (*Quercus L.-Carya Nutt.*) forest. The rounded shoulders of the dome gradually slope off to a nearly vertical incline of exposed granite. On these granitic shoulders are isolated pockets of soil

in cracks and depressions. The shallowest pockets of soil support only herbaceous plants; deeper pockets (100 cm in depth) support the stunted *Pinus pungens* that are the subject of this study. The study population occurs in a 50-m x 500-m area that extends along the southwest shoulder of Looking Glass Rock where the slope is 10–20° and elevation is 1040–1180 m. Hardwood tree species such as *Quercus prinus L.*, and *P. rigida*, both of which grow a few meters upslope in the deeper cap of soil, have apparently been unable to persist in these shallow pockets of soil. In 1976 there were 195 *P. pungens* individuals in the study population on Looking Glass Rock, with ages up to 95 years and diameters at breast height (dbh) up to 45 cm (Barden 1977). Fire-scarred trunk sections and tree-ring cores taken in 1976 from large pines near the study area indicated that a canopy-opening fire occurred on Looking Glass Rock about 1810, and that the most recent fire was in 1889. A 1976 review of U.S. Forest Service fire records and interviews with long-time employees confirmed that there were no forest fires on Looking Glass Rock during the period 1919–1976 (Barden 1977), nor

did fire occur there during the years 1976–1996 (pers. obs.).

By chance, climatic conditions before the 1976 and 1996 censuses contrasted sharply, as indicated by the Palmer Drought Severity Index (PDSI; National Climatic Data Center 1997). PDSI is a cumulative monthly soil moisture index based on deviations from average precipitation and temperature (i.e., the current month's deviations and the previous month's PDSI are used in the PDSI function to calculate the current month's PDSI value). Values of PDSI between +1 and -1 indicate normal soil moisture, -1 to -2 mild drought, -2 to -3 moderate drought, -3 to -4 severe drought, and < -4 extreme drought.

During the period 1960–1976, there were no long or severe droughts (Figure 2). In fact, from 1970 to 1976, PDSI was in the normal to wet range (> -1) for 66 consecutive months, the longest such period in the 103 years of weather records in western North Carolina (National Climatic Data Center 1997). In contrast, 1980–1989 was a decade of drought, with PDSI continuously below normal (< -1) from September 1984 to February 1989 (Figure 2), the longest such period in the 103-year data set. For the entire growing season of 1986 (March–October), PDSI was in the extreme drought range (-4 to -6); during the same period in 1988, it was in the severe-extreme range (-3 to -5). In July 1986 PDSI reached its lowest point in history, -5.76, which was nearly a full point below the previous record low of -4.81 set in September 1925. During the period 1989–1996, PDSI was generally in the normal range or above. Overall, between 1960 and 1996, PDSI fluctuated in an unpredictable way, but average July temperatures in the region increased by more than 1.5°C, a rate of 0.04°C per year (Figure 3).

METHODS

In June 1976 I began collecting demographic information on *Pinus pungens* by mapping, aging, and photographing individual pines in the study area from an easily relocated position (Barden 1977). Saplings < 5 cm diameter at the base were aged by counting terminal bud scars; larg-

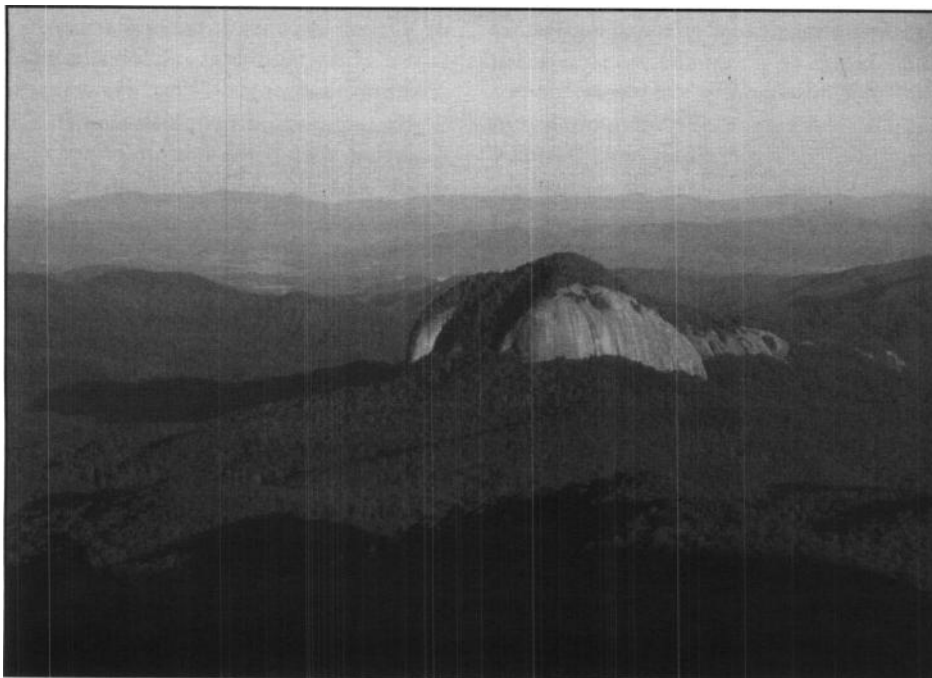


Figure 1. Looking Glass Rock, a 2.0-km x 0.5-km granitic dome 10 km northwest of Brevard, North Carolina, USA.

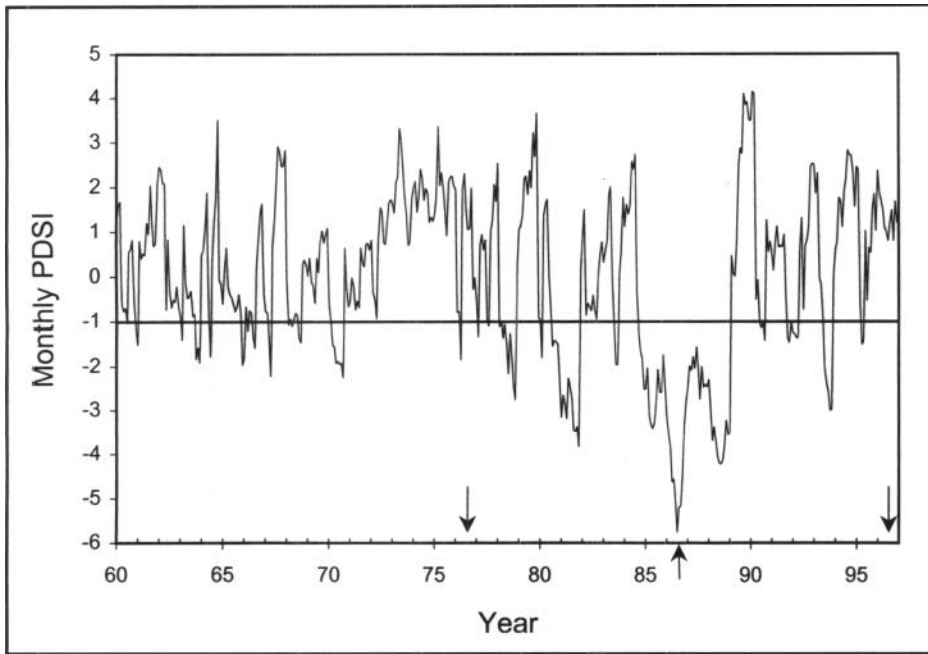


Figure 2. Monthly Palmer Drought Severity Indices for Division 1, Southern Mountains of western North Carolina, 1960-1996. Indices below the horizontal line indicate drought conditions. Arrows indicate dates of censuses of *Pinus pungens* at Looking Glass Rock study site.

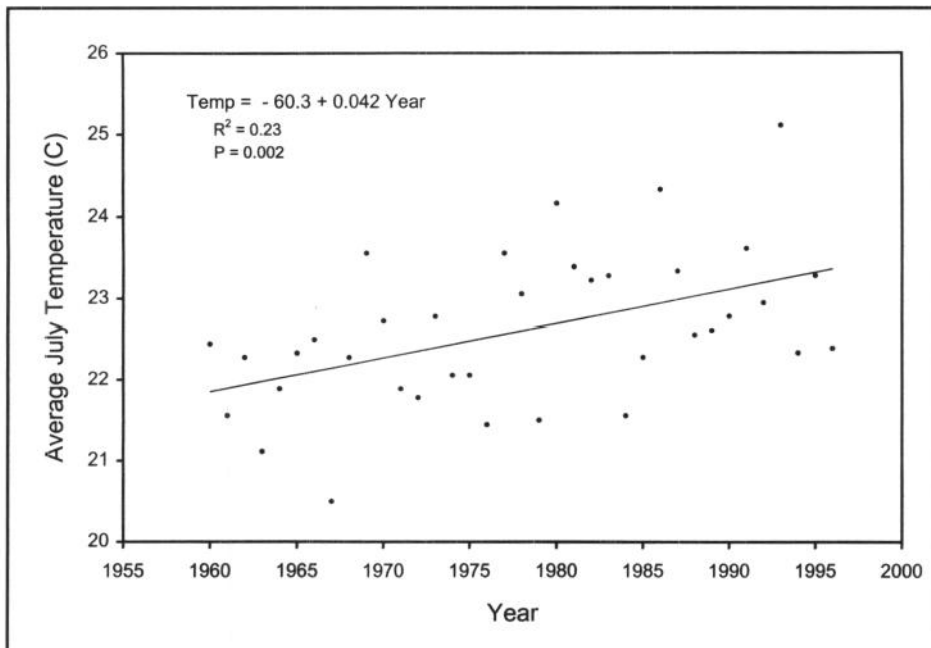


Figure 3. Average July temperature for Division 1 (Southern Mountains), North Carolina, 1960-1996.

er trees were aged by counting rings in increment cores taken near the base of the trees. I used a characteristic growth pattern created by droughts in 1925 and 1930 to cross-date cores (Hursh and Haasis 1931, Stokes and Smiley 1968). In June 1986 and 1996 I revisited each of the mapped

pinus and noted whether it had survived. In addition, I mapped and aged each pine seedling that had germinated and survived during the intervening decades.

In 1996 I investigated the effects of drought on tree growth by taking increment cores

from six study trees selected from across the study area. These trees ranged in size from 12 to 26 cm dbh and grew on sloping sites with shallow soil, where tree ring series tend to be more sensitive to changes in soil moisture. I took one core from near the base of each tree, avoiding upslope and downslope sides and areas near branches where ring patterns are likely to be distorted (Stokes and Smiley 1968). I dried the cores for a week, mounted them on wooden strips, sanded and polished them, and measured annual radial growth for 1980-1996 to the nearest 0.1 mm with an optical micrometer. I chose these years for analysis because they included a 17-year transition of PDSI that ranged from normal values to extreme drought and back to normal (Figure 2). I checked for missing rings by cross-dating tree cores, which was facilitated by a characteristic decline in growth during the years 1984-1986, when July PDSI values declined from moderately high to record low.

I standardized growth for each tree by fitting a quadratic curve to the annual growth increments of 1980-1996 with polynomial regression (Fritts and Swetnam 1989). I used a parabolic curve rather than a straight line to fit the data because annual growth declined from 1980-1986 and then tended to increase for the remaining years, in concert with the soil moisture index (Figure 2). For each tree, I divided the actual ring width of each year by the predicted value to calculate an index of growth, and then averaged growth indices for each year for the six trees (Fritts and Swetnam 1989). I used July PDSI as a representative indicator of soil moisture stress during the early to middle growing season, as suggested by Cook and Jacoby (1977), because the function used to calculate monthly PDSI includes moisture conditions from previous months. I checked the time series of growth indices and July PDSI values for serial autocorrelation with the Durbin-Watson test (Wesolowsky 1976), then used linear regression to analyze the growth indices as a function of July PDSI.

In 1977 and 1996 I studied seed dynamics of the population with identical protocol. I collected from one to five attached, sero-

tinous cones from each of three to five trees for each year of the preceding 11 years and tested viability of seeds stored in these cones (Barden 1979). I chose trees with the greatest abundance of cones. Older seeds were not available because cones had disintegrated or detached from the tree. Aging attached cones is feasible because only one whorl of cones is produced on a branch each year, and terminal bud scars are evident for several years. I heated each cone separately in an oven at 100°C until the scales opened, which usually required 1–2 minutes and could be discerned by a cracking sound. I then extracted the seeds, removed seed wings, discarded obviously aborted seeds, and planted seeds 1.7 cm apart in vermiculite in plastic trays. I watered the seeds once from below, covered them with cellophane, and kept them under continuous light at 21–25°C in a laboratory. As each seed germinated I re-moved the seedling without disturbing nearby seeds. Because cones of *Pinus pun-*

gens require 18 months to mature after fertilization (Mirov 1967), I assigned an age of 1 year to newly matured seeds and cones in figures and statistical analyses.

For each of the 11 years preceding both the 1977 and 1996 seed studies, I calculated average seeds per cone, then averaged the annual values for each 11-year period and compared the averages with a two-sample t-test. In addition, for each year preceding the two studies, I calculated the annual percent viability of seeds. I then used separate linear regression analyses for each time period to determine the change in viability with age of seeds stored in serotinous cones. Finally, for an overall comparison of viability of seeds stored in cones

during the two time periods, I used analysis of covariance

(AN-COVA) to compare the two regression lines (Sokal and Rohlf 1981). In 1977 and 1996 I also noted the age and condition (open or closed) of an additional 200 and 100 attached cones, respectively, to determine the percentage of cones of each age that had opened.

To quantify the total reproductive potential of the population over the two 11-year periods, 1967–1976 and 1987–1996, I calculated an annual index of released viable seeds by multiplying the annual average seeds per cone, the annual percent viable seeds, and the annual percent of cones open. I then averaged the

annual index values for each 11-year period and compared the averages with a paired t-test, with pairing based on age of seed.

RESULTS

Between 1976 and 1996 the *Pinus pungens* population produced new seedlings, despite the absence of fire (Figure 4), and during each of the two decades, the population of trees @ 10 years old increased (Figure 5). This increase was a consequence of both recruitment from the 0-to-9-year age class and high survival of older trees. For the 20-year period, 1976–1996, the survival rate for trees that had germinated before 1966 was 86%. During the same period, the youngest age class of pines declined by 92% (Figure 5). In 1976 the 0-to-9-year age class comprised 45% of the total population of 195 pines; by 1996 this age class comprised only 6% of the population. Overall, between 1976 and 1996, the entire population declined by 35% because of high mortality and low recruitment in the youngest age class.

During the period 1980–1996, annual radial growth of *Pinus pungens* was positively related to July PDSI (Figure 6; $F = 11.2$, $df = 1,15$, $P = 0.004$). Neither annual growth nor July PDSI was serially auto-correlated ($n = 17$, Durbin-Watson statistic = 1.8 and 2.2, respectively). In 1986,

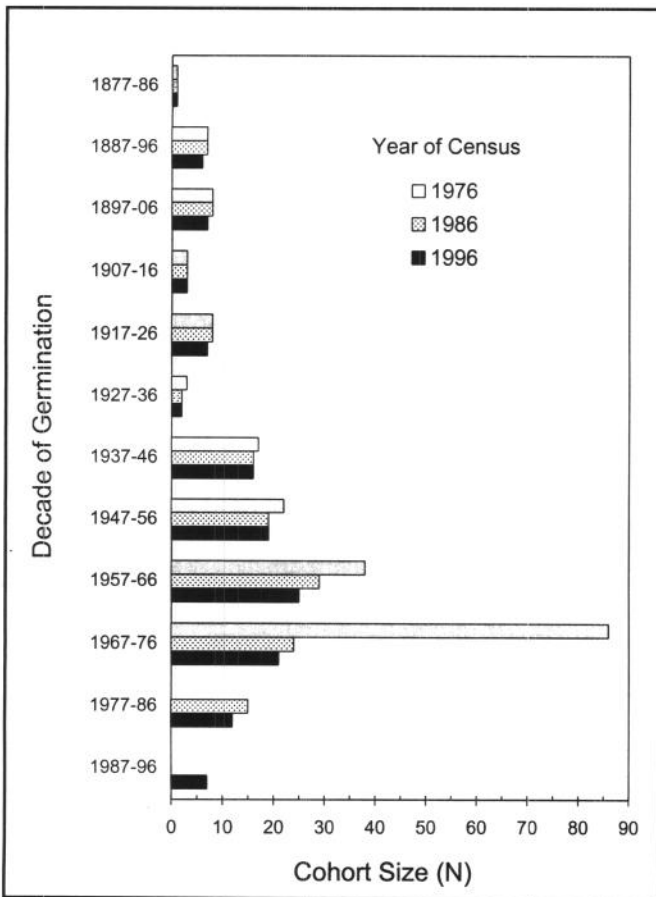


Figure 4. Age structure of the *Pinus pungens* population in 1976, 1986, and 1996, based on 10-year age-class cohorts.

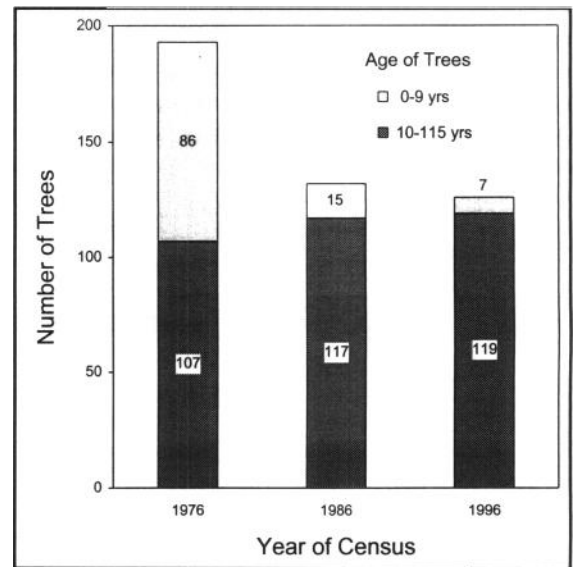


Figure 5. Age structure of the *Pinus pungens* population in 1976, 1986, and 1996, based on two age categories: 0–9 years and older trees (10–115 years).

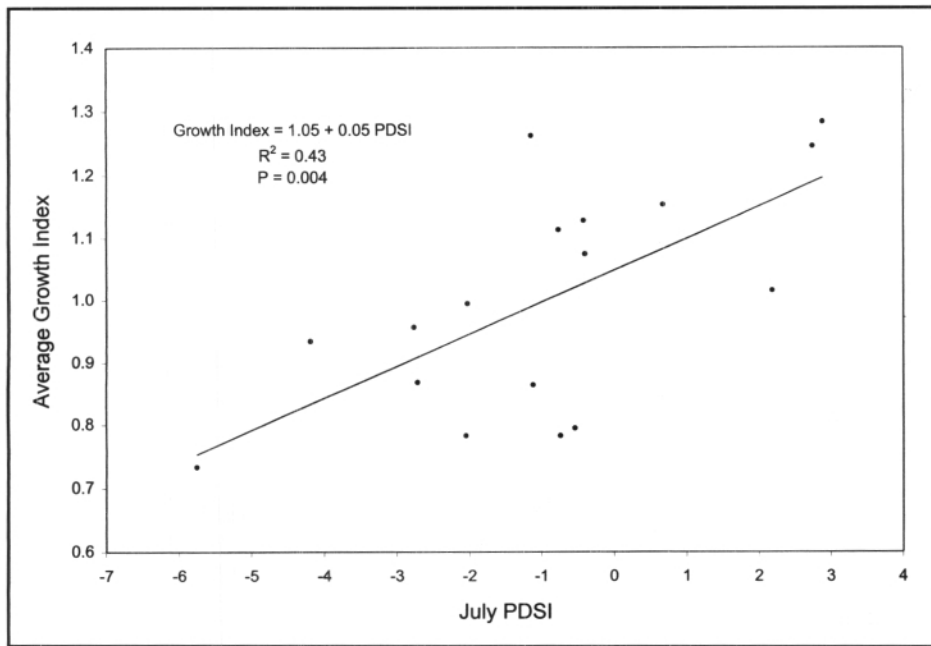


Figure 6. Average growth indices of six *Pinus pungens* individuals, as a function of July Palmer Drought Severity Index, 1980–1996.

when July PDSI was at its lowest point in history (-5.76), average radial growth for the six trees was 0.86 mm, which was 29% below the 17-year average of 1.21 mm year⁻¹. Overall, for each one-unit increase in PDSI, radial growth increased by 5%.

During the two 11-year periods preceding gennination studies in 1977 and 1996, the average numbers of seeds stored in serotinous cones were not significantly different (37 and 27 seeds per cone, respectively; $t = 1.4$, $df = 18$, $P = 0.18$). During both periods, seed viability declined significantly with seed age (Figure 7; for 1977, $F = 9.2$, $df = 1,9$, $P = 0.014$; for 1996, $F = 8.7$, $df = 1,9$, $P = 0.016$). The rates of decline were not significantly different for the two time periods ($F = 0.21$, $df = 1,18$; pooled slope = -2.6 percentage points per year). However, seeds maturing during 1967–1977 germinated at a higher rate than those maturing during 1986–1996 (ANCOVA adjusted mean germination rates = 32% and 18%, respectively; $F = 14.5$, $df = 1,19$, $P = 0.002$).

The temporal pattern of *Pinus pungens* cones remaining closed on trees differed between the two 11-year periods (Figure 8). In both 1977 and 1996, virtually all cones aged 1–2 years were closed. How-

ever, the two periods differed, in that, in 1996 nearly all cones aged 3–5 years were also closed, while in 1977, approximately 40% of cones aged 3–5 years were open. In 1977 the percentage of cones opened remained approximately 40% between ages 3 and 11 years, but, in 1996 there was

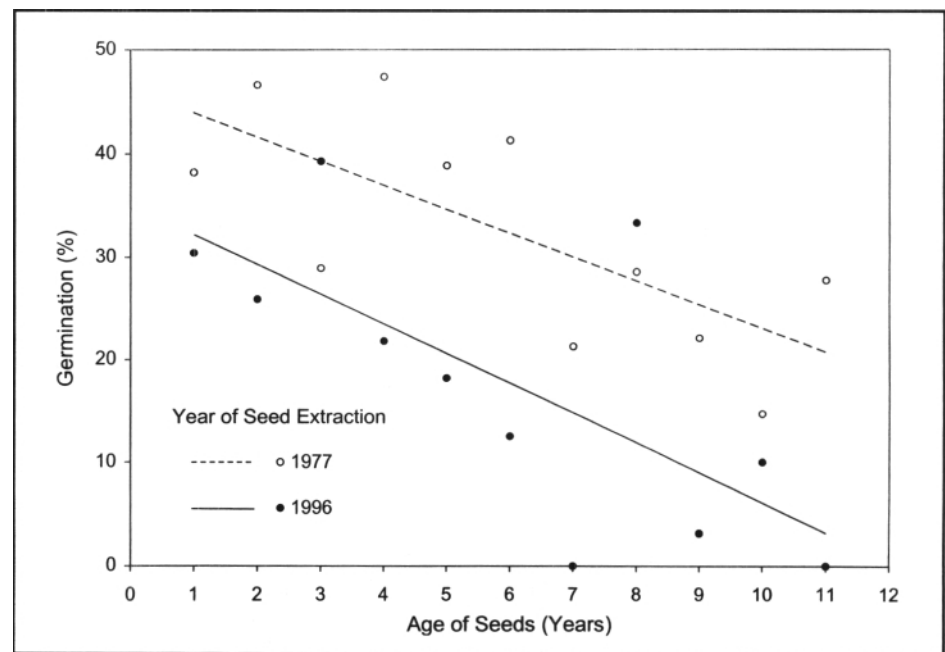


Figure 7. Germination of *Pinus pungens* seeds from serotinous cones aged 1–11 years, which were collected in 1977 and 1996.

more variation, with 40–80% of cones aged 6–11 years open. When the three indicators of reproductive potential were combined into a single index of released viable seeds, the average index for 1967–1977 was more than seven times greater than the index for 1986–1996 (Figure 9; $t = 3.19$, $df = 8$, $P = 0.013$). This large estimated differential in the indices of released viable seeds during the two periods was conservative, because cones were also more abundant on the trees in 1977 than in 1996 (pers. obs.).

DISCUSSION

Although the population of reproductive-age *Pinus pungens* (> 10 years) at this study site increased during the period 1976–1996, this increase may not continue during the period 1997–2006 unless survival and reproductive rates increase. Between 1976 and 1996 the age structure of the population changed from one with a large base in the young age classes, which is typical of a rapidly expanding population, to one with a small base in the young age class and a bulge in the mid-age class-es, which is typical of an aging or declining population (Figure 4). After the 1986 census, I predicted that recruitment would

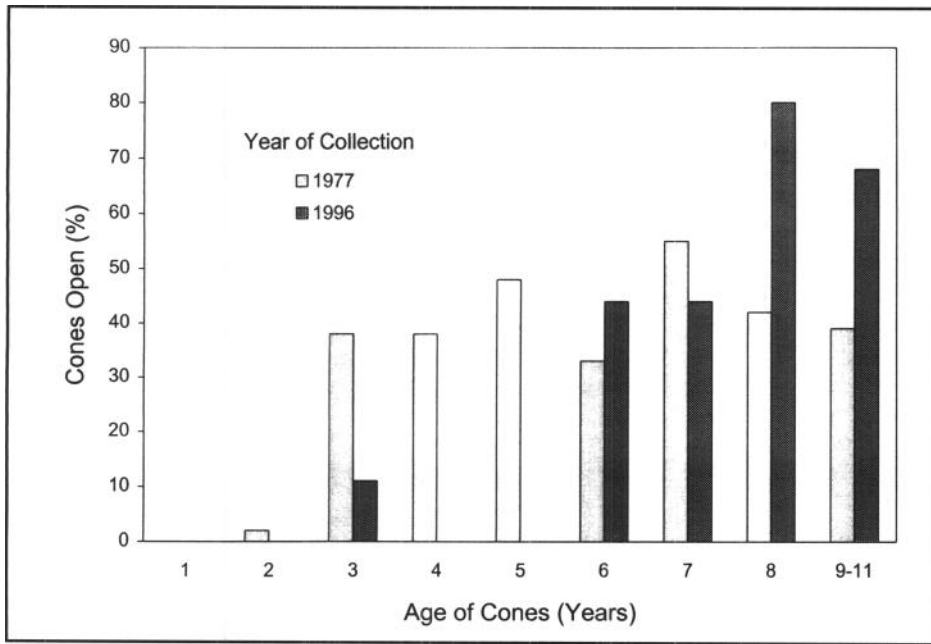


Figure 8. Percentage of *Pinus pungens* cones open while attached to trees, as a function of cone age (1–11 years), 1977 and 1996.

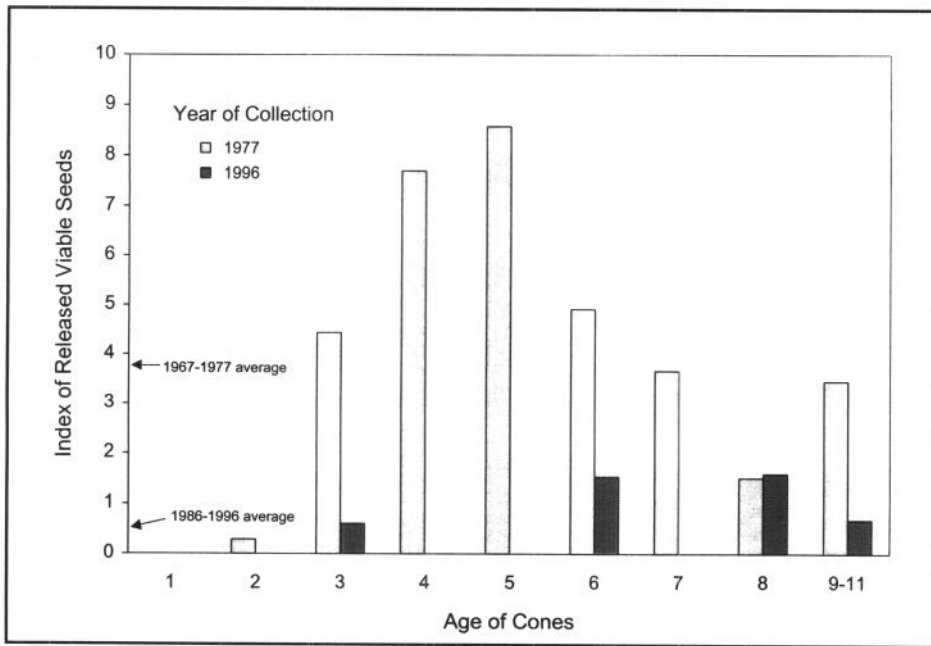


Figure 9. Indices of available, viable *Pinus pungens* seeds, as a function of cone age (1–11 years), 1977 and 1996. Arrows indicate averages of 3.8 and 0.5 for 1967–1977 and 1986–1996, respectively.

improve if precipitation returned to normal or above normal levels (Barden 1988). However, even though the PDSI was in the normal range or above during the years 1989–1996 (Figure 2), recruitment did not increase. Abrams and Orwig (1995) re-

ported an even more extreme failure in recruitment in a 320-year-old *Pinus rigida* stand growing on an extremely xeric rock outcrop site in southeastern New York. Although the population had surviving representatives from each of the previous

19 consecutive decades, 1780–1970, there were no recruits dating from the years 1970–1993. This failure of recruitment during 1970–1993 occurred despite above-normal precipitation.

Pedersen (1998) showed that the delayed effects of a severe drought may cause high mortality in oak stands for at least 10 years after the end of the drought. During 1989–1996 delayed effects of the extreme drought of the 1980s may have reduced production of viable *Pinus pungens* seeds on Looking Glass Rock (Figure 9). If drought was the cause of reduced recruitment and the benign climate of 1989–1997 continues, the size of the 0-to-9-year age class should be larger at the next census in 2006 than it was in 1996, unless the effects of the severe drought continue beyond 10 years. However, other factors, such as gradually increasing temperature (Figure 3), may also be responsible for poor recruitment during 1976–1996. High temperature may increase the rate of opening of serotinous cones (Williams and Johnson 1992) but may also reduce the production of viable seeds by desynchronizing pollen release and female strobilus receptivity or by inhibiting germination (Zobel 1969). High temperature (>28°C) may also reduce seedling survival by reducing root growth (Zobel 1969).

As the twenty-first century begins, conservation biologists are increasingly concerned that global climate change will reduce biological diversity (Delcourt and Delcourt 1998). Tree populations on extremely xeric sites are particularly well suited as indicators of climate change because they include both mature individuals, which can endure decades of inhospitable climate, and seedlings, whose survival rates are very responsive to climatic variation. Long-term monitoring of the *Pinus pungens* population on Looking Glass Rock may provide empirical confirmation of a predicted northward retreat of pine species in the southeastern United States (Iverson and Prasad 1998).

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Lawrence S. Barden, a Professor of Biology at the University of North Carolina at Charlotte, studies Piedmont prairie restoration, the federally listed endangered sun-flower Helianthus schweinitzii, and, at 10-year intervals, the demography of Pinus pungens.

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