Drought and Survival in a Self-perpetuating Pinus pungens Population: Equilibrium or Nonequilibrium?

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ABSTRACT: A 10-year follow-up study of recruitment and survival of table mountain pine *(Pinus pungens)* growing in shallow soil on a granite dome in western North Carolina showed that the population, which perpetuates itself without fire or other disturbance, has experienced long intervals of high survival and recruitment interrupted by brief episodes of low survival and recruitment probably caused by extreme drought. For these pines growing in shallow soil over bedrock, the Palmer Drought Severity Index was poorly correlated with episodes of low survival. A more appropriate drought index for the edaphic situation was the maximum number of consecutive rainless days in each 5-year age-class germination interval. Analysis of age-specific survivorship for the 1977-1986 decade showed that table mountain pines less than 30 years of age experienced lower survival rates during drought than older pines.

INTRODUCTION

In 1976 an unusual population of table mountain pine *(Pinus pungens* Lam.) was found growing on the rounded SW shoulder of Looking Glass Rock, a 1-km^2 granite dome near Brevard, in western North Carolina (Barden, 1977). The age structure of these pines, derived from increment cores, showed that this population was an edaphic climax which had perpetuated itself since the most recent fire in 1889 (Barden, 1977). Zobel (1969) had predicted that such a stand of *Pinus pungens* might be found on rock outcrops or shale slopes where hardwood species grow poorly. McIntosh (1950) found pine populations (*Pinus strobus, P. resinosa*, and *P. banksiana)* which, on the basis of size structure of the stands, appeared to be perpetuating themselves on sandstone and limestone bluffs in southwestern Wisconsin. However, the table mountain pine population on Looking Glass Rock is the first reported pine climax, based on known age structure and disturbance history, in the eastern United States (Barden, 1977).

In 1976 I interpreted the close fit of a log-linear curve to the age-structure data as evidence that the population was approaching equilibrium, that is, having relatively constant and approximately equal mortality and recruitment rates. Harper and White (1974) suggested an expanding population as an alternative interpretation for such data, but this explanation seemed unlikely because of the number of dead pines found in varying stages of decomposition (Barden, 1977). The carrying capacity of the site appeared to be set by the availability of pockets of soil deep enough to support drought-tolerant pines but too shallow to support hardwoods during summer droughts (Barden, 1977).

In 1986 I recensused the same trees, using detailed maps and fixed-point photographs from the 1976 study to relocate all members of the population. The purpose of the new study was to determine whether the population continued to exhibit the log-linear age structure after 10 additional years of recruitment and mortality. My reinterpretation of the cohort data, based on 5-year rather than 20-year age classes and a more critical analysis of weather records, differed sharply from conclusions of the earlier study, reflecting a new understanding of the importance of sporadic high morality in the population dynamics of the stand.

STUDY AREA AND METHODS

Looking Glass Rock is an oblong granite dome, 2.0 km by 0.5 km, which rises 300 m above the surrounding terrain to a maximum elevation of 1200 m. It is located 10 km NW of the nearest permanent weather station at Brevard, North Carolina, where the elevation is 660 m and the average annual precipitation is 167 cm, distributed relatively evenly throughout the year. The sides of the dome are exposed granite, nearly vertical in slope. A cap of soil on top of the dome supports an oak-hickory (*Quercus-Carya*) forest 75 ha in area. Around the edges of the forested cap, on the rounded shoulders of the dome, are shallow pockets of accumulated soil in cracks and depressions in the granite. The shallowest pockets support only herbaceous plants, but stunted table mountain pines (<10 m tall) survive where the soil depth is 10-40 cm. Growing with table mountain pine, though less abundant, is red cedar (*Juniperus virginiana* L.).

In 1976 I mapped the edge of the forested cap of soil on Looking Glass Rock from aerial photographs and then searched in the field for pine populations suitable for sampling. Trees were included in the 1976 analysis only if they grew in pockets of soil that were separated by exposed rock from the main cap of soil. This requirement insured that growing sites were extremely xeric, without undetected seepage of ground water into them. Depth of soil to bedrock was measured near each tree with a graduated iron probe. Permanent benchmarks were located on the rock, and each tree in the stand, including seedlings, was accurately mapped at a scale of 1:200 by measuring azimuth, distance and slope angle of the tree from the benchmarks. In addition, more than 150 photographs were taken showing locations of benchmarks and trees.

Seventy-eight trees which had been mapped and aged in 1976, but excluded from the earlier population analysis because they were growing in soil that was connected to the main cap of soil on Looking Glass Rock, were included in the 1986 analysis for three reasons: they were growing in shallower soil, on average, than trees included in the 1976 analysis (17.9 vs. 20.0 cm); including them did not alter the conclusions of the earlier study; and adding them to the 1986 analysis increased sample size by two-thirds. Mortality during 1977-1986 was determined by relocating each tree and noting its condition. New recruits during 1977-1986 were added to the maps for future demographic studies.

RESULTS AND DISCUSSION

In the 1976 study, the age structure was based on 20-year age classes, with one age class (40-59 years, germinated 1917-1936) deviating from the excellent fit of a log-linear curve:

Age class (Years):	0-19	20-39	40-59	60-79	80-99
Survivors, 1976:	126	37	11	12	8

($R^2 = 0.85$ with all years included; $R^2 = 0.96$ excluding 1917-1936, slopes of both lines significant at the $P = 0.05$ level). A severe drought in 1925, when total precipitation from April to August was only 7 cm (15% of normal), followed by a second drought in 1930, was reported as the probable cause of the small 1917-1936 age class (Barden, 1977).

In 1986 the age structure of young trees (<20 years old) differed sharply from that observed in 1976, with low survival of the 1967-1976 cohort and poor recruitment into the 1977-1986 cohort (Fig. 1, top). In 1976 there were 86 trees in the 0-9 year age class (44% of the 1976 population); by 1986 only 17 of these were still alive (20% survival), and the new 0-9 year age class contained only 11 trees (9% of the 1986 population; Fig. 1, top). The total population declined from 194 to 120 during the 1977-1986 decade.

It seemed likely that this decline was related to severe droughts of the 1980s. However, the Palmer Drought Severity Index (Karl and Knight, 1985), which incorporates the preceding month's Index with the current month's rainfall and average temperature to provide a cumulative measure of drought severity, proved inadequate as a correlate in this study. For example, during 1986 when the most severe drought in history lowered the Index below -6.00 in the southern mountain region of North Carolina (U.S. Department of Commerce, 1986), there were no deaths from May to October among the table mountain pines, including 11 new recruits which were less than 9 years in age.

A possible explanation for the incongruity between the low Palmer Drought Severity Index and high survival of pines during the 1986 drought involves rain water funnelling

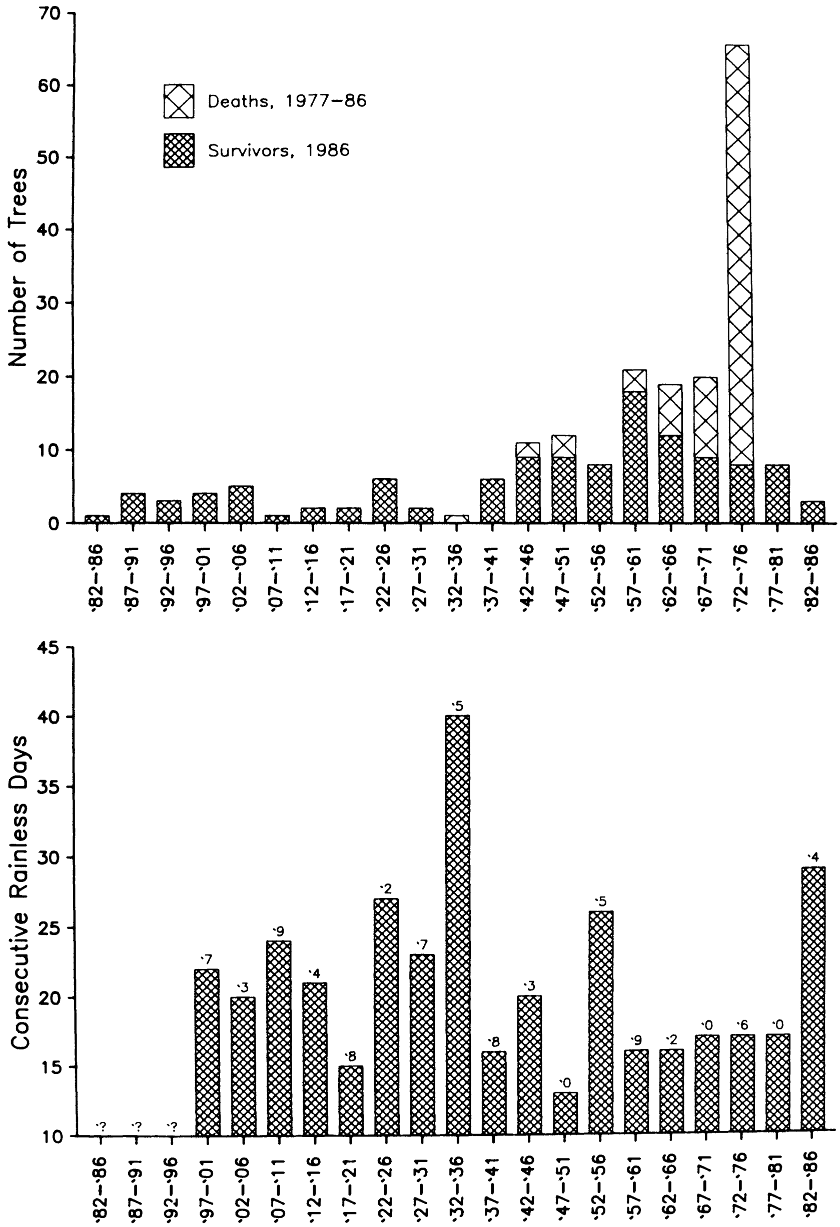

Fig. 1.—(Top) Germination dates of table mountain pines, 1882-1986 and survivorship, 1977-1986. (Bottom) Maximum rainless period during each 5-year interval. The year of occurrence is shown above each bar

on the rock. In 1986 I observed water from a short afternoon thundershower of ca. 1 cm collecting on relatively large areas of exposed granite (20-100 m^2), funnelling into the small pockets of soil supporting one or more pines and recharging the soil moisture. This observation suggested that a more ecologically meaningful index of drought experienced by the table mountain pines would be the number of consecutive rainless days above some threshold.

Accordingly, weather records from 1897-1986 for Brevard, North Carolina, were searched for all rainless periods of 10 or more consecutive days from April through September. During 1986 the longest rainless period was 18 days from 11-28 June, apparently not long enough to kill the drought-resistant pines. For all years the longest rainless period was 40 days in 1935, followed by 29 days in 1984 (Fig. 1, bottom). In addition, there were 3 other rainless periods of 24 days or more, in 1909, 1922 and 1955. These five droughts corresponded, with one exception, with 5-year cohorts that are small relative to surrounding cohorts (Fig. 1, top). The exception was that the 1922 drought occurred at the beginning of the 1922-1926 interval and therefore corresponds to the small 1917-1921 cohort rather than the larger 1922-1926 cohort.

In contrast to the 60-year interval 1897-1956 when long rainless periods occurred every 10-20 years, the 28-year interval 1956-1983 had no rainless periods longer than 17 days (Fig. 1, bottom). These 28 years of benign weather probably account for the large 1957-1976 cohort found in 1976, and the 29-day rainless period in 1984 explains the low survival of the 1957-1976 cohort revealed in 1986 (Fig. 1, top). Undoubtedly, some seedlings which germinated between 1976 and 1984 also died in the 1984 drought, but these uncensused recruits would not affect the conclusions of this study.

Despite the low survival of the 1957-1976 cohort to 1986 (37%), all of the trees older than 40 years survived the 1984 drought (Fig. 1, top). For trees 20-40 years of age in 1976, survival from 1976 to 1986 was 80%. Apparently, most of the trees that survived the 26-day drought in 1955 were also able to survive the 29-day drought in 1984.

During the years of benign weather, 1956-1983, many new recruits were able to survive on small pockets of soil or on pockets occupied by established trees. However, many of these sites had inadequate water reserves for recruit survival during the 29-day rainless period in 1984. Five such cycles of survival during the past century have apparently shaped the age structure of table mountain pine on Looking Glass Rock. The question of whether this population is in equilibrium in the sense of equal mortality and recruitment rates must be answered negatively. But neither does it fluctuate unpredictably. Rather, the two censuses of 194 and 120 trees may define a predictable ceiling and floor (*sensu* Strong, 1986) between which the population fluctuates in an unpredictable way.

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