AIR TEMPERATURE, HEAT SUMS, AND POLLEN SHEDDING PHENOLOGY OF LONGLEAF PINE[1]

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Abstract. Between 1957 and 1966, pollen shedding by longleaf pine (*Pinus palustris* Mill.) in southwestern Alabama peaked at dates ranging from February 23 to April 3. January 1 and 50°F was the combination of starting date and threshold air temperature that minimized annual variations in heat sums before the trees flowered. The heat sum required for peak pollen shedding declined as *the* season advanced. The regression Y = 19009 -89.26X, *in* which Y is the degree-hour heat sum above 50°F and X is days from January 1 through date of peak pollen shedding, accounted for nearly all observed annual variations in peak date. For the data from which the regression was computed, deviation of observed from expected date of peak pollen shed averaged 0.3 day. For eight subsequent observations, including two in North Carolina and one in northern Alabama, the deviation averaged 1.6 days.

INTRODUCTION

Flowering by the four major southern pines follows a consistent pattern (Dorman and Barber 1956), with slash pine (*Pinus elliottii* Engelm.) first, followed by longleaf (*P. palustris* Mill.), loblolly (*P. taeda* L.), and shortleaf pine (*P. echinata* Mill.). In the Gulf *States* (Wakeley 1954), slash pines normally shed their pollen in late January or early February, longleaf and loblolly pines in March, and shortleaf in April. A number of investigators have concluded that air temperature during the days or weeks before flowering is the major factor governing the time of pollen shedding by pines (Fielding 1957, Marcet 19.51, Millett 1944, Minshall 1947, Scamoni 1938, Snyder 1961).

Pollen shedding by longleaf pines has been observed for 15 years on the Escambia Experimental Forest in the Coastal Plains of southwestern Alabama, 2 years in the fall-line sandhills of North Carolina, and 1 year in the Mountain Province of northern Alabama. Southwestern Alabama data for the 10 years from 1957 through 1966 were analyzed to explore the relationship between air temperatures and longleaf flowering, and to determine the degree to which this factor may account for annual variations in the date of peak pollen shedding.

In studies of heat effects upon plant development, heat is usually expressed in degree-hours or degree-days above a biologically established threshold temperature. The heat unit system was developed in the eighteenth century, and most subsequent development and applications of the method have been in agriculture (Holmes and Robertson 1959). In most research, the heat sum required to attain a given stage of development has been assumed to be a fixed value, the "thermal constant," although actual constants have rarely been found in phenological studies. Heat sums associated with a phenological event for a given species normally vary from place to place, and from year to year in the same place. Difficulties in selecting the proper threshold temperature and starting date for heat accumulation have often been blamed (Schnelle 1955). Also, plant growth-temperature relationships may be nonlinear, seasonally variable, and affected by other environmental factors (Wang 1960).

A common departure noted for the thermal constant was a decrease with increasing altitude or latitude. For example, Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) in a valley bottom at an elevation of 1,000 ft needed from 800 to 900 degree-hours above 50°F for pollen shedding, while at elevations of 2,500 to 3,500 ft, pollen dispersal commenced after exposure to only 400 degree-hours (Ebell and Schmidt 1964). Phillips (1922) noted that fruit trees apparently required more heat before blooming in the South than in the North. Longleaf pines in the present study had an average of 9,862 degree-hours (above 50°F) between January 1 and peak pollen shedding in North Carolina in 1967 and 1968, while values for the same two years in southwestern Alabama averaged 11,341 degree-hours.

Such phenomena have been explained through "Linsser's law" (Waugh 1898, Abbe 1905), which states that a given stage of development is reached in a constant proportion of the growing season. A correction factor, total yearly heat sum or growing season heat sum for the locale, was applied as a divisor to the observed heat sum associated with a phenological event. The resulting proportional values were more nearly constant. Presumably, this procedure accounted for differences resulting from genetic adaptation of a species to varying climates, Sarvas (1967) proposed the same approach when he hypothesized that, within a species, subpopulations of trees are adapted to local climates and will all reach a given physiological phase of development at a constant percentage of the local average annual heat sum.

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This approach does not explain annual variation in heat sums for a species at a single location (Bradford 1922). A number of studies have indicated that the heat sum required for a particular plant development phase is less in a cool than a warm season (Katz 1952, Lana and Haber 1952, Schnelle 1955). If so, the heat sum should also be less in a cool than in a warm climate. For example, corn from a single genetic strain required a smaller heat sum to mature in Maine than in Virginia (Magoon and Culpepper 1932). This result suggests that genetic variations within a species may often be a comparatively minor factor in the observed geographic differences in springtime flowering phenology. Fow!er (1965) reported that in 1961 there was a difference of no more than 2 days in onset of pollen shedding among red pines (*Pinus resinosa* Ait.) in a planting representing nine climatic regions.

Schneider (1952) stated that year-to-year variations in the heat sum required to complete a plant development phase can be explained on the basis of time dependence. Thus, larger heat sums will be required for the same effect in early than in late flowering years. Total heat sum will be related to total development time. This hypothesis was also tested in the present study.

METHODS

Pollen shedding

Pollen traps like those described by Grano (1958) were exposed in a standard weather instrument shelter on the Escambia Experimental Forest (lat. 31° 00' N, long. 87" 05' W) at or just before the beginning of pollen shedding. Traps were changed two to four times weekly. The 'date and time of exposure and recovery of each trap were noted and duration of exposure recorded to the nearest 1/ 10 hour.

The density of longleaf pine pollen 'deposited on each trap was estimated by counting all grains under each of 10 systematically distributed 100× microscope fields per trap. Counts were converted to the average number of pollen grains per cm^2 and divided by the number of hours of exposure to give pollen deposition rate in grains per cm^2 per hour. Similar information was gathered in longleaf stands in Moore County, North Carolina (lat. 35° 16' N, long. 79" 17' W), in 1967 and 1968, and in Coosa County, Alabama (lat. 33" 06' N, long. 86" 19' W), in 1971.

Climatic data

Temperature records on the Escambia Experimental Forest are available only since February 1964 when a hygrothermograph was installed. I obtained local weather 'data covering the entire period of study from official Weather Bureau records for the Brewton, Alabama, weather station which is about 6.1 km north-northeast of the experimental area. Weather data in North Carolina came from the official weather station at Sanford, about 23 km northeast of the sampled stand. Data for northern Alabama came from a hygrothermograph maintained within the sampled stand.

Cumulative heat sums above the effective base or threshold temperature for flower development are a good expression of the temperature factor. The lack of thermograph records prevented direct computation of degree-hour heat sums, but I estimated sums from daily maximum-minimum temperatures by Lindsey and Newman's (1956) method. I tested the applicability of this method to winter temperature patterns near study areas by comparing degree-hour heat sums (above 50 "F) from a thermograph record with estimates derived from 'daily maximum-minimum temperatures. Comparisons included the months of January, February, and March for each year from 1965 through 1970, excluding only March 1965. All but three of 17 estimated monthly degree-hour sums were within 5% of true values, and 10 were within 2%. For the first 3 months (January through March), estimated values ranged from 1.8% high to 4.9% low and averaged 0.9% low.

Regression coefficients expressing the relationship of estimated over actual degree-hours for each of the 6 years ranged from 1.01 to 1.08, and coefficients of determination (r^2) from 0.94 to 0.97. Estimates of degree-hours tended to be low for low daily heat sums, and high for high values. The use of heat sums estimated from daily maximum-minimum temperatures instead of actual values from a thermograph trace is a source of error. However, the magnitude of this error in sums 'accumulated over a period of 8 or more weeks sbould be small.

The distance between stations providing temperature data and forest stands in which pollen was collected also represents a source of error. The magnitude of this error was checked by comparing monthly winter temperatures on the Experimental Forest from 1965 through 1970 with concurrent data from the Brewton weather station. Daily maximum temperatures on the forest averaged 2.4°F lower than those at the Brewton weather station, but minimum temperatures averaged 1.2°F higher. As a result, monthly mean temperatures at the two locations were fairly close, averaging 0.6°F lower on the forest. Year-to-year variations in differences between the two locations precluded use of a constant correction term.

Analyses

The analysis was 'designed to answer three questions: (1) What is the apparent threshold or base temperature for strobilus development? (2) What is the best starting date for accumulating heat sums? (3) Is the heat sum a constant?

In an initial screening, daily temperatures from the Brewton weather station were processed by computer to provide degree-hour heat sums through day of peak pollen shedding for all combinations of 12 starting dates (lo-day increments from November 1 through February 19) and 6 base temperatures (30°, 40°, 45°, 50°, 55°, 60°F). For each combination, I obtained mean annual heat sum and standard deviation. Assuming that the heat sum required for flowering might be related to development time, a regression of total heat sums over time, in days, from selected starting dates to peak pollen shed was also coonputed for each group. A regression and its standard error supplanted the mean and standard deviation for a given combination if the regression significantly (5-% level of probability) reduced variance in the heat sum. Mean, standard deviation or standard error as 'appropriate, and coefficient of variation were obtained for each of the 72 lo-year (1957–1966) groups.

After screening, I made similar analyses in the area of minimum residual variance. Included were all combinations of 10 starting dates (December 27 through January 5) and 14 base temperatures (41" through 54 °) .

The analyses were made to find the combination of starting date and base temperature that minimized annual variation in total heat sums to peak pollen shedding by longleaf pine. A major problem was selection of an effective method to evaluate the results. Neither standard deviation nor coefficient of variation alone is an adequate criterion for comparisons of residual variability among heat sums derived from different combinations of base temperatures and starting dates. Changing either starting date or base temperature will alter population characteristics by changing the size of group means. Statistical problems involved with such comparisons were discussed by Van der Bijl (1956).

Beyond a certain point, progressively lower base temperatures or later starting dates result in increasing heat 'sums with later flowering dates. This effect has been recognized before (Shelford 1930, Artz and Ludwig 1949, Schnelle 1955, Arnold 1959), and, when a termal constant was 'assumed, it was considered helpful in identifying incorrect base temperatures or starting dates.

The best starting date at a single base temperature can be estimated by minimizing standard deviation or standard error. A reliable 'determination of the effective base temperature for flower development is more difficult. Heat sums from different base temperatures for a single starting date are closely correlated. As the base temperature drops, group means increase, but the effect on variance progressively decreases. Analyses may provide 'some indications of the actual base temperature. A rather sharp increase in variance, in terms of coefficient of variation, can be expected as the selected base temperature rises above the effective base, because increasingly larger amounts of effective heat accumulations are being omitted from the sums. Coefficient of variation can be expected to decline at a relatively uniform rate with increments below the effective base temperature because of a progressive increase in mean values with little change in variance.

RESULTS

In 15 years of observation on the Escambia Experimental Forest, pollen shedding by longleaf pine peaked as early as February 23 and as late as April 3, a difference of 39 days. The average peak date was March 20, and the standard deviation was 10.3 days.

For all base temperatures initially screened, the starting date with the smallest residual variance was December 3 1 (Fig. 1). After December 3 1, residual variance increased despite a continuing decline in mean values. A secondary minimum consistently appeared with the November 21 starting date, after which residual variance increased again before declining to the December 31 low. Residual variance also generally declined as base temperature increased, but this change may be largely due to smaller mean values.

For most starting 'dates, lowest coefficients of variation were reached at the lowest base temperature, 30°F (Fig. 2). This result reflects the action of increasing mean values with proportionately smaller increases in variance. For the December 31 starting date, however, variation began to decline after 40°F and reached a low at 50°F. At the date-temperature combination of December 31 and 50°F, standard error amounted to 320 degree-hours and coefficient of variation 2.6%.

Screening analyses, therefore, indicated that the

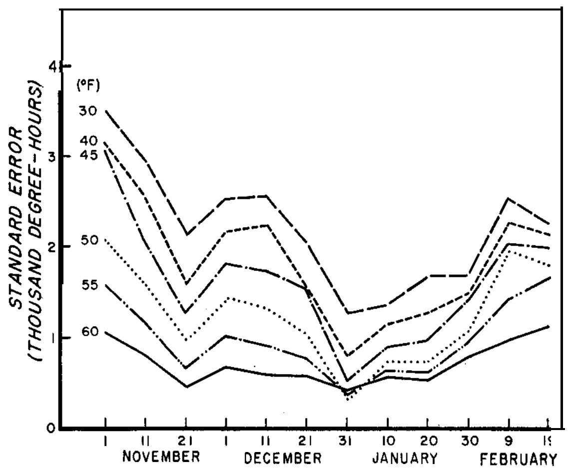

FIG. 1. Effect of starting date on standard deviation-standard error of degree-hours to peak pollen shedding for each of six base temperatures.

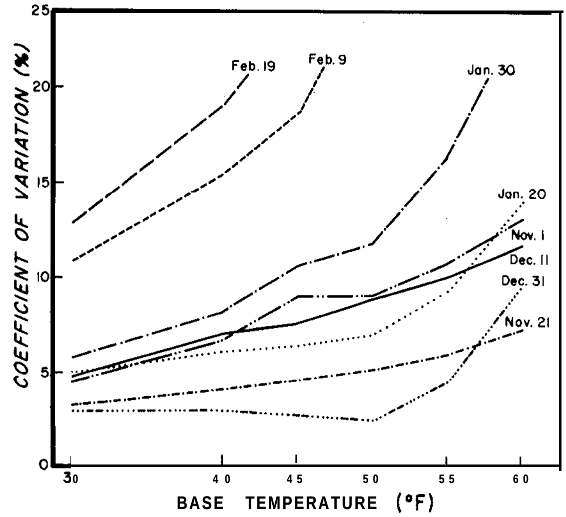

FIG. 2. Effect of base temperatures on coefficient of variation of degree-hours to peak pollen shedding for eight selected starting dates.

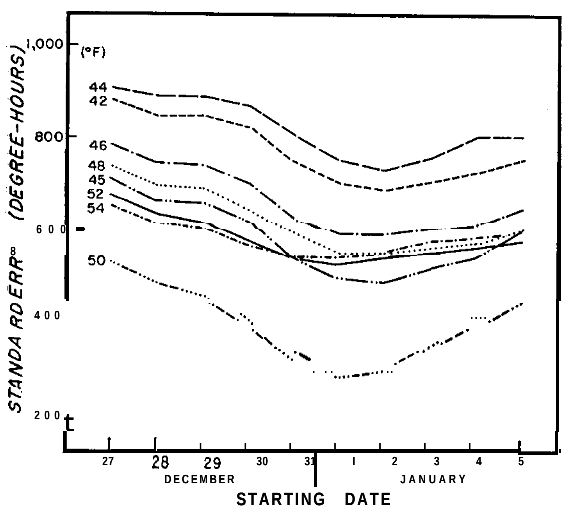

FIG. 3. Effect of starting date on standard deviation-standard error of degree-hours to peak pollen shedding for eight selected base temperatures near 50°F.

effective starting date and base temperature were somewhere near December 3 1 and 50°F. Further analyses included all combinations of the 10 starting dates from December 27 through January 5 and the 14 base temperatures from 41" through 54°F.

January 1 and 50°F was the best combination. That starting date minimized standard error (Fig. 3). The general upward trend of coefficients of variation with increasing base temperatures dipped somewhat at 45° but dipped considerably more at 50°F (Fig, 4).

Results indicate that the development of staminate strobili of longleaf pine is largely controlled by available heat in winter, the best expression of which was degree-hour heat sums above 50°F accumulated from

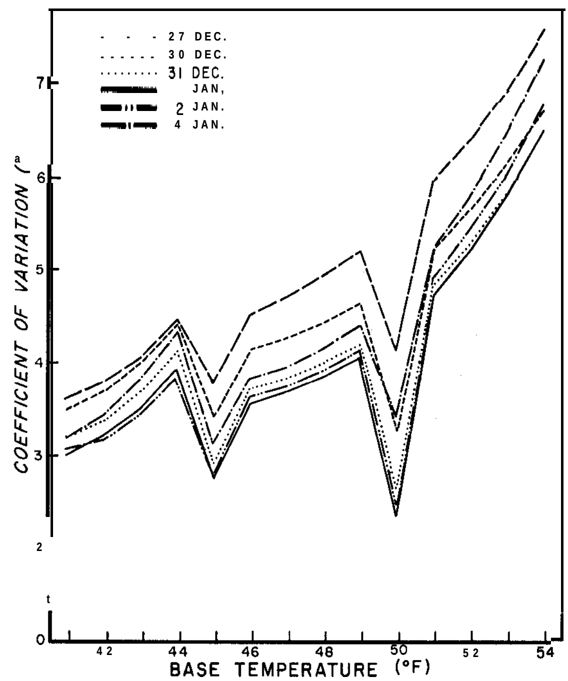

FIG. 4. Effect of base temperatures on coefficient of variation of degree-hours to peak pollen shedding for six. selected starting dates.

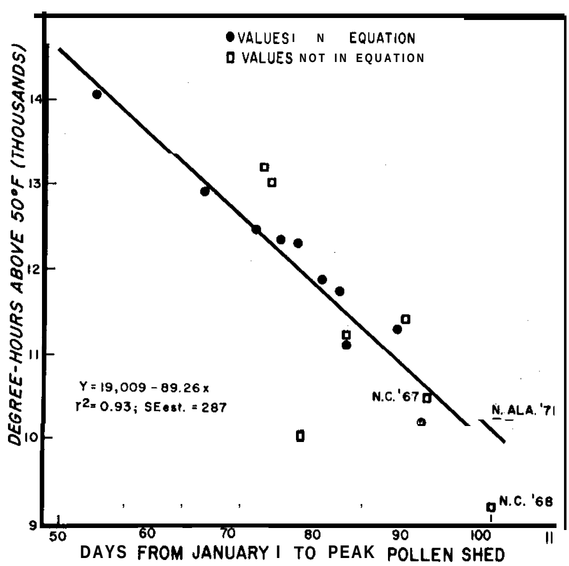

FIG. 5. Decline in heat sums to peak pollen shedding with later flowering dates.

January 1. The heat sum required to ripen staminate strobili was not constant but declined as development time increased. The regression expressing this relationship is: Y = 19009 – 89.26X, where Y is the degree-hour heat sum above 50°F from January 1 through day of peak pollen shedding and X is time, in days, for the same period (Fig. 5). The coefficient of determination (r^2) was 0.93, and the coefficient

TABLE 1. Comparisons of observed heat sums and time to peak pollen shedding by longleaf pine with expected values derived from regression

Date of peak pollen shedding	Degree-hours[a] from January 1 through day of peak pollen shedding			Time of peak pollen shedding in days from January 1		
	Expected	Observed	Difference	Expected	Observed	Difference
Escambia Experimental Forest, Alabama						
February 23, 1957	14189	14060	-129	55	54	−1
April 3, 1958	10708	10219	-489	94	93	-1
March 22, 1959	11779	11904		81	81	0
March 30, 1960[b]	10975	11335	+360	90	90	0
March 14, 1961	12493	12483	-10	73	73	0
March 8, 1962	13028	12941		67	67	0
March 18, 1963	12047	12313	+266	78	78	0
March 24, 1964[b]	11511	11156		85	84	−1
March 17, 1965	12225	12358	+133	76	76	0
March 24, 1966	11600	11786	+186	83	83	0
March 15, 1967	12404	13195		73	74	+1
March 31, 1968[b]	10886	11432	+546	90	91	+1
March 25, 1969	11511	11249	−262	86	84	−2
March 26, 1970	11422	10021		89	85	−4
March 16, 1971	12314	13041	+727	74	75	+1
Moore County, North Carolina						
April 4, 1967	10618	10537	-81	94	94	0
April 9, 1968[b]	10083	9187	-896	104	100	−4
Coosa County, Alabama						
April 12, 1971	9904	10249	+345	102	102	0

[a]Above 50°F.
[b]Leap years, extra day between January 1 and flowering date.

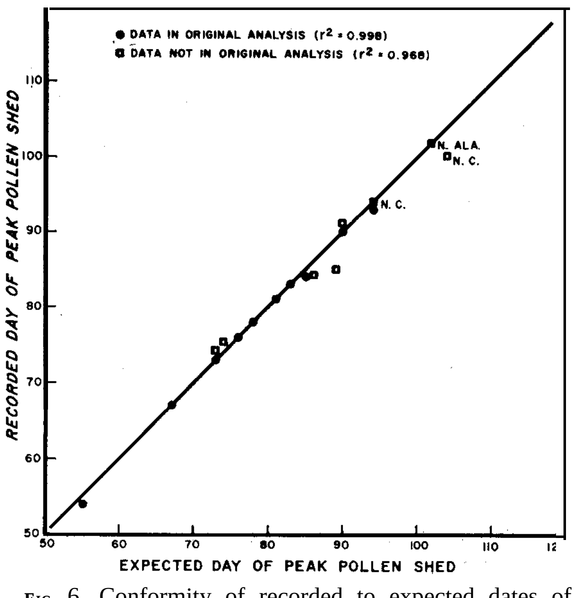

FIG. 6. Conformity of recorded to expected dates of peak pollen shedding by longleaf pine.

of variation 2.4%. Observed values for all years of record are shown with the regression.

The relationship between time and heat sums can also be expressed as a regression of the former over the latter. Because of the high degree of correlation between the two, however, the form of expression has very little effect on the relationship.

The heat sum-time regression was tested on the data from which it was derived and also on data from other areas and later years. Daily degree-hour heat sums experienced each year were accumulated from January 1 and plotted. The point of intersection of this accumulation with the regression line defines both the expected day and heat sum for peak pollen shedding that year. These expected values were determined for all years of record, and compared with observed values (Table 1) . Deviations of observed from expected degree-hour heat sums ranged from 10 to 1,400, averaging 214 degree-hours for the 10 years in the analyses, and 631 for the remaining 8. However, a single day oan have over 600 degree-hours, so much of the difference could be due to the heat sum added on the final day. Differences between observed and expected dates of peak pollen shed were remarkably small, even for those years and locations not included in the analyses (Fig. 6). Shedding peaked on the expected date in 7 of the 10 years included in the regression, and was 1 day early in the remaining 3. The peak day was also recorded on or within 1 day of the expected date in five of the eight subsequent observations. It was 4 days early in North Carolina in 1968 and on the Experimental Forest in 1970.

DISCUSSION

Apparently all or most of the heat above 50°F occurring on and after January 1 promoted the development of staminate strobili of longleaf pine. Why this should be the significant date is not clear. Perhaps a certain duration or degree of cold must be experienced before strobili will develop, and this was the average date by which the requirement was met.

What about the secondary minimum at the November 21 starting date? The increase in variance with progressively earlier starting dates consistently stopped during the first week in December and reversed during the last 10 days in November. The pattern suggests that staminate strobili development is promoted by temperatures above 50°F during a comparatively short time in late November and early December. During this period staminate flower buds emerge from the bases of vegetative buds. In 1968 some flower buds could be seen as early as November 27, and by December 5 had emerged on 80% of the flower-bearing shoots examined.

A decline in heat units required for peak pollen shedding with progressively later flowering dates is indicated by study results. The thermal requirement for flowering apparently is not constant, but variable, depending on total time for development. A linear form for this relationship was assumed for the analyses. However, it is possible that the heat sum over time relationship may actually be a curve, with a slope increasing toward the left as development time becomes progressively limiting, and diminishing toward the right as minimum required heat sum succeeds time as a limiting factor. For the range of values acquired from field observations, the linear expression of the relationship appears to be adequate.

The relationships between heat sums, time, and development of longleaf pine strobili suggested by results reported here agree well with Schneider's (1952) hypothesis of time dependence. A single regression accounted not only for year-to-year differences in beat requirements for flowering at a single location, but also 'for the latitudinal differences observed. Apparently, a larger than normal heat sum is needed to force early pollen shedding by longleaf pine, while an extended period of development will reduce total heat requirements. A similar relationship will probably apply to other plant species whose flowering is sequentially linked with that of longleaf pine.

Biological mechanisms behind the empirical relationships developed here are not clear and will require further study. Probably a series of complex physiological-environmental interactions are involved. On the surface, it seems that the time-heat sum relationship could result from either or both of two factors: a lower efficiency of heat utilization (slower development rate per unit of heat) early in the winter, or a base or threshold temperature for development that is relatively high early in the season and declines with time.

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