# Height Growth for Loblolly Pine Provenances in Relation to Photoperiod and Growing Season[1])

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## Introduction

In 1953 we started a study with loblolly pine (*Pinus taeda* L.) to assess the role of photoperiod in controlling the phenological behavior of the species. Would photoperiod be important in controlling plant behavior at latitudes of 30° or less where the maximum seasonal variation in photoperiod is less than two hours, or would seasonal variation in temperature or other factors prove more important?

Since the original measurements were made, other researchers have shown that photoperiod is a major factor in control of growth and phenology of southern pine (Allen and McGregor, 1962). However, a large number of geographic sources were used in this study and measurements were made on individual trees for three years. Statistical analyses show effects of daily rate of growth, frost free season, latitude and longitude of origin, initial size and other factors on the total yearly growth.

## Material and Methods

We acquired 31 lots of seed from widely dispersed parts of the geographic range of the species (*Table* 1). Philip C. Wakeley of the Southern Forest Experiment Station supplied 12 collections. The frost-free season of each region of the collection was estimated from the U. S. Department of Agrioulture Yearbook, "Climate and Man". Whenever possible, we acquired seed from several trees per locality and kept the seed from each tree separate. All seed was planted the same year in a uniform seed bed.

Two uniform experimental growth plots in the Austin Cary Memorial Forest near Gainesville, Florida were planted with rows of four seedlings (one-year-old) from each parent tree in the collection. Eight seedlings from the mixed tree collections from Wakeley's southern pine seed source study were planted in two locales within each test plot. Classical replicated planting designs were economically impossible with hundreds of trees to measure each week. Progenies from each seed source or mother tree were located at random in each plot. Progenies 124—53, 137—53, 143—53 and 147—53 were arranged photogenically in each plot and also planted again at random. Thus, sixteen of the thirty-one progenies were planted in two replications within each plot and the others were planted only once.

One test plot was set under floodlights which produced less than five foot candles at the ground level. The photoperiod was controlled by weekly adjustments of a time clock, so that from March 21st to September 21st, the photoperiod duplicated that of Maryland. The floodlights were shut off September 21st (the time of the Autumnal Equinox), since the days are shorter in Maryland than in Florida after this date. The other plot received only the normal daylight of Florida. The plants were sprayed regularly with an insecticide to control tip moths and other insects. The plots were cultivated and irrigated. A stake was driven flush with the ground by each seedling. Once each week the height of the seedling above the stake was measured to the nearest centimeter.

Individuals were arbitrarily classified as having ceased active growth when there was less than one centimeter of height growth for two succeeding weeks of measurement. Similarly in the spring individuals were declared to have initiated active growth during the first week when a height increment greater than one centimeter was recorded.

## Observations and Results

*Part I: Total Growth*

Under natural photoperiods, more than a two-fold variation in height growth occurred between the different loblolly pine provenances (*Figure 1*). Plants from a local source near Ocala, Florida, grew nearly 18 feet during the experiment. The plants from the northern-most latitude in Maryland grew barely 7 feet. The effect of the floodlights (creating long days) was to increase the growth of the northern sources considerably (*Figure 2*). However, even under

*Table* 1. — Loblolly Pine Seed Sources Used in Photoperiod Study.

| Accession | County or | State | Reference point Latitude | Reference point Longitude | Frost-Free** Season Days |
|---|---|---|---|---|---|
| 123—53 | Ocala | Florida | 29.2°N | 82.0°W | 290 |
| 124—53 | Ocala | Florida | 29.2° | 82.0° | 290 |
| 133—53 | Nashville | Georgia | 31.4° | 83.2° | 252 |
| 134—53 | Nashville | Georgia | 31.4° | 83.2° | 252 |
| 135—53 | Woodbine | Georgia | 30.8° | 81.7° | 266 |
| 136—53 | Woodbine | Georgia | 30.8° | 81.7° | 266 |
| 137—53 | Rome | Georgia | 34.2° | 85.2° | 217 |
| 138—53 | Rome | Georgia | 34.2° | 85.2° | 217 |
| 140—53 | Gray | Georgia | 30.0° | 83.7° | 240 |
| 141—53 | Gray | Georgia | 30.0° | 83.7° | 240 |
| 142—53* | Murfreesboro | N. C. | 36.4° | 76.9° | 196 |
| 143—53 | Murfreesboro | N. C. | 36.4° | 76.9° | 196 |
| 144—53 | Snow Hill | Maryland | 38.2° | 75.6° | 185 |
| 145—53* | Somerset Co. | Maryland | 38.2° | 75.7° | 181 |
| 146—53* | Pamlico Co. | N. C. | 35.2° | 76.7° | 245 |
| 147—53* | Onslow Co. | N. C. | 34.7° | 77.4° | 248 |
| 148—53* | Newberry Co. | S. C. | 34.3° | 81.7° | 221 |
| 149—53* | Clarke Co. | Georgia | 34.0° | 83.4° | 217 |
| 150—53* | Spalding | Georgia | 33.2° | 84.3° | 226 |
| 151—53 | Wilcox | Georgia | 33.2° | 84.3° | 226 |
| 152—53* | Hardeman Co. | Tennessee | 35.2° | 89.0° | 206 |
| 153—53* | Livingston Parish | La. | 30.5° | 90.8° | 255 |
| 154—53* | Pontotoc Co. | Miss. | 34.2° | 89.1° | 215 |
| 155—53* | Clark Co. | Arkansas | 34.1° | 93.2° | 216 |
| 156—53* | Angeline Co. | Texas | 31.3° | 94.6° | 247 |
| 24—53 | Blundale | Georgia | 32.6° | 82.3° | 251 |
| 25—55 | Arlington | Georgia | 31.5° | 84.6° | 242 |
| 26—55 | Dublin | Georgia | 32.5° | 82.9° | 238 |
| 27—55 | Townsend | Georgia | 31.5° | 81.4° | 257 |
| 28—53 | Hazelhurst | Georgia | 31.7° | 82.7° | 255 |
| 29—55 | Vienna | Georgia | 32.2° | 83.8° | 243 |

* Seed supplies by Philip C. Wakeley, Southern Forest Experiment Station from "Southwide Seed Source Study".
** Data from U. S. D. A. Yearbook 1941, "Climate and Man".

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*Figure 1.* — Comparative growth of four representative provenances in the normal photoperiod of Florida. The plants are four-years-old from seed. — Left-to-right: Florida source 124-53, Georgia source 137-53, North Carolina source 143-53, Maryland source 144-53 (intervals on range poles = 1 foot).

*Figure 2.* — Comparative growth of four representative provenances in Florida with the photoperiod prolonged to duplicate the daylength of Worcester Co., Md. — Left-to-right: Florida 124-53, Georgia 137-53, North Carolina 143-53, Maryland 144-53.

prolonged photoperiods northern sources did not grow as well in the Florida environment as the local source. This indicates that other factors than a shortened photoperiod are limiting the growth of the northern sources when they are grown in Florida. The local sources were unaffected by the prolonged photoperiod treatment. The height growth of the Ocala, Florida source in the floodlight plot was only one-half foot greater than in the normal Florida daylength plot.

The northern sources of loblolly pine produced only two whorls of branches per growing season while the local and other southern sources produced six to seven whorls of branches in the growing season. Maryland and northern sources responded to the prolonged photoperiods by increasing the number of branch nodes from two to four or more per year. Thus, loblolly pine is a multi-nodal species with racial variation in the number of nodes formed. The photoperiod-genotype interaction can produce varying numbers of nodes for a given race.

The southern sources of loblolly pine continued to have a perceptable bud elongation throughout the winter season. Some buds enlarged as much as ten centimeters during the winter months. There was no needle elongation during the winter, and the needles did not begin to elongate actively until after the time when weekly height increments were greater than two or three centimeters per week. The elongation of the buds of the northern sources during the same winter months was negligible.

*Part II: Duration of Growth*

The effect of the floodlights was to prolong the duration of seasonal growth *(Figures 3 a and 3 b)*. No differences in daily rate of growth could be detected within progenies as a result of photoperiod treatments. Both in the photoperiod plots and in the normal-day plots individual plants of a progeny made unsynchronized flushes of growth. Perhaps a more extensive design might have detected a photoperiod effect on daily rate of growth. The growth responses of the Summerset County, Maryland, and Silver Springs, Florida, sources show the striking interaction of seed source and photoperiod on duration of seasonal growth *(Figures 3 a and 3 b)*. Maryland source grew an extra 40 to 45 days under the increased photoperiod of the Maryland daylength plot. During these added 40 to 45 days of growth, the increased increment and branch development was achieved by the Maryland provenance.

Comparisons of the duration of growth in successive years shows that those individuals that tended to grow longer in one year performed in a similar manner in succeeding years *(Figures 3 and 4)*. This consistent behavior indicates significant individual variation within progenies as well as between provenances. The Florida sources started growth approximately 25 days earlier and continued growing approximately 85 days longer than the Worcester County and Sommerset County, Maryland, sources *(Figure 4)*. Hence without floodlight treatment the Silver Springs, Florida, source grew 110 days longer than the Worcester County, Maryland, source. Both the photograph *(Figure 1)*

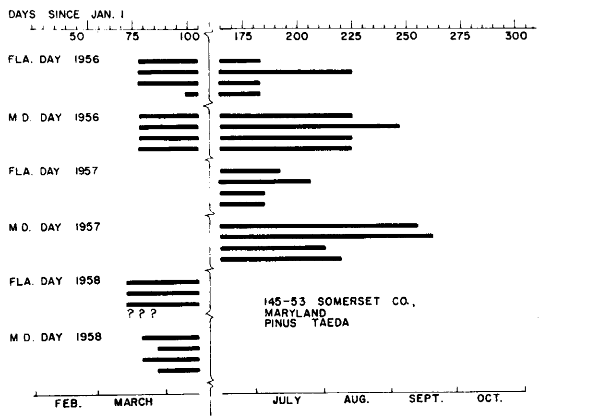


*Figure 3a.* — Comparative duration of growth of Somerset Co , Md., in different years and photoperiods. — Fla. day = normal daylength of Florida; Md. floodlight day = Florida daylength prolonged to duplicate Maryland daylength. Each bar represents a single tree. The plants are all half sibs.

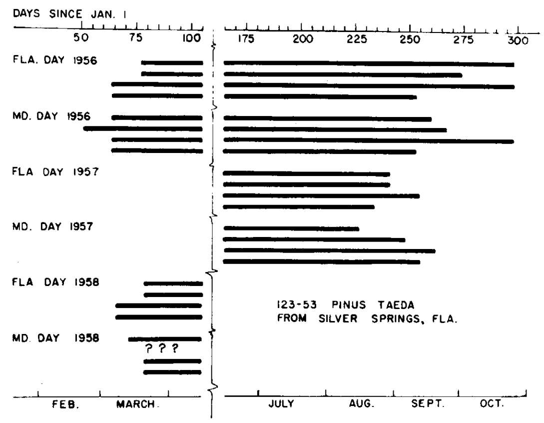


*Figure 3b.* — Comparative duration of growth of Silver Springs. Florida source in different years and photoperiods.

and bar graphs *(Figure 4)* indicate the clinal variation in duration of seasonal growth and in size of plants from different latitudes of origin.

*Part III: Variables Influencing Height Growth*

The variation in total height growth over three years was correlated with latitude of origin of the seed, the frost-free season where the seed originated, the duration of seasonal growth in Florida, and the daily rate of growth in Florida. A series of regression analyses was made in an attempt to rank these variables in order of their significance in explaining the observed variation in height growth. Growth during individual years of observation and total growth at the end of three years were analyzed for all plants in the normal day plots.

Interpretations of the analyses were difficult because nearly all variables were correlated with each other. Furthermore the distribution of some of the variables, such as frost-free season *(Table 1)* was not normal. A classic multiple regression analysis was made in which each variable was removed from the regression in all possible sequences and combinations. However, a precise statement of the contribution of each of these variables with the dependent variable growth is not possible because of their strong intercorrelation. The individual $R^2$ for terms in the regression vary depending on the sequence in which one or more of the variables is removed. The sum of the $R^2$ for each variable in the multiple regression is greater than 1. Throughout all of the analyses, differences in daily rate of growth can account for approximately 60 percent of the variation in total growth of the plant, and differences in duration of seasonal growth can account for approximately another 30 percent of the variation. The balance of the variation appears to be accounted for by initial height of the plants and the frost-free season that prevailed in the original habitats. The most satisfactory multiple regression equation for all trees and all seasons was as follows:

$$Y = -205.5 + 0.3083X_1 + 1.148X_2 + 356.6X_3 + 0.2820X_4$$

Where:

$Y$ = cumulative 3-year height growth of each plant in cm.;

$X_1$ = initial height of each plant at the end of the first growing season;

$X_2$ = the observed mean annual length of the growing season in Florida for each plant, based on a three year average;

$X_3$ = the observed average growth rate, as a mean of the three average daily growth rates computed for each of the three growing seasons, for each plant (cm/day);

$X_4$ = the number of frost-free days as given in "Climate and Man" for the locale nearest each seed source.

The multiple correlation coefficient ($R = 0.92$) was extremely high. The coefficient of determination showed the variables account for 85 percent of the variation in Y.

Independent correlation analyses show that all of the variables are correlated significantly with cumulative height growth *(Table 2)*. Surprisingly, in this analysis daily growth rate is not correlated with any variable other than initial height. This correlation between daily growth rate and initial height probably reflects seed size and other early environmental effects as described by CALLAHAM and HASEL (1961) for ponderosa pine.

In analyses by single years, average daily growth rate was highly correlated with duration of the growing season.

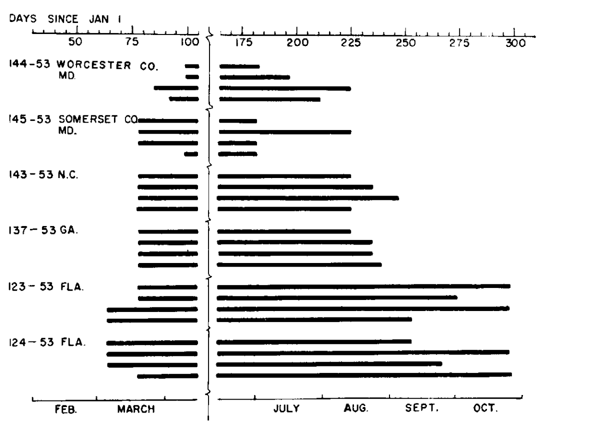


*Figure 4.* — Comparative duration of seasonal growth in 1956 by different sources when grown together in the normal photoperiod of Gainesville, Florida.

*Table 2.* — Coefficients of simple correlation between cumulative 3-year height growth (Y) and other variables (asterisks show statistically significant values).

| | $X_1$ | $X_2$ | $X_3$ | $X_4$ |
|---|---|---|---|---|
| Y | .31** | .50** | .81** | .41** |
| Init. Ht. ($X_1$) | — | .19* | .29** | —.068 |
| Length of Growing Season ($X_2$) | — | — | .09 | .48** |
| Growth Rate ($X_3$) | — | — | — | .17 |
| Frost-Free Season ($X_4$) | — | — | — | — |

Perhaps this was because daily growth rate was determined by dividing the total growth for the year by the observed duration of seasonal growth. However, in 1957 there was a strong negative correlation ($R = -0.516$) between the observed duration of seasonal growth in Florida and the average daily rate of growth. In 1956 there was a weaker positive correlation, and combined correlation for all three years was non-significant ($R = 0.09$). Cause for the yearly variation in the correlation coefficients between growth rate and duration of seasonal growth is a matter of speculation. The change in correlation could reflect the yearly variation in climate, although it is possible to rationalize any correlation obtained between these variables.

Another analysis was made substituting latitude and longitude of origin for frost-free season. Since frost-free season is highly correlated with latitude of origin, it was not unexpected that a good fit of multiple regression equation was obtained with this analysis. There was no correlation between the growth of the plants and their longitude of origin.

### Discussion

Eighty-five percent of the variation in the total growth of individual loblolly pine plants at the end of three years can be accounted for by the multiple regression analysis that includes variables of initial height, mean annual length of growing season, average daily growth rate, number of frost-free days and/or latitude of origin. Variation in height growth was shown to be controlled by the duration of the photoperiod. Other portions of the variation are doubtless due to such factors as genetic differences in the day and night temperature requirements and differences in the winter chilling requirements of the species (Perry 1960, Perry and Wang 1962).

True, greenhouse experiments demonstrate there are artificial photoperiods (20 hours or more) to which southern races of loblolly pine are responsive. However, the southern races of the species do not seem as sensitive to the fluctuating photoperiods of their natural environment as are the northern races. This lack of sensitivity to photoperiod is indicated by the persistent bud elongation from September to February, by December to January development of flower buds, and by the February 15 to March 15 flowering and start of active growth. All of this physiological activity by the local (Gainesville, Florida) race occurs when the natural photoperiods of the region are still relatively short, and intermittent temperatures of less than 20° F. are not uncommon. The condition of dormancy is hard to define even for plants that have a clear internal rest and winter chilling requirement. For these southern races of loblolly pine the definition becomes nigh impossible.

Kozlowski and Peterson (1962) in their study of seasonal growth of dominant, intermediate and suppressed red pine trees were able to show that the differences in height and growth of the specimen trees could be correlated with the differences in the length of the trees' growing season. Schütt (1962) indicated similar correlations between the duration of seasonal growth and the size of seedlings in one-year-old progenies of Scotch pine in Germany. Recent studies by Dietrichson (1964 a + b) with Norway spruce and Scots pine show that duration of growth is correlated with frost damage, stem-form and merchantable yields. Several attempts have been made to correlate differences in dry matter production with differences in photosynthetic rate. These attempts met with failure. Huber and Polster (1955) speculate that the failure may be due to the fact that some plants have a longer season of active growth than others. The results of this present investigation support their hypothesis by showing that about 30 percent of the variation in total growth can be accounted for by the observed variation in duration of seasonal growth. Hence, plant physiologists seeking to explain annual differences in dry matter production may expect the phenomena of photoperiodism and dormancy to account for a significant percentage of the variation in dry matter increment amongst individuals. At the same time, tree improvement workers should take care that the superior phenotypes they select are not superior merely because of a prolonged season of physiological activity. The genetic strains that ensue from such selections may be susceptible to frost damage as indicated by Dietrichson (1964 a + b).

### Summary

Three years of weekly measurements were made on individual trees from thirty-one seed sources of loblolly pine. One-half of the trees in this study were grown under the normal photoperiod of Gainesville, Florida, and half of the trees were subjected to an extended photoperiod regime equivalent to that of Worcester County, Maryland. The results of this study show a distinct response to the "natural photoperiod treatment" for plants of northern origin and little or no response by plants of southern origin. The response was primarily one of prolonged seasonal growth.

There was considerable variation in duration of seasonal growth between individuals and between provenances.

Height growth was significantly correlated with daily rate of growth, duration of seasonal growth, initial height, frost-free season and latitude of origin. Regression analyses showed differences in daily rate of growth could account for about 60 percent of the variation in height growth and differences in duration of seasonal growth could account for about 30 percent. The two variables account for about 85 percent of the variation in total growth when combined in a multiple regression analysis. The discussion indicates some of these results may concern both, physiologists and tree improvement workers.

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