Shoot Growth Patterns of Young Loblolly Pine

WILLIAM D. BOYER

Abstract. Most shoot elongation on *Pinus taeda* L. seedlings and saplings near Durham. North Carolina. was supplied by the first growth flush, which began about April I and ended in mid-May 1967. New growth per shoot declined with distance from the tree top. All leaders had three flushes and half had four. Variation in internode growth was dependent upon growth rate, not length of growth period, which was remarkably uniform among all sampled shoots. Day-to-day shoot growth during the first flush was highly variable. During a 17-day period that accounted for 42 percent of total elongation of the first flush, degree-hour heat sums above 50°F and solar radiation in langleys per day accounted for 93 percent of the variation in total daily growth and 76 percent of the variation in diurnal growth. The effect of temperature was positive. and solar radiation negative. Heat sums alone accounted for 94 percent of the variation in nocturnal growth. The threshold temperature for shoot growth was about 40°F at night, and averaged 50°F during the day. The apparent threshold temperature for diurnal growth increased with increasing intensity of solar radiation. Growth per unit of hear above threshold temperatures was almost the same during the day as at night. *forest Sci. 16: 472-482.*

Additional key words. *Pinus taeda,* temperature. relative humidity, solar radiation.

THROUGHOUT the 1967 growing season, selected shoots were observed on naturally seeded loblolly pine (*Pinus taeda* L.) seedlings and saplings near Durham. North Carolina. The time and rate of development of each successive growth flush and the amount and distribution of all new growth originating from each sample shoot were recorded. Shoot elongation was measured twice daily for a time during the first flush of spring growth in order to relate fluctuations in growth rate to recorded climatic variables. The first flush was chosen for these detailed observations because it was common to and concurrent among all sampled shoots. and because it accounted for most of the new growth. Observations were also limited to the peak period of shoot elongation, when growth rates are most susceptible to prevailing conditions of the external environment. Near the beginning and end of the period in which each flush is elongating, growth is governed more by physiologic conditions within each tree, and less by the immediate environment. Much of the present knowledge on variations in tree growth in relation to environmental variables, especially temperature, has been derived from small seedlings in greenhouses or growth chambers. This phase of the study was designed to explore the effects of important climatic factors on the shoot growth rates of larger trees tinder field conditions.

Procedure

Twenty open-grown loblolly pine trees were selected for study: 10 ranging from 3.5 to 5.6 ft tall are called seedlings in this paper, and 10 from 9 to 23 ft tall are called saplings. Soils in the study area are the eroded phase of White Store sandy loam. The growth of two lateral shoots, one on the north and one on the south side, was measured for each sample tree. The growth of seedling terminal shoots was also recorded.

Measurements

Buds. Lengths of the primary bud of all 50 sample shoots were measured on March 4, 1967. Secondary buds on the main shoot axis were counted at each-successive

node, and the numbers that developed into shoots were recorded. When growth was complete, new primary buds were measured and adjacent secondary buds were counted.

Shoots. Internode lengths of each sampled shoot were recorded at 2- to 4-day intervals beginning on March 4 and ending on September 18, 1967. Length of each growth flush is the distance between the bases of the initial bud and the next succeeding bud.

Shoots of the first growth flush were measured daily at 8 to 9 AM and 4 to 5 PM, beginning on the morning of April 20 and continuing through the morning of May 7. During this period, virtually all shoots, including the earliest and latest to start growing, were in their rapid growth phase. A morning measurement was missed on April 26 because of a heavy rainstorm. The total day consisted of a diurnal interval of 8 hr and the subsequent nocturnal interval of 16 hr. Shoot measurements for each interval were converted to growth rates in millimeters per 24-hr day to make all data directly comparable. At the end of the season, the numbers and lengths of all new shoots originating from each sample shoot were recorded by growth flush, whorl of origin, and axis.

Weather. All data, except solar radiation, came from a weather station in the clearing in which the sample trees were located. Maximum and minimum thermometers and a hygrothermograph were in a standard weather-instrument shelter. The station also had rain gages and totalizing anemometers at heights of 0.5 and 2 m. Solar radiation data came from an Eppley pyrheliometer on top of a building about a half-mile away. Climatic variables obtained were:

1. Air temperatures in degrees Fahrenheit.

a. Daily maximum and minimum temperatures for the 24 hr preceding each morning measurement.

b. Mean temperature for each measured interval of shoot growth (diurnal,

nocturnal, and daily), derived from the sums of hourly temperatures.

c. Temperature differential or the difference between succeeding maximum and minimum temperatures. For both diurnal and total daily (AM to AM) shoot growth, the temperature differential is the maximum during the day less the minimum the night before. For nocturnal growth, it is the minimum temperature during that night subtracted from the maximum of the preceding day.

2. Degree-hour heat sums for each growth interval were obtained by planimetering the area between the temperature trace on a hygrothermograph sheet and threshold temperatures of 40, 45, 50, and 55°F.

3. Solar radiation. Daily totals are expressed in langleys (cal/cm²).

4. Relative humidity. Mean percentages for each growth interval were obtained by summing hourly values and dividing by the number of hours.

5. Vapor pressure deficit. An average value for each growth interval, in inches of mercury, was calculated from mean temperature and mean relative humidity.

6. Wind was recorded in total miles at the 2 m height for 24-hr days ending each morning.

Analysis

Tests of significance for all analyses reported here were made at the 1-percent level of probability. An exception was made in step-wise multiple regression analyses. Regressions with two or more independent variables, even though significant at the 1-percent level, were discarded if the first independent variable was not significant at the 1-percent level, or if each additional independent variable did not contribute significantly at the 5-percent level.

Amount of *Shoot Growth.* New-growth on sampled north-side and south-side shoots was compared, for both seedlings and saplings, using *t* tests for paired replicates. Comparisons included total length of new primary shoots and total length of all new shoots originating from each sample shoot.

The relative importance of growth rate and duration of the growth period on total elongation of the first internode was explored by regression. Growth rate for each shoot was expressed as mean daily growth during the 5 days from April 30 to May 5. Duration of the growth period was defined as the days required for completion of 90 percent of total internode elongation (final internode length minus length of overwintering bud).

of Shoot *Growth.* Total new growth per shoot was related to vertical distance from the top of the tree through regression. Independent variables included both absolute and proportional vertical distances between the tree tops and both the bases and the tips of sample branches.

Bud *and Shoot* **Comparisons.** The relations between initial bud length, lengths of succeeding shoots, and length of the final bud were also explored by regression. Separate analyses were made for each of the three shoot locations on seedlings and two locations on saplings.

Shoot **Growth Rate.** Mean rate of growth for all 50 shoots was related to selected environmental variables by multiple regression. The twice-daily measurements provided data for analyses of diurnal, nocturnal, and total daily (AM to AM) growth. The independent variables are shown in Table 1. Unless otherwise indicated, values for these variables were derived from the same period as the dependent variable,. Heat sums above various threshold temperatures, mean temperature, and maximum temperature (for daytime intervals) are expressions of heat in the environment. Therefore, a series of multiple, step-wise regressions were run for each dependent variable. The first included all independent variables, and the succeeding included only one heat variable at a time. In this way the best expression of the heat influence, in terms of remaining variables, was identified.

Time and Amount of Shoot Growth

Some buds started elongating as early as March 7, and the season's growth was not complete until September 11. About 50

TABLE 1. *Variables included in **multiple** regression analyses of loblolly **pine shoot grow/h.***

Independent variables	Symbol	Growth period[a]		
		Diurnal	Nocturnal	Total day
Degree-hours above 40°F	DH_{40}	X	X	X
Degree-hours above 45°F	DH_{45}	X	X	X
Degree-hours above 50°F	DH_{50}	X	X	X
Degree-hours above 55°F	DH_{55}	X	--	
Solar radiation (current day or day before night) cal/cm²/day	SR	X	X	X
Maximum temperature (current day or day before night) °F	HT	X	X	X
Minimum temperature (current night or night before day) °F	LT		X	X
Mean temperature °F	MT	X	X	X
Temperature differential (maximum minus minimum) °F	TD	X	X	X
Relative humidity (percent)	RH	X	X	X
Vapor pressure deficit (mm Hg)	VPD	X	X	X
Wind (total miles per 24 hours)	W	—	—	X
Heat sum preceding interval[b]	DHP		X	X

[a] X indicates variables included in each regression analysis.

[b] Degree-hours over 50°F for day preceding current night, or midnight-midnight period preceding and including current total day.

percent of the sample shoots began active growth, 2 mm or more per day, during the first week in April. Terminal shoots were the first to begin growth and the last to stop; 91 percent of total height growth was complete by August 1. This growth period was a little longer than others have reported for loblolly pine. In Arkansas, seedlings of this species completed 93 to 96 percent of their height growth by August 1 (Williston 1951). Cessation of shoot growth about August 1 was reported by Reed (1939), who observed trees for 2 years in the same general area as the present study.

All seedling terminal shoots had three growth flushes, and half had four. Forty percent of seedling lateral shoots had three growth flushes, 55 percent had two, and 5 percent had one. Only 10 percent of sampled sapling shoots had two growth flushes; the remainder had one.

Total seasonal elongation of terminal shoots averaged 94.9 cm. Leaders with four flushes were longer (105.9 cmj than those with only three flushes (83.9 cm). initial heights of the two groups did not differ, and seedlings completing four flushes of terminal growth produced slightly less new growth on lateral shoots than did seedlings with only three.

Differences in the amount of new growth produced by north- and south-side shoots were not statistically significant. Seedling lateral shoots averaged 30.6 cm long on the south and 35.5 cm on the north side. Sapling south-side shoots averaged 16.6 cm long, and north-side 13.4 cm.

The average daily shoot growth rate recorded over 5 days during the period of rapid growth accounted for 80 percent of the differences in final lengths of the first internode. Duration of the growth period had no effect. According to Rehfeldt and Lester (1966), the rate and duration of elongation contributed about equally to total shoot elongation of red pine (*Pinus resinosa* Ait.). Nienstaedt and Olson (1961) reported that differences in duration of growth were mainly responsible for differences in height growth among eastern hemlock (*Tsuga canadensis* (L.)

Carr.) seedlings. However, Walters and Soos (1963) concluded that the amount of leader growth and length of the growing period were not correlated in the western conifers they studied.

The duration of each successive growth flush on individual shoots was remarkably uniform, regardless of when the growth occurred. The time required to complete 90 percent of total elongation of the first internode averaged 46.9 days for the 40 lateral shoots, with a standard deviation of 3.4 days. The growth period for leaders was longer, averaging 47.6 days. with a standard deviation of 2.4 days. Growth of the second flush lasted 39.2 ± 5.6 days for laterals, and 47.3 ± 3.7 days for leaders. The third flush lasted 39.1 ± 4.1 days for laterals and 37.1 ± 6.6 days for leaders. The fourth flush, on leaders only. lasted 42.0 ± 3.3 days.

While the duration of internode elongation was quite uniform among shoots, the dates when each growth flush commenced were not. By far the greatest variation in this respect occurred with the second growth flush of the 20 lateral shoots of seedlings, the first of which began growth on May 5, while the last did not start until July 5. By contrast, all but two of the 50 measured shoots commenced their first flush of growth within a 17-day period. Succeeding growth flushes of terminal shoots overlapped each other, but among laterals a considerable span of time, as much as 6 weeks, often separated the end of the first flush of growth and the beginning of the second. A long delay in the beginning of the second flush usually precluded a third flush.

Relations among lengths of initial buds, succeeding shoots, and final buds were statistically significant only for terminal shoots of seedlings and north-side shoots of saplings. In both cases, the final length of the first internode was related to initial length of the bud. The length of the final bud set on sapling north-side shoots was also related to the lengths of both the initial bud and the first internode. The applicable regressions for shoot or bud length are:

Regression r^2

Seedling terminals
First internode = -5.5 + 17.6
(bud length, mm) 0.76
Sapling north-side shoots
First internode = -35.9 + 12.5
(bud length, mm) .78
Bud set = -2.4 + 0.84 (bud
length, mm) .79
Bud set = -0.6 + 0.06 (first
internode length, mm) .87

Bengtson *et al.* (1967) reported a close correlation between terminal-bud length of slash pine (*Pinus elliottii* Engelm.) and subsequent height growth both in the spring (*r* = 0.97) and for the whole year (*i* = 0.91). Hanover (1963) reported a close correlation between terminal bud length and subsequent total seasonal elongation of ponderosa pine (*Pinus ponderosa* Laws.).

The average lengths of new growth originating from seedling shoots are apportioned to whorl of origin, growth flush, and axis in Table 2. Almost all growth of sapling lateral shoots was confined to the first flush: it averaged 320 mm

per south-side and 218 mm per north-side shoot. Only two of the 20 shoots produced second flushes, which amounted to an average of 7 mm per sample shoot, or 2.8 percent of the total annual growth. On lateral shoots of seedlings, the first flush provided 61 percent of all new growth. Most of the new growth on seedling terminals came from the second and third growth flushes.

The largest number of shoots per whorl, 3.9 including primary shoot, occurred along terminals. Seedling laterals averaged 2.5 and sapling laterals only 1.8 shoots per whorl. The number of buds failing to develop into shoots was low for the first growth flush, but much higher for the third and fourth growth flushes of terminal shoots, and the second and third flushes of lateral shoots (Table 3).

Total new growth per shoot was significantly related to vertical distance from the top of the tree. Distance expressed as a percent of tree height was a better expression than absolute distance. and distance from tree top to shoot tip was somewhat better than that from top to branch base

TABLE 2. *Average length*[a] of all new growth originating *from* shoots of 10 loblolly pine seedlings, by whorl, *growth flush*, und axis.

Growth Flush	Axes of first whorl[b]			Axes of second whorl			Axes of third whorl		Axes of fourth whorl		All whorls	Percent
	Primary	Secondary	Tertiary	Primary	Secondary	Tertiary	Primary	Secondary	Primary	Secondary		
											Millimeters —	Percent
				TERMINAL SHOOTS								
1	346	867									1,213	24.8
2		568	368	291	441						1,668	34.2
3		319	329		368	36	236	399			1,687	34.5
4		15	10		5			89	76	123	318	6.5
All	346	1,769	707	291	814	36	236	488	76	123	4,886	100.0
				LATERAL SHOOTS								
1	193	272									465	60.7
2		86	1	102	40						229	29.9
3		6	1		4		35	26			72	9.4
All	193	364	2	102	44			3.5	26		766	100.0

[a] For all selected sample shoots, whether indicated Bush or axis present or not.

[b] Main axis of a leader, or branch, is considered primary. An axis emanating from the main axis is considered secondary, and one from a secondary is considered tertiary.

TABLE 3. Average number of shoots and undeveloped buds arising from each existing growth whorl along primary *shoot* axis.

Growth whorl	Terminals			Laterals		
	Shoots	Buds	Total	Shoots	Buds	Total
			SEEDLINGS			
1	4.3	0.3	4.6	3.5	0.1	3.6
2	3.1	0.3	4.0	1.8	0.8	2.6
3	3.9	0.6	4.5	2.2	1.0	3.2
4	3.8	0.8	4.6	—	—	—
Final bud set	—	6.0	—	—	3.6	
			SAPLINGS			
1		—	—	2.1	0.1	2.x
2		—		1.0	1.0[a]	2.0
Final bud set					2.2	

[a] Based on **only one** shoot.

on the main stem. The best regression, total shoot lengths (cm) = 140.0 — 1.85 (proportional distance X 100), accounted for 46 percent of the observed variation in total new growth per lateral shoot.

The number of growth flushes, amount of secondary branching, and average shoot length all declined with increasing distance from the tree top, confirming similar observations reported for other conifers (Eggler 1961, Kozlowski and Ward 1961).

Rate of Shoot Growth

All shoots started elongating rapidly about April 1 (Fig. 1). Growth patterns of the first flush were virtually identical for all shoots, regardless of location. The second growth flush on terminal shoots covered a briefer period than that on laterals, primarily because growth of all terminals was still closely synchronized. The onset of the second growth flush in lateral shoots, varied widely from tree to tree. Hence growth curves for individual lateral shoots overlapped each other considerably, and the composite curve was much flatter and longer than that for terminals. The third flush lasted through mid-August. The fourth, on terminals only, began July 21 and continued until September 10.

Shoots on the south side grew faster than those on the north side during the early part of each growth flush, but slower toward the end. These differences were greater for saplings than for seedlings. They were the only observed responses that might be attributed to exposure. Rainfall patterns did not appear to affect shoot development. Except for a 2-week drought in June, however, rainfall was well distributed from mid-April through August (Fig. 1).

Daily shoot growth rates were highly variable during the period from April 20 to May 7 when measurements were recorded twice daily (Fig. 1). Significant contributions to regressions were made by no more than two recorded environmental variables for diurnal and total daily growth, while a maximum of three variables contributed to nocturnal growth. Twenty of 29 significant regressions, up to three of the most significant one-, two-, and three- variable regressions for each growth period, are listed in Table 4. Those omitted do not contain any independent variable not included in the listed regressions.

The results underscore the predominant influence of temperature on spring shoot growth of loblolly pine, as has been reported before for this and-many other species. Some expression of current temperature was the most important independent variable in every regression. The degree-hour heat sum above a threshold value of 50°F was in the best single-variable regression for both diurnal and nocturnal shoot growth (Fig. 2). These single-variable regressions accounted for a sur-

TABLE 4. *Significant* **regressions** for *relationships* **between loblolly pine shoot growth** and *environmental factors from* **April 20 through May 7.**

Growth period and equation	R^2	Standard error of estimate
Diurnal		
Y = 0.06 + 0.0111(DH_{50})**	0.59	1.39
Y = -12.50 + 0.255(*MT*)	.58	1.41
Y = -12.40 + 0.239(*HT*)	.58	1.41
Y = − 9.10 + 0.230(*HT*) − 0.0052(*SR*)	.78	1.05
Y = 2.80 + 0.0104(DH_{50}) − 0.0047(*SR*)	.76	1.11
Y = 1.92 + 0.0100(DH_{45}) − 0.0051(*SR*)	.75	1.14
Nocturnal		
Y = 1.71 + 0.0224(DH_{50})	.94	.62
Y = 0.90 + 0.0173(DH_{45})	.90	.76
Y = 0.19 + 0.0141(DH_{40})	.85	.95
Y = −0.02 + 0.0141(DH_{45}) + 0.0040(*DHP*)	.96	.52
Y = − 10.49 + 0.247(*MT*) + 0.0049(*DHP*)	.94	.63
Y = −0.79 + 0.0111(DH_{40}) + 0.0047(*DHP*)	.93	.66
Y = −3.39 + 0.0157(DH_{50}) + 0.0041(*DHP*) + 0.051(*RH*)	.98	.35
Y = −6.89 + 0.0167(DH_{50}) + 0.078(*HT*) + 0.045(*RH*)	.98	.39
Y = 0.41 + 0.0124(DH_{45}) + 0.0055(*DHP*) − 11.94(*VPD*)	.98	.42
Total day		
Y = − 14.33 + 0.330(*MT*)	.92	.64
Y = -0.48 + 0.0160(DH_{45})	.91	.67
Y = 0.52 + 0.0184(DH_{50})	.88	76
Y = 2.05 + 0.0172(DH_{50}) − 0.0025(*SR*)	.93	.63
Y = -20.29 + 0.248(*HT*) + 0.100(*RH*)	.82	.99

* Y = **mean shoot growth rate in mm per 24 hours.**

** **Symbols for independent variables are defined in Table I**

prising total of 94 percent of the observed variations in nocturnal growth, and a lesser 59 percent of diurnal growth.

The dominant influence of degree-hour heat sums on nocturnal shoot growth minimized contributions of additional variables. Other significant variables were expressions of temperature, usually heat sums, for the daylight interval immediately preceding the growth period, and average nocturnal humidity expressed as relative humidity or vapor pressure deficit. Both expressions of humidity were significant only in the presence of a second variable. All variables, except vapor pressure deficit, were additive in their effect. Together they accounted for as much as 98 percent of the observed variation in nocturnal shoot growth. The significant effect of the preceding day's temperature on night growth suggests some small lag or carryover of daytime growing conditions into the night hours.

After an expression of temperature, only one second variable, solar radiation, significantly influenced diurnal growth. Solar radiation along with degree-hour heat sum (DH_{50}) accounted for 76 percent of the variation in diurnal shoot growth.

Shoot growth rate was reduced as intensity of solar radiation increased. This reduction in growth probably results from increasing moisture stress in the tree associated with reduced turgor in ·elongating cells of the shoot. Fielding (1955) noted that during the day the apical shoots of Monterey pine (*Pinus radiafa* D. Don) sometimes actually shrink in length. Apparently, solar radiation may be more closely related to moisture stress conditions in the growing shoot than either relative humidity or vapor pressure deficit. These
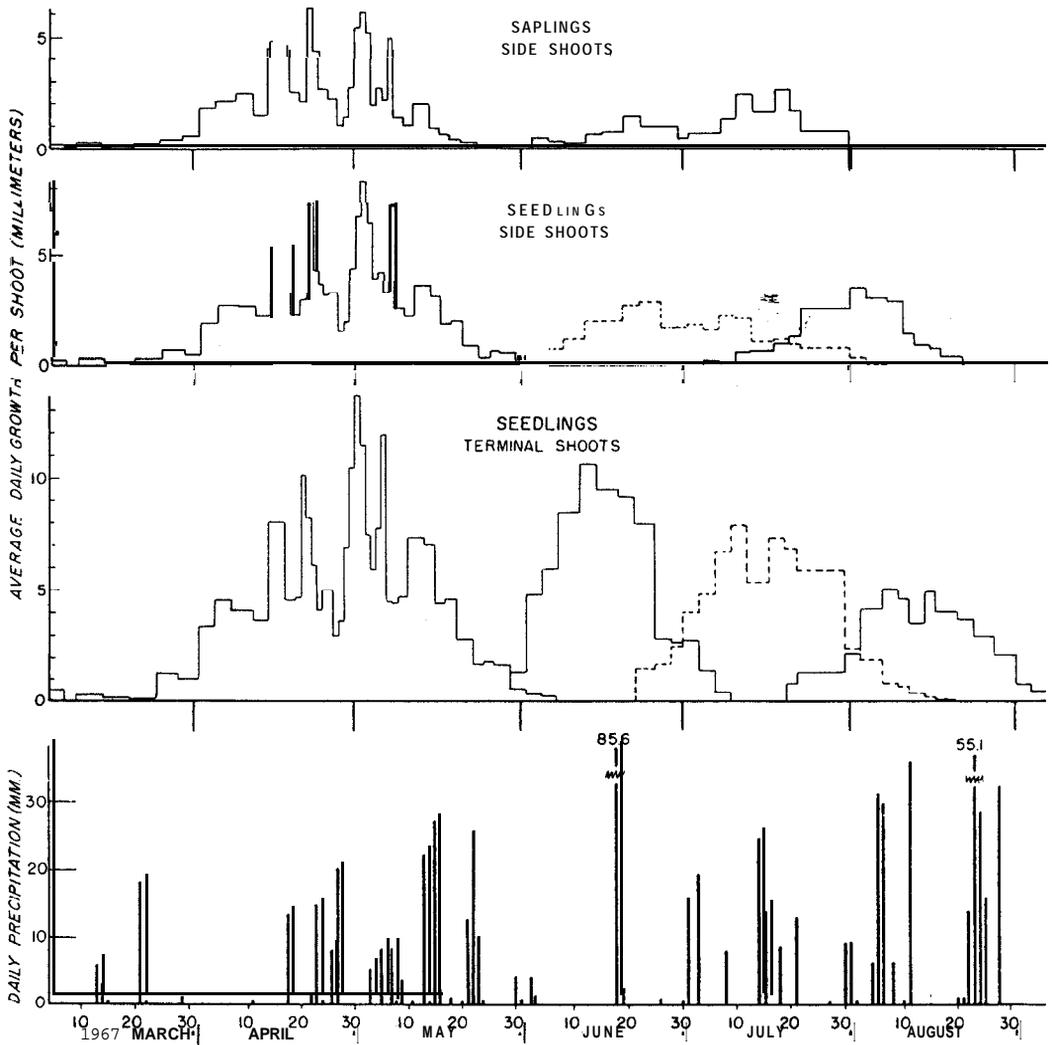
FIGURE 1. *Shoot growth of loblolly pine flushes and daily rainfall during one growing season. Each rate is an average for the seedlings on which the flush was present.*

latter two variables, however, are dependent on air temperature, while temperatures of shoots and foliage are likely to be considerably greater under high intensities of solar radiation. Solar radiation was negatively correlated with relative humidity ($r = -0.85$); it was not correlated at all with any expression of temperature or heat sums ($r = 0.1$ or less).

Depressing effects of solar radiation on tree growth have been reported before. Fielding (1960) observed that the mean internode length of Monterey pine seedlings was less in full sunlight than under

shade ranging from 6 to 30 percent of full sunlight. Logan (1959) noted that height growth of white pine increased with light intensity up to 55 percent of full sunlight, but leveled off above that point. Fritts (1960) reported that daily diameter growth of several hardwood species appeared to be inversely related to sunshine.

The best single-variable regression for total daily growth contained mean temperature for the 24-hr period of observation; it accounted for 92 percent of the variation in shoot growth. Those regressions with degree-hour heat sums were nearly as good.
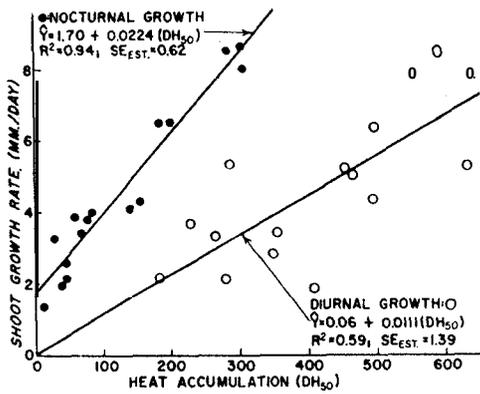
Figure 2. *Relation of* **degree-hour** *heat sums* (DH_{50}) *to diurnal and nocturnal shoot* **growth** *of loblolly pine during a 17-day* **period** *of rapid growth.*

Figure 3. *Relation of* **degree-hour** *heat sums* (DH_{50}) *and solar radiation* **(S R) t o** *total daily shoot growth of loblolly pine during a 17-day* **period** *of rapid growth.*

Only one of the two significant two-variable regressions was better than the best single-variable regression. It showed the positive influence of degree-hours above 50°F. plus the negative effect of solar radiation. This regression is shown is Figure 3 for zero solar radiation (dark) and 750 langleys per day. Also shown is the appropriate regression of shoot growth over heat sums alone. The location of this regression in the plane of the two-variable regression is, as expected, close to the mean solar radiation value for the period of observation.

The depressing effect of solar radiation on total growth for 24-hr days was about half that for daytime growth alone, suggesting that this effect is almost entirely confined to daylight hours. The average reduction in growth rate attributed to solar radiation for the 24-hr day was equivalent to 12.9 hr at the average rate loss prevailing during the daytime. Average day length (sunrise to sunset)-was 13.4 hr.

The average rate of shoot growth at night was nearly the same as during the day (0.196 vs. 0.199 mm/hour), despite lower temperatures at night. Consequently, the night growth rate, per unit of heat above 50°, was nearly double the daytime rate (Fig. 2). Diurnal growth was fastest on overcast days.

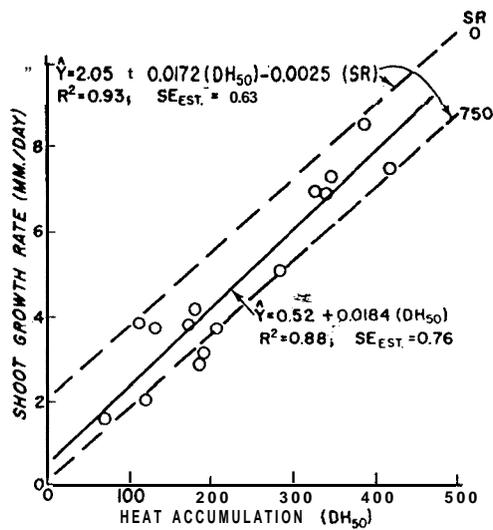Day-night differentials in shoot growth of pines have been reported before. Kienholz (1934) noted that 60 percent of

the leader elongation of red pine occurred at night, and reported a correlation of +0.74 between night growth and minimum temperature. He found no significant correlation between day growth and temperature. Reed (1939) observed that night growth of both loblolly and shortleaf pine in June and July was nearly twice as great as day growth. He reasoned that this differential was more closely related to diurnal and nocturnal evaporation than to any other factor studied. Fielding (1955) reported that the rate of shoot elongation of Monterey pine was much faster at night (3 PM to 9 AM) than during the day (9 AM to 3 PM). The fastest shoot growth occurred between 3 PM and midnight. Dahl and Mork (1959) noted that maximum growth of Norway spruce (*Picea abies* (L.) Karst.) also took place at night.

A day-night differential in threshold temperatures could explain the higher nocturnal growth rate per unit of heat above 50°F. The best single-variable regression for day growth, with DH_{50}, passes through the origin, suggesting that 50°F was the average threshold temperature. The regression for night growth that most nearly approached the origin was the one with a threshold temperature of 40°F.
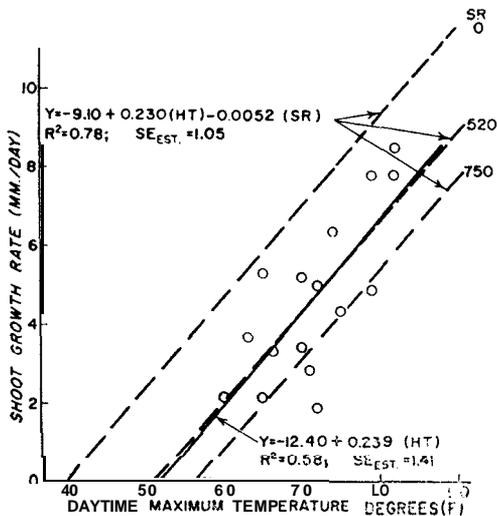
FIGURE 4. *Effects of maximum temperature (HT) and solar radiation (SR) on diurnal shoot growth of loblolly pine during a 17-day period of rapid growth.*

This value is probably close to the actual limit for shoot growth at night. when conditions for growth seem nearest the optimum. A 40°F threshold for shoot growth is also supported by the daytime regression of growth over maximum temperature (Fig. 4). When solar radiation is zero, the regression indicates that growth will not occur until the maximum temperature exceeds 39.6°F

The apparent threshold temperatures for daytime shoot growth are variable from day to day, and linearly related to total daily solar radiation. A given level of solar radiation seems to cause a uniform reduction in shoot growth rate over the entire range of air temperatures or heat sums experienced (Figs. 3 and 4). This uniform reduction in growth rate, in its effect on measured daytime shoot elongation, is equivalent to raising the temperature threshold for growth. It seems reasonable to assume that the depressing effect of solar radiation varies not only from day to day, depending on total daily radiation, but also with changing intensities of radiation during each day. On a clear day, the maximum effect should occur at midday and decline toward the morning and evening hours. The values given here

are, of course, averages for 8-hr days and therefore do not demonstrate changes in growth rate that might be expected during the course of the day.

When the depressing effect of solar radiation is removed, the effects of temperature on growth, both during the day and at night, appear to be nearly uniform.

Shoot growth rates given for diurnal and nocturnal measurement intervals are averages for periods of 8 and 16 hr, respectively. The 16-hr "nights" included some daylight hours, and the transition from night to day was included in the night averages. Night growth rate for the 11-hr dark period might be higher than that reported here for the 16-hr interval. However, the very small residual variation in night growth in comparison with that for day growth suggests that environmental factors responsible for the unexplained variation in day growth have little effect in the early morning and evening. Perhaps differential exposure of sampled shoots to daytime stress conditions is the major cause of unexplained variation in day growth, Highly uniform conditions prevailing at night apparently minimized growth variations.

The study was limited to one growing season and a single location. Longer studies under a variety of conditions will be required to determine the impact on growth rate and total shoot growth of the factors identified in the present study. Nevertheless, the results show that air temperature greatly influences growth rate of loblolly pine in the spring. They demonstrate a negative influence of solar radiation on diurnal growth and a lesser but positive effect of temperature on the preceding day and of relative humidity on nocturnal growth. In the study, almost all the daily variation in shoot growth was accounted for by these factors.

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