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R. M. Allen and N. M. Scarbrough

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# Morphology and Length Correlated in Terminal Flushes of Longleaf Pine Saplings

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*In longleaf pine* (Pinus palustris *Mill.) saplings growing in southern Mississippi the length of the first or spring flush was significantly correlated with that* of *the second flush; the correlation* of *length between flushes two and three was also statistically significant. The correlations were due more to similarities in internode elongation than to node* number.

*Flush length was closely correlated with number of* nodes *and with internode elongation in the second and third flushes. Probably because a severe spring drought in 1963 reduced the growth of only those trees with the greatest growth potential, length of the first flush of that year was correlated with number of nodes but not with internode elongation.*

*During periods of reasonably good* growing *conditions in the field, variation in node number accounted for almost three times more variation in flush length than did internode elongation. Over a range of annual environments, variation in number* of *nodes accounted for 47 percent of the variation in length of the spring flush and 74 percent of that of summer flushes.*

*No influence of one flush upon another was detected among the flushes of growth within a growing season. There was, however, a negative correlation between summer growth and spring growth in the following year.*

A thorough understanding of the elongation process could lead to improved methods for increasing height growth of southern pines. This paper is the second in a series that describes detailed studies of terminal shoot elongation. Reported here are correlations between some morphological characteristics of terminal flushes and the length they attain in longleaf pine saplings.

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**[1] Belle W. Baruch Professor of Forestry, Department of Forestry, Clemson University, Clemson, South Carolina. Experimental portion of this paper was carried out when the author was with the Southern Forest Experiment Station, USDA Forest Service.**

**[2] Forest Research Technician, Southern Forest Experiment Station, USDA Forest Service, Gulfport, Mississippi.**

A brief review of things already known about longleaf pine explains the approach taken in the studies described here. In pines, dwarf shoot primordia are formed in the axils of cataphylls or scales. The needles are initiated from the apical meristems of the short shoots.

In some respects, the pattern of terminal bud development in longleaf pine appears to follow that described by Sacher (5) for ***P. lambertiana*** Dougl. Initiation of dwarf shoot primordia for ***P. lambertiana*** begins in mid-May in Berkeley, California, and continues through most of the summer. Internodal elongation takes place in the winter bud in the following spring and essentially all of the activity is below the shoot apical meristem. The shoot apical meristem remains relatively inactive until sometime in the grand period of elongation, when it starts forming the next bud. According to Sacher (*5*), the winter bud is essentially a telescoped shoot which contains all of the nodes[3] of next spring's flush of growth.

Winter buds in longleaf pine probably do not start to form until sometime in late summer. In a study in southern Mississippi (*1*), the bud became readily distinguishable in August. It began elongating in late January, but there was no visible activity in the bud tip until about 40 days later. Rapid elongation of the second flush began about 30 days after the activity in the bud tip was noted and before the winter bud had elongated to 50 percent of its final length. This activity, as in ***P. Zambertiana,*** took place during the grand period of growth in the spring flush rather than after extension growth had ceased as in ***P. ponderosa*** Laws. (5) and ***P. resinosa*** *Ait.* (4).

The number of nodes in a given flush of longleaf pine is probably predetermined in the bud, and none are laid down after the bud starts to elongate. The growth of the shoot, then, is essentially a two-stage process, the formation of a bud and its subsequent elongation. A study in individual shoots of number of nodes, the product of bud formation, and length, the result of bud formation and elongation, should give some insight into the architecture of shoot growth. Therefore, some of the relationships between length of flush and number of dwarf shoots, i.e., fertile nodes, were examined.

## Methods and Results

Measurements were made in the fall of 1963 on the first three flushes of 1963 growth of longleaf saplings in a 5-year-old plantation on an old field. The numbers of dwarf shoots and lengths of the shoots bearing them were determined for the spring flush on 93 saplings and for the second

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[3] In the present discussion, the term "node" refers to the point of attachment of a cataphyll; the space between two succeeding nodes is the internode. Node does not refer to a branch whorl.

and third flushes of 61 of the saplings. In addition, length of the sterile cataphyll zone, diameter of the shoot at the midpoint of each flush, and average length of needles at the midpoint of each flush were recorded for 38 of the saplings.

Another measurement involved the phyllotaxy of the flushes. If the nodes are connected by imaginary lines, a number of helixes, or parastichies, may be projected upon the shoot (fig. 1) (2). The distance between the five parastichous intercepts nearest the midpoint of each flush was measured to estimate internode elongation (see arrows in fig. 1).

Similar measurements were made on the first flush of 1964 growth on 57 saplings from the same plantation.

Data were also obtained from 40 dominant longleaf pine saplings growing in a nearby plantation. These trees, which averaged about 20 feet tall, were cut in the fall of 1964, the length of each flush was measured, and dwarf shoots in each flush counted for the year 1961 through 1964.

The correlations between some growth components and total growth were determined both within and between the flushes.

The average length of the zone of sterile cataphylls was practically the same in all three flushes. This similarity is of doubtful importance because the length of the sterile zone of the spring flush relative to the length of the sterile zone in the third flush varied greatly among trees. The length of the sterile cataphyll zone was not

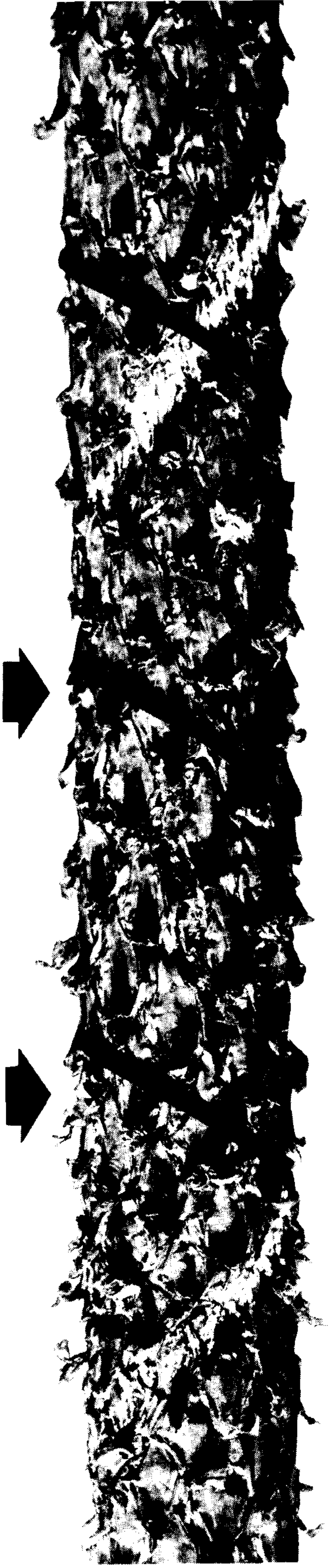

**Figure 1.** *Stem of longleaf pine sapling showing some of the parastichies that can be projected from the helical arrangement of the nodes.*

examined in detail as were other characteristics of shoots.

The spring flush was about three times the length of the second or third flush. Approximately the same difference was found in the number of nodes. Internode elongation (the distance between five parastichous intercepts) was about 21 percent greater in the spring flush than in either the second or third flush.

The spring flush had the largest diameter of the three flushes at time of measurements, but it also was the oldest. There was no difference in average needle length among the three flushes.

Mean values for the various measurements are given in table 1.

**Table 1.** – *Mean values of some characteristics of three consecutive flushes of longleaf pine saplings*

| **Flush** | **Length of zone of sterile cataphylls** | **Length of zone of dwarf shoots** | **Dwarf shoots** | **Internode elongation**[1] | **Stem diameter** | **Needle length** |
|---|---|---|---|---|---|---|
| | **Cm.** | **Cm.** | **No.** | **Cm.** | **Mm.** | **Cm.** |
| **First** | **2.8** | **47.4** | **415** | **10.0** | **29.0** | **39.8** |
| **Second** | **3.0** | **18.3** | **172** | **8.4** | **25.3** | **39.8** |
| **Third** | **3.0** | **15.1** | **150** | **8.2** | **22.1** | **38.0** |

[1] Distance between five parastichous intercepts.

## Correlation With Length

For 1963 data, correlations were computed between lengths of flushes and various attributes of the shoot within the flush for the first three flushes of growth in the 38 trees:

| Comparison | First flush | Second flush | Third flush |
|---|---|---|---|
| Length with number of nodes | 0.73* | 0.76* | 0.88* |
| Length with stem diameter | .10 | .06 | .12 |
| Length with internode elongation | .14 | .56* | .56* |
| Length with needle length | .17 | –.10 | .02 |

Length was not correlated with stem diameter in any of the flushes. Apparently those factors which are important in determining shoot length

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* Denotes statistical significance at the S-percent level of confidence-the level used throughout this paper.

are not important in determining initial shoot diameter. Shoot length was not correlated with needle length.

In the second and third flushes, length was positively correlated with number of nodes and estimated internode elongation. Evidently, in these two flushes the factors operating within the tree and in the environment to control the number of nodes that were formed similarly influenced internode elongation.

Spring flush length was correlated with number of nodes, but not internode elongation. To further explore the possible relation between number of nodes and flush length, the data were grouped and the two variables were plotted against each other in figure 2. While length was indeed correlated with number of nodes in the spring flush, the relationship was curvilinear. Length increased at a decreasing rate with increases in the number of nodes.

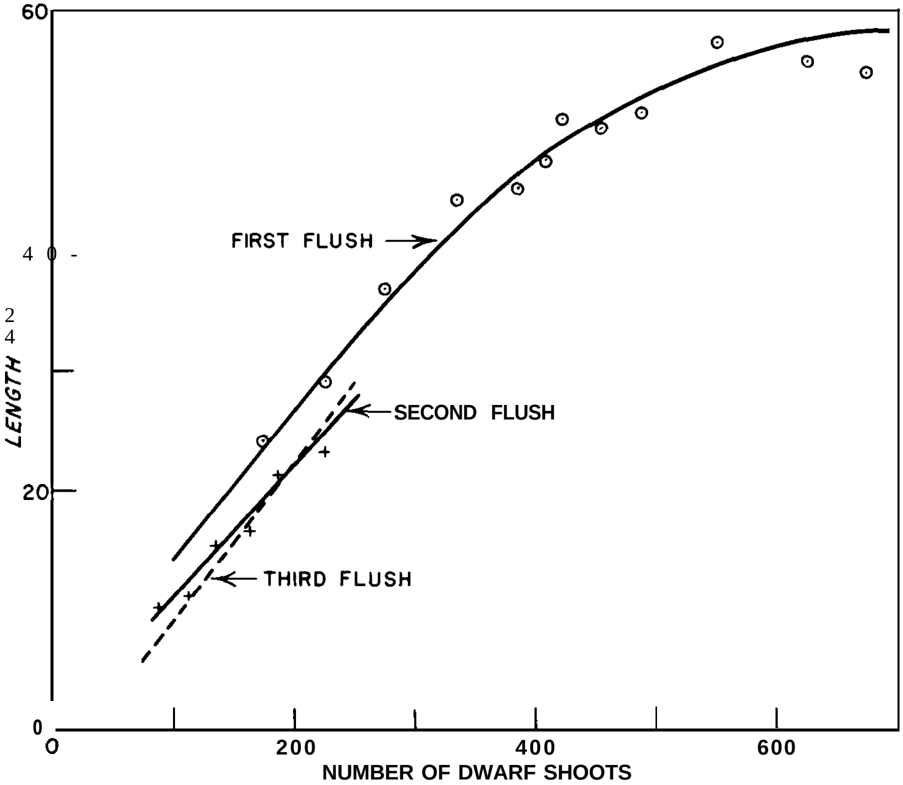

Figure 2. *The relation of flush length to number of dwarf shoots for the first three flushes of growth of longleaf saplings in 1963.*

To clarify growth relationships in the spring flush, internode elongation was plotted over number of nodes. The curve was constructed graphically with data from the spring flush of the 38 saplings (fig. 3). The linear coefficient of determination for the data of figure 3 was zero, but 74 percent of the variation in internode elongation was accounted for by the variation in node number with the curve.

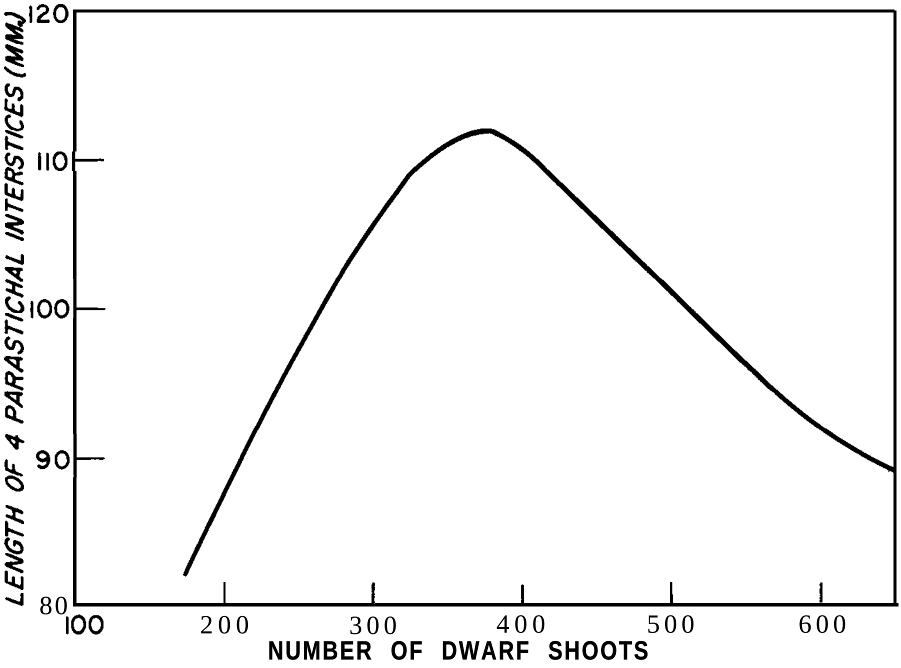

Figure 3. ***Relationship between length of internode and number of dwarf shoots in the spring flush of longleaf saplings.***

The effect of number of nodes on internodal elongation explained the curvilinearity in figure 2. Up to about 400 nodes, the increase in length of the spring flush was largely linear, but with further increases in number of nodes, the rate of increase in flush length declined due to the decreasing amount of internode elongation. The second or third flushes of these trees did not have over 400 nodes, and total length increased in about the same manner as in spring flushes with less than 400 nodes. These relationships between number of nodes and internode elongation also account for the lack of correlation between length and internode elongation in the spring flush when such correlation was found in the second and third flushes.

A biological explanation can be proposed for the curvilinear response of internode length with number of nodes. The very dry April 1963 (table

2) could have affected those saplings with many nodes more than those with fewer nodes-especially if saplings with relatively few nodes had a different pattern of elongation than those with many nodes. These possibilities were investigated.

Table *S.-Monthly rainfall at* Harrison *Experimental Forest, Saucier, Mississippi*

| Month | Year | | | | 1946-63 average |
|---|---|---|---|---|---|
| | 1961 | 1962 | 1963 | 1964 | |
| | | | *Inches* | | |
| January | 5.63 | 6.06 | 4.79 | 8.16 | 4.52 |
| February | 9.52 | 5.10 | 5.02 | 4.41 | 4.46 |
| March | 10.80 | 3.49 | 2.28 | 4.53 | 7.42 |
| April | 5.72 | 2.23 | .92 | 10.89 | 5.28 |
| May | 3.51 | 1.62 | 5.94 | 1.95 | 5.44. |
| June | 7.87 | 7.43 | 5.20 | 4.54 | 6.19 |
| July | 7.41 | 4.10 | 12.08 | 10.72 | 9.80 |
| August | 8.13 | 6.47 | 3.23 | 6.47 | 7.13 |
| September | 9.79 | 5.39 | 3.95 | 6.23 | 8.09 |
| October | 3.07 | 3.30 | .65 | 3.88 | 2.60 |
| November | 7.87 | 2.65 | 4.71 | 4.68 | 4.13 |
| December | 7.37 | 4.23 | 6.82 | 3.55 | 5.37 |
| Total | 86.69 | 52.07 | 55.59 | 70.01 | 70.43 |

***Elongation pattern&-To*** check the elongation pattern in a wet spring (1961), five saplings with an average spring flush length of 56 cm. (presumably averaging about 565 nodes as in figure 2) were compared with five saplings whose average spring flush length was 26 cm. (presumably averaging about 190 nodes). The saplings were untreated controls from a girdling-defoliation study described previously (1). Length of the spring flush was measured weekly from early February before elongation started until mid-May when elongation was completed in the spring flush on all saplings. The date when elongation started in the bud of the second flush was noted. Average weekly height increments (as percents of the total) of the two sets of trees are given in figure 4.

Saplings with the long spring flush made less of their growth prior to the appearance of the bud of the second flush than saplings with the

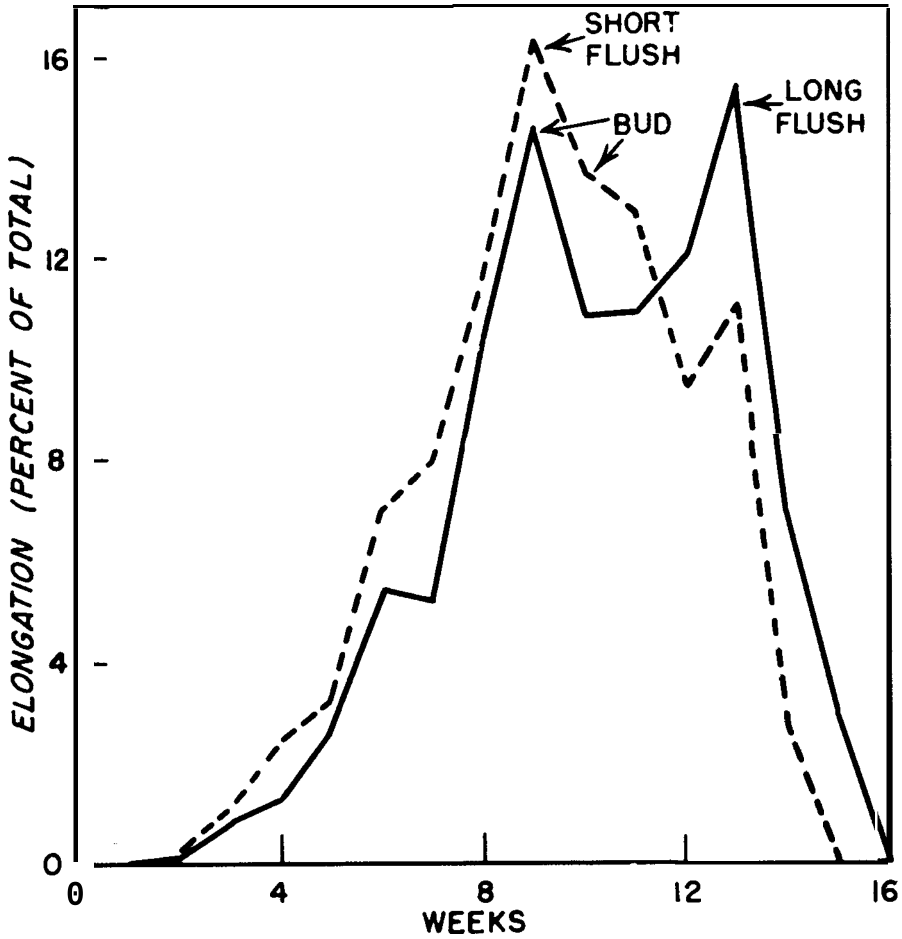

Figure 4. Periodic *growth (expressed as percent of the total) of the spring flush of longleaf saplings with a long spring or a short spring flush.*

short spring flush. A dry April would have more effect on those saplings making a long spring flush, because less of their growth would have occurred prior to the drought.

The reduction in growth rate, which caused the valley in the growth curve of the saplings with the long spring flush, coincided with an unseasonable cold period in early April. Although we do not know what the growth rates would have been had the cold weather not occurred, it seems apparent that the average response to cold by the trees which made a long flush of spring growth was different from that by trees which made a short flush.

*Moisture conditions.-In* contrast to 1963, moisture conditions were favorable during elongation of the spring flush in 1964 (table 2). To measure the effects of differences in growing conditions, the length of the spring flush, number of nodes, and internode length were recorded for 57 longleaf saplings in the same manner as in 1963. The data were grouped into classes and plotted in figure 5. The linear correlation coefficient between flush length and number of nodes was 0.83' (as determined from the individual tree data, not the grouped data). Furthermore, grouping and plotting internode elongation over number of nodes gave no suggestion of the curvilinearity found in 1963 and shown in figure 3.

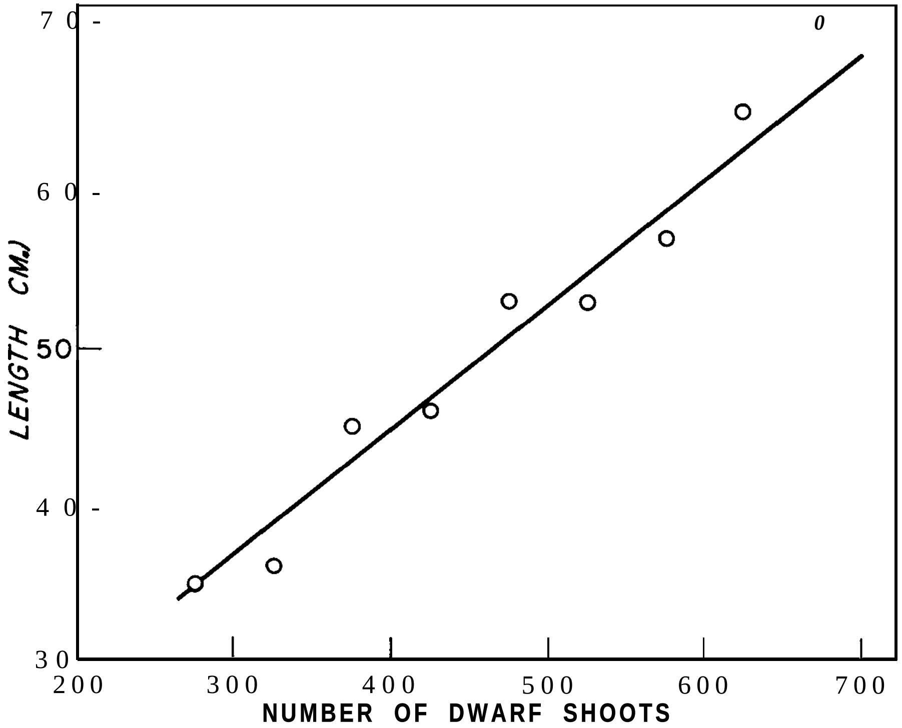

Figure 5. ***Relation of flush length to number of dwarf shoots for the first flush of 1964 growth.***

The correlation between flush length and internode elongation was 0.48' in 1964; it was 0.14 in 1963.

The curvilinear relationship obtained in 1963 between internode length and number of nodes was apparently due to drought in late April and early May. Saplings with a large number of nodes were probably affected more than those with fewer nodes because of the difference in growth patterns discussed in relation to figure 4. Also, saplings with more needles in the spring flush had greater transpiring surface, which may have caused internal water deficits in the shoot.

## Length of a Flush

To determine the relative importance of number of nodes and internode elongation in determining flush length, the third flush in 1963 (summer) and the first in 1964 (spring) were examined. These flushes were chosen because growing conditions were favorable during their formation and elongation. The correlation coefficients were:

| Comparison | Spring **flush** | **Summer flush** |
|---|---|---|
| Length with number of nodes | 0.83* | 0.88” |
| Length with internode elongation | .48* | .56* |

In the spring flush the multiple correlation coefficient of length (1) with number of nodes (n) and internode elongation (e) with 0.87’. The partial coefficients were about the same magnitude as the simple correlations: $R_{ln.e} =$ 0.82” and $R_{le.n} = 0.43^{*}$. The multiple correlation coefficient for the summer flush was $R_{lne} = 0.92^{*}$, and the partial correlation coefficients were $R_{ln\,e} =$ 0.88” and $R_{le\,n} = 0.53^{*}$. The similarity between the simple and the partial correlation coefficients show that the simple correlations were not materially influenced by intercorrelations.

In the above examples, which were chosen because of favorable environmental conditions, variation in number of nodes explained 77 percent of the variation among trees in the length of the summer flush and 69 percent in the spring flush. Variation in internode elongation explained 30 and 23 percent, respectively, of the variation in length of the two flushes. Thus, changes in number of nodes accounted for almost three times as much variation in flush length as did changes in internode elongation. It should be noted that the estimate of internode elongation was taken from the center of the flush and does not take into account the reduced elongation usually found at either end. Then too, the phyllotaxy was not consistent from tree to tree, and some experimental error may have been introduced into the internode elongation estimate by differences among trees in helical base. The node data were more precise but contained some error because variations in diameter were ignored. In spite of these deficiences, it seems apparent that in these examples more of the variability of flush length originated in the formation of the bud than in bud elongation.

The above examples, however, do not reveal what variation in number of nodes or internode elongation might contribute to the variation in flush length over a range in conditions, There was little difference in the variation explained by each between the second and the third flush in the 1963 data but there were differences in the relative contribution of each between the spring flush of 1963 and that of 1964.

We do not have additional data on internode elongation; however, the relationships between number of nodes and flush length were examined for the spring flush and for the summer growth[4] in 40 dominant longleaf pine saplings. For the summer growth, the amount of variation in length among trees explained by the number of nodes ranged from a low of 64 percent in 1964 to 81 percent in 1962; the average for all 4 years (1961 through 1964) was 74 percent. For the spring flush, the range was from 30 to 62 percent and an average of 47 percent of the variation in this flush's length was accounted for by variation in node number.

### Relations Between Flushes

Correlation coefficients were determined for the relation of length, number of nodes, and internode elongation between the different flushes:

| Comparison | Length | Number of nodes | Internode elongation |
|---|---|---|---|
| Between flush 1 and 2 | 0.43* | 0.33* | 0.64” |
| Between flush 1 and 3 | .24 | .16 | .46* |
| Between flush 2 and 3 | .39* | .12 | .72* |

The correlations in length were mainly due to a correlation in internode elongation. Evidently those factors controlling internode elongation were similar in each flush, but there was little evidence that early flushes influenced the number of nodes produced in subsequent flushes.

Conversely, the second flush did not materially influence the elongation of the first. This result was obtained in a separate study where the effect of the second flush on the spring flush was examined in the spring of 1964 on saplings in the plantation that provided data for length correlations.

Buds of the second flush were removed as soon as they were recognized (between April 20-23) on 10 saplings. The stumps were coated with lanolin immediately after removal of the buds. Each sapling was paired with an untreated control sapling that had approximately the same amount of elongation as the treated sapling at treatment time. Elongations of the spring flush of both treated saplings and controls were measured weekly from April 17 through May 21, when elongation ceased in the

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[4] Summation of the lengths of the zones bearing dwarf shoots of all flushes, except the spring flush, of a growing season.

spring flush. At no time was there any significant difference between the treated saplings and the controls, either in pattern or total amount of elongation of the spring flush.

Measurements on the 40 dominant longleaf saplings made it possible to determine the correlations between 1961 summer growth and 1962 spring growth, 1962 summer growth and 1963 spring, and 1963 summer and 1964 spring:

| Comparison | Correlation coefficient |
|---|---|
| 1961 summer: 1962 spring | – 0.13 |
| 1962 summer: 1963 spring | – .35* |
| 1963 summer: 1964 spring | – .26 |

Although the correlations were statistically significant in only one of the comparisons, it is important that in all three the tendency was for a negative relationship between summer growth and spring growth in the following year.

One might expect the correlation between number of flushes of summer growth and length of spring growth in the following year to be somewhat stronger than the length:length correlation. The number of flushes: spring growth correlations for the different years were:

| Comparison | Correlation coefficient |
|---|---|
| 1961 summer: 1962 spring | – 0.39* |
| 1962 summer: 1963 spring | – .30* |
| 1963 summer: 1964 spring | – .53* |

A still more valid comparison might be that between the number of summer flushes and number of dwarf shoots in the spring flush, because we are primarily concerned with effect of the summer growth on winter-bud formation, and the length of the spring flush is influenced by spring environment. The correlations of number of summer flushes:number of dwarf shoots on the spring flush for the different years were:

| Comparison | Correlation coefficient |
|---|---|
| 1961 summer: 1962 spring | – 0.59* |
| 1962 summer: 1963 spring | – .29 |
| 1963 summer: 1964 spring | – .42* |

There was no biological reason evident in the data for the lack of a significant correlation between number of flushes in the summer of 1962 and number of dwarf shoots on the 1963 spring flush.

The correlations show there was a negative relationship between summer growth and growth the following spring; those trees that grew more in the summer tended to grow less the following spring. Did the same relationship hold within the trees as among them? The relationship between the length of summer growth and the number of dwarf shoots of the spring flush within the trees was determined by using a covariance analysis[5] to remove the variation due to differences in vigor among trees. A significant negative linear regression coefficient indicated that in a year when a tree makes more than its average amount of summer growth the number of dwarf shoots is reduced in the first flush of the next year.

The same type of analysis was employed to see if the spring flush exerted any influence on the second flush in the same year. For 1961-1964, both length:length and the length:dwarf shoot relationships were analyzed. No significant relationship was obtained. It was concluded, therefore, that growth of the second flush is largely independent of spring growth within a tree.

## Discussion

It has been shown here that the number of nodes formed in the bud is an excellent index of the elongation potential of the terminal bud. The results also demonstrate the very important relationship between the variation in bud formation and that of flush length. The data strongly support Duff and Nolan's (3) observation that if conditions are favorable during bud formation the length of the resulting flush will usually be large despite the environmental conditions during extension growth. They also note that favorable conditions during extension growth will not usually offset the_ reduction in flush length attributable to a puny bud that resulted from unfavorable conditions during its formation.

Under weather conditions deemed favorable for both bud formation and extension growth, about three times as much of the variation in flush length among trees was accounted for by differences in the number of nodes than by differences in internode elongation in the longleaf pines studied. Under these conditions, variation in number of nodes explained 77 percent of the variation in length of a summer flush and 69 percent of that in the spring flush. On the average, however, 74 percent of the variation in summer growth and 47 percent of that in the spring flush were accounted for by the variation in node number.

The 1963 data showed how adverse weather, in this case growth, can reduce the growth of trees with a high growth potential and leave those trees with a lower potential relatively unaffected. In 1962, growth rates of trees making a long spring flush appeared to be affected differently

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[5] Dr. C. B. Loadholt of the Department of Experimental Statistics, Clemson University, did the covariance analyses.

by a period of cold weather than those making a short flush. These observations illustrate how adverse conditions can differentially affect the growths of individual trees.

The timing of the occurrences was no doubt of importance in both of these instances. Two trees in the same stage of growth, for example, might respond the same to a given adverse weather condition, but their responses might be considerably different if they happened to be in slightly different stages of growth. Many such events probably occur at random, and, although they are of considerable importance in contributing to the variation among trees in a given year, they may tend to average out over a long period. Not all of the responses to adverse weather conditions occur at random, however. Some trees, by virtue of their genetic constitution or their location in the stand, are not able to withstand or recuperate from the effects of adverse weather as well as other trees, and, as a consequence, they are at a competitive disadvantage.

Internode elongation in different flushes were correlated in individual trees. Correlation coefficients were: between flushes 1 and 2, 0.64’; 1 and 3, 0.46’; and 2 and 3, 0.72’. Node number ***was*** not as strongly correlated; the respective correlation coefficients were 0.33*, 0.16, and 0.12. Variation in the number of nodes from flush to flush within the tree is therefore viewed as being influenced more by external factors than is internode elongation.

An inverse relationship was observed between the amount of summer growth and the amount of spring growth the following year. The relationship may be one of time. When trees put on more than the average amount of summer growth they may simply have less reserves and time remaining in the growing season for the formation of the winter bud. Conversely, when trees make less than the average amount of summer growth they have more time for winter-bud formation. As a result, the length of the spring flush may be increased. Such relationships would tend to increase the amount of variation in terminal growth from one year to the next, especially in view of the fact that no influence of the spring flush on summer growth was detected.

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