THE SPROUTING OF SWEETGUM IN RELATION TO SEASON OF CUTTING AND CARBOHYDRATE CONTENT

KARL F. WENGER

SOUTHEASTERN FOREST EXPERIMENT STATION, FRANKLIN, VIRGINIA

Received December 7, 1951

Because vegetative succession in the range of loblolly pine is toward a hardwood climax, successful pine regeneration sooner or later requires reduction of hardwood competition. It would be a great deal easier to cope with the competing hardwoods if they could not sprout. All hardwood species in this type are capable of sprouting, however, although there are differences among species. To devise effective and efficient methods for controlling hardwoods, the forester must know how and why environmental conditions and characteristics of the parent stem affect sprouting.

In the southern Atlantic coastal plain, sweetgum (*Liquidambar Styraciflua* L.) is a major component of the hardwood understory. Its prevalence and its ability to sprout quickly, vigorously, and persistently make it one of the most serious competitors of pine seedlings.

Reports concerning other species indicate that site quality, size of the parent tree and season of cutting are the most important factors influencing the sprout growth of a species. Good sites result in more vigorous sprouting than poor sites (**25, 29**). Sprouting generally seems to increase with the diameter (at breast height) of the parent tree up to five inches and decreases with diameters above six inches (**20, 22**). Sprouting is least from stumps cut during the period of active growth and greatest from those cut during the dormant season (**6, 25**). Because of year-to-year variation in seasons, STOECKLER (**25**) related sprouting to phenological development and found that cutting when the leaves were nearly full size produced the least vigorous sprouts.

The seasonal trend of sprouting vigor is believed to be the result of the seasonal fluctuation of carbohydrate reserves (**1, 25**). Total carbohydrate reserves fluctuate in about the same pattern as sprouting vigor, declining sharply during spring growth to a minimum in early summer, building up to a peak in fall and going through a slight and gradual decline during the winter. This trend has been found in nearly every species studied, including fruit trees, forest trees, and woody shrubs (**12, 14, 18, 24**). ALDOUS (**1**) reported the absence of a seasonal trend in the carbohydrate content of buckbrush, but this finding is questionable in view of the consistency with which such a trend has been found in other species.

Presumably a plant will die if food reserves drop below some critical level. In Connecticut annual mowing of brush-invaded pastures for four years at different times during the year resulted in nearly complete disappearance of woody growth from plots cut in June, July, or August while

PLANT PHYSIOL. 28: 35-49
1953

plots cut in winter, April or May showed little change (5). Perhaps the treatment could be made more effective in the southern coastal plain where the longer growing season might permit more than one annual cutting.

Although the effects of site, season of cutting, and size of the parent tree probably hold in a general way for sweetgum in the southern coastal plain, the longer growing season might extend or shift the period of minimum sprouting. The presence of the overstory also might influence sprouting behavior. Accordingly, a study was begun in the spring of 1947 at the Santee Experimental Forest located in the Francis Marion National Forest 30 miles north of Charleston, South Carolina, to answer the following questions: (a) At what stage of plant development is sprouting least vigorous? (b) Does the destruction of successive generations of sprouts during a single season reduce sprouting vigor? (c) Is sprouting vigor related to the size of the parent stem? (d) How is sprouting vigor related to carbohydrate reserves? The effects of site quality on sprouting are equally important but the means available were not adequate for study of that factor.

Experimental procedure

An aggressive understory of nearly pure sweetgum in an old-field stand of loblolly pine on a moderately good site was chosen for the study. The size of trees used was restricted to less than three inches in diameter at breast height. Choice of trees was confined to those of seedling origin whenever possible.

SEASON OF CUTTING

For the determination of the period of minimum sprouting, 10 trees were cut every two weeks throughout the growing season, from April 28 to September 15, 1947. At the time of cutting, the stage of development of each parent tree was recorded in terms of size and texture of leaves, terminal shoot growth, terminal bud formation, and the progress of shoot hardening. One year after the parent stem had been cut the sprouts were counted, weighed, and measured.

The time of cutting the parent tree had no effect on the total height, total fresh weight, or number of sprouts produced per stump during the year after cutting. The relationships between the diameter of the parent tree at breast height (d.b.h.) and these sprout attributes were highly significant, however, and are expressed by the following equations: Total height in feet $= 2.0 + 14.0$ (d.b.h.); Total weight in grams $= -51.5 + 291.8$ (d.b.h.); Number of sprouts $= 4.3 + 6.6$ (d.b.h.).

Much of the variation in total height and weight was the result of differences in numbers of sprouts, which were not related to time of cutting. Variation from this source is eliminated if the height and weight of the average sprout from each stump are used. A regression analysis showed that both the height and weight attained by the average sprout in the year following cutting depended on the date of cutting (stage of phenological development) of the parent tree. Average height and weight were also related to the diameter of the parent tree. Figure 1 shows the effect of parent-tree diameter on average height of one-year-old sprouts and the trend of sprout height in relation to phenological development of the parent tree at the time of cutting. Stumps cut early in May, when the leaves that had emerged first were nearly full size, produced the shortest sprouts. This result agrees with those of other studies, but the second minimum, in August, has not been reported before. Fitting the curve by the method of least squares showed that this late summer minimum is a significant variation in the trend. The calculated curve limits the duration of the minimum period to about two weeks, although the data in figure 1 show that it actually lasted nearly six weeks for the year in question, beginning shortly after terminal buds were formed. Mortality of stumps was negligible.

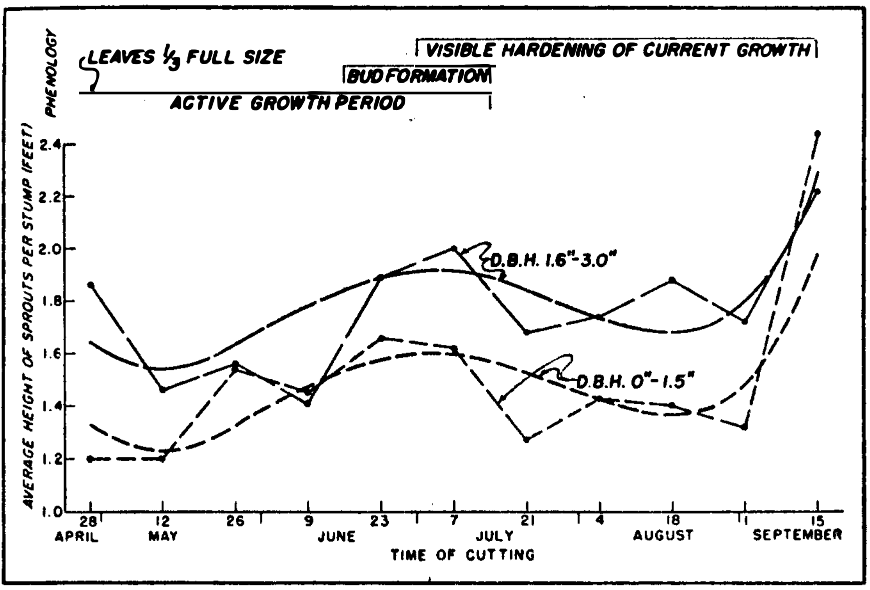

FIG. 1. Average height of one-year-old sprouts in relation to diameter and time of cutting of parent tree.

CUTTING SUCCESSIVE GENERATIONS OF SPROUTS

To study the effect of cutting successive generations of sprouts from the same stump, two cutting treatments were replicated six times within two diameter classes (0.0 to 1.5 inches, and 1.6 to 2.0 inches) on three initial cutting dates. Initial cutting dates were four weeks apart beginning April 28. On each initial cutting date 24 trees (12 in each diameter class) were cut; eight weeks later the sprouts were cut; after a second eight-week period the sprouts on 12 stumps (six in each diameter class) were cut again. The trees were chosen at the start, and treatments were randomly assigned. The interval of eight weeks between cuttings on the same stump was chosen after observing the growth of sprouts from the first cuttings on April 28. One year from the date of final cutting for each stump the sprouts were counted, weighed, and measured.

The dates of the final cuttings coincided with those for the season-of-cutting experiment, so that one-year-old second and third generation sprouts could be compared directly with one-year-old first generation sprouts. Third generation sprouts from stumps cut initially in May and June made most of their growth the following year; in fact, most third generation sprouts from the June cutting did not arise till the next spring. The mean values for the different levels of the three main classifications are presented in table I with significant differences marked by asterisks. As in the season-of-cutting experiment, stumps of larger trees produced both larger and more numerous sprouts.

TABLE I

SPROUT SIZES AND CARBOHYDRATE CONTENT ONE YEAR AFTER FINAL CUTTING BY FACTOR LEVELS (SUCCESSIVE CUTTINGS).

Factor levels		Sprouts per stump					Carbohydrate content	
		Number	Total height	Total weight	Average height	Average weight	Stump	Root
			ft.	*gm.*	*ft.*	*gm.*	*mg./gm.*	*mg./gm.*
Diameter of parent tree (inches)	0.0-1.5	8.6*	11.71*	162*	1.40*	19.8*	33.6	76.0*
	1.6-3.0	15.2*	26.11*	418*	1.72*	28.8*	28.8	44.8*
Number of sprout cuttings	0	13.0	20.95	326	1.62	23.6	27.6	56.7
	1	12.2	19.69	333	1.63	28.6*	30.0	57.1
	2	10.6	16.09	210	1.44	20.6*	33.6	67.3
Time of initial cutting	April 28	10.6	17.61	345	1.69	33.6**	24.6*	46.1*
	May 26	11.8	18.60	253	1.47	18.7*	30.0	56.7
	June 23	13.3	20.53	271	1.52	20.5*	36.6*	78.3*

*Vertically aligned asterisks indicate significant or highly significant differences.

Whether the number of sprout generations previously destroyed affected the number and size of sprouts in the final crop is somewhat uncertain. The one significant difference, that difference between the average weights of second and third generation sprouts, can be traced directly to exceptionally heavy second generation sprouts from a single large stump of the series started on April 28. The number, total height, average height, and total weight of third generation sprouts also were less than those of second generation sprouts, however, although the differences were too small to be significant. In view of the results achieved by Brown (5) with annual mowing of brush-invaded pastures, it is possible that there was a real trend toward lower vigor in successive generations of sprouts from the same stump.

The effect of time of initial cutting seems to have been expressed in the form, rather than in the number or height, of sprouts. Although the exceptionally high value mentioned above inflated the average weights of sprouts from the April 28 cuttings, the other sets begun on April 28 (all first and third generation sprouts and second generation sprouts from smaller stumps) were also heavier. Consequently, there is no reason to doubt that sprouts from cuttings started on April 28 were significantly heavier than sprouts from cuttings started later. Since the trend in height of these same sprouts was neither significant nor well-defined, the differences in weight suggest that the sprouts from the May 26 to June 23 cuttings were more slender than those from the cuttings started on April 28.

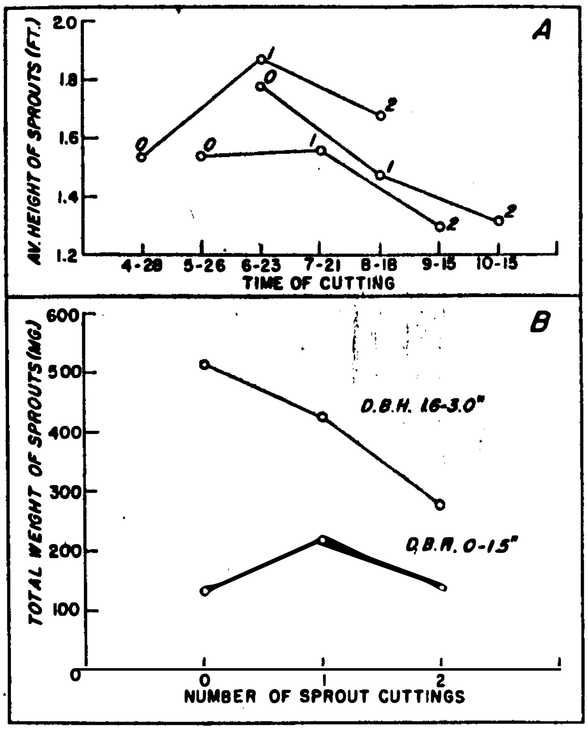

FIG. 2. The effect of number of cuttings, time of cutting, and parent-tree diameter on average height and total weight of one-year-old sprouts.

The interaction of the number of cuttings and time of initial cutting on the number of sprouts was also significant. In the series started on May 26, the number of sprouts increased with each additional cutting while in the series started on April 28 and June 23 the number of sprouts tended to decrease. There seems to be no reason why the number of sprouts should vary in that manner.

Figure 2 A shows the trends in average height on the same basis, although differences among them did not quite reach the 5% level of significance. Comparison of figure 2 A with figure 1 suggests that the number of sprout generations previously destroyed reduced sprouting vigor when cutting was started near the end of the period of active terminal growth or later but not when it was started before that time. Second and third generation sprouts (fig. 2 A) from cuttings started on April 28 were as tall as first generation sprouts (fig. 1) but third generation sprouts from cuttings started after April 28 were shorter than first generation sprouts. They were as tall as first generation sprouts from cuttings made at the time of minimum sprouting vigor, however (fig. 1). The comparison between figure 2 A and figure 1 also suggests that the variation among the trends in average height (interaction of number of cuttings and time of initial cutting on average height of one-year-old sprouts) is of greater significance than the statistical tests indicate.

The interaction of parent-tree diameter and number of sprout cuttings on total weight of sprouts per stump was also significant and is shown graphically in figure 2 A. Total weight of sprouts from parent trees of larger diameter followed a definite downward trend with number of cuttings while sprouts from smaller parent trees followed no well-defined trend. Mortality among stumps of the successive cuttings was negligible.

CARBOHYDRATE CONTENT

When the sprouts from treated trees were harvested one year after the final cutting, samples of stumps and roots were taken to determine the carbohydrate content after sprouting. When the sprouts from the seasonal cuttings, for which 10 trees were cut every two weeks during the growing season of 1947, were harvested in 1948, five of the 10 stumps were randomly selected and two samples were taken from each, one close to the point of sprout origin and one from the root close to but distinctly below the root collar. Samples were taken in the same way in 1948, one year after the date of final cutting, from all stumps and roots of the successive cuttings, for which three sets of 24 trees each had been treated during three periods beginning four weeks apart in 1947.

During the same year, 1948, a series of stump and root samples for carbohydrate determinations were taken from uncut trees to furnish control data. The original plan did not provide for a study of food reserves and no samples for carbohydrate determination were collected from check trees in 1947, when the initial cuttings were made. Collection of check samples the following year when the one-year-old sprouts from treated stumps were harvested was believed to be satisfactory, however, for, while the level of carbohydrate concentration may vary from year to year, its seasonal trend, judging from other studies, remains relatively constant. As quickly as possible after collection, usually within two hours, the samples were placed in an oven at 70° C, dried to constant weight, and stored to await carbohydrate analysis. The samples were ground in a Wiley mill to pass a 20-mesh sieve. One-gram portions were used in the analysis.

Carbohydrates were extracted by a modification of the enzyme digestion method described by HEPTING (11). The essential steps in that method are (a) the extraction of resins and oils with ether, (b) the digestion of starch to sugars by Takadiastase, (c) the removal of tannins and gums by lead acetate clearing, and (d) the acid hydrolysis of all sugars to glucose. A series of trials showed that the ether extraction of resins and oils was not necessary with sweetgum. Glucose was determined by the Shaffer-Somogyi method as described by HEINZE and MURNEEK (**10**).

The total, or absolute, quantity of carbohydrates as well as the concentration must be determined to locate the principal storage tissue. In addition, the weights of bark and wood must be in the same ratio as they are in the intact tree. Samples collected throughout the growing season accordingly were treated, before grinding, as follows: First they were trimmed to symmetrical sectors of the stem cross-section (the whole cross-section of smaller stems was used); then they were weighed; the bark was removed and saved; and finally the wood was weighed again. One-gram samples of wood and bark from both stems and roots were analyzed. The results are presented in table II. The separation by diameter classes was made because the ratio of bark to wood decreases with increasing diameter. The concentrations were as follows: Stem wood, 0.0285 gm. sugar/gm.; Stem bark, 0.0694 gm. sugar/gm.; Root wood, 0.1170 gm. sugar/gm.; Root bark, 0.0787 gm. sugar/gm. The small difference between stem bark and root bark was not significant, but all other differences were highly significant.

TABLE II

PROPORTION OF TOTAL CARBOHYDRATE RESERVES OF STEM AND ROOT FOUND IN WOOD AND BARK OF SWEETGUM.

Parent-tree diameter	Stems		Roots	
	Wood	Bark	Wood	Bark
In.	%	%	%	%
1	74.4	25.6	91.6	8.4
2	79.0	21.0	93.1	6.9
3	81.0	19.0	91.4	8.6

Although it was impractical to obtain stump and root weights to compare the total amounts of carbohydrates, it can be stated that the roots weighed more than the stumps in all cases. The root wood, therefore, contained by far the greatest amount of carbohydrate reserves.

In one study of sugar maple, with larger trees than those in this study, it was found that outer stem wood contained more carbohydrates than inner wood (**14**). Accordingly, some of the sweetgum samples were selected and divided into inner and outer portions, the outer portion including the growth of about two years. The differences in carbohydrate concentration were small and not significant. Apparently these trees were so young that the whole stem and root were still involved in transformation and translocation of carbohydrates in contrast to the larger sugar maple trees in which the differences probably were related to the inactivation of older stem wood.

Since the bulk of reserve carbohydrates are located in the wood (table II), the bark was not analyzed in the seasonal and successive cuttings or in the uncut trees. Figure 3 shows the seasonal trends of carbohydrate concentrations in the roots and stems of uncut trees and of the seasonal cuttings after sprouting. The trend for roots of uncut trees only was significant. There was no difference in carbohydrate concentration in roots or stems between trees of different diameters in either the uncut or the treated sets. Larger trees, then, contained the greater absolute quantity of carbohydrates.

The difference between the trends for uncut and treated trees was caused by sprout growth since the values for the uncut trees are, in fact, an estimate of what the treated trees would have had if they had not been cut. Root growth probably required the same amounts of carbohydrates in both cases unless some roots of the treated trees died after cutting. In that case the differences in figure 3 are less than the amounts of carbohydrates actually used by sprout growth.

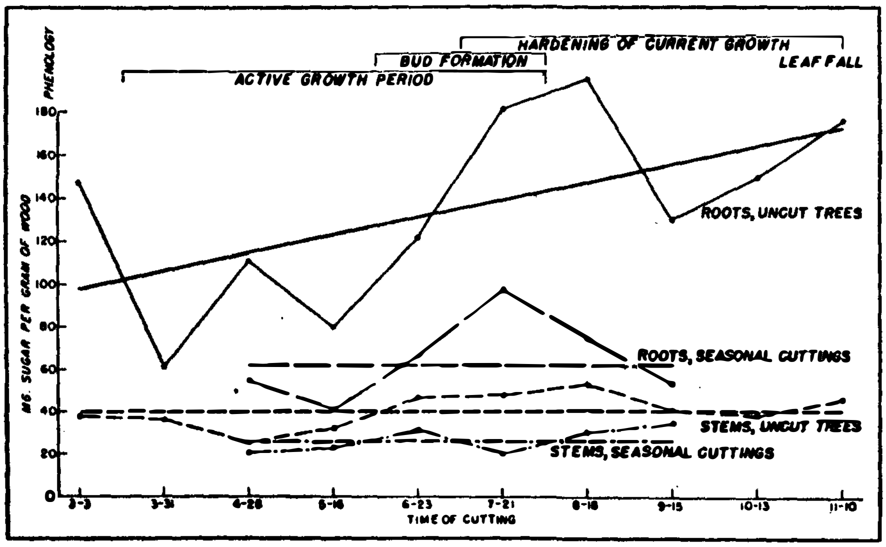

FIG. 3. Carbohydrate content of roots and stems of sprouted trees one year after cutting and of uncut trees.

Carbohydrate contents of stumps and roots of the successive cuttings are shown in table I. Roots of smaller trees had a significantly higher concentration after sprouting than those of larger trees. Carbohydrate concentrations in both stumps and roots were significantly higher for later initial cutting dates.

The interaction of number of cuttings and time of initial cutting on the carbohydrate concentration in the roots is shown in figure 4. The interaction was statistically significant, but the data showed that the difference responsible for significance should be attributed to chance rather than to treatment. The high value for single cuttings (0) made on June 23 was caused by an excessively high carbohydrate concentration in only one root. The main effect, number of cuttings (see table I), might have been significant if the value in question had been of the same order of magnitude as the two earlier single cuttings.

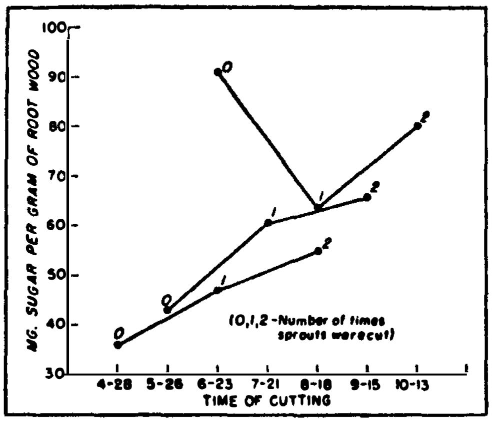

FIG. 4. The effect of number of cuttings and time of cutting on carbohydrate content of roots one year after final cutting.

Discussion

If the vigor of sprouting, expressed by the size attained by sprouts in one year, depended on the amount of reserve carbohydrates, larger stumps should produce larger sprouts because of the greater amount of reserve carbohydrates. This expectation implies a level of carbohydrate concentration that is critical for sprout growth. Considering also that the greater amount of foliage of the larger sprout clumps should produce a greater amount of carbohydrates, the carbohydrate concentration in the roots after growth of sprouts should be at least as high in the larger as in the smaller stumps. With respect to the change in size of sprouts in relation to the time of cutting, one would expect sprouts to increase constantly in size during the period of accumulation because carbohydrate concentration increases constantly during that period. These expectations apparently are realized with respect to diameter in the experiment on the season of cutting (figs. 1 and 3). In the successive cuttings, however, where the effect of diameter was determined more precisely, larger stumps contained a lower residual carbohy-

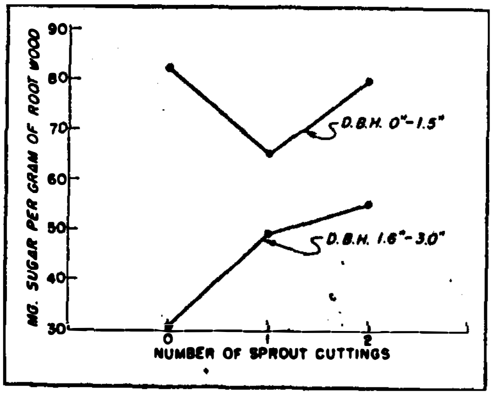

FIG. 5. The effect of number of cuttings and parent-tree diameter on carbohydrate content of roots one year after final cutting.

drate concentration than smaller stumps but produced larger and more numerous sprouts (table I). Seasonally, sprout growth and carbohydrate concentration were not well correlated: carbohydrates increased constantly during the accumulation period while sprout growth fell to a second minimum. The inverse relationship between sprout growth and carbohydrate content is shown in striking fashion upon comparing the effect of number of sprout cuttings on the total weight of sprouts from stumps of different sizes (fig. 2 B) with the carbohydrate content of the roots after sprouting (fig. 5) and is also evident upon comparing the trends of average sprout heights in figure 2 A with their root carbohydrate content after sprouting in figure 4.

It is clear, therefore, that under the conditions of these experiments, carbohydrates did not control the growth of sprouts but the amount of sprout growth determined the amount of carbohydrates used. Data recorded by several other workers support this conclusion; for example, FINCH (**8**) found that in regularly bearing apple varieties terminal growth was greater and carbohydrate content was less than in biennially bearing varieties in the off year while shyly bearing varieties were intermediate in both respects. In fruit trees (**12, 26**) the seasonal behavior of carbohydrates indicates that they are used in whatever amounts needed and the soluble products move whatever distance is required to reach the growing regions. There seems to be no obstacle to exhaustion of reserve carbohydrates throughout the plant to satisfy growth requirements, yet it has been demonstrated that food reserves within a short distance of the growing points usually suffice (**7**). Apparently under normal conditions, lack of carbohydrates usually is not the limiting factor in growth, but even under the most drastic treatments imposed in this study carbohydrates were not the limiting factor in the size sprouts attained. Had the treatments been continued in following years, carbohydrates might have become limiting.

Nitrogen, mineral nutrients and moisture supply are all, at times, critical in the growth of a plant. Certain facts indicate, however, that they, also, are not important in determining the seasonal trend of sprouting. Several facts about nitrogen metabolism should be noted in this respect: the carbohydrate–nitrogen ratio is more closely related to growth than nitrogen alone (**17**); meristematic regions maintain a higher nitrogen level than others (**15**); and the end of active growth is regarded as the result of carbohydrate accumulation (**28**), that is, the increase in the C/N ratio. But sprouts grow during the same season from the stumps cut after terminal growth of the parent trees has stopped, yet at this time the C/N ratio is higher in the stump than in the apical meristems. Evidently something other than carbohydrates or nitrogen determines the seasonal trend of sprouting vigor.

Variations in mineral nutrients or moisture supply also fail to provide a satisfactory explanation. The seasonal trend observed in this study is essentially the same as that recorded for many other species in many different places under what must have been greatly different soil moisture and fertility conditions.

A better explanation may be that the mechanism of apical dominance also controls the seasonal trend of sprouting vigor. Auxin inhibits the sprouting of lateral buds (**23**). It is produced by growing buds and young leaves and moves down the stem, where cambial activity follows its progress (**3, 4**). Its production in terminal buds follows a seasonal trend from an indetectible amount during the dormant season to a peak just before the most rapid growth in length, appearing first as the terminal buds begin to swell in the spring (**3**). Conceivably, then, the higher the auxin concentration in the stump of a tree at the time of cutting, the less vigorous the sprouts.

Because little is known about the relation of auxin to dormant buds, several assumptions must be made in accepting this explanation. In the portion of the tree stem where dormant buds are effectively suppressed, the auxin concentration must remain above the critical inhibitory level throughout the period of favorable growing conditions; the susceptibility of dormant buds to auxin inhibition must vary, otherwise all sprouts from cuttings made during the growing season would arise under the same degree of inhibition and would all be the same size; and the degree of inhibition under which sprouts arise must persist and affect their growth for at least a year. THIMANN (**27**) suggested that roots, stems, and buds all react similarly to auxin but at different concentrations, the optimum for stems being much higher than for buds; consequently it is possible that there might be seasonal differences in response as well. One case of apparent persistence of a hormone effect has been reported: APPLEMAN (**2**) found the vigor and yield of potato plants related to the size of the seed piece and attributed it to a growth hormone produced in an amount proportional to the size of the seed piece.

The second minimum of sprouting vigor may be related to changing day length. The phenological development of many southeastern forest tree species seems to be partly controlled by photoperiod (**13, 16**). If cessation of growth in length and terminal bud formation is brought about by shortening of the day, the sprouting of dormant buds would seem to be effectively checked even if auxin concentration dropped below the critical level. Upon cutting, the dormant buds in the stump would immediately gain the benefit of all of the disproportionately large root system and, since response to photoperiod can be modified by nitrogen supply (**21**), might be able to sprout and grow. The influence of suddenly increased nutrients would become progressively less until no longer effective as the days shortened. In this study most of the sprouts from stumps cut after the middle of August did not grow till the following season. This explanation requires the assumption that the inhibition exerted by shortened photoperiod also persists for at least a year.

While the proposed explanation is admittedly highly speculative, it is nevertheless probable that sprouting vigor is controlled by a hormone mechanism. STOECKLER (**25**) made double cuttings of aspen, first at a height of 36 inches and then at 12 inches after 3 to 24 hours. Stumps cut once produced many more sprouts than twice-cut stumps. Double cuttings with a three-hour interval produced fewer sprouts than those with longer intervals. These time intervals hardly permit the operation of anything but a hormone, or hormones. The results suggest positive, stimulating action rather than a negative one but it is quite likely that two or more hormones of different action affect sprouting vigor. If apical dominance is indeed a hormone effect, the successive cuttings in this study furnish another suggestion that hormone action is involved in sprouting vigor. Stumps cut once produced a total of 13 sprouts per stump; when sprouts were cut back once, a total of 22 sprouts was produced; when sprouts were cut back twice, a total of 30 sprouts was produced. Apparently buds that sprouted first immediately suppressed the remaining ones.

The positive relation between diameter of the stump and number of sprouts results from the greater opportunity for the formation of secondary dormant buds with larger diameter. Sweetgum does not seem to produce adventitious buds readily. Among all the stumps in this and another related study only one produced sprouts from what were unmistakably adventitious buds. There are not enough dormant buds formed during normal growth to account for the number of sprouts produced, but secondary dormant buds grow from bud initials in the axils of the scales of the parent bud (9, 19). Sprouts were frequently observed arising in horizontal rows in precisely the way Hahne (9) found secondary dormant buds arranged in pear. This lateral arrangement also reduces the tendency for buds that sprout first to inhibit others in the cluster, and a larger stump tends to produce more sprouts because a greater percentage of buds are laterally arranged.

The effect of parent-tree diameter on the size of sprouts is, most likely, the result of increased moisture and nutrients. Extension of lateral roots is more or less proportional to stem diameter, and the roots, spreading in all directions, tend to occupy a circular area. The roots of a two-inch tree, then, occupy not twice as much area, but more nearly four times as much as the roots of a one-inch tree, the area occupied increasing as the square of the relative increase in diameter rather than as a linear function of it. Sprouts from larger stumps therefore have relatively more moisture and nutrients available than those from smaller stumps and thus grow larger. This explanation is not in contradiction to the preceding discussion of possible hormone control of sprouting vigor. The seasonal trend, controlled by the postulated hormone mechanism, holds for all diameters, but at a higher level for larger diameters because of the greater supply of moisture and nutrients. The same holds true for the effect of site quality reported by other workers. Differences in sprouting vigor between sites are probably caused largely by moisture and nutrient differences but seasonal variations on a given site are attributable to the hormone system.

Summary

A study of sweetgum was made to determine (a) the time of least vigorous sprouting during the growing season in terms of phenological develop-

ment, (b) the sprouting vigor in relation to the size of the parent tree, (c) the effect on sprouting vigor of the destruction of successive generations of sprouts during the same growing season, and (d) the sprouting vigor in relation to carbohydrate reserves.

The seasonal trend of sprouting vigor (size attained by one-year-old sprouts) was studied by cutting trees at two-week intervals during the growing season. Another group was treated in such a way that first, second, and third generation sprouts could be compared at different times during the growing season. Observations of number, height, and fresh weight of sprouts were made one year after final cutting in all treatments. Diameter at breast height of all trees was recorded before cutting. When final observations were made, stump and root wood samples were collected from all treated trees and from uncut trees for carbohydrate determinations.

Sprouting vigor, expressed as the height or weight of one-year-old sprouts, followed a pronounced trend by date of cutting with two minima, the first when leaves that had emerged earliest reached full size and the second during the late summer hardening period. Sprout size was directly related to parent-tree diameter, large trees (1.5 to 3.0 inches) producing larger sprouts than small trees (0.0 to 1.5 inches).

The number of sprouts did not follow a seasonal trend but was dependent on diameter of stumps (parent-tree diameter), large stumps producing more sprouts than small stumps.

The destruction of successive generations of sprouts from the same stump during the same growing season apparently caused a decline in sprout vigor. Second and third generation sprouts from final cuttings made before September 15 were as tall as first generation sprouts, but third generation sprouts from final cuttings made on or after September 15 were much shorter than first generation sprouts. Sprouts from cuttings started on May 26 and June 23 were lighter in weight than those from cuttings started on April 26 but were not significantly shorter, suggesting that they were more slender. Sprouts from larger stumps decreased in total weight with number of generations previously destroyed while those from smaller stumps did not.

The study of carbohydrate reserves showed that, under the conditions of these experiments, the size and number of sprouts was not dependent on carbohydrate content.

The possible roles of nitrogen, other mineral nutrients, moisture, and hormones in determining the seasonal trend were discussed. It seems most likely that a hormone system related to that controlling apical dominance is the chief factor governing the seasonal trend of sprouting vigor.

The study was a cooperative project of the United States Department of Agriculture, U. S. Forest Service, and Duke University, Graduate School of Arts and Sciences. The assistance and support rendered by the following individuals is gratefully acknowledged: Dr. I. T. Haig and Dr. G. M. Jemison, while they were, respectively, Director, and Chief of the Division of Forest Management of the Southeastern Forest Experiment Station; Dr.

P. J. Kramer, Botany Department, Duke University; Dr. C. F. Korstian, Dean of the School of Forestry, Duke University; and the staff of the Central Coastal Plain Branch of the Experiment Station, Charleston, South Carolina.

LITERATURE CITED

1. ALDOUS, A. E. The eradication of brush and weeds from pasture lands. Jour. Amer. Soc. Agron. **21**: 660–666. 1929.
2. APPLEMAN, C. O. Special growth-promoting substances and correlation. Science **48**: 319–320. 1918.
3. AVERY, G. S., JR., BURKHOLDER, P. R., and CREIGHTON, H. B. Production and distribution of growth hormone in shoots of Aesculus and Malus, and its probable role in stimulating cambial activity. Amer. Jour. Bot. **24**: 51–58. 1937.
4. BOYSEN-JENSEN, P. Growth Hormone in Plants. Translated and revised by G. S. Avery, Jr. and P. R. Burkholder. McGraw-Hill Book Co., New York and London. 1936.
5. BROWN, B. A. Effect of time of cutting on the elimination of bushes in pastures. Jour. Amer. Soc. Agron. **22**: 603–605. 1930.
6. BUELL, J. H. Effect of season of cutting on sprouting of dogwood. Jour. Forestry **38**: 649–650. 1940.
7. CURTIS, O. F. The upward translocation of foods in woody plants. II. Is there normally an upward transfer of storage foods from the roots or trunk to the growing shoots? Amer. Jour. Bot. **7**: 286–295. 1920.
8. FINCH, A. H. Physiology of apple varieties. Plant Physiol. **10**: 49–72. 1935.
9. HAHNE, B. The origin of secondary dormant buds in deciduous fruit trees. Univ. California Publ. in Bot. **13**(5): 125–127. 1926.
10. HEINZE, P. H. and MURNEEK, A. E. Comparative accuracy and efficiency in determinations of carbohydrates in plant material. Missouri Agr. Exp. Sta. Res. Bull. 314. 1940.
11. HEPTING, G. R. Reserve food storage in shortleaf pine. Phytopathology **35**: 106–119. 1945.
12. ISHIBE, O. The seasonal changes in starch and fat reserves of some woody plants. Memoirs College of Sci. Kyoto Imp. U. Series B 11(1). 1935.
13. JESTER, J. R. and KRAMER, P. J. The effect of length of day on height growth of certain forest tree seedlings. Jour. Forestry **37**: 796–803. 1939.
14. JONES, C. H. and BRADLEE, J. L. The carbohydrate content of the maple tree. Vermont Agr. Exp. Sta. Bull. 358. 1933.
15. KARMARKER, D. V. The seasonal cycles of nitrogenous and carbohydrate materials in fruit trees. Jour. Pom. and Hort. Sci. **12**: 177–221. 1934.

16. Kramer, P. J. Effect of variation in length of day on growth and dormancy of trees. Plant Physiol. **11**: 127–137. 1936.

17. Kraus, E. J. and Kraybill, H. R. Vegetation and reproduction with special reference to the tomato. Oregon Agr. Exp. Sta. Bull. 149. 1918.

18. Leclerc du Sablon, M. Recherches physiologiques sur les matieres de reserves des arbes. Rev. Gen. Bot. **16**: 341–368; **18**: 2–25, 82–96. 1904; 1906.

19. Liming, F. G. Origin and growth of dormant buds in oaks. Jour. Forestry **38**: 226. 1940.

20. Little, S., Jr. Relationships between vigor of resprouting and intensity of cutting in coppice stands. Jour. Forestry **36**: 1216–1223. 1938.

21. Roberts, R. J. and Struckmeyer, B. E. The effects of temperature and other environmental factors upon the photoperiodic response of some of the higher plants. Jour. Agr. Res. **56**: 633–677. 1938.

22. Roth, E. R. and Sleeth, B. Butt rot in unburned sprout oak stands. U. S. Dept. Agr. Tech. Bull. 684. 1939.

23. Skoog, F. and Thimann, K. V. Further experiments on the inhibition of the development of lateral buds by growth hormone. Proc. Nat. Acad. Sci. **20**: 480–485. 1934.

24. Smyth, E. M. The seasonal cycles of nitrogenous and carbohydrate materials in fruit trees. Jour. Pom. and Hort. Sci. **12**: 249–292. 1934.

25. Stoeckler, J. H. When is plantation release most effective? Jour. Forestry **45**: 265–271. 1947.

26. Swarbrick, T. Studies in the physiology of fruit trees. I. The seasonal starch content and cambial activity in one- to five-year-old apple branches. Jour. Pom. and Hort. Sci. **6**: 137–156. 1927.

27. Thimann, K. V. On the nature of inhibitions caused by auxin. Amer. Jour. Bot. **24**: 407–412. 1937.

28. Thomas, W. Composition of current and previous seasons branch growth in relation to vegetative and reproductive responses in *Pyrus Malus* L. Plant Physiol. **7**: 391–445. 1932.

29. Zon, R. Management of second growth in the southern Appalachians. U. S. Forest Service Circ. 118, U. S. Dept. Agr. 1907.