

DIAMETER GROWTH OF SWAMP TUPELO:
SEASONAL PATTERN AND RELATION TO WATER TABLE LEVEL

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Abstract.--Patterns of diameter growth and the relation of diameter growth to water table levels were determined for 90-year-old swamp tupelo (*Nyssa sylvatica* var. *biflora* (Walt.) Sarg.) trees growing in an undisturbed habitat. Initiation and cessation of diameter growth varied from year to year and tree to tree. Initiation occurred over a 2½-month period (late March through May) and cessation over a 3½-month period (mid-July through October). Growth peaked in late May, declining only slightly in June through mid-July. Although growth occurred over a 32-week period, the average length of the growing season was 21 weeks, and within this 21 weeks there were nearly 6 weeks on an average in which no measurable growth occurred. Diameter growth during the May 2-July 25 period when 75 percent of growth occurred was related positively ($r^2=0.431$) to average water table level for the period. An analysis of the monthly relationships between water table and growth during this period revealed that higher water tables in April, June, and July and lower ones in May were related ($R^2=0.916$) to improved periodic growth.

Additional keywords: *Nyssa sylvatica* var. *biflora*, swamp drainage, growth initiation, intermittent growth, growth cessation.

INTRODUCTION

Swamp tupelo (*Nyssa sylvatica* var. *biflora* (Walt.) Sarg.) grows in head-water swamps and along black water rivers and streams of the South Atlantic and Gulf Coastal Plains. Although considerable data regarding growth and water relations of swamp tupelo seedlings are available (Harms 1970, Hook et al. 1970a, 1970b, 1971), similar knowledge for mature trees is limited. Such information as seasonal patterns and effects of ground water table levels (including flooding) is needed to predict changes in growth of mature swamp tupelo stands likely to result when natural water regimes in swamps and on surrounding lands are altered.

This paper reports on the diameter growth of swamp tupelo from data collected over a 6-year period from 9 swamp tupelo trees growing in an undisturbed swamp habitat.

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DESCRIPTION OF STUDY AREA

The study was established in the Bluebird Swamp which is about 200 hectares in size and is located on the Francis Marion National Forest, Berkeley County, South Carolina. Like many other nonalluvial or headwater swamps (Mattoon 1915) in the Carolina Coastal Plain, its water level is dependent upon precipitation and surface water draining from surrounding pine land, which is only a few feet higher in elevation. Although no well-defined stream channels are apparent, this headwater swamp drains into a small, intermittent creek, but during dry periods the water table drops below soil surface. The soil is a dark-colored Bayboro loam that is underlain with a gray-colored clayey horizon at 30 to 60 cm. The stand of swamp tupelo is even-aged (about 90 years old) and nearly pure in composition, with only a scattering of bald-cypress (*Taxodium distichum* (L.) Rich) and red maple (*Acer rubrum* L.) intermixed. On an average hectare there are 605 stems that are 12 cm dbh and larger, with 39 square meters of basal area, and 330 cubic meters of merchantable volume.

METHODS

Three plots with three trees each were established within a 30-hectare portion of the swamp. All trees selected were dominants; their diameters ranged from 30 to 38 cm and their heights from 25 to 30 meters. A well for observation of the ground water level was installed to a depth of 0.75 meter at the center of each plot. The bark was shaved at breast height and a dendrometer band (Liming 1957) was snugly fitted on each sample tree in March 1964.

Dendrometer band expansions and water table levels were measured at 2-week intervals throughout the 6-year period. Circumference measurements were read to the nearest 0.025 cm (0.01 inch) and the water table level to the nearest 3 cm (0.1 foot). Average diameter growth was calculated for each 2-week interval.

Multiple regression techniques were used to assess relationship of water table level and its fluctuation on diameter growth for various portions of the growing season.

RESULTS AND DISCUSSION

Seasonal pattern of diameter growth

The percentage of growth by biweekly periods (fig. 1) illustrates an average seasonal pattern of diameter for swamp tupelo trees measured in this study. Diameter growth for all trees reached its peak in late May, declined slightly in June through mid-July, and then dropped rather steadily from mid-July through mid-October when growth finally ceased. A great deal of variation occurred in this general seasonal pattern in that growth initiation, intermittency, and cessation differed from year to year and tree to tree.

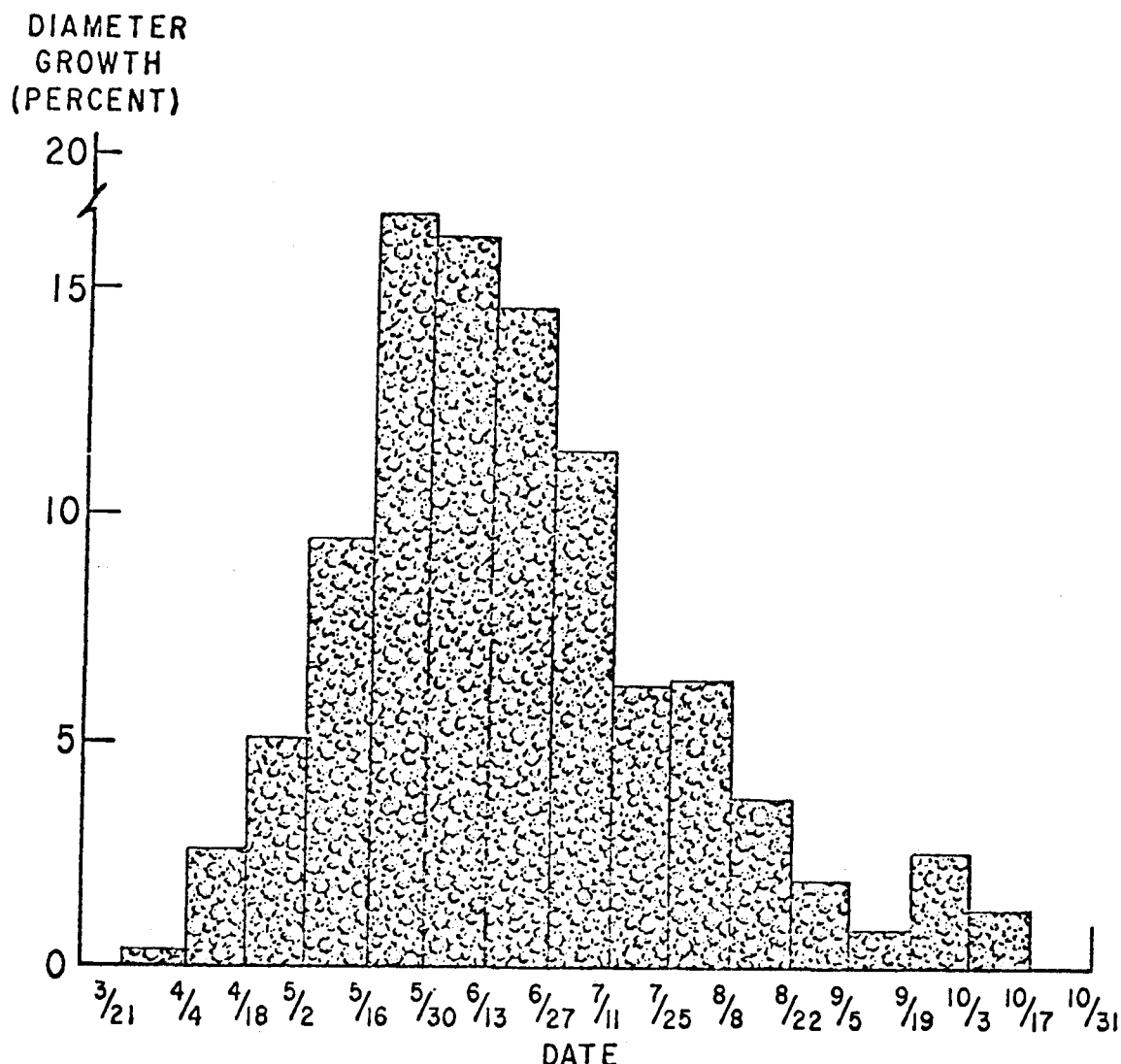


Figure 1.--Percentage of total diameter growth of swamp tupelo by biweekly periods (6-year average).

The initiation of measurable diameter growth varied from year to year by individual trees from late March until the end of May. Trees were usually in full leaf before their growth began. In the 6-year period, about two-thirds of the trees started their diameter growth by the end of April, but the remaining one-third did not begin growth until May. This growth initiation pattern is similar to that shown by water tupelo (*N. aquatica* L.) in southern Louisiana (Eggler 1955). Delayed growth initiation for diffuse porous hardwoods is presumably associated with the slow downward movement of auxin or other growth regulators from terminal buds (Kramer and Kozlowski 1960, Romberger 1963).

Although the 32-week period from March 21 to October 31 was the total time-span in which diameter growth was recorded, the average diameter growth

period was about 21 weeks. In the 6 years of the study, however, this period varied from year to year (19 to 24 weeks) and from tree to tree (18 to 24 weeks). Also, within this growing season there were nearly 6 weeks in which no measurable growth occurred, indicating that diameter growth of swamp tupelo is an intermittent process. Kozlowski and Peterson (1962) and Kramer and Kozlowski (1960) have found such to be the case for other species.

As with initiation, cessation of growth of individual trees occurred during a 3½-month period from mid-July to the end of October. In our 6-year study, 20 percent of the trees stopped diameter growth between mid-July and the first week in August, 30 percent between the first week in August and mid-September, and the remaining 50 percent from mid-September through October. None of the trees in the study were consistent from year to year in their growth cessation date. This 3½-month period of growth cessation also coincides with data for water tupelo in southern Louisiana (Eggler 1955).

Diameter growth and its relation to water table level

Cumulative annual diameter growth plotted as a sigmoid curve (fig. 2). Annual diameter growth, however, varied considerably in the six years of the study. Growth was low in 1964 (0.188 cm), 1967 (0.173 cm), and 1969 (0.157 cm); moderate in 1966 (0.226 cm) and 1968 (0.234 cm); and highest in 1965 (0.330 cm). Growth rate in 1965 exceeded that of other years from late May through July. In the 3 years with the poorest total growth, the rate slowed in mid-June rather than late July. Why did growth vary so much by year? One objective of our investigation was to determine if year-to-year variations in diameter growth of swamp tupelo were related to water, as measured by water table levels. The background for this hypothesis was the work we (Hook *et al.* 1970a) and others (Hosner and Boyce 1962, Dickson *et al.* 1965) had done with seedlings of swamp and water tupelo in which seedling growth was related to water regimes.

The most dominating feature of the natural habitat of swamp tupelo is water. Excess water restricts the normal aeration processes of soils and its presence, even for short duration, causes a number of chemical and microbiological changes in the root environment (Gambrell and Patrick (in press), McKee and Stolzy (in press)). Therefore, water can be assumed to be the dominant factor controlling plant growth in inundated soils.

The 12-week period (May 2-July 25) was chosen for the regression analyses of diameter growth and water table levels because swamp tupelo varies so much in its initiation of growth in the spring prior to this period and in its cessation in late summer and early fall after this period. Also, about 75 percent of the total annual growth occurs in this period.

The 12-week periodic growth was related positively ($r^2=0.431$) to average periodic water table level (fig. 3). However, using the average water table level for the 12-week period masks the effects that water levels in the different months of the growing season might have on growth. Indeed, the analyses of growth in the three 4-week periods (nominally, May, June, and July) indicate that this is the case (table 1). In these monthly analyses, the May (DG1) and July (DG3) diameter growth was related positively to the April and July water

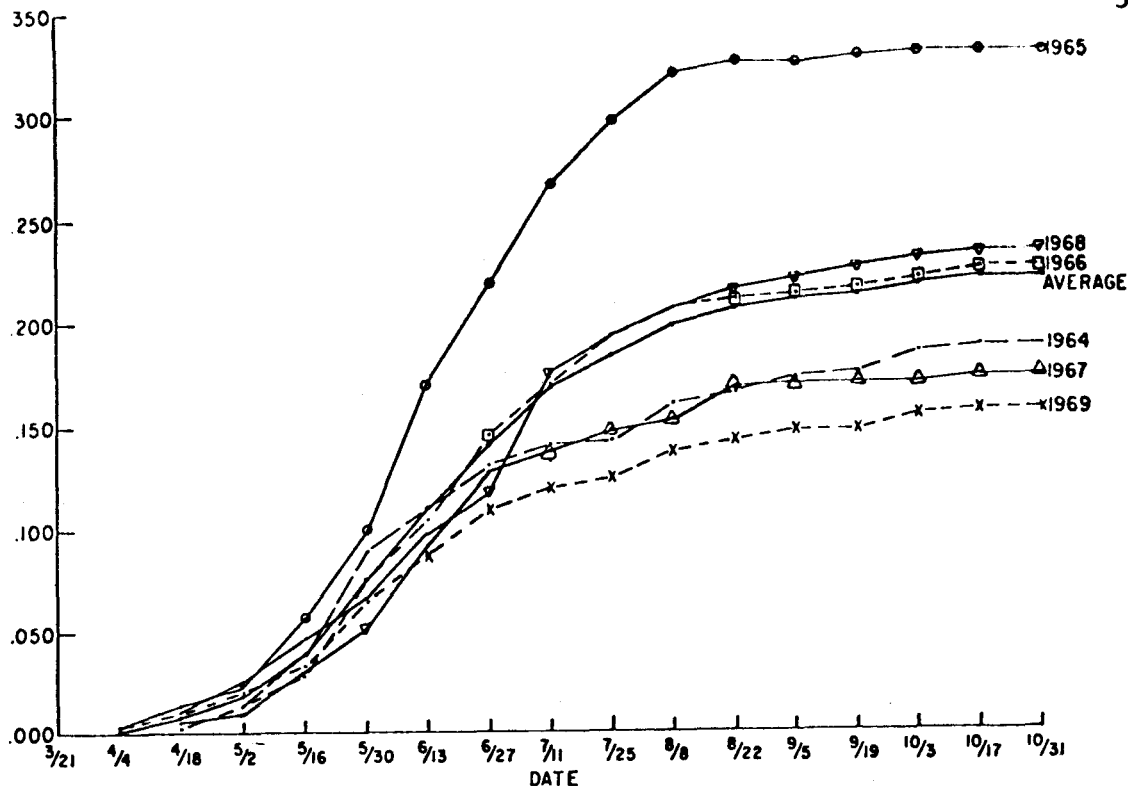


Figure 2.--Cumulative biweekly diameter growth by years for swamp tupelo.

DIAMETER
GROWTH (CENTIMETERS)

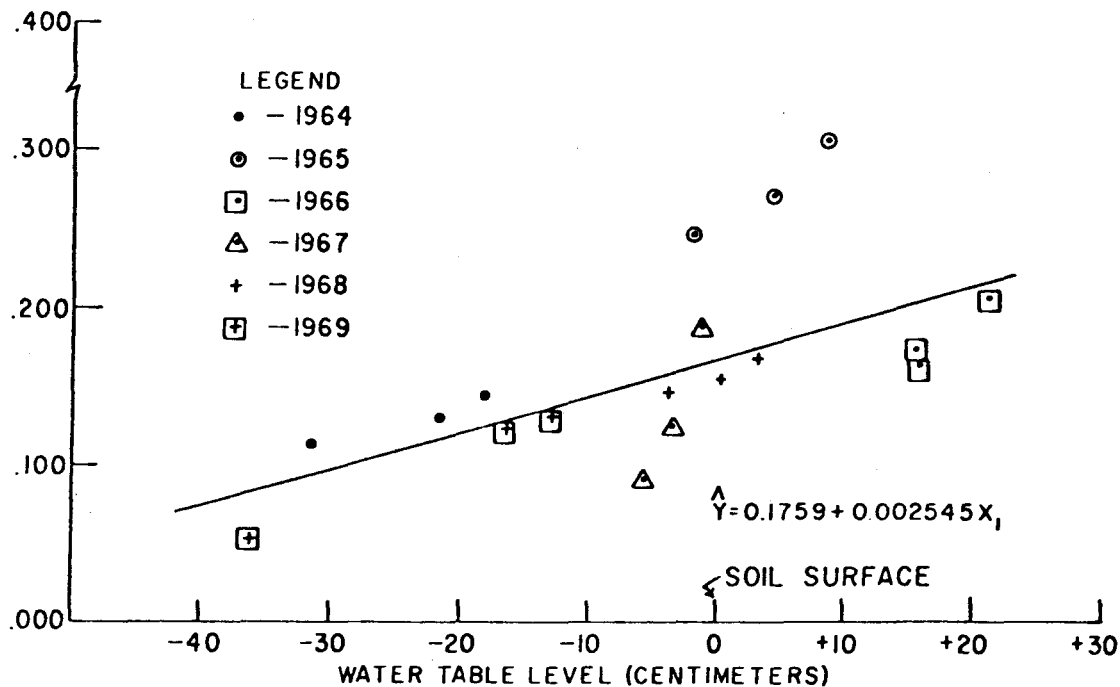


Figure 3.--Diameter growth of swamp tupelo during the May 2-July 25 period as related to water table level.

Table 1.--Regression coefficients for the relationships of water table levels and diameter growth of swamp tupelo by periods.

Water Table Level Periods ^{1/}	Diameter Growth Periods ^{1/}			
	DG1	DG2	DG3	DG4
	----- (b-coefficients) ^{2/} -----			
Y-Intercept	+0.04781	+0.07918	+0.02764	+0.10841
WTO	+0.00100	-----	-----	+0.00415
WTO ²	(NS)	-----	-----	(NS)
WT1	(NS)	-0.00095	-----	-0.00263
WT1 ²	(NS)	-0.00002	-----	(NS)
WT2	-----	+0.00111	(NS)	(NS)
WT2 ²	-----	(NS)	(NS)	+0.00002
WT3	-----	-----	+0.00149	+0.00390
WT3 ²	-----	-----	+0.00003	(NS)
R ²	0.4627	0.5875	0.7282	0.9158

^{1/} The periods are:

WTO = Average water table level (cm) from April 4 to May 2
 WT1 = Average water table level (cm) from May 2 to May 30
 WT2 = Average water table level (cm) from May 30 to June 27
 WT3 = Average water table level (cm) from June 27 to July 25
 DG1 = Diameter growth (cm) from May 2 to May 30
 DG2 = Diameter growth (cm) from May 30 to June 27
 DG3 = Diameter growth (cm) from June 27 to July 25
 DG4 = Diameter growth (cm) from May 2 to July 25

^{2/} A dash (--) in the table indicates that the water table level period was not included in the regression analysis. NS indicates that that variable was included in the analysis, but was nonsignificant.

table levels, respectively, but the June (DG2) growth was related negatively to water levels in May and positively to those in June. The same general relationship held when the 12-week diameter growth (DG4) was regressed against functions of the monthly water table levels (table 1). This periodic growth (DG4) was related positively to the April, June and July water levels and negatively to the May water table level and accounted for 91.6 percent of variation.

These results indicate that although diameter growth is, in general, positively related to increasingly higher water table levels, lower water tables in the early part of the growing season (May) are correlated with increased diameter growth. Thus, a fluctuation in the water levels during the growing season appears beneficial in terms of increasing growth for the whole season. From these data, the ideal growing season would have high water table levels in April, lower water table levels in May, followed by high water table levels in June and July.

Our results with swamp tupelo are similar to those obtained for water tupelo by previous workers. Silker (1948) found that flooding increased diameter growth in a water tupelo plantation near Wilson Reservoir in northwestern Alabama, and Klawitter (1964) showed that water tupelo growing in the Santee River Swamp, South Carolina, responded favorably to flooding throughout the year. Thus, swamp and water tupelo differ from most other tree species in that flooding tends to enhance growth.

Selection pressures on genetic traits are probably involved in these differences. Tupelos have been growing under flooded conditions for millennia and have developed traits which enhance survival and growth under very wet conditions. Hook *et al.* (1971) have concluded that anaerobic root respiration, oxygen transport from stem to roots, and toleration of high concentrations of CO_2 are adaptations which enable swamp tupelo to thrive in swamps. Tupelo rank poorly in capacity to compete with more mesophytic species on drier sites; this is not surprising since they are well acclimated to wet conditions. Our study and those of other workers (Silker 1948, Klawitter 1962, 1964) imply that practices that significantly lower water table levels in swamps probably would result in decreased growth of the tupelos. The net impact of drainage would be a profound change in the ecology of tupelo swamps.

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