

Effect of Swamp Size on Growth Rates of Cypress (*Taxodium distichum*) Trees

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ABSTRACT.—Growth rates of *Taxodium distichum*, tree species composition and environmental variables such as hydroperiod and organic matter depth were measured in small (<1-ha), medium (1–2-ha) and large (>5-ha) cypress swamps to determine if growth rates vary with swamp size and if biological and physical characteristics can provide an index to tree growth rates. Although trees grow faster in the centers of swamps, growth rates do not differ significantly among small, medium and large swamps, and they are highly variable within a given swamp. Overall tree basal area and *Taxodium* density are significant predictors of tree growth.

INTRODUCTION

Swamps dominated by cypress trees (*Taxodium distichum*) are a characteristic feature of landscapes in the southeastern United States. Although many of these swamps are less than 10 ha, together they account for approximately 3% of the land area in Florida alone (Bechtold and Knight, 1982). Because cypress swamps are so common and can be used as a source of wood products (Williston *et al.*, 1980) and sometimes for wastewater recycling (Ewel and Odum, 1984), interest in long-term sustainable management of them has increased. Research has been conducted on ecological relationships within cypress swamps (*e.g.*, Monk and Brown, 1965; Brown, 1981), but the variability, among swamps, of such basic parameters as tree growth rates and the factors that affect them is poorly understood.

Growth rates of many wetland tree species appear to be related to hydroperiod, the length of time that water stands above the soil surface. Fastest *Taxodium* growth rates are usually associated with intermediate hydroperiod (Mitsch and Ewel, 1979). Hydroperiods longer than 9 mo result in poor growth, regardless of water depth (Duever *et al.*, 1984b). On drier sites where reducing conditions in the soil may not persist so long, other species thrive, and *Taxodium* regeneration success is low (Marois and Ewel, 1983). However, nutrient inflow to a swamp may be just as important in controlling primary productivity as hydroperiod (Brown, 1981). Greater productivity of *Taxodium* at intermediate hydroperiods may be related to higher nutrient inflow than is found in swamps with short hydroperiods, and to more favorable redox conditions (and therefore greater nutrient availability) than are found in swamps with long hydroperiods.

In spite of variability in hydroperiod, virtually all cypress swamps have a characteristic layer of organic matter that increases in thickness from the edge of the swamp to the center, sometimes exceeding 1 m in depth (Monk and Brown, 1965; Coultas and Calhoun, 1975; Coultas and Duever, 1984). This organic layer has a high water-holding capacity and maintains soil moisture even when the water table is below the ground surface. It also plays an important role in nutrient storage, and fine roots are concentrated there (Hall and Penfound, 1943; Lugo *et al.*, 1984). The characteristic increase in tree size from edge to center in many cypress swamps is attributed to differential growth rates (Kurz and Wagner, 1953; Brown, 1981), which in turn may be related to increasing depth of organic matter (Duever *et al.*, 1984a).

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A very common type of swamp in Florida is the cypress pond, which is dominated by pond cypress trees (*Taxodium distichum* var. *nutans*) and often has standing water for more than 6 mo/yr (Marois and Ewel, 1983). There is no streamflow into or out of these swamps, and they vary in size from small (<1-ha), circular ponds, often called cypress domes, to larger (>10-ha) swamps that are much more irregular in size and shape. The objective of this research was to determine whether growth rates of *Taxodium* differ among cypress ponds of different sizes, and to identify physical and biological variables, such as those discussed above, that might provide an index to this component of swamp productivity.

METHODS

Study sites.—This study was conducted in the Withlacoochee State Forest in central Florida. This general region is called the Green Swamp, and its flat landscape is characterized by poorly drained pine stands interspersed with cypress swamps of various sizes and shapes. Three size classes of swamps were defined for this study: small (0.3–0.5 ha), medium (1–2 ha) and large (5–12 ha), and three swamps in each size class were selected. The small swamps are almost circular, they are deepest in the center, and the canopies have characteristic dome-shaped profiles. The larger swamps are irregular in both shape and profile.

Because our large swamps flow into other wetlands during exceptionally rainy years, it is likely that swamps larger than the ones we studied (and therefore with larger watersheds) would be categorized not as ponds but rather as “strands,” which are linear swamps with slowly flowing water. Therefore, the range of swamps that we examined spans the normal size range of cypress ponds in central and N Florida.

Merchantable timber had been removed from the three medium and three large swamps between 1925 and 1935, but no large-scale logging was carried out in the region after that. The history of the small swamps is not known, but they have almost certainly been logged during this century as well.

Swamp environment.—A staff gauge was placed in the deepest point of each swamp, and the water level was recorded approximately every 2 wk from March 1982 to March 1983. The mean water level, absolute fluctuation (standard error: SE), and relative fluctuation (coefficient of variation: CV) were calculated for each site.

Because organic matter in cypress ponds is typically deeper in the center than at the edge, organic matter depth was measured as close as possible to the center (defined as the point where water was deepest). In each swamp, three soil cores were taken to the A-1 horizon, which was less than 0.5 m deep in all the swamps and was primarily sand.

A nested analysis of variance and Duncan's multiple range test were used to detect differences in mean water levels and depths of organic matter at the deepest point among the three size classes of swamps and within each size class.

Floristic structure.—Structural characteristics of the vegetation were estimated from tree inventory data. In the small and medium swamps, 10-m × 10-m plots that had been established for another study were used as the basis for the inventory. All 28 plots in one small swamp were sampled, but because this proved to be too labor-intensive, only the plots along three transects were sampled in the other two small swamps (15 and 20 plots, respectively), and in all three medium swamps (30, 33 and 34 plots, respectively). In each of these swamps, one transect passed through the center, one ran along the edge, and one was midway between center and edge. Within the plots, the diameter at breast height (dbh, 1.3 m above the ground) was recorded for all trees that were greater than 3 cm dbh. If a tree had buttresses, which are common in *Taxodium*, the diameter was measured 45 cm above the butt swell.

In the large swamps, three transects were established perpendicular to the long axis of

the swamp. Thirty-one plots (10 m × 10 m) along the three transects in one of the large swamps were sampled as described above. To reduce the labor needed to obtain an adequate sample in these large, irregularly shaped swamps, the point-quarter method for sampling forest trees (Cottam and Curtis, 1956) was employed along the transects in the two other large swamps.

Basal area (m²/ha) and tree density (number of individuals/100 m²) were calculated for all tree species at each site and for *Taxodium* only. Analysis of variance and Duncan's multiple range test were used to determine significance of differences ($P < 0.05$) among the three swamp sizes. Importance values were calculated as the sum of relative values of density, basal area and frequency, with a maximum value of 300 (Curtis and McIntosh, 1951).

To determine if there were trends in diameter distributions related to swamp size, data were pooled for each swamp size. The mean percent of the total number of trees represented by each diameter class was then calculated for each swamp size class (small, medium, large).

Growth rates of trees.—*Taxodium* trees were sampled for growth rate determination according to a nested design. Four trees at each of three locations within each swamp were sampled: edge, midway between edge and center, and center. Growth rates and ages were obtained from increment cores extracted at breast height or 45 cm above the butt swell. An attempt was made to core the largest trees in each location, but this was not always possible because of the high incidence of heartrot. The cores were mounted on grooved wooden slats, sanded, and examined to distinguish true and false rings and to determine tree ages. Ring widths for the 30 most recent years were measured to the nearest 0.01 inch and then converted to metric units and to basal area increments, which are estimates of growth rates. Because the growth rates varied widely, all growth data were log-transformed for statistical analysis. Results are reported in the untransformed mode. ANOVA and Duncan's multiple range tests were used to evaluate significance ($P < 0.05$) of differences among swamps in both growth rates and ages.

Nested analyses of variance were also used to detect significant differences in growth rates and ages. A stepwise multiple regression was performed to determine which factors were most useful in predicting growth. The dependent variable was the mean log of the growth rate. Independent variables were total tree basal area, *Taxodium* basal area, total tree density, *Taxodium* density, number of species, mean water level, relative water level fluctuation, mean organic matter depth and mean tree age. Statistical analyses were performed with SAS (1982) at the University of Florida's Northeast Regional Data Center.

RESULTS

Swamp environment.—Because of exceptionally high rainfall during the year of our study, only two small swamps dried out completely, and then for only a short time. Consequently, hydroperiods of the swamps did not differ, although the water regimes suggest that large swamps would have the longest hydroperiods and small swamps the shortest (Fig. 1). There were significant differences in water level among small, medium and large swamps (Table 1). The cvs were highest for the small swamps, and the ranges of values for the medium and large swamps overlapped.

At the deepest point of each swamp, there was significantly less organic matter in the small swamps than in the medium and large swamps, which did not differ (Table 1). There were significant differences among mean organic matter depths within the medium and large size classes of swamps, but not within the smallest size class.

Floristic structure.—Twenty different species were recorded in the tree inventory. There was a strong negative correlation ($r = -0.91$) between the number of species and importance

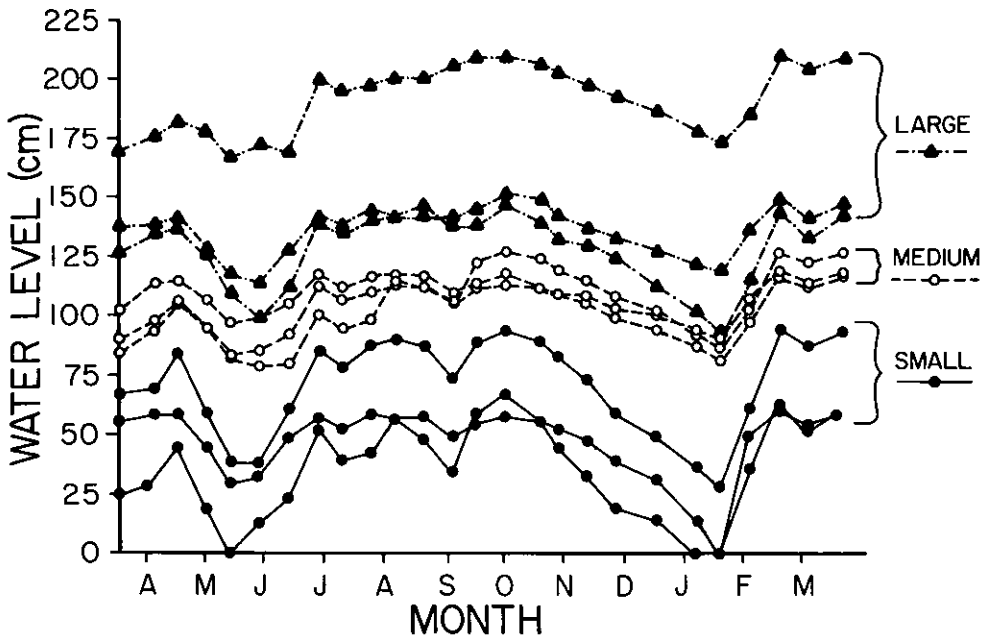


FIG. 1.—Biweekly changes in water level (March 1982–March 1983) in the nine study sites

value of *Taxodium* for the nine swamps. Medium swamps had the most species (12–15, $\bar{x} = 14$) and the lowest *Taxodium* importance values (171–181). The large swamps had the fewest species (4–9, $\bar{x} = 7$) and the highest *Taxodium* importance values (216–273). The small swamps were intermediate, with 10–11 species ($\bar{x} = 10$); *Taxodium* importance values ranged from 173 to 216.

Importance values for *Myrica cerifera* (wax myrtle), the next most common species, ranged from 12–50 with no clear trend related to swamp size. Only four other species had importance values greater than 20 in individual swamps [*Acer rubrum* (red maple), *Ilex cassine* (dahoon holly), *Nyssa sylvatica* var. *biflora*, (swamp black gum) and *Pinus elliotii* (slash pine)]. These species [along with *Quercus hemisphaerica* (laurel oak)] were present in at least seven of the nine swamps.

There were no significant differences in total basal area or *Taxodium* basal area among the three size classes, but density of all trees sampled and of *Taxodium* alone differed significantly among the three size classes (Table 1). Total density was significantly higher in the small and medium swamps than in the large swamps. *Taxodium* density was also higher in the small swamps than in the large swamps; values for the medium swamps did not differ significantly from either the small or large swamps. At least 75% of the total density was contributed by *Taxodium* in the three large swamps. The lowest values were among the small and medium swamps and were 58% and 59%, respectively.

Tree growth rates.—A nested analysis of variance showed no significant differences in growth rates among the three size classes (Table 1). Nor were there significant differences among swamps within each size class. There were significant differences in growth rates among all three of the sampling locations, with trees on the edges of swamps growing slowest, and trees in the centers growing fastest (Table 2).

TABLE 1.—Mean water level (standard error and coefficient of variation) and organic matter depths, basal area, tree density (standard error) and growth rates in nine cypress swamps in central Florida. Numbers with the same superscripts are not significantly different ($P < 0.05$)

	Small			Medium					Large		
	S1	S2	S3	M1	M2	M3	L1	L2	L3		
Area (ha)	0.3	0.3	0.5	2.0	1.8	1.3	5.3	11.1	9.2		
Mean water level (cm)	48 ^a	36 ^b	72 ^c	110 ^d	103 ^d	106 ^d	129 ^e	137 ^e	192 ^f		
(SE)	(2.9)	(4.0)	(4.0)	(1.6)	(2.2)	(3.0)	(3.0)	(2.0)	(2.9)		
(CV)	(31.5)	(57.4)	(28.5)	(7.4)	(11.1)	(14.5)	(11.9)	(7.5)	(7.7)		
\bar{x}	52 ^a	52 ^a	106 ^b					153 ^c			
SE	2.7	2.7	1.4					3.5			
Mean organic matter (cm)	3.7 ^a	5.0 ^{ab}	6.2 ^{ab}	25.2 ^c	11.5 ^{bc}	15.5 ^{cd}	21.8 ^{de}	21.0 ^{de}	34.2 ^f		
(SE)	(0.44)	(0.50)	(1.20)	(5.34)	(0.50)	(1.53)	(1.36)	(3.50)	(0.88)		
\bar{x}		4.9 ^a			17.4 ^b			25.7 ^b			
SE		0.54			2.41			2.40			
Basal area (m ² /ha)											
Total	44	59	56	56	53	54	53	58	67		
\bar{x}		53 ^a			54 ^a			57 ^a			
SE		4.6			0.9			4.1			
<i>Taxodium</i> only											
\bar{x}	40	51	50	50	47	46	52	51	66		
SE		47			48 ^a			56 ^a			
		3.5			1.2			4.8			
Tree density (no./100 m ²)											
Total	29.2	36.8	27.2	27.0	27.6	27.5	13.6	11.6	14.5		
\bar{x}	31.1 ^a				27.4 ^a			13.2 ^b			
SE	2.92				0.19			0.86			
<i>Taxodium</i> only											
\bar{x}	25.8	26.4	16.1	15.7	19.5	16.6	10.8	8.8	13.4		
SE		22.8 ^a			17.3 ^{ab}			11.0 ^b			
		3.34			1.15			1.33			
Growth rate (mm ² /yr)											
<i>Taxodium</i> only											
\bar{x}	954	693	960	937	996	1039	1422	1003	821		
		869 ^a			991 ^a			1082 ^b			
Range		362-1977			392-2340			365-2731			

TABLE 2.—Mean growth rate (mm²/yr) of four trees in each of three sampling locations. Overall means differ significantly at the 0.05 level

Swamp size	Location in swamp		
	Edge	Middle	Center
Small	624	806	1177
Medium	731	997	1245
Large	805	1145	1296
Range	569-1019	547-1379	873-1868
\bar{x}	720 ^a	983 ^b	1240 ^c

Analysis of covariance indicated that tree age did not have a significant effect on basal area growth over the last 30 yr. Nonetheless, there were significant differences in tree ages among three sizes of swamps. Trees in the small swamps averaged 69 yr, which was significantly younger than in either the medium (99 yr) or large (89 yr) swamps, which did not differ significantly from each other. There were also sampling location differences. Trees at the edge of a swamp were significantly older (93 yr) than trees in the center (79 yr), but neither differed significantly from trees midway along the radius (85 yr).

There were also differences in the diameters of trees in the three sampling locations. Trees at the edge (\bar{x} = 29.2 cm) and midway (\bar{x} = 30.4 cm) were significantly smaller than at the center (\bar{x} = 33.7 cm).

The analysis of covariance that was used in the nested model to test whether tree diameter varies with age must be interpreted conservatively, because the test statistics were approximated. The results suggest that tree age has a significant effect on diameter (r^2 = 0.63, P < 0.0001). The simple correlation between dbh and age was also significant (r^2 = 0.35, P < 0.0002), as expected, but the low correlation coefficient suggests that other factors, such as sampling location, are more important.

The nested procedure that was used to assess the relative variability of different levels in the sampling design (size of swamp, individual swamp, sampling location within swamp, and individual tree) in controlling growth rates facilitates comparison of these relationships (Fig. 2). Only 1% of the variability in growth rates was due to the size of a swamp or to characteristics of each individual swamp. There was more variability among trees within a sampling location (16%) than among locations within a swamp (10%). Almost 75% of the total variance was attributable to the year-to-year variation in growth rates.

Relationships among variables.—The three physical conditions that we studied were highly correlated with one another (Table 3). For instance, the small swamps had the lowest water level and shallowest organic matter. In large swamps, relative water level fluctuation was lowest and both water and organic matter were deepest.

The eight significant relationships between physical and floristic variables reflect the differences among swamps of different sizes, as discussed in the previous sections. The deepest water in the large swamps correlated positively with *Taxodium* basal area and negatively with tree density (total and *Taxodium* only). Correlations with mean organic matter depth and these structural characteristics followed the same pattern. There were positive relationships between relative water level fluctuations and density of all trees and of *Taxodium*. The small swamps, for instance, had the highest fluctuations and the highest densities.

Two significant correlations were found among the physical conditions and growth rate

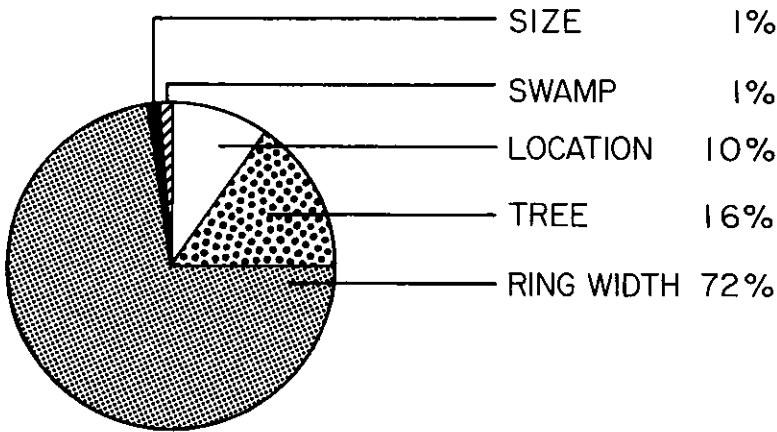


FIG. 2.—Relative variability in growth rates among all swamps at each level of the nested model: size classes, individual swamps within a size class, locations within the swamps, trees at each location, and ring widths within each tree

factors. A negative relationship existed between relative water level fluctuation and mean log of the growth rate and between relative water level fluctuation and mean tree age. No significant correlations were found among any of the floristic and growth variables.

In the stepwise multiple regression analysis, only total tree basal area and *Taxodium* density proved to be significant predictors of *Taxodium* growth rate in a swamp:

$$Y = 8.47 - 2.42 \times 10^{-2}X_1 - 3.19 \times 10^{-1}X_2$$

where

- Y = *Taxodium* growth rate;
 X_1 = total tree basal area;
 X_2 = density of *Taxodium*;
 $r^2 = 0.84$.

DISCUSSION

Impact of swamp environment on growth.—We found no significant differences in growth rates of *Taxodium* among ponds of different sizes. Nor were growth rates clearly correlated with the physical conditions that we measured; only relative water level fluctuation was inversely correlated with the log of the growth rate in the swamps. Although previous research demonstrated that *Taxodium* growth rates increase with increased nutrient availability (Brown, 1981; Nessel *et al.*, 1982; Lemlich and Ewel, 1984), any differences in nutrient availability that exist at our swamps must be masked by environmental conditions that allow the swamps to be nutrient sinks (*viz.* Dierberg and Brezonik, 1984). For instance, although larger swamps may have more inflowing water per unit area than smaller swamps because of their irregular shapes and longer perimeters, any additional nutrient subsidy may be offset by decreased opportunity for drydowns (Fig. 1) and mineralization.

Variability of Taxodium growth rates.—Results of our stepwise multiple regression analysis suggest that two biological variables, total tree basal area and *Taxodium* density, are the most useful for predicting overall growth rate. Variability among growth rates increases as level of aggregation decreases, from comparisons among swamp sizes to comparisons of

TABLE 3.—Correlation coefficients among physical and floristic variables. Only coefficients that were significant at the 0.05 level are included

	Mean water level fluctuation	Relative water level fluctuation	Mean organic matter depth	Basal area (all trees)	Density (all trees)	Number of species	Mean growth rate
Relative water level fluctuation	-0.82						
Mean organic matter depth	0.94	-0.74					
Basal area (<i>Taxodium</i>)	0.74		0.75	0.92			
Density (all trees)	-0.84	0.72	-0.73				
Density (<i>Taxodium</i>)	-0.80	0.79	-0.79		0.89		
<i>Taxodium</i> importance value					-0.70	-0.91	
Mean log of growth rate		-0.70					0.96
Mean age		-0.71					

locations within a swamp to comparisons of individual growth rings within a tree (Fig. 2). *Taxodium* is in fact very sensitive to changing environmental conditions, but the "environment" of one tree differs significantly from that of its neighbor. Brinson *et al.* (1981) were also unable to find simple relationships among properties of different wetlands and single environmental variables.

Location of an individual *Taxodium* within a swamp is a more important determinant of growth rate than the size of the swamp in which it is located. In spite of differences in water level, water level fluctuation, organic matter depth, tree density and basal area of *Taxodium*, average growth rates of large *Taxodium* trees are similar from swamp to swamp. Because overall tree basal area and *Taxodium* density were the only two factors that proved to be significant in predicting growth rates, perhaps inter- and intraspecific competition should be examined for their effects on *Taxodium* growth rates at different locations.

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