Comparative Biomass and Growth of Cypress in Florida Wetlands[1]

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ABSTRACT: Tree biomass and increase in biomass were determined for cypress (*Taxodium distichum*) in different systems in Florida. Ten trees were harvested to determine biomass regressions. Lowest biomass and tree growth rates were found in cypress-pine associations indicative of low water, in monospecific stands of cypress which are indicative of high water levels, and in a poorly drained cypress dome. Increases in individual tree growth ranged from 1.0 to 3.5 kg/y^{-1} in these groupings. Highest cypress tree growth rates were found in cypress-tupelo systems and cypress-hardwood systems. The latter are less dominated by cypress, however, so individual tree growth is greater (7.7 kg/y vs. 4.0 kg/y). Cypress-hardwood associations are known to be generally better drained than cypress-tupelo systems. Two experimental cypress domes currently receiving treated sewage effluent and groundwater showed high individual tree growth (5.0 and 4.2 kg/y, respectively), but little difference was noted between the two domes. Tree diameter increase showed normal cypress tree growth to be 1.0-2.0 mm/y with higher values of 2.8-3.3 in cypress-hardwood associations and the experimental cypress dome. Cypress in the poorly drained dome increased by only 2.0 mm/y.

INTRODUCTION

Cypress trees (*Taxodium distichum*) are found in a variety of wetland ecosystems throughout southeastern United States, along the Atlantic Coast and up the Mississippi River Valley to southern Illinois. Cypress-dominated ecosystems are characteristically still-water ponds or domes, fringes around lakes, floodplain backswamps or slowly flowing sloughs or strands.

The single feature common to all cypress habitats is standing water for at least part of the year. Cypress seedlings can only germinate on dry land (Demaree, 1932), so a fluctuating water level is necessary for a cypress system to survive over long periods. Mature cypress trees, however, can adapt to continual flooding (Matoon, 1916; Demaree, 1932; Dickson and Broyer, 1972).

Because cypress occurs in a wide range of wetland systems, it is possible to identify the hydrologic conditions by the trees that grow in association with the cypress. Cypress-hardwood associations are indicative of bottomland riverine forests and sloughs which experience a short hydroperiod (Carter *et al.*, 1973; Conner and Day, 1976). Here cypress do not dominate, and grow in association with species such as red maple (*Acer rubrum*), ash (*Fraxinus* sp.), box elder (*Acer negundo*), cottonwood (*Populus heterophylla*) and water oak (*Quercus nigra*). If drainage is poorer and the hydroperiod is longer in the riverine swamp, the cypress is found with water tupelo (*Nyssa aquatica*). The equivalent to water tupelo found in still-water ponds

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or domes with a similar hydroperiod but with stagnant water is swamp black gum (*Nyssa biflora*) (Penfound, 1952; Monk and Brown, 1965).

A cypress-pine association is indicative of severely drained conditions which allow slash pine (*Pinus elliottii*) or longleaf pine (*P. palustris*) to invade cypress. This condition was noted by the authors to be common in N-central Florida where drainage ditches lowered water levels near cypress domes. This association is also common at the edge of cypress domes where water is often intermittent and shallow (Monk and Brown, 1965). Cypress in pure stands generally indicate the other extreme of continuous high water. Several investigators (Penfound, 1952; Broadfoot and Williston, 1973) have stated that cypress is one of the swamp trees most tolerant to continual flooding. Anderson and White (1970) report on a cypress-tupelo swamp in southern Illinois where many hardwoods were killed when the water level was suddenly raised by a beaver dam.

While several ecological studies have been performed on the floristic structure of cypress swamps (*e.g.*, Hall and Penfound, 1939, 1943; Kurz and Wagner, 1953; Monk and Brown, 1965; Anderson and White, 1970; Montz and Cherubini, 1973), few data are available on the comparative growth of cypress in its various ecosystems and what factors may affect this productivity. Carter *et al.* (1973) made some measurements of net productivity of cypress in slough areas in the Big Cypress Swamp. Conner and Day (1976) recently reported on net productivity of a bottomland forest and a cypress-tupelo swamp in Louisiana. This study will present some biomass and tree growth data collected from Florida cypress swamps as part of an ongoing study of these wetlands as water conservation and nutrient recycling areas (*see* Odum *et al.*, 1977). Particular emphasis is paid to the variation in productivity among sites due to environmental variables, especially hydrologic conditions. Preliminary determinations of cypress growth in cypress domes subjected to high nutrient loadings from secondarily treated domestic wastewater and groundwater are also given.

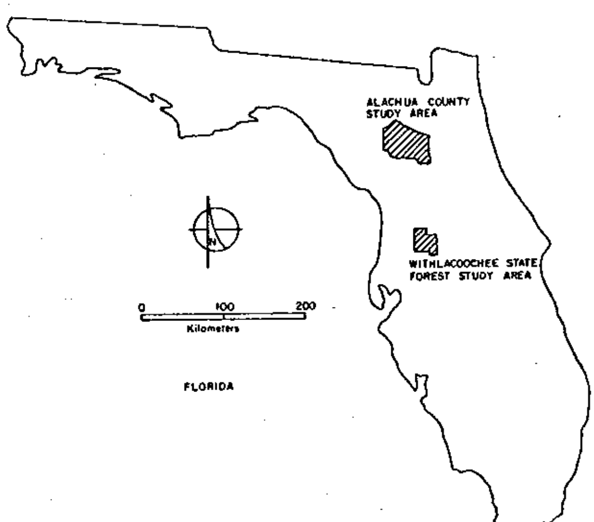

Fig. 1.—Location of two cypress study areas in Florida: Alachua County and Withlacoochee State Forest

METHODS

Study sites.—Two general areas with cypress wetlands in Florida were used in this study (Fig. 1). One area includes cypress dome ecosystems in Alachua County in N-central Florida. Three general sites within this area were utilized: (1) a cypress dome about 10 km NW of Gainesville in the Austin Cary Memorial Forest, where cypress trees were harvested for biomass regressions; (2) two experimental cypress domes 5 km N of Gainesville associated with an ongoing study of wastewater recycling and water conservation, and (3) a forest inventory site of two cypress domes near site (2) which is owned by Owens-Illinois Inc. and for which several years of cypress tree growth data were available. All sites were known to be dominated by pond cypress (*Taxodium distichum* var. *nutans*). These domes are located in an area dominated by the Ocala limestone formation (Eocene), overlying formations of Hawthorne sands, clays and limestones (Miocene) and surficial sands (Pleistocene). Solution holes that form in the Ocala limestone are thought to cause slight surface slumpages in Hawthorne and sand formations that in turn result in cypress domes (Pirkle and Brooks, 1959).

The two experimental domes mentioned above are part of an experiment being conducted to study the potential of these domes as areas of tertiary treatment for domestic wastewater and as areas of water conservation. Some preliminary results have been published elsewhere (Odum *et al.*, 1977). The two domes utilized here include one which received secondarily treated sewage at a rate of 2.5 cm/week (Sewage Dome) and a second dome which received an equivalent loading of hard groundwater (Groundwater Dome). The two domes at the Owens-Illinois site were characterized according to observed hydrologic conditions with one having very dry conditions and invading pine (Drained Dome) and the other having poor drainage conditions (Ponded Dome).

A wetland area in the Withlacoochee State Forest (Fig. 1) in W-central Florida was also included in the study due to the availability of cypress tree growth data. Parts of the forest are located in the NW corner of Green Swamp, a recharge area for the Floridan Aquifer and the headwaters of the Withlacoochee River. Because of slow drainage to the NW, this part of the state forest is dominated by cypress wetlands interspersed among pine flatwoods. No distinction was made between bald cypress (*Taxodium distichum*), if any, and pond cypress (*Taxodium distichum*) var. *nutans*) in data collected in this area.

Biomass.—Ten pond cypress trees, representative of the wide range of sizes encountered in most cypress domes, were harvested at the Alachua County Austin Cary Memorial Forest site for biomass determination. Diameter at breast height (dbh) and total tree height were measured with diameter tape and clinometer prior to felling each tree. The tree was cut at approximately 0.6 m above the ground surface with a chain saw, and the biomass was separated into leaves, small branches (less than 1 cm in diam), large branches and main stem. Wet weights were measured for each with a beam scale and subsamples were taken to determine moisture content. Total height and branch length were also measured on the felled trees. Roots of seven trees were pulled out with a tractor. Because of underlying clay layers, these roots had not penetrated more than 2 m deep. An estimate of 75% recovery was made, judging primarily from the taper of the roots (D. Post, Univ. of Fla., pers. comm.). Moisture content was determined for each set of roots and for stem cross sections by drying in a kiln at 100 C for 72 hr. Dry weights of leaves, branches, stem and roots plus stump were used as dependent variables (y) in regression analyses with the independent variable chosen as $x = \sqrt{\text{dbh x height}}$. Both dbh and height were expressed in centimeters. This independent variable was found most satisfactory for cypress by Carter *et al.* (1973). The regression equation had the form

$y = ax^b$ with a and b as regression coefficients. Biomass values were then determined for other cypress ecosystems by using the regression relations and dbh and height data for each cypress tree in that ecosystem.

Tree growth.—Changes in biomass ($\Delta B/\Delta t$) were determined for Alachua County and Withlacoochee State Forest study areas by utilizing data on changes in dbh over time. Spring-loaded aluminum dendrometers were used to record changes in dbh on 12 trees over a 1-year period at the Sewage Dome and Groundwater Dome in Alachua County. The two Owens-Illinois domes in Alachua County had four sets of dbh measurements for cypress trees over an 11-year period. Measurements of dbh at Withlacoochee State Forest were made at the beginning and end of a 6-year period in the 1960s by Florida Division of Forestry as a part of a Continuous Forest Inventory (CFI) data collection effort. Data from 21 circular plots of 809 m^2 each were used from this inventory. Biomass regressions developed from harvested trees were used together with changes in dbh to calculate change in total biomass change ($\Delta B/\Delta t$) for each cypress tree in the study plots over the measurement period.

Hydrologic conditions were inferred for cypress plots in Withlacoochee State Forest based on trees growing in association with the cypress. This led to determination of four classifications: (1) cypress hardwood; (2) cypress-tupelo; (3) cypress-pine, and (4) pure stand of cypress.

RESULTS AND DISCUSSION

Cypress harvest and biomass regression.—Data for the 10 pond cypress trees harvested in Alachua County are shown in Table 1. The dbh ranged from 8.4-36.8 cm and height varied from 7.8-24.9 m. Ground level diameter was generally from two to four times greater than dbh due to swollen buttresses characteristic of cypress (Kurz and Demaree, 1934). Most roots were found within 2 m of the surface because of underlying clay layers. The lateral spread of roots seemed to be one-third the height in most cases; no data on root distribution with depth were measured. Tree rings showed the trees to vary in age from 50-162 years. Constants for regression relationships used to determine pond cypress biomass were calculated from biomass data and are given in Table 2. A significant correlation was obtained for each relationship. Root biomass averaged 35% of total biomass. This is intermediate between 51% reported for mangroves (Golley *et al.*, 1962) and 11% reported for forested sphagnum bogs (Rodin and Basilevic, 1968).

Cypress biomass of study sites.—Regressions were used to determine cypress biomass in both Alachua County and Withlacoochee State Forest cypress wetlands. Results are summarized in Table 3. These calculations include only the contribution of cypress (>10 cm dbh) to total ecosystem biomass; data for calculating regressions were not found for other species present in the wetlands. However, since the two experimental cypress domes are almost exclusively cypress, biomass for these sites was characteristic of the entire ecosystem. The two other plots in Alachua County, the Drained Dome and the Ponded Dome, had low biomass values. These plots were located on the edges of cypress domes where trees are generally smaller (Vernon, 1947; Kurz and Wagner, 1953). Moreover, the plot in the Ponded Dome was only 50% cypress.

Four cypress associations were distinguished in the Withlacoochee State Forest according to presence of or absence of trees besides cypress. This enabled sites to be characterized according to their hydrologic regime. Subdominants in the cypress-hardwood site were ash, maple or water oak. These species are indicative of riverine systems with high water fluctuations and short hydroperiods. The cypress-tupelo sites included species of *Nyssa*, especially swamp black gum, as the subdominant. The

TABLE 1.—Pond cypress biomass data for trees harvested in Alachua County, Florida

	Tree number				
	1	2	3	4	5
Tree dimensions					
DBH, cm	8.4	11.2	12.7	15.0	19.0
Height, m	7.8	14.0	13.3	16.6	17.8
Age, years	52	50	66	66	63
Branch length, m	17.0	12.8	26.9	19.6	28.0
Height to 4-in diam, m	.8	2.2	4.6	6.4	11.1
Root depth, m	.9	.8	.8	.9	1.2
Root diameter, m	2.4	2.4	3.6	3.3	5.0
Ground diameter, cm	23.6	33.8	25.6	31.2	50.3
Dry weight, kg					
Leaves	.37	.80	1.7	.84	1.8
Small branch[a]	.57	1.3	2.7	2.3	3.5
Large branch	....	....	....	....	....
Total branch	.57	1.3	2.7	2.3	3.5
Stem	7.9	21.4	31.0	47.1	77.2
Stump[b]	5.2	7.0	4.2	6.7	18.8
Roots[c]	7.0	16.3	19.8	29.7	62.1
Total	21.0	46.8	59.4	86.6	163.4
Dry weight distribution % in:					
Leaves	1.7	1.7	2.9	1.0	1.1
Branches	2.7	2.8	4.5	2.6	2.1
Stem	37.6	45.7	52.2	54.4	47.3
Stump	24.7	15.0	7.1	7.7	11.5
Roots	33.3	34.8	33.3	34.3	38.0

TABLE 1.—(continued)

	Tree number				
	6	7	8	9	10
Tree dimensions					
DBH, cm	22.1	25.4	29.2	32.3	36.8
Height, m	16.8	18.0	20.6	20.9	24.9
Age, years	119	147	123-133	162	153
Branch length, m	16.5	37.1	40.9	45.5	45.5
Height to 4-in diam, m	12.4	14.2	16.9	17.5	18.1
Root depth, m	1.2	1.5	......	......	......
Root diameter, m	3.6	6.1	......	......	......
Ground diameter, cm	45.7	53.1	......	......	......
Dry weight, kg					
Leaves	1.6	3.8	4.2	2.5	5.8
Small branch[a]	2.9	6.8	5.4	6.3	7.8
Large branch	8.1	9.0	23.0	12.7	12.1
Total branch	11.0	15.8	28.4	19.0	20.9
Stem	116.5	161.4	218.5	258.6	399.4
Stump[b]	16.1	28.2	......	......	......
Roots[c]	69.1	158.8	......	......	......
Total	214.3	368.0	......	......	......
Dry weight distribution % in:					
Leaves	.8	1.0			
Branches	5.1	4.3			
Stem	54.4	43.9			
Stump	7.5	7.7			
Roots	32.2	43.1			

[a] Small branches are considered finger size (approximately 1 cm diam) and smaller

[b] Stump is considered to be the stem from ground level to the level at which the tree was cut (approximately 0.6 m above the ground)

[c] Seventy-five percent recovery of roots is assumed

cypress-pine association contained either slash pine or longleaf pine. Pure cypress stands had no other trees growing with the cypress.

Cypress biomass values ranged from 3.1-38.0 kg/m² for all Withlacoochee sites and averaged 13.5 kg/m². Table 3 gives the averages and standard errors for cypress biomass in the four associations. The cypress-tupelo association had the highest average (19.0 kg/m²) but also had the highest standard error range (14.3 to 23.7 kg/m²). The next highest cypress biomass was in the cypress-hardwood association. Cypress-hardwood sites had larger cypress trees than the cypress-tupelo sites (27.8 vs. 22.6 cm dbh), so the difference in biomass is reflected in the higher density of cypress in tupelo sites. There were 560 cypress/ha in the hardwood sites while the cypress-tupelo sites averaged 800 cypress/ha.

In both pure cypress stands and cypress-pine associations, size and biomass were substantially less than in hardwood and tupelo sites. These two areas probably represent the two extreme conditions for cypress. A pure stand of cypress is generally indicative of a high water level which excludes all other tree species, even *Nyssa* (Penfound, 1952). A cypress-pine association, conversely, reflectss a dry environment that has allowed water-intolerant pine to invade the cypress habitat.

Cypress tree growth.—Tree growth values for cypress in the ecosystems studied are given in Table 4. It is again stressed that these numbers are for cypress only and do

TABLE 2.—Regression analysis for pond cypress biomass

$$y = ax^b$$

y = biomass, g

$x = \sqrt{\text{dbh}\cdot\text{ht}}$

dbh = diameter at breast height, cm

ht = tree height, cm

	Number of trees n	Regression constants a	b	Correlation coefficient r
Leaves	10	7.16×10^{-2}	1.95	0.91
Branches	10	3.66×10^{-4}	3.20	0.95
Stem	10	8.25×10^{-3}	3.10	0.99
Stump and root	7	6.55×10^{-2}	2.68	0.95

TABLE 3.—Cypress biomass and numbers calculated for Alachua County and Withlacoochee State Forest study areas in Florida

Cypress ecosystem	Plot area (m²)	Cypress: % of total trees	No./ha	Mean dbh (cm)	Biomass (kg/m²)
Alachua County					
Sewage Dome	5272	95	510	23.7	13.6
Groundwater Dome	6900	80	720	21.0	17.5
Drained Dome	578	90	450	18.6 - 20.3[1]	6.8 - 8.4[1]
Ponded Dome	578	52	220	22.1 - 22.3[1]	5.1 - 5.3[1]
Withlacoochee State Forest					
Cypress-hardwood (4 sites)	3236[2]	62±12[3]	560±193[3]	27.8±3.6[3]	15.4±2.9[3]
Cypress-tupelo (6 sites)	4854[2]	80±5	800±159	22.6±2.2	19.0±4.7
Cypress-pure stand (4 sites)	3236[2]	100	580±193	19.5±0.8	9.5±2.6
Cypress-pine (7 sites)	5663[2]	76±8	460±154	20.3±1.3	10.1±2.1

[1] Range of values over 11-year period
[2] Combined area of all sites
[3] Average and standard error of site values

not reflect the entire ecosystem productivity. Biomass increase showed the same patterns as standing biomass did for different ecosystems. It is convenient to divide discussion on data into three categories.

The first category includes cypress ecosystems stressed by either too much or too little drainage. The ponded cypress dome in Alachua County had the lowest tree growth of any system examined. Both density of cypress and tree growth rates are lower than in any other cypress system considered. Larger cypress biomass increases were calculated for Withlacoochee State Forest cypress wetlands that were interspersed with pine trees and that were pure stands, and for the Drained Dome in Alachua County. Values at the Drained Dome and the cypress-pine system reflect competition stress from pine trees which have invaded following drainage. Growth in the pure cypress ecosystem is low, presumably because of water stress. Individual cypress trees in these three ecosystems were similar but low at 2.5-3.5 kg/y. The Alachua County dome had a very low value of 1.0 kg/y. Thus, either too low a water level, through increased competition, or too high a water level apparently due to flooding stress has a depressing impact on cypress productivity.

A second category includes cypress domes under experimental manipulation. Hydrologic conditions in both the Sewage and Groundwater domes are continual high water levels which could generally lead to lower productivities. However, each dome is receiving high levels of nutrients (ranges of total phosphorus were 0.1-0.7 mg-P/l and 0.5-6.8 mg-P/liter for the Groundwater Dome and Sewage Dome waters, respectively); this apparently contributes to greater productivities. The cypress dome receiving groundwater had a high cypress biomass increase for each tree of 4.2 kg/y while the value for the dome receiving sewage was 5.0 kg/tree. Indications are, therefore, that the two cypress domes are responding similarly to the input of additional nutrients although the Sewage Dome is receiving considerably more. The comparison, however, is not complete because measurements were begun only about 1 year after sewage application began. The effect of a forest fire which burned both domes prior to experimentation (Ewel and Mitsch, 1978) is also unclear. However, increase in biomass per tree is higher than that seen for the other two Alachua County domes discussed above. It is also higher than 3.1 kg/y for the harvested cypress trees listed in Table 1.

A third category includes a comparison of productivities of the cypress-hardwood

TABLE 4.—Cypress tree growth data measured in Alachua County and Withlacoochee State Forest study areas in Florida

Cypress ecosystem	Average diameter increase, mm/y	Increase in biomass	
		$kg \cdot tree^{-1} \cdot y^{-1}$	$g \cdot m^{-2} \cdot y^{-1}$
Alachua County			
Sewage Dome	3.0	5.0	253
Groundwater Dome	2.8	4.2	304
Drained Dome	1.5	3.5	159
Ponded Dome	0.2	1.0	22
Withlacoochee State Forest[1]			
Cypress-hardwood (4 sites)	3.3 ± 0.8	7.7 ± 2.9	336 ± 76
Cypress-tupelo (6 sites)	1.7 ± 0.2	4.0 ± 0.6	289 ± 58
Cypress-pure stand (4 sites)	2.0 ± 0.4	2.8 ± 0.7	154 ± 55
Cypress-pine (7 sites)	1.1 ± 0.2	2.5 ± 0.4	117 ± 27

[1] Values are average ± standard error

associations (riverine) and cypress-tupelo associations in Withlacoochee State Forest. Overall growth per cypress tree was much higher in the cypress-hardwood association than in the cypress-tupelo system (7.7 kg/y vs. 4.0 kg/y). Thus, cypress were growing much better in the hardwood association but there were fewer of them; maples, water oak and ash were important subdominants. The greater density of cypress in the tupelo association makes its overall cypress productivity higher. An analysis of variance showed significant differences ($\alpha = 0.05$) among the associations in tree growth, whether expressed as mm/y, $kg \cdot tree^{-1} \cdot y^{-1}$, or $g \cdot m^{-2} \cdot y^{-1}$.

Also shown on Table 4 are annual increases in diameter of cypress trees in the various ecosystems expressed as mm/y. Here, the cypress seem to be grouped in a range of 1.0-2.0 mm/y growth with these exceptions: (1) the ponded dome in Alachua County which showed an increase of only 0.2 mm/y over an 11-year period; (2) cypress-hardwood systems which had stem increases averaging 3.3 mm/y, and (3) the experimental domes which had values of 2.8-3.0 mm/y. A regression of the dbh vs. age of harvested trees listed in Table 1 gave a diameter increase of 1.6 mm/y; this sampling area had normal drainage conditions. Langdon (1958), on the other hand, found an increase of 4.6-5.3 mm/y for bald cypress in Louisiana, slightly higher than the value found for cypress-hardwood grouping here.

Plot productivity estimations.—An estimate of plot productivity was made by assuming that subdominant trees had the same growth characteristics and size as the cypress and that litterfall was related to total biomass according to litterfall turnover rate of 0.0165/year, a value measured at the Alachua County sites. Productivity values were divided by the percentage of trees that are cypress. This gave an average net productivity of 950 $g \cdot m^{-2} \cdot y^{-1}$ for the cypress-hardwood association and 760 $g \cdot m^{-2} \cdot y^{-1}$ for the cypress-tupelo association. A cypress-hardwood swamp and a cypress-tupelo swamp in Louisiana were found by Conner and Day (1976) to have

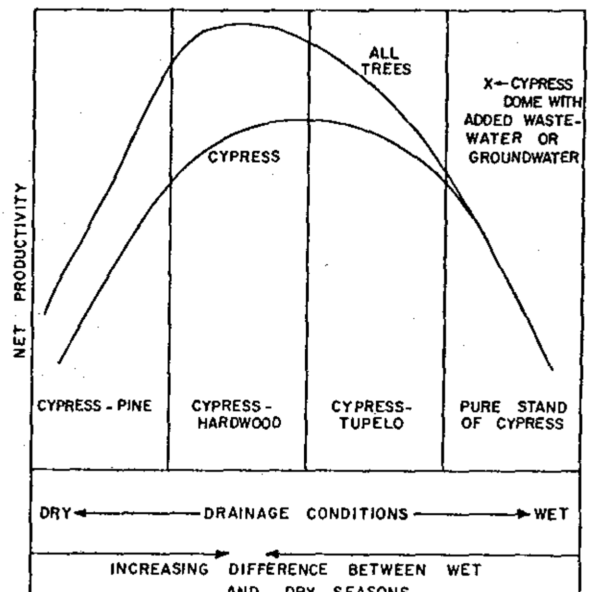

Fig. 2.—Generalized diagram showing the influence of drainage conditions on net productivity of cypress and cypress ecosystems

productivity values of 1374 $g \cdot m^{-2} \cdot y^{-1}$ and 1120 $g \cdot m^{-2} \cdot y^{-1}$, respectively.

Carter *et al.* (1973) reported on measurements of cypress productivity in S Florida in both undrained and drained cypress strands. Productivities were 858 $g \cdot m^{-2} \cdot y^{-1}$ for the undrained swamp and 387 $g \cdot m^{-2} \cdot y^{-1}$ for the drained swamp. This seems to contradict the findings in Alachua County where the Drained Dome maintained a higher productivity than the Ponded Dome. However, a cypress strand is a slow-flowing system with many species (especially red maple) in common with the cypress-hardwood riverine system. Conditions are thus equivalent to a highly productive cypress-hardwood system; drainage would force the system towards a dry, low productivity cypress-pine association.

Cypress tree growth and environmental conditions.—Cypress tree growth and ecosystem productivity have been shown to vary in different types of cypress ecosystems. The relationships between cypress and ecosystem productivity for different drainage conditions in which cypress is found are summarized in Figure 2. The effect of artificially adding wastewater with nutrients is also shown. On the basis of this figure some generalizations about the importance of environmental variables in productivity of cypress system in Florida can be made.

1. Cypress-hardwood associations, found primarily in riverine and flowing strand systems, have the most productive cypress trees. The short hydroperiod favors both root aeration during the long, dry periods and elimination of water-intolerant species during the short, wet periods. The continual supply of nutrients with the flooding river system conditions may be a second important factor in maintaining these high productivities. Although highest productivities per cypress tree are found in this system, the cypress is also least dominant.
2. Total cypress production in $g \cdot m^{-2} \cdot y^{-1}$ in the cypress-tupelo association is similar to the cypress-hardwood association. However, cypress are more numerous in the cypress-tupelo association and thus the growth rates of individual trees are less. Here the water levels are not extreme but the hydroperiod tends to be longer than in the cypress-hardwood association (Conner and Day, 1976).
3. Cypress tree growth is generally slow in pure stands of cypress. This condition probably indicates relatively high water levels that do not even allow for survival of *Nyssa* (Penfound, 1952). *Nyssa aquatica* in a southern Illinois cypress swamp under study by the senior author recently suffered high mortality rates when water levels were raised by beaver dams.
4. Cypress tree growth is likewise low in dry conditions where pine has invaded. There is some evidence that cypress grows much faster in dry conditions when competition is eliminated. However, in Florida, cypress is at an extreme competitive disadvantage relative to the several species of pine well-suited to dry conditions of the upland. Fire could eliminate cypress completely from these systems if conditions remained dry (Ewel and Mitsch, 1978).
5. The addition of both secondary sewage with high nutrients and groundwater with some nutrients may increase cypress tree growth over levels found in natural cypress domes. No evidence is yet available that sewage application results in higher productivities than equivalent groundwater application.

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LITERATURE CITED

ANDERSON, R. C. AND J. WHITE. 1970. A cypress swamp outlier in southern Illinois. *Ill. State Acad. Sci.*, **63**:6-13.

BROADFOOT, W. M. AND H. L. WILLISTON. 1973. Flooding effects on southern forest. *J. For.*, **71**:584-587.

CARTER, M. R., L. A. BURNS, T. R. CAVINDER, K. R. DUGGER, P. L. FORE, D. B. HICKS, H. L. REVELLS AND T. W. SCHMIDT. 1973. Ecosystem analysis at the Big Cypress Swamp and estuaries. U.S. Environ. Prot. Agency Region IV, Atlanta. EPA 904/9-74-002.

CONNER, W. H. AND J. W. DAY, JR. 1976. Productivity and composition of a bald cypress-water tupelo site and a bottomland hardwood site in a Louisiana swamp. *J. Bot.*, **63**: 1354-1364.

DEMAREE, D. 1932. Submerging experiments with *Taxodium*. *Ecology*, **13**:258-262.

DICKSON, R. E. AND T. C. BROYER. 1972. Effects of aeration, water supply and nitrogen source or growth and development of tupelo gum and bald cypress. *Ibid.*, **53**:626-634.

EWEL, K. C. AND W. J. MITSCH. 1978. The effects of fire on species composition in cypresss dome ecosystems. *Fla. Sci.*, **41**:25-31.

GOLLEY, F., H. T. ODUM AND K. WILSON. 1962. The structure and metabolism of a Puerto Rican red mangrove forest. *Ecology*, **43**:9-19.

HALL, T. F. AND W. T. PENFOUND. 1939. A phytosociological analysis of a cypress-gum forest in southeastern Louisiana. *Am. Midl. Nat.*, **21**:378-395.

——— AND ———. 1943. Cypress-gum communities in the Blue Girth swamp near Selma, Alabama. *Ecology*, **24**:208-217.

KURZ, H. AND D. DEMAREE. 1934. Cypress buttresses and knees in relation to water and air. *Ibid.*, **15**:36-41.

——— AND K. A. WAGNER. 1953. Factors in cypress dome development. *Ibid.*, **34**:157-164.

LANGDON, O. G. 1958. Silvical characteristics of bald cypress. USDA S.E. Forest Exp. St. Pap. 94. 7 p.

MATOON, W. R. 1916. Water requirements and growth of young cypress. *Proc. Soc. Am. For.*, **11**:192-197.

MONK, C. D. AND T. W. BROWN. 1965. Ecological considerations of cypress heads in north central Florida. *Am. Midl. Nat.*, **74**:126-140.

MONTZ, G. N. AND A. CHERUBINI. 1973. An ecological study of a bald cypress swamp in St. Charles Parish, Louisiana. *Castanea*, **38**:378-386.

ODUM, H. T., K. C. EWEL, W. J. MITSCH AND J. W. ORDWAY. 1977. Recycling treated sewage through cypress wetlands in Florida, p. 35-67. *In:* F. M. D'Itri (ed.). Water renovation and reuse. Marcel Dekker Press, New York—Basel.

PENFOUND, W. T. 1952. Southern swamps and marshes. *Bot. Rev.*, **8**:413-446.

PIRKLE, E. C. AND H. K. BROOKS. 1959. Origin and hydrology of Orange Lake, Santa Fe Lake and Levys Prairie Lakes of north central Florida. *J. Geol.*, **67**:302-317.

RODIN, L. E. AND N. I. BASILEVIC. 1968. World distribution of plant biomass, p. 45-52. *In:* F. E. Eckardt (ed.). Functioning of terrestrial ecosystems at the primary production level. UNESCO, Paris.

VERNON, R. O. 1947. Cypress domes. *Science*, **105**:97-99.

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