# AN OLD-GROWTH CYPRESS STAND IN OKEFENOKEE SWAMP

G. Ronnie Best

Center for Wetlands, University of Florida, Gainesville, FL 32611.

David B. Hamilton[1] and Gregor T. Auble

Institute of Ecology, University of Georgia, Athens, GA 30602.

ABSTRACT - A remnant stand of old-growth pond cypress in Okefenokee Swamp, Georgia, was studied. The rooting media is a shallow-flooded, strongly acid, deep peat soil. Cypress is the dominant feature of the old-growth community towering well above the subcanopy of broad-leaved evergreen trees. Although Taxodium has the greatest basal area for trees, its importance value in the tree class is superceded by Gordonia >> Taxodium >> Persea ~ Magnolia > Nyssa. However, Taxodium dominates overall community structure in basal area (35.18 $m^2$/ha for Taxodium; 60.06 $m^2$/ha for community) and importance value (20.6%). Tree diversity ($\bar{H}$), based on six species, for the community is 1.80 with a maximum possible diversity of 2.58. Taxodium replacement is lacking indicating its eventual demise as the community dominant. Replacement predominantly by Gordonia and secondarily by Magnolia and Nyssa appears to be the successional trend for this old-growth cypress community.

## INTRODUCTION

Few areas exist in the Southeast where man's activities have not disturbed natural areas. Even the once pristine Okefenokee Swamp has been drastically altered during the past century through extensive logging (Hopkins, 1947; Izlar, 1984b) and canal digging (Hopkins, 1947). Natural perturbations by fire have often been complicated by man's intervention (Cypert, 1961; Izlar, 1984a). Nonetheless, isolated areas do exist where perturbations by man have had little impact on natural communities. This paper describes such a community, a unique remnant stand of old-growth pond cypress (Taxodium ascendens) occurring in a shallow peaty area of the Okefenokee. Apparently, the community has not been sufficiently disturbed in the last few centuries to alter its natural succession to a bay swamp dominated by broadleaf evergreen hardwoods. This bay swamp represents a variation of the bayhead community that Monk (1966) considered to be climax on seasonally flooded areas.

### Description of the Study Area

The stand lies on the northeastern perimeter of Grand Prairie in the southeastern section of the Okefenokee Swamp, Georgia. The stand appears to be an undisturbed remnant of a more extensive Taxodium-dominated swamp forest in the eastern portion of the Okefenokee. Duever (1979), who treated the

[1]Present address: U.S. Fish and Wildlife Service, Ft. Collins, CO 80526.

site as an example of a large "tree house" (a peat-formed island), estimated the size of the area to be about 1000 m in diameter. Canopy trees in the site range between 30 and over 90 cm in diameter at breast height and over 30 m in height, suggesting the area was most certainly spared from logging in the early part of the century. Several of these canopy trees are 400-500 years old or older (Duever, 1979). Fire scars on the larger trees and several of the younger understory trees indicate that the area has been burned, though not severely, during recent fires. Numerous completely burned trunks exist on the outermost perimeter of the forest facing Grand Prairie indicating the forest may have covered a greater area than it presently does.

## METHODS

A detailed census of woody plants was conducted on two separate occasions during the summers of 1978 and 1979. The 1978 census was part of an intensive site-specific study on this unique stand, whereas the 1979 census was part of a comprehensive survey of major woody communities in Okefenokee Swamp. During both surveys, large quadrats with smaller nested quadrats were used to survey the larger and smaller classes of individuals. Vascular plant nomenclature follows Radford et al. (1968).

During the 1978 census all woody plants greater than 1 m in height were measured by tree, sapling, or seedling classes. The tree size class (individuals with a 10 cm or greater diameter at breast height [dbh]) was sampled in nine 10-m x 20-m plots. The sapling size class (2-10 cm dbh) was measured in four 5-m x 10-m plots nested within the first four tree quadrats. Seedlings (woody plants $\geq$1 m in height but <2 cm dbh) were sampled in four 2-m x 4-m plots also nested within the larger 10 quadrats. Species and breast height diameter were recorded for all individuals greater than 1.3 m (standardized "breast height" for this study). Species and height were recorded for plants between 1 and 1.3 m in height.

The 1979 census was part of a more comprehensive survey of all major woody plant communities throughout the swamp. Two quadrat sizes were used for all size classes. Individuals with a dbh of less than 5 cm were sampled in eight 2-m x 4-m plots located randomly within a larger bounded 20-m x 40-m quadrat randomly placed well within the stand to minimize forest edge effect. Woody plants larger than 5 cm dbh were sampled in four 10-m x 20-m plots also located within the larger bounded quadrat. Species, breast height diameter, and whether or not the trees were live or dead were recorded for all individuals. Data in this report are based only on live individuals.

Importance values were calculated for woody plants by summing data on relative frequency, density and dominance (basal area), and converting to a basis of 100%. Importance values were calculated for trees (which included all individuals with the potential to attain upper canopy stature) and shrubs as separate size classes, and for all woody plants as a whole. Species diversity ($\overline{H}$) for the tree size class was calculated as follows:

$$\overline{H} = \sum \rho_i \log_2 \rho_i \qquad (1)$$

where $p_i$ is the sampling probability. The statistic used for calculating diversity was:

$$H' = c/N \left(N \log_{10} N - \sum n_i \log_{10} n_i\right) \quad (2)$$

where N is the total number of all individuals, $n_i$ is the total number of individuals of each species, and c = 3.321928 to convert from $\log_{10}$ to $\log_2$ (Lloyd et al., 1968). The maximum diversity possible ($H'_{max}$) for the site was calculated using the function:

$$(H'_{max}) = \log_2 N. \quad (3)$$

Since the diversity of a community depends on the number of species and their pattern of distribution (i.e., clumped, even, etc.), a measure of site homogeneity, or evenness ($J'$), was calculated using the following method as described by Zar (1974):

$$J' = \frac{\overline{H}}{H'_{max}}. \quad (4)$$

Tree species data from the 13 10-m x 20-m quadrats were used for diversity calculations.

## RESULTS

The old-growth cypress stand in the Okefenokee Swamp is characterized by three relatively distinct tiers of woody plants. The lower stratum is dominated by shrubs that generally do not exceed 4 m in height. The dominant shrubs are Lyonia lucida (fetterbush), Clethra alnifolia (sweet pepperbush), Smilax laurifolia (laurel greenbrier), and Itea virginica (virginia willow). Vaccinium arboreum (sparkleberry), Leucothoe racemosa (sweetbells lencothoe), Rhus radicans (poison ivy), Vitis spp. (wild grape), and Lyonia ferruginea (staggerbush) are also present, but to a much lesser extent. Numerous tree seedlings and saplings also occupy this stratum. This layer, although occasionally patchy, is relatively continuous throughout.

The middle stratum covers a large zone, ranging from 4 m to slightly over 15 m in height, and, like the shrub layer, is relatively continuous. This layer is dominated at the lower level by Ilex cassine (including coriacea) (dahoon) (generally treated as shrubs except when used to parallel data presented by others on diversity), and at the upper level by Gordonia lasianthus (loblolly bay) and an occassional large Magnolia virginiana (sweet bay). Persea palustrus (red bay) and Nyssa sylvatica var. biflora (black gum) are also common components in the middle stratum.

A large void approximately 10 m wide separates the middle tree stratum from the upper tree stratum. This stratum consists solely of Taxodium ascendens. The Taxodium canopy generally occupies a span between 20 and 30 m. The upper canopy distribution is very spotty, with usually one or two and sometimes four or five Taxodium merging their canopies.

Additional descriptive information used to characterize the old-growth cypress stand is presented in Table 1. In this study woody plants are treated either as trees or shrubs based on their potential to attain upper canopy status. Gordonia is the most frequently encountered tree individual as reflected in its high frequency and density. However, its dominance relative to structure is overshadowed by Taxodium with a basal area of 35.18 $m^2$/ha, almost triple that of Gordonia (13.46 $m^2$/ha). Persea, Magnolia, and Nyssa combined contribute less than 15% to the total basal area of trees in the site. The relative contribution to the community by individuals in the tree stratum as expressed by importance value (sums of relative frequency, density, and dominance converted to a basis of 100%) is dominated by Gordonia followed by Taxodium >> Persea ~ Magnolia > Nyssa.

Total stem density for woody plants greater than 1 m high is 27,339 stems/ha, quite similar in density to the 28,386 stems/ha reported by Schlesinger (1978) for a relatively unique deep-water cypress community in the western portion of Okefenokee Swamp. However, in Schlesinger's site Taxodium comprises 8% of all woody plants, whereas only 0.5% of the woody plants are Taxodium in the old-growth community. In both sites composition of the remaining individuals is dominated by several commonly shared shrub species. A cypress community in the Great Dismal Swamp, Virginia, has a density of 1560 stems/ha for individuals with a breast height diameter greater than 2.54 cm (Dabel and Day, 1977). That compares to 1739 stems/ha for the same size distribution (excluding shrubs) in the old-growth community.

The apportionment of individual species contribution to basal area is often used to assess community dominance since it is a measurement of the utilization of resources by a species (Whittaker, 1970). Total basal area for the site (Table 1) is 60.06 $m^2$/ha with 94% (56.25 $m^2$/ha) in tree species and 6% (3.91 $m^2$/ha) in shrubs. Schlesinger's (1978) deep-water cypress community has a community basal area of 80.35 $m^2$/ha with 8.6 $m^2$/ha in standing dead yielding a comparable live plant basal area of 71.75 $m^2$/ha. Dabel and Day's (1977) cypress community has a basal area of 59.3 $m^2$/ha. These basal areas are remarkably similar considering that the basic similarity between the communities is that they are occasionally or regularly flooded swamps with Taxodium as the dominant canopy species. Dissimilarities in community structure is apparent when one realizes that Taxodium comprises 86% of the basal area in the Okefenokee deep-water cypress community (Schlesinger, 1978), 47% in the cypress community in the Great Dismal Swamp (Dabel and Day, 1977), and 59% in the old-growth Okefenokee cypress community (Table 1). Based on these data, it is apparent that the old-growth cypress community is more similar to the more distal and younger ( ~130 years; personal communication: F. P. Day) cypress community in the Great Dismal Swamp, probably because of a similarity in flooding regime, than to the more proximal deep-water cypress community in Okefenokee Swamp.

The understory consists of a dense layer of woody vegetation. The denseness of the shrub layer is more apparent when one realizes there are, on the average, almost 2.5 stems/$m^2$. Most species of this layer are broad-leaved, mostly evergreen shrubs. Ilex, treated as a shrub though intermediate in stature between shrubs and trees, dominates the shrub component primarily because of its moderately high density and high basal area relative

to other shrub species. Based on importance value, Ilex > Lyonia ∿ Clethra >> Smilax >> Itea as significant contributors to the shrub layer.

When all woody plants within the community are considered as a whole, there is a shift in the relative importance value of certain species. Taxodium replaces Gordonia as the dominant tree, and Ilex shares its dominance in the shrub layer with Clethra and Lyonia. When viewed from the whole community perspective the dominance of basal area by Taxodium supercedes the higher frequency and density of Gordonia, resulting in Taxodium having a 25% higher community importance value than its nearest competing tree species, Gordonia, or any other dominant woody plants. Ilex also shifts in significance in the shrub layer becoming more similar in importance value to Clethra and Lyonia.

The reproductive success of the tree species may be ascertained by comparing the densities (Table 2) of seedlings (<2 cm dbh and >1 m high), saplings (2-10 cm dbh), and trees (>10 cm dbh). Gordonia, Persea, and Magnolia have sufficient numbers in both the seedling and sapling size class to sustain their potential contribution as canopy species. Considering that about 14% of the trees are Nyssa, the complete absence of Nyssa seedlings and the relatively few saplings is not understood. It is questionable whether or not there are sufficient numbers in the smaller size class to establish Nyssa in the canopy. However, even as a potential contributor to the upper canopy, Nyssa is still an immature tree with most of its representatives in the smaller size class of trees. The lack of reproductive success for Taxodium is quite apparent especially since there are no individuals smaller than the 26 cm dbh size class (actually the smallest Taxodium individual recorded was 30 cm dbh). In fact, the mean breast height diameter for Taxodium sampled during the surveys was 53.1 cm (standard error [S.E.] ± 9.6 cm).

Only six tree species (i.e., woody plants with 10 cm dbh) occur in the site, though a few large slash pine (Pinus elliottii) are clumped near the outer edge. These are Taxodium, Gordonia, Magnolia, Nyssa, Persea, and Ilex. Ilex is, in this case, treated as a tree since it has a few individuals in the tree size class and is often treated as such by other authors. Tree diversity ($\bar{H}$) (Table 3) in the site is 1.80 (S.E. ± 0.09); considering there are only six species, the maximum diversity ($H'_{max}$) possible for this community is 2.58. For the plant community described, the estimated evenness ($J'$) of the population distribution pattern is 0.70. These data correspond more closely to diversity values for bayheads ($\bar{H}$ = 1.75) than for cypress domes ($\bar{H}$ = 1.16) (Monk, 1966, 1968), although the similarity in species numbers and composition more closely match those for cypress domes. Partial accounting for these discrepancies lies in the fact that the old-growth cypress community in the Okefenokee is more similar to a floodplain cypress community than to cypress dome communities. In fact, Taxodium dominates cypress dome communities, accounting for 60% of the average importance value (based on the sum of relative frequency and density) with the other species common to the old-growth community accounting for only 16% of the average importance value (Monk and Brown, 1965). A comparison of similar data (Table 1) for the old-growth community reveals that Taxodium contributes only 7% to the average importance value.

## DISCUSSION

The old-growth cypress stand in the Okefenokee Swamp consists of an overstory of tall, rather widely spaced Taxodium and a three-tiered understory. The subcanopy has a relatively uniform distribution, is of medium height, and is dominated by Gordonia. The canopy of Ilex melds the subcanopy with the dense shrub layer. The dense shrub layer, although patchy, covers much of the ground surface.

The larger Taxodium in the stand are rather old with estimated ages of 445, 528, and 587 years for three individuals cored by Duever (1979). Duever states that ring quality for Taxodium is "fair-good" (based on a sample size of 126 trees over all of Okefenokee Swamp). Therefore, it is safe to assume that at least several of the older Taxodium have been present in the site for over 400 years. If one assumes some reliable correlation between age and diameter, and given that the 587-year-old Taxodium is 96 cm dbh, then the younger Taxodium must be older than 100-150 years. This figure corresponds with the estimated time of encroachment of the bay species. Selected individuals of Gordonia, a community codominant with Taxodium, have estimated ages of 67, 73, and 91 year for three of the larger trees (ring quality, fair-good; N = 38) (Duever, 1979). Three larger Magnolia have estimated ages of 122, 124, and 145 year. However, ring quality for Magnolia is "poor-fair" (N = 58), and can be used to estimate site age only in conjunction with the other species. The few Pinus elliottii observed at one edge of the site have ages of 98, 124, and 140 year (ring quality, good; N = 32). These are in the upper limits of known ages for P. elliottii (Pomeroy and Cooper, 1956; Hebb and Clewell, 1976). Therefore, based on estimated ages (Duever, 1979) and size class distribution (Table 2), it is apparent that successful establishment of Taxodium has not occurred in the last 100-200 year, indicating long-term succession towards a community dominated by evergreen hardwoods, locally known as bay swamps. This trend concurs with the succession model suggested by Hamilton (1978, 1984) for Okefenokee Swamp and by Monk (1968) for woody swamps in north-central Florida.

Taxodium presently dominates the stand in stature, basal area, and overall community importance. However, Gordonia has already gained a dominant position of importance as a tree species and is replacing Taxodium in community importance. Gordonia currently comprises 22.4% of the community basal area. This plus its significance as a dominant component of the canopy, as reflected in its high frequency and density, makes Gordonia a serious competitor as the potential single community dominant to replace Taxodium. This trend differs considerably from the successional trend of cypress-to-bay communities for this region as noted by Monk (1968) where bay communities are codominated by Magnolia and Persea and to a lesser extent Gordonia. Even a slash pine-to-bay successional community in the panhandle of Florida is becoming dominated by Magnolia with Nyssa and Persea as secondary codominants. Gordonia are not even present in this latter community (Hebb and Clewell, 1976).

The significance of Gordonia as a dominant community component is not well understood, and may be related to numerous factors. However, the process through which terrestriallike communities develop in Okefenokee Swamp

results in the creation of numerous variable-sized peat islands scattered throughout the swamp (Cypert, 1972). By being somewhat isolated from terrestrial communities, plant species invasion would be restricted. Gordonia seeds, much like P. elliottii seeds, are wind disseminated, increasing the potential for dispersal to remote areas. These species are expected to gain an early advantage in encroaching on habitable sites. Seeds of Persea, Magnolia, and Nyssa, on the other hand, are much larger and are probably restricted to dispersal primarily by animals or on rare occasion by floating to a site during flood events. Based on the apparent restricted water flow pattern in this section of the Okefenokee, seed transport to this site by flooding is highly improbable. Although mature, seed-producing individuals do occur in the site, it is still not known whether or not Persea, Magnolia, or Nyssa will become codominants in the canopy. Magnolia has a sufficient number of seedlings and saplings and may eventually share canopy dominance with Gordonia. The trend for Nyssa is not clear, yet evidence suggests it will not secure a dominant role in community structure. However, based on our observations and on those of Duever (1979) regarding Persea, it appears that Persea is stressed in communities in the Okefenokee. Almost all individuals of Persea observed in the present study, except for seedlings and a few small saplings, consisted of only one or two small live apical branches; the primary bole was generally dead. This concurs with observations of Duever (1979). He states "the larger red bay (Persea) were invariably hollow..." (p. 32). Thus, Persea is not expected to increase in importance in the community, even with the eventual demise of Taxodium, and may eventually be all but eliminated from the site.

## CONCLUSIONS

The apparent eventual demise of Taxodium as the community dominant and the replacement with evergreen hardwood species in this old-growth cypress community supports the successional scheme for these swamp communities (Hamilton, 1978, 1981; Monk, 1968). The old-growth cypress stand cannot be perpetuated without major disturbance because there are no Taxodium in the understory to succeed it. Disturbances of the last 100-200 years, including numerous fires and attempts to drain the swamp, have not been of sufficient magnitude to alter the successional trend in the community. This stand will eventually be a Gordonia-dominated bay swamp, a variation of the red bay–sweet bay community type occurring within the peaty swamp series described by Penfound (1952).

Acknowledgments-This study was supported by NSF grants DEB-76-12292 and DEB-78-08842. We thank P. Anderson, G. Gibson, D. Jennings, D. McPherson, V. Osteen, and B. Vaughn for field assistance and Frank P. Day for his careful review of the manuscript. This is Contribution Number 26, Institute of Ecology, University of Georgia, Okefenokee Ecosystem Investigations.

## REFERENCES

Cypert E. (1961) The effects of fires in the Okefenokee Swamp in 1954 and 1955. Am. Midl. Nat. 66, 485-503.

Cypert E. (1972) The origin of houses in the Okefenokee prairies. Am. Midl. Nat. 87, 448-458.

Dabel C. V. and Day Jr. F. P. (1977) Structural comparisons of four plant communities in the Great Dismal Swamp, Virginia. Bull. Torrey Bot. Club 104, 352-360.

Duever M. J. (1979) Ecosystem analysis of Okefenokee Swamp: Tree ring and hydroperiod studies. Okefenokee Ecosystem Investigations, Technical Report No. 5. University of Georgia, Athens. 72 pages.

Hamilton D. B. (1978) Vegetation mapping and successional relations. In Integrated Studies of the Okefenokee Swamp Ecosystems II. Biogeochemical Aspects of Hierarchial Level Structures (Report of Research Accomplished). A proposal and project report to NSF (eds B. C. Patten [PI] et al.), pp. 351-370.

Hamilton D. B. (1984) Plant succession and the influence of disturbance in Okefenokee Swamp. In Okefenokee Swamp: Its Natural History, Geology, Geochemistry (eds A. D. Cohen, D. J. Casagrande, M. J. Andrejko, and G. R. Best), (this book).

Hebb E. A. and Clewell A. F. (1976) A remnant stand of old-growth slash pine in the Florida panhandle. Bull. Torrey Bot. Club 103, 1-9.

Hopkins J. M. (1947) Forty-five years with Okefenokee Swamp. Ga. Soc. Nat. Bull. No. 4, 69 pages.

Izlar R. L. (1984a) Fire and climate in the Okefenokee swamp-marsh complex. In Okefenokee Swamp: Its Natural History, Geology, Geochemistry (eds A. D. Cohen, D. J. Casagrande, M. J. Andrejko, and G. R. Best), (this book).

Izlar R. L. (1984b) Okefenokee logging operations: A burbon and branch water success story. In Okefenokee Swamp: Its Natural History, Geology, Geochemistry (eds A. D. Cohen, D. J. Casagrande, M. J. Andrejko, and G. R. Best), (this book).

Lloyd M., Zar J. H. and Karr J. R. (1968) On the calculation of information-theoretical measure of diversity. Am. Midl. Nat. 79, 257-272.

Monk C. D. (1966) An ecological study of hardwood swamps in north-central Florida. Ecology 47, 649-654.

Monk C. D. (1968) Succession and environmental relationships of the forest vegetation of north-central Florida. Am. Midl. Nat. 79, 441-457.

Monk C. D. and Brown T. W. (1965) Ecological considerations of cypress heads in north-central Florida. Am. Midl. Nat. 74, 126-140

Penfound W. T. (1952) Southern swamps and marshes. Bot. Rev. 18, 413-445.

Pomeroy K. B. and Cooper R. W. (1956) Growing slash pine. USDA Farmers' Bull. 2103, 28 p. Washington, D.C.

Radford A. E., Ahles H. E. and Bell C. R. (1968) Manual of the Vascular Flora of the Carolinas. University of North Carolina Press, Chapel Hill.

Schlesinger W. H. (1978) Community structure dynamics and nutrient cycling in the Okefenokee cypress swamp-forest. Ecol. Monogr. 48, 43-65.

Whittaker R. H. (1970) Communities and Ecosystems. Collier-Macmillan Ltd., London. 158 pages.

Zar J. H. (1974) Biostatistical Analysis. Prentice-Hall, Inc., Englewood Cliffs, N.J. pp. 35-38.