Ecology, 61(6), 1980, pp. 1412–1421

THE EFFECTS OF FLOODING ON THE SWAMP FOREST IN LAKE OCKLAWAHA, FLORIDA[1]

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Abstract. A 26-km stretch of the Oklawaha River in north-central Florida was impounded in 1968, forming a 5265-ha reservoir and flooding 1620 ha of mixed deciduous hardwood swamp to depths up to 3 m. Carolina ash (*Fraxinus caroliniana* Mill.), baldcypress (*Taxodium distichum* [L.] Rich.), red maple (*Acer rubrum* [L.]), and swamp tupelo (*Nyssa silvatica* var. *biflora* [Walt.] Sarg.) were the important tree species, with smaller amounts of cabbage palm (*Sabal palmetto* [Walt.] Lodd), button bush (*Cephalanthus occidentalis* L.), and several species of oak and elm. Tree mortality 3 yr after flooding was closely related to water depth, but it also varied with species and diameter. All trees of all species had died in those parts of the reservoir flooded in excess of 1.3 m. Mortality decreased progressively as prevailing water depth decreased below 1 m. At 0.8 m mortality averaged 41%, at 0.7 m it averaged 17%, and at 0.2 m it averaged 2%, about the same as natural mortality in unflooded areas of the swamp. Baldcypress, swamp tupelo, and cabbage palm were the most flood tolerant. The oaks were least tolerant. Measurements at the end of the fourth, sixth, and seventh growing seasons showed that the rate of mortality had dropped to low but still above-natural levels. Under all flooding depths mortality was least in the larger trees, those >38 cm in diameter. Trees <13 cm in diameter suffered the greatest losses. As depth of water increased, the proportion of the root systems killed by flooding increased, and the amount of starch in tissues of living roots decreased.

Key words: baldcypress; Carolina ash; hardwood swamp; red maple; reservoir flooding; soil aeration; swamp flooding; swamp tupelo.

INTRODUCTION

Lake Ocklawaha is located in Putnam and Marion Counties in north-central Florida and forms part of the north and west boundary of the Ocala National Forest. The lake, also known as Rodman Reservoir, is a 5265-ha impoundment constructed as a part of the Cross Florida Barge Canal. It came into existence in the fall of 1968 with the closing of a dam across the Oklawaha River near the community of Rodman.

The lake is a long and relatively narrow reservoir extending generally west and south from Rodman Dam a distance of about 26 km to Eureka, where another dam was constructed, but not closed, across the Oklawaha River (Fig. 1). Contained almost entirely within the floodplain of the river, the lake is generally <2 km wide over most of its length, though it widens to >3 km in the vicinity of Rodman Dam. When the lake is filled to capacity at a pool elevation at the dam of 6 m above mean sea level, the average water depth is about 2 m.

Construction of the Cross Florida Barge Canal was halted in 1971, when it was about one-third complete, to permit an assessment of the changes that the completed works would cause in environmental relationships of the region. As part of this assessment, the

[1] Manuscript received 17 August 1978; revised 17 March 1980; accepted 19 March 1980.

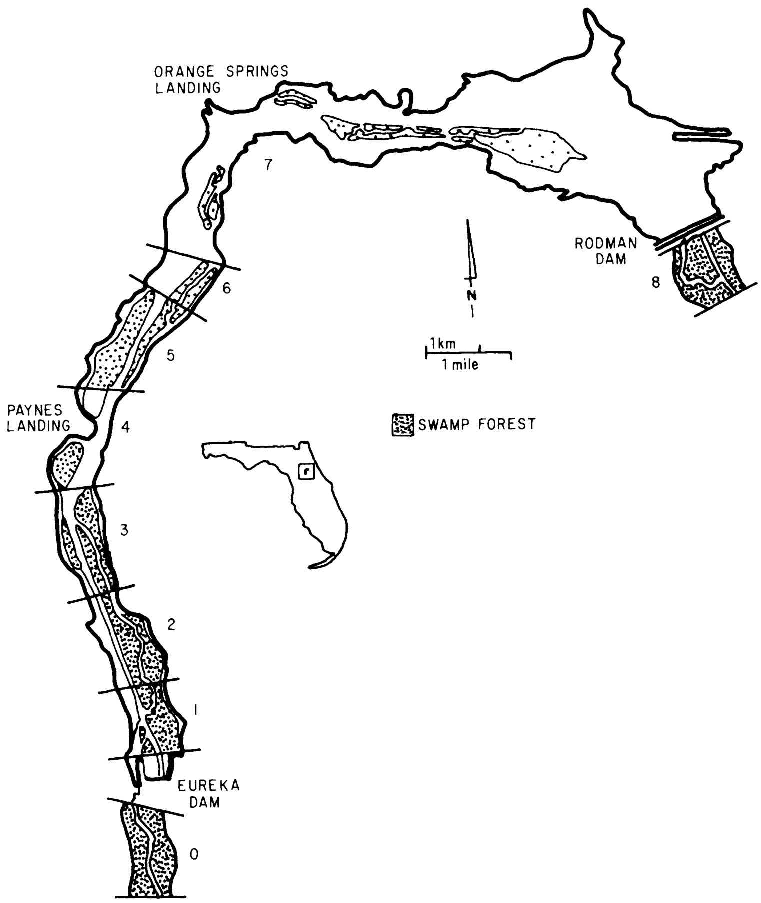

FIG. 1. Lake Ocklawaha, showing areas of swamp forest and the boundaries and numbers of sample populations. Inset map of Florida indicates location of lake.

authors undertook to document the effects of flooding on the swamp forest impounded when Rodman Dam was closed. Our objectives were to investigate the relationship of flooding depth to mortality of the major tree species and to determine the physiological responses of the tree roots to flooding.

This report is based on the results of field and laboratory studies made between the spring of 1972 and the fall of 1975.

The Oklawaha Ecosystem

The Oklawaha River is one of the principal waterways of Florida. Rising in a chain of lakes in the central peninsular highlands, it flows north and then eastward for about 113 km before joining the St. Johns River a few miles below Lake George.

Flooding on the river normally occurs in early fall each year, and in the area now occupied by the reservoir, water levels averaged 0.3 to 0.6 m above spring and summer lows. Maximum levels can exceed the average by as much as 0.9 m. Low flows are usually in May (United States Forest Service 1973).

Precipitation over the Oklawaha basin varies greatly during the year. About half the annual rainfall of 1270 to 1397 mm occurs in the summer, from June through September. Late fall and early spring tend to be dry. The average temperature is about 21°C, and while below-freezing temperatures may occur between November and April, frost rarely persists for more than 24 h. The growing season is about 300 d (Monk 1965).

The floodplain of the river is relatively narrow, ranging from 0.8 to 1.6 km in width. The floor of the floodplain is uneven, with numerous hummocks and hollows interspersed with drainageways and sloughs of varying depth. The hollows and sloughs generally have mucky bottoms. The soils are mucks and sandy loams underlain by freshwater marls and mucks. The most common soil series were Terra Ceia Muck, Placid Mucky fine sand, and soils of the Anclote-Tomaka association.

The dominant plant community is a swamp forest of mixed deciduous hardwoods. The major species are Carolina ash (*Fraxinus caroliniana* Mill.), pumpkin ash (*F. profunda* [Bush] Bush), baldcypress (*Taxo-*

dium distichum [L.] Rich.), red maple (*Acer rubrum* L.), swamp tupelo (*Nyssa sylvatica* var. *biflora* [Walt.] Sarg.), cabbage palm (*Sabal palmetto* [Walt.] Lodd), and button bush (*Cephalantus occidentalis* L.). A fuller discussion of the ecosystem is given by Monk (1966) and by the environmental statement prepared by the Forest Service for the Oklawaha River (United States Forest Service 1973).

When Rodman Dam was closed, all but about 1620 ha of the swamp forest had been cleared by cutting or by being crushed into the ground with heavy machinery. The uncut forest was left to provide habitat for fish and wildlife. The subsequent flooding of the reservoir, however, placed the remaining forest under chronic stress because of the artificially high and stable water levels. While tree species in river swamps are well adapted to temporary, seasonal flooding, many cannot survive the stress imposed by a constantly high water level. As a result, extensive mortality had occurred in the flooded forest by the time construction of the canal was halted. However, much of the river channel and its bordering forest were still intact in the southern end of the reservoir. In 1972, 3 yr after flooding, an aerial survey showed that about 460 ha on both sides of the river for a distance of about 13 km north of Eureka Dam were still forested with living trees. Most of the trees along the remaining 13 km of the river within the reservoir were dead.

Methods and Procedures

Field studies

The principal objective of this study was to evaluate the effects of flooding on the forest as a whole; therefore, it was necessary to establish a series of sample plots throughout the swamp so that we could obtain data that represented the entire population of trees. To accomplish this sampling efficiently, aerial photographs were used to divide the surviving forest into six arbitrary subpopulations occupying areas, each about 1.6 km long, northward from Eureka Dam (Fig. 1). A seventh population was designated to include the open water area of the reservoir above Rodman Dam. This population contained few live trees and was not sampled. Two unflooded control populations were established outside the reservoir, one above Eureka Dam, and one below Rodman Dam. These populations, 0 and 8, represented undisturbed forest against which the flooded forest was compared. Circular 0.04-ha plots, randomly located on the aerial photos, were established in April 1972. The numbers of plots per population varied with area and number of trees. Most populations had 10 plots, population 6 had 4, population 5 had 18, and population 4 had 8. A total of 80 plots was installed.

The data collected included species identification, diameter at breast height (dbh) of all trees living and dead, and an estimate of stress based on appearance of the live crowns (i.e., color, leafiness, and general vigor). The plots were first measured in April 1972 after the forest had been flooded for three growing seasons. At that time the surface water depth on each plot was also measured. The pool elevation at Rodman Dam was then at 5.5 m above mean sea level.

The second measurement, in November 1972, followed the fourth growing season, and the third measurement, in February 1975, the sixth growing season. A fourth measurement, in August 1975, was made a few months before the end of the seventh growing season.

The stress estimates based on crown condition proved to be too subjective for a physiological evaluation of the effects of flooding. In an effort to obtain an objective and quantifiable measure of stress, we developed a procedure for examining the root systems of the trees so that we could observe the physiological condition of the roots. We assumed that the presence of living roots <2.5 mm in diameter indicated a functioning root system. Conversely, the absence or death of these small roots was taken to indicate a dead or declining root system.

The root system of each tree to be sampled was quartered by imaginary lines running through the trunk in north-south and east-west directions. A large lateral root was located in each quadrant and partially excavated with spade and bucket auger as deeply as necessary to determine whether it met our criterion for a viable, functional root. If the first root was dead, a second was examined. The presence of one living lateral root having small absorbing roots was enough to classify the quadrant as viable.

Roots were excavated on 10 plots in population 5 in April 1972 and on all 80 plots in November1972; none were examined in 1975. On each of the plots visited, the roots of the 10 living trees 2.5 cm and larger in dbh nearest the plot center were examined. Root samples were collected from the first baldcypress, swamp tupelo, ash, and red maple trees encountered, tagged as to condition, and placed in plastic bags on ice in a portable cooler for subsequent microscopic examination.

Laboratory studies

A random selection of the root samples obtained in the field were examined to evaluate the amount of food reserves (stored starch) in different tissues as an indication of tree vigor. Fresh longitudinal sections of roots were cut free-hand and stained with an iodine solution (1.8% IKI in water; Johansen 1940) to ascertain the presence of starch grains in roots of cypress, gum, ash, and red maple. The amount of starch present in the storage tissues was quantified by assigning a numerical rating as follows: tissues devoid of starch grains (0); scattered and sparse (1); light to moderate levels (2); abundant in all storage cells (3); and high concentrations in all storage cells (4).

TABLE 1. Water elevation of Lake Ocklawaha from 1968 through September 1975.

Date	Reservoir elevation (m above mean sea level)	Approximate duration (mo)
Sept. 1968, dam closed	4.1	8
May 1969–June 1969	4.3	2
July 1969–Nov. 1970	5.9–6.2	16
Dec. 1970–Aug. 1972	5.5	20
Aug. 1972–Feb. 1973	4*	6
Feb. 1973–Dec. 1974	5.5	23
Dec. 1974–Mar. 1975	4.6	4
Mar. 1975–Sept. 1975	5.5	7

* An elevation of 4 m above mean sea level is approximately the natural pre-flooded surface elevation of the Oklawaha River from the north end of population 5 and southward.

TABLE 2. Average depth of water above the soil surface in the tree populations with the reservoir level at Rodman Dam at 5.5 m above mean sea level.

Population number	Plot category	Surface water depth (cm) $\bar{x} \pm$ SE
0	Control	29.2 ± 4.6
1	Reservoir	20.3 ± 6.6
2	Reservoir	52.1 ± 5.1
3	Reservoir	65.8 ± 5.1
4	Reservoir	82.3 ± 6.1
5	Reservoir	107.2 ± 5.6
6	Reservoir	120.6 ± 9.6
8	Control	24.1 ± 4.8

Data analysis

Data for the most numerous taxa—ash, maple, cypress, and gum—were segregated by species, while oak, palm, button bush, etc. were lumped as "others." The data were summarized by population for each measurement date and tabulated as number of trees per hectare by species and also by 13-cm diameter classes. Multiple regression analyses were computed to provide indications of the importance of dbh, species, and water depth to tree survival.

The data obtained from the root excavations were summarized for each tree. The trees were scored as having none (0), one, two, three, or four quadrants with dead roots and assigned to viability class I, II, III, IV, or V. Trees with no dead root quadrants were generally healthy and vigorous and were assigned to class I; those with dead roots in all four quadrants were placed in class V. The number of trees in each class was expressed as a percentage of the 10 trees excavated in each plot. The root sampling scheme did not permit analysis of the data by species.

RESULTS

Between the fall of 1968, when Rodman Dam was closed, and August of 1975, when the last tree measurements were taken, the average water levels of Lake Ocklawaha varied considerably (Table 1). There were both natural, seasonal fluctuations because of variation in the amount of water coming in from the Oklawaha River and also fluctuations due to changes in elevation maintained at the spillway by the Corps of Engineers. Except for a 6-mo period in the middle of the 4th yr when the pool elevation was at 4 m above mean sea level, the forest was continuously flooded to depths exceeding the natural water levels that existed prior to impoundment.

Average elevation of the river decreases about 2.7 m between Eureka at the south end of the reservoir and Orange Springs landing near the north end. Hence, at a reservoir elevation at Rodman Dam of 5.5 m above mean sea level, water depth increased from a few cm above the soil surface at Eureka Dam to 2.7 m or more at Rodman Dam. Table 2 shows the average depth of water above the soil surface in each tree population when the reservoir elevation at Rodman Dam was at 5.5 m above mean sea level.

Summary data of tree numbers and mortality for each species are given in Table 3. The data were originally recorded as number of living and dead trees present on the date of measurement but are presented to show mortality as a percentage of the sum of living and dead trees tallied in April 1972. This value was taken to approximate the number of living trees present in 1968 when Rodman Dam was closed. Mortality on each date was thus calculated from the cumulative number of trees dying since April 1972. No adjustment for natural mortality since 1968 has been attempted, but the data from the control populations indicate that the rate of natural mortality was not very great.

The data show that there is a relationship between depth of flooding and mortality; as the prevailing water depth increased, mortality for all species increased. Except for the April 1972 measurement, when water depth on all plots was measured, the actual depths at the later dates varied from those shown, but the relative difference in depth between the populations was similar.

Mortality in population 6 was essentially complete after 3 yr of flooding to depths of 1.2 m or more; for this reason the plots were not measured in 1975. In population 5, after 3 yr 68% of the trees had died in water averaging 107 cm deep, and in population 4 where the water averaged 82 cm deep, 41% of the trees had died. As water depth decreased upriver in populations 3, 2, and 1, tree mortality was correspondingly less. The data from the control plots in populations 0 and 8 indicate that natural mortality for the same period was on the order of 2–6%; thus there probably were only small flooding-caused losses in populations 1 and 2, where mortality averaged 4% or less.

The species varied in their susceptibility to damage from flooding (Table 3). Baldcypress and swamp

TABLE 3. Cumulative percent mortality of trees in Lake Ocklawaha by population and species.*

Population number	Area (ha)	Water depth Apr 1972 (cm)	Species	Fall 1968	Apr 1972	Nov 1972	Feb 1975	Aug 1975
				n	% mortality			
				Reservoir plots				
1	88	20.3	Ash	926	2	2	3	3
			Maple	178	0	4	4	4
			Cypress	106	0	2	2	2
			Gum	72	0	0	0	3
			Others	361	4	4	4	4
			Total	1643 ± 9.3†	2	2	3	3
2	89	52.1	Ash	783	4	4	4	4
			Maple	153	3	3	3	3
			Cypress	62	0	0	0	0
			Gum	25	0	0	0	0
			Others	212	6	6	19	24
			Total	1235 ± 6.7	4	4	6	7
3	90	65.8	Ash	556	24	24	24	25
			Maple	282	16	22	22	22
			Cypress	79	3	3	3	3
			Gum	54	5	5	5	5
			Others	153	5	6	35	35
			Total	1124 ± 8.3	17	18	20	21
4	26	82.3	Ash	684	52	58	65	66
			Maple	178	50	58	60	68
			Cypress	230	12	16	16	16
			Gum	72	3	14	14	14
			Others	25	40	50	90	90
			Total	1189 ± 7.7	41	47	52	54
5	130	107.2	Ash	580	91	94	97	99
			Maple	170	77	77	77	77
			Cypress	205	11	13	13	13
			Gum	79	31	59	59	59
			Others	54	55	100	100	100
			Total	1088 ± 7.9	68	76	81	82
6	35	120.6	Ash	1023	99	100	...	...
			Maple	173	100	100	...	...
			Cypress	25	50	50	...	...
			Gum	131	91	91	...	...
			Others	12	40	40	...	...
			Total	1364 ± 10.0	97	98	...	...
				Control plots				
0	175	29.2	Ash	832	1	2	5	5
			Maple	264	1	2	2	2
			Cypress	220	2	4	4	4
			Gum	62	0	0	0	0
			Others	398	3	3	7	9
			Total	1776 ± 12.8	2	3	5	5
8	171	24.1	Ash	1487	7	8	12	13
			Maple	249	2	7	7	7
			Cypress	25	0	0	0	0
			Gum	99	2	2	2	2
			Others	282	4	9	24	32
			Total	2142 ± 9.7	6	8	13	14
Averages for populations 0 and 8			Ash	1158	5	6	10	10
			Maple	257	2	4	4	4
			Cypress	121	2	4	4	4
			Gum	79	0	0	0	0
			Others	343	4	5	14	18
			Total	1958	4	6	9	10

* Base for mortality calculations: number of trees per hectare in Fall 1968 = living + dead tallied April 1972.
† Standard error in percent is given for each population total.

TABLE 4. Cumulative mortality of trees in Lake Ocklawaha by population and diameter class.*

Population number	Area (ha)	Water depth Apr 1972 (cm)	Dbh class (cm)	Fall 1968	Apr 1972	Nov 1972	Feb 1975	Aug 1975
				n	% mortality			
					Reservoir plots			
1	88	20.3	2–13	907	2	2	2	2
			14–26	413	2	2	4	4
			27–39	180	3	3	4	4
			40+	143	0	2	2	2
			Total	1643	2	3	3	3
2	89	52.1	2–13	524	7	7	10	12
			14–26	437	2	3	4	5
			27–39	170	0	0	1	1
			40+	104	2	2	2	2
			Total	1235	4	4	6	7
3	90	65.8	2–13	482	22	22	23	25
			14–26	353	17	17	18	19
			27–39	170	12	17	22	22
			40+	119	4	6	10	10
			Total	1124	17	18	20	21
4	26	82.3	2–13	559	51	54	61	63
			14–26	301	49	64	70	73
			27–39	146	22	25	31	31
			40+	183	12	15	15	15
			Total	1189	41	47	52	54
5	130	107.2	2–13	457	78	89	97	97
			14–26	378	72	77	81	83
			27–39	106	65	65	67	67
			40+	147	27	38	40	42
			Total	1088	68	76	81	82
6	35	120.6	2–13	593	100	100	...	...
			14–26	561	98	98	...	...
			27–39	99	100	100	...	...
			40+	111	78	82	...	...
			Total	1364	97	98	...	...
					Control Plots			
0	175	29.2	2–13	969	0	4	6	6
			14–26	437	3	3	6	6
			27–39	217	0	2	2	2
			40+	153	10	10	10	10
			Total	1776	1	3	5	5
8	171	24.1	2–13	1213	10	12	17	19
			14–26	692	1	2	7	7
			27–39	138	4	4	7	9
			40+	99	2	5	8	8
			Total	2142	6	8	13	14
Averages for populations 0 and 8			2–13	1091	5	9	12	13
			14–26	563	2	2	7	7
			27–39	178	1	3	3	3
			40+	126	8	8	8	8
			Total	1958	4	5	9	10

* Base for mortality calculations: number of trees per hectare in Fall 1968 = living + dead tallied in April 1972.

blackgum, the naturally water-tolerant swamp species, were much more resistant to deep flooding than ash and maple, the most common species in this swamp. In population 5, 91% of the ash and 77% of the maple had died 3 yr after flooding. In population 6, which together with population 7 had suffered the most, 99% of the ash, 100% of the maple, 50% of the baldcypress, and 91% of the swamp blackgum were dead.

Among the species present in small numbers were cabbage palm, laurel oak (*Quercus laurifolia* Michx.) and water oak (*Q. nigra* L.). Because oaks do not tolerate long periods of continuous flooding, all those

TABLE 5. Relationships between species mortality in April 1972 (Y) and water depth (x_1) and dbh (x_2) as described by the regression: $Y = a + b_1x_1 + b_2x_2 + b_3x_1x_2$.

Species	Intercept a	Water depth b_1	Dbh class b_2	(Water depth) × (Dbh class) b_3	R^2
Ash	−13.6566	.9112	−.2372	−.0066 NS*	.60
Maple	−16.6169	.8099	−.0736 NS	−.0010 NS	.50
Cypress	2.0812	.1035	−.1248 NS	.0028 NS	.05
Gum	−17.2886	.6699	.1899	−.0231	.36
All species	−15.8294	.8120	.0424	−.0175	.41

* NS: coefficient not statistically significant. All others significant at the 5% or 1% level.

present in populations 3, 4, and 5 were dead after 3 yr (Gill 1970). No oaks in populations 1 and 2 had died. There were numerous palms scattered throughout the forest, but very few of them had died because of flooding.

Table 4 lists mortality by 13-cm diameter classes. These data show that trees larger than about 26 cm dbh survived much better than smaller ones, probably because the smaller trees tended to be shorter and usually have less well-developed crowns and root systems. These factors would make smaller trees much more likely to succumb to stress than the larger, dominant ones. However, as flooding depth increased to the maximum measured in populations 5 and 6, even the largest trees suffered extensive mortality.

Multiple regressions of the April 1972 data were computed to provide a quantitative indication of the importance of water depth, species, and dbh class to tree survival relationships summarized in Tables 3 and 4. The percentages of dead ash, maple, cypress, and gum were taken as dependent variables, and water depth, dbh class, and the interaction of water depth and dbh were taken as independent variables. All regressions were statistically significant but because of the large variation among plots the R^2 values ranged from .05 to .60 (Table 5). Water depth accounted for more of the variation in mortality than any of the other variables. Dbh class was significant only in the regressions for ash and gum and in the regression for all species combined. The interaction of water depth and dbh was significant only for gum and the combined species regressions. These results are illustrated in Fig. 2.

Plot measurements taken in November 1972 and during 1975 showed only small increases in mortality, and no change in the trends observed earlier. Trees had continued to die in all populations but not at the high rate recorded in April 1972. Not only was mortality much reduced, but it also appeared to be holding at the same rate in all populations. Losses continued to be greatest in the smaller size classes and among the less flood-tolerant species. The trees that survived in populations 4 and 5, mainly cypress and gum, had apparently become adapted to the deep water, although they had a generally unhealthy appearance. Numerous branches were dead, leaving the crowns composed largely of epicormic shoots that had sprouted from the main stem and the larger branches.

Physiological effects

The severity of the effects of flooding on the root systems varied markedly with water depth, as shown in Fig. 3, where the percentage of trees in each via-

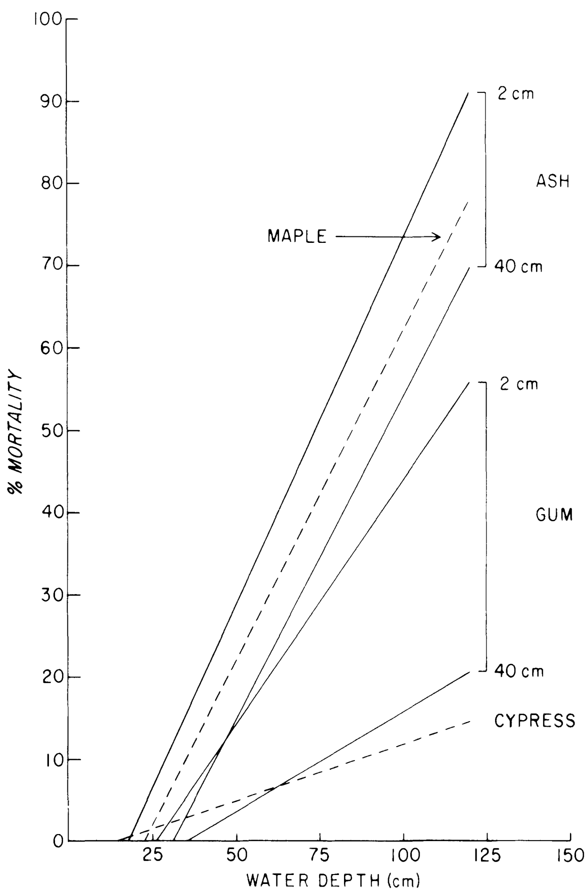

FIG. 2. The effect of water depth and dbh on mortality of four species. Dbh was a factor only for ash and gum: response is plotted for the 2-cm and 40-cm classes. Trends for maple and cypress are shown for their mean dbh, 24 cm and 33 cm respectively.

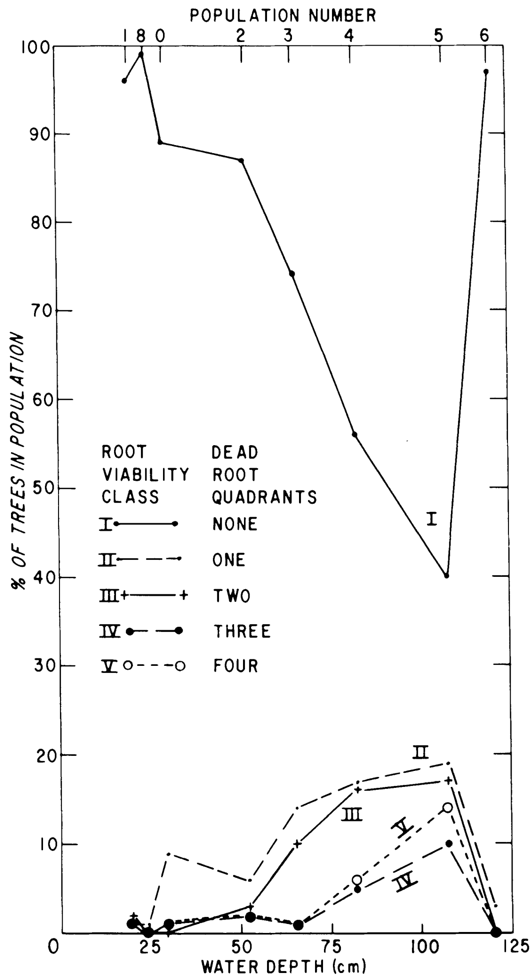

FIG. 3. Effect of water depth on the percentage of trees in the various root viability classes in each population.

bility class is plotted for each population in relation to the water depth that prevailed when the roots were measured.

Most of the trees in control populations 0 and 8 had living roots in all four quadrants. Trees in population 1 had as high a proportion of root systems in viability class I as the control populations. Population 1, at the south end of the reservoir, had not been flooded quite as deeply as either of the controls (Table 2). In contrast, root systems in the other populations within the reservoir were clearly influenced by water depth. The proportion of healthy trees declined from 87% in population 2 to 44% in population 5. Population 6 appeared to be an exception to the trend; however, the April inventory that established the high proportion of trees with apparently good root systems in this most deeply flooded population was made after 97% of its trees were already dead. The remaining 3%, only about 37 trees per ha, apparently had become adapted to flooding, and consequently, viable roots were found in all quadrants of most of the root systems. The majority of the survivors were palms, the remainder being scattered baldcypress, maple, and tupelo.

As water depth increased, the proportion of trees having dead roots in two or more quadrants also increased. In population 4, with a water depth of 82 cm, 33% of the trees had dead roots in at least two quadrants, and 11% had roots dead in three or four quadrants. In population 5, at a depth of 107 cm, 24% of the trees had dead roots in three or four quadrants.

The laboratory examination of the viability and physiological condition of the root samples brought in from the field also suggested a relationship between mortality and flooding depth of the populations.

Observations of starch content were first made on randomly selected roots of the same species from population 0, representing low stress, and population 5, representing high stress, in an attempt to show overall population differences in food reserves. Although the majority of trees of all species in population 5 showed lower average starch reserves than the same species in population 0, there was considerable variation among trees in the amount of starch observed. This variation arose because the random selection of root samples from the same populations included vigorous as well as stressed trees.

To eliminate the confounding effect of the mixed root samples, another set of observations was made in which root category was purposefully selected. The objective was to determine if the amount of food reserves in the roots was associated with a particular category. Thus, trees with zero or one and three or four root quadrants dead in populations 3, 4, and 5 were selected and examined for starch content. In populations 0, 1, and 2, the trees with three or four root quadrants dead were not sufficient in number to supply a meaningful sample. Microscopic examination showed that there were distinct and readily observable differences in starch content between healthy trees of categories 0 or 1 and the low-vigor trees of categories 3 or 4 (Table 6). The average rating for the trees in categories 0 or 1 indicated that abundant starch was present in the xylem of the roots; in the trees of categories 3 or 4, the rating showed sparse to light amounts of starch in the system. The amount of starch in the phloem and cortex was somewhat less, but the relative difference between the groups was even greater. There were, however, no clear-cut differences among species.

DISCUSSION

The patterns of tree mortality observed in Lake Ocklawaha reflect the species' tolerance to prolonged flooding and their ability to adapt to the change in soil conditions that occurred when the swamp was flooded. The relative flood tolerance and sensitivity to water depth of the major species are well illustrated by the regression lines plotted in Fig. 2.

TABLE 6. Rating of stored starch in root tissues of cypress, swamp tupelo, and ash (6 trees of each) sampled by root quadrant category from populations 3, 4, and 5 in Lake Ocklawaha, November 1972.

	Number of quadrants with dead roots							
	0–1				3–4			
Species	Tree	Xylem	Phloem	Cortex	Tree	Xylem	Phloem	Cortex
Cypress	1	3*	3	1	4	1	0	0
	2	2	2	1	5	1	0	0
	3	3	2	1	6	2	1	1
Swamp tupelo	1	4	2	1	4	0	0	0
	2	3	1	1	5	2	0	0
	3	3	2	0	6	1	1	0
Ash	1	3	3	2	4	2	1	0
	2	4	3	1	5	1	1	0
	3	2	2	1	6	0	0	0
Average of all species		3.0	2.2	1.0		1.2	0.4	0.1

* Numerical rating of starch content stained with iodine-potassium iodide and observed microscopically: 0—none; 1—sparse; 2—light to moderate; 3—abundant; and 4—high concentration.

Ash and maple were the most sensitive of the four species to flooding and responded alike to increasing water depth. Tree size had no apparent effect on mortality of maple, indicating that large trees died as readily as small trees when flooded. Large-diameter ash were, however, more resistant to flooding than small ones but no more resistant in deep than in shallow water. These species frequently persist in swamps with shallow, periodic flooding regimes such as the Oklawaha, but do not occur in swamps that are normally deeply flooded during the growing season (Penfound 1952). They respond to flooding by developing an adventitious root system on the stem at the waterline; ash has the further capacity to regenerate a few new secondary roots that exhibit some anaerobic characteristics, and therefore tends to be more flood tolerant than maple (Hook and Brown 1973). Such adaptations are apparently sufficient to sustain both species in infrequently flooded conditions but not under prolonged or deep flooding. We observed that adventitious roots had developed on both ashes and maples in all of the plots that were flooded.

Cypress was least sensitive to water depth and gum was intermediate. Tree size did not influence cypress mortality, but as Fig. 2 shows, small gum were much more prone to die as water depth increased than large gum. Baldcypress and swamp tupelo thrive in the swamp habitat because, in part, of a number of root adaptations. Hook et al. (1971) have shown that, under flooded conditions, tupelo species have or can develop secondary roots, so-called water roots, that oxidize their rhizosphere, have a high capacity for anaerobic respiration, and can withstand relatively high concentrations of carbon dioxide and other gases. However, these researchers found that even tupelo can be severely restricted in growth or killed by excessively high concentrations of carbon dioxide, such as can accumulate under deep or prolonged flooding (Hook et al. 1970). The ash and maple in Lake Ocklawaha had produced no water roots, but our examinations of baldcypress and swamp tupelo showed that they were developing water root systems although the roots were sparsely distributed, especially in the deeply flooded portions of the lake.

Hook and Brown (1973) found that tolerance of a species to flooding is related to its ability to produce a system of water roots when subjected to prolonged flooding or soil saturation. When newly flooded for more than a few days, secondary roots die. Flood-tolerant species will replace these roots in a short time with new, succulent, relatively unbranched secondary roots. Intolerant species cannot replace secondary roots, and as a result, the trees die. Whether or not water roots are produced depends on the nature and duration of flooding. Our observations in other swamps indicate that few water roots are produced on trees in infrequently flooded soil. Annual, periodic flooding such as occurs on the Oklawaha River is not conducive to abundant production of flood-tolerant roots. Rather, more or less continuously saturated soil is required (Hook et al. 1970, Harms 1973). The creation of Lake Ocklawaha caused an unnatural condition of deep, continuous flooding with relatively slow-moving water. This condition probably resulted in a rapid depletion of soil oxygen and buildup of compounds toxic to roots so that even the flood-tolerant baldcypress was unable to generate new roots sufficient to maintain life in the most deeply flooded areas (Patrick 1973). The data on root system viability (Fig. 3) and root tissue starch content (Table 6) are indicative of the severity of the morphological and physiological stresses imposed by flooding. Although the sampling methodology did not permit us to evaluate species differences, it was quite apparent that root structure and function had been adversely altered by the prolonged flooding.

Tree diameter appears to be a factor in survival under flooded conditions for some species. The relationship is probably indirect, with size being a measure of tree vigor and root surface available for production of water roots. The data collected were not sufficiently detailed to allow these variables to be evaluated.

The effects of flooding on the trees in Lake Ocklawaha are similar to those reported in the literature for water impoundments of bottomland forests in other regions of the United States (Green 1947, Yeager 1949, Hall and Smith 1955). Penfound (1949) and Eggler and Moore (1961) reported on the effects of flooding on trees in Lake Chicot, a cypress-gum swamp in Louisiana. This impoundment is the only one described in the literature that is comparable to Lake Ocklawaha in species and climate. In Lake Chicot, baldcypress was the most common species, followed by water tupelo, water elm (*Ulmus americana* L.), and button bush. Depth of the lake appeared to be about 2 m at the spillway. Water management involved a fall and winter drawdown with spring and summer flooding to control aquatic vegetation. After 4 yr flooding, only 3% of the baldcypress in an area flooded in excess of 0.6 m had died, but 67% of the water tupelo and 86% of the button bush were dead. At the end of 18 yr, 50% of the baldcypress, all of the button bush and water elm, and 72% of the water tupelo had died. All of the live tupelo were sprouts growing from the stumps of broken and decayed trees. Eggler and Moore (1961) estimated that half of the living cypress growing in deep water had dead tops.

In Lake Ocklawaha the low, nearly constant rate of mortality after the 3rd yr, regardless of water depth, is evidence that the remaining trees were adapting to the new conditions. Because severity of stress is related to water depth, decline and death can be expected to develop more gradually in the shallower parts of the lake. Baldcypress and swamp tupelo may well adapt to and be little affected by water depths of 0.6 m or less but the less tolerant ash and maple will eventually die.

Acknowledgments

The planning and execution of this study were conducted by a multidisciplinary team of Federal, State, and university researchers and technicians under the auspices, initially, of the Council on Environmental Quality and, later, the United States Army Corps of Engineers.

Literature Cited

Eggler, W. A., and W. G. Moore. 1961. The vegetation of Lake Chicot, Louisiana, after eighteen years' impoundment. Southwestern Naturalist **6**:175–183.

Gill, C. J. 1970. The flooding tolerance of woody species—a review. Forestry Abstracts **31**:671–688.

Green, W. E. 1947. Effect of water impoundment on tree mortality and growth. Journal of Forestry **45**:118–120.

Hall, T. F., and G. E. Smith. 1955. Effects of flooding on woody plants, West Sandy dewatering project, Kentucky Reservoir. Journal of Forestry **53**:281–285.

Harms, W. R. 1973. Some effects of soil type and water regime on growth of tupelo seedlings. Ecology **54**:188–193.

Hook, D. D., and C. L. Brown. 1973. Root adaptations and relative flood tolerance of five hardwood species. Forest Science **19**:225–229.

Hook, D. D., C. L. Brown, and P. P. Kormanik. 1971. Inductive flood tolerance in swamp tupelo (*Nyssa sylvatica* var. *biflora* [Walt.] Sarg.). Journal of Experimental Botany **22**:78–89.

Hook, D. D., O. G. Langdon, J. Stubbs, and C. L. Brown. 1970. Effect of water regime on the survival, growth, and morphology of tupelo seedlings. Forest Science **16**:304–311.

Johansen, D. A. 1940. Plant microtechnique. McGraw-Hill, New York, New York, USA.

Monk, C. D. 1965. Southern mixed hardwood forest of north central Florida. Ecological Monographs **35**:335–354.

———. 1966. An ecological study of hardwood swamps in north central Florida. Ecology **47**:649–654.

Patrick, Jr., W. H. 1973. Evaluation of soil properties as affected by flooding in the Oklawaha River-Rodman Reservoir area. Appendix 24. Final environmental statement. Proposal for Oklawaha River, Ocala National Forest, Florida. United States Forest Service, Washington, District of Columbia, USA.

Penfound, W. T. 1949. Vegetation of Lake Chicot, Louisiana, in relation to wildlife resources. Proceedings of the Louisiana Academy of Science **12**:47–56.

———. 1952. Southern swamps and marshes. Botanical Review **18**:413–446.

United States Forest Service. 1973. Final environmental statement: proposal for Oklawaha River, Ocala National Forest, Florida. United States Forest Service, Washington, District of Columbia, USA.

Yeager, L. E. 1949. Effect of permanent flooding in a river-bottom timber area. Illinois Natural History Survey Bulletin **25**:23–65.