South Carolina Coastal Zone Management Program

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Title: Total Phosphorus, Total Nitrogen and Total Organic Carbon Distributions in a Southeastern Coastal Plain River

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INTRODUCTION

Coastal plain streams and rivers are often closely linked to forested floodplain swamps (Kuenzler, et. al., 1980). Floodplain forests occur in lowlands that border streams and rivers which seasonally inundate them (Wharton, et. al., 1982). These riverine floodplain ecosystems include not only the structural elements such as the stream or river, the swamp forest, the atmosphere, the soil and the fauna but also the functional and metabolic attributes such as primary productivity and nutrient cycling (Vannote, et. al., 1980).

The one-way flow generated by gravity in streams and rivers has far reaching consequences for every aspect of their ecology. Characteristics of flow which are influential are water velocity, stream discharge and turbulence. Flow velocity is itself influenced by a combination of channel characteristics such as topographic slope, width and depth. The nature of the mineral substrate, the concentrations of dissolved and suspended materials and temperature, are further factors which play important ecological roles (Townsend, C.R. 1980). However, for coastal plain rivers and streams as examplified by the site of this study, tidal influences which have been observed up to 77 km upstream are capable of modifying the nutrients and organic carbon concentrations and dynamics of delta systems.

Lotic ecosystems are not isolated entities. Streams and rivers interact with the atmosphere at their surface and with the land at their edges, and it is across these boundries that movements of materials and energy take place. Two intriging features of such lotic systems are a dependance for the majority of their energy supply on import of organic matter elaborated in the terrestrial system through which they flow (watershed) and the utilization of a great deal of organic input during the fall-winter periods of lowest annual temperature (Cummins, 1974). This lotic communities are generally heterotrophic and temperature compensated by having organisms that can process organic matter at reasonable rates below normal temperature optima.

Nutrient cycling in aquatic ecosystems responds to and influences water quality and primary productivity of streams and rives. Water flow, water quality, and patterns of nutrient cycling are all interacting variables in stream ecosystem functioning. Ripariam ecosystems along small, low-order streams are buffer zones where excessive nutrients and sediments from upland disturbances may be trapped and assimilated. For larger streams and rivers like the Lower Santee River, overbank flow of water during flood events provides an opportunity for upstream flows to come in contact with the bordering floodplains (Brinson, et. al., 1981). This aequeous transport system provides path-ways for exchange between river channel and floodplain through lateral imports, sedimentation and export of elements and organic matter.

The vectors transporting energy and materials between a terrestrial landscape and its aquatic subecosystem have been categorized as meterorological, geologic and biologic (Likens, et. al., 1974). The ecosystem-watershed concept, which originated with the Hubbard Brook Watershed Ecosystem Study, provides an important framework for research into contemporary processes in many environments (O'Sullivan, 1979). In many watershed ecosystems, inputs, outputs, and internal processes are affected by cultural factors. Many effects of Man upon environmental systems are thus transmitted and expressed via the material pathways of ecosystem watershed (Meyer and Tate, 1983; Mulholland, et. al., 1979).

One of the most dramatic anthropogenic effects on stream ecosystems has been the alteration of water flow patterns for hydropower generation. In 1941, 88 percent of the water flow in the Santee River in S. C. was diverted for hydropower generation. Due to unforseen siltation problems associated with the diversion, plans to redivert 80 percent of the originally diverted water flow back into the Santee river have been authorised. Stream flow changes of this magnitude affect riverine ecosystem functioning and river-floodplain interactions. Study of Santee Swamp located above Lake Marion, which serves as headwaters for the Lower Santee River, docummented significant reduction in nutrient concentrations with little or no oxygen depletion as the waters coursed through the swamp (Kitchens, et. al., 1975). However, at present, very little is known about the distributions of nutrients and organic matter in the lower Santee River which is the area directly affected by the rediversion. Therefore the purpose of this study was to document the spatial and temporal distributions of total nitrogen, phosphorus, and organic carbon along the lower Santee River.

MATERIALS AND METHODS

Description of the Study area

The Santee River originates in the Appalachian Mountains of North and South Carolina. Via a number of tributaries above Lake Marion, the river traverses the piedmont, meander across the coastal plain and empties into the Atlantic Ocean 75 km northeast of Charleston, S. C. (Fig. 1). The Santee river is a tertiary river formed by the Saluda, Broad, and Congaree rivers in South Carolina and the Wateree River from North Carolina. The 43,512 km^2 river basin is inhabited by 58% of South Carolina's population.

Until 1941, the Santee, with an annual discharge mean of 525 $m^3 s^{-1}$, was the fourth largest river on the U.S. east coast. The construction of Wilson Dam in 1941, created Lake Marion, South Carolina's largest lake with a 450 km^2 surface area (Fig. 2). In order to effectively harness

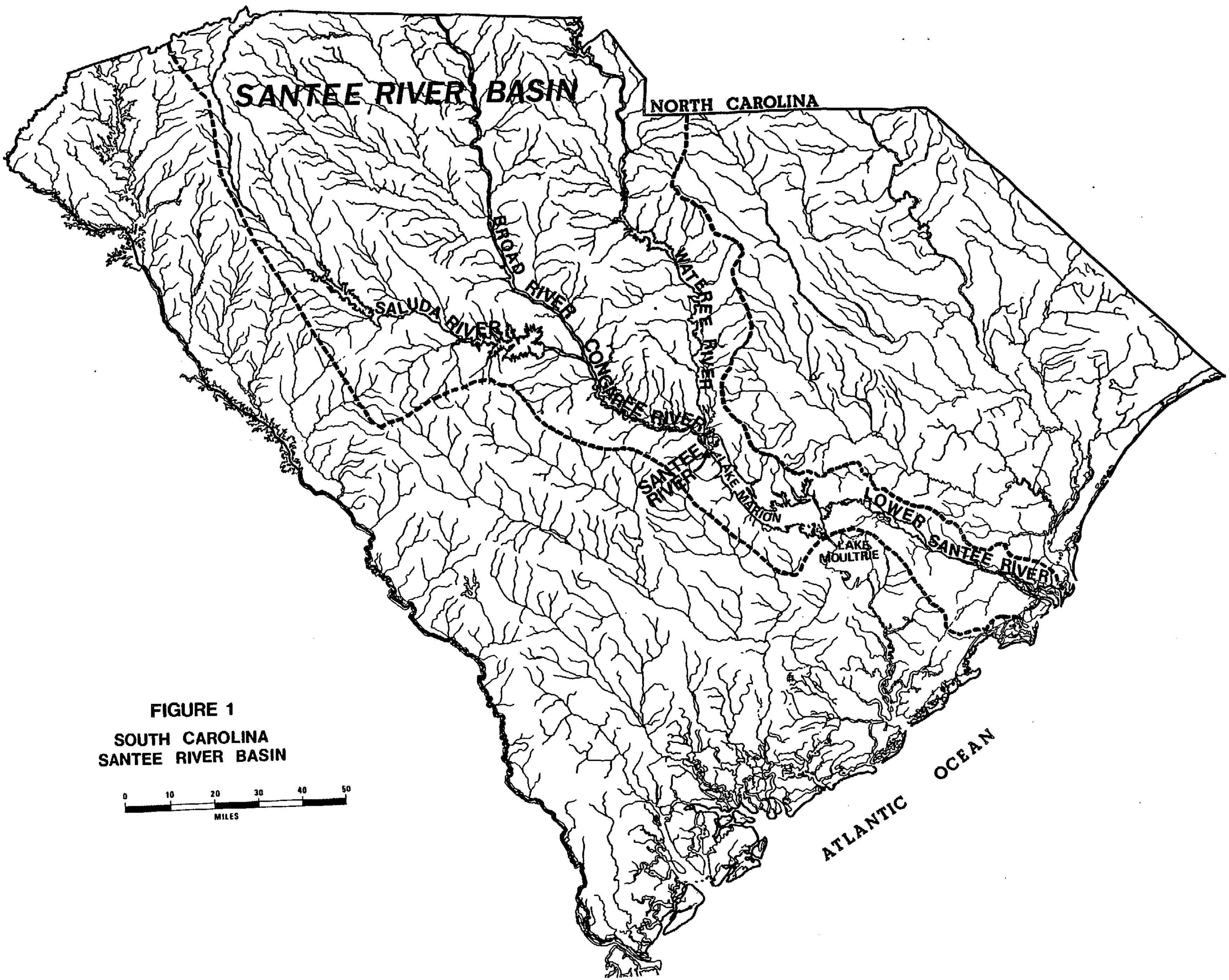

FIGURE 1
SOUTH CAROLINA
SANTEE RIVER BASIN

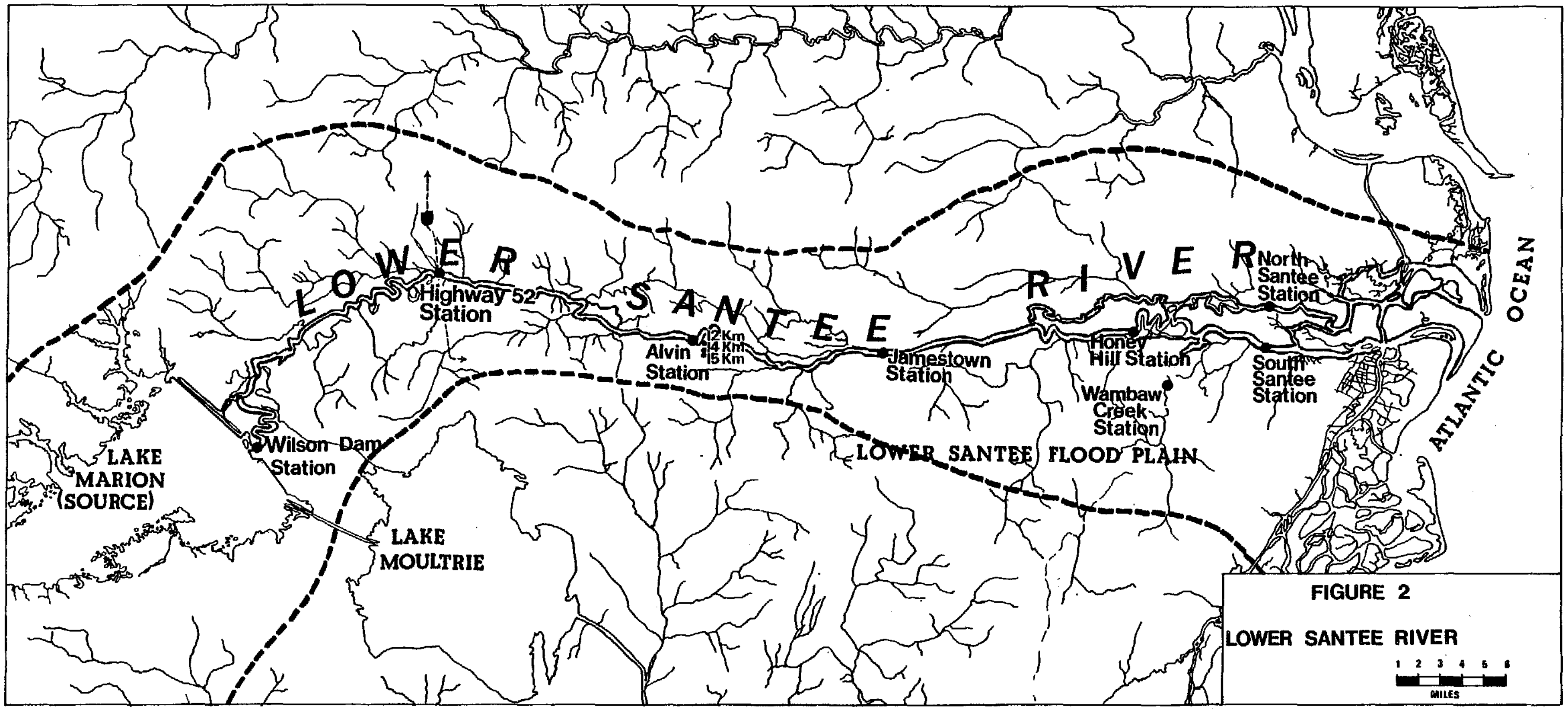

FIGURE 2

LOWER SANTEE RIVER

hydroelectric power from the Santee, Lake Marion was connected through a 12 km diversion canal to Lake Moultrie of Cooper river. Thus 88% of the Santee flow was channeled into Cooper river (Bjorn Kjerfue, 1976). Presently, the Santee River annual mean discharge is $74m^3s^{-1}$. Among other less documented impacts, the Santee-Cooper project apparently led to severe shoaling problems in Charleston Harbor. To alleviate this shoaling problem and associated dredging costs, the Army Corps of Engineers has been authorized to modify the existing Santee-Cooper system by rediverting approximately 80 percent of the previously diverted discharge back into the Santee river. The rediversion project is expected and predicted to produce environmental impacts on aquatic, riparian and coastal habitats (F.I.S, U. S. Army Corps of Engineers, 1975).

The specific site of this study is the Lower Santee River which lies within the tail of the Santee river basin and stretches 140 km from the Wilson Dam to the Atlantic Ocean (Fig. 2). The Lower Santee River has its headwaters from Lake Marion's hypolimnium and its hydrography during moderate dishcarge conditions showed that 73 and 27% of the discharge reached the ocean via North and South Santee distributaries respectively (Kjerfüe, et. al., 1978). The Lower Santee River sub-basin drainage area is 1942 km^2. A major feature of the Lower Santee River is the extensive forested floodplain which spans 2 to 8 km wide along the 140 km river stretch from Lake Marion to the Coast. The total floodplain area has been measured as 520.2 km^2 producing a floodplain-subbasin area ratio of 0.27 (Lowry and Osemene, 1984). Table 1 shows the distribution of the floodplains area with reference to the Seven Stations studied.

We introduce the concept of Wetland Factor (WF). This we define as the Wetland area between two adjoining sampling stations on the river channel divided by the distance between the two stations (river reach). It is the wetland area in km^2 per unit length of the riverine reach in km. We propose that it is a rational method for easy projection of the floodplain area bordering a river segment. Riverine floodplain are not evenly distributed along the river stretch. A riverine reach with a WF of 2 has twice the floodplain area of the river segment with a WF of 1. The headwater reach for the Lower Santee River (WD-HW52) has a WF of 4.2 km^2/km while the estuarine delta reach (N and S Santee - Atlantic Ocean) has a WF of 7.7 km^2/km.

The land use of the Lower Santee River subbasin was determined to be 62.5% wooded floodplain forest, 7.1% of cropland, 5.0% of pasture land while the rest, 25.4% is urban and industrial developments (Lowry and Osemene, 1984). The vegetation of the floodplain is a mix of bottomland hardwoods and cypress-tupelo associations plus various stages of succession in logged area. The bottomland

Table 1. The distribution of Wetland (Floodplain) area to the Sampled Stations on the Lower Santee River Channel in South Carolina.

River Reach	Stations	Distance between Station in km	Wetland area in km2	% of Total Wetland area	Wetland Factor*
1	WD - HW52	37	155.5	30	4.2
2	HW52 - AL	30.6	100.6	19	3.3
3	AL - JT	14.5	59.8	12	4.1
4	JT - HH	17.7	17.6	3	1.0
5	HH - N & S Santee	20.9	39.0	8	1.9
6	N. and S. Santee Delta - Ocean	19.3	147.8	28	7.7

$$* \text{ Wetland Factor (W.F.)} = \frac{\text{Interstation Floodplain Area in km2}}{\text{Interstation distance in km}}$$

hardwoods include sweetgum, green ash, American elm, water hickory and other species which require deeper water tables and shorter flood durations than the cypress-tupelo associations (McKellar, et. al., 1981).

The seasonal patterns of Lower Santee river flow include winter-spring periods of highflow which ranges from 312 $m^3 S^{-1}$ in late December to 496 $m^3 S^{-1}$ in late April and a summer-fall periods of low flow which range from $28 m^3 S^{-1}$ in June to $14 m^3 S^{-1}$ in November. Presently large winter-spring flood releases from the Marion Lake Dam into the Lower Santee River increase the annual mean flow to about $80 m^3 S^{-1}$. These flood releases cause periodic inundation of the entire floodplain (U.S.G.S., Columbia 1984).

Research Design

In order to study the nutrients and organic carbon dynamics, 7 approximately equidistant stations were set up on the Lower Santee River main channel. These stations from upstream to downstream were Wilson Dam (WD) located 140 km upstream, Highway 52 (HWY 52 or Russeleville) located 103 km, Alvin (AL) located 72 km, Jamestown (JT) located 58 km, Honey Hill (HH or Pleasant Hill Landing) located 40 km, North Santee at highway 17 (NS) located 21 km and South Santee at highway 17 (SS) located 17.7 km upstream respectively. In this paper, the Wilson Dam station is refered to as the source or headwater station, the stations from HW52 to HH are referred to as the riverine stations while the stations SS and NS on highway 17 are collectively refered to as the delta or estuarine or coastal stations.

Replicate water samples were obtained from each of these stations, once a month from March 1983 to February 1984. This period covered the annual hydrologic and ecologic seasonal cycles. The Honey Hill and Alvin Stations were sampled for ten (10) and nine (9) consecutive months respectively. The North and South Santee river stations in the river delta were consistantly sampled within the last hour of ebb-tide flow to insure maximum riverine effects on nutrient concentrations. Salinity and specific conductivity were also measured at each station. Samples were immediately embedded in ice and transported to the laboratory where they were processed and preserved for later analyses. Samples were generally processed within 4 hours of collection. Except for samples processed for all subspecies of organic carbon which were preserved by freezing at - 20^{o}C, all precessed subsamples were chemically preserved from bacterial activities with 0.1 ml of 2% mecuric chloride solution and stored at refrigerator temperature (4^{o}C) until analysed. The respective sub-samples were analysed for total nitrogen, total phosphorus and organic carbon within 10 days from the sampling data. Approximately 672 processed water samples were analysed.

Analytical Methods

Total phosphorus was assayed first by oxidizing all the organic phosphorus to ortho-phosphate ions by adding a strong oxidizing acid-fersulfate solution to samples and holding them for 1 hour at 132°C autoclave high temperature and pressure (Menzel and Corvin, 1965). The orthophosphate ions was determined spectrophotometrically after reaction with acid-molybdate solution (Murphy and Riley, 1962).

Total nitrogen was assayed by first oxidizing all the particulate and dissolved organic nitrogen to nitrate ions by adding strong alkaline persulfate solution and heating for 1 hour at 132°C autoclave high temperature and pressur (D'Elia, et. al., 1977). The spectrophotometric method of Alkaline Hydrazine Reduction followed with diazotization was then used to determine the concentrations of total nitrogen in each water sample (E.P.A. - NPDES, 1979). It must be emphasized that in our hands we found this technique to be pH sensitive to color development. See appendix 1 for the complete procedure.

The Total organic carbon was determined as the sum of the dissolved organic carbon (DOC) and particulate organic carbon (POC) of each sample. The highly precise carbondioxide-infra red rays absorption standard method was utilized (Menzel and Vaccaro, 1964). For the POC, the cupric oxide dry method of glass ampule preparation was used (Hutchinson, 1983). The Horiba PIR - 2000 (Oceanic International Co., Texas) infra-red analyser was used for organic carbon analyses.

RESULTS

Hydrology

The Lower Santee River daily discharge and monthly mean discharge data for the period of study was obtained from the U.S.G.S. in Columbia. Only provisional discharge data was available at the time of this paper. However, history has shown that the confirmed discharge data are usually identical to the provisional data. The discharge measurements were made at Pineville gage station which is 3.9 km downstream from the Wilson Dam.

The monthly mean and daily discharge data are plotted in Figure 3. The river discharge on the date of sampling is represented on the graph as "day-discharge". This is compared with the month's mean discharge as determined by U.S.G.S.

The graph showed that the time from December to April represents the period of high discharge (354 to $496 m^3 S^{-1}$), while the time from May to November represents period of Low river discharge (8.5 to $57 m^3 s^{-1}$). In general, discharge on the sampling day was similar to the monthly mean discharge. However, there is a significant difference between April day discharge ($57 m^3 S^{-1}$) and April month mean discharge (496 $m^3 S^{-1}$).

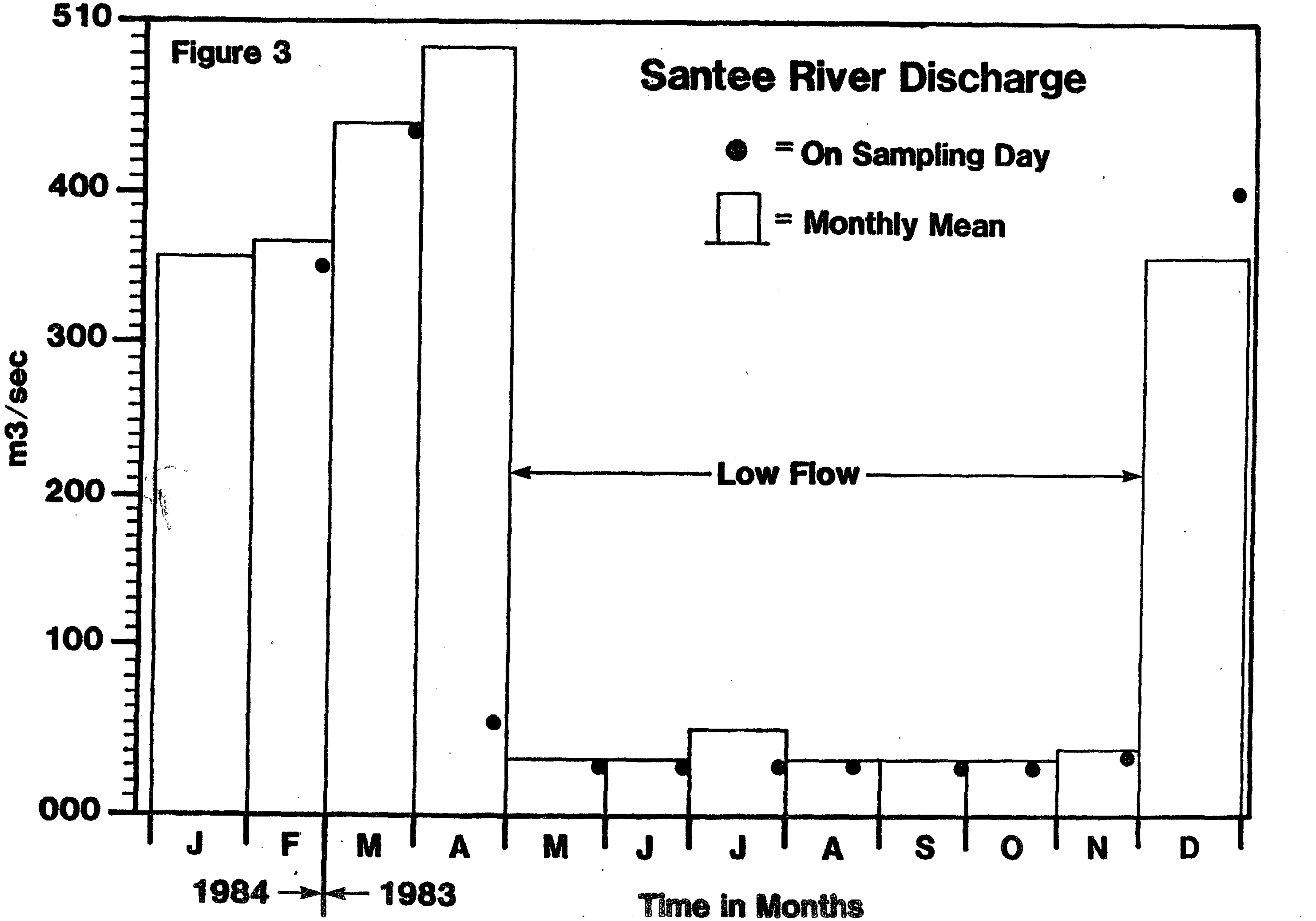
Santee River Discharge
= On Sampling Day
= Monthly Mean
Low Flow
m3/sec
510
400
300
200
100
000
J
F
M
A
M
J
J
A
S
O
N
D
1984
1983
Time in Months

Figure 3

Total Phosphorus

Temporal Variability:

Variations in the total phosphorus concentrations of the surface water during the period of study are shown in the six-panel graph in Fig. 4. At the headwater station (WD), the graph shows a relatively high TP concentration (6.0 to 5.0 mg-at/L) during the winter months from late December to late March. This was followed by a gradual and steady decline from spring to late August when a minimum was observed as 1.25 mg-at/L. A sudden rise in TP concentration was observed in the Fall season months of September to mid December (Fig. 4a).

The riverine stations downstream to H.H Station (Fig. 4b-e) reflect similar pattern as the source water station but with higher nutrient variability. This increase noise would be expected since interstation tributaries and overland flow from agricultural areas contribute some phosphorus to the river channel. Also the Wetland Factor (WF, Table 1) varies between stations and contributes to the variability.

The estuarine delta stations (N and S Santee distributaries stations) present quite a different temporal trend (Fig. 4. f.). The overlay plot of TP concentrations observed at the two delta stations show no significant difference between the north and south channel stations even though 73% of the discharge flow through the N. Santee to the Ocean.

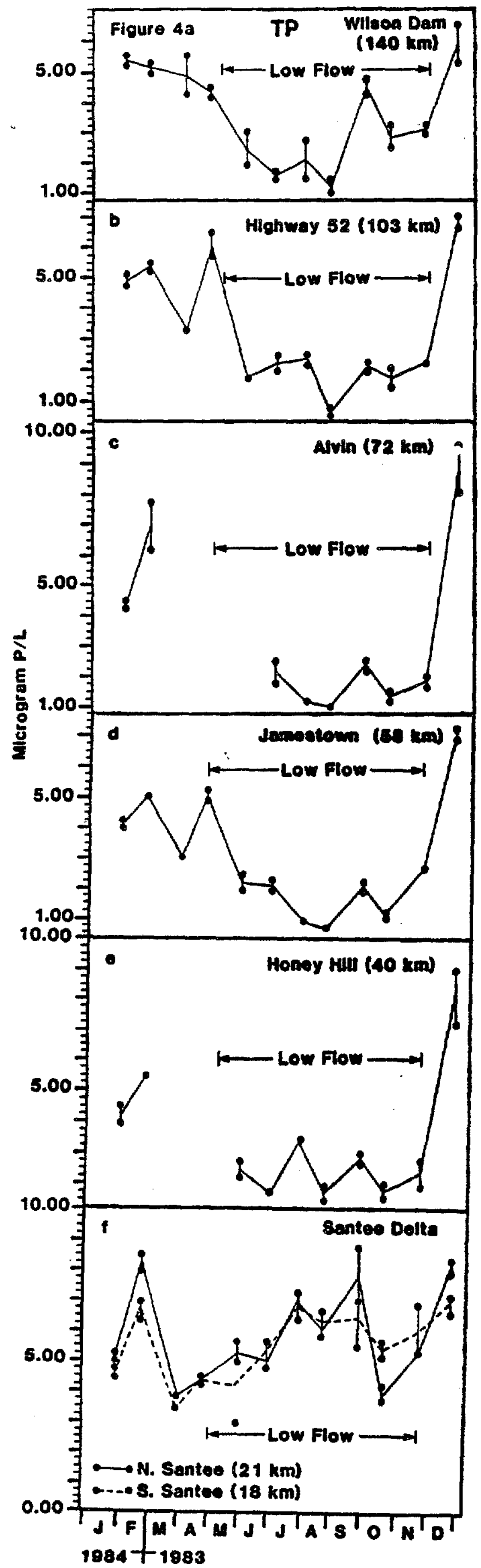
Figure 4a
TP
Wilson Dam (140 km)
Low Flow
b
Highway 52 (103 km)
c
Alvin (72 km)
d
Jamestown (58 km)
e
Honey Hill (40 km)
f
Santee Delta
N. Santee (21 km)
S. Santee (18 km)
Microgram P/L
10.00
5.00
1.00
0.00
J F M A M J J A S O N D
1984 1983

The major differences observed between these delta stations and the upstream riverine stations are relatively higher TP concentrations (3.75 to 8.5 mg-at/L) especially in the summer and fall. This complex annual pattern perhaps reflects a combination of influences from upstream riverine and floodplain effects and from the intertidal marshes of coastal delta. Eventhough, we sampled these stations during ebb flow, water quality parameters in this area are affected to some extent by previous high tides and upstream dispersion.

Spatial Variability:

The spatial distribution of TP concentration observed at the 7 stations between Wilson Dam and the delta region is shown on the three-panel graphs (Fig. 5a-c). The delta stations show significantly rising TP concentration (3.25 to 6.00 ug-at/L) as the water flows towards the Ocean. Fig. 5a presents the phosphorus pattern during the winter floodperiods. We observed that TP concentrations at all stations were consistently higher than the annual means observed for each station. We observed also that the general delta nutrient spike is not present probably because of increased flushing secondary to high river discharge.

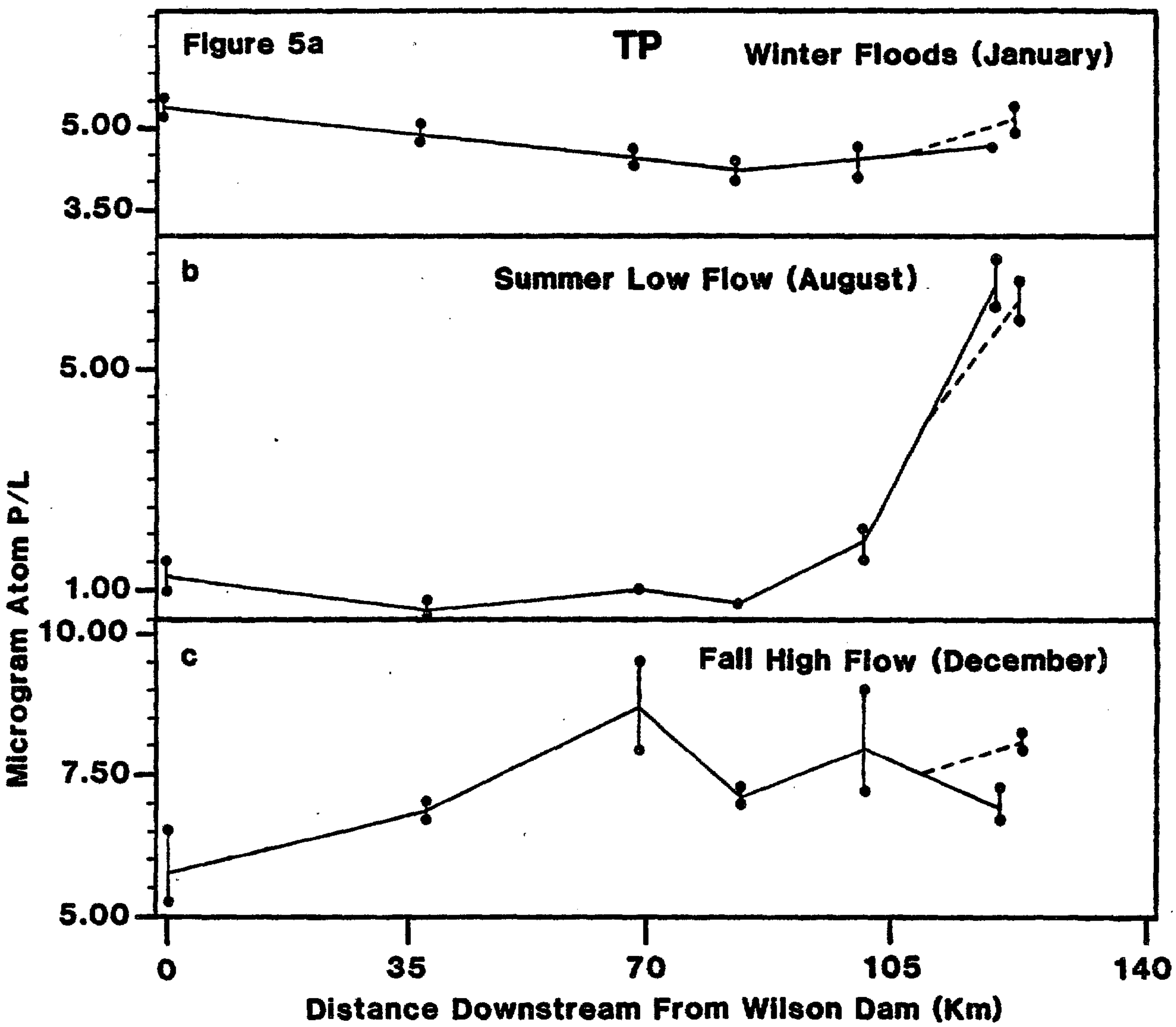

Figure 5a
TP
Winter Floods (January)
5.00
3.50
b
Summer Low Flow (August)
5.00
1.00
10.00
c
Fall High Flow (December)
7.50
5.00
Microgram Atom P/L
0
35
70
105
140
Distance Downstream From Wilson Dam (Km)

Fig. 5b reflects the pattern of the TP concentrations observed for each station during the month of August (Summer low flow). A consistently low TP concentration is observed all through the headwaters and riverine stations (1.25 to 1.00 ug at/l). This decline may be due to increased use of inorganic P during these summer months of maximum sunlight and optimum temperatures for primary productivity. The tidal effects of coastal estuarine areas are reflected in the delta TP concentration spike (1.50 ug at to 6.25 ug-at P/l). Fig. 5c reflects the upstream to downstream TP concentration trends during the end of December. The double effects of initial winter floods which connects the nutrient dynamics of the channel with that of its floodplains, and the increased liter fall and dry fallout of the preceeding fall season could explain the consistently high TP concentrations (5.75 to 8.75 ug-at P/liter) observed at all stations. During this period the flusing effect of the increased riverine dishcarge may have abrogated the usual riverine delta nutrient spike.

Total Nitrogen

Temporal Variability:

Seasonal variations in total nitrogen (TN) at each station are shown in Figs. 6a-e. The TN seasonal pattern is similar to that observed for TP with high fall and winter concentrations (13 to 26 ug-at N/L) and low spring and summer concentrations (4.0 to 6.5 ug-at N/L). Low TN

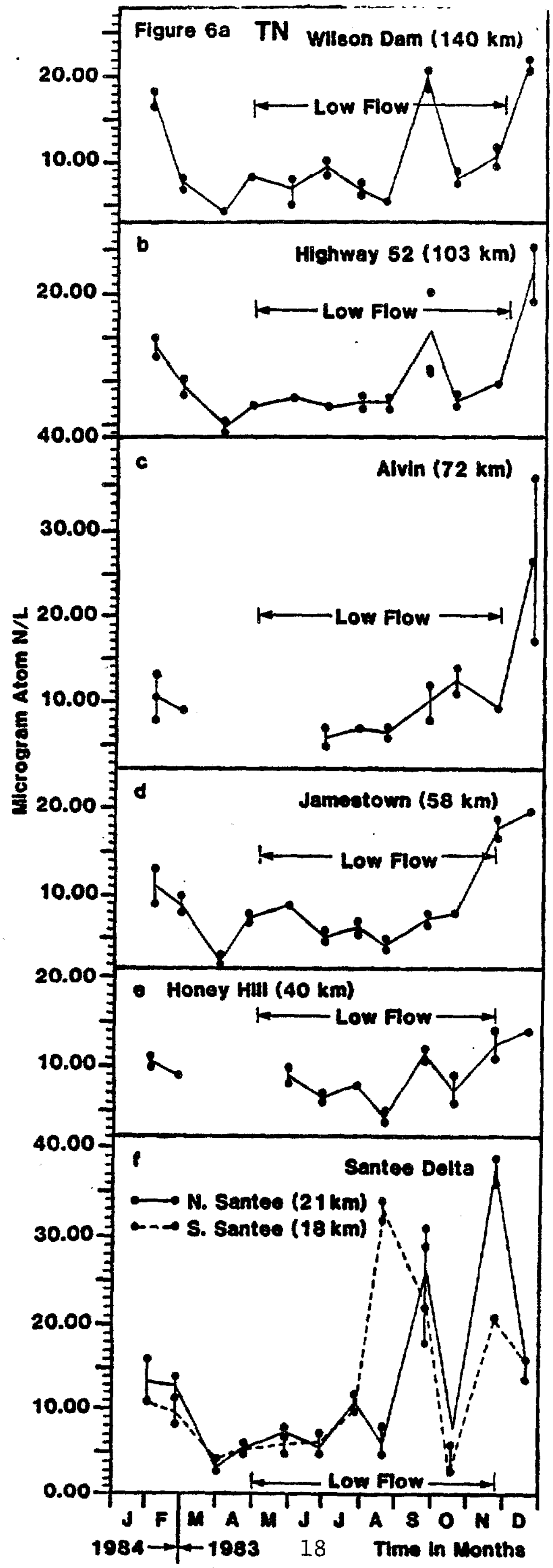

Figure 6a TN Wilson Dam (140 km)
Low Flow
20.00
10.00
b Highway 52 (103 km)
Low Flow
20.00
40.00
c Alvin (72 km)
Low Flow
30.00
20.00
10.00
Microgram Atom N/L
d Jamestown (58 km)
Low Flow
20.00
10.00
e Honey Hill (40 km)
Low Flow
20.00
10.00
f Santee Delta
N. Santee (21 km)
S. Santee (18 km)
Low Flow
40.00
30.00
20.00
10.00
0.00
J F M A M J J A S O N D
1984 1983
Time in Months

concentrations (3-5 ug-at N/L) were observed in August for the headwaters and all riverine stations. Maxima TN concentrations (32 to 38 ug-at N/L) were observed at the delta stations during the months form August to December. The pattern we observed for the two delta stations are relatively similar (Fig. 6-f).

Spatial Variability

The graphs in Fig. 7a-c reflect the spatial variations in TN concentrations. During the winter floods (J-Mar) gradual decrease in TN concentration from 17.5 to 11.0 ug at/l was observed from source waters of WD to the delta stations. This suggests that the riverine reach and its floodplains are sinks for TN species (Fig. 7a). The summer low flow (Fig. 7b) presents low TN concentrations of 5.0 to 6 ug at N/L for the riverine stations, however, very high TN concentrations (34.0 ug at/l) was observed during this time (August) for the north Santee delta station. This suggests that miximum tidal effects occur during summer low flow periods. High TN concentrations of 20.5 ug at/l at the headwaters and 17.0 ug at/l at the delta stations were observed during the initial fall-winter flood periods (Fig. 7c), suggesting that the floodplains upstream may be functioning as nitrogen sources while the coastal wetlands may function as nitrogen sinks.

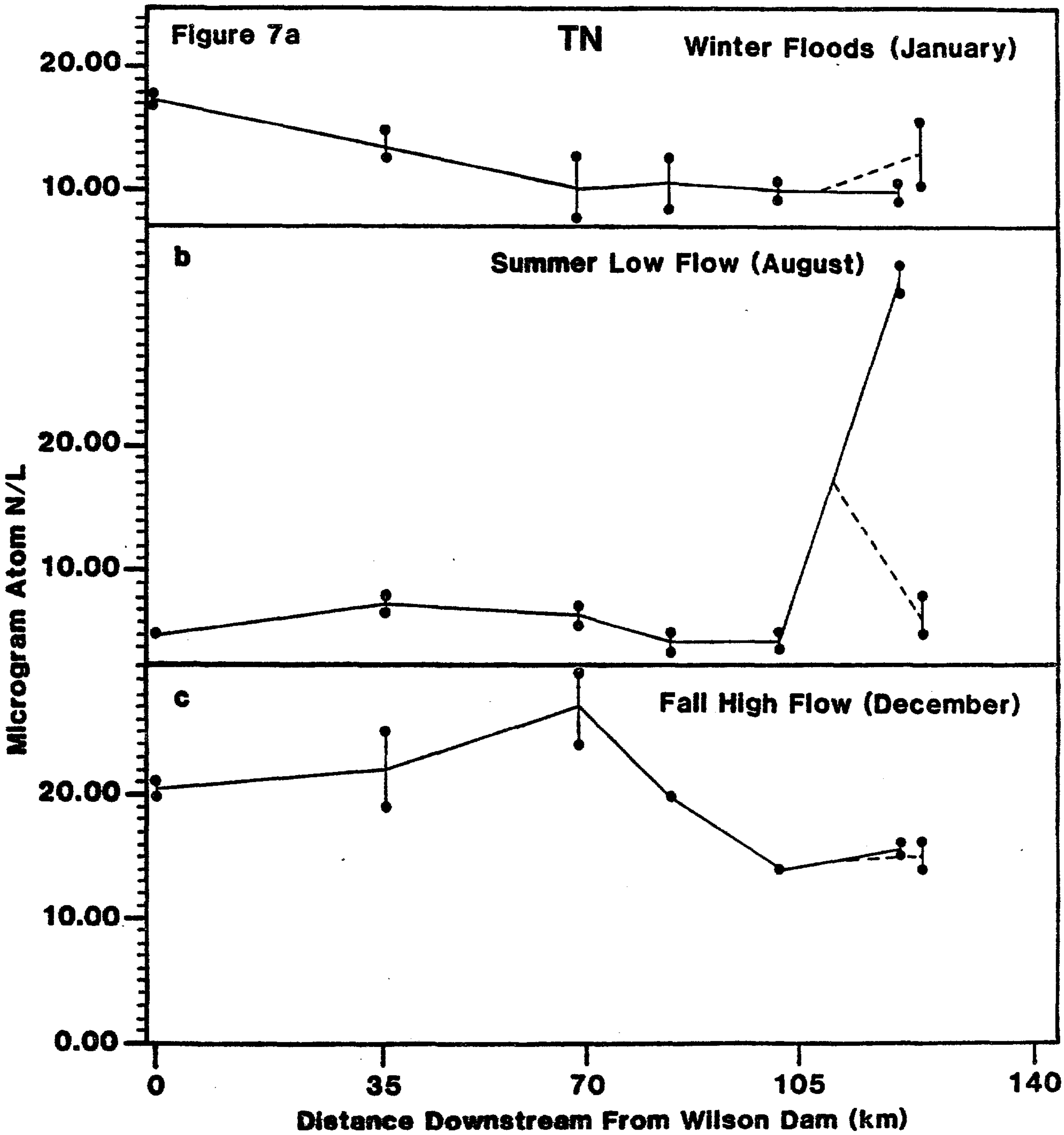

Figure 7a
TN
Winter Floods (January)
b
Summer Low Flow (August)
c
Fall High Flow (December)
Microgram Atom N/L
20.00
10.00
0.00
0
35
70
105
140
Distance Downstream From Wilson Dam (km)

Total Organic Carbon

Temporal Variability:

The graphs for the temporal trends of total organic carbon (TOC) (Fig. 8a-f) are a bit sketchy due to analytical problems (POC-June and July missing data). The sources water at WD station show a decline in TOC concentrations from 8.5 mg/l in late summer to 5.0 mg/l in late fall (Fig. 8a). This was probably due to possible autumn decline in organic carbon production in Lake Marion. The riverine stations through Honey Hill (HH) reflect similar decline from late summer but with sharp increase with December flood conditions suggesting a floodplain source of organic carbon with the first month of flooding. The estuarine stations (N and S. Santee) show a linear decline from maximum levels of 19 mg/l in late summer to levels less than 7 mg/l in December.

Spatial Variability:

The Lower Santee River TOC spatial trends are presented in Fig. 9a-d. The annual TOC mean concentrations show a gradual increase from 6.0 mg/liter at Wilson Dame (WD) to near 12 mg/liter in the estuarine stations (Fig. 9a). The winter flood (Jan) period suggests slight linear increase in TOC downstream from Wilson Dam suggesting TOC input from floodplain (Fig. 9b). The summer-fall low flow periods

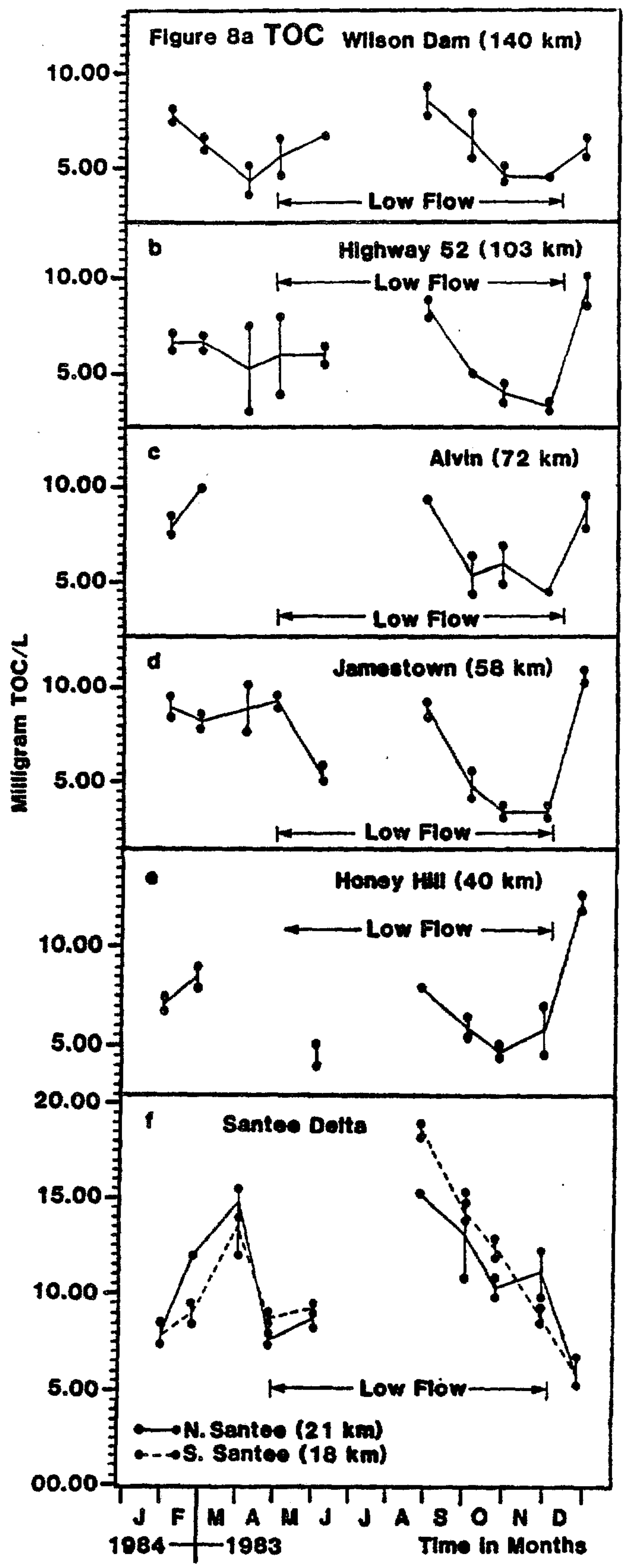

Figure 8a TOC Wilson Dam (140 km)
Low Flow
b Highway 52 (103 km)
Low Flow
c Alvin (72 km)
Low Flow
d Jamestown (58 km)
Low Flow
e Honey Hill (40 km)
Low Flow
f Santee Delta
Low Flow
N. Santee (21 km)
S. Santee (18 km)
Milligram TOC/L
10.00
5.00
20.00
15.00
00.00
J F M A M J J A S O N D
1984 1983
Time in Months

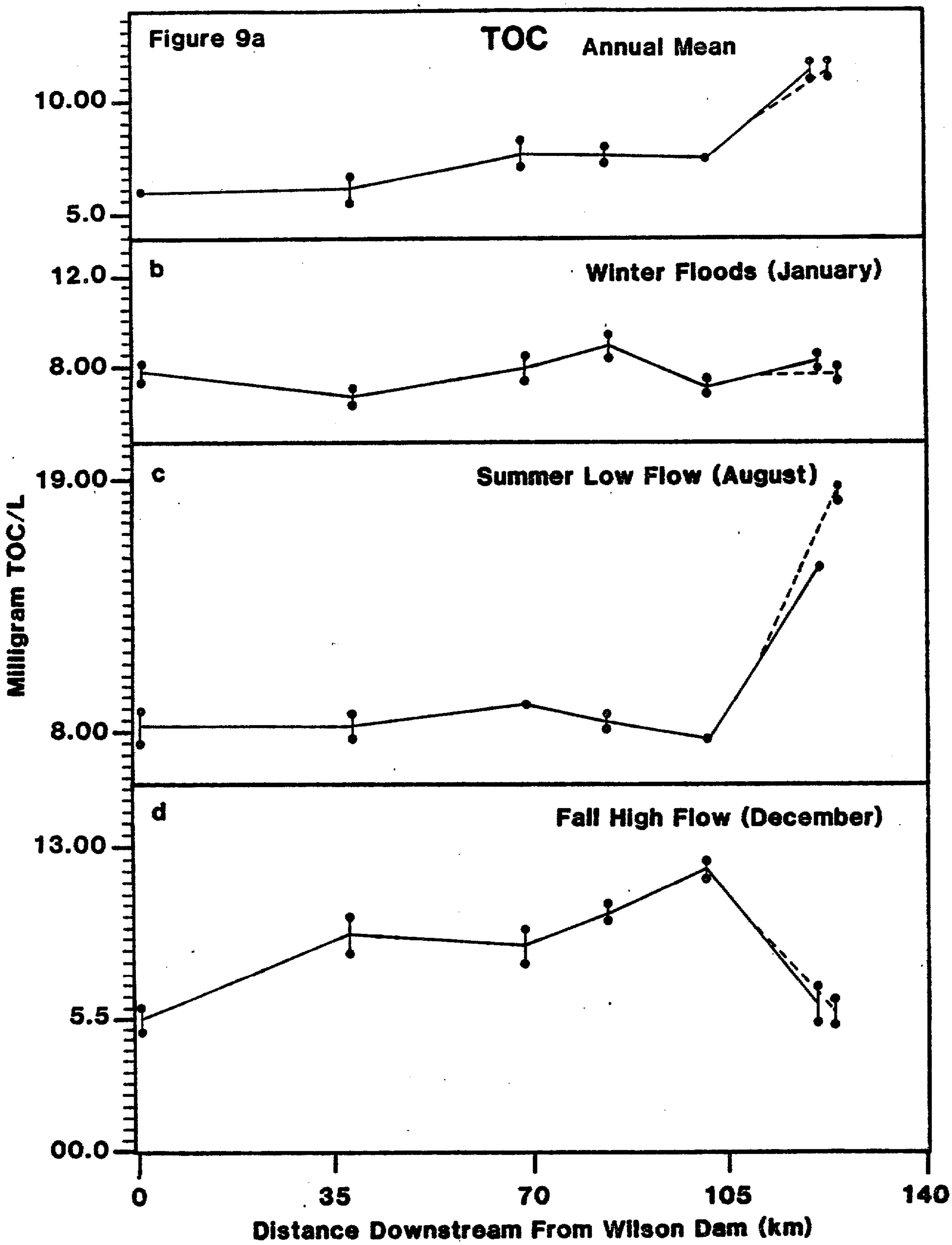
Figure 9a
TOC Annual Mean
b
Winter Floods (January)
c
Summer Low Flow (August)
d
Fall High Flow (December)
10.00
5.0
12.0
8.00
19.00
8.00
13.00
5.5
00.0
Milligram TOC/L
0
35
70
105
140
Distance Downstream From Wilson Dam (km)

(August) show small changes in riverine stretches (8.0 to 9.0 mg/liter) but with sharp increase to peak values approaching 20 mg oc/liter in the delta region suggesting source of organics from coastal wetlands (Fig. 9c). The dramatic effects of late fall and initial flood events is reflected in Fig. 9d. There is a gradual increase 5.5 mg/liter from the source water of Lake Marion (WD) to concentrations near 13 mg oc/liter at the HoneyHill station suggesting maximum floodplain source of OC. However a sudden drop in the organic carbon concentration was observed for the same period at the coastal stations suggesting estuarine dilution or consumption of organic rich river water during this period.

Discussion

Hydrologic effects-- Recent literature suggests that the hydrolic regime of most southeastern floodplain-river ecosystems are characterized by the periodicity and timing of water input, the flushing rate, the quantity and velocity of river discharge downstream and the topographic gradient of the ecosystem (Elder and Mattraw, 1982; Kuenzler, et. al., 1980; Tate and Mayer, 1983).

Much of the work done on 3rd to 6th order coastal streams and rivers shows that the highest floods resulting in maximal innadation of the forested floodplains occur in late winter and early spring. In this study we document that the Lower Santee River experienced high discharge from the month of December to April, and low discharge from May to November. During winter and early spring, the discharge (354 to 496 $m^3 s^{-1}$) is high enough to innadate the entire floodplain forests that boaders the entire river stretch. The Lower Santee River hydrologic characteristic is similar to those reported for most southeastern coastal-lain rivers.

Flood events in streams contribute significantly to annual material export from watersheds (Leopold, et. al., 1964; Aormann et. al., 1974; Johnson et. al., 1976). Material export is a function of both stream water concentration and dishcarge rate. The hydrologic characteristics of the Lower Santee River floodplain system, as well as the productivity of the floodplain vegetation, are important factors effecting nutrient concentrations and dynamics in the river water. The role of hydrologic factors is complex. The concentrations of some dissolved materials are diluted at high discharge (Leopold et. al., 1964; Johnson and Needham, 1966) while others, particularly phosphorus and nitrogen are increased (Turner et. al., 1975; Long and Cooke, 1978). A small woodland stream is almost totally enclosed by its ripariam vegetation such that direct litter fall in the stream is an important component of the allochtonous input (Cummins, 1977). For a large river, direct litter fall into the main channel is of monor significance. Flooding is the mechanism by which detritus deposited on the flood plain may be transported. The major role played by the Santee River winter-spring high flow, other than increase nutrient flux, we find to be the transport of organic carbon and nutrients from the bordering flooplain forest bed into the river channel. This aeqneous transport provides pathways for exchange between the river channel and floodplain through lateral import or exports of elements and organic matter.

Temporal effects

The temporal variations of N and P along the Lower Santee River were similar. The seasonal patterns (Figs. 4 and 8) document high winter levels, low summer levels and with intermediate spring and fall levels. The source water for this river is Lake Marion and similar seasonal patterns have been observed and reported for lakes (Pearl et. al., 1975; Horne and Goldman 1972). Seasonal nutrient variation has also been reported for riverine systems (Naiman and Gibert 1978; Elder and Mattraw, 1982).

The most rationale ecological explanation for these seasonal fluctuations should be the variable rates of nutrients cycling, however the well docummented lateral transport from bordering wetlands complicates the ecological explanation. The natural characteristics of TP concentrations and river flow rates derived from hydrograph and chemograph has been reported to peak almost always before the flow peaks and the TP concentrations declines to low flow values before the flow returns to its approximate steady flow range of values (Verhoff et. al, 1982).

The temporal variabilities we observed for TOC (Fig. 8) are high summer concentrations followed by a late summer and fall decline. This can be explained as the ecological effects of high primary productivity in spring and summer and autumn decline of organic carbon production. However the sharp increase in TOC concentrations observed in December may be explained by hydrologic effects of lateral transport of organic carbon from the inuudated floodplain forests. Elder and Mattraw (1982) have documented the importance of flooding on organic carbon flux from wetland systems. Particulate material transport from the floodplain is almost entirely dependent on flood events with adequate flow velocity. Timing has been emphazied as important since major litter-fall production always occurs in late autumn (Elder and Cairns 1982).

Spacial effects -- TP, TN and TOC.

The TP and TN concentrations show marked difference between the riverine stations (HWY52 to HH) and the delta stations (N and S Santee). Within the riverine stations there is a gradual decrease from the upstreams to downstream. This suggests more nutrient uptake in the riverine stretch and or the nutrient sink effects of the bording floodplain forests. The mechanisms of nutrient removal by wetlands are not well understood and may depend on the hydrology of the ecosystem. Some studies of wetlands have indicated only seasonal or temporary removal of nutrients or even net releases of nutrients (Lee et. al., 1975). Mechanisms suggested for the nutrient sink effects include nitrification and subsequent denitrification across an anaerobic interface (Engler and Patrick, 1974), uptake by growing vegetation (Kitchens et. al., 1975; Klopatek, 1975; Boyd et. al., 1977, Brinson, 1977; Tilton and Kadlec, 1979) and sedimentation (Yarbro, 1979). The delta stations show a spike in the concentrations of TP and TN. However since this spike in nutrient concentration is not observed during periods of high riverine discharge, we interpret the spike as due to maximum estuarine tide effects which peaks during the months of low flow. The spacial pattern observed for TOC is the reverse for TP or TN. There is a gradual increase of TOC concentrations from upstream to downstream delta station. This we interpret as the bordering floodplain forest and delta wetlands functioning as TOC source to the river channel. This is borne out by the dramatic increase in TOC upstream during initial flood events in winter. At the same time the usual delta spike concentration is lost due to increase flushing. The increase in TN, TP, TOC during flood periods has been reported to be due to mobiliztion of particulate subspecies during flood periods (Elder, 1983; Lambon and Hern, 1983).

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ESTIMATION OF BIOMASS AND PRIMARY PRODUCTIVITY OF MATURE AND EARLY SUCCESSIONAL FOREST SITES ON THE SANTEE RIVER FLOODPLAIN

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ESTIMATION OF BIOMASS AND PRIMARY PRODUCTIVITY OF MATURE AND EARLY SUCCESSIONAL FOREST SITES ON THE SANTEE RIVER FLOODPLAIN

ABSTRACT

The productivities of two study sites in a coastal South Carolina alluvial river swamp forest were studied from May 1983 to May 1984. The two sites were a mature bottomland hardwood (BLH) forest and an early successional scrub/shrub type forest. Aboveground net primary productivity was determined from measurements on litter-fall, stem growth and harvested samples of the herbaceous understory. Annual stem growth of the BLH site was estimated by regressing diameter breast height and dry weight biomass. The annual stem growth at the scrub/shrub site was determined by a random harvest technique. The annual increase in stem biomass for the BLH was 1232 g drywt/m2/yr. The scrub/shrub site stem biomass increase was 909 g drywt/m^2/yr. Litter-fall was measured at 654 g drywt/m^2/yr and 499 g drywt/m^2/yr for the BLH and scrub/shrub sites respectivly. Herbaceous layer productivity was measured using a peak biomass by species method. Herbaceous layer production was 132 g drywt/m^2/yr for the BLH and 152 g drywt/m^2/yr for the scrub/shrub site. Estimated total aboveground net primary productivity (NPP) was determined as the sum of the increase in stem biomass, litter-fall and herbaceous layer biomass. The NPP of the BLH site was 2018 g drywt/m^2/yr and the scrub/shrub site NPP was 1560 g drywt/m^2/yr. The NPP and biomass measurements of these two sites were consistent with productivity data from similar sites in the southeast.

INTRODUCTION

The Santee River is formed by the confluence of the Congaree and Wateree Rivers about 51 miles downstream from Columbia, South Carolina, and flows 143 miles to the Atlantic Ocean. The Santee originally had an average annual flow of 17,400 cfs and was the fourth largest river on the east coast of the United States. The Santee River basin drains about 16,768 square miles in North and South Carolina. In 1941 the South Carolina Public Service Authority (PSA) significantly altered the flow regime of the Santee River by constructing a dam and a diversion canal to develope the hydro-electric power potential on the coastal plain. At that time almost 90% of the Santee Rivers flow was diverted into the Cooper River. The flow on the Santee is now controlled by releases made from Wilson Dam on Lake Marion.

The Cooper River Rediversion Project was designed to alleviate shoaling and dredging problems in Charleston Harbor. Completion of this project will cause the Santee River to be returned to within 80% of its original flow. Table 1. indicates annual average flow regimes for the Santee River.

TABLE 1.
Average annual flow regimes
for the Santee River
(from McKellar et al. 1981)

	Flow (cfs)*
Before 1941	17,500
After diversion	2,000
After rediversion (planned completion date Jan, 1985)	14,000

* cfs = cubic feet/sec = 0.0283 m^3/sec

The flow on the Santee River increases during the winter-spring period, from the normal controlled flow of 500-600 cfs, increasing the annual mean flow to 2,000 cfs.

The Santee River floodplain spans from 2 to 8 km along the 70 km distance from Wilson Dam to the coastal zone. The high productivity of this area is important in that it maintains timber production, fish and wildlife habitats and contributes many "free" values to the region by maintaining natural flood control, water storage and water quality (Wharton 1970, Wharton et al. 1976). The floodplain ecosystem also exports significant amounts of organic detritus, which plays a major role in downstream coastal ecosystems (Brinson et al. 1981, Wharton et al. 1982, and Elder and Mattraw 1982). The higher flow on the Santee River after rediversion will mean that the floodplain will be inundated by water at a greater frequency, depth and duration. Trees put under stress because of this increased flow will not be able to reproduce or maintain themselves. The majority of bottomland species can not survive two years of continuous flooding (Broadfoot and Williston, 1973).

SITE DESCRIPTION

Mature bottomland hardwood site: near Alvin, S.C.

A bottomland hardwood community in the Francis Marion National Forest, representative of the surrounding forestland, was choosen as the site for this particular productivity study. The total area of the site measured 6000 m^2 (50 m x 120 m) and was approximately 0.4 km from the Santee River.

Species analysis of the stand was obtained by the point-centered quarter technique (Cottom and Curtis, 1956). Table 2 describes a summary of the vegatation analysis. The overstory species that were most important were red maple (*Acer rubrum*, average dbh = 14.7 cm, importance value = 47.04), sweetgum (*Liquidambar styraciflua*, dbh = 26.2 cm, IV = 34.65) and green ash (*Fraxinus pennslyvanica*, dbh = 53.1cm, IV = 47.38). Other overstory species found include American elm (*Ulmus americana*), water oak (*Quercus nigra*), overcup oak (*Quercus lyrata*), laurel oak (*Quercus laurelifolia*), sycamore (*Platanus occidentalis*) and water hickory (*Carya aquatica*). Overstory species are defined as those species capable of reaching dominant or subdominant positions in the forest canopy. The understory consisted almost entirely of three species. Sugarberry (*Celtis laevigata*, dbh = 14.8 cm, IV = 43.27), ironwood (*Carpinus caroliniana*, dbh = 10.1 cm, IV = 39.10) and possumhaw (*Ilex decidua*, dbh = 7.9 cm, IV = 38.09). American holly (*Ilex opaca*) and hawthorn (*Crategus sp.*) were also found. The understory species are defined as those not able to obtain canopy height in a forest setting.

The herbaceous layer of the site consisted mostly of green briar (*Smilax sp.*), sedges (*Carex sp.*), bignonia (*Anisostichus capreolata*) and composites (*Senecio sp.*). Other herbaceous plants found include lizard tail (*Suarurus cernuus*), poison ivy (*Rhus radicans*), and blackberry (*Rubus sp.*). Table 3 summarizes the herbaceous plant species found at the site.

On the average water was in the floodplain about 10% of the year (35 - 40 days). The total rainfall in the Francis Marion National Forest during the year of the study was 151.5cm average temperature was 65.4° F. (U.S.G.S. 1982-1983).

Early successional scrub/shrub site: near Germantown, SC

The scrub/shrub site was an approximately 19 ha area that was clearcut in 1976 using a high-lead skidding operation (U.S. Forest Service). This type of clearcutting leaves large amounts of stumps, logs, hummucks and other debris which offer sufficient seed bed for a variety of bottomland species. The black willow (Salix nigra, average dbh = 10.0cm, importance value = 68.30) became established shortly after the clearcutting and was by far the largest tree species found (Allen, U.S.Forest Service, 1962). The most important tree species found at the site were the black willow, red maple (dbh = 1.8cm, IV = 37.68), baldcypress (Taxodium distichum, dbh = 0.5cm, IV = 35.32), green ash(dbh = 1.3cm, IV = 25.58), and water tupelo (Nyssa aquatica, dbh = 1.7cm, IV = 24.45). Shrub species found included virginia tea (Itea virginiana, dbh = 0.6cm, IV = 17.41), American holly (dbh = 1.2cm, IV = 8.25) and possumhaw (dbh = 0.7 cm,IV = 8.09). Table 4 shows a summary of the woody vegatation analysis at the clearcut site determined by the quadrat sampling technique.

The herbaceous layer of the clearcut site consisted mostly of sedges (Carex sp.), blackberry (Rubus sp.), and composites (Scenecio sp.). Other herbaceous plants found included bignonia, Christmas fern (Polystichum acrostichoides), lizard tail, and cat-tail (Typha sp.). Table 5 summarizes the herbaceous plant species found at the site.

On the average water was in the floodplain about 10% of the year (35 - 40 days). The total rainfall during the year of the study was 177.3 cm and the average tempature was 64.2°F. (U.S.G.S. 1982-1983).

METHODS AND MATERIALS

Mature bottomland hardwood site:

Stem biomass was determined by using the point-quarter technique (Cottom and Curtis, 1956). Twenty points were selected at random and the closest overstory or understory tree (greater than 5 cm dbh) in each quarter was identified, cored to determine latest increment growth, and measured for point to plant distance and dbh. There were a total of 80 trees sampled. Tree biomass was determined by the regression equation log drywt = 1.9757 + 2.5371 log dbh (Monk et al. 1970). This equation gives whole tree weight for general hardwood species. Annual diameter increase was estimated by subtracting the ring increment for the growing season from the measured dbh. The difference in the starting and ending tree biomass as determined by the regression equation was the annual increase in wood biomass.

Litter-fall was collected on a regular basis (averaging every 50 days). The litter was collected in 18 1 x 1 m traps made of burlap and pvc piping. The samples were sorted into leaf, wood, reproductive and other unidentifiable material. All components of the sample were dried at 70^{o} C until a constant weight was obtained. The sum of the average monthly litter-fall collections in $g/m^2/yr$ was used to calculate organic matter loss in the study site during the year.

Biomass of the understory-herbaceous layer was measured by using the harvest method (Whittaker, 1975). Twenty-one 0.5 x 0.5 m quadrats were collected at five different times during the year (representative of the growth seasons for different herbaceous plant species). The samples were separated into species and dried at 70^{o} C to a constant weight. Productivity of the herbaceous layer was estimated using a peak biomass by species method (Whigham et al. 1978).

Scrub/shrub site:

Stem biomass at the clearcut site was measured by using the harvest method (for trees less than 5 cm dbh) and regression equations (for trees greater than 5 cm dbh). Fifteen 10 x 10 m quadrats were harvested and all trees with dbh less than 5 cm were taken. All the samples were separated into species, measured for basal diameter (db), dbh, height, age, latest ring increment and dried to a constant weight. The biomass of trees with a dbh greater than 5 cm was measured by the regression equation of log drywt = 5.0284 + 2.0903 log dbh (natural log). This equation was generated from measurements made on 196 hardwood trees in the sample. Annual wood production for harvested trees was estimated two ways:

1. Estimated volume increment x average density.
2. Regression on differences in starting and ending dbh's.

The estimated volume increment (evi) was determined by the equation of Whittaker and Woodwell (1968):

$$\begin{aligned} evi &= 0.5\,(3.1415)\,(\text{height})\,(r^2-c^2) \\ \text{where } r &= \text{tree radius} \\ c &= r - i \\ i &= \text{annual wood radial increment at db.} \end{aligned}$$

The evi was then multiplied by the average density of each tree (determined by tree weight / tree volume) to determine the wood production for each tree sampled.

Annual wood production was also determined by using the regression equations that were generated from sampling at the clearcut site. The difference in starting biomass and ending biomass was the annual wood production. Wood production for the large trees was estimated as the total biomass divided by the age of the stand times the area sampled. (wood production for large trees = total biomass / age(8 years)x 150 m^2). This was actually an underestimate of the large tree productivity but increment cores were not taken so there was not a precise measurement.

Litter-fall collections were made on a monthly basis (averaging every 50 days) in 18, 1 x 1 m traps constructed as above. The litter was separted into component parts (leaf, wood, reproductive and other), and dried to a constant weight. The sum of the average monthly litter-fall in $g/m^2/yr$ was used to calculate organic matter loss during the year.

The productivity of the herbaceous layer was estimated using the harvest technique and peak biomass by species method as described above.

TABLE 2.
SUMMARY OF THE VEGATION ANALYSIS BY THE POINT-QUARTER TECHNIQUE
FOR THE MATURE BOTTOMLAND HARDWOOD SITE.

SPECIES	no.	rel. density	rel. dominance	rel. frequency	importance*
green ash	7	8.75	27.52	11.11	47.38
sugarberry	13	16.25	11.15	15.87	43.27
sweetgum	9	11.25	13.88	9.52	34.65
red maple	15	18.75	12.42	15.87	47.04
ironwood	12	15.00	8.23	15.87	39.10
possumhaw	13	16.25	7.56	14.28	38.09
overcup oak	2	2.50	5.68	3.17	11.35
sycamore	2	2.50	4.46	3.17	10.13
water oak	1	1.25	3.89	1.59	6.73
A. elm	2	2.50	0.67	3.17	6.34
laurel oak	1	1.25	0.18	1.59	3.02
baldcypress	1	1.25	3.31	1.59	6.15
A. holly	1	1.25	0.23	1.59	3.07
hawthorn	1	1.25	0.47	1.59	3.31
total	80	100	100	100	300

* Importance value = rel. density + rel. dominance + rel. frequency (Curtis and M[c]Intosh, 1951)

TABLE 3.
SUMMARY OF THE HERBACEOUS PLANT SPECIES
AT THE MATURE BOTTOMLAND HARDWOOD SITE

species*	%occurance **
sedges (*Carex sp.*)	100
bignonia (*A. capreolata*)	100
greenbriar (*Smilax sp.*)	100
cane (*Arundunaria sp.*)	80
Composites (*Senecio sp.*)	100
lizard tail (*S. cernuus*)	80
poison ivy (*R. radicans*)	100
clearweed (*Pilea pumila*)	80
V. creeper (*P. aquinquifolia*)	60
blackberry (*Rubus argutus*)	80

** %occurance = no. of times found in sampling
*ref.(Radford, Ashels and Bell, 1983)

TABLE 4.
SUMMARY OF VEGATION ANALYSIS BY THE QUADRAT SAMPLING TECHNIQUE
FOR THE SCRUB/SHRUB SITE

SPECIES	no.	rel. density	rel. dominance	rel. frequency	importance*
black willow	14	3.58	56.67	8.05	68.30
red maple	86	21.99	1.99	13.70	37.68
baldcypress	84	21.48	0.14	13.70	35.32
green ash	42	10.74	1.14	13.70	25.58
w. tupelo	48	12.28	1.90	10.27	24.45
w. oak	14	3.58	9.21	8.05	20.84
sweetgum	9	2.30	10.92	4.62	17.84
virginia tea	40	10.23	0.33	6.85	17.41
w. hickory	13	3.32	1.90	3.42	8.64
ironwood	1	0.26	6.91	1.20	8.37
A. holly	10	2.56	1.03	4.62	8.25
possumhaw	12	3.07	0.40	4.62	8.09
A. elm	3	0.77	4.52	0.07	6.49
privet	4	1.02	1.80	1.20	4.02
silverling	7	1.79	0.42	1.20	3.41
cottonwood	1	0.26	0.64	1.20	2.10
sycamore	1	0.51	0.06	1.20	1.77
pine	1	0.26	0.00	1.20	1.46
total	366	100	100	100	300

Importance value = rel. density + rel. dominance + rel. frequency
(Curtis and M^{c}Intosh, 1951)

TABLE 5.
SUMMARY OF THE HERBACEUOS PLANT SPECIES
AT THE SCRUB/SHRUB SITE

species*	%occurance **
sedges (Carex. sp)	100
blackberry (Rubus sp.)	100
composites (Senecio sp.)	100
greenbriar (Smilax sp.)	20
clearweed (Pilea pumila)	60
poison ivy (R. radicans)	100
bignonia (A. capreolata)	100
fern (P. acrostichoides)	80
lizard tail (S. cernuus)	60
pennywort (Hydrocotlye sp.)	60
rush (Juncus effusus)	40
cat-tail (Typha sp.)	40

** % occurance = no. of times found in sampling
*ref. (Radford, Ashels and Bell, 1983)

Net primary production:

Aboveground net primary productivity was determined as the sum of the stem biomass increase, litter-fall and herbaceous layer biomass. Underground biomass which may account for as much as 30% of the total biomass in some forest ecosystems (Mitsch and Ewel, 1979) was not included due to the difficulty in sampling. Consumption by herbivores was also not included. Total aboveground net primary productivity can be calculated using Newbould's (1967) equation:

$$Pn = \hat{}B + L + G$$

where Pn = net productivity (aboveground) during time(^T)
^B = biomass change during (^T)
L = litter-fall during (^T)
G = grazing by herbivores during (^T)

RESULTS

Biomass of the mature bottomland hardwood site:

Stem biomass of the mature bottomla hardwood site was calculated by regressing dbh and whole tree dry weight. There where 160 trees sampled (trees greater than 5 cm dbh) with a biomass range of 918 g dry weight to 6,574,000 g dry weight. The average tree biomass was 564,000 (+/- 93,700) g dry weight. Table 6. summarizes the BLH site biomass by species.

The biomass of the herbaceous layer was determined by the harvest technique. A peak biomass by species method was used to determine total production. This method more accurately assesses productivity than taking the average biomass of monthly samples. Table 7 summarizes peak biomass estimates for the BLH site. A total of 132 g drywt/m^2/yr was determined as the herbaceous layer productivity.

TABLE 6.
Summary of the BLH site biomass*
by species

species	#	ave. dbh(cm)	biomass(g)	ave. biomass(g)
overstory				
green ash	16	53.13	42,835,596	2,677,224
cottonwood	3	48.26	5,134,596	1,711,373
baldcypress	1	51.56	2,072,929	2,072,929
A. elm	3	8.97	118,837	39,612
l. oak	3	5.84	27,510	9,170
o. oak	3	51.71	10,585,369	3,528,456
red maple	24	14.68	3,772,387	157,182
sweetgum	21	26.19	10,912,080	519,622
sycamore	3	29.46	1,950,039	650,013
w. hickory	1	58.89	2,889,648	2,889,648
w. oak	2	40.28	3,229,013	1,614,507
total	80	29.70	83,527,528	1,044,094
understory				
A. holly	2	4.32	6,260	3,130
sugarberry	29	14.78	5,049,100	174,106
hawthorn	1	7.37	13,708	13,708
possumhaw	25	7.94	599,162	23,966
ironwood	23	10.11	1,006,522	43,761
total	80	10.94	6,674,753	83,434
grand total	160	20.32	90,202,281	563,764

* biomass determined by regression equation of Monk (1970)

$$\log \text{drywt} = 1.9757 + 2.5371 \log \text{dbh}$$

TABLE 7.
Summary of peak biomass estimates by species
for the BLH site

species	peak month *	biomass(g/m^2)	%
<u>Smilax sp.</u>	October	36.9	27.9
<u>Carex sp.</u>	May	26.5	20.1
<u>Senecio sp.</u>	May	18.8	14.2
<u>A. capreolata</u>	December	17.1	12.9
<u>Rhus radicans</u>	May	8.0	6.1
<u>Arundunaria sp.</u>	October	4.9	3.8
<u>Rubus sp.</u>	May	3.9	2.9
<u>Pilea pumila</u>	May	2.2	1.7
<u>Suarurus cernuus</u>	May	1.4	1.1
<u>P. aquinquefolia</u>	May	1.3	1.0
others	-	5.7	4.3
shrub	October	5.3	4.0
total		132.0	100

*Samples were taken in May(83),July,October,December,May(84)
(n = 21, 0.5 x 0.5 m quadrats / month)

Biomass of the scrub/shrub site:

Stem biomass of the scrub/shrub site was measured by using the harvest technique for trees less than 5 cm dbh, and by regression for trees greater than 5 cm dbh. There were 366 trees harvested with 15, 10 m^2 samples. A total dry weight of 124,787 g (832 g/m^2) was recorded. The average tree weighed 340 +/- 33 g. Table 8 lists the biomass of the harvested trees by species. There were 25 trees with a dbh greater than 5 cm. The biomass of these trees was estimated by regression to be 712,973 g dry weight (4753 g/m^2). The average tree weighed 28,518 +/- 5,700 g. Table 9 lists the biomass of the large trees (not harvested) by species.

Biomass of the harvested trees was also calculated by regression. The total biomass was estimated to be 115,489 g dry weight (n = 279, 87 trees did not attain breast height or 1.37 m) or 770 g/m^2. (table 8)

Biomass of the herbaceous layer was 167 g/m^2. Table 10 summarizes the species and biomass of samples taken in May(83), July, October, December and May(84).

Litter-fall

Mature BLH site:

Litter-fall at the mature BLH site was 654 $g/m^2/yr$. The litter was separated into leaf, wood and reproductive components. Leaf weight accounted for 73.5% (478 $g/m^2/yr$) of the total, wood weight 13.8% (90 $g/m^2/yr$) and reproductive 12.7% (82 $g/m^2/yr$). The peak of litter-fall occured between early October and early December, accounting for 57% of the total weight lost. Reproductive components reached a peak of

34% between May and June, with a low of 7% between October and December. Wood weight reached its peak between January and Febuary (40%) and a low of 4% between October and December. (table 11)

Scrub/shrub site:

Litter-fall at the clearcut site was 499 $g/m^2/yr$. Leaf weight accounted for 78% (389 $g/m^2/yr$) of the total, wood 13% (65 $g/m^2/yr$) and reproductive components 9% (45 $g/m^2/yr$). The peak of litter-fall occured between October and December accounting for 54% of the total weight lost. Reproductive components reached a peak of 15% between July and October and a low of 1% between October and December. Wood weight reached a peak between December and January with 51%, with a low between July and October of 3%. (table 11)

TABLE 8.
Biomass of harvested trees
at the scrub/shrub site

species	#	ave. dbh(cm)	biomass(g)	ave. biomass(g)
green ash	42	1.33	18288	435
silverling	7	0.76	1693	242
ironwood	1	3.50	4037	4037
cottonwood	1	1.14	184	184
baldcypress	84	0.48	7667	91
possumhaw	12	0.72	1662	138
american elm	3	2.67	5172	1724
water hickory	13	1.68	10941	842
american holly	9	0.77	2754	306
virginia tea	40	0.59	3153	78
oak	9	2.05	13133	1459
pine	1	0.00	12	12
privet	4	1.60	2699	675
red maple	81	1.26	28810	356
sweetgum	6	1.55	4507	751
sycamore	2	0.19	62	31
water tupelo	46	1.48	18523	403
black willow	5	0.86	1486	297
total	366	1.05	124787	341

(115489 regression calculation n=279)

TABLE 9.
Biomass* of large trees (> 5cm dbh)
at the scrub/shrub site.

species	#	ave. dbh(cm)	biomass(g)	ave.biomass(g)
american holly	1	5.16	4720	4720
red maple	5	10.11	133657	26731
oak	5	7.74	62159	12432
sweetgum	3	9.80	57130	19043
water tupelo	2	6.53	15452	7726
black willow	9	15.13	439855	48873
total	25	10.92	712973	28519

* determined by regression: log wt = 5.0284 + 2.0903 log dbh

TABLE 10.
Summary of peak biomass estimates by species
for the scrub/shrub site

species	peak month*	biomass(g/m^2)	%
Carex sp.	May	52.2	31.2
Senecio sp.	May	24.1	14.4
Rubus argutus	December	18.6	11.1
Rhus radicans	May	7.8	4.7
Juncus effusus	October	6.6	3.9
Smilax sp.	May	4.7	2.8
P. quinquefolia	May	4.6	2.8
Suarurus cernuus	May	4.4	2.6
Typha latifolia	May	3.9	2.3
A. capreolata	May	3.4	2.0
others	October	30.5	18.2
shrub	October	6.4	3.8
total		167.2	100.0

* samples were taken in May(83), July, October, December and May(84).

Annual wood production

Bottomland hardwood site:

The annual increase in stem biomass was 1232 $g/m^2/yr$ (the difference between starting and ending biomass). The productivity and area was estimated for each tree sampled (n = 80). Table 12 summarizes production by species at the BLH site. Approximately 86% of the wood production occured in the overstory species with 14% in the understory.

Table 11.
Litter-fall (%) component
BLH and scrub/shrub sites

sample day	component	BLH(g/m^2)	scrub/shrub(g/m^2)
0-49 (May 83)	total(%)	27(4)	40(8)
	leaf	14	34
	wood	3	4
	reprod	10	2
49-83	total(%)	43(6)	27(5)
	leaf	24	21
	wood	7	3
	reprod	12	3
83-150	total(%)	102(15)	71(14)
	leaf	70	58
	wood	21	2
	reprod	11	11
150-210	total(%)	383(57)	277(54)
	leaf	339	258
	wood	16	18
	reprod	28	1
210-244	total(%)	63(9)	36(7)
	leaf	31	18
	wood	21	18
	reprod	11	0
244-276	total(%)	25(4)	7(1)
	leaf	11	5
	wood	10	2
	reprod	4	0
276-375 (May 84)	total(%)	29(4)	51(10)
	leaf	4	11
	wood	15	18
	reprod	10	22
total (376 days)	total(%)	671(100)	515(100)
	leaf	493	404
	wood	93	65
	reprod	85	46

TABLE 12.
Annual wood production by species
at the BLH site.

species	#	production($g/m^2/yr$)	% of total
green ash	7	597.4	48.4
sweetgum	9	185.9	15.1
w. oak	1	88.2	7.2
sugarberry	13	81.0	6.6
red maple	15	79.1	6.4
sycamore	2	48.7	3.9
possumhaw	13	46.7	3.8
ironwood	12	41.4	3.4
o. oak	2	40.7	3.3
baldcypress	1	17.0	1.2
l. oak	1	2.2	0.2
hawthorn	1	2.2	0.2
A. elm	2	1.2	0.1
A. holly	1	0.6	<0.1
total	80	1232.3	100

Scrub/shrub site:

The annual increase in stem biomass at the clearcut site was 908 g drywt/m^2/yr. The productivity was estimated by harvesting 150 m^2 (366 trees), the dry weight of which was 314 g/m^2/yr. The large tree annual wood production estimated by regression was 594 g/m^2/yr. Table 13 summarizes production by species at the scrub/shrub site.

Aboveground net primary production

BLH site:

The NPP of the BLH site was the sum of stem biomass increase (1232 g), litter-fall (654 g) and herbaceous layer biomass (132 g). The total NPP was 2018 g dry weight /m^2/yr.

Scrub/shrub site:

The NPP for the scrub/shrub site was 1560 g dry weight/m^2/yr. Stem biomass increase, litter-fall and herbaceous layer biomass were 908 g, 500g and 152 g dry weight /m^2/yr respectively. Table 14 summarizes the NPP for both sites.

TABLE 13.
Annual wood production by species
at the scrub/shrub site.

species	#	production($g/m^2/yr$)	% total
b. willow	14	370.4	40.7
r. maple	86	177.5	19.5
oak	14	79.3	8.7
w. tupelo	48	61.1	6.7
sweetgum	9	59.9	6.6
g. ash	42	43.5	4.8
w. hickory	13	28.6	3.1
baldcypress	84	24.4	2.7
elm	3	12.7	1.4
ironwood	1	11.7	1.3
A. holly	10	11.1	1.2
silverling	7	8.4	0.9
privet	4	8.1	0.9
V. tea	40	6.0	0.7
possumhaw	12	5.6	0.6
cottonwood	1	0.4	<0.1
sycamore	2	0.3	<0.1
pine	1	<0.1	<0.1
total	391	909.1	100

Table 14
Net primary productivity values
for BLH and scrub/shrub sites

	BLH	Scrub/shrub
litter-fall/day (g dry wt/m^2/yr)	1.8	1.4
litter-fall (g dry wt/m^2/yr)	654	499
Herbaceous layer biomass (g dry wt/m^2/yr)	132	152
Increase in stem biomass (g dry wt/m^2/yr)	1232	908
NPP (g dry wt/m^2/yr)	2018	1560

DISCUSSION

Floodplain swamp forests are among the most productive ecosystems due to several subsidies offered to the floodplain by the watershed and river, including particulate and dissolved organic matter, water, clays and silt and nutrients (Wharton et al. 1982). The estimated productivities of the two sites on the Santee river floodplain were consistent with other studies (Conner and Day, 1976). The flooding regime of wetland areas is important in maintaining this high amount of productivity. Gosselink et al. (1981) stated: "Forest production appears to peak at the once-per-year flood frequency if flooding is during the winter because this regime furnishes the optimum environment for plant growth in terms of nutrient input by flood waters, summer soil moisture and possibly aerobic conditions during the summer leading to inorganic nutrient release from organic debris". This corresponds with Odum's (1978) illustration of the effect of flooding on productivity. Productivity is low with stagnant and abrasive flood regimes, whereas it peaks with seasonal flooding. With an operation schedule of 15 hours at full capacity (24,500 cfs) and 9 hours of zero discharge (U.S. Army Corps of Engineers, 1976), simulated stage curves (U.S. Army Corps of Engineers, 1976) indicate that the pulsing discharge would cause overbank flooding approximately 50% of the time in the upstream reaches of the river. At lower reaches of the river this pattern would cause overbank flooding essentially 100% of the time. After rediversion the Santee floodplain may be flooded for about 50% of the time over a typical annual cycle (McKellar et al. 1981) instead of the normal 10-15% prior to rediversion. Brink (1954) surveyed areas where flood conditions persisted and found that herbaceous plant species such as sedges (*Carex sp.*) and rushes (Juncus sp.) were severly affected but returned when the flooding ceased. The lethality of the waters was associated with temperature, depth, duration, movement and physical destruction (deposition of silt). Hosner (1958) studied the effects of inundation upon seedlings of six bottomland hardwood species. He found that only willow (*Salix nigra*) survived complete inundation during the growing season. The other species according to flood tolerance were green ash, sweetgum, box elder (*Acer negundo*), cottonwood and silver maple (*Acer saccarinum*). After 32 days of inundation only the willow seedlings survived (based on death of above-ground parts and roots). Demaree (1932) experimented with *Taxodium sp.* and found that for baldcypress to become established, the seeds must sprout when they are not submerged, and the seedlings must grow to a sufficient height during the first year to stay above flood level. The flow regime of the Santee after rediversion will prevent any regeneration of new forest growth because there will be a constant stress from flooding on the floodplain ecosystem.

The ultimate result of the rediversion on the Santee floodplain may be the loss of productivity due to the mortality of bottomland hardwood areas and dominance by baldcypress-water tupelo areas. The cypress-tupelo swamp was found to have lower net primary productivity (Conner and Day, 1976). Table 15 shows an analysis of the predicted impacts and loss of productivity to the floodplain.

TABLE 15.
(from Mckellar et al. 1981)
Productivity in the Santee floodplain
I. before rediversion
II. after rediversion

Association	%cover	total area (km^2)	gross productivity $gC/m^2/yr$	gC/yr
I. bottomland hardwood	75	82.5	1944	19.7
cypress-tupelo	25	27.5	1399	4.7
total				24.4
II. bottomland hardwood	37.5	41.3	1944	9.9
cypress-tupelo	12.5	68.7	1399	11.8
total				21.7

change - 2.7

CONCLUSION

Net primary productivity for 'average forests' is between 0.5 and 5.0 g/m2/day (182.5-1850 g/m2/yr) (Odum, 1959). The estimates of the NPP for the Santee floodplain are within or near this range. High productivity in riverine swamps is extremely important to coastal ecosystems and to fish and wildlife. A comparison of productivities for wetland areas of the southeastern United States (table 16) substantiates the fact that swamp forest production is highly dependent upon the flow regime and is an important part of the regions environmental resources.

TABLE 16.
Comparison of swamp forest productivies
in the southeastern U.S.

Area	source		density (#/ha)	wood prod. g/m²/yr	npp
still water					
Cypress dome (young) Fla.	S. Brown	1981	2150-3900	335-501	750-1230
Cypress dome (mature) Fla.	S. Brown	1981	3951	541	956
Cypress dome (sewage) Fla.	S. Brown	1981	2573	1060	1794
Cypress forest (Okefenokee swamp)	Schlesinger	1978	1465	330	595
flowing water					
Cypress floodplain Fla.	S. Brown	1981	1644	1086	1607
BLH La.	Conner & Day	1976	1710	800	1574
Cypress-tupelo	" "	1976	1235	500	1140
Tupelo gum (alluvial swamp) NC	Brinson et al	1980	2590	*	*
BLH (mature) SC	this study	1984	833	1232	2018
Scrub/shrub (successionary) SC	this study	1984	26080	908	1560

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Modeling the impacts of a river diversion on bottomland forest communities in the Santee River floodplain, S.C.

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Abstract

LEONARD PEARLSTINE, HENRY MCKELLAR, and WILEY KITCHENS. U.S. Fish and Wildlife Service, Slidell, Louisiana and University of South Carolina, Columbia, South Carolina. Modeling the impacts of a river diversion on bottomland forest communities in the Santee River floodplain, SC.

The U.S. Army Corps of Engineers is completing a river diversion project that will substantially modify water flow in a coastal plain river of South Carolina. Phased discharges from power plant operations on this diversion are expected to cause extensive flooding of the bottomland forest.

To study the impact of the altered hydrologic regimes on the growth and succession of the forested floodplain, a bottomland hardwood succession model was developed by modifying an earlier upland forest model by Shugart and West. Interactions of river flow and site elevation in the model determine flooding patterns and depth of the water table. These hydrologic parameters are then used as major controls for seed germination, tree growth, and tree mortality. Individual species responses to these parameters over time control succession and species composition on the simulated site. Coupling the simulation model with a geographical information mapping system has permitted rapid visual inspection of predicted bottomland community changes in the Santee floodplain. The model predicts a loss of up to 97% of the existing bottomland forest to open water or soil conditions too wet to support tree species; an alternative water release schedule may retain much of this area as cypress-tupelo.

Introduction

Moisture appears to be one of the most critical factors influencing the distribution of forest species within a river floodplain (Hook and Brown, 1973; Bedinger, 1978; Teskey and Hinckley, 1977). Species are distributed along moisture gradients as a result of their tolerance to flood duration and frequency (Bedinger, 1971; Johnson and Bell, 1976). Flooding is most critical during the growing season. Tree species cannot colonize or survive year-to-year flooding lasting more than 50-60% of the growing season (Hall and Smith, 1955), although year-round root inundation may be tolerated in isolated years (Gill, 1970).

During the dormant season, floods have little effect on the growth of most species (Hall and Smith, 1955; McAlpine, 1961; Bedinger, 1978).

Flood stress on woody species is predominantly due to lack of oxygen near the roots (Kramer, 1951). Anaerobiosis has been shown to develop within hours of flooding (Gill, 1970). Those species that best tolerate flooded conditions appear to depend on one or a combination of adaptations. Anatomical adaptations such as aerenchyma formation and adventitious rooting allow oxygen flux from the air or oxygen-rich water to the roots. Metabolic adaptations decrease root oxygen demand (Gill, 1970).

The complex interactions among hydrology, geochemistry, and biology in forest ecosystems are not well understood. However, several simulation models have been developed which successfully predict tree growth and succession in a variety of upland and bottomland applications (Botkin, 1972a; Shugart and West, 1977; Phipps, 1979). In this paper we document modifications of earlier models and the further development of a forested floodplain simulation model.

This model (FORFLO) is designed to predict tree growth, productivity, and changes in species composition in response to river flow modifications.

To examine its effectiveness and practical application, the FORFLO model was used to predict the consequences resulting from a river diversion on the Santee River floodplain forest community in South Carolina. The results of that study are reviewed in this report. In addition, FORFLO is currently being implemented along the lower Atchafalaya River, Louisiana, where a combination of river building, natural subsidence, and levee construction by the U.S. Army Corps of Engineers complicates predictions of species change. FORFLO will also soon be implemented to assist management decisions in the greentree reservoir at Felsenthal National Refuge in Arkansas.

Area Description and River Flow Modifications

The Santee River, South Carolina, was once the fourth largest river on the east coast with average annual flows of 17,500 cubic feet per second (cfs). In 1941, the South Carolina Public Service Authority diverted 88% of the Santee's flow through two newly created lakes and into the Cooper River in order to develop hydroelectric power potential (Figure 1). After the 1941 diversion, the Cooper River had a discharge of approximately 150 times its former flow rate, and the Santee River carried only 10% of its former flow. However, the Santee River still floods typically during late winter and early spring due to release of floodwaters from an upstream reservoir. This periodic flooding continues to support a bottomland hardwood forest along most of the length of the Santee's oversized floodplain. High flows on the Cooper River after the diversion carry large quantities of sediments creating shoaling problems in the navigation channels in Charleston Harbor. Maintenance of the main navigation channels in the harbor requires intensive year-round dredging. The U.S. Army Corps of Engineers, the South Carolina Ports Authority, and the United States Navy dredge an average total volume of about 10.2 million cubic yards of sediment from the harbor per year (U.S. Army Corps of Engineers, 1966). Dredging currently costs about $1.00/yd^3 (J. Saddler, S.C. Ports Authority, personal communication, 1981), or $10.2 million dollars per year to maintain Charleston Harbor.

To alleviate this shoaling problem and the associated dredging cost, the Army Corps of Engineers was authorized by Congress in 1968 to redivert most of the water flow back into the Santee River. The rediversion involves construction of an 18.5-km long canal from Lake Marion back into the Santee River (Figure 1). An additional hydropower plant is being constructed on the rediversion canal near St. Stephen to take advantage of some of the remaining hydrostatic head. For the Cooper River, the Army Corps of Engineers has stipulated (preliminarily) that a weekly average flow of 3,000 cfs must not be exceeded if shoaling in Charleston Harbor is to be effectively reduced (U.S. Army Corps of Engineers, 1975). The magnitude of changes in mean annual discharge patterns between the 1941 diversion project and the planned rediversion are summarized in Table 1.

The floodplain is the major ecological feature of the coastal plain which will be impacted by the rediversion. Studies by McKellar et al. (1981 and

1984) suggested that the rediversion as planned would inundate much of the Santee floodplain and result in an extensive decline in the bottomland forest.

McKellar et al. suggested that loss of floodplain productivity may be decreased substantially if, during the critical early months of the growing season (April, May, June, July), the power plant on the rediversion canal would be operated with just one of its three turbines. This would allow a maximum of 8,000 cfs to pass through the rediversion canal; the rest of the flow would be shunted to the Cooper River.

The seasonal patterns of river flow for present conditions and for the rediversion options discussed above are shown in Figure 2. These long-term average trends indicate a winter-spring period of high flow and a summer-fall period of low flow. After the rediversion, the Santee River would be returned to within 80% of its original (pre-diversion) flow rate with seasonal patterns including flood stages and periods of low flow. Cooper River flows would be held at a weekly 3,000 cfs average as stipulated by the Corps. The results of the modified rediversion proposed by McKellar et al. would be reduced flow to the Santee during the early growing season with a corresponding increase on the Cooper during these months (Figure 2).

Development of the Model

A major objective of this research was to develop a floodplain forest model (FORFLO) to quantitatively predict changes in Santee floodplain forest in response to alternative plans of river flow modification.

The FORFLO model was developed by modifying the forest simulator FORET (Shugart and West, 1977), a southern deciduous forest succession model which simulates the growth, reproduction, and competition of each tree in a mixed-species 1/12-ha (radius = 16.29 m) forest stand. Tree position is not explicity considered. FORET is itself a modification of a previous forest model, JABOWA, developed by Botkin et al. (1972a and 1972b). In this paper, we present those modifications required for modeling the Santee floodplain forest succession in response to river flow conditions. Detailed descriptions of aspects of the model retained from FORET and JABOWA are provided in the references listed above. Figure 3 is a conceptual flow diagram of the FORFLO model. Parameters used to describe tree behavior in the model are presented in Table 2.

Computed Flood Conditions

In the FLOOD subroutine, flooding duration and height are calculated from the hydrologic regime of the river based on stage-discharge relationships for the study site. This subroutine is specific for 19 kilometers of the Santee River floodplain between Lake Mattassee and Jamestown (Figure 1); however, it can be modified for other regions by substituting an appropriate equation for river stage vs. discharge. The relationships for the study area are shown in Figure 4. The flooding regime of the study plot is determined by considering the elevation of the simulation plot and the relationship between river flow and river stage.

The hydrologic regime is entered in the model as the mean and standard deviation river flow twice monthly for a year. River flow for any given year in the simulation is stochastically determined by its mean and standard deviation for each half-month period.

Two water discharge sources are provided for total river flow input to the FLOOD routine. One source represents the seasonal pattern of watershed discharge based on water release patterns from Lake Marion. The other represents inputs due to the rediversion and can be easily manipulated to examine alternative water release options. Both sources are summed in the model to determine total flow and flood conditions in the study area.

A nine year (1970-1978) bimonthly average of river flows was derived from U.S. Geological Survey data for the Santee River. Average bimonthly discharge into the Cooper River for the same time period are taken from South Carolina Public Service Authority data. The U.S. Army Corps of Engineers (1975) has stipulated that discharge into the Cooper River cannot exceed a 3,000 cfs weekly average after the rediversion. Therefore, present monthly average discharge into the Cooper River minus 3,000 cfs were used for the rediversion canal flow.

For the Santee floodplain study area, the relationship between river flow and river stage was derived from U.S. Army Corps of Engineers data (1976). These relationships are shown in Figure 4 at Lake Mattassee and at Jamestown. The equation of the curve at Lake Mattassee is

$$Y = -9.55 + 1.595 \ln(X) \qquad (1)$$

($r^2 = 0.995$) where Y is the river stage in meters above mean sea level (MSL), and X is the river flow in cubic feet per second (cfs). The equation of the curve for both locations was taken to be the same except there is a 3.2 meter elevation drop from Lake Mattassee to Jamestown. Because the drop in river stage elevation from Lake Mattassee to Jamestown was assumed to be linear, the elevation difference per kilometer was computed as a simple proportion equal to 0.1657 m/km. River stage at any location in the study area can be derived from the modified equation

$$Y = -9.55 + 1.595 \ln(X) - (0.1657D) \quad (2)$$

where D is the distance, in kilometers, of the plot downstream from Lake Mattassee.

To predict flooding patterns for a simulation plot, a single value is entered for plot elevation. For the Santee floodplain study area, the University of South Carolina Computer Service Division developed a detailed topograhic map of the study area using data from available 15 minute and 7.5 minute USGS quadrangles. Supplementary elevation data were obtained from the U.S. Coast and Geodetic Survey (horizontal and vertical control stations) and the U.S. Army Corps of Engineers (floodplain cross sections, Santee River bank-to-bank profiles, and several logging road traverses). Linear interpolations were performed for selected streams when surrounding elevation data and contour intervals were sufficient for computation. The value entered into the model for the river stage at which the plot will first be flooded was derived by locating the plot on a one foot interval version of this contour map.

In the FLOOD subroutine, river stage is calculated for each half-month period and compared to the elevation of the plot. Duration of flooding on the plot is derived from the length of time the plot was flooded during the year. During flood conditions, flood height is taken to be equal to the difference between the plot elevation and the river stage. The site is defined as flooded when the water level is 15 cm below the plot elevation or higher. Under these conditions, the soil is assumed to be saturated. When river stage drops below 15 cm from the plot elevation, water level on the plot is no longer considered to be influenced by river stage, and is assumed to be equal to the average water table depth in the plot.

Seed Germination and Sprouting

For most tree species, seeds will not germinate when the ground is flooded (Fowell, 1965). From Fowell, the period of the year when each species germinates is entered in the model. If the simulation plot is continuously flooded during the germination period for a species, that species is not allowed to germinate. Two exceptions in the floodplain are black willow and eastern cottonwood. These trees are allowed to germinate regardless of flood conditions.

If a species is allowed to germinate, flood duration during the growing season is one of the environmental conditions that determines whether the seedlings will survive. The calculated flood duration of the plot is compared to the flood duration tolerance of the species. If the flood duration of the plot is within the range of flood tolerance for the species, then a switch is set which indicates that flood conditions are adequate for survival of the seedling in the BIRTH subroutine. This approach is similar to that used by Phipps (1979) except that Phipps used percent duration when flooding was greater than 10%, and flood frequency instead of flood duration where duration was less than 10%. Bedinger (1971) had earlier found this to be the most explicit description of the relationship between flooding and species distribution at the White River National Wildlife Refuge, Arkansas. Because of the stochastic nature of the FORFLO model, it cannot calculate flooding more than a year in advance and, therefore, it cannot calculate flood frequency. Flooding is always described in the model by percent duration. In the future, attention should be directed to other environmental and physiological factors that might account for the relationship described by Bedinger.

As in the Shugart and West model (1977), the subroutine BIRTH is essentially a series of switches which test whether conditions are favorable for seedling survival of each tree species. From the list of species which can survive, the species and numbers of seedlings which are allowed to germinate in the model are randomly selected. FORET uses four switches testing for exposed mineral soil, leaf litter covering the soil, recruitment as determined by temperature, and animal browsing intensity.

Because soils are such an important determinant of species composition in bottomland forest, we have expanded the soil characteristic qualifiers for species survival in two ways related to soil cover and soil texture. Germination of many species is reduced, but not terminated by an inappropriate soil cover. Therefore, FORFLO examines the species preference for either exposed mineral soil or a leaf litter cover testing for a strong or moderate preference. This simply adds an intermediate condition to the same FORET model switches mentioned above. If there is no preference and if soil cover is appropriate, then germination is not reduced. If the soil cover is inappropriate because of a moderate preference for the other type, then germination is reduced by half. If the preference is strong for the other type, then germination will not occur for that species. Litterfall determines the leaf cover and organic content of the soil in the model and is a function of leaf area as described by Shugart and West (1977).

A test for the appropriate soil texture has also been added to the BIRTH subroutine. Species are described by their preference for clay, loam, or sandy soils. As above, if a species has no preference or the soil texture on the plot is appropriate, then germination is not restricted. A species is not allowed to survive on an inappropriate soil texture if that species has a strong preference for some other soil texture; survival is reduced for a species with a moderate soil texture preference on an inappropriate texture. Since loam is intermediate to sand and clay, survival is reduced less if the inappropriate texture is loam than it is if the texture is sand or clay.

Trees may also be recruited into the model by stump sprouting. When a tree dies, stump sprouts may be introduced if the tree was in the proper size range for its species. The number of sprouts is randomly selected and is also species-dependent.

Tree Growth and Mortality

Shugart and West (1977) described the growth equation for a tree in optimal conditions as:

$$\frac{dD}{dt} = \frac{GD\ (1 - DH/D_{max}H_{max})}{(274 + 3b_2D - 4b_3D^2)} \qquad (3)$$

where D is the diameter at breast height in centimeters, H is the height of the tree in centimeters, D_{max} and H_{max} are maximum recorded diameters and heights, respectively, for each individual species, and G, b_2 and b_3 are growth rate parameters for each tree species. This equation assumes that a tree under optimum conditions will grow to two-thirds of its maximum height at one-half of its maximum age. The derivation of this equation is treated in detail by Botkin et al. (1972a and 1972b) and Shugart and West (1977). The optimum growth curves for some selected species are shown in Figure 5.

This optimum growth is reduced by multiplying the equation by modifying parameters for stand crowding, S(BAR); temperature factors, T(DEGD); and shading tolerance, r(AL). S(BAR) is a crude expression of competition for soil moisture and nutrients. S(BAR) is a function which compares the total biomass of the simulated 1/12 ha circular plot with the maximum recorded biomass in the area. S(BAR) is equal to one for open stands with no crowding and approaches zero as the plot biomass approaches the maximum. Knight and McClure (1981) have estimated maximum biomass in South Carolina lowland hardwood stands to be 336,700 kg green weight/hectare.

T(DEGD) is a value derived from a parabolic function ranging from zero to one which assumes that each species has an optimum temperature for photosynthesis. Growing degree-days were used as an index of these thermal effects. The growing degree days for the simulated plot were calculated as the sum over a year of the deviations of mean daily temperatures above 42° F, which was taken to be the base temperature below which trees are not growing. A 30 year monthly average of temperatures for the Central Region, South Carolina is shown in Figure 6. The equation which derives T(DEGD) uses minimum and maximum values of growing degree-days to represent the extremes between which each species can grow. Minimum and maximum values are obtained by comparing species range maps with lines of constant growing degree-days. Botkin et al. (1972a) found that the extremes of a species range closely follow growing degree-day isotherms. For a simulated plot in a region whose growing degree-days approach one of the extremes, the value of T(DEGD) for that species will approach zero. The value of T(DEGD) will be one if the plot is in the middle of the species range.

An expression of shade tolerance, r(AL), was modified for the FORFLO model. Shugart and Botkin recognize two classes of shade tolerance - tolerant and intolerant - and describe r(AL) by the equation

$$r(AL) = 1.0 - \exp[-4.64(AL - 0.05)], \text{ shade tolerant;} \quad (4)$$

$$= 2.24[1.0 - \exp(-1.136(AL - 0.08))], \text{ shade intolerant} \quad (5)$$

where AL is the available light scaled between 0(no light) and 1(max. light). The light available to any individual tree is a function of the leaf area shading that tree from above. The height of the trees on the simulated plot is calculated as a simple function of the trees' diameter. The FORFLO model introduces a third, intermediate shade classification. Points midway between the shade tolerant and shade intolerant curves were fitted to a modified Michaelis-Menten function

$$r(AL) = [1.87(AL - .064)]/(.5 + AL - .064), \text{ intermediate tolerance.} \quad (6)$$

The shade tolerance curves are shown in Figure 7.

In addition to the functions reducing optimum growth given above, a water table function was added to the FORFLO model to model floodplain conditions. The water table function, H(WTAB), modifies the growth equation to express species tolerance of water levels on the simulation plot during the growing season. The height of the water level for each half-month period determined in the FLOOD subroutine is taken for each half-month in the early growing season-April through July. These water level heights are compared to the height of each tree of a species. If the water level is more than 3/4 the height of the tree (during flooded conditions), it is assumed that the tree will not grow during that half-month period (H(WTAB)=0).

If this condition is not met then H(WTAB) is a continuous exponential function which compares water level on the simulation plot for each half-month period during the growing season, to the optimum water table depth for each species. Relationships between water table depth and species growth are not well understood however. Phipps (1979) derived a general equation

$$H(WTAB) = 1. -0.05511(T - W)^2 \qquad (7)$$

which is used in FORFLO. T is the water level (or water table depth) on the simulation plot and W is the optimum water table depth for each species. H(WTAB) is one when the water table is at an optimum depth for the species, and it approaches zero as the water table rises or falls away from the optimum. Baldcypress and water tupelo both have a wide range over which they will grow optimally (Eyre, 1980; Harms, 1973). Eyre reports that cypress may be flooded ten feet deep or more and show evidence of oxidation at flood depths up to four feet. Four feet was taken to be the maximum depth of flooding for both cypress and water tupelo before growth would be reduced. The two curves for the hypothesized relationship between floodplain tree growth rate and water table are shown in Figure 8. Optimum water table depths for the species used in the simulations are from Phipps (1979), Teskey and Hinckley (1977), Gosselink et al. (1981) and Wharton et al. (1982).

The FORFLO growth equation (3) with modifying functions is

$$\frac{dD}{dt} = \frac{GD\ (1 - DH/D_{max}H_{max})}{(274 + 3b_2D - 4b_3D^2)} \cdot S(BAR) \cdot T(DEGD) \cdot r(AL) \cdot H(WTAB) \quad (8)$$

When predicted growth is reduced to less than 10% of optimum conditions by a combination of modifying factors, the probability of the tree's death is increased greatly (subroutine KILL).

Other Subroutines

The subroutine PLOTIN assigns the initial number, age, and DBH of trees of each species to the plot at the beginning of the simulation. Age and DBH of each tree is determined from a normal distribution with a mean and standard deviation specified for each species. Age and DBH use the same degree of randomness in this routine so that for an individual tree, the magnitude and direction of the deviation from the mean is the same. For example, if a particular tree's age is 0.5 times the standard deviation age plus the mean age, that tree's DBH will be 0.5 times the standard deviation DBH plus the mean DBH.

The subroutine OUTPUT calculates biomass and net production of trees on the plot using equations from Johnson and Bell (1976) and understory production values from Conner and Day (1976). A printed output is then provided for biomass, production, the number of stems, flood duration, and the hydrologic regime for each year. An option in OUTPUT is to run the model repeatedly and print the results as importance values.

Other support routines in the model are essentially the same as in Shugart and West (1977), and do not affect the ecological interpretation of FORFLO simulations.

An Application to the Santee River Floodplain

To examine the usefulness of the FORFLO model in predicting successional trends, the model was used to simulate impacts of the rediversion project on floodplain forest along the Santee River.

Comparison with Field Conditions

The study site used to test model response is located about halfway between Lake Mattassee and Jamestown (Figure 1), and has been documented by the Charleston Office of the U.S. Fish and Wildlife Service (USFWS) with a single transect through it (Karen Harper, USFWS, personal communication, 1983). In addition, the University of South Carolina (USC), Department of Environmental Health Sciences has completed a preliminary tree survey of the site (Parks and Williams, 1983).

For a preliminary test of model response, initial conditions were provided to represent species composition in a site representative of wetter conditions before the original diversion. Baldcypress (Taxodium distichum), water tupelo (Nyssa aquatica), and water hickory (Carya aquatica) were the predominant species with considerably fewer numbers of overcup oak (Quercus lyrata), sweetgum (Liquidamber styraciflua), green ash (Fraxinus pennsylvanica), and red maple (Acer rubrium) also present. Present patterns of river flow were then simulated and the model was run for a 50 year period to examine the resulting species composition predicted for present conditions by the model. Because of the stochastic properties of the model and the small (1/12 ha) size of the simulated plots, the model was run 50 times and the results averaged. The results at year 50 are shown in Figure 9. Importance values (the sum of relative density, relative frequency, and relative dominance; Curtis, 1959) are used in the figure to describe observed and predicted forest composition. The species listed along the bottom of the graph in Figure 9 are all the species that were available to the model for recruitment. The model predicts the occurrence of 100% of all of the tree species in the study area, documented either by the U.S. Fish and Wildlife Service or by the University of South Carolina study. In addition, the model predicts the minor occurrence of sassafras (Sassafras album) and loblolly pine (Pinus taeda), two species which were not observed in either field study. However, since loblolly pine occurs in other floodplain sites in South Carolina with similar flood regimes (Warton et al., 1982) this deviation is not considered significant.

For the typical mix of bottomland hardwoods in the area, the model also predicted importance values close to the range of those observed for major species. Although there was some divergence in species importance documented by the two field studies, the model generally predicted importance values for each major species within 10 units of one or both of the field studies. The model underestimated the importance of green ash by 40-47% and overestimated the importance of water hickory by 3-5 fold. It cannot be determined from the conflicting field results whether baldcypress has been overestimated by the model.

The importance values for water hickory and possibly baldcypress appear to be high in the FORFLO output because the model was initialized with these species and they are slow to die under the new water regime. No new germination of these species is occurring in the model. If the model is allowed to continue to run up to year 200, baldcypress decreases steadily to a very low importance of 6 units and water hickory is completely removed from the plot while American elm (Ulmus americana) increases in importance to 21 units. The slow replacement of baldcypress and water hickory is apparently due to the conservative equation used by Phipps (1979) and in this model to describe tree growth response to the water table.

An additional weakness in this comparision is that the initial species mix was only a best guess. Model runs initialized with different numbers, DBH, or ages of species will result in different importance values in the first fifty years. If the model is allowed to continue running beyond year 50, however, the species selected by the model continue to agree with observed tree species. By year 200 initial conditions have far less impact on importance values.

Model Simulations of the Santee-Cooper Rediversion

Both the proposed and the modified rediversions were simulated along a 35.6-mile reach of the Santee River forested floodplain from the rediversion site downstream to Jamestown (Figure 1). In the proposed rediversion, flow to the Santee River from Lake Marion remains the same, flow to the Cooper River is reduced to 3,000 cfs as stipulated by the U.S. Army Corps of Engineers, and the remaining flow is added to the Santee River flow via the rediversion canal (Figure 2). The modified rediversion is the same as the proposed pattern except that during the early growing season (April-July) flow through the rediversion canal is reduced to that which can pass through one turbine of the canal's power plant. This option allows flow to exceed 3,000 cfs on the Cooper River only during these four months of the growing season. Thus, the modified rediversion attempts to preserve the bottomland forest in the Santee floodplain by reducing flooding during the trees' critical growth period.

Maps of the areal extent of present habitat types compared to the two options as predicted by the FORFLO model are shown in Figure 10. The later two maps were derived by running the FORFLO model at 1/2 foot intervals and recording the elevation at which one classification became more dominant than another. For example, bottomland hardwood is replaced by cypress-tupelo as elevation decreases and flooding subsequently increases. At each elevation interval, 50 replicate model simulations of 200 years each were run. Two-hundred years allows for most species replacement and stabilization of any new species composition that might occur. The most likely outcome of an introduced flood regime is recorded by averaging the 50 replicate runs. The immature bottomland forest (bottomland shrub/scrub) covering so much area in the present-conditions map is the result of clearcutting by landowners in anticipation of rediversion. The nonforested wetted soils classification only means that the moisture regime is too wet to support forest cover. The classification does not necessarily mean there must be standing water on the site all year, although the soil will usually be saturated. Much of this area may support emergent vegetation or very moisture-tolerant shrubs such as buttonbush (Cephalanthus occidentalis). Most striking in these maps is the loss of bottomland forest: a 97% loss of bottomland hardwoods for the proposed rediversion or an only slightly improved 94% loss for the modified rediversion. The difference in the two options is primarily that bottomland hardwoods under the modified rediversion scenario are more likely to succeed to cypress-tupelo rather than open water, thus maintaining a forest cover. The acreage of the habitat types under the three conditions is shown in Table 2.

Conclusion

From the two rediversion alternatives examined, the FORFLO model indicated that large tracts of bottomland hardwood habitat would be lost in either case study. However, the modified rediversion plan, based on reduced waterflow during the growing season, predicted that a forest cover of primarily cypress-tupelo would be maintained. This project thus demonstrated that mathematical modeling can be useful in synthesizing complex ecological relationships for the study of successional trends. The integration of ecological modeling and spatial mapping, as in this project, can provide a valuable tool to the resources manager who needs to forecast the extent of change a floodplain modification may bring about.

Options to improve FORFLO are primarily focused on routines describing water relations in the model. The equation used in FORFLO to relate tree growth to depth of the water table is purposely conservative because this relationship is not well studied. An increased understanding of water relations would benefit modeling efforts to successfully predict floodplain forest succession.

The suite of environmental conditions (water table, flooding, temperature) an individual tree has adapted to are often more important than a general optimum for that species. A substantial change in a site's environment can cause rapid loss of the existing trees even when that change is within the limits of the species tolerance (Robert Johnson, U.S. Forest Service, personal communication, 1984). Work is presently underway to incorporate species acclimation into future modeling attempts. A principle result would likely be the speeding up of the successional process after a major change in environmental conditions such as a river diversion. This may be one reason the model appears to be slow in replacing species such as water hickory.

Projects are underway to adapt FORFLO to model the Atchafalaya River Basin in Louisiana and the greentree reservoir in the Felsenthal National Refuge, Arkansas. These studies will increase the species list the model can handle, introduce elements to handle sediment subsidence and accretion, and provide opportunities to validate the model.

Bottomland forest wetlands are ecologically and economically important for wildlife habitat, timber resources, detrital output to downstream marshes, downstream flood mitigation, water quality improvement, and scenic quality. Predictive models such as FORFLO can assist our understanding of bottomland forest succession interrupted by changing environmental conditions. Such models are effective quantitative prediction tools that can assist resource managers in planning river basin management alternatives.

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Table 1. Annual average flow regimes for the Santee and Cooper Rivers.

TIME	Flow (cfs)*	
	Cooper River	Santee River
Before Diversion in 1941	100	17500
After Diversion	15500	2000
After Planned Rediversion	3000	14500

*cfs = cubic feet/second = 0.0283 m3/sec.

Table 2. Parameters used in the FORFLO model.*

Species Name	DMAX	DMIN	G	B3	B2	ITOL	AGEMX	SND	SMN	SMX	12345	W	FR1	FR2	GW1	GW2	KSL	KPF
Acer rubrum	13395.	1810.	222.2	.1479	46.62	1	150.	3.	12.0	100.	FTTTF	.60	.00	30.0	5	14	1	0
Carpinus caroliniana	10820.	2420.	142.1	.2592	48.20	1	150.	2.	6.0	70.	TTTFF	.60	.00	16.0	5	14	0	0
Carya aquatica	11100.	5800.	159.0	.0959	41.24	2	250.	3.	6.0	70.	TFFTF	.30	10.00	40.0	8	11	0	0
Carya tomentosa	12652.	4105.	98.1	.1900	49.41	3	300.	1.	12.0	200.	TTTFF	2.10	.00	5.0	8	12	1	0
Celtis laevigata	12560.	4820.	100.0	.3846	70.00	2	200.	2.	6.0	30.	FTFTF	.60	5.00	25.0	4	7	0	0
Cornus florida	10947.	3686.	88.7	.5360	40.81	1	100.	3.	12.0	200.	TTTFF	1.80	.00	2.0	4	8	0	0
Fraxinus pennsylvania	9900.	1600.	188.6	.1518	43.14	2	150.	1.	6.0	50.	FFTFF	.90	8.00	30.0	4	7	0	0
Liriodendron tulipifera	10947.	3686.	174.8	.0440	32.35	3	300.	2.	12.0	200.	TTFTF	.60	.00	4.0	5	8	4	1
Liquidambar styraciflua	10947.	5526.	140.0	.1009	38.50	3	250.	2.	12.0	100.	FTFTF	1.00	6.00	20.0	4	7	3	0
Nyssa aquatica	9300.	6000.	95.6	.0444	23.32	2	300.	1.	6.0	50.	FTFFF	.00	30.00	60.0	3	14	1	0
Pinus echinata	9461.	5526.	96.7	.3266	64.51	3	300.	2.	6.0	20.	TFFFF	2.00	.00	4.0	4	6	3	0
Pinus taeda	10820.	5730.	101.5	.1790	53.00	3	350.	0.	.0	0.	FTFFF	1.80	.00	4.0	14	6	1	0
Platanus occitentalis	9900.	3500.	93.0	.0388	28.42	2	500.	2.	6.0	50.	TTFFF	.60	.00	20.0	7	10	0	0

Table 2. continued.

Species Name	DMAX	DMIN	G	B3	B2	ITOL	AGEMX	SNO	SMN	SMX	12345	W	FR1	FR2	GW1	GW2	KSL	KPF
Populus deltoides	10000.	1600.	309.0	.0388	28.42	2	150.	1.	6.0	30.	TTFFT	1.02	.00	20.0	7	16	3	0
Prunus serotina	10947.	3899.	138.6	.0830	35.57	3	250.	3.	12.0	200.	FFFTF	1.10	.00	1.3	5	10	0	0
Quercus alba	10204.	2966.	100.3	.0740	36.37	2	400.	2.	12.0	40.	TFFFF	2.40	.00	2.0	17	20	1	0
Quercus falcata	10947.	5526.	82.6	.0780	33.57	2	400.	2.	12.0	30.	FFFFF	1.80	.00	5.0	5	10	1	0
Quercus laurifolia	11800.	6000.	184.8	.0860	31.97	2	150.	3.	6.0	12.	TFFTF	1.00	.00	20.0	17	20	3	0
Quercus lyrata	9600.	5300.	128.5	.1221	41.47	2	250.	1.	6.0	12.	FTFTF	.60	5.00	30.0	17	20	3	0
Quercus michauxii	10200.	5000.	117.0	.0508	27.89	2	300.	1.	6.0	12.	TTFTF	1.00	.00	30.0	17	20	1	1
Quercus nigra	10700.	5500.	114.9	.0866	32.74	2	250.	2.	6.0	12.	TTFTF	1.50	10.00	15.0	5	9	1	0
Salix nigra	11200.	2900.	169.8	.1348	24.15	3	70.	3.	6.0	30.	TFFFT	.50	.00	20.0	7	11	2	1
Sassafras albidum	10947.	3686.	135.8	.1039	34.79	3	200.	3.	12.0	200.	TTFFF	2.00	.00	4.0	5	9	1	0

Table 2. continued.

Species Name	DMAX	DMIN	G	B3	B2	ITOL	AGEMX	SND	SMN	SMX	12345	W	FR1	FR2	GW1	GW2	KSL	KPF
Taxodium distichum	11800.	5300.	82.9	.0242	18.61	2	400.	0.	.0	0.	TTFFF	.15	30.00	50.0	4	12	1	0
Ulmus americana	12560.	2200.	85.5	.0465	22.40	2	300.	2.	6.0	240.	TTFTF	1.50	.00	20.0	5	10	1	0

*DMAX and DMIN are maximum and minimum degree-days respectively. G, B3 and B2 are the growth equation (3) (text) parameters for each species. ITOL is the shade tolerance class. Class 1 is shade tolerant and equation (4) is used to calculate the growth modifier. Class 2 is intermediate and uses equation (6) while class 3 is shade intolerant and uses equation (5). AGEMX is the maximum recorded age of each species. SND is the tendency to reproduce vegetatively and SMN and SMX are minimum and maximum size trees (cm, DBH) that will stump-sprout. Reproduction switches (12345) are used in the BIRTH subroutine and take values of T (true) or F (false). Switch 1 is T if the species prefers sandy soil. Switch 2 is T if the species prefers clay soil. Switches 1 and 2 are both T if the species prefers loam. If switch 1 and 2 are both F the species has no soil texture preference. Switch 3 is T if species recruitment is reduced by a hot year. Switch 4 is T if the species is a preferred food of deer or small mammals. Switch 5 is T if the species can't germinate when the plot biomass is high. W is the optimum depth to the water table (m) and is used to calculate the growth modifier in equation (7). FR1 and FR2 are the range of annual flood durations (percent) tolerated by the species during germination. GW1 and GW2 are the range of half-month periods during which the species will normally germinate (e.g., 1 = first

Table 2. Continued.

half of January; 24 = last half of December). KSL measures the degree of preference for soil cover. 0 is no preference. 1 and 2 are moderate and strong preferences, respectively, for exposed mineral soil. 3 and 4 are moderate and strong preferences, respectively, for littercover. KPF measures the degree of preference for soil texture. 0 is a moderate or no preference; 1 is a strong preference.

Table 3. Habitat types in the Santee River floodplain study area.

	Hectares*		
	Present	Proposed Rediversion	Modified Rediversion
Nonforested, wetted soils	743	6655	3060
Cypress-Tupelo	1962	1918	5512
Bottomland hardwoods	7362	257	417

*Hectares = 2.47 Acres

Figure Captions

Figure 1. Location map.

Figure 2. Seasonal discharge patterns for the Santee-Cooper Rivers.

Figure 3. Overview diagram of the FORFLO forest floodplain succession model. Symbols are from Odum, 1983.

Figure 4. Stage discharge relationships for stations on the Santee River.

Figure 5. Optimum growth curves for some selected species as described by the FORFLO model.

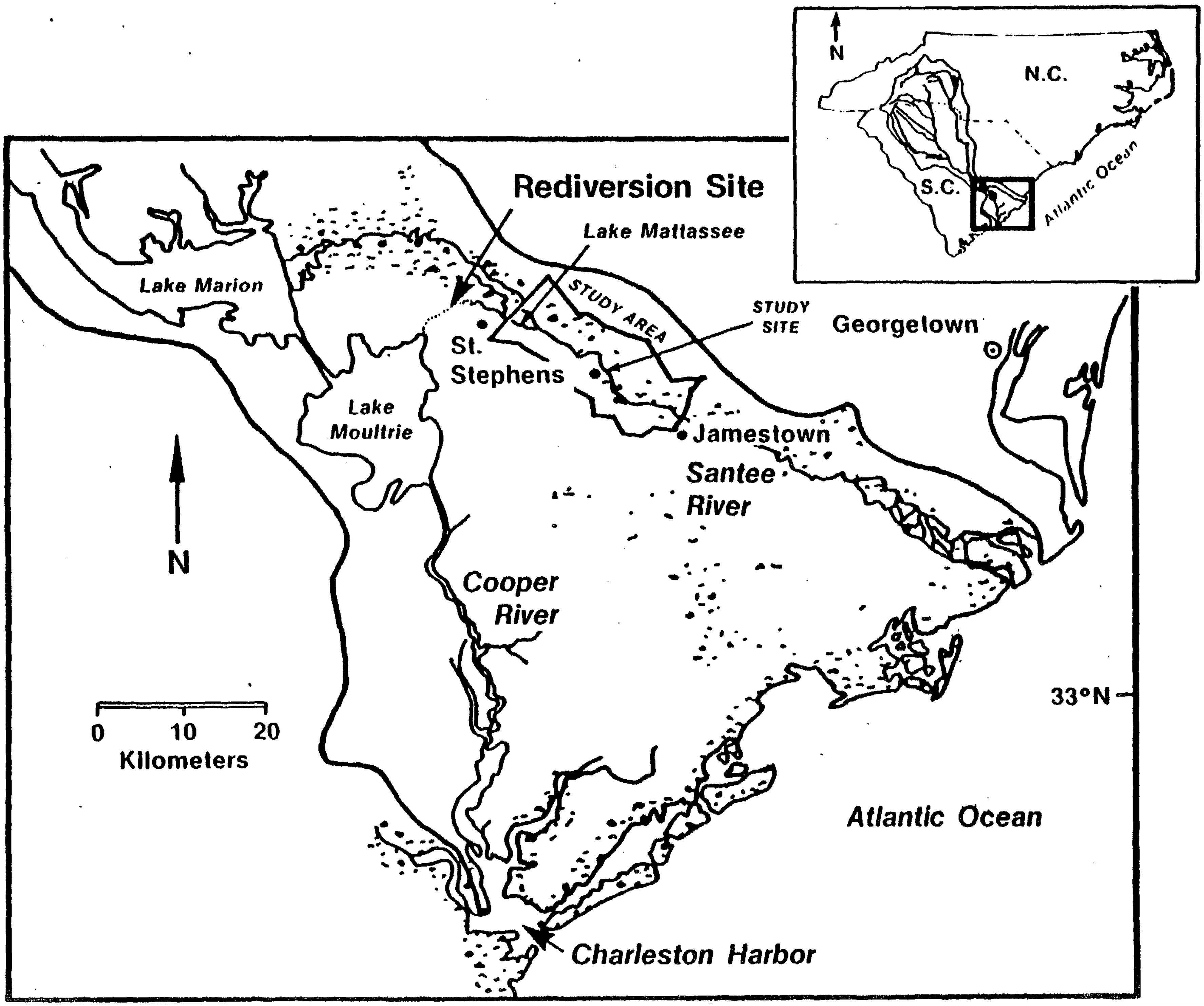
Figure 6. Sine curve fitted to 30 year monthly average temperatures for the central region, South Carolina. $Y = 63.6 - 16.95 \ln [(2\pi/365)(\text{time}-105)]$ Reference: N.O.A.A, 1973.

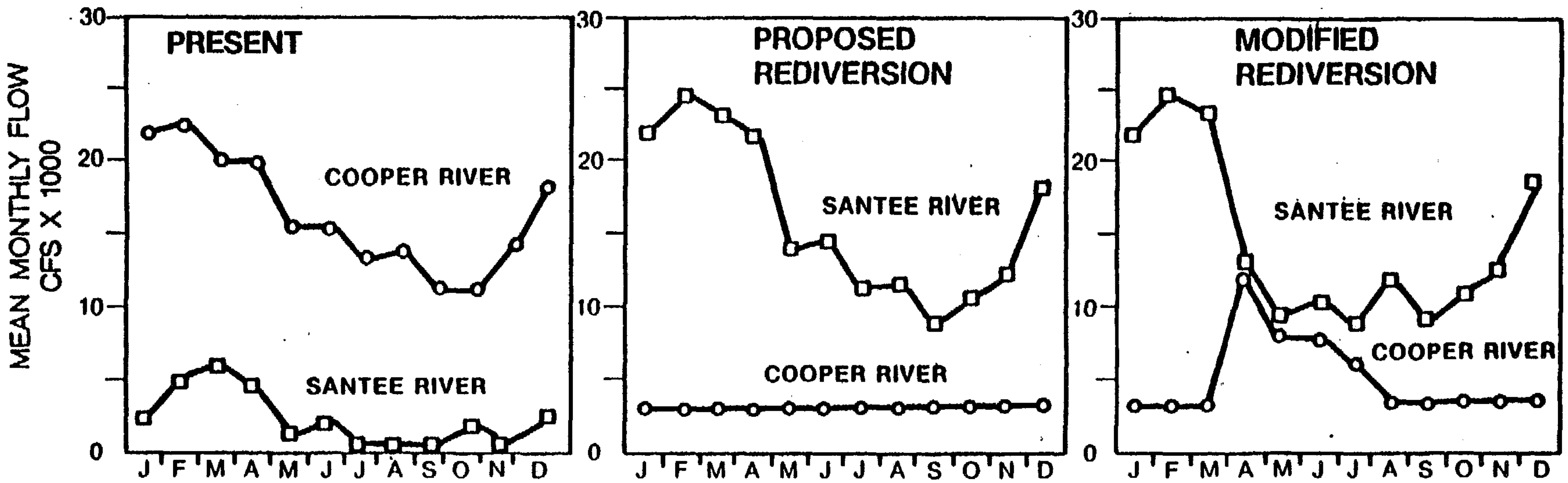
Figure 7. Available light growth modifier.

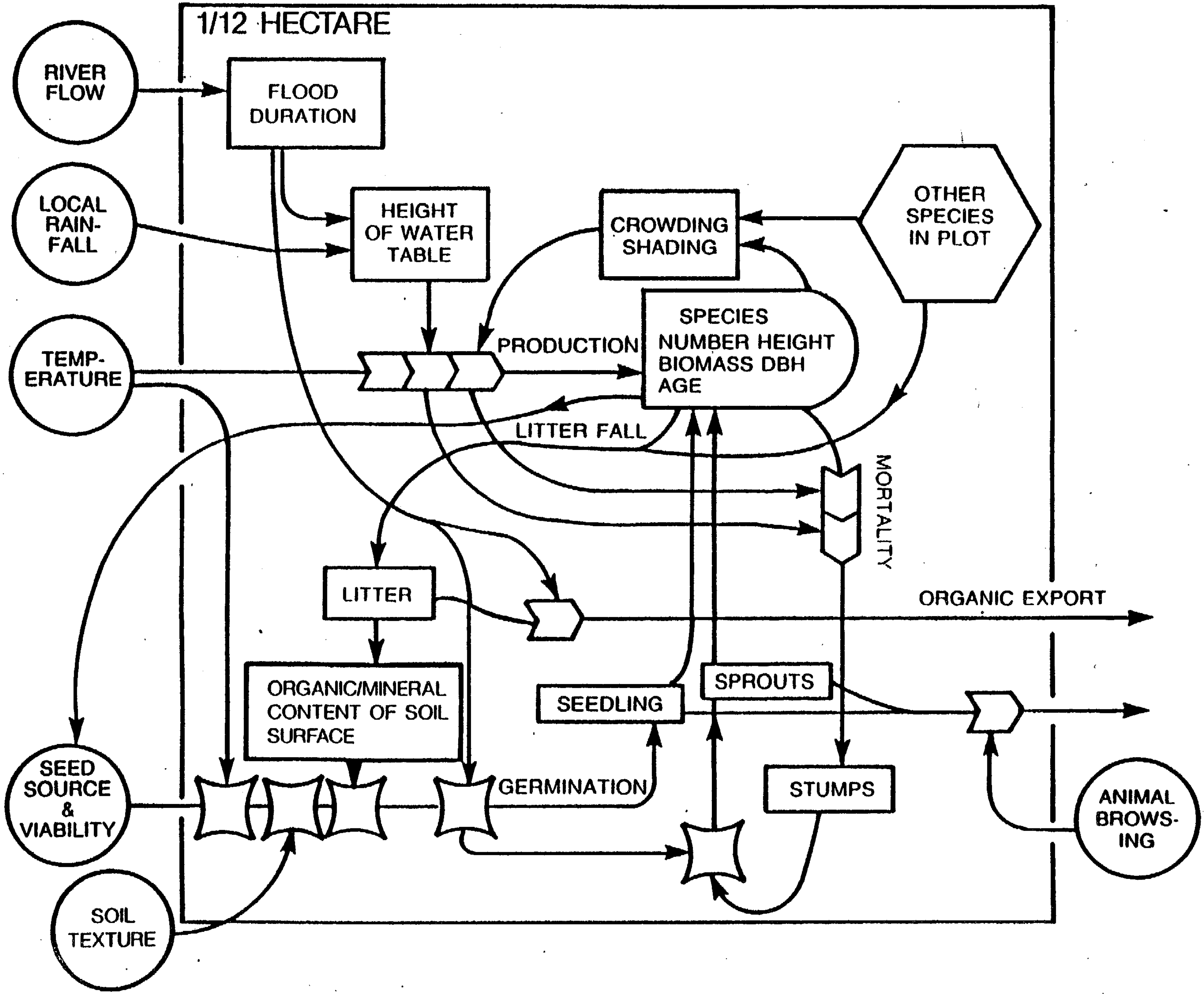
Figure 8. Water table growth modifier.

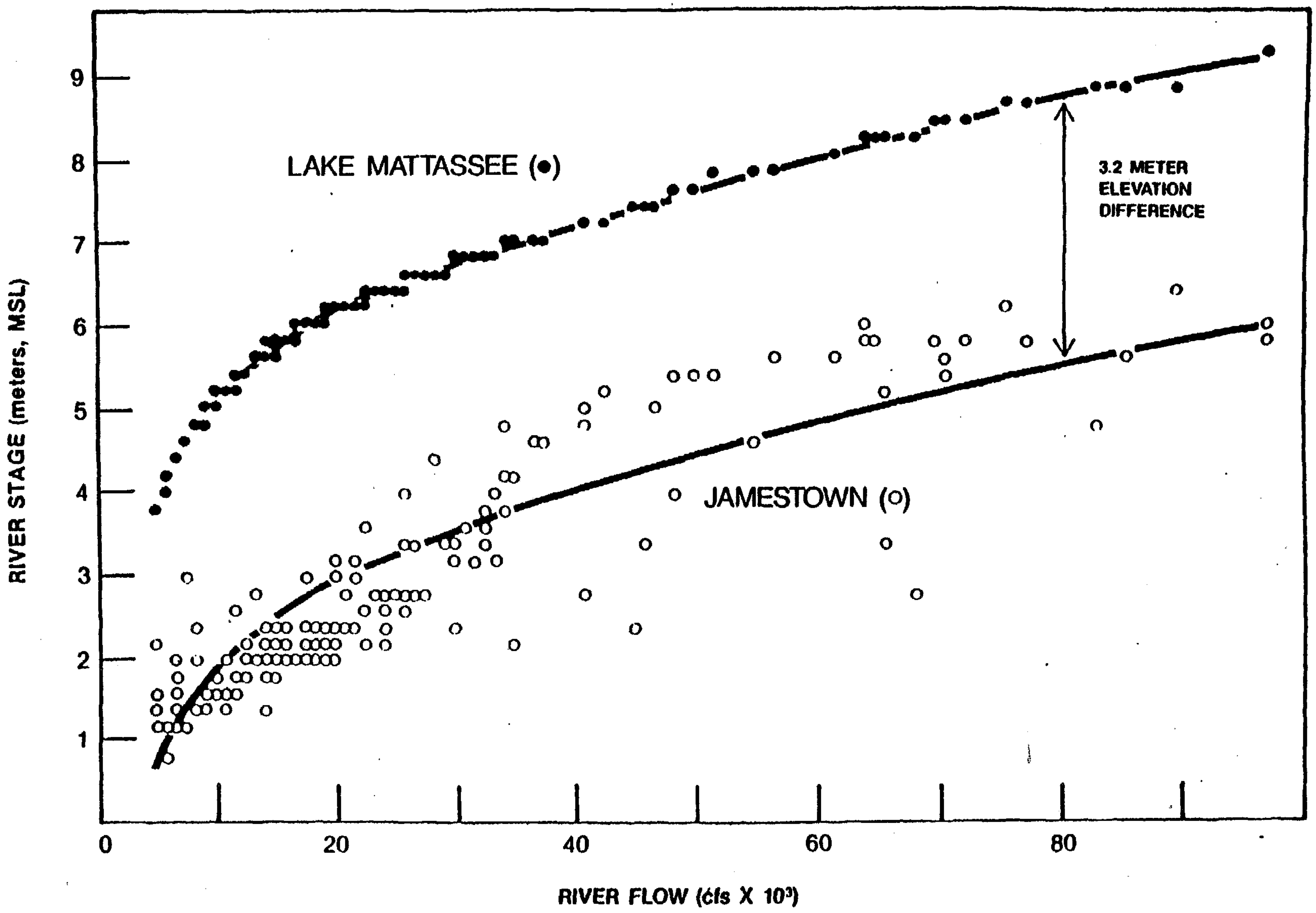
Figure 9. Comparison of model results with field observations.

Figure 10. Areal extent of habitat types currently and as predicted by FORFLO after the rediversion.

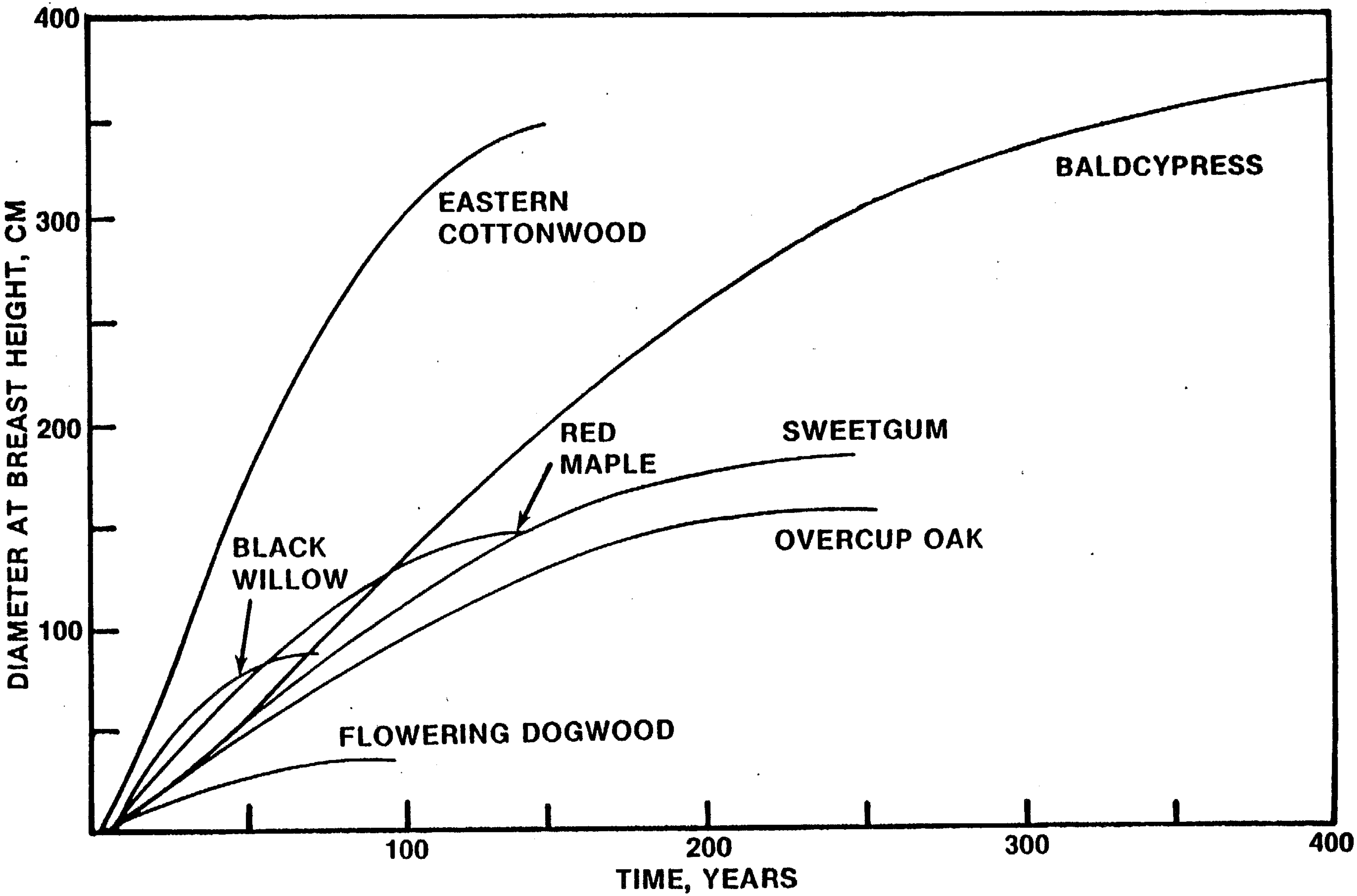

Rediversion Site
Lake Mattassee
STUDY AREA
STUDY SITE
Lake Marion
St. Stephens
Lake Moultrie
Jamestown
Georgetown
Santee River
Cooper River
N
0 10 20
Kilometers
33°N
Atlantic Ocean
Charleston Harbor
N.C.
S.C.
Atlantic Ocean


MEAN MONTHLY FLOW
CFS X 1000
PRESENT
COOPER RIVER
SANTEE RIVER
PROPOSED
REDIVERSION
SANTEE RIVER
COOPER RIVER
MODIFIED
REDIVERSION
SANTEE RIVER
COOPER RIVER
30
20
10
0
J F M A M J J A S O N D

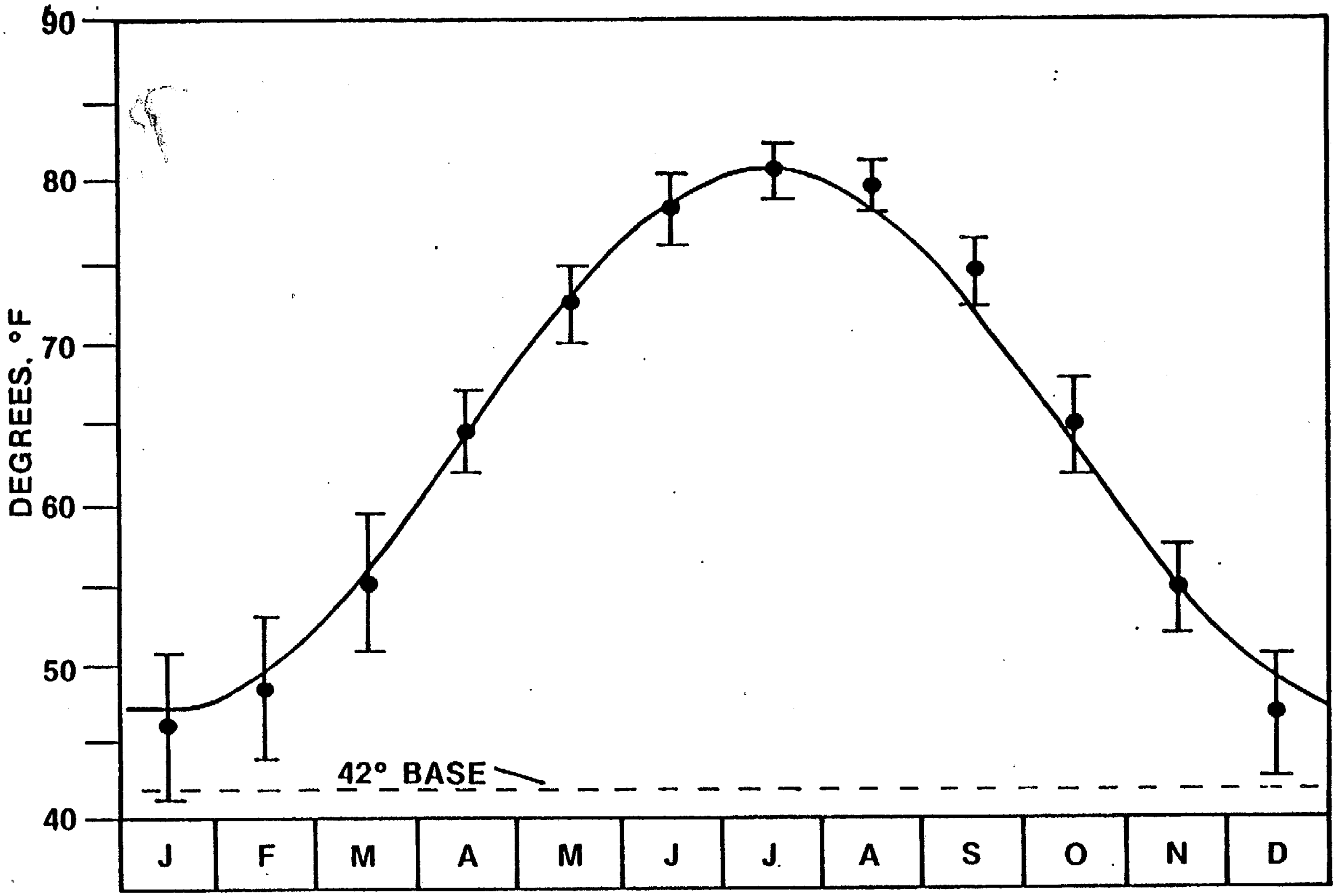

1/12 HECTARE
RIVER FLOW
FLOOD DURATION
LOCAL RAIN-FALL
HEIGHT OF WATER TABLE
CROWDING SHADING
OTHER SPECIES IN PLOT
TEMP-ERATURE
PRODUCTION
SPECIES NUMBER HEIGHT BIOMASS DBH AGE
LITTER FALL
MORTALITY
LITTER
ORGANIC EXPORT
ORGANIC/MINERAL CONTENT OF SOIL SURFACE
SEEDLING
SPROUTS
SEED SOURCE & VIABILITY
GERMINATION
STUMPS
ANIMAL BROWS-ING
SOIL TEXTURE



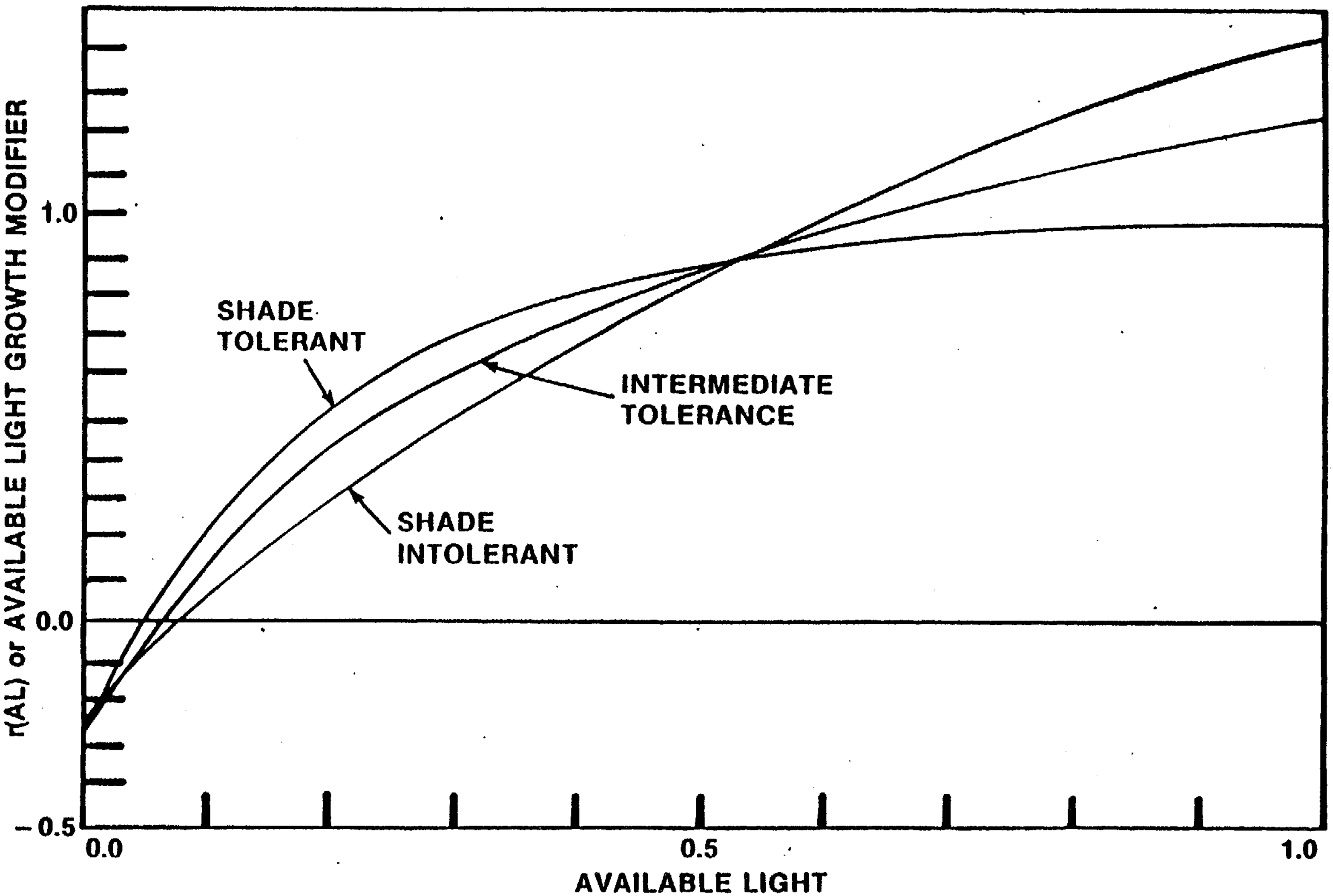
LAKE MATTASSEE (•)
3.2 METER
ELEVATION
DIFFERENCE
JAMESTOWN (o)
RIVER STAGE (meters, MSL)
RIVER FLOW (cfs X 10³)
0
20
40
60
80
1
2
3
4
5
6
7
8
9



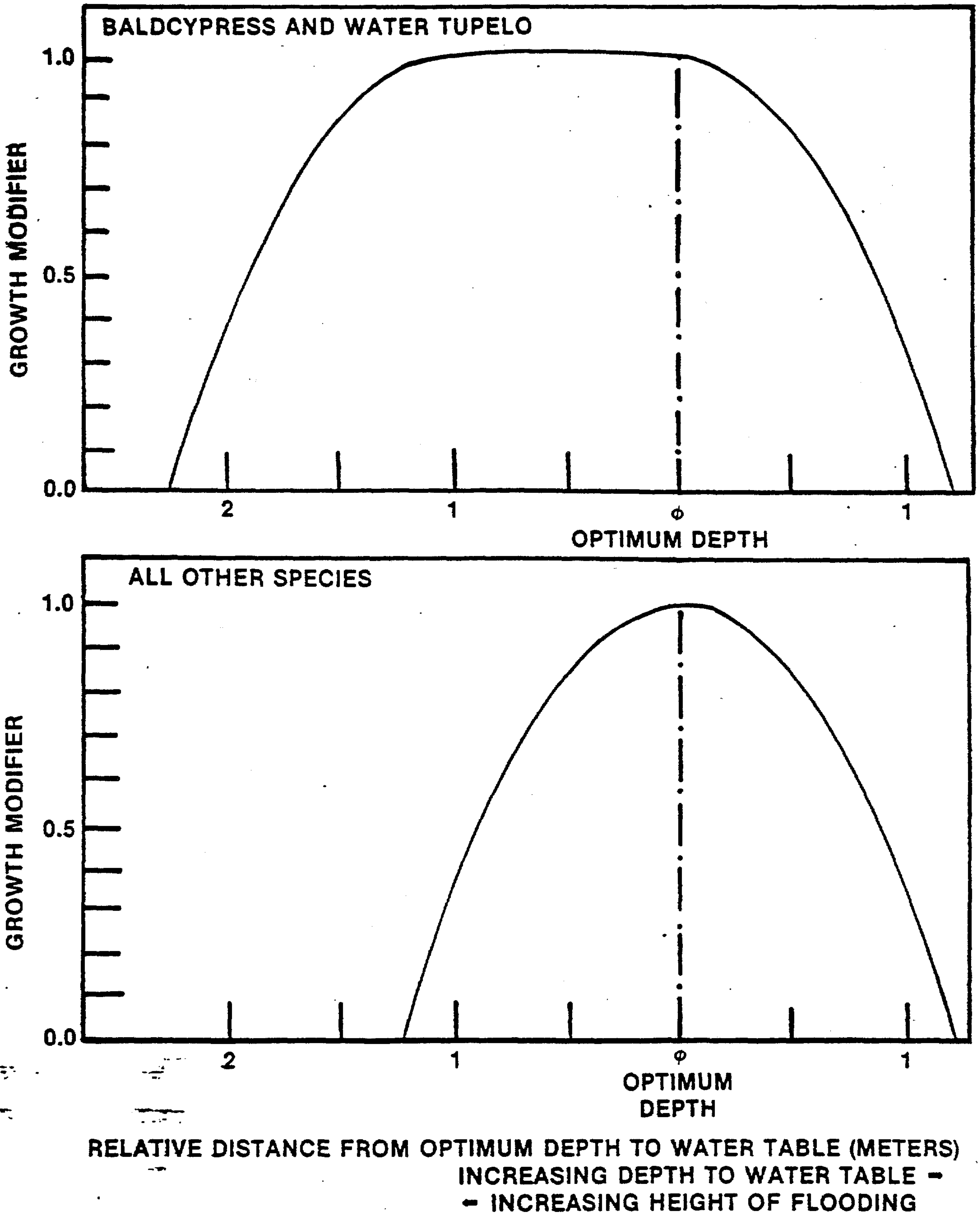
400
300
200
100
DIAMETER AT BREAST HEIGHT, CM
EASTERN
COTTONWOOD
BALDCYPRESS
RED
MAPLE
SWEETGUM
OVERCUP OAK
BLACK
WILLOW
FLOWERING DOGWOOD
100
200
300
400
TIME, YEARS

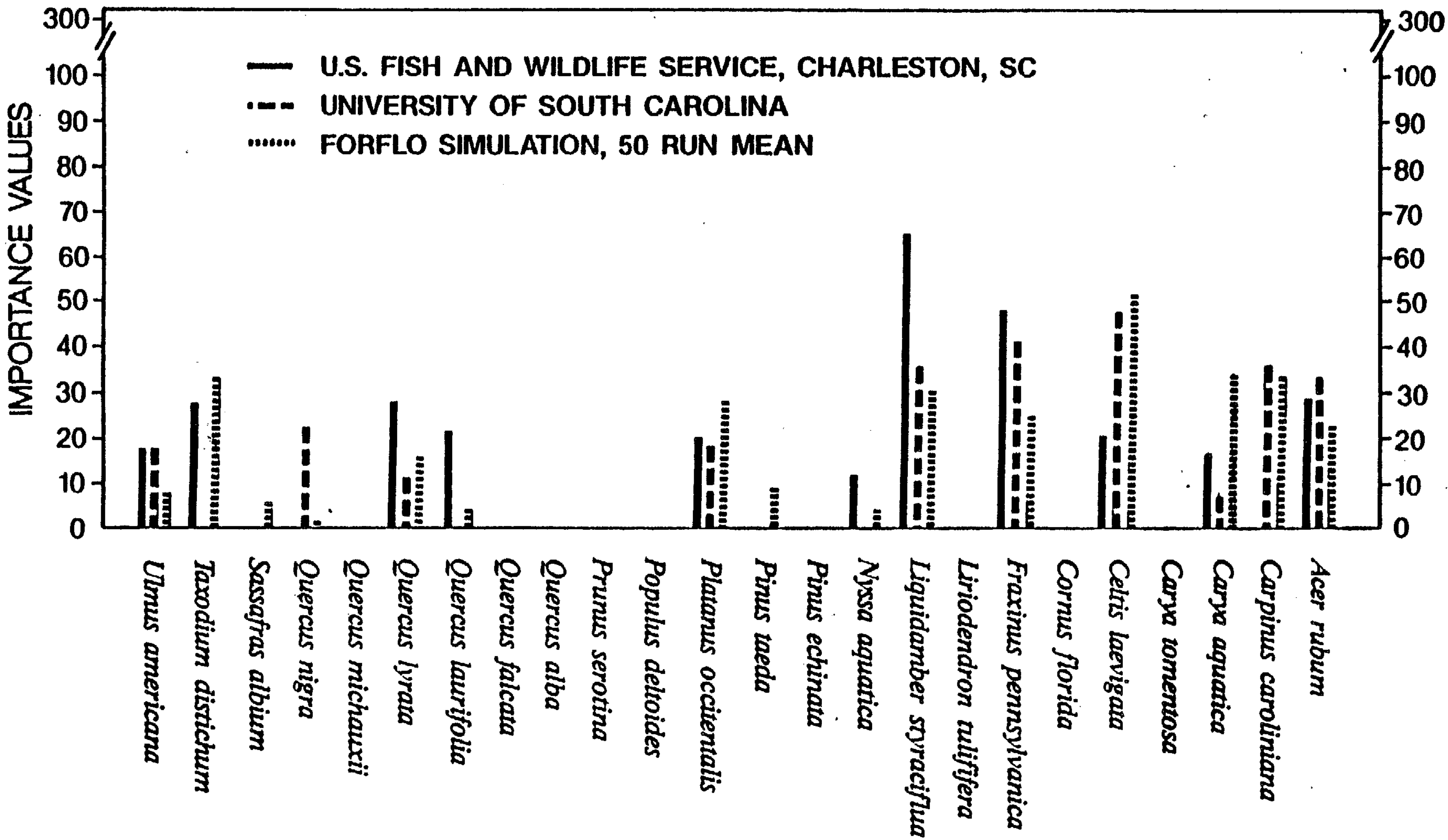


90
80
70
60
50
40
DEGREES, °F
42° BASE
J
F
M
A
M
J
J
A
S
O
N
D

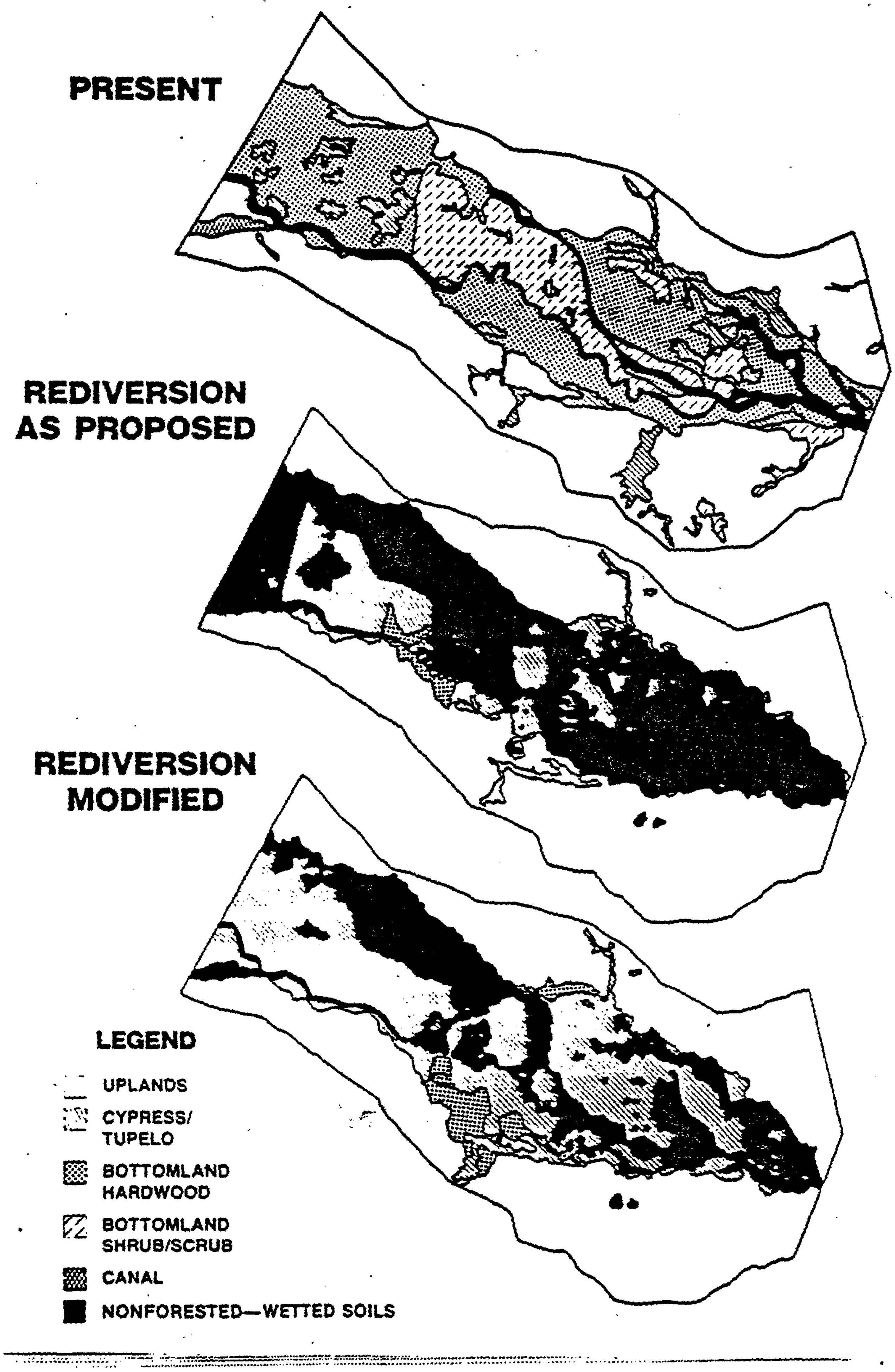


SHADE
TOLERANT
INTERMEDIATE
TOLERANCE
SHADE
INTOLERANT
r(AL) or AVAILABLE LIGHT GROWTH MODIFIER
1.0
0.0
-0.5
0.0
0.5
1.0
AVAILABLE LIGHT


BALDCYPRESS AND WATER TUPELO
GROWTH MODIFIER
1.0
0.5
0.0
2
1
ϕ
1
OPTIMUM DEPTH
ALL OTHER SPECIES
GROWTH MODIFIER
1.0
0.5
0.0
2
1
φ
1
OPTIMUM DEPTH
RELATIVE DISTANCE FROM OPTIMUM DEPTH TO WATER TABLE (METERS)
INCREASING DEPTH TO WATER TABLE →
← INCREASING HEIGHT OF FLOODING



IMPORTANCE VALUES
U.S. FISH AND WILDLIFE SERVICE, CHARLESTON, SC
UNIVERSITY OF SOUTH CAROLINA
FORFLO SIMULATION, 50 RUN MEAN
300
100
90
80
70
60
50
40
30
20
10
0
Ulmus americana
Taxodium distichum
Sassafras albium
Quercus nigra
Quercus michauxii
Quercus lyrata
Quercus laurifolia
Quercus falcata
Quercus alba
Prunus serotina
Populus deltoides
Platanus occidentalis
Pinus taeda
Pinus echinata
Nyssa aquatica
Liquidamber styraciflua
Liriodendron tulififera
Fraxinus pennsylvanica
Cornus florida
Celtis laevigata
Carya tomentosa
Carya aquatica
Carpinus caroliniana
Acer rubum


PRESENT
REDIVERSION
AS PROPOSED
REDIVERSION
MODIFIED
LEGEND
UPLANDS
CYPRESS/
TUPELO
BOTTOMLAND
HARDWOOD
BOTTOMLAND
SHRUB/SCRUB
CANAL
NONFORESTED—WETTED SOILS