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ABOVEGROUND PRODUCTION IN SOUTHEASTERN FLOODPLAIN FORESTS: A TEST OF THE SUBSIDY–STRESS HYPOTHESIS

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Abstract. It has been hypothesized that periodically flooded forests have higher rates of aboveground net primary production than upland forests and near-continuously flooded forests, but a competing hypothesis holds that the benefits of periodic inputs of nutrients and water may be diminished by stresses associated with anaerobic soils or drought. To test these hypotheses, we measured groundwater table depths and aboveground productivity in floodplain forests of South Carolina and Louisiana. We established paired plots on locally dry, intermediate, and wet topographic positions across three hydrologic transects in each state. These plots encompassed upland hardwood, bottomland hardwood, and cypress swamp forests. Measurements of leaf litterfall, wood production, and groundwater table depth were made in 1987 and 1988. We then used mean growing-season water depth (MWD) to group the plots into three classes: wet (>0 cm), intermediate (0 to -60 cm), and dry (<-60 cm).

Aboveground net primary production (NPP) on wet plots (2-yr mean ± 1 SD = 675 $\pm$ 271 g·m^{-2}·yr^{-1}) was significantly lower than on intermediate and dry plots ($P \leq 0.02$). There was no significant difference between intermediate and dry plots (107 $\pm$ 189 and 1038 $\pm$ 91) g·m^{-2}·yr^{-1}, respectively). In addition, aboveground NPP on intermediate plots was not significantly different from 22 temperate upland forests in the literature.

Combining our data with data from the literature, we found that aboveground NPP on wet plots was negatively related to MWD with a slope of -5 g·m^{-2}·yr^{-1}·cm^{-1}. On sites with evidence of hydrologic disturbance ($>25\%$ dead stems) the slope of this line was 5 times greater (-24 g·m^{-2}·yr^{-1}·cm^{-1}).

We conclude that the subsidy–stress hypothesis does not adequately describe patterns of NPP across Southeastern U.S. floodplain forests. Conditions of periodic flooding and flowing water do not often lead to high rates of productivity compared with upland forests. However, extensive flooding is nearly always a significant stress on forest productivity, particularly when the flooding regime has been recently perturbed through levee construction or impoundment. Our data support a more complex interaction between subsidy and stress factors.

Key words: flooding regime and net primary production; flooding stress and floodplain forest production; floodplain forests, southeastern United States; hydrologic disturbance and net primary production; hydrologic disturbance in floodplain forests; Louisiana, USA; net primary production in bottomland hardwood forest; South Carolina, USA.

INTRODUCTION

Aboveground net primary production in Southeastern floodplain forests of North America varies from about 200 to 2000 g·m^{-2}·yr^{-1} (Conner 1994). The conceptual models that have been proposed to explain this variation (Mitsch and Ewel 1979, Odum 1979, Brinson et al. 1981, Taylor et al. 1990, Odum et al. 1995) propose that flooding may have either positive or negative

effects on plant growth depending on the timing, duration, and hydrologic energy of flood events. In Odum's (1979) adaptation of the subsidy–stress model[6] for swamp forests, he proposed that the highest rates of production occur with periodic floods of short duration due to subsidies of nutrients and water, while stagnant flooding or floods of long duration cause physiological stress and result in lower production. The model suggests that upland forests are relatively unproductive because they lack flooding subsidies.

Odum's hypothesis was based primarily on work by Conner and Day (1976) in Louisiana cypress swamps that suggested productivity is related to flooding regime as follows: seasonal flooding > slow-flowing floods of long duration > continuous stillwater flooding. Brinson et al. (1981) recognized that this ranking corresponded to a gradient in hydrologic throughput: flowing water

> sluggish flow > still water. Mitsch et al. (1979) reported a positive correlation between discharge in the Cache River, Illinois, and annual stem increment in cypress (*Taxodium distichum*) trees, presumably due to increased rates of phosphorus deposition during years of high flow. Brown (1981) explicitly linked nutrient subsidies to hydrologic regime when she reported a positive correlation between phosphorus-input rates and primary production in Florida cypress swamps.

An important assumption of Odum's (1979) hypothesis is that the forests being compared are mature and in equilibrium with the hydrologic regime. In a steady-state condition bottomland tree species are expected to be physiologically and morphologically adapted to the flooding regime at a given position along a hydrologic gradient (Sharitz and Mitsch 1993). Flooding is considered a stress if the productivity of a forest composed of highly flood-tolerant tree species is lower than a nearby upland forest composed of tree species adapted to drier conditions. Likewise, flooding is considered a subsidy if productivity is higher than on nearby upland sites. Subsidy and stress are judged relative to upland forests assuming that all forests are optimally suited to the hydrologic regime. Stress by this definition is not a perturbation but is instead a chronic drain on metabolic energy that cannot be entirely overcome through species replacement or adaptation (Lugo 1978).

In a subsequent paper, Odum et al. (1979) defined subsidy and stress more traditionally (see Lugo 1978) by emphasizing the response of steady-state ecosystems to perturbations. They defined stress as an ''unfavorable deflection'' and subsidy as a ''favorable deflection'' in ecosystem performance (e.g., productivity) following a disturbance. By this definition subsidy and stress are judged in relation to the productivity of the same site prior to the perturbation.

Most studies of productivity in Southeastern United States floodplain forests have focused on deepwater cypress–tupelo (*Nyssa aquatica*) swamps (Conner 1994), which lay on the wet side of the subsidy–stress curve. Largely overlooked are extensive areas of bottomland hardwood forest that occur on floodplain terraces between deepwater cypress–tupelo and upland forests (Sharitz and Mitsch 1993). Although generally drier than cypress–tupelo swamps, bottomland hardwood forests receive water and sediments during seasonal flood events. Taylor et al. (1990) used a subsidy–stress model to suggest that bottomland hardwood forests should have higher productivity than either nearby upland forests or more extensively flooded cypress–tupelo swamps.

An alternative hypothesis by Mitsch and Rust (1984) holds that the benefits of improved fertility and water status may be diminished by the physiological stresses associated with anaerobic soils or drought. They proposed that winter floods will increase production through deposition of nutrient-laden sediments (Mitsch et al. 1979, Brown 1981) and through improved soil moisture during the growing season (Broadfoot 1967). However, production may be reduced if flooding causes an anaerobic rooting zone during the growing season (Hook and Brown 1973), or if water availability declines during periods of low rainfall (Dickson and Broyer 1972). In this model, the hydrologic regime may impose subsidies and stresses in a single growing season, thereby moderating the influence of any single factor on production. The Mitsch and Rust (1984) model can be considered a more complex expression of the subsidy–stress hypothesis proposed by Odum (1979) and Taylor et al. (1990). All of the aforementioned hypotheses were based on data from a relatively small number of sites, and remain largely untested.

Many previous studies in Southeastern U.S. swamp forests have reported only stem increment or wood production (Mitsch and Ewel 1979, Birch and Cooley 1983, Mitsch and Rust 1984, Brinson et al. 1985, Dicke and Toliver 1990, Conner and Day 1992*a*, Robertson 1992, Keeland and Sharitz 1995), or only leaf production (Brinson et al. 1980, Gomez and Day 1982, Conner and Day 1992*b*). Most studies that have reported total aboveground NPP have not reported groundwater-table data (Conner and Day 1976, Johnson and Bell 1976, Brown 1981, Conner et al. 1981, Brown and Peterson 1983, Muzika et al. 1987, Conner et al. 1993). Published studies that provide total aboveground production and groundwater-table data for the same sites are relatively few (Appendix 1).

The juxtaposition of upland, bottomland hardwood, and cypress–swamp forests in the Southeastern U.S. offers an ideal arena in which to test the subsidy–stress hypothesis. Our objective was to test the hypothesis that periodically flooded forests generally have higher productivity than other Southeastern U.S. forests. Although the primary goal of our work was to test predictions on patterns of productivity across hydrologic gradients (Odum 1979, Taylor et al. 1990, Odum et al. 1995), we also assessed the effects of hydrologic perturbation (Odum et al. 1979) on some sites.

DESCRIPTION OF STUDY AREAS

In South Carolina and Louisiana we established five transects across flooding gradients and one transect across a hydrologic-disturbance gradient. The three South Carolina transects were located in a single watershed within the Savannah River Site near Aiken on the Upper South Atlantic Coastal Plain. The three Louisiana transects were located in separate watersheds of the Gulf Coastal Plain.

South Carolina transects

Savannah River.—The Savannah is a relatively large river that discharges into the Atlantic Ocean. Our transect at the Savannah River swamp (SR) was located on the upland edge of the 2.5-km-wide river floodplain. Flooding on the most frequently flooded plots (SR-1 and 2) was a function of input from nearby

tributaries into the Savannah River floodplain and a periodic backwater effect at the confluence (downstream) with Steel Creek during high discharge in the Savannah River (Hardegree et al. 1995). On most of the sites in our study, the position of the groundwater table during non-flooded periods was determined by groundwater discharge within the watershed. However, groundwater tables on the SR-3 and 4 plots were primarily determined by local runoff and the presence of a slowly permeable soil horizon between 30 and 60 cm depth (Megonigal et al. 1993). Median water velocities are lower in the Savannah River swamp (10–38 cm/s) than in the river channel (67–85 cm/s) (Newman 1986). The soils are chiefly poorly drained clays and loams (Typic Fluvaquents).

Upper Three Runs.—Upper Three Runs Creek (UTR) is a fifth-order stream and a tributary of the Savannah River. Water levels on the transect were influenced by overbank flooding from the Savannah River, which caused water to back up onto the creek floodplain (Hardegree et al. 1995). Median channel velocities range from 20 to 40 cm/s. The soils are poorly drained clays and loams (Typic Fluvaquents). This transect did not include a relatively dry site.

Meyers Branch.—Meyers Branch (MB) is a third-order stream and a tributary of Steel Creek. Median water velocities range from 18 to 31 cm/s. The soils are sandy and grade from Cumulic Humaquepts (high organic-carbon content) to Typic Quartzipsamments (Megonigal et al. 1993). Tree cores suggest that larger individuals of cypress were removed in selective logging of the area in the late 1940s (Muzika et al. 1987).

Louisiana transects

Verret Basin.—The Verret Basin swamp (VB) is located between Bayou Lafource and the Atchafalaya floodway (Conner et al. 1993). The site is characterized by slow flow rates (no velocity data are available). Near-continuous flooding is due partly to rapid rates of subsidence (Conner and Day 1988). Soils are Typic Fluvaquents that formed from clayey and silty sediments of the Mississippi and Atchafalaya Rivers.

Barataria Basin.—The Barataria Basin swamp (BB) transect was located at the upper end of the Barataria Bay estuary, between the Mississippi River and Bayou Lafourche (Conner and Day 1992*a*, *b*). These plots represented a hydrologic disturbance gradient with naturally flooded plots that received flowing waters from Bayou Chevreuil (BB-NAT1 and NAT2) and impounded plots that were continuously flooded and stagnant (BB-IMP1 and IMP2). The soils are poorly drained silts and clays (Typic Fluvaquents).

Pearl River Swamp.—The Pearl River Swamp (PR) lies between the West Pearl and Pearl Rivers. Flow rate data are not available, but annual median discharge is 48 m^3/s. Because flooding occurs primarily by overbank flow across the Pearl River levee, backwater sloughs may experience deep flooding in the spring and dry periods during the summer. Soils along the transect vary from Aeric Fluvaquents to Typic Fluvaquents (Faulkner and Patrick 1992). In terms of topographic relief and vegetation, the Pearl River sites were more similar to sites in South Carolina than in Louisiana.

Study plots and vegetation

In most cases, we chose sites on each transect to represent locally dry topographic highs, locally wet topographic lows, and intermediate elevations. Exceptions were made for the Barataria Basin transect, where the sites were established on a hydrologic-disturbance gradient, and for the Upper Three Runs transect, which did not have a dry site.

Flooded plots in both regions were dominated by cypress and water tupelo as is typical of frequently flooded deepwater swamps in the Southeastern U.S. (Table 1). The intermediately flooded plots in South Carolina, and on the Pearl River transect in Louisiana, were dominated by a variety of bottomland hardwood species including swamp tupelo (*Nyssa sylvatica* var. *biflora*), tulip poplar (*Liriodendron tulipifera*), sweetgum (*Liquidambar styraciflua*), ash (*Fraxinus* spp.), and several species of oaks (*Quercus* spp.). The upland end of these transects supported loblolly pine (*Pinus taeda*) and sweetgum. Rapid subsidence and increasing water levels in the Verret Basin account for the large percentage (50%) of dead stems on the flooded plots. The abundance of *Fraxinus* in BB-IMP-2 and the Verret Basin plots is also evidence of hydrologic disturbance. In terms of vegetation and hydrology (Fig. 1), the paired plots at the BB-IMP site were very different and will be referred to separately as BB-IMP1 and BB-IMP2. The vegetation at the naturally flooded Barataria Basin site (BB-NAT) was typical of other relatively undisturbed and frequently flooded forests in our study.

MATERIALS AND METHODS

Production

We established paired 20 m × 25 m plots (0.05 ha) at each site, except on the Verret Basin transect where the plots were 20 m × 50 m (0.1 ha). Litterfall was collected at monthly intervals from 10 randomly located 0.25-m^2 nylon-screen traps per plot between April 1987 and April 1989. Traps were located ≈1 m above the forest floor to prevent loss or leaching during flood events. We tested the adequacy of our sampling effort by placing 20 traps on two plots in each state; the mean litterfall in 10 traps was within the 90% confidence interval of the larger sample. We use the term "leaf litter" in reference to all non-woody litter including flowers, fruits, and seeds that typically account for <10% of the non-woody litterfall total (Megonigal and Day 1988). Leaf litter was separated from woody litter and dried to constant mass at 65°C.

Stem production was estimated for 1987 and 1988 from

TABLE 1. Species composition and structure of upland and swamp forests in South Carolina and Louisiana, USA.

Transect and plot number	Species†	Basal area (m²/ha)	Stand‡		
			Density (stems/ha)		
			Live	Dead	Dead/ Live
South Carolina					
Savannah River					
SR-1 and 2	*Nyssa aquatica*	46.0	900	30	0.03
	Taxodium distichum				
SR-3 and 4	*Quercus* spp.	29.3	330	20	0.07
SR-5 and 6	*Pinus taeda*	31.5	520	40	0.08
	Quercus spp.				
Upper Three Runs					
UTR-1 and 2	*Nyssa sylvatica*	47.1	570	30	0.06
	Taxodium distichum				
UTR-3 and 4	*Nyssa sylvatica*	27.0	350	0	0
	Quercus spp.				
Meyers Branch					
MB-1 and 2	*Taxodium distichum*	35.3	620	40	0.06
MB-3 and 4	*Liriodendron tulipfera*	43.0	600	10	0.02
	Nyssa sylvatica				
MB-5 and 6	*Pinus taeda*	24.1	360	20	0.06
	Liquidambar styraciflua				
Louisiana					
Verret Basin					
VB-1 and 2	*Diospyros virginiana*	26.6	530	265	0.50
	Taxodium distichum				
VB-3 and 4	*Fraxinus* spp.	28.1	575	90	0.16
	Taxodium distichum				
VB-5 and 6	*Quercus* spp.	28.9	450	35	0.08
	Fraxinus spp.				
	Celtis laevigata				
Barataria Basin§					
BB-Nat1 and Nat2	*Nyssa aquatica*	54.5	930	130	0.14
	Taxodium distichum				
BB-Imp1	*Fraxinus* spp.	22.3	400	0	0
	Celtis laevigata				
	Liriodendron styraciflua				
BB-Imp2	*Fraxinus* spp.	13.6	480	120	0.25
Pearl River					
PR-1 and 2	*Taxodium distichum*	46.2	550	20	0.04
	Nyssa sylvatica	47.1	570	30	0.06
PR-3 and 4	*Liquidambar styraciflua*	36.7	630	30	0.05
	Carya aquatica				
PR-5 and 6	*Liquidambar styraciflua*	39.4	450	70	0.16

† Species that account for 50% of the basal area, listed in order of dominance.
‡ Basal area and density data are for all stems ≥10 cm diameter at breast height. Values are the average of paired plots.
§ Nat = natural; Imp = impounded.

annual changes in wood biomass calculated using allometric equations based on stem diameter at breast height (dbh, ≈1.3 m) as the independent variable (Appendix 2). Diameter was measured above the butt swell on large cypress trees. The dbh of stems ≥10 cm was measured at the end of a length of chain (≈10 cm long) that we hung from an identification tag on the tree. The "standard chain" method allowed us to make measurements a safe distance below the tag's nail, which often caused the trunk to swell. We assumed that the contribution of wood from stems <10 cm dbh and herbs was a relatively small fraction of aboveground net primary production because the growth rates of saplings are typically low due to light availability, and the productivity of saplings is dominated by leaves (Whittaker et al. 1974), which we recovered in litter traps. None of our sites had an important shrub component. Aboveground net primary production (aboveground NPP) was calculated as the sum of leaf litter and wood production. Woody litter was not included because we assumed that all wood production was accounted for by the allometric equations that were based on measurements of whole-plant wood biomass.
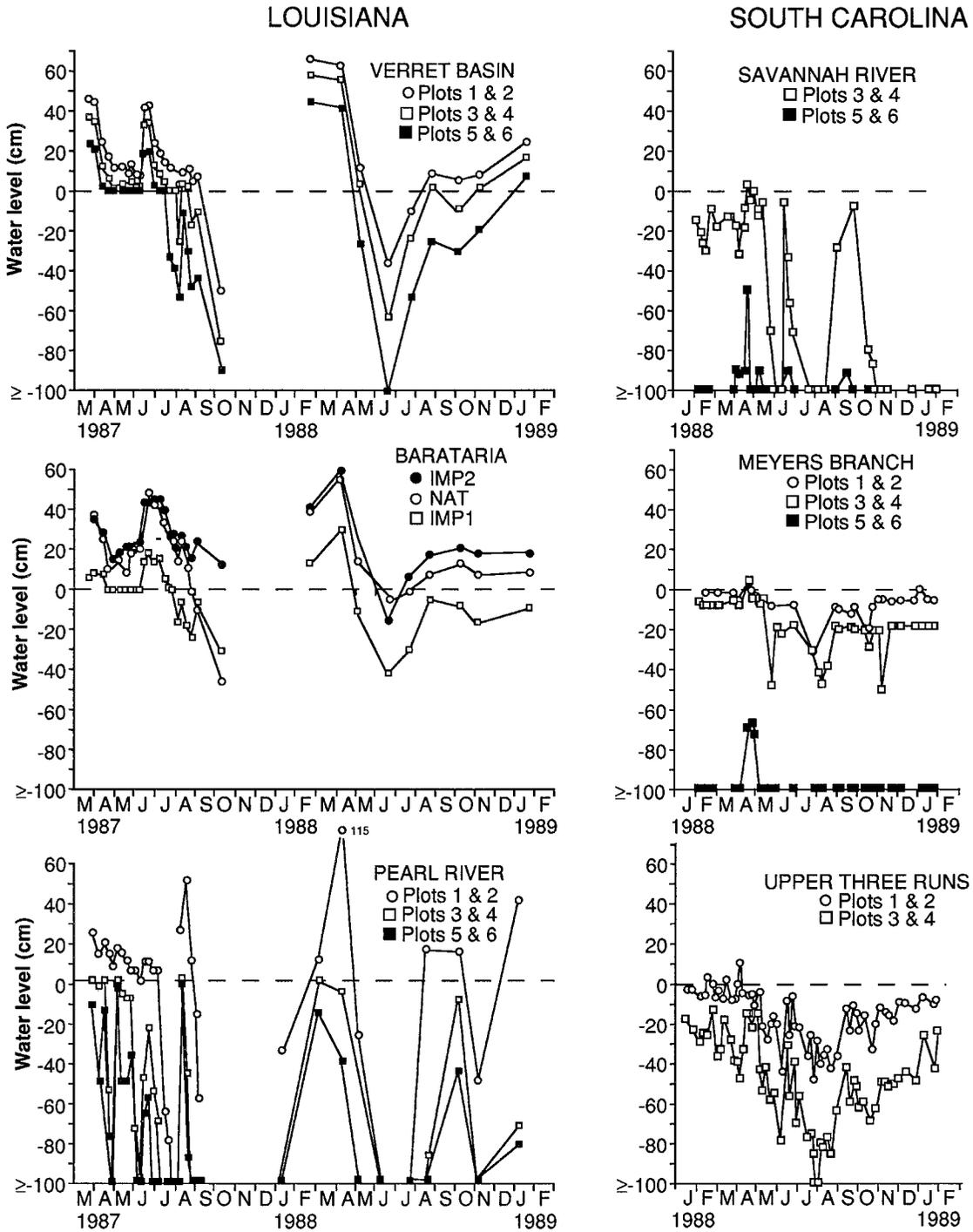
FIG. 1. Water-table depths relative to the soil surface on 17 forested sites in South Carolina and Louisiana, USA. The figure does not show the Savannah River flooded site (SR 1 and 2), which was continuously flooded to an average depth of 60 cm.

Hydrology

Rivers and streams are a source of water for bottomland hardwood forest soils primarily during flood events, while groundwater is the dominant water source during periods of base flow. The groundwater table establishes the depth of the aerobic–anaerobic interface in soils, a feature known to regulate many biogeochemical processes affecting plant productivity (Mitsch

and Gosselink 1993). We established groundwater wells to monitor the position of the groundwater table between flood events.

Our methods for measuring groundwater table and flooding depth varied between sites and regions. In South Carolina, a single fixed-position staff gauge was used for the SR-1 and 2 plots that were continuously flooded. In Louisiana, we measured above-surface flooding as the average water depth at 20–30 points per plot. Water-table depths were determined in perforated 6-cm (internal diameter) polyvinyl chloride pipes installed to depths of 90–100 cm at each position along the flooding gradient (dry, intermediate, wet). The wells were lined with pea gravel and the surface was packed with clayey subsoil from the site (Faulkner et al. 1989). In South Carolina and at the Pearl River transect in Louisiana we used a single well placed midway between the pair of plots at each position. At the other Louisiana sites we installed a well on every plot. Measurements in Louisiana were made weekly in 1987 and monthly in 1988; in South Carolina measurements were made at least once a month during 1988 only. We express groundwater-table depths relative to the soil surface so that positive values indicate flooding and negative values indicate a subsurface groundwater table.

We placed each of our plots on a common hydroperiod scale by calculating mean growing-season water depth (MWD) as the average groundwater depth for the period March to November. Groundwater-table depths >90 cm below the soil surface were assigned a value of −90, which corresponded to the bottom of our most shallow wells. We use the term *water depth* to encompass both groundwater-table depth and flooding depth. Because water depths were measured at regular intervals, MWD values explicitly incorporate the duration of soil saturation and flooding. We defined *wet* plots as having MWD values >0 cm, *intermediate* plots had values between 0 and −60 cm, and *dry* plots had values < −60 cm. A threshold of −60 cm was chosen because it delineated the plots in our study with hydric soils (intermediate and wet) from those with non-hydric soils (Soil Conservation Service 1991, Faulkner and Patrick 1992, Megonigal et al. 1993). Rainfall data for the South Carolina sites was obtained from the Savannah River Laboratory Weather Center operated by the Savannah River Plant (Aiken, South Carolina, USA).

Statistical analysis

Differences in production among the reclassified flooding regimes (based on MWD) were tested by analysis of variance (SAS Institute 1987: GLM procedure) using the mean of paired plots on each site. We used contrasts to test our a priori hypothesis that productivity was higher on intermediately flooded sites than wet and dry sites in this study, or upland sites in the literature. We used the SAS Institute (1987) Reg procedure for regression analyses, Means procedure for paired *t* tests, and Ttest procedure for unpaired *t* tests; homogeneity of slopes was determined by analysis of covariance using the GLM procedure.

RESULTS

Hydrology

Between-region differences in flooding regime were evident in groundwater-depth data (Fig. 1) and the mean growing-season water depth (MWD) values (Table 2). Most of the wet plots were in the Barataria Basin and the Verret Basin; SR-1 and 2 were the only wet plots in South Carolina and they were continuously flooded to a depth of roughly 60 cm (data not shown). The low-elevation sites at Meyers Branch, Upper Three Runs, and Pearl River that we considered to be locally wet had intermediate values on a common MWD scale. Note that the MWD values do not reflect the temporal variability in water table depth—the PR-1 and 2 and the MB-3 and 4 plots had similar MWD values but very different patterns of soil saturation and flooding.

Leaf and stem production

Leaf production on wet plots (395 g·m^{-2}·yr^{-1}) was lower than on intermediate plots ($P = 0.0007$), but intermediate and dry plots were not significantly different (689 g·m^{-2}·yr^{-1}, Fig. 2). The lowest leaf production in both regions occurred on sites with continuous or near-continuous flooding (BB-IMP2, BB-NAT, VB-1 and 2, and SR-WET), while leaf production on sites with periodic exposure of the soil surface was relatively high (Pearl River and all South Carolina plots except SR-WET). The Pearl River sites produced more leaf litter (665–855 g·m^{-2}·yr^{-1}) than other sites in Louisiana (138–598 g·m^{-2}·yr^{-1}), regardless of topographic position. Leaf production averaged 62 ± 11% (mean ± 1 SD) of aboveground net primary production (NPP) and did not change significantly between 1987 and 1988 in either region (paired *t* test, $P > 0.25$; Table 2).

Flooding regime did not consistently affect wood production. Wood production was lower on wet plots than on intermediate plots in 1988 ($P = 0.0006$), but not in 1987 (Fig. 3). This difference between flooding regimes in 1988 was due mainly to significantly higher stem production on intermediate and dry plots in South Carolina ($P \leq 0.05$, paired *t* test, mean increase of 202 g·m^{-2}·yr^{-1}). In Louisiana, wood production was not significantly different between 1987 and 1988, regardless of topographic position.

Aboveground net primary production

Aboveground NPP was lower by ≈30% on sites with MWD values >0 cm compared to sites with MWD values <0 cm (Fig. 3). Wet sites had significantly lower aboveground NPP than intermediate sites in both years ($P \leq 0.02$), but there was no significant difference between the intermediate and dry sites. In addition,

TABLE 2. Leaf, wood, and total aboveground production on paired plots in South Carolina (for 1988) and Louisiana (for 1987 and 1988). Mean growing-season water-depth (MWD) values were calculated for the months of March to November.

| | MWD (cm) | | Production ($g \cdot m^{-2} \cdot yr^{-1}$) | | | | | |
| | | | 1987 | | | 1988 | | |
Plot†	1987	1988	Leaf	Wood	Total	Leaf	Wood	Total
SR-1-WET	⋯	60.0	501	166	667	453	197	650
SR-2-WET	⋯	60.0	482	213	695	314	287	601
SR-3-INT	⋯	−49.5	767	288	1055	737	593	1330
SR-4-INT	⋯	−49.5	680	367	1047	629	411	1040
SR-5-DRY	⋯	−88.0	668	339	1007	634	467	1101
SR-6-DRY	⋯	−88.0	607	386	993	638	440	1078
UTR-1-INT	⋯	−20.1	690	330	1020	700	361	1061
UTR-2-INT	⋯	−20.1	776	290	1066	768	432	1200
UTR-3-INT	⋯	−34.8	593	232	825	686	280	966
UTR-4-INT	⋯	−34.8	581	302	883	695	570	1265
MB-1-INT	⋯	−9.4	713	188	901	644	509	1153
MB-2-INT	⋯	−9.4	837	338	1175	972	704	1676
MB-3-INT	⋯	−21.5	625	226	851	713	524	1237
MB-4-INT	⋯	−21.5	654	224	878	652	500	1152
MB-5-DRY	⋯	−87.4	799	31	830	792	294	1086
MB-6-DRY	⋯	−87.4	832	136	968	794	461	1255
VB-1-WET	12.3	20.2	339	652	991	361	237	598
VB-2-WET	11.6	18.9	316	225	541	317	204	521
VB-3-WET	0.2	11.0	529	381	910	598	435	1033
VB-4-WET	0.6	11.1	504	629	1133	582	326	908
VB-5-INT	−35.9	−30.9	556	437	993	592	389	981
VB-6-INT	−41.7	−13.2	551	716	1267	558	410	968
BB-IMP1-INT	−2.2	−1.3	514	380	894	561	332	893
BB-IMP2-WET	27.9	28.3	185	92	277	138	64	202
BB-NAT1-WET	17.9	19.7	486	416	902	487	285	772
BB-NAT2-WET	18.0	20.5	484	319	803	493	331	824
PR-1-INT	−6.2	−16.0	745	229	974	680	598	1278
PR-2-INT	−6.2	−16.0	767	470	1237	709	422	1131
PR-3-INT	−52.8	−65.9	741	867	1608	855	280	1135
PR-4-INT	−52.8	−65.9	707	843	1550	737	649	1386
PR-5-DRY	−68.4	−76.4	665	482	1147	672	533	1205
PR-6-DRY	−68.4	−76.4	779	169	948	709	125	834

† Designations indicate Transect, plot number, and MWD class (wet, intermediate, or dry; see *Materials and methods: Hydrology*). For explanation of transect abbreviations see Table 1.

aboveground NPP on the intermediate and dry sites in our study was not significantly different ($P = 0.26$) from values reported for 8 North Carolina upland forests (Peet and Council 1981) and 14 temperate deciduous forests (Cole and Rapp 1981, Fig. 3). The highest rates of aboveground NPP we measured occurred on the PR-3, PR-4, and MB-2 plots (>1400 $g \cdot m^{-2} \cdot yr^{-1}$), all of which had an intermediate flooding regime.

Production did not vary significantly with hydrologic regime on intermediate ($r^2 = 0.12$, $P = 0.08$) or dry ($P = 0.77$) sites (Fig. 4), but water depth/duration was negatively correlated to aboveground NPP at MWD values >0 cm. This pattern held when we included published data from other Southeastern U.S. swamp forests (numbered points in Fig. 4, Appendix 1). In the expanded data set, the slope of the MWD–NPP relationship was more negative on sites that showed evidence of severe hydrologic alteration ($>25\%$ dead stems, Table 1) than on sites with comparatively unaltered hydrologic regimes. Production declined by a rate of -5 $g \cdot m^{-2} \cdot yr^{-1} \cdot cm^{-1}$ MWD ($r^2 = 0.78$, $P = 0.0001$) on wet sites with relatively unaltered hydrologic regimes and -24 $g \cdot m^{-2} \cdot yr^{-1} \cdot cm^{-1}$ MWD ($r^2 =$

0.67, $P = 0.02$) on hydrologically altered sites. Thus, the stress associated with inundation increased by fivefold when forest communities were not in equilibrium with the current hydrologic regime.

DISCUSSION

Our results do not support the hypothesis that periodic, short-duration floods increase forest production relative to adjacent upland forests or regional upland forests (Odum 1979, Taylor et al. 1990, Odum et al. 1995). Aboveground NPP (net primary production) was remarkably similar among upland hardwood, bottomland hardwood, and cypress–tupelo forests at MWD (mean growing-season water-depth) values <0 cm (Figs. 3 and 4), and there were no significant differences in aboveground NPP between Southeastern U.S. upland sites in the literature and the dry or intermediate sites in this study (Fig. 4). This result is consistent with other studies on bottomland hardwood forests. Mitsch and Rust (1984) found only weak or insignificant correlations between tree-ring width and historical records of flooding in a bottomland hardwood forest in Illinois, and Johnson and Bell (1976) reported similar rates of
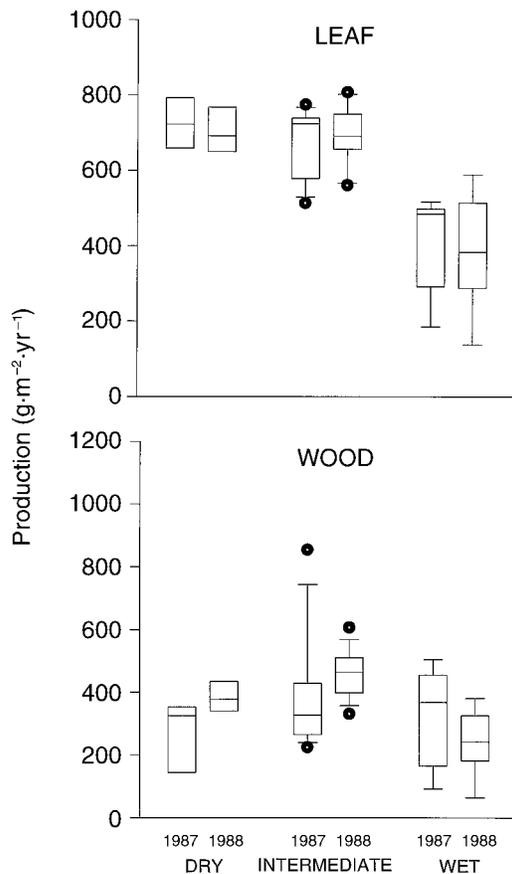
FIG. 2. Box plots of leaf and wood production (paired plots averaged) for sites classified as dry ($n = 3$), intermediate ($n = 9$), or wet ($n = 5$) according to mean growing-season water depth. Boxes encompass the 25th to 75th percentiles in productivity; horizontal caps represent the 10th and 90th percentiles; circles are the 5th and 95th percentiles. The median (50th percentile) is indicated with a horizontal line inside the box.

aboveground NPP in an upland forest (1150 g·m^{-2}·yr^{-1}) and a bottomland hardwood forest (1090 g·m^{-2}·yr^{-1}). Periodic floods and shallow groundwater tables do not necessarily improve the productivity of unmanaged forests in the Southeastern United States.

Gosselink et al. (1981) investigated the relationship between forest productivity and hydrologic regime by plotting the aboveground NPP of wetland and upland forests in the literature against a rough estimate of inundation frequency. We reexamined their data and found that aboveground NPP of "seasonally flooded" swamp forests (1306 ± 410 g·m^{-2}·yr^{-1}, mean ± 1SD) was ≈30% higher than mesic upland forests (1002 ± 271 g·m^{-2}·yr^{-1}), a difference that was nearly significant (t test, $P = 0.08$). Their estimate for upland forests was similar to our estimate (1000 ± 261 g·m^{-2}·yr^{-1}), but they reported greater aboveground NPP for seasonally flooded forests than we do for intermediate sites (1107 ± 189 g·m^{-2}·yr^{-1}). The primary difference between the

two data sets is that we have a larger sample size ($n = 18$ vs. 6 observations), and their data set does not include bottomland hardwood forests. There was no overlap of sites from the literature between the two data sets. The large standard deviation (SD) for seasonally flooded sites in the Gosselink et al. (1981) study was due to two sites with rates of aboveground NPP >1600 g·m^{-2}·yr^{-1}. Early reports of unusually high rates of aboveground NPP in a few periodically flooded forests (Brown 1981, Conner et al. 1981) may have exaggerated the benefits of flooding subsidies.

Our results are consistent with a model by Mitsch and Rust (1984) in which the benefits of water and nutrient subsidies are negated by the physiological stresses imposed by anaerobic soils or drought, i.e., subsidies and stresses may occur simultaneously and cancel one another (Lugo 1978). The potential benefits of soil inundation are apparent in observations of increased aboveground NPP in green-tree reservoirs (Broadfoot 1967). Winter floods in these hardwood forests presumably improves soil water availability during the growing season. Foster (1992) found that shallow groundwater tables and occasional summer floods kept the soil water potential above −0.5 MPa throughout the summer in a bottomland hardwood forest in Indiana. Measurements of stomatal conductance, pre-dawn and minimum daily leaf water potential, and soil-to-leaf hydraulic conductance in box elder (*Acer negundo*) trees suggested that net photosynthesis was not under stomatal control at these soil moisture levels (Foster 1992). The benefits of sediment deposition are sup-
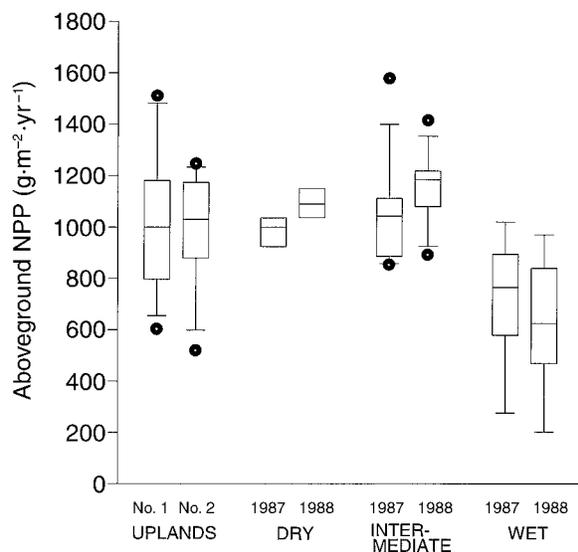

FIG. 3. Box plots of aboveground net primary production (NPP) (paired plots averaged) for sites in this study and upland sites from two literature sources. The sites in upland study no. 1 (Cole and Rapp 1981, $n = 14$) are widely distributed temperate forests, and those in study no. 2 (Peet and Council 1981, $n = 8$) are hardwood stands in the Duke Forest, North Carolina, USA. The data convention is as in Fig. 2.
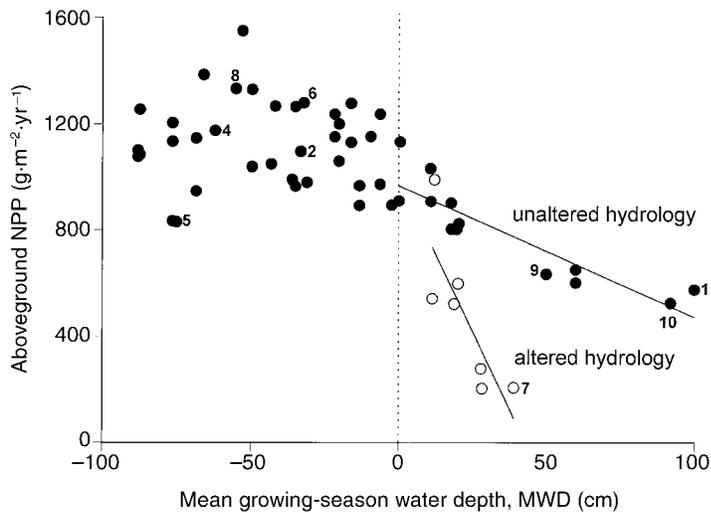
Fig. 4. The relationship of aboveground net primary production (NPP) to mean growing-season water-depth values (MWD; Table 2). Because we have no 1987 water-level data for South Carolina, these values were excluded. Numbered points are sites from the literature (see Appendix 1). The vertical line at 0 cm MWD is the y intercept for regressions. Hydrologically altered sites in our study (○) had >25% dead stems, and Mitsch et al. (1991) report a large number of dead stems on their C2 (no. 7) site. Regression equations for plots with MWD > 0 cm are: Production = 965.5 − 4.8 MWD for unaltered sites; Production = 1007.6 − 23.5 MWD for altered sites.

ported by reports of positive correlations between sediment-associated nutrient inputs and aboveground NPP in cypress swamps (Mitsch et al. 1979, Brown 1981). On the other hand, periodic flooding may cause stress since anaerobic and reduced conditions can persist in the rooting zone of bottomland hardwood soils for periods of several weeks during the growing season (Faulkner and Patrick 1992, Megonigal et al. 1993). Although bottomland hardwood trees can tolerate short periods of soil saturation, greenhouse studies demonstrate that most species exhibit better growth in unsaturated soils than saturated or flooded soils (Dickson and Broyer 1972, Hook and Brown 1973, Kozlowski 1984, Day 1987, Jones et al. 1989). Even shallow flooding can decrease rates of photosynthesis and stomatal conductance (Peterson and Bazzaz 1984, Will et al. 1995). Likewise, drought can be expected to lower growth rates due to a lack of soil moisture (Dickson and Broyer 1972), though very few field studies have investigated this possibility (Foster 1992). Although there is evidence to support the individual components of the Mitsch and Rust (1984) model, no study has investigated the extent to which these components interact to determine the NPP of bottomland hardwood forests. Our data are consistent with simultaneous subsidy and stress interactions, but studies are needed that investigate each of these processes from a more mechanistic viewpoint.

A component of the Mitsch and Rust model (1984) that is not commonly considered is the role of drought stress. One largely untested hypothesis in the literature is that a decrease in root biomass relative to shoot biomass (a common response to flooding) reduces drought tolerance because there is less root surface area for water uptake during dry periods (Kozlowski 1985, Sun et al. 1995). There may be additional morphological and physiological trade-offs such that trees are incapable of tolerating both drought and flooding. For

example, the capacity of roots to perform and tolerate alcoholic fermentation is lower in wetland trees raised in drained soils compared to those raised in flooded soils (Keeley 1979). Hook and Brown (1972) and Keeley (1979) have speculated that stem morphology characteristics that maximize O_2 transport to root systems will decrease the ability of trees to control transpiration losses during periods of drought. Because bottomland hardwood tree species must adapt to hydrologic regimes on sites that are alternately inundated and unsaturated to depths >1 m, they may be particularly sensitive to annual extremes in precipitation and runoff.

Our data analysis and the various conceptual models we tested each quantified the hydrologic regime somewhat differently. The models of Odum (1979) and Mitsch and Rust (1984) were based on flow rate and the duration of flood events. Although Odum's (1979) flooding categories were labeled as "stagnant, slowly flowing or seasonally flooded," it is commonly understood that sites with flowing water are generally seasonally flooded (Brinson et al. 1981). Taylor et al. (1990) used flood frequency and duration during the growing season to define hydrologic gradients in Southeastern U.S. bottomland hardwood forests. We quantified flooding regime in a parameter that incorporated the depth and duration of not only flooding, but also soil saturation during non-flooded periods. Our hydrologic categories corresponded well to the categories used by Odum (1979) and Odum et al. (1995). The wet sites generally had stagnant (BB-IMP2) or slow-flowing water (VB-WET, SR-WET), with the exception of the BB-NAT site that had flowing water. Likewise, most intermediate sites had flowing water and were periodically inundated (UTR, MB, PR). Nearly one half of our plots would be categorized as periodically flooded with flowing water (Fig. 2, site descriptions), a condition that subsidy–stress models pro-

posed should yield unusually high rates of primary production.

A primary benefit attributed to periodic inundation by flowing water is deposition of nutrient-laden sediments (Mitsch et al. 1979). A sediment deposition rate of 8.6 mm/yr delivered 19 g P·m^{-2}·yr^{-1} to an Illinois cypress swamp, compared to inputs of only 0.14 g P·m^{-2}·yr^{-1} from throughfall (Mitsch et al. 1979). Other studies in southeastern bottomland hardwood forests have reported sediment deposition rates ranging from 2.4 to 2.8 mm/yr (Cooper et al. 1987, Hupp and Bazemore 1993). Conner and Day (1988) measured sediment deposition rates of 2.7 mm/yr at VB-3 and 4, 8.8 mm/yr at VB-1 and 2 and 6.0 mm/yr for swamps in the Barataria Basin. Although we did not measure sediment deposition rates at other sites in our study, it is reasonable to assume, given the flooding regime, that they also received periodic inputs of sediments and nutrients.

Flooding stress

The use of aboveground NPP data to detect stress (i.e., reductions in whole-plant growth) is problematic because it often affects leaves, roots, and stems disproportionately (Day 1987, Keeley 1979). Furthermore, the characteristic symptoms of stress are generally time dependent and vary with the magnitude and persistence of the stressor (Lugo 1978, Larcher 1995). At the onset of stress, trees can maintain relatively high rates of metabolism by mobilizing carbohydrate reserves in stems and roots (Harms et al. 1980, Kozlowski 1992). Given a limited supply of carbohydrates, trees may invest in the production of new leaf tissue rather than new wood (Waring and Schlesinger 1985:34). For example, water tupelo trees that suffered a complete insect defoliation early in the growing season did not produce new wood until they had produced a second flush of leaves (Conner et al. 1981). In such cases, a pattern of reduced wood growth, but relatively constant leaf production, may indicate the onset of stress. On the other hand, the same pattern can occur without a change in whole-plant production due solely to shifts in carbon allocation. For example, in a 3-yr study on cypress saplings, continuous and periodic flooding regimes produced similar rates of leaf production and whole-plant production (root plus shoot), but continuously flooded saplings allocated more carbon to boles than to roots (Megonigal and Day 1992). As a result, the same whole-plant production yielded greater wood biomass and annual tree-ring increments under continuously flooded conditions (Young et al. 1993). Thus, annual variations in wood growth alone cannot be used as an unambiguous sign of stress.

When flooding stress is chronic, it will eventually deplete carbohydrate reserves (Harms et al. 1980) and reduce the photosynthetic capacity of trees (Pezeshki et al. 1996). Because reductions in photosynthetic capacity due to stress are often manifest as lower leaf biomass or leaf area, rather than lower rates of photosynthesis per se (Brown 1981, Neufeld 1983, Luxmoore et al. 1995), leaf litterfall is a reliable measure for detecting chronic stress in forests. In two consecutive years, leaf litterfall was 38% lower on plots with mean growing-season water depths above the soil surface (i.e., MWD > 0 cm) than on drier plots; aboveground NPP also was significantly lower on wet plots in both years. Low rates of leaf litterfall on wet sites is strong evidence that low rates of aboveground NPP were due to stress and not to shifts in root–shoot allocation. Furthermore, the monotonic decline in aboveground NPP with increasing MWD is evidence that stress was caused by excessive flooding. Similar relationships have been observed for patterns of leaf production across gradients of nutrient stress (Brown 1981) and salinity stress (Brinson et al. 1985).

Chronic flooding stress was particularly severe on VB-1 and 2, BB-IMP2, and plot C2 of Mitsch et al. (1991), all of which had large numbers of standing dead trees as evidence of an increase in hydroperiod during recent decades (Table 1, Mitsch et al. 1991). Levee construction and impoundment on plots BB-IMP2 and C2 has apparently changed the hydrologic regime from periodic flooding to near-continuous flooding. In addition to levee construction, the VB-1 and 2 plots are currently experiencing vertical accretion deficits of 10.8 mm/yr due to sea-level rise and subsidence (Conner and Day 1988). On these plots, the slope of the relationship between aboveground NPP and MWD was 5 times more negative than sites with relatively unaltered hydrologic regimes (Fig. 4). The apparent reduction in aboveground NPP caused by an increase in the depth/duration of flooding on hydrologically altered sites is an example of perturbation stress as described by Odum et al. (1979) and Lugo (1978). Flooding stress was particularly severe on these sites because the forest community is not in equilibrium with the hydrologic regime (Harms et al. 1980). Given that hydrologic regimes can be changed much more quickly than plant communities are able to respond through species replacement, such perturbations are likely to be common in the Southeastern U.S. If provided sufficient time it is possible that the productivity of hydrologically altered sites may eventually recover. However, regeneration of forest species will be less likely because most woody seedlings, even those of wetland species, require an exposed soil surface to germinate and must attain a minimum size before they can survive inundation (Jones et al. 1994). If forests do regenerate, we predict from the negative slope of the regression relationships that the maximum productivity of the site will have been permanently lowered to a level determined by the new MWD value.

Hydrologic perturbations at the VB-1, VB-2, and C2 plots have apparently reduced aboveground NPP even though cypress was a canopy dominant. It seems counterintuitive that an increase in flooding should lower

the productivity of forests that are dominated by extremely flood-tolerant species such as cypress or water tupelo (Harms et al. 1980), but these species develop morphologically and physiologically different primary root systems under periodic and continuous flooding regimes (Hook et al. 1971, Megonigal and Day 1992). The large, succulent water roots of continuously flooded trees have a higher tolerance for anaerobic respiration and an improved capacity for oxidizing the rhizosphere than roots developed under periodic flooding (Keeley 1979). Although flood-tolerant species have the ability to generate entirely different root systems when flooded as seedlings (Hook and Brown 1973, Megonigal and Day 1992), they are unlikely to entirely retain this capacity as trees (Keeley 1979). For example, Harms et al. (1980) found that water roots were "sparsely distributed" on mature cypress and tupelo trees three years after a change from periodic to continuous flooding in a water reservoir. They also observed that mortality of cypress and water tupelo increased linearly with water depth following impoundment. Thus, increased flooding frequency can impact productivity even on the wet extreme of the flooding continuum.

Temporal variation in carbon allocation

Much of the within-stand variation in aboveground NPP between 1987 and 1988 was due to changes in wood production (Fig. 2). Wood production changed by an average of $81 \pm 151\%$ (mean ± 1 SD) between 1987 and 1988 on a per-plot basis, while leaf production changed by just $9 \pm 8\%$ (Table 2). As we discussed earlier (see *Flooding stress*), it is problematic to interpret annual variations in wood growth in terms of subsidy–stress responses. If we assume that similar rates of leaf production in 1987 and 1988 indicate that the photosynthate supply was similar in the two years, then large fluctuations in wood production could have been due entirely, or at least in part, to changes in carbon allocation between stems and roots (Day and Megonigal 1993). The significant increase in wood production (202 g·m^{-2}·yr^{-1}) between 1987 and 1988 on South Carolina intermediate and dry plots coincided with an increase in April, May, and June rainfall of 14 cm, suggesting that improved soil water availability may have caused a shift in carbon allocation that favored stem growth. This relationship between spring rainfall and growth is the basis for using cypress tree rings to reconstruct past climates (Stahle and Cleaveland 1992). Shifts in carbon allocation and carbohydrate storage may help explain the temporary increase in radial growth that has been observed immediately after the impoundment of cypress (Stahle et al. 1992, Young et al. 1995).

Summary and Conclusions

We tested the subsidy–stress hypothesis by comparing the aboveground NPP of wetland and upland forests in equilibrium with their hydrologic regime (Odum 1979, Taylor et al. 1990, Odum et al. 1995). The subsidy–stress hypothesis was inadequate for predicting relative rates of aboveground NPP across hydrologic gradients in Southeastern U.S. floodplain forests. Aboveground NPP in wetland and upland forests was comparable at mean growing-season water depth (MWD) values <0 cm regardless of the extent of soil saturation and flooding (Figs. 3 and 4). Instead, our data support a hypothesis by Mitsch and Rust (1984), who suggested that the benefits of improved water and nutrient availability due to shallow groundwater tables and flooding can be offset by the physiological stresses imposed by anaerobic soils or drought.

Unusually high rates of aboveground NPP (>1400 g·m^{-2}·yr^{-1}) were observed on MB-2, PR-3, and PR-4, all of which were periodically flooded (Table 2). Plot PR-4 was the only plot with high rates of aboveground NPP in two consecutive years. High rates of aboveground NPP on these sites may reflect situations where the interaction of subsidy and stress factors happened to be optimal for the existing tree species, edaphic conditions, and site history. It is possible that periodic floods create the potential for high rates of NPP, but that negative influences on tree growth typically prevent high rates from being realized. Although the aboveground NPP of dry and intermediate plots in our study was slightly greater (90 g·m^{-2}·yr^{-1}) than our estimate for regional upland forests, it appears that unusually high rates of NPP are not typical of bottomland hardwood forests.

In accordance with the subsidy–stress hypothesis, aboveground NPP was lowest on the wet end of the hydrologic gradient. This observation is also consistent with the model proposed by Mitsch and Rust (1984), which allows subsidy–stress factors to vary in importance depending on local conditions. In cases where MWD values were >0 cm, the stress associated with an anaerobic rooting zone overcame the tree's ability to cope through morphological and physiological adaptations (Hook 1984) and flooding emerged as the single most important factor regulating NPP.

The "push–pull" models proposed by Odum (1974) and others (see Lugo 1984), and the generalized version of the subsidy–stress model proposed by Odum et al. (1979), were concerned with the responses of ecosystems to natural and anthropogenic perturbations. We found evidence that impoundment and levee construction decreased NPP compared to relatively undisturbed forests growing in similar hydrologic regimes. These sites would be expected to respond with increased NPP to other perturbations such as fertilization or moderate drainage. Thus, the subsidy–stress hypothesis may be most appropriate for predicting the responses of Southeastern U.S. floodplain forests to environmental perturbations.

Unfortunately, the practical problems of measuring root production has limited most field studies to col-

lecting aboveground growth data only. Yet the observation that wetland trees can shift carbon allocation between roots and shoots, without a corresponding change in whole-plant production, makes it difficult to interpret aboveground NPP data in terms of plant vigor or stress. Physiological measurements such as photosynthetic capacity, stomatal conductance, transpiration, nutrient-use efficiency, and carbohydrate storage provide a more objective basis for detecting stress in plants. We now need in situ investigations of the physiological responses of wetland trees to perturbation in order to evaluate and quantify anthropogenic impacts on these ecosystems.

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APPENDIX 1

Published studies of leaf and wood production in Southeastern U.S. floodplain and swamp forests. We selected sites with data sufficient to calculate mean growing-season water depth, and we excluded small ombrotrophic basin systems such as cypress domes. The site-column numbers correspond to points in Fig. 4.

Site	Production ($g \cdot m^{-2} \cdot yr^{-1}$)		MWD† (cm)	Sources
	Leaf	Wood		
1. Intensive site	231	344	100	Schlesinger 1978‡
2. Cedar	656	441	−33	Megonigal and Day 1988
				Day et al. 1988
3. Maple–gum	624	450	−43	Day et al. 1988
4. Cypress	619	557	−62	Day et al. 1988
5. Mixed hardwood	582	249	−75	Day et al. 1988
6. C1	468	812	−32	Mitsch et al. 1991§
7. C2	63	142	39	Mitsch et al. 1991§
8. H1	420	914	−55	Mitsch et al. 1991§
9. H2	136	498	50	Mitsch et al. 1991§
10. H3	253	271	92	Mitsch et al. 1991§

† Mean growing-season (March to November) water depth. Positive values indicate inundation, and negative values a subsurface groundwater table on average.

‡ Water depth from W. H. Schlesinger, *personal communication.*

§ Average of 1982 and 1983 data in Mitsch et al. (1991): Fig. 2.

APPENDIX 2

Allometric equations for calculating wood production. All equations (except for *Pinus taeda*) were developed from trees collected in bottomland hardwood and swamp forests. Equations are of the form: $M = f(D)$, where M is mass in pounds or kilograms; D is diameter at breast height (dbh) in inches or centimeters, and f is a parameterized function of D. The r^2 for regressions were always ≥ 0.98 and usually 0.99.

Species[†]	Mass	Function	dbh range (cm)
Liquidambar styraciflua[1]	M	$1.69699(D^2)^{1.27523}$	10–28
	M	$1.68032(D^2)^{1.27729}$	>28
Nyssa sylvatica[1]	M	$2.43427(D^2)^{1.16974}$	10–28
	M	$1.30697(D^2)^{1.29943}$	>28
Lireodendron tulipfera[1]	M	$1.23262(D^2)^{1.31950}$	10–28
	M	$2.24272(D^2)^{1.19469}$	>28
Quercus alba[1]	M	$2.20767(D^2)^{1.26916}$	10–28
	M	$1.56965(D^2)^{1.34028}$	>28
Quercus laurifolia[1]	M	$2.89221(D^2)^{1.21296}$	10–28
	M	$10.22597(D^2)^{0.94962}$	>28
Quercus nigra[1]	M	$3.15067(D^2)^{1.21955}$	10–28
	M	$5.99898(D^2)^{1.08527}$	>28
Other *Quercus* spp.[1]	M	$2.97559(D^2)^{1.21433}$	10–28
	M	$2.89492(D^2)^{1.22006}$	>28
Carya spp.[1]	M	$3.00150(D^2)^{1.20454}$	10–28
	M	$1.62114(D^2)^{1.33298}$	>28
Other species[1]	M	$2.54671(D^2)^{1.20138}$	10–28
	M	$1.80526(D^2)^{1.27313}$	>28
Acer rubrum[1]	M	$2.39959(D^2)^{1.20030}$	10–28
Fraxinus spp.[1]	M	$2.66900(D^2)^{1.16332}$	>10
Celtis spp.[2]	$\log_e M$	$0.566 + (1.25157 \log_e D^2)$	>10
Quercus lyrata[3]	$\log_e M$	$0.486 + (1.25829 \log_e D^2)$	>10
Quercus nuttalli[4]	M	$2.83658 D^{2.38225}$	>10
Nyssa aquatica[5]	$\log_{10} M$	$-0.919 + 2.291 \log_{10} D$	>10
Taxodium distichum[6]	$\log_{10} M$	$-0.97 + 2.34 \log_{10} D$	>10
Pinus taeda[7]	$\log_{10} M$	$1.56 + (2.59 \log D) +$	>10
		$1.57 + (2.01 \log_{10} D)$[‡]	

[†] Sources of equations and appropriate units for M and D: 1 = Clark et al. 1985, pounds and inches; 2 = Schlaegel 1984*a,* pounds and inches; 3 = Schlaegel 1984*b,* pounds and inches; 4 = Schlaegel and Wilson 1983, pounds and inches; 5 = Muzika et al. 1987, kg and cm; 6 = Scott et al. 1985, kg and cm; 7 = K. McLeod, *personal communication,* kg and cm.

[‡] The first term is boles and the second is branches.