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FLOOD PULSE DYNAMICS OF AN UNREGULATED RIVER FLOODPLAIN IN THE SOUTHEASTERN U.S. COASTAL PLAIN

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Abstract. Annual flooding in low-gradient rivers is recognized as an important subsidy between the river and its broad adjoining floodplains. Unfortunately, relatively few low-gradient rivers are unregulated and retain their natural "flood pulse" behavior in most developed regions of the world. Furthermore, attempts to quantify flood inundation dynamics of any river floodplain are scarce. We used aerial photography to delineate the degree of floodplain inundation and GIS to quantify flooded areas on the forested floodplain of a 6.3-km reach of the Ogeechee River, an unregulated sixth-order river in the southeastern USA. A regression was used to quantify the relationship between discharge and percentage floodplain inundation. Using 58 years of daily discharge data obtained from a U.S. Geological Survey gaging station, we converted daily discharge into daily percentage inundation and produced an inundation-duration curve, which describes the percentage of time that a particular inundation level is exceeded. This showed, for example, that >50% of the floodplain was inundated 15% of the time (54 d/yr) and that 100% was inundated 3.6% of the time (13 d/yr) for the average year. At 50% inundation, system width exceeded channel width by 19 times. In a relatively wet year, we showed that 50–100% of the floodplain was inundated for several months during the winter–spring. Even in a relatively dry year, >20% of the floodplain (seven times the river width) was inundated for several months. The long-term pattern over a period of 58 years (1938–1995) showed considerable fluctuation in inundation and recession occurring throughout most years, with the highest peaks found during winter and spring. The floodplain failed to reach 50% inundation in only four of 58 years. However, in six years, >50% of the floodplain was inundated for at least 30% of the time (i.e., four months of the year). Floods of 50% inundation typically had a duration of at least 30 d. Thus, although inundation may fluctuate considerably within a year, much of the floodplain can be inundated for a relatively long duration. Description of such long-term patterns is essential for understanding natural hydrodynamics of unregulated rivers, particularly as attempts are made to restore previously altered systems. The flood pulse for this forested floodplain river is less predictable and floods are of shorter duration than the large tropical rivers for which the flood pulse concept was originally conceived. Unlike tropical rivers where seasonal patterns of flooding are driven by precipitation, flooding in the Ogeechee River is primarily controlled by seasonal differences in evapotranspiration. Description of inundation dynamics is critical to understanding how plants and animals adapt to a habitat that shifts from dry to lentic to lotic, and in quantifying production of aquatic organisms and ecosystem processes.

Key words: discharge; floodplain; flood pulse; hydrologic model; hydrology; inundation; land–water interactions; long-term research; river swamp; unregulated river; wetland.

INTRODUCTION

Flooding in low-gradient rivers has become recognized as an essential ecological interaction between a river channel and its associated floodplain (Junk et al. 1989, Ward 1989*a*, *b*, Bayley 1995, Toth et al. 1995). This contrasts sharply with the historical view of flooding as a disturbance or catastrophic event, whether one is talking about ecological stress (e.g., Resh et al. 1988, Hildrew 1998) or as a hazard for humans (e.g., Newson 1994). Thus, depending on the system in question, flooding can fit into one of two ecological themes: the ecology of disturbance (e.g., Pickett and White 1985, Michener and Haeuber 1998) or the ecology of land–water subsidies (e.g., Odum et al. 1979, Ward 1989*b*, Megonigal et al. 1997), both of which have a major influence on the structure and function of ecosystems. This paper addresses the phenomenon of flooding in low-gradient floodplain rivers. If we are to understand the ecological and conservation requirements of such systems from physiological adaptations to ecosystem pathways, it is essential that ecologists first be able to characterize the hydrodynamic properties of such systems.

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The predictable advance and retreat of water from a river channel to its floodplain and the hydrological and biological interdependence between them has been called the flood pulse concept (Junk et al. 1989, Bayley 1995). In some respects it is an extension of the river continuum concept (Vannote et al. 1980) which emphasized longitudinal linkages between downstream and upstream processes, but ignored lateral connections with the floodplain (but see Cummins et al. 1983). The flood pulse concept postulates that unaltered large river systems derive the bulk of riverine animal biomass from biological production within floodplains and not from downstream transport of organic matter (Junk et al. 1989).

Besides the hypothesized interdependencies between channel and floodplain, inundation of the floodplain creates a shallow aquatic environment several times the area of the river channel itself (e.g., Cuffney and Wallace 1987, Toth et al. 1995, Hamilton et al. 1996, Junk 1997). The timing, frequency, and duration of inundation throughout this temporary aquatic environment play a major role in defining plant community composition and distribution (e.g., Clark and Benforado 1981, Lugo et al. 1990, Messina and Conner 1998), affecting ecosystem processes such as methane emissions (e.g., Pulliam 1993, Hamilton et al. 1995), providing temporary habitat for fishes that migrate from the main channel (e.g., Ross and Baker 1983, Welcomme 1985, Fernandes 1997), and in serving as habitat for a diverse assemblage of aquatic invertebrates (e.g., Wharton et al. 1981, Gladden and Smock 1990). Thus, the ecological importance of flooding is far broader than as a simple subsidy of organic matter to the main channel.

The flood pulse and all its ramifications cannot be fully understood without quantification of its most essential component: its inundation dynamics. Inundation dynamics can be defined as the temporal and spatial pattern of floodplain inundation, such as occurs continuously within a year and over many years. Inundation dynamics are dependent on both flow (i.e., discharge) dynamics and the delineation of floodplain areas, both of which have been described in considerable detail for many river systems. On the one hand, long-term discharge records, such as the excellent database developed by the U.S. Geological Survey (USGS), are available for many rivers and have been invaluable in recent years for understanding natural flow dynamics of rivers (e.g., Poff and Ward 1989, Poff 1996, Poff et al. 1997). Such understanding is particularly important in efforts to restore natural functions of regulated rivers (e.g., Dahm et al. 1995, Toth et al. 1995, Richter et al. 1996, 1997, Poff et al. 1997, Puckridge et al. 1998). On the other hand, delineation of wetlands and floodplain areas is also well described. The U.S. Army Corps of Engineers has described the frequency with which floods of a given magnitude occur for many rivers throughout the USA (e.g., the 100-yr floodplain). Delineation of the floodplain area of large tropical rivers also has been well described (e.g., Junk 1997). However, neither discharge patterns nor floodplain delineation alone can define inundation dynamics. Such hydrological behavior has been described for relatively few systems, and has yet to be incorporated into the flood pulse paradigm.

Discussions of the flood pulse concept and river–floodplain interactions have tended to focus on large and mostly tropical rivers (Junk et al. 1989, Bayley 1995, Junk 1997). Rivers in the Northern Hemisphere often are considered so altered by human intervention (Dynesius and Nilsson 1994) that one must look to tropical rivers to understand the importance of river–floodplain interactions. However, there are several medium-size unregulated rivers, particularly in the southeastern U.S. Coastal Plain (Benke 1990), that contain several characteristics associated with the flood pulse concept (e.g., Cuffney and Wallace 1987, Benke and Meyer 1988, Pulliam 1993). Such characteristics include a low gradient, broad floodplains, and frequent flooding. While many of these rivers have flow regimes altered from damming and channelization, a few have survived major interventions and continue to display natural inundation behavior.

The objective of the present paper is to quantitatively describe the flood pulse in one of these remaining unregulated Coastal Plain rivers, the Ogeechee River in eastern Georgia. Here we develop a procedure for describing the flood pulse through quantification of the river's inundation dynamics. Cuffney and Wallace (1987) developed the first predictive model of inundation on the Ogeechee floodplain based on river stage. Their model and a modified model by Pulliam (1993) were based on actual inundation data at 80 points distributed along a relatively narrow band of floodplain covering ~0.05 km^2. In contrast, we employ low-altitude aerial photography to characterize inundation at different flood stages along a considerably longer reach, and further describe long-term patterns of inundation extent, duration and frequency using a 58-yr record of discharge from a USGS gaging station. We then discuss how this quantification has broad implications regarding ecosystem function and river management, and how it relates to previous characterizations of the flood pulse concept.

STUDY SITE

The Ogeechee River is a sixth-order river located almost entirely in the Georgia Coastal Plain, with only the uppermost 5% in the Piedmont Plateau. At our study site (32°09′ N, 81°25′ W) downstream from Eden, Georgia, the river drains an area of 6861 km^2, has a low gradient (20 cm/km), and is 63 km from its mouth near Savannah (Fig. 1). The river meanders through a floodplain swamp (or bottomland forest) characterized by swamp blackgum (*Nyssa sylvatica* var. *biflora*) and bald cypress (*Taxodium distichum*) at the

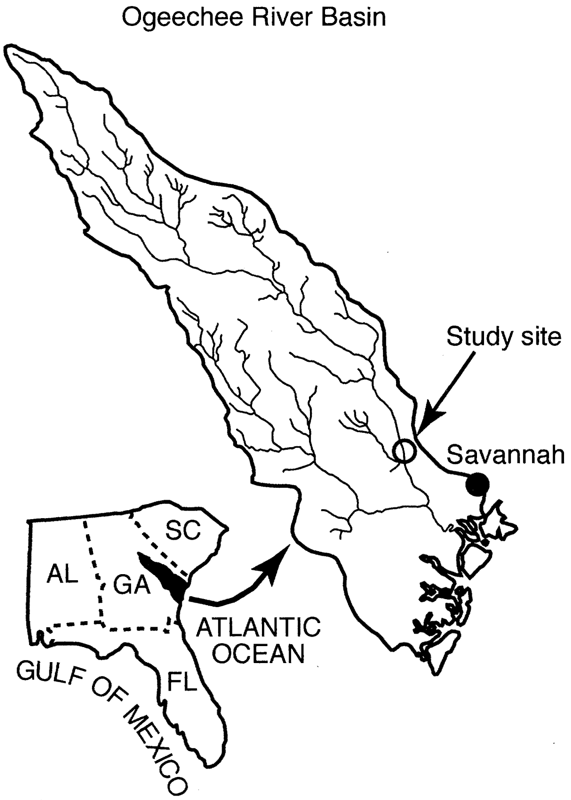

FIG. 1. Location of the study site on the Ogeechee River, Georgia, USA.

lowest elevations (for summary of major trees and shrubs see Pulliam [1993]). The edge of the river swamp is relatively well defined by an upland area that has frequently been converted to agriculture and pine forest. Upstream, the floodplain has a total area ~150 km^2 (Pulliam 1993). In our 6.3-km study reach, channel width averaged 33 m and floodplain width was 1.2 km, or 37 times the width of the channel. Mean river discharge was 67 m^3/s based on a 58-yr record at a USGS gaging station located at Eden. Water temperatures typically ranged from 8°C in winter to 30°C in summer, with mean temperature of 19°C.

The Ogeechee River has been the subject of ecosystem research for most of a decade. Studies have included analysis of channel and floodplain organic matter dynamics (e.g., Cuffney and Wallace 1987, Meyer et al. 1997), invertebrate production (e.g., Benke and Parsons 1990, Benke 1998), trophic interactions between dissolved organic matter, bacteria, and invertebrates (e.g., Meyer et al. 1987, Edwards and Meyer 1990), ecosystem metabolism (Edwards and Meyer 1987, Meyer and Edwards 1990), and river–floodplain interactions (e.g., Roberts et al. 1985, Cuffney 1988).

METHODS

Aerial photographs were taken with a Pentax Super ME 35 mm single-lens reflex camera with a 28 mm lens held in a camera port of a Cessna 172 aircraft so that the plane remained parallel to the land surface. Black-and-white infrared film (Kodak High Speed Infrared) was used with a Wratten No. 25 filter. Flights were taken on four clear days at different river stages (0.5 to 2.7 m gage height) to photographically record the extent of flooding. All flights were taken during winter months (1984–1985) when there was minimum leaf cover. The plane was flown at an altitude of 1500 m (±50 m) and ground speed of 40 m/s (±4 m/s). A succession of photographs (usually 12) was taken over a 6.3-km reach of river (from the U.S. Route 80 bridge at Eden to the Interstate Route 16 bridge) where ecological studies were being conducted. Photographs included river channel and floodplain and overlapped each other by ~33%. A fifth level of inundation (2.9 m stage) was obtained from a false color infrared print from a NASA (National Aeronautics and Space Administration) high altitude flight in February 1981. A final level of inundation (100%) was obtained from field observations on dates when the highest portions of the floodplain were flooded.

Boundaries of wet and dry areas for each date were manually traced from photographs for the 6.3-km reach of river. All tracings of separate dates were then combined onto a single map. This map was then digitized using ARC-INFO software, and planer surface areas between lines of inundation determined.

Percentage of inundation of the defined river–floodplain map was regressed against river discharge obtained from the USGS gaging station. Given the inundation–discharge relationship, we then converted 58 yr of daily discharge values (21 186 d from 1938 to 1995) obtained from the USGS Internet website[5] to daily percentage inundation. Inundation level also was converted to relative system width; i.e., the number of times the inundated river–floodplain exceeded the channel width. The model assumes an instantaneous response of inundation to discharge. On the declining arm of the hydrograph, however, actual inundation will not fall as rapidly as that predicted from the decline in discharge, particularly if some of the water is retained in residual pools. Thus, the model is conservative in predicting inundation levels, and the actual inundation patterns should be smoother than patterns predicted by the model.

Duration curves were determined from daily discharge, inundation, and relative system width. The actual number of days (out of 21 186 d) that the river exceeded a given discharge was determined and converted to percentage of time a discharge was equaled or exceeded. Discharge was then plotted against percentage of time discharge was equaled or exceeded to obtain a discharge duration curve (e.g., Gordon et al. 1992). The same procedure was employed to obtain an

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[5] URL = ⟨http://water.usgs.gov⟩

inundation–duration curve, (substituting inundation for discharge), and a system-width duration curve.

The statistical relationship that we use to estimate floodplain inundation is a relatively simple type of predictive model, but one well-suited for our purposes. Other, more sophisticated, physically based models are frequently used to predict river flooding, and particularly to predict sediment transport and over-bank deposition (e.g., Simm et al. 1997, Nicholas and Walling 1998). Modeling efforts often utilize digital elevation models (DEMs), which represent floodplain topography, as an essential component of the model. While high resolution DEM data are often desirable in predictive models, such data are logistically difficult and expensive to obtain at a meaningful vertical resolution in environments such as the Ogeechee River, where terrain is complex with modest topographic relief. DEM data are not available for the Ogeechee River. The aerial photograph-based method we employed is substantially less expensive than that associated with acquisition of DEM data, and is conceptually easy to transfer to other sites. For the limited purpose of inundation prediction, our method appears appropriate.

In order to examine the relationship between precipitation and discharge, we obtained daily precipitation and air temperature data for Millen, Georgia, from 1940 to 1995 (56 yr) from the University of Georgia State Climate Office website.[6] Millen is located about halfway between the headwaters of the Ogeechee basin and our study site (~90 km upstream of study site). Mean monthly precipitation was compared to mean monthly discharge calculated with data obtained from the USGS website for Eden for these same years. Mean monthly evapotranspiration for the Ogeechee basin was calculated as precipitation minus runoff, and does not account for recharge or discharge from groundwater storage.

RESULTS

The floodplain of the 6.3-km reach of the Ogeechee River covered a surface area of ~7.5 km^2 and showed considerable topographic complexity, based upon inundation patterns observed at different discharge levels (Fig. 2, Table 1). Numerous sloughs and small channels extend deep into the floodplain. In some locations, such as where studies were done along transects by Cuffney (1988) and Pulliam (1993), one side of the river floods more frequently than the other (i.e., near Interstate 16 bridge; Fig. 2).

The percentage of floodplain inundated (arcsine transformed) was strongly related to river discharge (r^2 = 0.98; Fig. 3). The floodplain was completely inundated when river discharge reached 255 m^3/s. However, even when discharge was very low, water could be found in sloughs and ponds (Fig. 2).

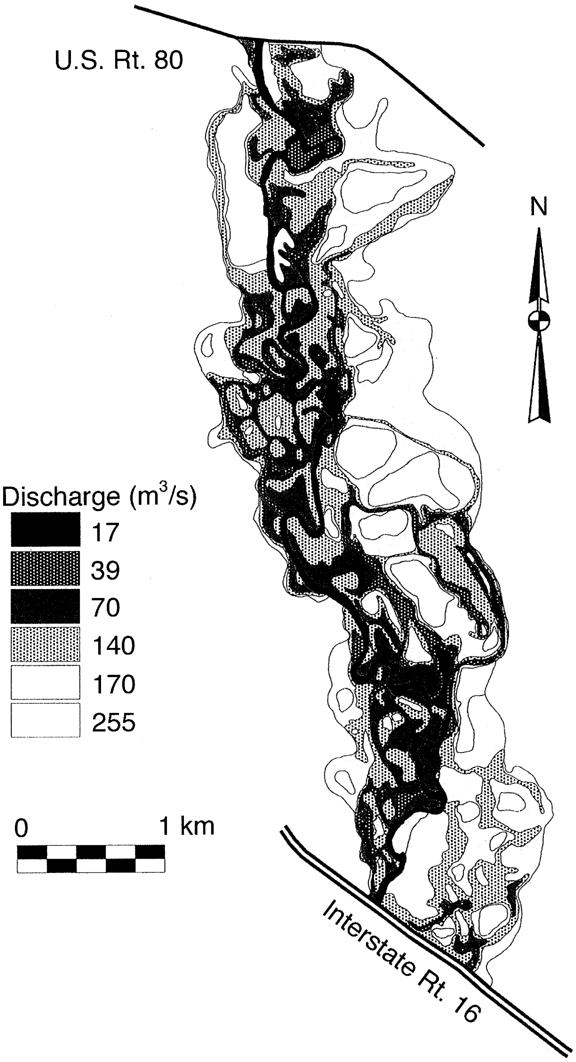

FIG. 2. Floodplain inundation levels for a 6.3-km reach of the Ogeechee River floodplain. Inundation levels correspond to discharges measured at the USGS gaging station at Eden, Georgia, USA (see Table 1). Blackened area for 17 m^3/s includes the small portion of the floodplain inundated at this discharge plus the channel.

The discharge–inundation relationship was used to predict floodplain inundation over a 58-yr period (Fig. 4). Such predictions assumed that this relationship existed during the entire period. Given that river geomorphology changes through time, the relationship is going to vary over time. The most conservative interpretation would be that inundation predicted from discharge for any given year is that which would have occurred if geomorphology had been constant. We doubt that the relationships would have changed so much as to have significantly affected our predicted inundation values.

Comparison of our predicted inundation levels (Fig. 4) with our own field observations and those of Pulliam (1993) suggests that at low discharge the degree of

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[6] URL = ⟨http://www.bae.uga.edu/climate⟩

TABLE 1. Discharge, cumulative area of floodplain inundated, percentage of floodplain inundated, number of days per year cumulative area is inundated, and relative system width at various river stages (mean gage height) along a 6.3-km reach of the Ogeechee River.

Mean gage height (m)	Discharge (m^3/s)	Cumulative area inundated (km^2)	Percentage inundated	Days per year inundated	Relative system width†
0.52	17	0.10	1.4	291	1.5
1.31	39	0.46	6.2	183	3.2
2.01	70	1.73	23.3	114	9.4
2.74	148	3.61	48.4	43	18.3
2.89	170	6.14	82.2	33	30.3
3.20	255	7.46	100.0	13	36.9

Notes: Discharge and river stage are from the USGS gaging station at Eden, Georgia. Areas inundated are from digitized inundation maps created from aerial photographs (Fig. 2).

† Relative system width = the number of times the inundated river–floodplain exceeded the channel width.

inundation is often underestimated. Pulliam (1993) found that his modification of the Cuffney and Wallace (1987) model was inaccurate when inundation was predicted below the 2.2-m stage because local rainfall and groundwater inputs accumulated in pools without direct input from the river (also see Williams 1998). Our model is subject to the same limitations for a stage as high as 2.2 m, which predicts an inundation of 25%. Thus, the horizontal line at an inundation of 25% on Fig. 4 indicates that inundation values predicted below this level are often underestimated. This inaccuracy at low inundation levels, however, has little effect on our interpretations and conclusions.

The long-term record of inundation showed that extensive flooding occurred almost every year and that there was considerable predictability in seasonal patterns. Floods of >50% inundation occurred in all but four years (1945, 1950, 1968, 1988) during the 58-yr period. In six years, >50% of the floodplain was inundated for at least 30% of the time (i.e., four mo of the year). The greatest inundation was in 1964, when >50% of the floodplain was inundated for more than half the year.

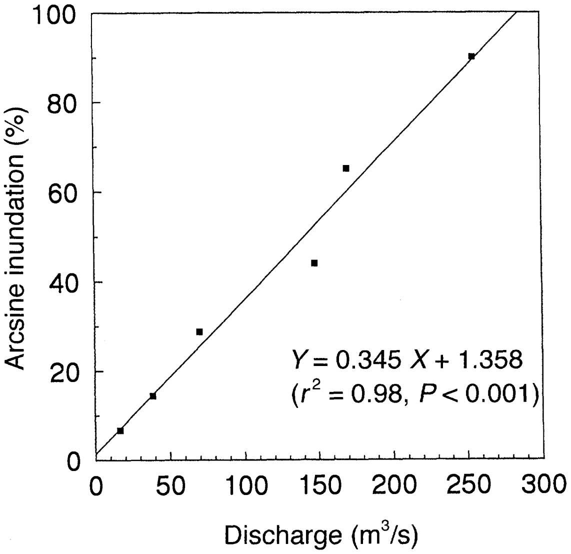

FIG. 3. Linear regression of percentage floodplain inundation (arcsine transformed) for a 6.3-km reach of the Ogeechee River vs. discharge measured at the USGS gaging station at Eden, Georgia, USA.

The highest percentage of inundation usually occurred early in each calendar year with substantial declines for the rest of the year (Fig. 4). Flooding sometimes occurred later in the year, often due to tropical storms, but only rarely were floods as great as those during the winter–spring. The year 1964 represents the most obvious exception over the 58-yr period. Inundation was typically high early in the year, followed by a decline in early summer, but this was followed by a series of high flood events throughout summer and fall. The typical winter–spring flooding in 1965 resulted in almost continuously high flooding (>50% inundation) for most of 18 straight months. The difference between winter–spring and summer–fall flooding is also illustrated by examining mean duration of floods. Twenty of 58 years had floods of >50% inundation that exceeded 30 d in duration (i.e., number of consecutive days >50% inundation). In some years, more than one flood of 30-d duration occurred. However, in only one of 20 years did a 30-d flood (>50% inundation) occur during the summer–fall period (21 June–20 December), with the rest occurring during the winter–spring (21 December–2 June).

Comparison of the years 1982 and 1983 helps illustrate the relationships between daily discharge, percentage inundation, and relative system width for two distinctly different years (Fig. 5). Mean discharge for 1982 (52 m^3/s) was lower than the long-term mean discharge of 67 m^3/s, representing a relatively dry year (Fig. 5A). Only two peaks of discharge during winter exceeded 100 m^3/s for ~2-wk duration. Even with this relatively dry year, however, at least 20% of the floodplain (>7 times the river width) was inundated for several months of the year, including two small floods in the summer months (Fig. 5B, C). Mean discharge for 1983 (83 m^3/s) was higher than the long-term mean discharge, representing a relatively wet year (Fig. 5A). In contrast to 1982, high fractions of the floodplain (50–100%) were inundated, and relative system width

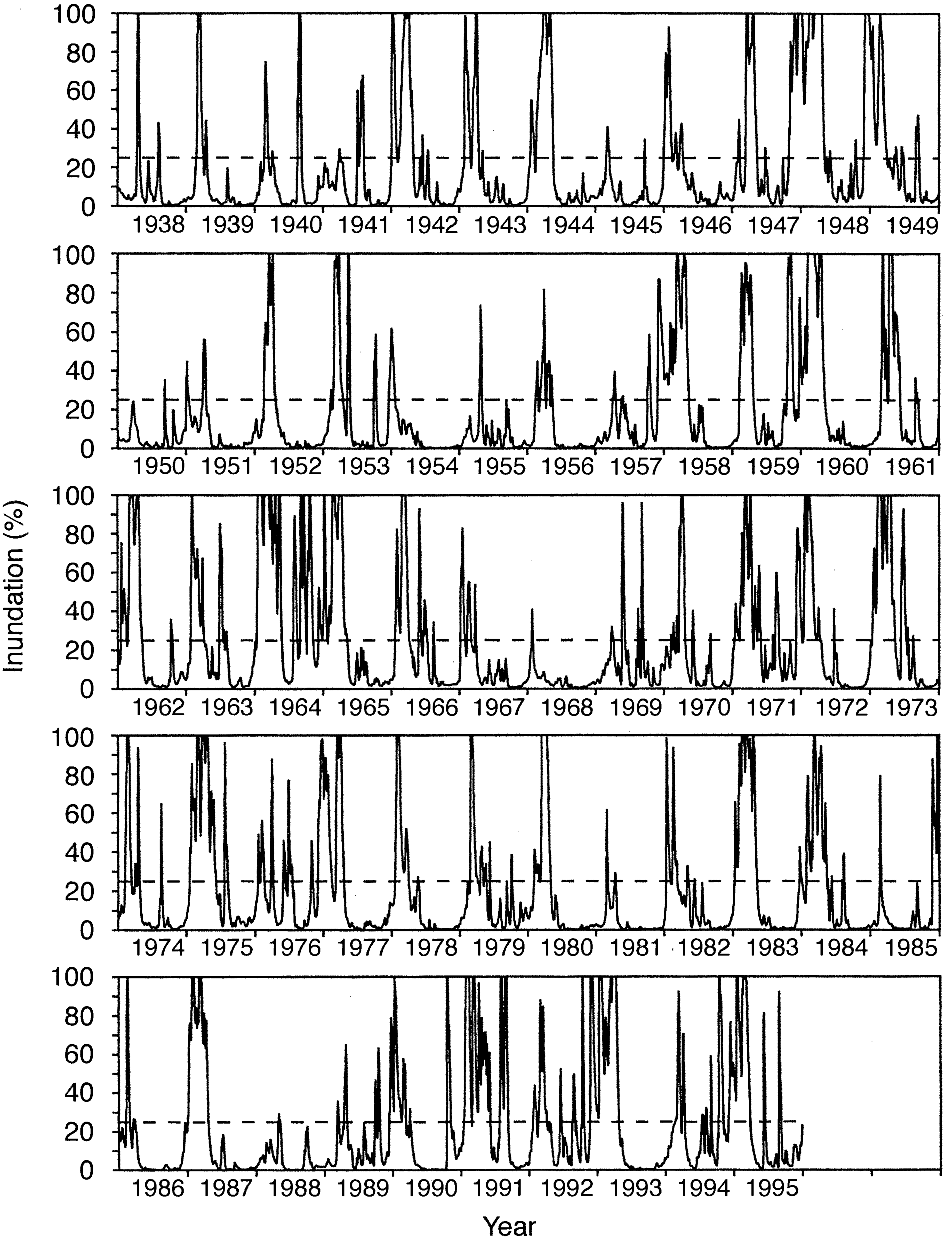

FIG. 4. Long-term pattern of floodplain inundation predicted from the discharge–inundation relationship shown in Fig. 3, and 58 calendar years (1938–1995) of daily discharge data obtained from USGS gaging station at Eden, Georgia, USA. The dashed lines represent the 25% inundation level, below which the predictive model is less reliable.

exceeded 25 for extensive periods of time during the winter (Fig. 5B, C). However, both discharge and floodplain inundation throughout the summer were continuously low.

The discharge–duration curve (Fig. 6A), based on the 58-yr record of flooding (Fig. 4), had a typical shape showing a continuous decline of discharge with increasing frequency of occurrence. For example, a discharge of 123 m^3/s was equaled or exceeded 15% of the time, but a discharge of 38 m^3/s was equaled or exceeded 50% of the time. Because of the linear relationship between discharge and percentage inundation (arcsine transformed), the inundation–duration curve had a similar shape to the discharge–duration curve, and showed that substantial fractions of floodplain were inundated for extensive periods of time (Fig. 6B). For example, >50% of the floodplain was inundated 15% of the time (i.e., 54 d/yr), and 100% was inundated 3.6% (13 d/yr; Table 1). Similarly, relative width of the river–floodplain system (number of times river–floodplain width exceeded channel width) was high for several weeks of the year (Fig. 6C, Table 1).

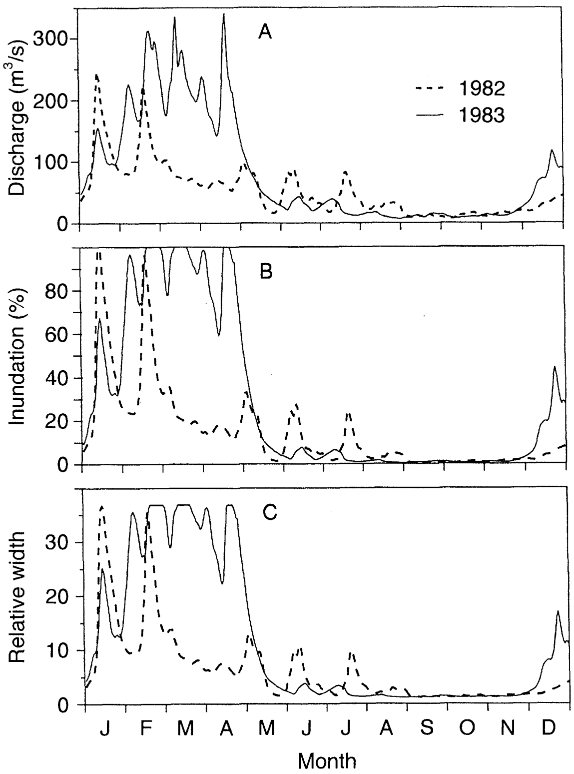

FIG. 5. Examples of the annual pattern of (A) discharge, (B) percentage floodplain inundation, and (C) relative system width for a 6.3-km reach of the Ogeechee River floodplain. Mean discharge was lower than average in 1982 (mean = 52 m³/s), and higher than average in 1983 (83 m³/s).

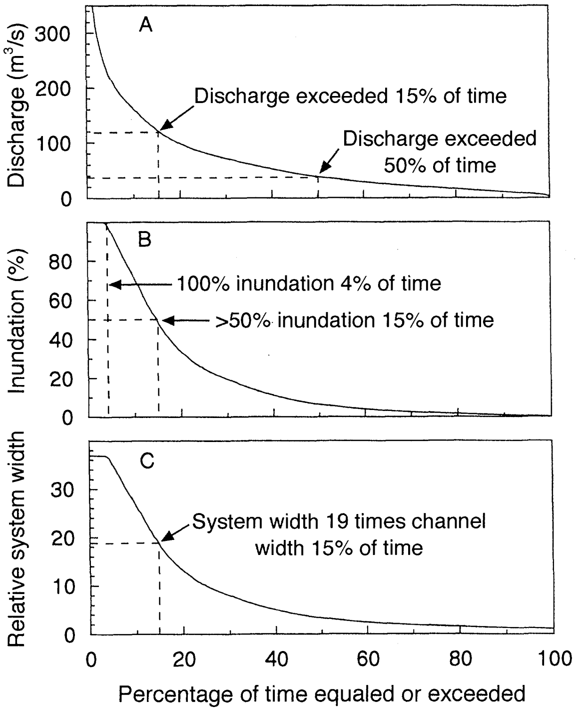

FIG. 6. Duration curves (percentage of time at which value equaled or exceeded) for (A) discharge, (B) percentage floodplain inundation, and (C) relative system width. All curves are based on 58 years of daily discharge data (1938–1995) from the USGS gaging station at Eden, Georgia, USA. Curves for inundation and system width are based on regression in Fig. 3. Relative system width is the number of times mean width of inundated area exceeds channel width (33 m).

The relative width was 19 times the channel width at 50% inundation (15% of the time) and 37 times the channel width at 100% inundation.

Comparison of mean monthly discharge (expressed as centimeters of runoff) with mean monthly precipitation for 56 yr (1940–1995) showed a surprisingly poor relationship between these two variables (Fig. 7). While mean monthly runoff was much higher in January–April than in June–September, the three highest months of precipitation were June, July, and August. Only in October and November were both discharge and precipitation consistently low. Mean monthly evapotranspiration (precipitation − runoff) closely tracked mean monthly air temperature.

DISCUSSION

A major point of this paper is that description of the *dynamics* of floodplain inundation, not simply patterns of main-channel stage or discharge, is necessary to quantify the flood pulse concept. It is water on floodplain surfaces, not discharge per se, that creates new aquatic habitat, shapes geomorphology, and provides a fluid medium for exchange of living and nonliving matter. Furthermore, we have shown that natural floodplain inundation is not limited to large tropical rivers,

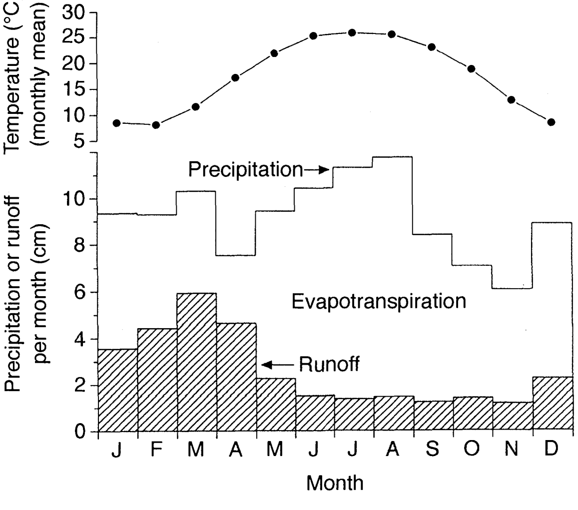

FIG. 7. Monthly means for air temperature, precipitation, runoff, and evapotranspiration in the Ogeechee River basin calculated from 56 years of daily values (1940–1995). Daily temperature and precipitation were for Millen, Georgia, and discharge was from Eden, Georgia, USA. Evapotranspiration was calculated as precipitation minus runoff and does not account for potential monthly differences in groundwater storage.

but represents an important phenomenon in a medium-sized subtropical river of North America as well. Unfortunately, rivers with such characteristics have become quite scarce. The Ogeechee River is one of relatively few unregulated rivers remaining in the southeastern U.S. Coastal Plain (or anywhere in the contiguous 48 United States; Benke 1990). Information on natural inundation patterns is thus all the more essential for understanding the hydrological requirements necessary to maintain natural ecological functioning of river–floodplain systems; e.g., for describing physiological requirements of wetland plants, quantifying habitat for aquatic animals, and measuring ecosystem processes that are influenced by flooding. Furthermore, our understanding of variability among riverine ecosystems from different regions will depend on their inundation dynamics, as well as other aspects of their natural flow regime (e.g., Poff and Ward 1989, Poff et al. 1997, Richter et al. 1997). Such understanding must be linked with efforts to restore natural discharge and flooding regimes in regulated rivers (e.g., Dahm et al. 1995, Toth et al. 1995, Richter et al. 1996).

Inundation of the Ogeechee River floodplain

We have shown that inundation of the Ogeechee River floodplain is a natural event of high frequency that greatly expands the effective river width in virtually every year. Some years with high rainfall may have continuous inundation for several consecutive months (e.g., Figs. 4 and 5B). In other years, droughts may result in relatively small amounts of inundation, particularly during the summer. In almost all years, however, substantial inundation occurs for at least one month in winter–spring due to over-bank flooding. Additional inundation of up to 25% of the floodplain may occur by filling of pools from local rainfall and groundwater inputs (Pulliam 1993, Williams 1998; A. C. Benke, *personal observations*). Thus, inundation of floodplains associated with medium-sized rivers in the southeastern U.S. Coastal Plain is a common event of relatively long duration.

The results of our model are difficult to compare with previous Ogeechee River inundation models of Cuffney and Wallace (1987) and Pulliam (1993). They developed separate predictions for the high-elevation east floodplain and the low-elevation west floodplain and did not develop weighted values for the extended floodplain as we did. Also, we would not expect their results to exactly match our own because our estimates were based on a much larger area (7.5 km^2) and incorporate additional areas of higher elevation. We therefore predicted 100% inundation at a somewhat higher stage (3.2 m) than they did (2.8 m). Thus, while their patterns of inundation coincide well with ours for comparable years, their inundation percentages appear to be somewhat higher (Fig. 8 in Pulliam 1993).

It is important to recognize that inundation of the Ogeechee River floodplain is not simply a gradual increase in the amount of floodplain soils that are covered by water. As the river rises, it inundates low-lying portions of the floodplain (<2 m stage) by backing into sloughs and connecting with residual pools. Above the 2-m stage (~23% inundation), flow becomes measurable in the floodplain and carries ~13% of total river discharge (Roberts et al. 1985). At the 3.1-m stage (almost 100% inundation), flow through the floodplain increases to ~51% with a mean velocity of 0.22 m/s (Roberts et al. 1985). As the river falls, velocity and flow decline, and some water is retained in residual pools. Short-term fluctuations in inundation (e.g., Fig. 5B) and current velocity mean that habitat characteristics, organic matter exchanges, and the ability of fish to migrate between floodplain and river channel often are in a state of change. Because of this variability in lentic and lotic conditions within a topographically complex floodplain (Fig. 2), it would be inappropriate to describe the inundation as a moving littoral zone, as has been described for tropical systems (see Fig. 2 in Junk et al. 1989).

Inundation in other systems

Comparable studies of river–floodplain inundation are scarce on a global scale, with few attempts at cross-system comparisons or to incorporate such phenomena into the flood pulse concept. However, a few recent studies are noteworthy. Hamilton et al. (1996) used remote sensing (Nimbus-7 satellite) to describe inundation patterns in the large Pantanal wetland (Paraguay River) of South America, which could reach a total inundation area of 110 000 km^2 (vs. 150 km^2 in the Ogeechee). The Paraguay River has an even lower gradient than the Ogeechee (2.5 cm/km vs. 20 cm/km), has 19 times (1260 m^3/s) the average discharge, and except for gallery forest along the rivers, aquatic and semiaquatic plants primarily characterize the floodplain during the rainy season. Using monthly estimates of inundation (in contrast to our daily estimates), they developed a correlation between Paraguay River stage and inundation area and were able to reconstruct regional inundation patterns over the past 95 years. Hamilton et al. (1996) found highly regular seasonal inundation peaks, although the predicted amplitude of the floods showed considerable variability (~10% to 100% inundation) when viewed over the entire 95-yr period. Sippel et al. (1998) used the same approach for the Amazon River floodplain over a 94-yr period, and also found highly regular seasonal inundation peaks, but the amplitude of peaks was less variable between years (~50% to 100% inundation). Such predictable seasonal variation is consistent with the original description of the flood pulse concept (Junk et al. 1989), although amplitude can vary considerably between years. The smoothness of the inundation patterns in the Pantanal and Amazon is apparently due to their extremely large size, but it also may be due in part to the use of monthly inundation values, in contrast to our daily predictions.

Toth et al. (1995) used floodplain elevation data and historical stage data to predict the floodplain inundation that occurred in the Kissimmee River system, Florida, prior to channelization in the 1960s. This river, which is similar in discharge (63 m^3/s) to the Ogeechee River (67 m^3/s), had a wider floodplain (1.5–3.0 km vs. 1.2 km), a lower slope (6.6 cm/km vs. 20 cm/km), and was characterized by a broadleaf marsh rather than a forested floodplain. It also was undoubtedly unique among North American rivers in having an extremely high inundation frequency. At the wettest of two sites, 100% of the floodplain was inundated 35% of the time and 39% of the floodplain was inundated 86% of the time (Toth et al. 1995).

Gladden and Smock (1990) approximated floodplain inundation for a single year in the forested floodplains of two small (2.5–3.0 m wide) Coastal Plain streams in Virginia. Although no long-term predictions were made, they found that one of the floodplains was continuously inundated at >75% coverage for >9 mo, while the other one was only inundated at >20% for ~6 mo. Localized differences in geomorphology probably prevent a general model from being developed in these small streams.

In all four cases (Pantanal, Amazon River, Kissimmee River, and Virginia stream), floodplain inundation occurred for a longer duration than we found in the Ogeechee River floodplain. Both the Pantanal and the Kissimmee are high inundation systems in which the floodplain flora is composed of small aquatic plants rather than forests. The Kissimmee system is currently undergoing a major restoration after being largely destroyed by channelization and drainage, while the Pantanal may soon experience a similar fate due to a large navigation project on the Paraguay River (Hamilton et al. 1996). Although duration of inundation for the Ogeechee floodplain is shorter than that for the Pantanal and the historic Kissimmee floodplain, its characterization should be of considerable use for ecological understanding and management of other forested Coastal Plain streams in the southeastern United States.

Flood pulse of the Ogeechee River

Our inundation model and climatological data from the Ogeechee River provide the opportunity to make a direct comparison with the flood pulse of tropical rivers (Junk et al. 1989, Bayley 1995, Junk 1997). As mentioned above, the Ogeechee River and other rivers of the southeastern U.S. Coastal Plain possess physical characteristics similar to those of large tropical flood-pulse rivers, even though they are much smaller; e.g., low gradient, broad floodplains, and frequent floods. The inundation pattern that we have described for the Ogeechee River also is clearly reminiscent of the flood pulse originally described by Junk et al. (1989). Flooding occurs almost every year in the winter–spring, but with an amplitude and duration that are more variable than observed during the rainy season in large tropical rivers. A notable difference is the unpredictable occurrence of short-duration floods during summer months in the Ogeechee.

Although the flood pulse in the Ogeechee River is superficially similar to those observed in large tropical rivers, comparison of climatological data shows that factors producing floods are distinctly different. Precipitation in the tropics is strongly seasonal, ranging from ~4 cm/mo in the dry season to ~30 cm/mo in the wet season in central Amazonia, and is clearly the major factor driving the seasonal flood pulse of the Amazon River (Irion et al. 1997). Air temperature, on the other hand, varies little over the year, with monthly means ranging from only 26°C to <28°C.

In contrast, the seasonal pattern of runoff (and flooding) in the Ogeechee basin appears to be influenced primarily by seasonal variation in temperature and evapotranspiration, not precipitation. Although seasonal variation in evapotranspiration is only slightly greater in the Ogeechee (<3 to >10 cm/mo) than in the tropics (~5–9 cm/mo; Irion et al. 1997), it is sufficient to override the relatively small seasonal differences in precipitation (i.e., 9–10 cm/mo in winter vs. 11–12 cm/mo in summer; Fig. 7). The effect of evapotranspiration is most obvious in June–August when precipitation is at its highest, yet runoff is low. If precipitation is sufficiently high in summer, it can override evapotranspiration losses and produce summer flooding, but such events usually are of lower amplitude and shorter duration than winter floods (Fig. 4).

It is possible that seasonal differences in recharge and discharge from groundwater storage may play a role in the Ogeechee patterns because storage is ignored in our calculation of evapotranspiration (as precipitation − runoff). For example, the apparently high values for evapotranspiration in December–January may be partly the result of recharge since runoff is lower in these months than in February–April. It also is possible that seasonal differences in evaporation are enhanced by water extraction and irrigation practices in the basin. However, we believe that natural seasonal differences in evapotranspiration are primarily responsible for flooding patterns. Records for such patterns in the basin have been observed from 1900 to present.

Our comparison between the Ogeechee River and tropical rivers demonstrates that regional climate determines which hydrological factor dominates seasonal differences in discharge and flooding. Rainfall, spring snowmelt, and groundwater exchange have received considerable attention in characterizing discharge patterns (e.g., Poff and Ward 1989, Poff 1996). However, evapotranspiration appears critical to the timing of the flood pulse in the Ogeechee basin, and is likely to be important over much of the southeastern USA (Muller and Grymes 1998).

Junk et al. (1989) considered predictability and duration to be critical features of the flood pulse concept because few organisms are able to take advantage of unpredictable floods of short duration, and biological activity would be limited. Flooding is highly predictable and monomodal in most large tropical rivers, but unpredictable and polymodal in smaller rivers (Junk 1997). Clearly, the flood pulse of the Ogeechee is less predictable and occurs for shorter duration than most large tropical rivers (compare Figs. 4, 5, and 7 with patterns described by Hamilton et al. [1996] and Sippel et al. [1998]). Consideration of long-term averages would suggest that the Ogeechee is monomodal (Fig. 7), but examination of individual years shows considerable fluctuation within any single year (Figs. 4 and 5B). The much smaller size of the Ogeechee seems primarily responsible for the lack of smoothness in inundation patterns in comparison to the large tropical rivers for which the flood pulse was envisioned. However, it would be interesting to know whether a tropical river comparable in size to the Ogeechee was similar in terms of predictability and flood duration.

Importance of flooding to organisms and ecosystems

The qualitative importance of flooding to floodplain organisms and ecosystem processes is well recognized (Junk et al. 1989, Bayley 1995, Molles et al. 1998). However, quantification of the flood pulse is necessary for defining aquatic habitats for animals and examining how inundation patterns affect plant distributions and ecosystem processes. For example, the inundation model provides temporal and spatial estimates of habitat available to fishes migrating from the main channel for foraging and spawning (Ross and Baker 1983, Welcomme 1985, Fernandes 1997). The model also can be useful for studying relationships between flooding, spatial distribution of plants, and their physiological adaptations in bottomland forests (e.g., Clark and Benforado 1981, Lugo et al. 1990, Messina and Conner 1998). Application of an earlier inundation model of the Ogeechee River already has proved valuable in studying litter decomposition (Cuffney and Wallace 1987) and gas emissions from floodplain soils (Pulliam 1993).

The inundation model also makes it possible to examine the relative importance of floodplain invertebrates within the context of an entire river system. Stream ecologists historically have viewed the benthic zone of the main channel as the primary habitat for aquatic invertebrates. Previous studies of Coastal Plain rivers, including the Ogeechee, have expanded this view to include submerged snags, which support a taxonomically rich and productive invertebrate assemblage (e.g., Cudney and Wallace 1980, Benke et al. 1984, Benke and Wallace 1997). However, aquatic invertebrate populations also are abundant in the Ogeechee floodplain (Cuffney and Wallace 1987, Anderson 1995; A. C. Benke, *unpublished data*) in spite of the lower predictability and duration of floods envisioned by Junk et al. (1989). These floodplain invertebrates are of potentially great importance because floodplain areas are many times that of the main channel. Even though habitats within the floodplain undergo considerable fluctuation (i.e., water-logged soil to standing water to flowing water), many organisms are able to persist with either short life-spans, high vagility, or desiccation resistance. At moderate inundation (e.g., 25%) the invertebrate assemblage is characterized by lentic taxa, but lotic taxa invade as discharge and flow through the floodplain increases (A. C. Benke, *personal observations*). An inundation model makes direct comparisons between main channel and floodplain assemblages possible. For example, Smock et al. (1992) found that 67–95% of invertebrate production occurred in the floodplain rather than the channel of two forested streams much smaller than the Ogeechee.

CONCLUSIONS

An important theme of modern ecology is that knowledge of long-term ecological dynamics is essential for understanding the natural properties of ecosystems. The 58 years of discharge data available from the United States Geological Survey was invaluable for quantifying long-term inundation patterns on the Ogeechee River. Such information can be used in correlating inundation with both structural and functional aspects of river–floodplain ecosystems, comparing flood pulse dynamics among different rivers, and in providing a benchmark for river restoration. Understanding the natural inundation regime of river–floodplain systems provides a key for ensuring the long-term integrity of these systems, and is critical if we are to know how restored rivers are supposed to behave hydrologically. It is also important to understand how climatological variables in different regions of the world interact to produce seasonal patterns of discharge and flooding.

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