The Flood Pulse Concept in River–Floodplain Systems

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Abstract

The principal driving force responsible for the existence, productivity, and interactions of the major biota in river–floodplain systems is the flood pulse. A spectrum of geomorphological and hydrological conditions produces flood pulses, which range from unpredictable to predictable and from short to long duration. Short and generally unpredictable pulses occur in low-order streams or heavily modified systems with floodplains that have been levelled and drained by man. Because low-order stream pulses are brief and unpredictable, organisms have limited adaptations for directly utilizing the aquatic/terrestrial transition zone (ATTZ), although aquatic organisms benefit indirectly from transport of resources into the lake system. Conversely, a predictable pulse of long duration engenders organismic adaptations and strategies that efficiently utilize attributes of the ATTZ. This pulse is coupled with a dynamic edge effect, which extends a “moving lateral” throughout the ATTZ. The moving lateral provides prolonged stagnation and allows rapid recycling of organic matter and nutrients, thereby resulting in high productivity. Primary production associated with the ATTZ is much higher than that of permanent water bodies in unmodified systems. Fish yields and production are strongly related to the extent of accessible floodplains, whereas the main river is used as a migration route by most of the fishes.

In temperate regions, light and/or temperature variations may modify the effects of the pulse, and anthropogenic influences on the flood pulse or floodplains frequently limit production. A local floodplain, however, can develop by sedimentation in a river reach modified by a low-head dam. Bioflocs of slowly flowing rivers turn into floodplain habitats, becoming separated from the main channel by levees.

The flood pulse is a “moving process” and is distinct from concepts that emphasize the continuous processes in flowing water environments such as the river continuum concept. Floodplains are distinct because they do not depend on upstream processing efficiencies of organic matter, although their nutrient pool is influenced by periodic lateral exchange of water and sediments with the main channel. The pulse concept is distinct because the position of a floodplain within the river network is not a primary determinant of the processes that occur. The pulse concept requires an approach other than the traditional limnological paradigms used in lotic or lentic systems.

river/floodplain/ecosystem theory

Résumé

Les inondations occasionnées par la crue des eaux dans les systèmes courts d’eau-prairies inondables constituent le principal facteur qui détermine la nature et la productivité du biotope dominant de même que les interactions existant entre les organismes biotiques et ceux-ci et leur environnement. Ces crues, passagères, dont la durée et la prévisibilité sont variables, sont produites par un ensemble de facteurs géomorphologiques et hydrologiques. Les crues de courte durée, généralement imprévisibles, surviennent dans les réseaux hydrographiques peu variés ou dans les rivières qui ont connu des transformations importantes suite à l’endiguement et au drainage des plaines inondables par l’homme. Comme les crues surviennent dans les réseaux hydrographiques d’ordre inférieur, elles sont brèves et imprévisibles, les adaptations des organismes sont moins limitées et qui a lait à l’exploitation des ressources de la zone de transition existant entre le milieu aquatique et le milieu terrestre (ATTZ), bien que les organismes aquatiques profitent indirectement des détritus transportés dans le solus loco. Inversement, une crue prévisible de longue durée favorise le développement d’adaptations et de stratégies qui permettent aux organismes d’exploiter efficacement l’ATTZ. Une telle crue s’accompagne d’un effet de bordure dynamique qui fait en sorte que l’ATTZ devient un “limite mobile”. Dans ces circonstances, il n’y a pas de stagnation prolongée et le recyclage de la matière organique et des substances nutritives se fait rapidement, ce qui donne lieu à une productivité élevée. La production primaire dans l’ATTZ est beaucoup plus élevée que celle des masses d’eau permanente dans les réseaux hydrographiques non modifiés. Le rendement et la production de poissons sont également nés à l’endiguement de la plaine inondable, tandis que le cours normal de la rivière est utilisé comme voie de migration par la plupart des poissons.
production of poisons are detrimental to the stability of the plant community, and that the size of the
environnent and the temperature can modify the effects of the plant on the system. In the

Dans les rivières temporaires, les variations de l'implantation et de la température peuvent modifier
les effets de la végétation et de la température sur les plantes anodines. L'effet de la température
et de la végétation sur l'équilibre des systèmes hydrologiques est important. En effet, les

Les eaux des cours d'eau modifiées par un niveau de base élevé. Aussi, les rivières des cours d'eau à faible
débit se transformeraient en étangs anodines suite à la formation de levées alluviales qui se forment au

La chlorophylle des plantes se transformant par le cours d'eau. Cette situation est différente des cas
précédemment mentionnés car elles sont même plus favorables pour la transformation de la matière organique
en atmosphère et de la décomposition n'est pas altérée dans les eaux eutrophiques avec le canal principal. Le
Le canal est un phénomène particulier par rapport à la présence de substances anodines dans le

Hydrologists think of rivers as labyrinths in the hydrological cycle, which transports runoff water from the continental to
the sea or to the censer of endorheic basins (Curry 1972). Since water is a good solvent and flowing water provides
living energy, water transport by rivers is linked with the transport of dissolved and solid substances. However,
precipitation and river discharge typically vary significantly during the annual cycle. At low discharge rates, river flow in
well-defined channels, but at high water in natural systems wide floodplains are recurrently inundated.

Rivers-floodplain systems provide important habitats for biota, and ecologists have tried to link the biota of river systems
with local environmental conditions and to adopt existing paradigms from other aquatic systems. These attempts have
met with two problems: (1) the division of ecology into terrestrial ecology and limnology; and (2) the classification
of water bodies into more or less closed, limnetic systems with accumulating characteristics (lakes, ponds) as outlined in
traditional limnology texts (Ruttner 1952) and open, lotic systems with discontinuous characteristics (streams, rivers);
(Dybas 1970). The transient nature of aquatic habitats in
floodplains resulted in biased treatment or in their omission. When studying floodplains, ecologists restricted them
to river channels; when studying floodplains, they concentrated on floodplain lakes, often treating them as
climatologic lakes.

One recent theoretical construct in river ecology, the river continuum concept (RCC) (Vannote et al. 1980), is based on the
hypothesis that a continuous gradient of physical conditions exists from headwater to mouth. Analogous to
the energy equilibrium theory of fluvial geomorphologists, the RCC states that structural and functional characteristics
of stream communities are adapted to form the most probable position or minima state of the physical system. Pro-
duction and consumer communities establish themselves in
harmony with the dynamic physical conditions of a given river reach, and downstream communities are fashioned to
capitalize on the inefficiencies of upstream processing. Both upstream inefficiency (leakage) and downstream adjustment costs are predictable. Therefore the RCC purports to provide a framework that permits us to integrate predictable and
observable biological features of lotic systems (Vannote et al. 1980).

In our view, the RCC suffers from two basic limitations: (1) it was developed on small temperate streams but has
been extrapolated to rivers in general; and (2) it was based on a concept that had been elaborated for the river
basins in a geoclimatological sense but was in fact restricted to habitats that are permanent and lotic.

Most papers that discuss the RCC recognize these limitations (Winterbourne et al. 1981; Barham and Luke 1982;
Minsball et al. 1983; Minsball et al. 1985; Staatz and Hipler 1985; Sedell et al. 1980) but fail to consider the biolo-

geographical isolation of systems within the seasonal, aquatic habitats of floodplains. It may prove acceptable to
modify the RCC to account for brief and unpredictable floods in low-order streams, even for catastrophic floods which
change the physical environment and "reset" systems (Cummins 1977; Fisher 1983). However, as the size of a
floodplain increases, usually along with increasing river
discharge, the frequency of floods decreases, and their duration and predictability increase. These changes result in a
distinct geomorphological and hydrological system with an
increasing ratio of periodically lotic to anoxic areas. This sys-
tem results in adaptations of biota that are distinct from those in systems dominated by stable lotic or
habitat ecologies.

Recently, the importance of river-floodplain systems to terrestrial systems and tropical regions has been shown by Lamb (1959), Hoek and Basil (1976),
Ryjan and Sahm (1979), Welcomme (1979, 1985,
1989), Bayley (1980, 1981, 1983), junk (1980, 1984), and junk and Wel-
comme (1985) based on their experiences in tropical sys-
tems. Amore and Bravard et al. (1986), who
analyzed the impact of flood regulation on plant and animal
communities of the Rhone R. floodplain, stressed the
importance of lateral and vertical dimensions of the river-

floodplain system. Davies and Walker (1985) emphasized
that considerable modification of the RCC was required before it could be applied to large river systems.

In this paper we synthesize evidence that supports a com-
plementary concept, the "flood pulse"; that attempts to explain the relationship between the biota and
the environ.
ment of an unmodified, large river–flowplain system. This concept is based on our experiences in relatively pristine systems in the neotropics and Southeast Asia and in the Upper Mississippi R. We derive this concept from the known ecology of typical biota that have adjoined the geomorphology and hydrology of large river–flowplain systems.

The Flood Pulse Concept

We propose that the pulsing of the river discharge, the flood pulse, is the major force controlling biota in river–flowplain systems. Lateral exchange between flowplain and river channel, and nutrient recycling within the flowplain have more direct impact on biota than the nutrient spiraling discussed in the RCC (Van Rens et al. 1980). We postulate that in unaltered large river systems with flowplains in the temperate, subtropical, or tropical belt, the overwhelming bulk of the riverine animal biomass derives directly or indirectly from production within the flowplains and not from downstream transport of organic matter produced elsewhere in the basin.

The effect of the flood pulse on biota is principally hydrological. We postulate that if no organic material except living animals were exchanged between flowplain and channel, no qualitative and, at most, limited quantitative changes would occur in the flowplain (Bayley 1989). The relative importance of imported versus recycled inorganic nutrients in flowplains is not clear and probably varies between systems. Given similar hydrological conditions, the longitudinal position of a flowplain in the drainage network is of little importance with respect to the biota.

The Highway Analog

Faunal life histories in unaltered large river–flowplains can be viewed as analogous to vehicles on a highway network. Were non-territorial to investigate this network, they would observe numerous bodies traveling in opposite directions and might well surmise that resources for those bodies were derived from the highways. If funds permitted a detailed study, it would reveal that four-wheeled creatures need to leave highways periodically for sustenance, along with their apparently symbiotic occupants. Eventually, major sources of production would be identified in farms, oil fields, and mines, vessels consuming and distributing resources via the highway network as a response to production cycles and short-term economic changes.

The life histories of major plant and animal groups, in particular fish, in large river–flowplains are beginning to be understood sufficiently to contribute to the theory that the river network in a river–flowplain system is in many ways analogous to a highway network with the vehicles corresponding to the fish, deciduous, herbivores, and/or omnivores support large fisheries in the main channel (Petretti 1978, 1982; Wolcomer 1979; Quinn and Basquin 1985), but the highest yields are associated with adjoining flowplains (Richardson 1921; Lowe-McConnell 1964; Petretti 1983) and most of their production is derived from flowplain habitats (Wolcomer 1979; Bayley 1983). The main channel is used principally as a route for gaining acceas to adult feeding areas, nurseries, spawning grounds, or as a refuge at low water or during winter in temperate zones. An analogous situation is found in large north-temperate and arctic rivers where most of the ichthyomass is anadromous; here the main feeding grounds are found in the delta area and in the sea (Grinnell 1953; Andrews and Lear 1956; Forster 1968; Roy 1989).

We will describe the functions of the flowplain and main channel in large river–flowplain systems with respect to the biota and evaluate the links between them and the nonflowable watershed in the light of recent data.

Definition of a Flowplain

Terms applied to classical limnological and terrestrial systems can be inappropriate for explaining concepts in river–flowplains. This is not merely a semantic discussion because the classical terms are understood to define features and functions in their respective systems. The "active flowplain" of a river is defined by North American hydrologists as the area flooded by a 100-year flood (Bhowmik and Stahl 1979). This period is arbitrary, longer than most existing records, and has little ecological meaning. Bayley (1981b) noted that huge areas of shallow, very acidic, largely deoxygenated swamp occur in the Peruvian Amazon. These areas are distinct from the main channels and inimicable to the bulk of aquatic animals. He proposed an active flowplain that excluded these peripheral swamps in order to compare fish production and fishery yields among systems.

We define flowplains as "areas that are periodically inundated by the lateral overflow of rivers or lakes, and/or by direct precipitation or groundwater; the resulting physio-chemical environment causes the biota to respond by morphological, anatomical, physiological, phenological, and/or ethological adaptations, and produce characteristic community structures. This ecological delineation recognizes that flooding causes a perceptible impact on biota and that biota display a defined reaction to flooding. Further, it implies that the impact of water level pulsing on biota is independent of the nature of its source and that there are many ecological similarities between flowplains adjacent to, for example, puling lakes or reservoirs and puling rivers. The definition encompasses a wide hydrological spectrum from short- to long-duration, floods and fast unpredictable to predictable timing. Our examples from large river systems exhibit predictable flood pulses of long duration. We have termed the flowplain area the "aquatic/terrestrial transition zone" (ATTZ) because it alternates between aquatic and terrestrial environments. We use this term to stress our more specific definition of flowplain, because "flowplains" has often been defined to include permanent lentic and lotic habitats. The insile edge of this aquatic environment that traverses the flowplain (ATTZ) we have termed the "moving littoral." The flowplain or ATTZ has unique properties that have been considered to contribute a specific ecosystem (Link 1981; Odum 1988).

Hydrologists consider the river and its flowplain as one unit since they are inseparable with respect to the water, sediment, and organic budgets. We term this unit the "River–flowplain system." Therefore, this system con-
The hydrological regime of rivers reflects the climate of its upstream catchment area. Low order streams have an irregular flood pattern with numerous peaks because they are strongly influenced by local precipitation. This influence generally diminishes with increasing size of the watershed and is almost imperceptible in the hydrograph of very large rivers. The hydrological buffering capacity of a large catchment area results in a rather smooth and predictable flood curve. In mainly tropical or subtropical systems with large watersheds, the hydrograph reflects seasonality in precipitation, and typically shows only one pronounced flood peak per year. A few tropical rivers, e.g., the Zaire R., show two flood peaks due to two rainy seasons in their catchment areas. In temperate and cold climates, the impact of precipitation on the hydrograph is modified by the temperature regime. For example, minor flooding occurred in autumn in the Upper Mississippi R. prior to dam construction (Gribbough and Anderson 1980a) because evapotranspiration rates decrease as temperature drops. Also, water accumulates as snow and ice in winter, which then contributes to the spring flood by melting.

Due to the size of large river basins, the effects of seasonal climatic changes may be felt downstream only after several weeks or even months. This time lag can be of ecological importance in downstream parts of large river systems. In the central Amazon the river is still rising at Manaus after the termination of the major rains; the flood peak follows the rainy season by 4-6 weeks. On the lower Mississippi R., cold water from melting snow in the head waters causes the temperature in the backwaters of the floodplain to be much higher (Bryan et al. 1976; Holland et al. 1983).

The shape of the hydrograph depends not only on the discharge characteristics of the river, but also on valley slope, floodplain size, and vegetation. Although the Illinois R. has a mean discharge of only 627 m$^3$/s (Fitzgerald et al. 1986), it has protected floods characteristics of a much larger river because it occupies a wide valley river carved by the ancestral Mississippi and Teays rivers. Because the valley has filled with alluvium, its gradient is very flat and the river drops only 1.6 cm/km.

At a given rate of discharge increase, the water level rises more slowly as the floodplain begins to fill. In larger floodplains the rate of rise is slower, the period of inundation increases, and more lentic habitats develop. As the water recedes, processes in the floodplain become less dependent on the river channel and more subject to local climatic events. During the terrestrial phase, the amount and distribution of local rains greatly affects the composition and productivity of plant communities as well as the life cycles of many animals. When local precipitation at low water is high, floodplains are forested, e.g., in the middle and upper Amazon, Zaire, and Mississippi rivers. Conversely, when local precipitation is low, savannas with gallery forest develop, e.g., in the floodplains of the lower Nile, Zambezi, and Volta rivers. Some lakes and swamps are isolated from the main channel for many months or even years. Their hydrological regimes are therefore independent of the main channel except during periods of high water.
Nutrients

According to hydrologists, a river's chemistry reflects its catchment area. This holistic view has been applied success- fully to streams with respect to their nutrient budgets (Hyne 1972; Yannone et al. 1986). Nutrients can routinely be divided into inorganic and organic fractions; these in turn can be subdivided into ionic compounds, dissolved solids, and particulate matter. The flow system receives all classes of nutrients directly from the main channel, and its basic nutrient status would be expected to correspond to that of the river. Floodplains, however, tend to establish their own cycles since organisms and environmental conditions that influence the biogeochemical cycles differ considerably from those in the main channel. The efflux of rain, runoff, groundwater, and input from floodplain tributaries may also be important.

The Inorganic Fraction

Gaseous Compounds

Gases such as CO₂, O₂, H₂S, CH₄, and N₂ are produced and/or consumed in the floodplain independently of processes in the main channel in systems with slow, regular flood pulses. Residence time of floodwater water and temperature modify concentrations. The lack of persistent thermal and chemical stratification in most Arcticflaya floodplain lakes is due to the short period of light conditions during warm weather (Bryan et al. 1974). In contrast, the water column becomes chemically stratified over large areas after entering the Amazon floodplain: the daily thermocline with a temperature difference of 1–3 °C is insufficient to inhibit circulation. Deeper than 2 m during periods of several weeks or even months. Large amounts of organic material under decomposition at high temperatures result in high rates of oxygen consumption and CO₂ release near the bottom. Hypoxic, or even anoxic conditions accompanied by H₂S and CH₄ production, are often found at a few meters depth (Schmidt 1973a; Meleck and Fisher 1983; Junk et al. 1983).

In addition to nitrogen input from the river, high nitrogen fluxes to and from the atmosphere occur. These fluxes are related to oxygen levels and to organisms in water and soils, both of which change drastically between flood and dry periods. Denitrification in wetlands is well documented (Kemp and Day 1984) and has even been tried in the treatment of wastewater (Dierberg and Brezonic 1984). Various nitrogen-fixing organisms, e.g., cyanobacteria and bacteria, that are often associated with higher plants such as Leguminosae counteract denitrification by fixing atmospheric nitrogen (Heller 1969; Richter et al. 1985). Despite the high potential for denitrification, Brinon et al. (1980) consider Copaia-cypress swamps to be nitrogen sinks due to high nitrogen levels in the litter.

Dissolved Solids

River water is the major source for dissolved inorganic compounds, including plant nutrients. Abiotic and biotic processes in the floodplain, however, may considerably alter the total amount and ionic composition of dissolved materials. Increased evaporation may raise salinity in back- waters above the levels found in the river, or precipitate in acid climatic zones. Biogenic modifications are reported from Amazonian floodplain lakes where ten to twentyfold increases in total salinity have been measured in small pools at low water (Furch et al. 1983). A major change in ionic composition, such as an increase in potassium, has been associated with phytocline deposition of aquatic and terrestrial macrophytes (Furch 1984a, 1984b; Furch et al. 1983).

Further changes in ionic composition result from dilution by local rains or by mixing with lateral inflows of surface and ground water from forested areas. During low river stages in the Amazon, water seeping through floodplain sediments has an electric conductance up to 200 times that of the Amazon R. water, with high levels of iron and manganese (Iron and Jank, unpublished data).

Levels of dissolved nutrients are seldom limiting factors for primary production in the main channels of large rivers. In the floodplain, however, phosphate and/or nitrogen often limit productivity, and inflowing river water replen-ishes the nutrient levels, as shown for phytoplankton production in Amazonian floodplain lakes (Fisher 1979). In lake and swamp habitats receiving minimal influence from the Amazon R., autotrophic phytoplankton (flagell- ate Euglenophytes and Pyrrophytes) predominated during low water levels in association with minimal inorganic nutrients (Bryan et al. 1976; Seger and Bryan 1981).

Little is known concerning the amount of dissolved inor- ganic compounds released from the floodplain into the main channel, and findings are contradictory for phosphorus (Yaboo 1983) and nitrogen (Brinon et al. 1983). Release and storage may be related to the flood cycle and to vegetation cover, and in temperate regions, to the growth cycle of the vegetation (Klopatek 1978; Brinon et al. 1980). Because large floodplains represent a mosaic of habitats with different physical and chemical conditions supporting diverse biotic communities, they may see either as a sink, or as a source with respect to each nutrient, depending on the circumstances.

Particulate Matter

Particulate organic matter in suspension is intrinsically considered an unimportant source of plant nutrients in the river channel. Consequently, such particles hinder growth of phytoplankton and submergent aquatic macrophytes due to shading. In floodplains, however, they become a basic part of the nutrient pool available to primary producers in the dry phase and during part of the wet phase. Fertility of flood- plains depends largely upon the quality of deposited sediments. Brown (1983) states that transport and deposition of sandy and kaolinitic material produce an interior floodplain (e.g., Rio Negro in Brazil), whereas the montmorillonite and illite of the Amazon and Mississippi rivers result in high floodplain fertility. However, an impoverishment of some mobile elements (Fe, Mn, Zn) was detected in the upper 10 m-layer of Amazon sediments, which are only a few hundred years old (Iriin et al., unpublished data). Conversely, weathering of the sediments, which is accelerated in tropical climates, adds dissolved inorganic materials,
The Organic Fraction

According to the RCC, aquatic animal communities of low-order streams depend mainly upon material from the nonflooded watershed. Medium-order streams have an increased instream production. Fauna of high-order rivers lacking floodplains depend mainly on organic material from upstream areas because primary production in the main channel is very low (Vannote et al. 1980).

Practically all litter must be processed by microorganisms if it is to become attractive to higher consumers. A considerable portion continues to be practically indigestible, such as fine particulate organic material in the Amazon main channel (Hodges et al. 1986). Ensel et al. (1986) reported that humic materials comprised 60% of the dissolved organic carbon of the Amazon main channel; this carbon in turn made up about 50% of the total organic carbon. The comparably low BOD of the water from the main channel of the Amazon itself contrasts sharply with values in its floodplain (Junk, unpublished data).

Part of the organic carbon transported in the main channel passes on to the floodplain. This amount, however, is negligible in comparison with in situ production of organic material in the floodplains of rivers (Bayley 1989). Estimates of the productivity of the Amazon floodplain show that annual primary production is of the same order of magnitude as the total amount of carbon transported by the river to the Atlantic Ocean (Richie et al. 1980; Junk 1985a).

The direct impact of floodplains on the carbon budget of main channels is not well known. Some evidence suggests that floodplains can be a source for particulate and dissolved carbon (Chowdhury et al. 1982; Martins 1982; Junk 1985a; Furne and Junk 1985; Grubaugh and Anderson 1989). Conversely, retention mechanisms, such as settling of sediments, uptake by organisms, and retention of most macrophytes by stranding or trapping during falling water (Junk 1980) contribute to the recycling of most carbon in the floodplain and strongly reduce leakage to the river channel. Carbon export from floodplains also depends on hydroperiod, flushing rate, and in temperate regions, on the growth cycle of floodplain vegetation. Data from floodplains are limited, but Odum and de la Cruz (1967) estimated that the rate of export of organic material from a Georgia tidal marsh was directly proportional to volumetric flow rates.

Gosslink et al. (1981) assumed that flooding during winter and spring provides more detritus to main channels than during summer in temperate regions. In the tropics, consistently high temperatures favor high production and rapid processing of organic material throughout the year.

Biota in the River Channel

The channel is well defined in large, pristine rivers, and is delineated from the floodplains by natural levees and/or a marked increase in water velocity. In rivers modified by navigation dams, such as the Mississippi, broad, slow-flowing main channel borders are found on either side of the narrow main channel, which is defined by the thalweg (Fremling et al. 1989). These borders, which constitute a developing floodplain, are discussed separately below; however, the main channels of modified rivers have much in common with those in more pristine systems.

Plants

Great water depth, high suspended load, considerable turbulence, and strong current make the main channel unfavorable for primary production. Aquatic macrophytes and periphyton normally colonize shores and in some translucent tropical rivers, rocky substrates (Podosomaceae). In slow-flowing tropical and sub-tropical rivers floating macrophytes may become important. Phytopatomplankton density increases with stream order, transparency, and decreasing current velocity, but absolute values are low (e.g., Berner 1951). In most large rivers, physical factors, in particular light, rather than mineral nutrients limit primary production (Fisher 1979). Average primary production per unit area in the main stems of large turbid river systems such as the Amazon, Mekong, Ganges, and Mississippi can be only a small fraction of that in their floodplains. The extent to which floodplain water bodies contribute to populations of potamoplankton and floating macrophytes in large rivers is unknown. The considerable increase of potamoplankton downstream of reservoirs, e.g., in the Nile (Brook and Reddick 1954; Talling and Reddick 1967; Ham- merton 1976) and the increase of floating macrophytes in the Amazon main channel at rising and high water (Junk 1970) are due to high production of these plants in associated lentic habitats.

Invertibrates

Little information is available about colonization by animals of the bottoms of large rivers. The bed loads of large rivers in alluvial plains, e.g., the Mississippi, are sandy (Schumm 1977). Large river channels mostly consist of a monotonous sequence of slowly moving sand dunes unstable for benthic colonization. Turbid river channels, for example, transports its bed load of coarse sand as dunes 6–8 m high (Stioli 1984). High suspended load hinders benthic and epizoic animals (Hynes 1970). Junk (1973) found a decrease in number and biomass of principally filter-feeding pericon in flowing macrophyte vegetation as amounts of inorganic suspended increased.

Although some invertebrates can live in the dominant sandy substrates of main channels (e.g., the clandoeite Giliotis, Cephalopoda, Robackia, and Sarcithra (Coffman and Ferrington 1984)), densities are low. Berner (1951) and Norris et al. (1968) indicated average fresh invertebrate biomass in the main channel of only 0.001 g m\(^{-2}\) and 0.007–0.048 g m\(^{-2}\), respectively, for the Missouri R., and attributed these low values to shifting substrates, silhouette, fluctuating water levels, swift current, and absence of aquatic vegetation. In the Archaflayola distributary, which receives 80% of the Mississippi R. discharge, Bryan et al. (1976) reported a mean quantity of 327 benthic individuals per m\(^{2}\) in riverine habitats compared with densities up to ten times greater in floodplain habitats.

Logs and rocks provide stable substrates for organisms in a channel environment that is otherwise dominated by shifting alluvium. Over 10 logs were pulled from channels in the lower 1600 km of the Mississippi during a 5-year period (Harmon et al. 1986). The average fresh animal biomass colonizing logs in the Kaskaskia R., Illinois, varied between 0.57 and 1.65 g m\(^{-2}\) (Nilsen and Larimore 1973). Nord
Vertebrates

Vertebrates, particularly fish, are important components in the main channel. In subtropical and tropical rivers, fresh-water dolphins, capybaras, manatees, hippos, turtles, and crocodiles may contribute considerably to the main channel biomass. White whales and seals occur in arctic rivers; beavers, muskrats, and otters in temperate rivers; and waterfowl and shorebirds in both. However, few higher animals have adapted to utilize main channel habitats exclu-

Because the ATTZ has pronounced aquatic and terrestrial phases, there are strong selective pressures on aquatic organisms to colonize it at rising or high water because of the feeding opportunities (Bonnet et al. 1969; Welcomme 1979; Bayley 1983, 1988). Conversely, terrestrial organisms that occupy nonflooded habitats along the floodplain border are adapted to exploit the ATTZ at low water levels (Shappe and Osborne 1971; Fredrickson 1979; Davies 1985).

In low-order streams, the level of adaptations to flooding is rather low. Few organisms, unpredictable floods correspond to catastrophic events that periodically "reset" the physical and biotic environment (Cummins 1977; Fisher 1983). Obligate aquatic organisms concentrate notably in the main channel because flood periods are too short and irregular to develop profitable strategies for occupying the ATTZ. The predictable and prolonged flood pulse typical of large rivers favors the development of anatomical, morphologi-

In the humid tropics, regular flooding and drying of floodplains promote a pronounced seasonality in an otherwise eutrophic environment. Many Amazonian floodplain trees show distinct annual growth rings, because inundation causes a "physiological winter" through oxygen stress (Wuebbles 1985, 1986). Seed production is tied with the flood for dispersal by water or by fish (Gottschalk 1978; Golding 1980). Terrestrial invertebrates from central Amazonian floodplain forests show a defined reproduction period (Adis and Malmert 1960; Pfeffer 1986) after poly-

Except for limited amounts of potamonkton, brachionus, and paramecium, the list of the main channel coincides to the river shoreline, to islands, or in the main chan-

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Because many vertebrates living in the main channel depend on the floodplain for food supply, upwelling, and shelter, they have developed strategies to utilize Periodically available habitats. High mobility is required, as witnessed by the extensive migrations referred to earlier. Such strictly aquatic animals as fish and manatees depend on the flood cycle of the river, which controls access to the floodplain. Others less strictly aquatic, such as hippos, beavers, or capybaras, make feeding trips out of the water.

The importance of lateral migration of animals between the floodplain and main channel of larger river systems has been underestimated because modern civilization has sub-

Life cycles of biota utilizing floodplain habitats are related to the flood pulse in terms of its annual timing, duration, and the rate of rise and fall. Timing is important in temper-

The flood pulse is hypothesized to be the driving force behind species "flood pulse", creating a "physiological winter" through oxygen stress (Wuebbles 1985). Seed production is timed with the flood for dispersal by water or by fish (Gottschalk 1978; Golding 1980). Terrestrial invertebrates from central Amazonian floodplain forests show a defined reproduction period (Adis and Malmert 1960; Pfeffer 1986) after poly-

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in these areas access to their great plasticity in coping with habitat change.

Fish that depend on seasonal colonization of floodplain habitats dominate the fisheries, the biomass, and the production in river–floodplain systems (Bonetto et al. 1970a; Weil- 
combe 1979; Bailey 1971a; Goulding 1981; Bailey 1983; Littlejohn et al. 1982). Spawning of many species occurs at 
the beginning or during some period of the rising flood, resulting in timely colonization of the floodplains for feed- 

ing and shelter (Bayley 1983, 1988; Holland et al. 1983; 

Weilcombe 1985). Conversely, when the water recedes, fish find refuge in main channels, in residual floodplain 
water bodies, or in permanent tributaries (Weilcombe 1979).

Adults of many species show seasonality in food uptake related to flood cycles, as shown for the Rupununi R. by 
Lowe-McConnell (1964) and for the large rivers of the Amazon basin by Goulding (1981) and Ribeiro (1983). Periods of fasting coincide with low or falling water levels and are associated with decreases in seasonal fat con- 
tent in many adult fish (Junk 1983b). Studies of diets at ris- 
ing and high water show that many species directly use 
pollen, fruits, seeds, and the small portion of terrestrial insects that drop into the water from the canopy of the forest 
(Goulding 1980).

Detritus plays a major part in the food web in floodplains 
(Weilcombe 1983). Fish are major detrivores in the tropics. For example, fine particulate organic matter (FPOM) is consumed directly by the highly specialized Prochilodontidae and Caimanidae in South America, and by Citharinidae and Lebistes species in Africa (Bowen 1984; 

FPOM is also an important feature of the gut contents of large catostomids and Dorosoma in large N. American 
rivers, but its nutritional importance has only recently been 
indicated (Abbott 1988). Most of the commercially impor-
tant fishes are bottom forage utilizing macroinvertebrates, 
which in turn ingest detritus (Fremling et al. 1989).

The importance of remnant floodplain areas in the Missis-
sippi and its tributaries was indicated by Risotto and Turner (1985), who found that 55 % of the variation in average fish catch was explained by bottomland hardwood area (as a proxy 
to floodplain area), fishing effort, and latitude. 

Because floodplain areas are now controlled by manmade levees and not all floodplains are forested, the relationship 
might be improved with direct measurements of the active 
of the floodplain area.

Adaptations to survive hypoxic conditions favor the 
colonization of periodically stagnant waters typical of many 
floodplains. Air breathing and other adaptations to low oxygen 
concentrations are frequently found in neotropical fishes 
(Carter and Beauge 1931; Kramer et al. 1978; Junk et al. 1983), other tropical floodplain rivers (Weilcombe 
1979), and in fish of the Mississippi drainage (e.g., gars, 
Lepisosteus spp. and bowfin, Amia calva; see also Marvin and Heath 1968).

In the temperate Upper Mississippi R. floods can reduce the 
overwinter survival of young-of-the-year freshwater 
fishes (Aphloiodon gastrurae) by the influx of channel 
water at 0°C into backwater thermal refuges where the tem- 
perature is 4°C (Bodeenleger and Sheehan, in press). The 
winter biology of fishes in large North American rivers has 
been little studied, and the recruitment of other species may 
be strongly affected by winter temperatures and flood pat- 
terns. From spring through summer, the timing and dura-

of the flood is critical to species which gain access to 
the ATTZ, and permanent backwaters for feeding and spawning. Ideal conditions for spring spawners occur dur-

ing years in which the flood and temperature rise are cou- 
pled; conversely, recruitment is poor if the flood retreats 
too soon during the warm growing season (Fig. 1). Finger 
and Stewart (1987) found that the timing and duration of 
flooding controlled the year-class dominance of spring- 
versus summer-spawners in Missouri floodplain forests.

In polar, sub-arctic, and taiga rivers the timing of the flood 
is predictable because of massive snow melt in the 

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creating an inhospitable environment for fishes (Roy 1989). The severe springtime conditions may explain why fish in high latitudes avoid the flood by spawning in the fall (R.A. Ryder, personal communication).

Tree growth is mainly retarded by floods because the thalweg becomes desaturated (Huffstein 1968; Huffman et al. 1981). Graslin et al. (1981) posulated that floods during winter or spring have a positive effect on the floodplain forest because they distribute nutrients and water to the soil before plant growth commences. Data on flood tolerance of tree species often appears to be contradictory because the timing of floods relative to growing cycles and growing periods is not stated (Dister 1980).

The Mississippi R. is a major migratory flyway for waterfowl, shorebirds, gulls, and eagles. The "drilling ducks" (mallard, pintail, greenwing and bluewing teal, black duck) utilize mast in floodplain forests, winter grain in adjacent harvested fields, and invertebrates associated with macrophytes in shallow water bodies, as well as the seeds, tubers, and plant leaves in the floodplain (Belrose 1941). The diving ducks (canvasback, lesser scaup) utilize submerged macrophytes and macroinvertebrates that grow in deeper water (Thompson 1973). Aquatic and moist-soil vegetation in the Illinois and Upper Mississippi floodplains requires a period of shallow, stable water levels during the winter growing season (Belrose et al. 1978). The summer's primary production is made more accessible to migratory waterfowl by the autumn rise in water levels. If an autumn flood does not occur, manures of refugees and duck clubs create one by pumping water from the river into the floodplain. They also pump water out of the same impoundments if the flood is too slow to release in the summertime, so they can still milk or allow native plants to grow (Belrose et al. 1979).

Flood Pulsing and Plant Community Structure

Under given climatic conditions, plant communities become established in the ATZ of large rivers according to the flood regime. Every place in this zone can be considered a point on a gradient reflecting the degree of annual flooding. Every plant has its optimum position on this gradient. The optimum, however, can be modified by such factors as stability, structure, and fertility of the substrate, groundwater level, and biogeochemical processes (e.g., accumulation of organic material, oxygen fixation, and interspecific competition) (Linsey et al. 1961; Bedinger 1979; Burgess et al. 1973; Johnston and Bell 1976; Bell 1980; Dister 1980; 1983; Graslin et al. 1981; McKnight et al. 1981; Distributions of animals are also affected by this gradient in spite of their mobility (Wharton et al. 1981; Larson et al. 1981). Basic changes in plant community structure occur mainly through a shift of the gradient, such as a rise of the floodplain surface due to additional inorganic or organic sediment deposition (allotrophic or autotrophic succession), a lowering by erosion, or a change in the hydrograph due to climatic change, tectonic movement, or human influence such as the construction of a dam or lateral dikes.

Plant communities, however, are characterized by smaller changes. There is strong pressure on communities to proceed to a later successional stage when the period of the flood pulse is reduced. The shape of the pulse often varies within large limits, thereby causing communities to respond. Annual plants react to annual differences whereas forest communities are affected by extreme annual floods, droughts, or even periods of successive years of extreme flood events that may occur every 10, 20, or 100 years. Establishment of tree seedlings in low-lying areas requires a period of exceptionally low water for several years, as Demarest (1952) found for Taxodium distichum. Aquatic communities tend to fill up periodically isolated water bodies with organic debris, thereby causing autogenic succession to marsh and swag vegetation when the flood pulse fails. This process has been estimated to require about 200 years in the temperate Rhône R. (Amoros et al. 1986).

Extreme floods clean these water bodies and "reset" community toward earlier successional stages. Reset can be especially severe when floods occur during the ice season in temperate rivers because trees and channels can be scoured by wind- or water-driven ice (Sigfusson 1964). Consequently, the observed community structure in floodplains is a result of short-, medium-, and long-term effects of the flood pulse. Shelford (1934) estimated that about 600 years were required to develop the late submaximal tullip-deer-oak communities on the lower Mississippi R. Most communities receiving the full amplitude of the flood pulse can be viewed as being in a dynamic equilibrium at an early successional level (puls-stability, tenue Oulm 1959; see also Margalef 1968).

Flood Pulsing and Production

Primary and secondary production in the river-floodplain system is the sum of production during terrestrial and aquatic phases. As indicated previously, the basic fertility of the floodplain depends on the nutrients status of the water and on the sediments deriving from the river. This fertility, however, may be modified by tributaries and by runoff from the local catchment area of the floodplain. Length, amplitude, frequency, and predictability of the flood pulse determine its occurrence, life cycles, and abundances of primary and secondary producers and decomposers, abundances which affect the level of exploitation and regeneration of the nutrient pool as well as its supply. Graslin and Turner (1979), proposing a cladocentric or wetland systems according to a hydrodynamic energy gradient, suggested that a positive relationship existed between productivity and water flow. Their theory may be valid within limits in a river-floodplain system; however, short-duration pulsed can flush out considerable organic matter and nutrients into the main channel (or into the estuary from a salt marsh as shown by Teal [1962]) and limit in situ productive processes and access by aquatic animals. In such systems, the aquatic ecologist studying production is concerned with how the ATZ benefits the river or the permanent lentic areas in the floodplain. Conversely, slow inundation of the same floodplain allows sufficient time for in situ processes along the moving littoral (Fig. 2), which traverses the ATZ with each pulse. Aquatic and terrestrial ecologists studying production in river-floodplain systems with slow pulsing should be concerned with how the river benefits the floodplain.

The flooding phase of the moving littoral (Fig. 2) finds its closest parallel to a reservoir in the process of being flooded (Wood 1951), with mineralized products from any preceding aquatic cycle and the current terrestrial one being
Fig. 2. The moving littoral in the transition zone (ATTZ) of a river-floodplain system in the central Amazon, with estimates of annual production (P) and biomass (B). Estimates are as dry weight per hectare. The H2S zone has no dissolved O2. The indicated zones are as follows: (1) Phytoplankton C14 (Schmidt 1970b), (2) annual terrestrial plants, (3) perennial grasses, (4) floodplain (varzea) forest, and (5) emergent macrophytes (from Junk 1985c and unpublished data). Phytoplankton are not included, but preliminary data on phytoplankton from T. R. Fisher (pers. comm.) indicate a total productivity in the floodplain of the same order as phytoplankton (Bayley 1989).

released into the water. The various sources of primary production have high values (Fig. 2) but varying production to biomass ratios. When integrated over areas appropriate for each season in the floodplain, phytoplankton contributed less than 6% of the total carbon production in the central Amazon varzea floodplain (Junk 1985a; Bayley 1989).

Most carbon sources, including considerable detrital biomass, are important to some animals at some time (Wolcomme 1979, 1985; Junk 1984), but their quantitative importance is unknown. Organic material produced in floodplains varies considerably with respect to consistency, protein content, digestibility, and availability, that result in large differences in decomposition time and in the types of organisms involved in decomposition processes. Phytoplankton and periphyton are easily decomposed in only a few hours or days. In the Amazon, aquatic and terrestrial herbaceous plants lose about 50% of their weight after 2-3 weeks in water (Howard-Williams and Junk 1976). Tree leaves vary widely according to species; some are as quickly decomposed as herbaceous plants whereas others remain little modified throughout months and even years. Softwood plants are destroyed in a few years, whereas hardwood plants may remain little modified for years and even decades (Junk, unpublished data).

Strong evidence suggests that the change between terrestrial and aquatic phases accelerates the decomposition of organic material, as the circumstantial evidence of Wood (1951) indicated. Terrestrial arthropods play an important role in the decomposition of leaf litter and wood as shown for cockroaches by Imrler and Furth (1979) and for termites by C. Marius (pers. comm. to WJ). Oxygenation of sediments during dry periods promotes processing of organic material; later, when reflowing occurs, plant nutrients are recycled into the water, thereby enhancing productivity. This effect, sometimes in combination with a crop planation or fallow period for an entire year, has been utilized for many years in European fish culture. Wood (1951) proposed the management of water levels in impoundments by changing them seasonally to increase fish production. Lam-bou (1959) suggested that the processes described by Wood explain the high productivity of backwater lakes due to natural water fluctuations at the Mississippi floodplain. In the Amazon floodplain during the period of rising water, mean growth increments by weight of 12 common fish species were 60% higher than during the remainder of the year (Bayley 1988).

Food supply in fertile floodplains during the flood phase can be so abundant that factors other than food may limit individual growth and population density of fish and other aquatic animals. Limitations during the flood phase include spawning success, lack of habitats with sufficient dissolved oxygen (Junk et al. 1983), and predation (Bayley 1983). Limitations at low water include higher levels of predation, a probable reduction in food supply, or even death by drought. Bayley (1988) found that growth of juveniles of 11 abundant fish species tested did not indicate a density-dependent relationship with potentially competing species guilds during the period of rising water. Only two out of eight species indicated density-dependency at F.<0.5 during the shorter falling-water period.

The preceding ideas have very little to do with traditional concepts of productive processes in rivers. The RCC predicts that lower reaches of river systems have low ratios of production to respiration (P/R) due to processing of material from upstream and reduced in situ production. Wissmar et al. (1981) noted that Amazon floodplain lakes have high respiration rates, and Melack and Fisher (1983) noted that carbon loss due to respiration exceeds the carbon contributed by phytoplankton. However, these are limnological perspectives that describe only part of the system. The evidence offered here for the lower reaches of the river-floodplain system indicates high in situ production
and low importation of organic matter from upstream. Therefore, we predict high P/R ratios for large river-floodplain systems.

**Flood Pushing and Diversity of Habitats and Species**

Sediments, which are deposited in the floodplain in well-defined geomorphological units, form bars, levees, awakes, oxbows, backwaters, and side channels. Flowing water grades sediments according to grain size. The floodplain soils are stratified horizontally and vertically in a small scale pattern (Irons et al. 1983; Amsden et al. 1986), but the wind-induced transport of sediment may modify the water-induced sediment pattern.

The main river and its connecting channels represent the lotic part of the river-floodplain system; oxbow lakes, abandoned channels, and backwaters represent the lentic one. Both harbor sets of organisms which colonize the much more extensive, periodically flooded ATTZ and increase species numbers occurring in the floodplain. Differences in the duration of flooding, in soil structure, and in vegetation result in small-scale habitats in the form of meadows,捎 roughly parallel zones. This arrangement multiplies the edge effect far beyond that represented by the main channel and its islands. In addition to these topological edges, there are many physicochemical eddies in the form of sharp vertical and horizontal boundaries in oxygen, temperature, dissolved or suspended matter; in the main channel these are encountered only at confluences with tributaries or near the substrate. In the Amazon, oxygen levels in surface water may drop from about 5 mg/L in the main channel to 0.5 mg/L in the floodplain 50 m away (Junk et al. 1983).

Habitats shift horizontally and vertically according to the water level (Fig. 2). In addition to this instability due to the moving littoral is another instability caused by sediment deposition and erosion by the river. Depending on the position of the river channel and its dynamics, habitats may be ephemeral or rather stable over decades or centuries. This affects such stationary organisms as trees.

Flooded areas inside and adjacent to the floodplain perimeter, as well as emergent vegetation or the floodplain forest canopy, can be termed terrestrial habitats. All of them harbour an abundance of plants and animals that colonize the ATTZ, increasing considerably the total number of plants and animals occurring in the system.

No attempt to explain the total diversity in all habitats has been made; however, studies on specific plant and animal groups show some tendencies and some apparent inconsistencies. Species diversity would be expected to be limited in aquatic and terrestrial taxa that are sedentary and experience the full impact of the physiological stress resulting from the change between the aquatic and terrestrial phase. Wöhrle (1983) showed that the central Amazon floodplain forest has a much lower plant species diversity than the nonflooded forest. Salis et al. (1986), however, state that high diversity in tree species characterizing the upper Amazon lowland forests occurs in existing and extinct floodplains, but they did not present species numbers or diversity indices. They describe a mosaic of small habitats created by large-scale, continuous disturbance by lateral erosion and sedimentation from the river channel, with high diversity between habitats. They reason that the high diversity in the relatively short-lived habitats of the present floodplains was due to insufficient time to allow competitive exclusion, supporting Connell's (1978) intermediate disturbance hypothesis. In the former floodplain formations that are about 5,000-10,000 years old, habitats are very stable, and the high species diversity between habitats was attributed by them to allopatric speciation.

Diversity should be expected to increase with the ability of organisms to avoid the physiological stress in the ATTZ. High diversity in floodplains occurs in mobile groups, such as fish (Lowry-McConkey 1972; Welcomme 1985) and nonaquatic birds (Rasmussen and Parker 1983).

The drastic change between terrestrial and aquatic phases results in high seasonal losses for most plant and animal populations, but these losses tend to be recovered by quick growth, early maturity, high reproduction rates for r-strategy organisms (Plauser 1970), and fast dispersal. Many of the most persistent and productive aquatic weeds (e.g., Eichhornia crassipes, Salvinia auriculata, Ceratophyllum pteridis, and Alternanthera philoxeroides) are endemic to neotropical river-floodplain. In floodplains they are periodically decimated by the dry phase, allowing coexistence of many plant species with similar habitat requirements. In hydrologically stable conditions, they become dominant due to their strong competitive ability. Conversely, many perennial weeds in agricultural crops dominate in the early successional stages of floodplain vegetation at low water levels due to their strategy traits and recurrent disturbance of the ATTZ by the flood pulse (Smith and Waters 1986; Wilf, unpublished data).

Many plants and animals show an impressive resilience with respect to short-term catastrophic events; an example is the rapid response of fishes following extreme drought, overfishing, or pollution. The capacity of these highly effective reproduction strategies and to their mobility which allows access to dispersed low-water refuges, fish recover quickly when the flood pulse returns (Welcomme 1979). An alternate strategy is effective only when sufficient nutrient and food resources are available to fully utilize the growth potential. Floodplains of extremely low nutrient status may therefore lose K-selection (Plauser 1970), such as Magnalipis and Walker (1989) have indicated for Amazonian freshwater shrimp.

If we consider the total number of species in a river-floodplain system, circumstantial evidence suggests that a physical factor, the flood pulse, produces and maintains a highly diverse and dynamic habitat structure, thereby allowing a high species diversity despite stresses in the ATTZ. This in contrast with the intermediate disturbance hypothesis of Connell (1978) and parallels the observations of Statzner and Higler (1986) and Statzner (1987) who noted that physical factors (stream hydraulics) affected zonation patterns of benthic invertebrates, and that longitudinal zones of transition were associated with higher species richness.

**Man-Made River-Floodplains**

Dams have altered the hydrology and created artificial sedimentation basins covering thousands of square kilometres in rivers worldwide. Dams construction continues. For example, about 100 large reservoirs totalling 100,000 km² are projected to utilize the hydropower potential of Amazon R. tributaries (Junk and Melo 1987).
The hydrological changes often remove the flood pulse from floodplains downstream and sometimes permanently inundate floodplains upstream.

In the longer term, sedimentation and the modified flood pulse produce man-made river-floodplains. The 26 main navigation dams on the Upper Mississippi River downstream from Minneapolis, Minnesota, divide the river into reaches where the entire floodplain width is currently inundated, but where sedimentation is creating shallows that will become levees, side channels, or backwaters, and eventually floodplains (Fig. 3A to H). Of course, former floodplains now behind manmade levees will remain isolated from the river, assuming no long-term changes in flood stages or flood protection policy. The new floodplain downstream from some of these dams will experience the full amplitude of the flood cycle because the dams maintain water depths for navigation only during low flows but have little effect on flood levels. Indeed, the gates are raised completely out of the water and the relatively low earthen walls that connect the locks and gates to the bluffs are overtopped during floods. The extent to which these developing floodplains contribute to secondary production, fish yield, and waterfowl utilization should be measurable during the next 50 years, assuming that other factors (e.g., pollution) remain constant or are taken into account. Thus the flood pulse concept can be investigated by measuring changes in one system through time since the navigation dam construction.

Even now, in an intermediate stage of succession in the Mississippi pools, the channel borders, not the main channel, are centers of production. Concentrations of particulate and dissolved organic carbon, plankton, and microbes are higher closer to the fringing plant beds and diminish toward the channel (Fig. 3C, E, and D). The greatest biomass of benthic macroinvertebrates are the burrowing filterers and collectors (mayflies of the genus Hexagenia and sphaerid clams, Macruriidium and Sphaerium), which occur in beds just offshore of the macrophytes (Fig. 3F). These invertebrates apparently did not appear in high densities (up to 100 000 clams/m²) in the oldest pooled reach of the Mississippi R., the Keduk Pool, until the 1960's (Gale 1969; Sundansky et al. 1979), when sedimentation raised the channel border bottom to the 1-m euphotic zone, thereby triggering autotrophic production by macrophytes. Diving ducks, which feed on concentrations of these invertebrates, only began using this pool in substantial numbers in the mid 1960's (Mills et al. 1966; Thompson 1973; P.C. Bellrose, pers. comm.). If phytoplankton or upstream sources had floated the clams and mayflies, dense populations of these invertebrates should have been present in Keduk Pool (but evidently were not) when Ellis (1931a, 1931b) made his biological surveys 18 years after the dam was closed, which was sufficient time for the accumulation of substrate suitable for burrowers. Organic matter was not being trapped behind upstream dams before it could enter the pool because these dams were not constructed until the late 1930's and early 1940's. The historical evidence from the Upper Mississippi R. that supports the idea that a high level of secondary production requires a nearby center of primary production, rather than long-distance transport of organic matter from upstream sources via the main channel.

Conclusions

From a hydrological aspect, floodplains are part of the drainage system of rivers and are periodically affected by transport of water and dissolved and particulate material. From an ecological point of view, they represent transition zones (ATTZ) that alternate between aquatic and terrestrial states and link river channels with permanent lentic bodies and permanently dry land. Most large river systems have geomorphological settings that produce floodplains that are large relative to the lotic surface area (Welcomme 1985), and, in unmodified watersheds, produce a pulse of long duration that results in extensive but temporary lentic areas covering the ATTZ. Conversely, flood pulses of short duration, which are typical of low-order streams or of some modified systems, are associated with ATTZ's that are frequently covered by flowing water for short periods.

Fig. 3. A section of lower Keduk Pool on the Upper Mississippi (A-D) with a projection of the stabilized system by the end of the century (E-H) (amplified data from R. V. Anderson, R. E. Sparks, J. W. Grobaugh, K. S. Luhinski, and R. W. Gordon).
The flood pulse is the driving force for river-floodplain system development through the dynamic equilibrium. The system responds to the rate of rise and fall and to the amplitude, duration, frequency, and regularity of the pulses. A variety of physical structures in combination with the flood pulse results in great habitat diversity. This diversity is coupled with the dynamic effect of the moving littoral, which extends the edge effects of the littoral over the entire floodplain, thereby rendering channel banks bordering lotic zones insignificant by comparison. Organisms tend to invade the floodplain from the terrestrial side also. Regular pulsing coupled with habitat diversity favors high diversity of aquatic and terrestrial plants and animals, despite considerable stress that results from the change between terrestrial and aquatic phases. 

Aquatic and terrestrial productivity of river-floodplain systems depend mainly on the nutrients status of the water and sediments, on the channel, and on the flood pulse. Cycles specific to the floodplain, however, are decoupled from some extent from the nutrient status of the main channel. The moving littoral provides permanent substrates, thereby allowing the rapid recycling of organic matter and nutrients and resulting in a productivity that we predict to be greater than if the ATTZ were either permanently inundated or dry. Primary production associated with the ATTZ is much higher than that of permanent water bodies in unmodified systems and can often extend that of permanent terrestrial habitats.

Transport of organic carbon from upstream catchment areas into the floodplain (signalling) is of little importance to the productivity of the system. Conversely, primary and secondary production of the floodplains is estimated to 20% of the main channels. A major component of energy transfer between floodplains and main channels is affected by animal migration, in particular of fish that migrate upstream for considerable distances. Some bird species transport nutrients from terrestrial areas or flood mudflats, where they feed, to floodplain lakes, where they rest and feed. Other species do the reverse. The main function of the river channel in relation to plants and animals in the river-floodplain systems is that of a migration route and dispersal route to access resources and refuges.

In conclusion, for those interested in the principal driving forces responsible for the structure, function, and evolutionary history of the biota in river-floodplain systems, we believe that the concept offered here will prove of heuristic rather than merely descriptive value. There is a fundamental dichotomy in the river-floodplain system: both continuous (e.g., the RCC) and batch processes occur. The latter, represented by the flood pulse concept, is dominant in systems with floodplains (ATTZs), in particular when the pulse is regular and of long duration. It is distinct because processes in floodplains do not depend on efficient processing of organic matter upstream, although their inorganic nutrients pool may be replenished with periodic lateral inflows of water and sediments from the main channel. The pulse concept differs in that the position of the floodplain in the system relative to the river network is not a primary determinant of the processes that occur, although hydrological circumstances do not normally favor floodplain development in extreme upper reaches. However, examples do occur in upper reaches, such as the Parnassal of the Paratib system and the extensive Bolivian and Peruvian floodplains in the Amazon.

This concept implies an approach to studying the system different from the traditional limnological paradigms for either lotic or lentic systems. The space and time scales appropriate for understanding the mechanisms differ from those relative to longitudinal processes in lotic channels. We hope that the flood pulse concept will help ecologists improve the design of studies and frame hypotheses that will lead more directly to a better understanding of river-floodplain systems. This is an urgent goal considering the modifications that continue to be proposed and that are sometimes put into practice in many tropical and temperate systems.

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(Addressees of personal communications follow references)