Riparian Ecosystems: Conservation of Their Unique Characteristics[1]

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Abstract.--Riparian ecosystems have two essential characteristics: laterally flowing water that rises and falls at least once within a growing season; and a high degree of connectedness with other ecosystems. Other pulses such as fire and hurricanes may also be important in ecosystem maintenance. Changes in hydroperiod or amplitude of water level fluctuation produce the most dramatic changes in riparian communities. Changes in neighboring ecosystems, which have high rates of exchange of energy and nutrients with riparian ecosystems, may also have significant effects.

INTRODUCTION

Riparian ecosystems occur in both fresh and salt water; not all have distinct channels; and dominant vegetation may vary from low, herbaceous growth to tall trees with high basal area (Table 1). Is there, then, a set of unique characteristics that justifies regarding riparian wetlands as a distinct class of ecosystems? This paper identifies two such characteristics and discusses the effects of human-induced perturbations on the stability of riparian ecosystems.

Table 1.--Examples of Riparian Ecosystems

	Fresh Water	Salt Water
Forested	River swamps Bottomland hardwoods Cypress strands Bosques	Riverine mangroves
Nonforested	Some marshes Some peatlands	Tidal marshes

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PULSES IN RIPARIAN ECOSYSTEMS

One characteristic that distinguishes riparian ecosystems from other wetland ecosystems is the lateral movement of water through the ecosystem together with water level fluctuation, comprising a significant pulse in the physical environment. This pulse may occur daily in coastal ecosystems, annually in temperate or seasonal ecosystems, or irregularly within a year. Perhaps the most important feature is that both high and low extremes occur within a single growing season. A riparian ecosystem at any time therefore has an upstream and a downstream end, although the directionality itself may be reversed.

Diversity in wetland ecosystems seems to be inversely proportional to the length of time during the growing season that soils are saturated. Crawford (1976) pointed out that species of trees that are flood-intolerant are unable to detoxify end-products of glycolysis in the roots because of anoxia. Flood-tolerant species can either decrease glycolytic activity in anoxic conditions or detoxify the end-products of glycolysis. Several such species are capable of withstanding a short flooding period, although the longer the hydroperiod, the fewer the number of tolerant species. Wistendahl (1958) observed that slight differences in topography and depth of flooding had a significant effect on vegetation species composition in a floodplain. Franz and Bazzaz (1977) documented the narrow range of elevations within which each tree species in a floodplain is found, reflecting small but distinct differences among species not only in tolerance of mature trees to flooding but in requirements for seed germination and seedling survival as well. Among the most flexible species of trees found in riparian ecosystems are cypress (*Taxodium distichum*) in the Southeast, box elder (*Acer negundo*) in the Southwest, and red maple (*Acer rubrum*) in the Northeast.

Riparian wetlands that are dominated by herbaceous plants also show zonation imposed by hydroperiod, although substrate may play an important role also. Sawgrass, wet prairie, and sloughs, for instance, are three major community types in the Everglades that are differentiated by hydroperiod, but that show site-to-site variation in species composition (Goodrick 1974).

The hydroperiod pulse may carry a pulse in nutrient input as well. However, peak nutrient availability may not necessarily coincide with peak nutrient input. Changes in pH and oxygen concentrations that accompany water level changes may affect availability of nitrogen, phosphorus, and other nutrients (see discussion by Klopatek 1978). Consequently, strategies for adapting to extremes in both moisture and nutrient availability may be common in riparian wetlands.

One unique characteristic of riparian wetlands is therefore the presence of moving water that carries with it a nutrient subsidy and that completes at least one cycle during a growing season. This pulse strongly affects both species composition and growth dynamics of the ecosystem.

Fire is another pulse that often affects riparian ecosystems. Ewel and Mitsch (1978) showed that fire is probably a common factor in many cypress ecosystems. Duever et al. (1976) suggested that in the absence of fire many of the cypress swamps in south Florida could eventually develop into mixed hardwood forest. More frequent fires would convert the swamps into shrubby marshes or sloughs. Hofstetter (1974) reported that fire is essential to the continued existence of sawgrass communities in the Florida Everglades.

Periodic incidence of fire is not restricted to southeastern riparian ecosystems. Killingbeck and Wali (1978) reported that the oldest trees in a North Dakota gallery forest were only 80 years old, even though the presence of the forest is recorded from presettlement times. They noted the observation of a long term local resident that prairie fires frequently invaded the forest, killing some of the larger trees.

When fire has been a long-term evolutionary force in an ecosystem, it very often becomes a subsidy as well, speeding decomposition and remineralization of the litter and keeping competing tree seedlings from assuming dominance (Mutch 1970). This may be particularly true in riparian ecosystems, where the effect of fire appears to be more selective than it is in upland ecosystems.

Another pulse that affects riparian ecosystems in coastal areas is provided by hurricanes, which blow in from offshore at irregular intervals, bringing high-speed winds and increased water and salinity levels many kilometers inland. A simulation model based on current biomass and metabolism data from mangrove ecosystems in south Florida predicted that these ecosystems would reach steady-state 23 years after starting from an early stage of succession (Lugo et al. 1976). These authors cited other reports on mangrove forests in south Florida and in Puerto Rico that suggested that maturity is reached after 20 to 25 years, and that the average hurricane frequency in this region is 20 to 23 years. The long-term periodic stress of high winds and subsequent increased salinity on coastal ecosystems may therefore have a strong influence on shaping metabolic patterns in an ecosystem and determining the level of complexity that it may reach.

These three pulses (flooding, fire and hurricanes) occur at short (less than one year), moderate (one to ten years), and long (20-25 years) intervals, respectively, yet each has a measurable effect on ecosystem structure and function. E. P. Odum (1971) pointed out that communities become adapted to such pulses and that their optimum function depends on them. The pattern of superposition of the variety of pulses to which a riparian wetland is exposed may clearly play a role in determining the levels of diversity and productivity that it achieves.

CONNECTEDNESS OF RIPARIAN ECOSYSTEMS

The second characteristic of riparian ecosystems that contributes to their uniqueness is their high degree of connectedness with other ecosystems. Waide and Webster (1976) reviewed the concept of connectedness, which is the number of links between organisms in an ecosystem. The concept is applied here to the next higher level, the number of links between ecosystems in a watershed. A riparian ecosystem by definition at any point receives inputs both from upstream and from the surrounding watershed and delivers them downstream, sometimes in an altered form. Nutrient and seed inputs are therefore important water-borne links between upstream (and upland) ecosystems and riparian ecosystems. Riparian ecosystems in turn may serve as seed sources for downstream ecosystems and may alter nutrient inputs as well, exporting them in more oxidized (or more reduced) forms.

Do animals provide another link between these communities? Hunt (1975) showed that terrestrial insects often form a significant proportion of the food of salmonid fishes in both lotic and lentic environments. W. E. Odum (1971) found that most of the sport and commercial finfish of the Gulf of Mexico depend at some stage in their life cycles on mangrove detritus. The rapidity with which insects reinvaded defaunated mangrove islands (Simberloff and Wilson 1969) suggests a high degree of connectedness of these ecosystems with neighboring ecosystems. Mangrove islands are not riparian ecosystems, but riverine mangroves would probably demonstrate the same response.

Bird concentrations in riparian wetlands are often very high. Hubbard (1977) reported that two river valleys in New Mexico support 16-17% of the entire breeding avifauna of temperate North America. Diversity is higher among water birds than land birds in Florida, in spite of significant losses of wetland habitat during the last century (Robertson and Kushlan 1974). Diversity of birds in a wetland is not necessarily related to vegetation diversity. Weller (1978) pointed out that variety in structure is more important than variety in vegetation composition to increasing diversity of birds nesting and feeding in marshes. Birds clearly provide important linkages between ecosystems, particularly in temperate climates where long-range migrations are common. The seasonal pattern of movement between types of ecosystems (aquatic, riparian and nonriparian wetlands, and terrestrial) is difficult to analyze, however. Nonmigratory populations may restrict their activities more to a single ecosystem. Howe (1977) described a strong relationship that had evolved between a bird and a tropical wet forest tree common in floodplain forests and theorized that plants that have specific and predictable habitat requirements and that have a particularly nutritious resource should be able to attract and establish coevolutionary relationships with foragers such as birds and insects.

Sheppe and Osborne (1971) found that less than half the species of mammals in the vicinity of the Kafue Flats along the Zambezi River regularly use the floodplain. Small mammals found on the floodplain, which is up to 40 km wide in places and floods to a depth of 5 m, either seek refuge from high water on emergent levees along the river or move long distances to the margins. Cowan and Holloway (1973) reported that 40% of the species of deer in the world that are threatened inhabit swamps, riparian forests, and floodplains that are located within a relatively arid environment. Some of these species have been able to adapt themselves to new environments, showing more plasticity than threatened species in upland environments. It seems more likely, then, that terrestrial vertebrates inhabiting riparian wetlands either restrict their movements to these areas or perhaps move outward into surrounding areas to feed. But upland vertebrates seldom invade the wetland areas.

Connectedness with upstream and downstream ecosystems is therefore an important characteristic of riparian wetlands. Most of the flow of energy and nutrients seems to be water-borne, but animals may provide significant linkages with surrounding ecosystems as well. Net energy flows associated with animal populations seem to be from upland to wetland ecosystems and from wetland to aquatic ecosystems.

STABILITY OF RIPARIAN ECOSYSTEMS

Waide and Webster (1976) conducted an analysis of the effects of different levels of connectedness on ecosystem stability, using a linear model for their analysis. They analyzed neighborhood stability, which is related to the magnitude of the response of the system to its forcing functions. They concluded from this analysis that when interrelationships in an ecosystem are primarily donor-controlled, rather than recipient-controlled, higher degrees of connectedness lead to greater stability. Their hypothesis is applicable at the watershed level, and the relationships between ecosystems in a watershed may actually fit a linear model more closely than do the relationships between organisms in an ecosystem. The primary linkages in a watershed are the unidirectional flows of water-bearing nutrients. Linkages provided by animal movements are nonlinear (e.g., simultaneously donor and recipient-controlled) but are probably less significant to the total energy flow.

Waide and Webster's analysis suggests that wetlands that are fed by more diverse watersheds may have higher stability. This is supported by the observation that terrestrial vertebrates in particular may move out from riparian wetlands but not necessarily into them, recalling Margalef's (1963) principle that energy tends to flow toward the more mature system in a mosaic of different systems, and assuming that greater stability comes with maturity.

Stability, however, may also be evaluated as the response of a system to a human-induced perturbation. In the analogy between an ecosystem and a watershed, the river and associated wetlands that drain the watershed may be equivalent to top carnivores, since water and the nutrients it carries converge on these ecosystems in the same way that energy in the stricter sense converges on the higher trophic levels (H. T. Odum, in press). Presumably, top carnivores would suffer more than lower trophic levels from perturbations affecting the ecosystem (see discussion in Ricklefs 1976). Riparian wetlands, therefore, may be relatively stable in an unperturbed world, but actually occupy sensitive niches in the watershed system when human-induced perturbations are considered.

Stability relative to such perturbations is believed to be comprised of two components: resistance and resilience (Webster et al. 1975). Resistance is defined as the ability of an ecosystem to withstand change from perturbation, and resilience is the ability of an ecosystem to return to its initial state after change induced by perturbation. Management of riparian ecosystems must therefore take into account both aspects of stability in determining the overall impact of management practices.

MANAGEMENT OF RIPARIAN ECOSYSTEMS

The benefits provided by riparian ecosystems can be summarized as: 1.) benefits that can be taken advantage of without destroying the essential characteristics of the ecosystem (fish and wildlife production, flood control); and 2.) benefits that may be extracted from the ecosystem only by leaving a scar of variable magnitude and duration (navigation, reservoir siting, timber production). The stability of each of the major kinds of ecosystems will be analyzed with respect to its abilities to provide the second class of benefits.

Hydroperiod Manipulation

Changes in hydroperiod may be brought about by either direct or indirect actions. Direct actions would include flooding or draining of the basin, and evaluation of their effects may be fairly straightforward. Channelization moves water more rapidly from upstream to downstream, and might drain the surrounding riparian ecosystem, allowing establishment of upland species. However, development that occurs elsewhere in the watershed may also have significant effects on water flows, such as by increasing runoff or diverting runoff directly into a water source. Zoning of land use activities and development clearly must be implemented on a watershed basis in order to guard more effectively against these indirect effects.

The most sensitive characteristic of riparian ecosystems is clearly the dependence of species composition on hydroperiod and depth of flooding. Disturbance of hydroperiod may drastically change the ability of floodplain species to maintain their dominance. It is apparently not always possible to detect the seriousness of a change until trees die; many will continue growth and not demonstrate stress until their abrupt death (Green 1947). Tolerances of individual species to changes in hydroperiod have been documented (see review by Gill 1970), and it should be possible to rank the tolerances of different floodplain communities to change.

Community tolerance may be inversely proportional to diversity. In the Southeast, cypress-dominated ecosystems may sustain the longest hydroperiod, but there are clearly limits to their flexibility: regeneration is not possible without an occasional complete drawdown, and significant increases in depth may not be tolerated for long period. Both forested and herbaceous wetlands are probably equally intolerant to flooding and drainage, since in both cases decreased hydroperiod would make a site habitable to far more species. Resistance and resilience to changes in hydroperiod may therefore be low. Resilience may actually be lower than resistance because germination and growth requirements of seedlings are often more stringent than survival requirements of the adult plants. However, if the original hydroperiod is restored, resilience may be fairly high.

Increased Nutrient Loading

Wetlands are currently favored sites for testing the ability of natural ecosystems to absorb the nutrients in secondarily treated wastewater, reducing the need for constructing expensive advanced wastewater treatment systems. Both forested and nonforested wetlands throughout the country have proven to be able to absorb excess nutrients without substantial harm to ecosystem structure or function. Nessel (1978) showed that cypress trees in a sewage-enriched cypress strand sustained increased growth rates for more than 40 years. Both ash and cypress increased growth rates over a 20-year period in a swamp containing ash, (Fraxinus profunda), cypress, and black gum (Nyssa sylvatica) trees (Boyt 1976). Sloey et al. (1978) reported continued reduction of nitrogen and phosphorus levels in agricultural runoff going through a marsh over a 50-year period, during which phosphorus appeared to accumulate in the sediments.

In short term studies, net productivity of a freshwater marsh increased over a one-year period of sewage application in central Florida (Dolan 1978). Whigham and Simpson (1976) found that some herbaceous species in a freshwater tidal marsh were eliminated from enclosures receiving effluent. Wentz (1976) reported no significant effect of sewage effluent disposal on species composition in a Michigan peatland.

In all cases, sediments appeared to serve as the primary nutrient sink. In the sewage-enriched systems, nutrient concentrations increase in the foliage of the trees and in roots of both trees and herbaceous species. Dorge (1977) found that phosphorus storage in the sediments of a riverine cypress swamp in Illinois far exceeded storage in all other compartments in the ecosystem. Sediments in riparian ecosystems therefore appear to be the primary absorbing unit in both undisturbed and sewage-enriched riparian ecosystems. However, some river swamps may have little or no sediment accumulation, although it is not clear whether increased nutrient loading would damage such systems.

Riparian ecosystems seem to be capable of tolerating increased nutrient loading without substantial changes in tree species composition, although composition of herbaceous species may change. Sediments appear to be capable of storing large quantities of phosphorus in particular. Restrictions on use of wetlands for sewage disposal are probably more closely related to detrimental effects of increased hydroperiod than to nutrient loading itself.

Fire Regulation

Changes in fire periodicity and/or severity may be critical. Gunderson (1977) found that periodic surface burns tend to arrest succession in a cypress swamp, but that a severe burn caused by increased growth rates of understory because of logging or drainage may completely destroy both hardwood and cypress stands. Both too much and too little fire must therefore be guarded against. However, because fire periodicity is usually more random than hydroperiod, small changes may be less damaging.

Resistance to change in fire periodicity in an otherwise unperturbed system may be moderate. Increased fire incidence will destroy fuel resources and may prevent seedling establishment. Decreased fire incidence may allow fuel to accumulate, increasing the severity of a subsequent fire. Resilience, however, will depend on the existence of a seed source. Any portion of a riverine system may therefore be resilient as long as propagules are continually washed from upstream to replace losses from downstream sections. Herbaceous ecosystems that depend more on wind or animals to transport propagules may be more resilient. Least resilient are upstream portions of ecosystems and ecosystems with large areas and slow flows, where migration of propagules to the burned area may be slow. Resilience in any riparian ecosystem will decrease with the severity of the fire, especially if peat beds are destroyed (Ewel and Mitsch 1978).

Some geographic areas, such as the Southeast, are clearly more sensitive than others to changes in fire periodicity. Hofstetter (1974) pointed out that lightning-caused fires in Florida were historically most common during the summer wet season, and probably did not cause extensive damage. Charcoal and ash deposits that have been found deep in peat deposits indicate that fires occasionally started before the summer rains or during an exceptionally dry spell and probably were very destructive. The combined effect of increased incidence of human-caused fire and lowering of water tables has been far more dry season fires, which tend to be much more destructive. In areas such as the prairie states where fire is presently less prominent an ecological factor than it was in the past, it would be useful to document the effect of fire removal on the remaining natural ecosystems.

Timber Harvest

Bottomland hardwoods and floodplain forests have traditionally been favored sites for harvesting timber. However, removal of most of the large old trees in the late nineteenth and early twentieth centuries was an extractive process, and sustained yield was not an object. Moreover, dikes built to gain access to trees in the broader forests often affected water flow patterns. Resistance to timber harvest actually depends only on accessibility of the timber, and few large swamps have not been cut over at least once.

Resilience of floodplain forests seems to be fairly high, although a combination of high-grading and site alteration may have increased regeneration time for many of the forests. Lee (1945) found that canopy closure in forests growing on natural levees in floodplain forests in Indiana occurred after 36 years. Turner (1931) reported that American elm (Ulmus americana) and silver maple (Acer saccharinum) achieved dominance in 40 years in communities developing on artificial levees along the Illinois River. Cottonwoods (Populus deltoides) 40 feet tall were found together with black willow (Salix nigra) on a 15-year-old island in the Wabash River (Lindsey et al. 1961). During the first winter after a drawdown of the Rodman Reservoir in the former basin of the Oklawaha River, Florida, cypress seedlings proliferated along the banks, suggesting that forest regrowth would be fairly rapid if the natural hydroperiod were restored. When a forested area upstream of a harvested area is left intact, it will act as a seed source for downstream areas. If these riverine forests are habitats for rare or endangered populations, however, removal of large sections of forest should be avoided.

Mangrove forests are able to recover rapidly from localized cutting. However, changes in salinity that may accompany drainage and cutting may reduce seed germination (Holdridge 1940).

Resilience in forests with a broad expanse and little topographical change may be more dependent on seed storage in the sediments and less on upstream seed sources. Alteration of water flow by diking may decrease seed access to all areas of the swamp and may cause ponding, decreasing the probability that seeds will germinate. Construction of dikes should therefore either include culvert systems or be oriented to disturb water flow patterns as little as possible. Clear cuts in such areas should be restricted to small areas so that seed transportation is rapid. One large paper company in Florida is currently experimenting with the use of 16-hectare clearings in bottomland swamp. Their plan includes a rotation scheme and buffer strips. Such a design may be economical on a long-term basis, especially if buffer strips can be chosen specifically to include seed trees of the most desireable species.

CONCLUSIONS

One unique characteristic, hydroperiod (and, in some cases, fire), determines the resistance of the community. The shorter the hydroperiod, the less tolerant an ecosystem will be to an increase in hydroperiod; decreasing hydroperiod will probably cause changes in any riparian ecosystem. Another unique characteristic, connectedness, determines resilience. Connectedness, however, is a double-edged sword, for while it ensures seed and nutrient inflow after a disturbance, it also increases the battery of impacts to which an ecosystem may be exposed. In preserving the roles that these ecosystems play in a watershed, therefore, the periodic influence of flooding and fire must be maintained. Connectedness may be depended upon to speed regrowth of a harvested ecosystem, but its effect on increasing sensitivity to impacts generated elsewhere in the watershed must be recognized as well.

LITERATURE CITED

Boyt, F. L. 1976. A mixed hardwood swamp as an alternative to tertiary wastewater treatment. Master's thesis, Univ. of Florida, Gainesville.

Cowan, I. McT., and C. W. Holloway. 1973. Threatened deer of the world: Conservation status. Biol. Conserv. 5:243-250.

Crawford, R. M. M. 1976. Tolerance of anoxia and the regulation of glycolysis in tree roots. Pages 387-401 in M. G. R. Cannell and F. T. Last (eds.). Tree Physiology and yield improvement. Academic Press, N.Y.

Dolan, T. J. 1978. Effect of secondarily treated effluent on a central Florida freshwater marsh ecosystem with estimation of phosphorus budget. Master's thesis, Univ. of Florida, Gainesville.

Dorge, C. L. 1977. Phosphorus cycling in a southern Illimois cypress swamp. Master's thesis, Ill. Inst. Tech., Chicago.

Duever, M. J., J. E. Carlson, L. A. Gunderson, and L. Duever. 1976. Ecosystem analysis at Corkscrew Swamp. Pages 707-737 in H. T. Odum and K. C. Ewel (eds.). Cypress wetlands for water management, recycling and conservation. Third Annual Report to National Science Foundation and the Rockefeller Foundation. Center for Wetlands, Univ. of Fla., Gainesville.

Ewel, K. C., and W. J. Mitsch. 1978. The effects of fire on species composition in cypress dome ecosystems. Fla. Sci. 41:25-31.

Franz, E. H., and F. A. Bazzaz. 1977. Simulation of vegetation response to modified hydrologic regimes: A probabitistic model based on niche differentiation in a floodplain forest. Ecology 57:176-183.

Gill, C. J. 1970. The flooding tolerance of wood species - a review. For. Abstr. 31: 671-688.

Goodrick, R. L. 1974. The wet prairies of the northern Everglades. Pages 47-51 in P. J. Gleason (ed.). Environments of south Florida: Present and past. Miami Geol. Soc. Mem. 2.

Green, W. E. 1947. Effect of water impoundment on tree mortality and growth. J. For. 45: 118-120.

Gunderson, L. H. 1977. Regeneration of cypress, *Taxodium distichum* and *Taxodium ascendens*, in logged and burned cypress strands at Corkscrew Swamp Sanctuary. Master's thesis, Univ. of Florida, Gainesville.

Hofstetter, R. H. 1974. The effect of fire on the pineland and sawgrass communities of southern Florida. Pages 201-212 in P. J. Gleason (ed.). Environments of south Florida: Present and past. Miami Geol. Soc. Mem. 2.

Holdridge, L. R. 1940. Some notes on the mangrove swamps of Puerto Rico. Caribb. For. 1:19-29.

Howe, H. F. 1977. Bird activity and seed dispersal of a tropical wet forest tree. Ecology 58:539-550.

Hubbard, J. P. 1977. Importance of riparian ecosystems: Biotic considerations. Pages 14-18 in R. R. Johnson and D. A. Jones (tech. coords.). Importance, preservation and management of riparian habitat: A symposium. USDA For Serv. Gen. Tech. Rep. RM-43. Rocky Mtn. For. Range Exp. St., Fort Collins, Colo. 80521

Hunt, R. L. 1975. Use of terrestrial invertebrates as food by salmonids. Pages 137-151 in A. D. Hasler (ed.). Coupling of land and water ecosystems. Springer-Verlag, New York.

Killingbeck, K. T. and M. K. Wali. 1978. Analysis of a North Dakota gallery forest: Nutrient, trace element, and productivity relations. Oikos 30:29-60.

Klopatek, J. M. 1978. Nutrient dynamics of freshwater riverine marshes and the role of emergent macrophytes. Pages 195-241 in R. E. Good, D. F. Whigham, and R. L. Simpson (eds.). Freshwater wetlands: Ecological processes and management potential. Academic Press, New York.

Lee, M. B. 1945. An ecological study of the floodplain forest along the White River system of Indiana. Butler Univ. Bot. Stud. 7:155-175.

Lindsey, A. A., R. O. Petty, D. K. Stirling, and W. van Asdell. 1961. Vegetation and environment along the Wabash and Tippecanoe Rivers. Ecol. Monogr. 31:105-156.

Lugo, A. E., M. Sell and S. C. Snedaker. 1976. Mangrove ecosystem analysis. Pages 113-145 in B. C. Patten (ed.). Systems analysis and simulation in ecology. Academic Press, New York.

Margalef, R. 1963. On certain unifying principles in ecology. Am. Nat. 97:357-374.

Mutch, R. W. 1970. Wildland fires and ecosystems - A hypothesis. Ecology 51:1046-1051.

Nessel, J. 1978. Distribution and dynamics of organic matter and phosphorus in a sewage-enriched cypress swamp. Master's Thesis. Univ. of Florida, Gainesville.

Odum, E. P. 1971. Fundamentals of ecology. 3rd ed. W. B. Saunders Co., Philadelphia. 574 pp.

Odum, H. T. The value of wetlands as domestic ecosystems (to be published in J. Kusler (ed.). Wetlands Symposium. Envir. Law Inst., Washington, D. C.

Odum, W. E. 1971. Pathways of energy flow in a South Florida estuary. Univ. Miami Sea Grant Tech. Bull. 7.162 pp.

Ricklefs, R. E. 1976. The economy of nature Chiron Press, Portland, Ore. 455 pp.

Robertson, W. E., Jr., and J. A. Kushlan. 1974. The southern Florida avifauna. Pages 414-452 in P. J. Gleason (ed.). Environments of south Florida: Present and past. Miami Geol. Soc. Mem. 2.

Sheppe, W., and T. Osborne. 1971. Patterns of use of a floodplain by Zambian mammals. Ecol. Monogr. 41:179-205.

Simberloff, D. D., and E. O. Wilson. 1969. Experimental zoogeography of islands. The colonization of empty islands. Ecology 50: 278-296.

Sloey, W. E., F. L. Spangler, and C. W. Fetter, Jr. 1978. Management of freshwater wetlands for nutrient assinilation. Pages 321-340 in R. E. Good, D. R. Whigham, and R. L. Simpson (eds.). Freshwater Wetlands: Ecological processes and management potential. Academic Press, New York.

Turner, L. M. 1931. Plant succession on levees in the Illinois River Valley. Trans. Ill. State Acad. Sci. 24:94-102.

Waide, J. B., and J. R. Webster. 1976. Engineering systems analysis: Applicability to ecosystems. Pages 329-371 in B. C. Patten (ed.). Systems analysis and simulation in ecology. Academic Press, N. Y.

Webster, J. R., J. B. Waide, and B. C. Patten. 1975. Nutrient recycling and the stability of ecosystems. Pages 1-27 in F. G. Howell, J. B. Gentry, and M. H. Smith (eds.). Mineral cycling in southeastern ecosystems. ERDA Symp. Series, CONF-740513.

Weller, N. W. 1978. Management of freshwater marshes for wildlife. Pages 267-284 in R. E. Good, D. F. Whigham, and R. L. Simpson (eds.). Freshwater wetlands: Ecological processes and management potential. Academic press, N. Y.

Wentz, A. W. 1976. The effects of simulated sewage effluents on the growth and productivity of peatland plants. Ph.D. Diss., Univ. of Michigan, Ann Arbor.

Whigham, D. F. and R. L. Simpson. 1976. The potential use of freshwater tidal marshes in the management of water quality in the Delaware River. Pages 173-186 in J. Toubier and R. W. Pierson (eds.). Biological control of water pollution. Univ. of Pennsylvania Press, Philadelphia.

Wistendahl, W. A. 1958. The floodplain of the Raritan River, New Jersey. Ecol. Monogr. 28:129-153.