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CHANGES IN THE FUNCTIONING OF WETLANDS ALONG ENVIRONMENTAL GRADIENTS

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Abstract: One of the prevalent gradients in wetlands is the continuum of depth and frequency of flooding. While much emphasis has been placed on the importance of hydrology as a driving force for wetlands, few other perspectives have emerged to demonstrate unifying patterns and principles. In contrast to the wetness continuum, the functioning of wetlands can be separated into two broad categories: (1) landscape-based transitions that occur within a wetland or group of similar wetland types and (2) resource-based transitions that allow comparisons of the flow of water and processing of nutrients among very different wetland types. Landscape-based continua include the transition from upstream to downstream in riverine wetlands and between aquatic and terrestrial ecosystems within a wetland. Along the upstream-downstream continuum, sources of flood-water delivery change dominance from ground-water discharge and overland runoff, as in low order streams, to dominance by overbank flooding, as in high order streams. With increasing size, properties related to the aquatic-to-terrestrial transition are replaced by properties related to wetland-atmospheric exchanges and by landscape maintenance, the latter not normally acknowledged as a wetland function. Resource-based continua include the extremes of (1) sources of water to wetlands (precipitation, overland flow, and ground water) and (2) the variation in inflows and outflows of nutrients and sediments. Emphasis on water source forces consideration of controls beyond the wetland's boundaries. A broader view of biogeochemical functioning is gained by categorizing wetlands into groups based on the exchange of nutrients and sediments among landscape units rather than on serving as a sink or source for a particular element. Based on this analysis, the less frequently flooded or saturated portions of wetlands are no less functionally active than wetter portions; the functions are simply different. Efforts to classify wetlands according to their hydroperiod do little to reveal their fundamental properties.

Key Words: environmental gradients, landscape continua, landscape maintenance, non-point source, stream hydrology, stream order, water quality.

INTRODUCTION

Wetlands are often described as transitional ecosystems that represent continua between strictly aquatic and strictly terrestrial ecosystems. The nature of such environmental gradients in ecosystems was hotly debated in the early decades of this century by Clements (1916), who overstated the integrity of the biotic community and interactions among species populations, and Gleason (1926), who countered that the abundance of individual species responds only to prevailing environmental conditions (Hagen 1992). These opposing perspectives can be applied to wetlands by paraphrasing the debate as a question:

"Are wetland ecosystems and the continuum that they represent along moisture gradients discrete assemblages (i.e., recognizable integrated units or communities) or are they simply a coexistence of organisms that opportunistically and independently colonize an area that has abiotic features conducive to their life history characteristics?"

A narrow view of the Gleasonian approach suggests that as flooding becomes less frequent along a wetland continuum, reduced soil moisture and relief from waterlogging stressors progressively result in the establishment of more mesophytic or xerophytic species. This places emphasis on the response of plant species to the wet-to-dry continuum. A narrow view of the Clementsian approach is that discrete changes will occur in biotic communities along the same continuum.

To some extent, these extreme views represent a false dichotomy for wetlands, in part because undue emphasis is placed on the single variable of wetness, and in part because the dichotomy oversimplifies some of the more complex ecosystem properties such as energy flow and food-web support, sediment balance and biogeochemical cycling, and ecosystem interactions and landscape-level patterns. By placing undue emphasis on the wetness gradient, more specific adaptations to stress tend to be obscured, such as responses of plants to soil-water sulfide toxicity (Mendelssohn and McKee 1988, Koch and Mendelssohn 1989), iron toxicity (Benckiser et al. 1984), and growth effects due to ethylene production (Tang and Kozlowski 1984). Although hydroperiod (duration and timing of flooding) is a common metric that captures the temporal dimension of wetness, it does not provide a scale for non-flooded conditions in which the saturated zone migrates vertically as the water table fluctuates below the surface. However, even consideration of below-surface saturation does not encompass relevant properties such as the position of the wetland in the landscape, the sources of water and its elemental composition, and the size of the wetland itself. While Gleason and Clements were trying simply to *explain how* ecosystems change along environmental gradients, the current challenge presented by wetlands is to better *understand why* different wetlands function[1] differently and how their functioning responds to natural and human-induced disturbances and stressors.

If it is true that wetter wetlands either possess more functions or carry them out more intensively than drier ones, then evidence should be developed to demonstrate this. In contrast, if functions change for other reasons or in ways not predictable from a wetness index (i.e., hydroperiod), the factors truly responsible for functional changes need to be evaluated for how they vary among wetland types and not just between the wet and dry extremes of a single wetland.

The gradients or continua chosen for discussion here fall into two broad categories: (1) landscape-based continua that vary within a wetland or geographically connected network of wetlands and (2) resource-based continua that allow comparison of functioning between disparate wetland types. Of the landscape- based continua, the upstream-downstream gradient is the most complex and is most apparent in riverine wetlands (i.e., floodplains). The aquatic-to-upland transition is the most common and familiar and most directly reflects the wetness variable. In contrast, resource-based continua are more conceptual and need not be geographically restricted. The examples discussed depict wetlands as donating, receiving, and conveying water. The nutrient and sediment analysis goes beyond the concept that wetlands function merely as sinks by providing a more objective framework for assessing the relationship between wetlands and their inputs and outputs.

LANDSCAPE-BASED FUNCTIONING

Transitions between Floodplains of Low Order and High Order Streams

Flood-water storage and water-quality maintenance are two well-established functions of riverine wetlands. However, there has been little information synthesized on whether and how these functions may change along the continuum from streamside riparian zones in head-water regions (first order streams) to broad floodplains such as those along the Mississippi River (tenth order). As the size of floodplains (considered here equivalent to wetlands) covaries with stream order and hence discharge, so does the ratio between two dominant sources of water delivered to floodplain surfaces.

Before these sources are examined, it is first necessary to establish a relationship between stream order and floodplain surface area. Figure 1a illustrates the pattern of a hypothetical drainage network that can be classified as first, second, and third order streams, etc. Length and number of streams are inversely proportional to stream order as estimated by Leopold et al. (1964) in Table 1. From their estimates of length and number of streams for each order in the United States, I made assumptions about corresponding floodplain widths in order to roughly estimate surface areas. I assigned a floodplain width of 3 m to first order streams and a doubling thereafter with each increment in stream order (Table 1). Note that no data are known to be available to validate these assumptions. While other reasonable estimates would result in different details of specific widths and changes in width, the magnitudes and direction of change would be similar enough to allow the same conclusions to be drawn. These metrics were used to estimate total floodplain surface area for each stream order by multiplying the total length times the chosen floodplain width. The distribution of surface area estimates among stream size classes changes little, from 4,449 km^2 to 9,391 km^2, slightly greater than a doubling, while the length dimensions change by orders of magnitude (Table 1).

The assumptions and calculations above provide insight into how riverine floodplain wetlands function in water quality improvement with possible implications for their management and protection. One could ask if different emphasis should be placed on different stream orders in a program to promote the use of riparian zones as sinks for nutrients or sediment. Unless precluded by some overriding policy reason, it would seem that each stream order should be given roughly

[1] Functioning (or function) is used to describe phenomena such as flood-flow alteration, biogeochemical cycling, and habitat maintenance including contributions to biodiversity. The emphasis in this paper is on hydrology at the landscape level and on sources and sinks of nutrients and sediments. Functioning continues to occur whether or not society utilizes the wetland. Values of wetlands, in contrast, are the societal perception of the functioning of wetlands. Values change depending on culture, technology, and other market and nonmarket forces while functioning remains unaffected. Most functions ascribed to wetlands have corresponding societal value.

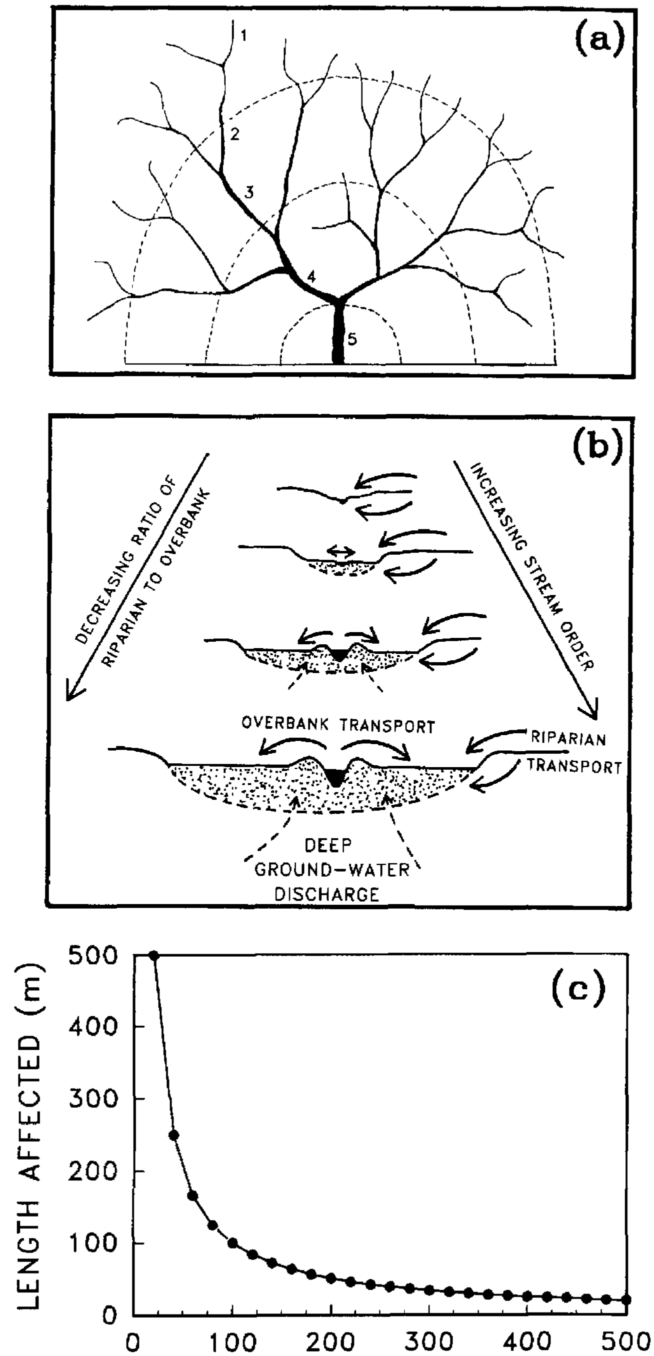

Figure 1. (a) Drainage network showing stream order following the nomenclature of Strahler (1952). (b) Cross sections of riverine wetland (floodplains) showing the downstream trend in overbank transport and riparian transport of water to the floodplain surface. Although deeper ground-water discharge is important in maintaining base flows, it assumes relatively less importance during flood events in comparison with non-channelized overland runoff and surficial ground-water sources. (c) Change in length of floodplain affected by 1 hectare of disturbance as a function of floodplain width.

Table 1. Relationship between stream order and other dimensions of stream configuration. First 4 columns are from Leopold et al. (1964).

Stream Order	Number	Average Length (km)	Total Length (km)	Estimated Flood-plain Width (m)	Flood-plain Surface Area (km^2)
1	1,570,000	1.6	2,526,130	3	7,578
2	350,000	3.7	1,295,245	6	7,771
3	80,000	8.5	682,216	12	8,187
4	18,000	19.3	347,544	24	8,341
5	4,200	45.1	189,218	48	9,082
6	950	103.0	97,827	96	9,391
7	200	236.5	47,305	192	9,082
8	41	543.8	22,298	384	8,562
9	8	1,250.2	10,002	768	7,681
10	1	2,896.2	2,896	1,536	4,449

equal consideration because of the small differences in floodplain area.

However, a very different conclusion is reached if one considers how the water quality functions of riparian wetlands differ across a continuum of stream orders. This difference is determined by the source of water in flood events and the manner in which water is delivered to the wetland surface. Besides precipitation, which is virtually a constant for wetlands within a given climatic region, the ratio of riparian transport to overbank transport decreases rapidly from upstream to downstream (Figure 1b). (Riparian transport is the movement of water from the upland to the floodplain by nonchannelized overland flow and by ground-water contributions to quickflow following storms. Overbank transport is flooding that results from discharge exceeding bankfull capacity.) This assumes that, with successive increments in stream order, riparian transport to the floodplain remains roughly constant per unit of stream length, while overbank transport to the floodplain increases with increasing stream order because of increasing discharge downstream.

Before identifying which stream orders should receive priority in management for water quality improvement, we first should review the processes that contribute to water quality functioning of riverine wetlands. Several studies have verified that so-called "riparian buffers" or streamside and floodplain zones of vegetation are highly active in reducing nutrient and sediment concentrations of overland and subsurface flows moving from agricultural uplands to the channels of low order streams. Work done independently in Georgia (Lowrance et al. 1984a, 1984b), at two sites in North Carolina (Jacobs and Gilliam 1984, Cooper et al. 1987, Cooper and Gilliam 1987), and in Maryland (Peterjohn and Correll 1984) all illustrate that riparian transport, as defined above, is not only the major pathway by which water from uplands is delivered to wetland surfaces, but the upland-wetland interface is a major sink for potential water pollutants such as nitrate, ammonium, particulate and dissolved phosphorus, and sediments. Except for the dissolved pollutants that may be transported by deeper aquifers to the stream channel, riparian transport is virtually the only pathway by which non-point-source pollutants are transported to floodplain surfaces. In contrast to riparian transport, channelized flow bypasses contact with the floodplain until episodes when discharge exceeds channel capacity (Whigham et al. 1988). (Nutrient and sediment removal in the studies cited was not restricted to jurisdictional wetlands but occurred also in the slopes between agricultural fields and the floodplain.)

The relatively greater importance of riparian transport in nutrient removal and sediment deposition can be illustrated by assessing the consequences of applying a fixed area of disturbance to a riparian wetland on a low order stream and one applied to a high order stream. Figure 1c is a plot of the dimensions of floodplain wetlands of 1 ha in surface area with varying widths and lengths. The curve begins at a floodplain that is 20-m wide and 500 m in length and ends downstream with a floodplain that is 500-m wide and 20 m in length. Now assume that the 1 ha is disturbed by draining, permanently removing forest cover, paving the surface with impervious surface, or filling with spoil. The question becomes, "How is the riparian functioning of nutrient removal and sediment deposition affected at different points along the curve?" The shape of the curve shows that the length affected is very sensitive to small changes in floodplain width below 150 m. With diminishing width of floodplain, the effect of a 1-ha disturbance exponentially increases the length affected. Alternatively stated, for floodplains 150-m wide or greater (roughly a fifth order stream, Table 1), there is correspondingly minor change in the length of floodplain affected (less than 75 m) by disturbance.

Assuming that riparian transport is the most critical step in water quality improvement of non-point runoff, the shape of the curve in Figure 1c suggests that more emphasis should be placed on avoiding impacts to wetlands associated with low order streams than those next to higher order streams. In fact, the steepness of the curve argues that the greatest emphasis be placed on maintaining the integrity of first and other low order streamside environments for water quality improvement because a given area of disturbance will affect them proportionately more than wetlands of higher order streams. Hence, it is not simply the *surface area* of wetland that should remain the focus of attention but also the *length* of this resource. Management programs for wetlands that are oriented to protect water quality ought to reexamine their use of surface area units (hectares, km^2, etc.) in setting goals and should consider instead using units of length (meters, kilometers). Inventories that track temporal changes in wetland area alone fail to express gains and losses in the most meaningful terms.

The order-of-magnitude differences in length with increasing stream order (Table 1), indicate that length of riparian wetland is a better index of potential for enhancing water quality than area. In contrast to the argument made earlier for distributing management efforts approximately evenly among stream orders, lower order streams are where efforts would best contribute toward meeting goals of improved water quality in the context of non-point sources of pollution. This perspective is antithetical to the Nationwide Permit No. 26 (Section 404 of the Federal Water Pollution Control Act), which authorizes up to 10 acres (4.0 ha) of filling and associated activities in headwater and isolated wetlands.

Transitions between Aquatic and Terrestrial Ecosystems

In one of the most widely accepted definitions of wetlands, they are portrayed as "transitional between terrestrial and aquatic systems" (Cowardin et al. 1979). Several functional effects of this transition emerge as the shape and the size of wetlands vary. The shape of wetlands, which influences the edge-to-area ratio, may be important for the relative success of interior and edge species (Diamond 1975, 1976). Shape also is related to contiguity, especially important for the movement of animals in riparian corridors (Harris 1985, Gosselink and Lee 1989). The importance of wetland size is well established for large, wide-ranging animals such as black bear (Hellgren and Vaughn 1987). Large size is a dominant attribute of extensive wetlands such as the Everglades of Florida, the lower Mississippi River Delta marshes and swamps, the pocosin peatlands of southeastern U.S.A., the extensive peatlands of the boreal and northern temperate regions of North America and Eurasia, and the tundra of the Arctic.

What has not been addressed by these examples is the consequences of losing transitional properties as size increases. In other words, what alternative properties do wetlands acquire that may compensate for the loss of transitional functions, such as the removal of sediments and nutrients from runoff and the interspersion of habitats along ecotones? Transitional properties are replaced instead by those related to atmospheric exchanges. For example, extensive boreal peatlands have a demonstrated capacity to neutralize acid deposition (Bayley et al. 1986). Peatlands of recently glaciated regions are one of the few large areas on Earth that continue to be a significant atmospheric sink for carbon dioxide (Harden et al. 1992). Each of these two functions is dependent on size, not on transitional properties.

Landscape maintenance is yet another function of extensive peatlands. It takes on two forms. The first is control over surface topography, which, in turn, affects drainage patterns. Patterned fens and bogs represent the epitome of this function whereby peat accumulation alters drainage patterns and raises water tables (Sjörs 1961). The peatland literature is rife with papers (1) describing cross-sectional profiles that show a much more varied topography before peat deposition, and (2) illustrating feedback controls among topography, accretion of peat, hydrology, water chemistry, and species composition of the plant community (Moore and Bellamy 1974). Because such peatlands not only change landscape patterns but become the landscape itself, all other wetland functions are derived from landscape maintenance.

Landscape maintenance reaches its greatest significance and is best revealed where the very existence of landscape would be threatened were it not for the continuation of landscape functions. This occurs where rising sea level intersects land that had originally accumulated peat under the influence of local atmospheric and drainage controls. Rather than becoming submerged and transforming from emergent wetland to the open water of an estuary, accretion of peat keeps pace with the rate of rising sea level to maintain emergent wetland. This has been described for a portion of North Carolina's pocosins as part of the overall interaction of wetlands and rising sea level (Brinson 1991).

The landscape functions just described have one thing in common: they occur where the area of wetlands far exceeds that of uplands. Unlike more typical landscapes where wetlands occupy 1 to 10 percent of the surface area, the ratio between wetlands and uplands is reversed. In each of the examples cited above, large portions of the wetlands are publicly owned as national wildlife refuges and national parks. The functions carried out by these large land holdings are highly dependent on size.

RESOURCE-BASED CONTINUA

Up to this point, properties of wetlands have been emphasized that transcend the notion that they are merely transitional phases of aquatic and terrestrial end members. The two gradients described below conform even less to continua of wetness. In the first case, wetlands fall into three categories: those that supply water to drainages downslope from them, those that receive water primarily from ground water, and those that transport large volumes of water across surfaces from one location to another in the landscape. In the second gradient, wetlands are arrayed according to the relative strengths of their inflows and outflows of nutrients and sediments.

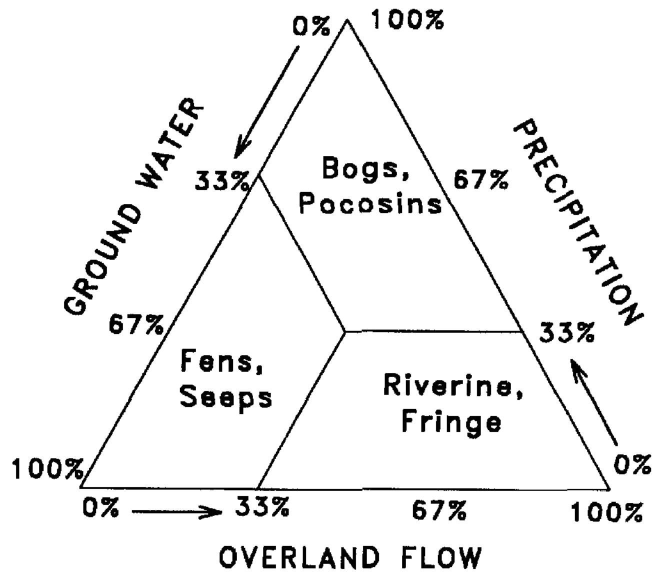

Figure 2. Ternary diagram illustrating the three sources of water to wetlands and their probable relationship to several wetland types.

Functional Variations in Response to Sources of Water

Wetlands can be classified by the relative importance of three sources of water: precipitation, ground water, and overland (surface) flow (Figure 2). At one extreme, precipitation-dominated wetlands, especially ombrotrophic bogs, are poor in nutrients, have low primary productivity and decomposition rates, and do not support extensive food webs (Moore and Bellamy 1974). Because they are isolated from influxes originating from overland transport of nutrients and sediments, they have little opportunity to influence the quality of ground water and surface water; hence, their interactions with the atmosphere through acid deposition and carbon dioxide exchanges become a dominant group of functions as described above. Because the balance between precipitation and evapotranspiration determines water storage in these wetlands, they may be more directly affected by climate change than other wetland types.

Ground-water-dominated wetlands depend on aquifer discharge to maintain saturated soils. They often occur on or near slopes where ground-water flows intercept the land surface (Novitzki 1978, Winter 1988).

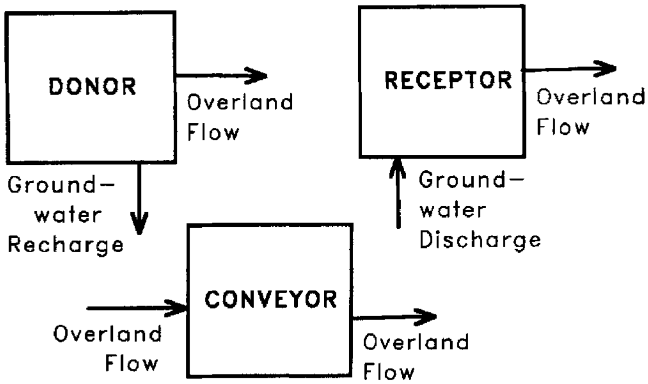

Figure 3. Nomenclature for wetland types based on landscape-level hydrologic movement. Donor wetlands "donate" downstream or to ground water but receive water only via precipitation. Receptor wetlands receive mostly groundwater discharge and lose water by overland flow. Conveyor wetlands are dominated by overland flow and are most capable of moving sediment.

They have little capacity to accumulate and store surface water because of drainage from the sloping wetland surface. Ground-water-dominated wetlands generally maintain higher levels of primary productivity than precipitation-dominated ones (Ingram 1967, 1983) because the continuous flow of the former supplies both nutrients and oxygen, thus mitigating some of the stressful conditions generally associated with saturated soils, such as toxin accumulation.

Riverine wetlands also may be dominated by ground-water sources. These may be apparent as seeps and rivulets at the floodplain surface (Porcher 1981) or obscured from view as deep ground-water inputs to the alluvium (Roulet 1990). Ground-water sources often dominate in arid climates where precipitation and overbank flooding are negligible by comparison. In contrast, channelized stream flow may be an important source of ground water for the underlying aquifer in "losing" streams of arid regions (i.e., channel discharge decreases downstream) (Zimmermann 1969).

Dominance by overland flow is in stark contrast to ground water in timing, hydraulic resistance, and capacity to transport sediments. Overland flows are generally episodically driven by rainfall or overbank flooding, while ground-water sources are buffered to varying degrees depending on the size and permeability of aquifers. Overland flows do not encounter resistances even remotely approaching those of ground water. With a greater capacity for kinetic energy, overland flows are capable of transporting sediments and other particles from uplands to wetlands and between locations within a wetland. Sediment trading in floodplain systems, from cutbanks downstream to point bars, illustrates the relative resistance to transport by larger particle sizes and, by inference, the preferential transport of smaller particle sizes to lower energy environments downstream or to backswamps (Leopold et al. 1964).

What are the implications of these extremes in water source to the functioning of wetlands? In precipitation-dominated wetlands, overland flows, when they occur, result in the flux to surrounding ecosystems of dissolved forms of nutrients and organic matter. Hydraulic energy is seldom sufficient to transport much particulate material. Consequently, these wetlands function as suppliers of water and dilute nutrients to downstream ecosystems (Brinson 1988). (In some cases they may supply water for aquifer recharge, although their tendency to maintain surface water storage implies that their sediments are relatively impermeable to infiltration.) Precipitation-dominated wetlands can be characterized as *donor* wetlands because they are not "recipients" of overland flows of water from other landscape units (Figure 3). As such, they are analogous to upland interfluves that supply water to headwater streams and to underlying aquifers by infiltration.

In contrast, ground-water-dominated wetlands are dependent on receiving water from aquifers that normally are recharged by extensive uplands, at times quite distant from the wetland (Siegel and Glaser 1987). Consequently, they are vulnerable to competition for water in the aquifer by such activities as (1) consumptive withdrawal by municipalities (Brown 1984) and (2) diversion from the aquifer by impervious surfaces, such as parking lots and buildings. Activities that degrade water quality in the recharge area may also eventually influence wetlands at discharge points. Other properties of ground-water-dominated wetlands are slow flow (low kinetic energy), insufficient turbulence to transport sediment, and location on fairly stable geomorphic surfaces. Because such wetlands are dependent on receiving water from aquifers of adjacent landscape units, they can be characterized as *receptor* wetlands (Figure 3).

Wetlands dominated by overland flows include both tidal and riverine wetlands. Tidal wetlands that receive twice daily flooding not only convey considerable quantities of water across their surfaces, but the cumulative effects of regular flooding result in long hydroperiods. Riverine wetlands have much less regular and frequent flooding, and flood waters originate by overbank transport not only from upstream tributaries but also by riparian transport from upland runoff. Due to the transient nature of the flow and the strong hydraulic energy of these currents, tidal and riverine wetlands function more as intermediaries to water flow than the donor or receptor wetlands; consequently, they may be called *conveyor* wetlands (Figure 3). The strong hydraulic energy provided by currents of overland flows influence geomorphic structure more than is apparent in other types. In contrast to donor and receptor wetlands, conveyor wetlands engage in active landscape modification by moving sediments from one locality to another.

The use of such terms as donor, receptor, and conveyor to characterize wetlands is not meant to proliferate terminology but to highlight distinct extremes in water sources and movement and implications of these extremes for functioning at landscape scales. Granted, wetlands maintained by ground-water seeps act not only as receptors but also "donate" water to ecosystems downstream from them, as do conveyor wetlands. The term "receptor" is intended to draw attention to the principal water source by emphasizing its vulnerability to change when "upslope" ground-water dynamics are altered. Receptor wetlands are perhaps more vulnerable than others to inadvertent contamination because they depend upon aquifers that are "invisible" to the casual observer. Donor wetlands, on the other hand, are distinguished by the low concentrations of nutrients and sediments that they export because they lack sources that have had long periods of contact with soils. The term "conveyor" places more emphasis on the communication between various localities within the landscape than on internal processes of wetlands. The portrayal of rivers as conduits for the movement and dissipation of hydraulic energy and materials is consistent with the conveyor term. The donor-receptor-conveyor categories also draw attention to the connectivity among wetlands (Ewel 1979) and how they are integrated in the landscape by sources and movements of water. Their degree of wetness is incidental to this perspective, but their position in landscape gradients is not.

Variations in the Exchanges of Elements and Sediments

The sources and hydrodynamics of water have a strong influence on the biogeochemical processing of dissolved elements and the transport and deposition of sediments. These relationships are the basis for several generally applicable and accepted principles regarding elemental cycling in wetlands: (1) longer residence times allow greater modification of water quality (Kadlec 1978), (2) efficiency of nutrient removal (outputs divided by inputs) increases with the rate of input (loading) up to a level at which efficiency either reaches a plateau or decreases (Nichols 1983), (3) wetlands that receive low loadings of nutrients may function more as nutrient transformers than sinks (i.e., they operate at low efficiency) (Elder 1985, Mulholland 1992), (4) nitrogen tends to be lost to the atmospheric sink via the nitrification-denitrification couple, while phosphorus accumulates in sediments and can only be removed by burial (Patrick and Khalid 1974), (5) most wetlands function as elemental sinks because they are intrinsically depositional landforms, (6) biomass accumulation by vegetation seldom represents a significant long-term sink for nutrients (Klopatek 1978, Brinson 1985, but see Lowrance et al. 1984b for riparian forests with net accumulation), and (7) organic carbon can both accumulate and be exported at the same time (Mitsch and Gosselink 1986). There are probably exceptions for each of these "principles." Regardless, they are representative of the findings of much of the research that has been conducted on the influence of wetlands on water quality. This diversity of perspectives on biogeochemical functioning is not likely to be explained by simple gradients in hydroperiod or depth of flooding.

The range in biogeochemical variability among wetlands can be demonstrated more systematically by considering four combinations of element/sediment inflow and outflow: high and low fluxes of inflows combined with high and low fluxes of outflows (Table 2). ["From low inflow to high outflow" indicates that there are low fluxes to the wetland surface and high fluxes (i.e., exports) from the wetland. These flows refer mostly to overland flow and subsurface transport rather than atmospheric exchanges such as precipitation, nitrogen fixation, and denitrification.] The second column of Table 2 lists several elements, groups of compounds, or other constituents that tend to follow the corresponding combination. Finally, a probable interpretation of the responsible functions is given, including documented examples of the combinations, if available.

Low Inflow, Low Outflow. Wetlands in relatively undisturbed landscapes may receive water that is quite low in nutrients from upland runoff and from wetlands located upstream. Consequently, they are unlikely to further "improve" water quality by reducing concentrations of nutrients and sediment. In a study of the Apalachicola River, Florida, Elder (1985) reported that the principal effect of the river's floodplain was not removal or production of nitrogen or phosphorus but transformation from one nutrient form to another (Table 2). Likewise, coastal plain streams show little longitudinal change in conductivity during base flow because (1) strong mechanisms are lacking to either increase or decrease the concentrations of total ions and (2) ground-water discharge along the length of the stream is derived from a homogeneous water source (Mulholland et al. 1981).

Low Inflow, High Outflow. This combination of fluxes for nutrients and sediments is most likely to occur in disturbed wetlands where slow but long-term accumulation processes are reversed by changes in drain-

Table 2. Combinations of inflow and outflows of nutrients and sediments in wetlands. "Low inflow, low outflow" indicates that both inflows and outflows are low and fluxes are roughly similar. If examples are available that represent these combinations, they are cited.

Flux or Combination	Element, Compound, or Constituent	Probable Interpretation	Example and Source
Low Inflow, Low Outflow	Total N and P	Transformation active; no source or sink.	Apalachicola River and Floodplain (Elder 1985)
	Conductivity	Flowthrough with homogeneous ground-water supply.	Riverine wetlands (Mulholland et al. 1981)
Low Inflow, High Outflow	Nitrate, phosphate	Oxidation of soil organic matter.	State change from accretion to subsidence (Crisp 1966)
	Sediments	Reduced sediment inflow.	Net erosion below dams (Williams and Wolman 1984)
	Organic carbon (OC) in peatlands	Reducing environment impedes oxidation of OC.	Ombrotophic bogs (Clausen & Brooks 1983, Brinson 1991)
High Inflow, High Outflow	Plant nutrients	Autumn die-off of SAVs and emergent marsh vegetation.	Tidal freshwater marshes (Simpson et al. 1983)
	Phosphorus	Saturation of soil exchange sites.	Fen receiving wastewater (Kadlec 1985)
High Inflow, Low Outflow	Nitrate	Flow from aerobic to anaerobic environment.	Upland to riparian forest (Jacobs & Gilliam 1983)
	Dissolved oxygen	Transport through or over sediment rich in organic matter.	Coastal plain stream swamp (Mulholland 1981)
	Phosphate, suspended sediments	Reductions in nutrients from upland disturbance.	Riparian zones in agricultural areas (Cooper et al. 1987, Cooper and Gilliam 1987)

age patterns or land use. Input-output analysis of an eroding peatland demonstrated that it was a net exporter of nitrogen and phosphorus (Crisp 1966). For sediments, channelization may lead to destabilization of the alluvial fill and massive degradation of the stream channel (Hupp and Simon 1991). Although floodplains are not exclusively wetlands, sediments stored in them can be remobilized and exported below newly constructed dams because the dams release water that is relatively free of sediment and thus has a high capacity to entrain and transport sediments. Williams and Wolman (1984) report a net increase in sediment transport between the point just below the dam (low inflow of sediment) to points further downstream (high outflow). Finally, although neither sediment nor dissolved nutrient, dissolved organic carbon inputs to donor wetlands are negligible, while downstream exports are much higher than the corresponding exports from uplands (Mulholland and Kuenzler 1979).

High Inflow, High Outflow. While there are few documented examples of this combination occurring under natural conditions, the work by Kadlec (1985) on phosphorus loading to a peatland illustrates that wetlands cannot function perpetually as sinks for all nutrients because sites of sorption become saturated. A seasonal example of this combination would be freshwater tidal marshes that release nutrients during the massive decomposition of biomass in the fall that had accumulated during the previous growing season (Simpson et al. 1983). While not specifically an inflow but rather short-term internal nutrient loading, peatlands may release nutrients for export following peat fires and from oxidation that follows water-table drawdown during droughts or with the installation of drainage ditches.

High Inflow, Low Outflow. This combination has captured the most attention in relation to the water quality functioning of wetlands. It applies to the riparian buffer strips of low order streams as demonstrated by studies in Maryland (Peterjohn and Correll 1984), North Carolina (Cooper et al. 1987), and Georgia (Lowrance et al. 1984b). Nitrate originating from overland runoff and discharge from the surficial aquifer is removed primarily by denitrification. Because most wetlands are depositional environments, this combination also applies to suspended sediments that accumulate in the low energy environment of floodplains.

While the emphasis on inflow-outflow combinations has been on specific elements and compounds, the broader perspective is on wetlands as landscape units similar to the donor, receptor, and transformer roles described earlier. A preoccupation with duration and depth of flooding would obscure not only the array of biogeochemical process that are common in wetlands, but would tend to divert attention away from processes that depend on landscape position. While wetness is important in determining plant species composition, habitat quality, and on-site soil conditions, gradients of moisture do little to explain the transport of water and water-borne materials through the landscape.

CONCLUSIONS

1. When single environmental factors such as wetness become the main focus for explaining changes in the functioning of wetlands, there is a tendency to overlook alternative sources of variation. Consideration of other factors such as position of the wetland in a drainage network, size of the wetland, sources of water, and biogeochemical inflows and outflows reveals a rich variety of perspectives of practical importance. The relationship of these factors to the degree of wetness is usually incidental.

2. Headwater streams tend to set the biogeochemical state (i.e., nutrient content) of the larger drainage network. Consequently, riparian buffer strips adjacent to headwater sources are a crucial first step in the movement of water from uplands to streams. Opportunities for wetlands to alter water quality are far lower by the time the water reaches the higher order streams. In downstream reaches, infrequent overbank flooding is the only remaining mechanism by which the channel flow can come in contact with the floodplain wetland surface. From a water quality perspective, alterations of wetlands on low order streams should be subjected to much greater scrutiny than they currently receive. The current emphasis on the surface area impacted may be misplaced because these linear landforms should be managed according to their length, not their surface area.

3. Existing terminology for wetlands does little to draw attention to patterns occurring at landscape scales. By using the term "receptor" for seepage wetlands that are dominated by ground-water discharge, attention is focused on the primary source of water and its vulnerability to loss by competing flows and to contamination by upland activities that may appear to be decoupled from influences on wetlands. Corresponding terminology for rain-fed bogs and interfluves is "donor" wetland, and for riverine floodplain wetlands is "conveyor" wetland.

4. Although much emphasis has been placed on the water quality functioning of wetlands, the tendency to think of them only as nutrient and sediment sinks ignores the enormous degree of variation that exists within a wetland, between wetland types, and among individual nutrients and compounds.

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