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CHAPTER 9

THE CHARACTERISTICS OF WETLAND ECOTONES

Marjorie M. Holland, Dennis F. Whigham and Brij Gopal

ABSTRACT

Wetlands occur in almost every type of landscape, providing a wide range of natural functions of value to humanity. They are among the earth's most productive ecosystems and are absolutely essential to many plant and animal species, especially migratory birds. More specifically, there is evidence to suggest that the boundaries between wetlands and other ecosystems are among the most important components of wetlands. In a landscape context, wetlands and wetland ecotones are important transition zones between uplands and aquatic ecosystems. They are sites where nutrient concentrations change as water flows between terrestrial and aquatic ecosystems, and are thus important buffers between uplands and open waters. Research questions are suggested in two categories: (1) *issues related to both wetland patches and ecotones, and* (2) *issues related specifically to wetland ecotones.*

INTRODUCTION

Wetlands provide a wide range of valuable functions for humans (Mitsch and Gosselink 1986, Bedford and Preston 1988). They have local and international significance as regulators of the hydrologic cycle and they improve water quality. Wetlands also provide important habitat for freshwater and marine organisms, and are critical to many bird species as breeding sites and staging areas during migration. It is, in part, the importance of wetlands for bird migration and for essential faunal habitat that has led to a variety of international agreements addressing wetland conservation and management (Maltby 1986, Hollis *et al.* 1989). Yet, in a landscape context, wetlands are also important regulators of nutrient and sediment fluxes between terrestrial and aquatic ecosystems (Forman and Godron 1986, Mitsch and Gosselink 1986).

Little is known, however, about the ecotones between wetlands and other types of ecosystems. In this chapter we focus on the characteristics of wetland ecotones, especially ecological processes occurring in them. Finally, we identify research areas requiring attention in responsible management plans for wetland patches and ecotones.

DEFINITION OF WETLANDS AND WETLAND ECOTONES

Wetlands are defined as lands transitional between terrestrial and aquatic systems where the water table is at or near the surface or the land is covered by shallow water (Cowardin *et al.* 1979). Wetland ecosystems have one or more of the following three attributes: (1) they support, at least periodically, hydrophytes, (2) the substrate is classified predominantly as an undrained hydric soil, and (3) the substrate is saturated with water or covered by shallow water at some time during the growing season each year.

Wetlands occur over a wide range of hydrologic conditions, and the common terms used to describe them have a long history (Denny 1985, Mitsch and Gosselink 1986, Symoens 1988). It is necessary, therefore, to go beyond the wetland definition to consider wetlands and wetland ecotones in the context of an accepted classification system. The system we chose is the one adopted in the United States (Cowardin *et al.* 1979). However, we have chosen to divide the six major categories listed in that system into two types: tidal wetlands and inland wetlands (Table 9.1).

Tidal wetlands. Exchanges of material between open water ecosystems and tidal wetlands occur once or twice daily in response to tidal cycles. Salinity is an important driving factor in coastal tidal wetlands, but its importance decreases upstream where wetlands influenced by salt water are gradually replaced by freshwater tidal wetlands (Odum *et al.* 1984).

Inland wetlands. Most wetlands are not along coastlines but in interior regions. Frayer *et al.* (1983) estimate that 38 × 10^6ha, or about 95% of the total wetlands of the conterminous United States, are inland. Exchanges of materials between the three types of inland wetlands (Table 9.1) and adjacent ecosystems are likely to change on a seasonal basis in response

Table 9.1 Types of tidal and inland wetland ecosystems. From Mitsch and Gosselink (1986)

1. Tidal Wetland Ecosystems
    - Tidal salt marshes
    - Tidal freshwater marshes
    - Brackish tidal wetlands
2. Inland Wetland Ecosystems
    - Inland freshwater marshes
    - Northern peatlands
    - Swamps

to precipitation patterns. There are many types of inland wetlands. The categories listed in Table 9.1 are three of the most widespread types in North America. Readers are referred to chapters in this volume by Pinay *et al.* and Pieczyńska for discussions of riverine wetlands and lake edge wetlands, respectively.

Inland freshwater wetlands are usually characterised by (1) soft-stemmed emergent species including cattail (*Typha*), arrowhead (*Sagittaria*), pickerelweed (*Pontederia*), phragmites (*Phragmites australis*), manna grass (*Glyceria*), and sedges (*Carex*), (2) a shallow water regime, and (3) generally shallow peat deposits. These wetlands are ubiquitous in North America. Examples of regions where marshes dominate include the prairie pothole region of the Dakotas (USA) and Canada, and the Everglade region of Florida (Mitsch and Gosselink 1986).

Northern peatlands are associated with the deep peat deposits of the north temperate regions of North America, such as areas found in the states of Wisconsin, Michigan, and Minnesota and most of the Canadian provinces. Bogs and fens, the two major types of northern peatlands, occur over a wide range of conditions. The thick peat deposits develop in old lake basins or form as blanket bogs, which expand across the landscape.

Swamps, according to a United States definition, are wetlands dominated by trees or shrubs. They often have standing water for most if not all of the growing season (Mistch and Gosselink 1986). Swamps occur in a variety of nutrient and hydrologic conditions and, in southeastern United States, are often dominated by various species of cypress (*Taxodium*), ash (*Fraxinus*), maple (*Acer*), and sour gum (*Nyssa*).

Ecotones. Wetlands, like all ecosystems, have internal and external boundaries separating distinct vegetation patches. Some wetland ecotones are clearly delineated, while for others it is difficult to distinguish where one patch ends and the other begins. In this paper we accept the working definition of a MAB/SCOPE working group (Holland 1988): An ecotone is a zone of transition between adjacent ecological systems, having a set of characteristics uniquely defined by space and time scales and by the strength of the interactions between adjacent ecological systems. The use of *ecological system* here is analogous to that of *patch*, and may refer to wetland patches and contiguous upland or open water patches. Throughout this chapter the term *wetland ecotone* is analogous to *landscape boundary*, *transition zone*, or *wetland boundary*. Although we recognise that wetland patches are heterogeneous internally, we present little information on ecotones within wetlands because of the lack of published papers on their characteristics.

We can categorise wetland ecotones into four types (Table 9.2). Most coastal and inland wetlands, referred to as patch bodies by Johnston and Naiman (1987), have lateral boundaries connecting them to adjacent upland and open water ecosystems. Johnston and Naiman (1987) use the phrase

Table 9.2 Comparison of the types of flows that dominate ecotones in tidal and inland environments

Type of Wetland (patch body)	*Type of Ecotone*	
	Upland-wetland	*Wetland-open water*
Tidal	Ecotone dominated by flows from wetland. Variations in flow generally small and predictable.	Ecotone dominated by flows from estuarine area. Variations in flow may be large or small but usually predictable.
Inland	Ecotone dominated by flows from upland. Large variations with high unpredictability.	Ecotone dominated by flows from open water. Large variations but mostly predictable.

patch body to describe volumetric landscape units, which have boundaries with upper and lower strata in addition to boundaries with adjacent patches. The connections across ecotones can be through either lateral or surficial boundaries. Surficial boundaries separate overlying patch bodies, while lateral boundaries separate patch bodies that are adjacent to each other on the same plane. Transfers across surficial boundaries have a vertical direction, while transfers across lateral boundaries are primarily horizontal (Johnston and Naiman 1987).

In both tidal and inland wetlands, vertical transfers may occur across at least five surficial boundaries (Figs. 9.1 and 9.2), while horizontal transfers may occur across at least five lateral boundaries. Transfers across surficial boundaries include transfers from aerobic to anaerobic soils, from aerobic soils to surficial vegetation and litter, from vegetation and litter to aerobic soils, from open water to the atmosphere, and from open water to aerobic soils. Transfers across lateral boundaries include transfers from the upland to the wetland (upland-wetland ecotone), or from the wetland into open water (wetland-open water ecotone), from groundwater aquifers into soils, or across vegetation zones with each zone dominated by different species (wetland-wetland ecotones).

WETLAND PATCHES AND ECOTONES AS LANDSCAPE FEATURES

Most landscapes contain wetland ecosystems that often form transitions (ecotones) between upland and open water ecosystems, and water flowing through the landscape will usually cross several wetland ecotones (Fig. 9.3). The example given in Fig. 9.3 demonstrates that most landscapes contain more than one wetland and that wetlands often form a continuum between the uplands and downstream tidal ecosystems. The figure illustrates three common types of ecotones in the landscape: upland-wetland, wetland-wetland, and wetland-open water. In this example, surface water and

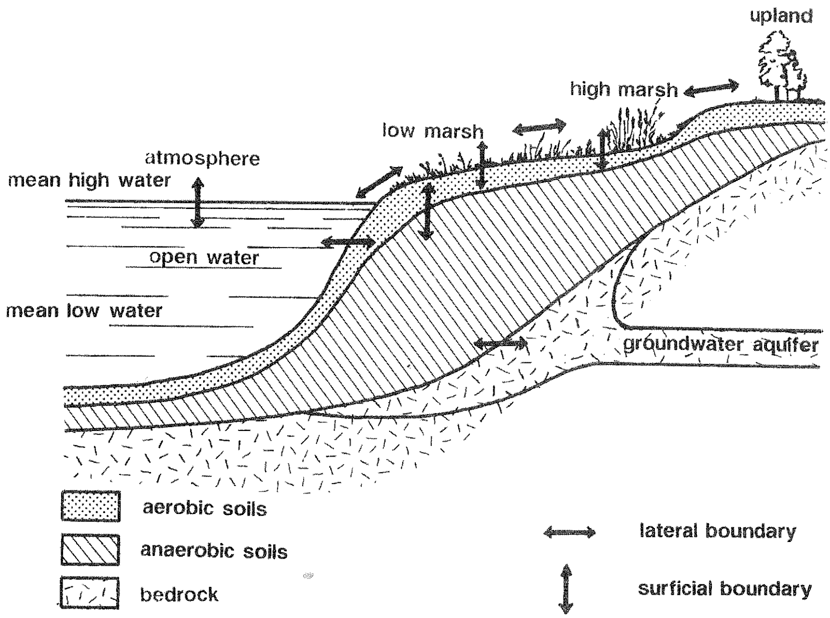

Figure 9.1 Generalised diagram showing ecotones between tidal wetlands and adjacent systems. Refer to Johnston and Naiman (1987) for discussion of lateral and surficial boundaries

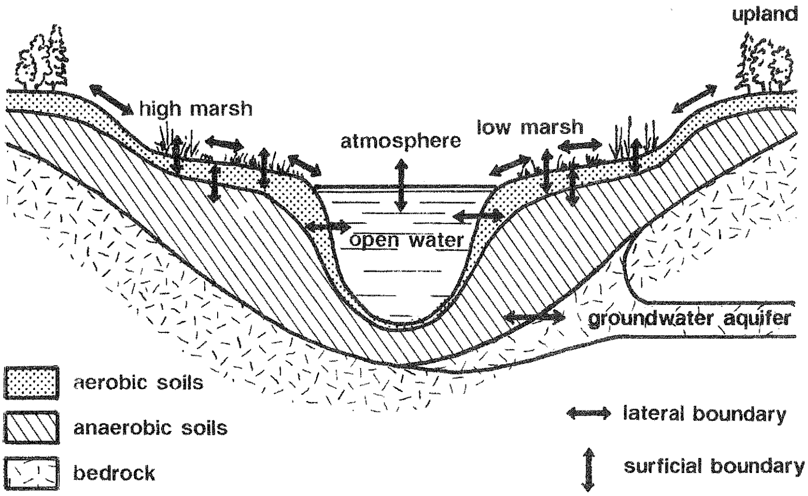

Figure 9.2 Generalised diagram showing ecotones between inland wetlands and adjacent systems. Refer to Johnston and Naiman (1987) for discussion of lateral and surficial boundaries

groundwater would first flow from upland habitats (forests and cultivated fields) across the upland-wetland ecotone into the riparian forest. The second ecotone would be the wetland-open water ecotone between the

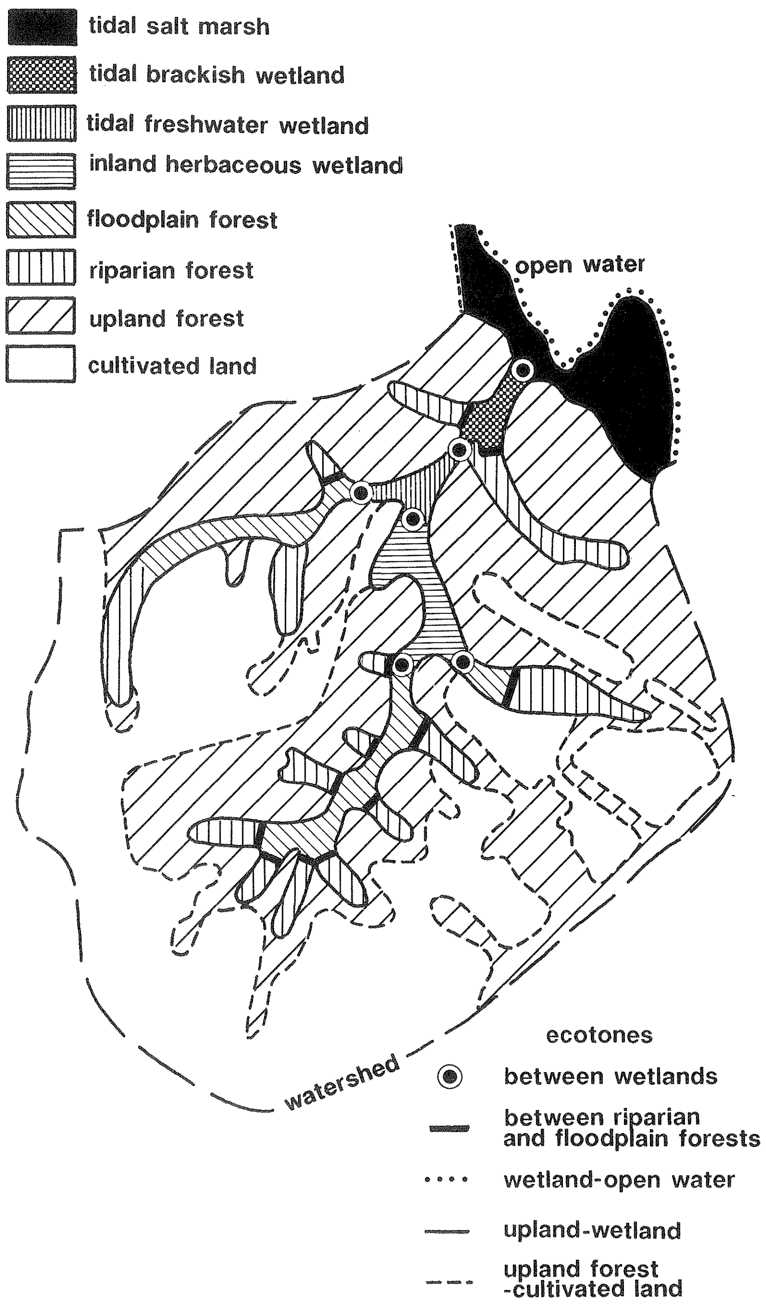

Figure 9.3 Generalised diagram of representative wetland patches and ecotones within a drainage basin. Adapted from Whigham *et al.* (1988)

riparian forest and the first order stream. Once in the stream channel, water would move along the wetland continuum, passing from riparian forests into floodplain forests. Changes in water quality parameters would occur *in situ* in the stream channels except during flooding events when water in the streams would cross the open water-wetland ecotone and come into contact with the wetland surface.

Water leaving the floodplain forests would, in some situations, pass through wetland-wetland ecotones formed where floodplain forests meet inland herbaceous wetlands. Water passing through inland herbaceous wetlands often moves as sheet flow across the surface rather than in distinct stream channels. The next downstream ecotone would be the wetland-wetland ecotone at the transition between the inland herbaceous wetland and the floodplain forest. Except during flooding periods, water would remain in the streams as it moved through floodplain forests. After the water had flowed through the wetland-wetland ecotone between the floodplain forest and the tidal freshwater wetland, interactions between the streams and the wetland would occur twice daily in response to tidal flooding. The topographically lowest ecotone in the landscape is formed between the salt marsh and the open water ecosystem. In addition to the ecotones described, all of the wetlands also have an upland/wetland ecotone at the border between the uplands and the wetlands. Overall, water moving through this typical coastal plain (USA) landscape would pass through 7 different types of wetlands and across 10 ecotones. As will be shown later in this chapter, important changes in water quality occur as water moves across ecotones, and the changes may be more dramatic in some ecotones than in others.

Upland-wetland and wetland-open water ecotones (Fig. 9.3) may be rather static, but more often they are dynamic in both space and time (Johnston and Naiman 1987). Wetland-open water ecotones can change in space as wetlands expand into open water areas (ponds, lakes, and impoundments) or as wetlands erode. For example, high velocity current will often scour away sediments and vegetation, causing erosion (Johnston and Bell 1976, Shure and Gottschalk 1985). On the other hand, low velocity currents will allow sediment deposition, thus increasing wetland vegetation (Holland and Burk 1982, 1984).

Longer-term shifts in the position of ecotones within coastal landscapes are common and often result from variations in sea level (DeLaune *et al.* 1987). In climates where blanket bogs are formed, upland-wetland ecotones shift towards the uplands as wetlands expand over the landscape (Richardson 1981). Humans also influence the position of ecotones (Hackney and Yelverton 1990), as do animals (Naiman *et al.* 1986, 1988). Changes in the position of ecotones may also occur over shorter periods and may be reversible (Brinson *et al.* 1985, Zedler and Beare 1986).

STRUCTURAL AND FUNCTIONAL DYNAMICS

Physical characteristics

Structural and functional characteristics of wetland ecotones are influenced primarily by hydrologic regimes, but other factors may at times be important (Johnston and Naiman 1987). Hydrologic conditions affect many abiotic factors, including salinity, soil anaerobiosis, and nutrient availability. Since hydrology is the primary forcing function in wetlands, the biotic characteristics of wetlands and wetland boundaries are almost always controlled by hydrologic changes (Niering 1987). Differences in the magnitude (depth of submergence by tides and waves), frequency, and duration of the hydrologic interactions between ecosystems result in a variety of conditions within ecotones over different spatial and temporal scales.

Physical features of the environment play an important role in determining the biotic characteristics of ecotones in tidal wetlands. Tides, patterns of sediment movement, freshwater inputs, geological history, geographical location, and shoreline structure, combined with human land use and animal activities, all influence the development and extent of ecotones in tidal wetlands. The interaction of tides, sediments, and geological history in determining changes in wetland ecotones has been well documented for the northeastern USA (Bloom 1964, Bloom and Ellis 1965, Redfield 1972, Orson *et al.* 1987), but is less well known for other regions.

Orson *et al.* (1987) demonstrated the importance of the interaction between physical characteristics in a study of tidal wetland development in the Pataguanset River estuary, Connecticut, USA. They showed that as coastal submergence progressed over 3500 yr, salt marsh-upland ecotones replaced upland-freshwater marsh ecotones and, once established, were able to extend landward over submerging uplands and seaward over emerging mud flats. The acceleration in the relative rates of eustatic sea level rise over the last few centuries may have significant effects on future development of coastal wetlands (Flessa *et al.* 1977, Harrison and Bloom 1977, McCaffrey 1977, Boesch *et al.* 1983), and the study of this phenomenon will have implications for predicting the locations of future wetland-upland ecotones.

The same physical features, except for tides, are also important in determining the development of inland wetlands and associated ecotones. The interaction of climate and geology in determining changes in wetland ecotones has been well documented for lake-sedge and fen-*Sphagnum* peatland ecotones in extreme northern and southern regions of the northern hemisphere (Pigott and Pigott 1959, 1963; Heinselman 1970, Moore and Bellamy 1974, Moss 1980, Mitsch and Gosselink 1986).

Shallow basins only a few meters deep fill in by sedimentation, by peat accumulation at the margins, and by encroachment of vegetation from upland towards open water (Moss 1980). Pigott and Pigott of the northern hemisphere (1959, 1963) demonstrated the developmental complexities of inland wetland ecotones in studies of Malham Tarn, Yorkshire, England. About 12-13,000 yr B.P., just after the lake formed, tundra vegetation predominated in the adjacent upland. During ensuing years, emergent plants, including various species of Poaceae and Cyperaceae, colonised the wetland-open water ecotone, and peat developed. A few thousand years ago the peat mat built up above the level of groundwater. At that point rain became the main water source, and through leaching the peat became acidic enough to allow *Sphagnum* to dominate. In recent centuries a general drying has allowed cotton grass (*Eriophorum vaginatum*) to invade. Cotton grass peat now forms the most recent peat layer (Pigott and Pigott 1959, 1963). Thus the interaction of climate and substrate has caused lake-sedge and fen-*Sphagnum* ecotones to change dramatically over time. Recent initiatives to understand global environmental change (Risser 1985, Holland 1988) may recast the importance of these and similar studies in predicting future locations of upland-inland wetland boundaries should major climatic shifts occur.

Functional characteristics: ecotones of tidal wetlands

Ecotones are important and dynamic components of landscapes and are active sites for retention and transformation of nutrients (Peterjohn and Correll 1984). The term *retention* implies that materials are retained within the ecotone. Retention is usually accomplished when nutrients are assimilated into and stored in plant biomass or buried in the substrate. Transformation refers to a change in form and, in this instance, the transformation of nitrogen into NO_2 by denitrification.

Wetland-open water ecotones (*surface water*). Many studies of tidal wetlands have focussed on import-export characteristics (Nixon and Lee 1985), and in some investigations ecotones were considered (Bertness 1984, 1985; Hopkinson and Schubauer 1984, Mitsch and Gosselink 1986). In general, ecotones receive high nutrient and sediment inputs, especially in particulate form. Sediments near the lateral ecotone between the wetland and the tidal creek are better oxidised, and concentrations of toxic compounds are lower than those of sediments in the surficial ecotone between the tidal wetland and flooding tidal waters (Mendelssohn *et al.* 1982).

The study of Wolaver *et al.* (1983) in a Virginia (USA) salt marsh is probably representative of changes occurring in the surface water ecotone between tidal wetlands and open water ecosystems. Using an experimental flume, they were able to show significant exchanges between the flooding water on the incoming tide and the wetland surface. It should be noted, however, that the pattern was not the same for all nutrients examined or for all seasons. Nitrite was the only nutrient to show a net export across the surficial ecotone between the wetland surface and the open water. There was a net uptake of NH_4-N, NO_3, PO_4, dissolved organic N, dissolved organic P, particulate N, and particulate P from the surface water by the wetland surface. Seasonal uptake patterns were associated with vegetative metabolism as well as with microbial activities at the substrate surface.

There is less known about interaction occurring across wetland-wetland ecotones between tidal wetlands and upstream inland wetlands. The location of the ecotone, usually based on salinity (Brinson *et al.* 1985), can vary in both space and time. During periods of high freshwater discharge, the ecotone occurs further downstream than it does during periods of low freshwater discharge. Brinson *et al.* (1985) conducted a study of a coastal estuarine system in North Carolina where a brackish tidal wetland was contiguous to a forested inland freshwater wetland. During the course of the study there was a regional drought, and brackish water intrusion into the forested wetland resulted in increased mortality of trees, lower production rates, and changes in the patterns of nutrient-cycling. All these changes occurred at the boundary between the tidal and inland wetlands.

Wetland-open water ecotones (*groundwater*). Exchanges of groundwater with surface water occur slowly in tidal wetlands except at the ecotone between the wetland and the adjacent open water ecosystem (Agosta 1985, Jordan and Correll 1985, Yelverton and Hackney 1986, Harvey *et al.* 1987). Between floods the sediments drain more completely in this narrow zone than in high marsh areas, because of differences in sediment grain size and because the area also contains numerous animal burrows. The exchange of nutrients between marsh and open water is much greater than between open water and aerobic or anaerobic soils (Jordan and Correll 1985, Harvey *et al.* 1987). Most groundwater leaving tidal wetlands comes from surface water infiltrating the sediments, which moves back towards open water. The slow movement of groundwater from interior areas of tidal wetlands can affect the nutrient composition of groundwater flowing across the lateral boundary from the substrate to open water (Agosta 1985). In a few situations, however, there is significant mixing between true groundwater and open water (Valiela *et al.* 1978).

Exchanges across ecotones similar to those just described for saltwater tidal wetlands also occur in freshwater and estuarine tidal wetlands. Whigham and Simpson (1978) studied a tidal freshwater wetland in New Jersey, USA, finding significant changes in the nutrient composition of tidal water when it flowed over the surficial ecotone between the wetland surface and the overlying water. In another study in the same ecosystem, Simpson *et al.* (1981) studied distribution patterns of heavy metals discharged into the wetland from a storm drain. Most metals (lead, mercury, and others) were removed from the water column within a few metres of where the discharge pipe entered the wetland ecotone. The authors attributed the reduction in concentrations of heavy metals to deposition and sedimentation within the marginal (ecotonal) areas of the wetland.

Functional characteristics: ecotones of inland wetlands

The flow of surface and subsurface water through inland wetlands is also variable (Cowardin *et al.* 1979, Mitsch and Gosselink 1986), but unlike that of tidal wetlands, it is almost always in one direction (Table 9.2). Like tidal wetlands, inland wetland groundwater is usually anaerobic. Aerobic conditions may be present only in a shallow surface layer. In many nontidal wetlands, periods of low hydrologic inputs are characterised by a lowering of the water table, draining of sediments, and an increase in the depth of the aerobic zone. These wetting and drying cycles play an important role in the nutrient dynamics of inland wetlands (Howard-Williams 1985).

Processes occurring in inland wetlands are also strongly influenced by their drainage basins (Livingston and Loucks 1979, Porter 1981), the chemical composition of waters flowing into the basins (Richardson *et al.* 1978), and the sediment load of the surface water (Jaworski and Raphael 1978, Stuckey 1978). Jaworski *et al.* (1979), for example, attributed declines in the abundance of floating-leaved and submerged aquatic plants in undiked wetlands along western Lake Erie (USA) to a local surface runoff across upland-wetland ecotones. They recommended a wetland management strategy that included a corridor of terrestrial vegetation to protect the wetlands from excessive turbidity and nutrient loading from upland runoff.

The amount of surface water available to most inland wetlands depends on hydrologic inputs from precipitation or from upstream ecosystems (Howard-Williams 1985). In some inland wetlands, surface flow occurs in distinct drainage channels and there appears to be little exchange of materials across the wetland-open water ecotone between streams and adjacent wetlands except during floods (Kuenzler *et al.* 1977, Mitsch *et al.* 1979, Brinson *et al.* 1984, Brinson 1988, Whigham *et al.* 1986). In some inland wetlands, streams are not present and water moves as sheet flow over the surface. In those instances, there are clear patterns of interaction between the water column and the wetland across the ecotone (Verry and Timmons 1982, Richardson and Marshall 1986).

Wetland-open water ecotones (surface water). Vitt *et al.* (1975) and Vitt and Bayley (1984) studied peat systems in Canada and characterised nutrient movement across the ecotone between the wetland and open water. The concentration of calcium in surface water decreased as water flowed across the wetland, with greatest changes at the ecotone between the wetland and open water (Vitt *et al.* 1975). In Manitoba, Vitt and Bayley (1984) examined the relations between vegetation and water chemistry in four bogs where changes in pH and concentrations of Na^+, K^+, Ca^{++}, and Mg^{++} were greatest at the wetland-open water ecotone.

Verhoeven *et al.* (1988) studied nutrient relations between wetlands and adjacent open water ecosystems in the Netherlands. Changes in electrical conductivity (a measure of the overall nutrient content) of surface water decreased most rapidly in the ecotone when the wetland surface was flooded from an adjacent ditch. The authors suggested that changes were due to active plant nutrient uptake in the ecotone. Vermeer (1985), working in the same areas as Verhoeven *et al.*, found similar conductivity patterns. He also showed that changes in concentrations of nutrients were greater near the ecotone between ditches and the wetland (Fig. 9.4).

Verhoeven *et al.* (1988) further demonstrated the conditions under which this ecotone effect may be important. When the vegetation in contact with open water is a floating mat (i.e. typical of earlier stages of fen succession), mat elevation will adjust to water level changes in the adjacent ditch or pond. Therefore, water flooding the wetland from the ditches will always be in contact with the floating mat, and it can be expected that significant interactions will occur at the surficial ecotone. When vegetation becomes anchored to the bottom (i.e. characteristic of later stages of succession), the mat does not adjust to changing water levels. Floodwaters then have little contact with vegetation, resulting in less nutrient uptake at the surficial ecotone.

Wetland-open water ecotones (*groundwater*). There have been fewer studies of nutrient transformations occurring as groundwater moves across wet-

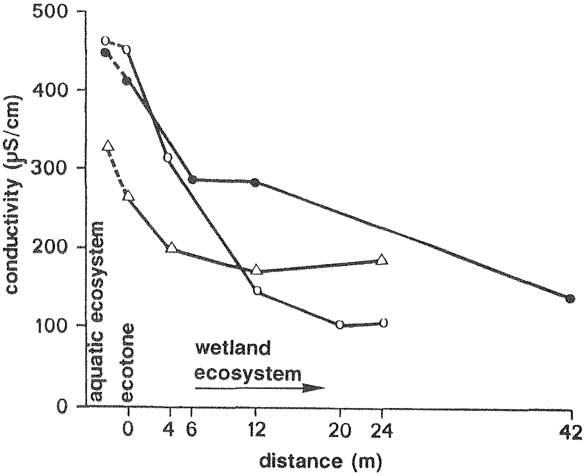

Figure 9.4 Differences in conductivity measured in the ground and ditch water along three wet grassland transects (means of 10 samples). Adapted from Vermeer (1985)

land-open water ecotones. Verhoeven *et al.* (1988) compared conductivity changes occurring in groundwater moving from open water to adjacent wetlands in the Netherlands. Similar to patterns they found for surface water (see section above), the greatest changes occurred at the wetland ecotone for metals and nutrients in subsurface water (Fig. 9.5). The ability of peat systems to retain nutrients, especially P, has been demonstrated clearly by Richardson and Marshall (1986), and it would be expected that many of the chemical transformations occur as groundwater crosses wetland-open water ecotones of peat systems. Richardson and Marshall (1986) have also shown that the peat substrate can become saturated with P, losing its uptake capacity. This suggests that under conditions of high nutrient loading, ecotones may have a limited ability to retain phosphorus and other nutrients.

McKnight *et al.* (1985) studied the distribution and characteristics of humic substances in Thoreau's Bog, Massachusetts, USA, where the upper moss (*Sphagnum*) layer was the primary site of dissolved organic carbon (DOC; <0.5 μm diameter) production. They showed the greatest changes in interstitial DOC concentrations at the ecotone between the bog and a central area of open water. Similar results were found by Gaudet (1979), who demonstrated that nutrients from upstream sources were more effectively retained when passing through a floating mat of vegetation in an African lake compared with periods when water from upstream areas was transported directly under the vegetative mat and into the lake.

Verhoeven *et al.* (1988) give an interesting example of how blockage of a surficial boundary between wetland vegetation and the underlying stratum can have an important impact on nutrient exchanges. In groundwater discharge areas there is a net movement of water out of the aquifer, across the ecotone, and into the substratum of the wetland. Although the groundwater is often polluted from nearby agricultural areas, most nutrients are adsorbed by the wetland substrate and do not reach the substrate surface where vegetation assimilation would occur. This situation is, however, limited to a few decades, since the adsorptive ability of the peat layer will ultimately be exceeded (Richardson and Marshall 1986).

Seischab (1987) sampled interstitial and subsurface water along a transect crossing several vegetative ecotones ranging from deciduous and evergreen wetland forests to herbaceous and open water areas. We compared the percentage change in nutrient concentrations (positive or negative) as water moved across ecotones between the eight different wetland types with the percentage change as water moved within homogeneous patches (Table 9.3). The greatest change occurred across the ecotones, demonstrating the importance of ecotones in regions with multiple wetlands.

Upland-wetland ecotones (surface water). Upland-wetland ecotones have been shown to be important for surface water and groundwater quality

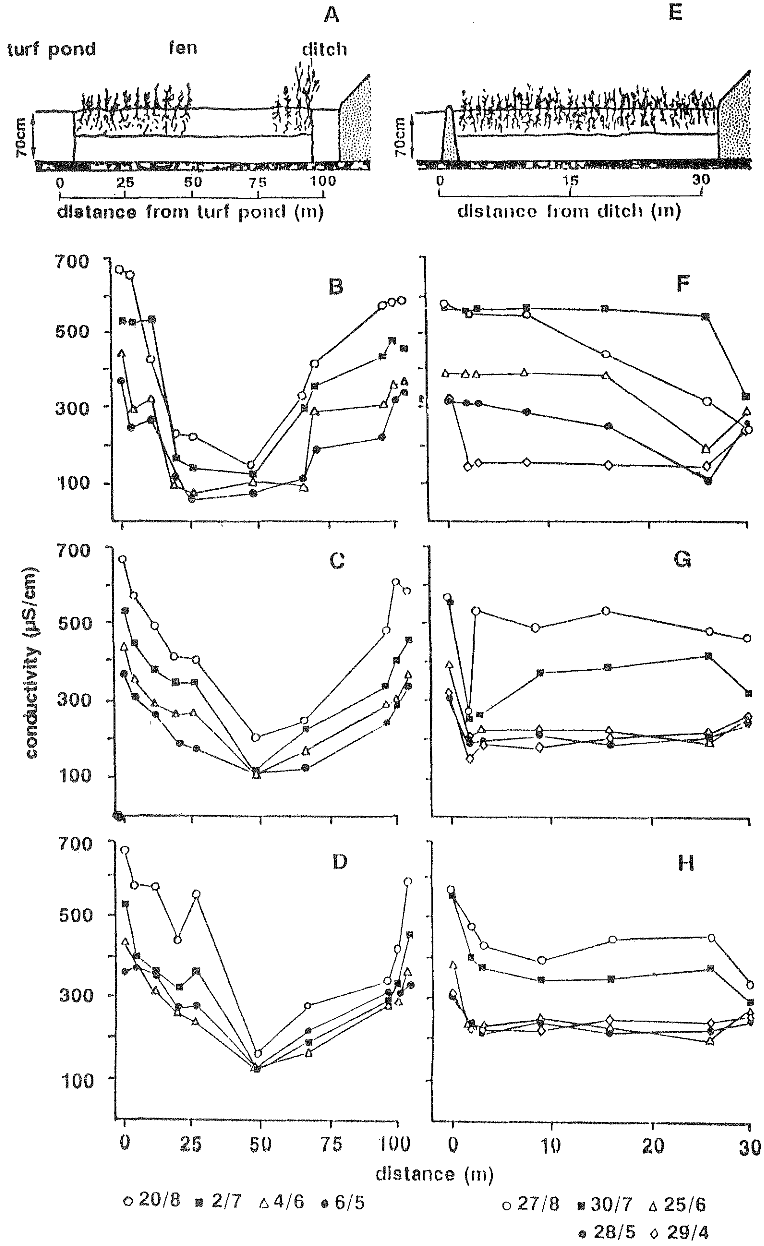

Figure 9.5 Electric conductivity of water samples along transects in the Molenpolder fen (A-D) and the Westbroek I fen (E-H). A and E: Schematic representation of the transects. B and F: Conductivity at the soil surface. C and G: Conductivity 20 cm below soil surface. D and H: Conductivity 60 cm below soil surface. Adapted from Verhoeven *et al.* (1988)

Table 9.3 Percentage change in water quality parameters for pairs of sampling sites within and between different zones of vegetation. Values are means, independent of whether the changes were positive or negative. From Seischab (1987)

Parameter	*Within Zone*	*Between Vegetation Zones*
pH	1.68	5.25
Conductivity	5.96	37.69
Calcium	6.66	32.61
Magnesium	6.77	21.93
Nitrate	56.48	78.75

(Peterjohn and Correll 1984, 1986; Cooper *et al.* 1986, Schnabel 1986). This is particularly true where the upland areas are dominated by agricultural practices, which export large amounts of sediments and nutrients.

Sediments eroded from uplands primarily move in surface water. This is also the primary pathway for phosphorus movement in agricultural landscapes, since most phosphorus is attached to sediment particles (Lowrance *et al.* 1984, Pionke *et al.* 1986). Nitrogen moves primarily in subsurface water as dissolved nitrate, ammonium, and organic nitrogen (Peterjohn and Correll 1984, 1986).

Surface water containing sediment and nutrients passes through the upland-wetland ecotone as overland flow. When overland flow is not channelised, there is ample opportunity for water to come into contact with the surface litter layer. As the intensity of runoff increases, overland flow often becomes channelised flow, there is less contact between the water and the litter, and there is less retention of sediments and nutrients. This has been shown by Jordan *et al.* (1986), who found that sediment transport through a coastal plain landscape occurred primarily during large storms when the retention ability of upland-wetland ecotones in riparian forests was bypassed.

The velocity of surface water slows as it passes through the surface litter layer in the ecotone, trapping sediments and adhering nutrients. Whigham *et al.* (1986) found that the litter layer within riparian forests retained large amounts of sediment and that some phosphorus was trapped along with the sediment. Most phosphorus, however, passed through the riparian zone, since deposited sediments had low phosphorus concentrations compared with the finer sediments (clays) passing through to the adjacent aquatic ecosystem. Much of the phosphorus attached to the fine sediments was retained by wetlands further down the hydrologic gradient (Whigham *et al.* 1988). Compared with phosphorus, most nitrogen is removed from subsurface water at the upland-wetland ecotone (Peterjohn and Correll 1984). The primary mechanism for nitrogen removal in the ecotone appears to be denitrification driven by inputs of nitrate-nitrogen in groundwater from the upland, the presence of reduced sediments in the ecotone, and the high organic matter content of the soil.

Upland-wetland ecotones (*groundwater*). In contrast, the movement of groundwater across upland-wetland ecotones is even more dynamic and potentially important as a landscape feature. Schnabel (1986) showed that more nitrate was removed from groundwater during periods of low hydrologic discharge than during periods of high discharge across an upland-wetland ecotone. During periods of high discharge, more water moves across the ecotone as overland flow, and there is less contact time for vegetative uptake and microbial transformation of nutrients (Pionke *et al.* 1986). Schnabel (1986) found nitrate concentrations decreased by more than 50% within 16 m of the upland-wetland ecotone when those conditions prevailed. Peterjohn and Correll (1984, 1986) and Lowrance *et al.* (1984) report similar results. Gilliam *et al.* (1986) found high rates of denitrification also occurred near the wetland-open water ecotone when surface aerobic and subsurface anaerobic zones were present.

Subsurface processes discussed so far are primarily mediated by microbial metabolism (Lowrence *et al.* 1984, Peterjohn and Correll 1984). The role of vegetation in nutrient retention at ecotones is less clear. Fail *et al.* (1986) conducted one of the few ecotone studies where measurements of plant nutrient uptake were made. These authors tested the hypothesis that vegetation in a wetland (riparian forest) was important in retaining nutrients transported from adjacent upland agricultural areas. They found primary production and nutrient uptake rates were higher in the upland-wetland ecotone receiving high nutrient inputs from the uplands. This suggests that vegetation at the upland-wetland ecotone is responsive to changes in nutrient availability. While they did not indicate spatial patterns in rates of biomass and nutrient accumulation, high rates of root production within the first 8 m of the ecotone suggest that the ecotonal areas are important for nutrient retention.

Lateral and longitudinal exchanges across ecotones

Examples given in the previous section allow us to formulate some general statements about the importance of wetland ecotones in landscapes: (1) Hydrologic characteristics probably have the greatest role in determining the fate of materials moving across wetland ecotones. With few exceptions, hydrologic and nutrient inputs across wetland ecotones vary temporally, and the ability of nutrients to be retained or transformed within an ecotone is negatively related to how quickly water moves across the ecotone as surface water or groundwater. (2) The movement of material across ecotones in tidal wetlands is more predictable than in inland wetlands (Table 9.2). (3) Interactions across wetland-open water ecotones dominate patterns of nutrient exchange within tidal wetlands (Wolaver *et al.* 1983). (4) Exchanges across the upland-wetland ecotone are not important in estuarine areas unless significant amounts of groundwater from upland areas discharge into the tidal wetlands (Valiela *et al.* 1978). (5) During periods of extreme tidal events (spring and storm tides), coastal ecotones are probably not important as sites for sediment and nutrient exchange. (6) The movement of materials across wetland-open water ecotones in inland environments is probably more variable and less predictable than in tidal areas (Table 9.2). When surface and groundwater flows through riparian zones into first order streams across a lateral wetland-open water boundary, important nutrient transformations occur (Schnabel 1986, Ford and Naiman 1989). Once the water has entered the aquatic system, it moves downstream to higher order streams. Compared with streams, however, there is much greater retention and transformation capacity where water from the stream flows across wetland ecotones (e.g. in impounded areas), as shown by Naiman *et al.* (1986) for landscapes containing beaver-created impoundments. (7) When the capacity of upland-wetland ecotones is exceeded (e.g. during storms), downstream wetlands and wetland ecotones become important (Whigham *et al.* 1988). (8) Wetland ecotones provide an important buffering capacity within landscapes.

Biotic characteristics of wetland ecotones

Biotic diversity. It has been suggested that ecotones support relatively high biological diversity (Patten *et al.* 1985). Wetland ecotones can have a high species diversity, but species diversity for a particular wetland boundary may be affected by a variety of factors (van der Maarel 1976), and thus may be difficult to predict. In a New England (USA) inland freshwater marsh complex, Burk (1977) found vascular plant species diversity to be lowest at the wetland-open water ecotone, higher in the middle of the marsh, and highest at the upland-wetland ecotone. Similarly, in several tidal marshes sampled in northeastern United States, vascular plant species diversity was generally lowest at the wetland-open water ecotone, higher in the wetland center, and highest at the upland-wetland ecotone (Senerchia-Nardone and Holland 1985, Senerchia-Nardone *et al.* 1986). However, in other instances, upland-wetland ecotones may be sharp and have few species, if any. We believe that the answer to the question about higher biodiversity in wetland ecotones needs to be addressed with additional lateral transect studies crossing from uplands to wetlands to open water patches, and focussing on species richness in the wetland-upland or wetland-open water ecotones.

Primary production. Conditions stressful in other environments may increase primary production in plants adapted to wetland ecotones. For example, Sharma and Gopal (1977) studied biomass structure in the cattail (*Typha* *elephantina*) along a gradient from open water through wetland to upland. In the dry upland stand, flooded occasionally for a short period, aboveground biomass was small, maximum biomass was obtained in the middle stand which was flooded frequently, and the permanently flooded stand had intermediate values (Sharma and Gopal 1977). It seems important for future studies to focus on analyses of productivity at wetland-upland or wetland-open water ecotones.

Community structure. Historic names for different kinds of wetlands (e.g. marshes, fens, bogs, swamps) imply general recognition of distinctive associations of plants that are readily recognised and, at least loosely, comprise a community. One reason these associations have been so clearly identified is that zonation patterns in wetlands are often thought to be sharp, with abrupt boundaries that call attention to vegetation change, and by implication to the uniqueness of each zone (Mitsch and Gosselink 1986).

Recent evidence suggests that in at least one wetland species, several phenotypes have evolved (Keeley 1979). Phenotypes may allow different populations within the same species to tolerate different environmental conditions, and thus to survive not only within a wetland, but also at the wetland-open water and upland-wetland ecotones. Keeley (1979) has reported population differentiation in tupelo (*Nyssa sylvatica*) along a soil moisture gradient from upland sites, which are never flooded, to floodplain wetlands, which are periodically flooded and drained, to permanently flooded swamps. Upland plants were very intolerant of flooded soils. In contrast, swamp plants were quite tolerant of flooded soils. The floodplain population produced a distinctly flood-tolerant phenotype, but not nearly as tolerant of flooded conditions as the swamp phenotype. Keeley (1979) concluded that floodplain plants apparently have been selected to be similar to upland plants under drained conditions and swamp plants under flooding, and one consequence of this is that their tolerance of flooded conditions is intermediate. Thus selection may have preserved genotypes capable of acclimating to either drained or flooded conditions, with the result that the phenotypes are optimally adapted to neither. It appears at least in the case of *Nyssa sylvatica* that phenotypic gradients have developed across wetland ecotones. Similar work on other wetland transition zone species would help in understanding their physiological and genetic survival strategies.

Community development. Much thought has been devoted to the question whether wetlands always develop into drier terrestrial habitats, and thus if wetland ecotones are invaded by upland species, or if open water is invaded by wetland plants, or both (Odum 1971, Livingston and Loucks 1979, Holland and Burk 1984, Niering 1987). Certain species are especially likely to invade other communities because of life history traits such as arrival time, growth rates, and longevity patterns (Glenn-Lewin 1980, Noble and Slatyer 1980, Hibbs 1983). Van der Valk (1981) presents an approach to wetland succession where the presence and abundance of each species depends on its life history and its adaptation to the environment of a site. Traditional theories of the relation of wetland succession and the climax state to diversity, stability, and resilience might well be reconsidered (Livingston and Loucks 1979, van der Valk 1981, Niering 1987). There is growing evidence that continuous disequilibrium due to periodic physical disruption is necessary for the continued high productivity of wetlands and associated systems. As long as fluctuating hydrologic conditions persist, a wetland ecotone will remain in a state of *pulse stability* (Odum 1971). In low energy situations, Welling *et al.* (1988) have shown that ecotones between different vegetation types change very little once species have become established. It would thus appear that many wetland ecotones are influenced by biotic interactions and that physical conditions are only important under certain conditions.

Anthropogenic stabilisation of such systems often reduces productivity. Wetland ecotone management goals based solely on concepts of homeostasis and stability could be disruptive to the functioning of the wetland itself, as well as to adjacent systems (Livingston and Loucks 1979). To assist present wetland ecotone managers, research is needed to identify traditional, low-intensity management techniques that have successfully maintained or enhanced the functions of ecotones in the past, and thus have promoted sustainable utilisation of wetland patches and ecotones (Clark and Holling 1984, Hollis *et al.* 1988).

Recognition of the importance of wetland ecotones

The importance of upland-wetland ecotones has been recognised by some state governments in the United States, and legislation has been passed to ensure that they are maintained (Holland and Balco 1985). New Jersey now requires a 50 m buffer zone between uplands and wetlands (Tubman 1988); this legislation was based in part on a scientific wetland-upland buffer delineation model (Roman and Good 1986). How variable can that width be at different locations in the landscape to reach desired water quality goals? Is the maintenance of the upland-wetland ecotone more important at some locations in the landscape than others? We believe that upland-wetland ecotones are most efficient in areas that are topographically lower in the landscape where soils have both aerobic and anaerobic layers, important requirements for denitrification (Peterjohn and Correll 1984, Whigham *et al.* 1988). Ecotones topographically higher on the landscape might efficiently intercept sediments and nutrients in surface water but would be less efficient at intercepting nutrients in groundwater, because the shallow groundwater would most often be aerobic.

In the highly managed landscape of the Netherlands, the length of wetland-open water ecotone is high compared to the area of wetland. During dry periods, there is a net movement of water into wetlands from the extensive ditch systems. Polluted river water is the hydrologic source for those exchanges, and wetland-open water ecotones play an important role in intercepting nutrients before they reach the interior of wetlands (Verhoeven *et al.* 1988). Thus, in the Netherlands, wetland-open water ecotones have an important assimilative capacity for aquatic pollutants.

CONCLUSION

We summarise this chapter by presenting a list of significant research questions. They are divided into two categories: (1) issues related to both wetland patches and ecotones, and (2) issues related specifically to wetland ecotones.

Issues related to wetland patches and ecotones

1. What role does vegetation play in nutrient uptake, especially in upland-wetland ecotones during the growing season? There is evidence to demonstrate that vegetation can play an important role in removing nutrients from the substrate and groundwater (Peterjohn and Correll 1984, Fail *et al.* 1986). We do not know, however, how variable this characteristic is among different types of wetlands nor the importance of the ecotone itself. This last issue is of particular importance because the little data available suggest that upland-wetland ecotones may be important landscape features for the interception of nutrients, especially nitrogen.

2. How does the assimilative capacity of the wetland ecotone compare with the assimilative capacity of the wetland patch? Most investigations have focussed on wetland patches, but not on ecotones. However, evidence given in this chapter suggests that the wetland boundary may be the most important part of the wetland. Is this observation true, and is it true for all types of wetlands?

3. Can the assimilative capacity of wetland patches and ecotones be enhanced or maintained through management? This question is obviously important, yet there is little information directly addressing it.

4. At what temporal or spatial scale are research results most useful for decision making and management? Wetland research takes time, can be expensive, and usually considers only one wetland at a time. Most questions asked of wetlands ecologists, however, deal with issues at several scales, many of which focus on landscape issues (Di Castri and Hadley 1988, Holland 1988). It would be productive to consider several

hierarchical levels, including both wetland patches and ecotones. An example would be to consider all wetlands in a drainage basin (Fig. 9.3). The goal would be to determine which types of wetlands and ecotones are most important in intercepting nutrients and sediments. This approach has the potential to identify emergent processes by moving from a single wetland boundary to a wetland and then to a series of wetlands in a drainage system.

Issues related specifically to wetland ecotones

1. At what level of human investment have ecotones been maintained and restored in the past, and is there any evidence of positive benefits from those actions?
2. Does the nutrient retention efficiency of wetland ecotones, particularly in tidal wetlands, change when the edge-to-area ratio is altered? If boundaries are important to wetland function, there should be a relation between nutrient retention capacity and the size (area) of the boundary or the ratio of ecotone length to patch volume (patch body).
3. How does the assimilative capacity of upland-wetland ecotones vary under different topographic and geologic settings, and between different types of upland and wetland ecosystems?
4. Along definable hydrologic gradients, are wetland ecotones topographically higher in the landscape more important in retaining and transforming nutrients than ecotones lower in the landscape?
5. How important are wetland-open water ecotones, especially in landscapes where a high percentage of the surface water volume occurs in lakes and ponds? In those situations, is the ratio of wetland area to open water more important than the length of wetland ecotone?
6. Do wetland ecotones support high biological diversity? This question needs to be addressed with additional lateral transect studies crossing from uplands to wetlands to open water ecosystems, and focussing on species richness in the wetland-upland or wetland-open water ecotone.
7. Is primary production higher in wetland-upland or wetland-open water ecotones than in the wetland patches themselves?
8. Have wetland plants evolved several phenotypes to allow the coexistence of different populations of the same species within a wetland, as well as at the wetland-open water and upland-wetland ecotones?

Strategies for future research

Research provides valuable information to decision makers. Yet, for scientists, perhaps the most difficult question to answer is what research should be done when the information base is small and the need for information is great. We believe that field research and simulation modelling both need to be accomplished and coordinated so that the results will be useful to both scientists and resource managers. Based on our review, we suggest the following priority areas:

- Study the importance of upland-wetland ecotones in a variety of landscapes simultaneously.
- Characterise the relationship between wetland size, hydrologic characteristics, and dimensions of the ecotone on the assimilative capacity of the wetland patches and ecotones.
- Use existing management questions to develop a series of experiments that will test our ability to maintain or enhance the functions of wetland ecotones.
- Identify traditional, low-intensity management techniques that have successfully maintained or enhanced the functions of wetland ecotones in the past.
- Utilise existing descriptive and predictive models to identify parameters of wetland patches and ecotones that need to be better understood.
- Establish lateral transects crossing from uplands to wetlands to open water ecosystems and assess biological diversity in wetland-upland and wetland-open water ecotones.

Towards a management of wetland patches and ecotones

Wise use of wetland patches and ecotones requires action on a broad scale, giving consideration to all factors affecting wetlands and the drainage basins of which they are a part. A fundamental understanding of ecosystem and hydrological processes is necessary for good management (Hollis *et al.* 1989). Careful synthesis and integration should ultimately result in national wetland policies that include consideration of upland-wetland and wetland-open water ecotones. Major items for developing such policies may include:

- A national inventory of wetland patches and ecotones
- Identification of the benefit and values of these wetland patches and ecotones (Simpson 1985)
- Definition of the priorities for each site in accordance with the needs of, and socio-economic conditions in, each country
- Proper assessment of environmental impact before development projects are approved, continuing evaluation during the execution of projects, and full implementation of environmental conservation measures that

take full account of the recommendations of this process of environmental assessment and evaluation

- Use of development funds for projects that permit conservation and sustainable utilisation of wetland resources

Realisation that wetland patches and ecotones cannot be managed in isolation from upstream inputs and downstream impacts has led to the development of wetland legislation and policies at the local and national level in many developed countries (Holland and Balco 1985, Roman and Good 1986, Tubman 1988). In addition to the creation of parks and reserves, legislation may require that alteration of wetlands and stream courses tributary to, and downstream from, the protected site be subject to regulation (Verhoeven *et al.* 1988). Most wetland patches and ecotones in developing countries retain a wide range of their natural functions (Gaudet 1979). Many rural economies in Africa and in Southeast Asia depend on the utilisation of these wetland patches and ecotones. Accordingly, it is neither practical nor desirable that all extractive activity be precluded from all wetland systems (Hollis *et al.* 1988). Rather, mechanisms for sustainable utilisation of wetland patch and ecotone resources need to be developed and promoted (Clark and Holling 1984), and this can be accomplished through solid interdisciplinary research that has vision for the future.

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