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Wetlands are Ecotones: Reality or Myth?

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ABSTRACT

Wetlands have been traditionally viewed as ecotones and as transitional communities between "land" and "water". While the edges of many wetlands and some wetland types may possess ecotonal qualities, relatively few are ecotones between dryland and open water. The concept of ecotones has been overstated and, in many cases, misapplied to wetlands. Reference to wetlands as transitional habitats between land and water implies that wetlands are temporary habitats evolving naturally into either upland habitats or deep water, which for the most part, does not occur except due to major climatic changes and other processes that significantly alter the current hydrology. Wetlands collectively are no more ecotones or transitional habitats than other habitats along the soil moisture continuum from deserts to deep water. The concept of ecotones is best applied to individual plant communities rather than to broad habitat types such as wetlands. The paper uses examples of North American wetlands to support these claims.

INTRODUCTION

Wetlands are environments subject to permanent or periodic inundation or prolonged soil saturation sufficient for the establishment of hydrophytes[1] and/or the development of hydric soils or substrates[2]. Given regional differences in hydrologic regimes, climate, soil-forming processes, and geomorphologic settings, a vast assemblage of wetland plant communities and hydric soil types have developed worldwide. Numerous terms have been applied to individual wetlands because of these differences. Some common wetland types include salt marsh, tidal marsh, alkali marsh, fen, wet meadow, wet prairie, alkali meadow, shrub swamp,

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[1]Hydrophytes are individual plants growing in water or on substrates (e.g., soils) that are periodically subject to anaerobic conditions due to excessive wetness. See Tiner (1991) for details.

[2]Hydric soils are soils that are saturated at or near the surface (by flooding or high groundwater tables) usually frequently and long enough to promote the development of anaerobic reducing conditions that affect plant growth and promote the establishment of erect (self-supporting) hydrophytes. Hydric substrates are permanently or nearly permanently inundated or saturated substrates lacking erect hydrophytes; they are mostly non-vegetated areas (e.g., the bottoms of the shallow water zone of permanent waterbodies), but may be vegetated with submerged species or floating-leaved plants.

wooded swamp, bog, muskeg, wet tundra, pocosin, mire, pothole, playa, salina, salt flat, tidal flat, vernal pool, bottomland hardwood swamp, river bottom, lowland, mangrove forest, tropical rainforest, and floodplain swamp. Within regions, wetlands naturally occur in landscape positions where surface water collects for some time and/or where ground water discharges permanently or periodically. Common wetland landforms include: (1) depressions surrounded by upland and with or without a drainage stream, (2) relatively flat low-lying areas (floodplain) along major waterbodies (e.g., rivers, lakes and estuaries) usually with fluctuating water levels, (3) broad flat areas lacking drainage outlets (e.g., interstream divides), (4) vast expanses of arctic and subarctic lowlands where a permafrost layer occurs near the surface (muskegs), (5) sloping terrain below sites of ground water discharge (e.g., springs, seeps, toes of slopes and drainageways), (6) slopes below melting snowbeds and glaciers, and (7) flat or sloping areas adjacent to bogs and subject to paludification processes.

Wetlands have been considered to be ecotones or ecotonal habitats between land and water by some scientists (Mitsch and Gosselink 1986, among others). While certain wetland plant communities or portions of wetlands may indeed represent such ecotones, the concept of ecotones has been greatly misapplied to and overused for wetlands. The majority of wetlands are not ecotones between dryland and aquatic communities, but are relatively distinct communities along the soil moisture continuum. These wetlands do not occur between upland and large waterbodies, but are instead essentially surrounded by upland except perhaps for a small shallow drainage stream. Reference to wetlands as transitional habitats between land and water is a similar overstatement. Most wetlands are relatively stable spatially, although some may appear unstable due to plant community dynamics. The latter changes, however, tend to occur within a wetland rather than between the wetland and the adjacent habitat. In this paper, I will provide specific examples of North American wetlands to support these propositions.

WHAT IS AN ECOTONE?

An ecotone has been defined as a transition zone of tension between two or more communities (Clarke 1954, Odum 1959). This zone emphasizes the "struggles" between adjacent communities brought about by physical conditions (e.g., soil, drainage, and pH) and/or biological competition. Ecotones may vary in scale from broad transitions of vegetation (e.g., sometimes more than 100 km in width) between major vegetation communities to narrow belts of transition between adjacent plant communities, such as the edge of the forest next to a grassy field, a streambank beside a meadow, or the transition from a soft bottom to a hard bottom marine community. Clarke's concept of ecotone requires that there be tension between the communities and he admits that this is difficult to demonstrate for large geographic areas (Clarke 1954). Odum (1959) suggests that the ecotone is a tension belt of considerable linear dimension that is narrower than the communities on either side.

Physical conditions in the ecotone are different from those in either adjacent community. Ecotones may be preferred habitats for some species, so certain plants

and animals may only occur in these areas and may be absent or virtually absent from the bordering communities. Clarke (1954) gave the margin of a pond where willow and cattails predominate as an example of an ecotone. In his opinion, this community is a transition between land and water where certain animals are present that are not found elsewhere in the pond and the adjacent plant community. These animals include turtles, frogs, herons, red-winged blackbirds, muskrats, and a host of aquatic invertebrates.

An important, yet often overlooked, requisite of an ecotone is that "the ecotone inhabitants owe their existence to the presence of the particular conditions on each side and that the ecotone assemblage would disappear or be considerably modified, if the bordering communities or conditions were removed or seriously changed" (Clarke 1954, p. 412). The "edge-effect" is typified by ecotones, leading to increased variety and diversity of organisms (Odum 1959). From my perspective, this would seem to restrict the concept of ecotones mostly to areas relatively narrow in width but possibly quite long in length (the edges) between adjacent communities as suggested by Odum (1959).

The difference between an edge and an ecotone should be emphasized. An edge is any recognizable boundary between two adjacent communities. It is usually defined by an observed change in the plant community. This change may be abrupt as the edge between a lake and a rock cliff or a floating bog mat and open water, or it may be more gradual and transitional in nature. An edge may be an ecotone when there is a zone of tension between the two communities. While there may be a zone of tension between any two communities, the concept of an ecotone seems to imply a tension zone more than just a few centimeters in width. It should be wide enough to be of ecological significance. Evidence of this tension is usually reflected by vegetation patterns on "land", while substrate differences have been used to identify ecotones in submerged marine systems (Odum 1959). Areas of low topographic relief, such as the Gulf-Atlantic Coastal Plain, may have relatively broad ecotones where environmental conditions change gradually over considerable distances creating transitional communities where plant species from adjacent habitats intermix. This situation applies equally to wetlands and non-wetlands (aquatic and terrestrial communities).

ECOTONAL WETLANDS

Wetlands have been considered "ecotonal communities" presumably because: (1) many wetlands occur between dryland and permanent waterbodies and, therefore, appear as the first sign of "land" (a substrate or soil at least periodically exposed to air), (2) many wetland plant communities appear transitional in their composition, containing species unique to wetlands mixed with true aquatic species or mesic terrestrial species[3], and (3) a belief that the vegetation of wetlands would

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[3] For purposes of this paper, "aquatic" species are those plants that live exclusively in open water habitats; they may tolerate only brief periods of exposure to air. "Terrestrial" species are defined as plants that typically occur on dryland (upland) sites. "Wetland" species are those plants that occur in wetlands (e.g., marshes, swamps and bogs) with a higher frequency than in uplands.

eventually succeed into an upland plant community. The term "terrestrialization" has been used to define the latter process - hydrarch succession (Kangas 1990).

Wetlands occurring in the shallow water zone of lakes and rivers are classic examples of ecotonal communities (Fig. 1). These wetlands are permanently inun-

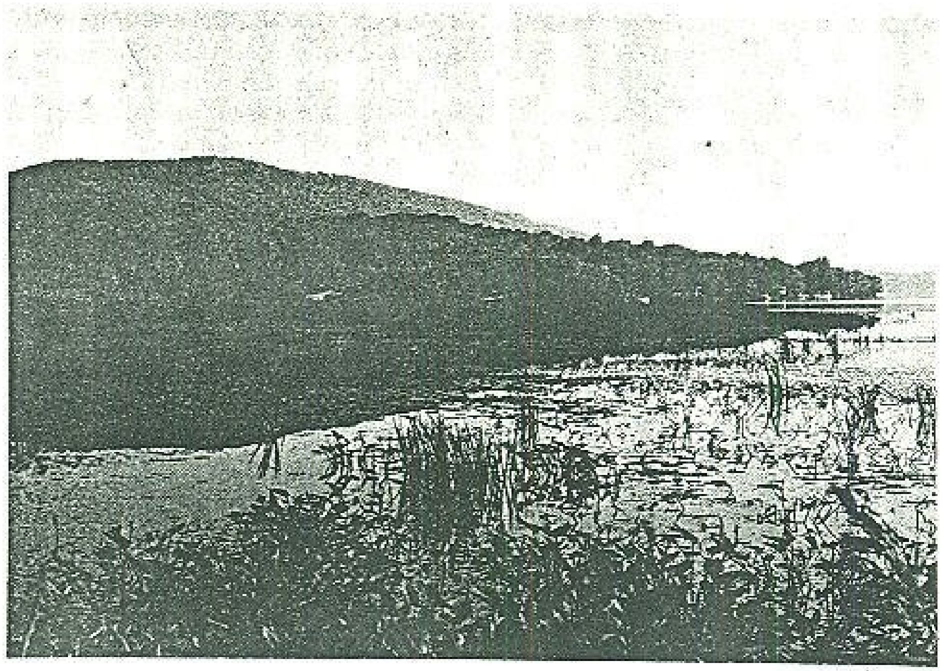

Fig. 1. Example of an ecotonal wetland in eastern North America. Emergent wetland species, including pickerelweed (*Pontederia cordata*), are intermixed with a floating-leaved aquatic species, such as white water lily (*Nymphaea odorata*), in this semi-permanently flooded wetland.

dated or nearly so throughout the growing season in most years. They tend to be dominated by aquatic species in deeper areas, by a mixture of aquatic and obligate emergent[4] hydrophytes in shallower water, and by the latter in sites flooded for long periods. Emergent species usually cannot survive near permanent inundation deeper than 1.5-2.0 m as suggested by Sculthorpe (1985) and Cowardin et al. (1979), while aquatic species typically cannot survive long periods of exposure to air. The shallow water marsh appears to be an ecotone between the adjacent

[4] "Emergent" refers to plants that are free-standing, self-supporting and therefore includes both herbaceous (non-woody) and woody plants.

aquatic bed and seasonally flooded marsh. One would expect that the plant composition in this area would change depending on water conditions. In wet years, aquatic species may be expected to predominate the site, while in dry years pronounced summer drawdown could result in an extension of the seasonally flooded marsh community. Consequently, there is noticeable tension in this zone. This situation commonly occurs in certain prairie pothole wetlands in North America. Kantrud et al. (1989) and van der Valk and Davis (1976) describe vegetative patterns and dynamics in these wetlands.

The upper edges of many wetlands also appear as transitional or ecotonal plant communities. Here wetland plant species are intermixed with mesic terrestrial species to form what some have called the "transition zone" (Environmental Laboratory 1987). This very condition has made it virtually impossible to use vegetation alone for defining the upper limits of wetlands (Federal Interagency Committee for Wetland Delineation 1989, Sipple 1985, 1988, Tiner 1988). Rather than being ecotonal between land and water, these communities are ecotonal between wetland and dryland (upland). Obligate hydrophytes, especially aquatic bed species, are conspicuously absent from these communities. The limits of these wetlands can only be established by assessing soil properties, since the plant community is dominated by facultative type[5] species that occur in both wetlands and nonwetlands to varying degrees.

Many macrophytic species (obligate hydrophytes) occur only in wetlands, while many others (facultative wetland plants) are more common in wetlands than in non-wetlands. The wettest wetlands (permanently or semipermanently flooded) often have both wetland species and aquatic species, but lack terrestrial plants. Conversely, the driest wetlands (seasonally saturated in the root zone or temporarily flooded) typically have terrestrial and wetland species, but aquatic species are absent. Moreover, the terrestrial species found in these areas have adapted in some way to living in periodically anaerobic soils, with shallow root systems being perhaps the most common adaptation (Tiner 1991). These species exemplify the tension and transitional nature of this zone. The wettest and the driest wetlands, therefore, may also be considered ecotones, but not necessarily ecotones between water and dryland.

It appears then that ecotonal wetlands may be largely restricted to plant communities at the two edges (waterward and landward) of wetlands or to the wettest and driest of wetlands. These communities reflect a zone of tension where species common to communities on either side of this zone intermix with perhaps some species characteristic of the transition zone itself. The community at the waterward edge reflects tension between the aquatic community and the seasonally flooded wetland, whereas the landward edge community contains members of the neighbouring wetlands and upland communities. Even where wetlands occur between land and water, one cannot simply say that the plant community of the wetland contains both aquatic and terrestrial species growing side by side. In the

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[5] In the United States, species occurring in wetlands have been rated in five "wetland indicator" categories based on their frequency of occurrence in wetlands: 1. Obligate Wetland (>99%), 2. Facultative Wetland (67-99%), 3. Facultative (34-66%), 4. Facultative Upland (1-33%) and 5. Upland (<1%) (Reed 1988).

case where a wetland complex contains both aquatic and terrestrial species, the wetland is usually composed of at least two different plant communities (one wetter and the other drier). One undoubtedly begins to realize that wetlands have unique characteristics that clearly set them apart from either land or water.

Conceptually, wetlands occupy the wetter portion of the soil moisture continuum (Fig. 2). They range from shallow water to a zone saturated near the surface

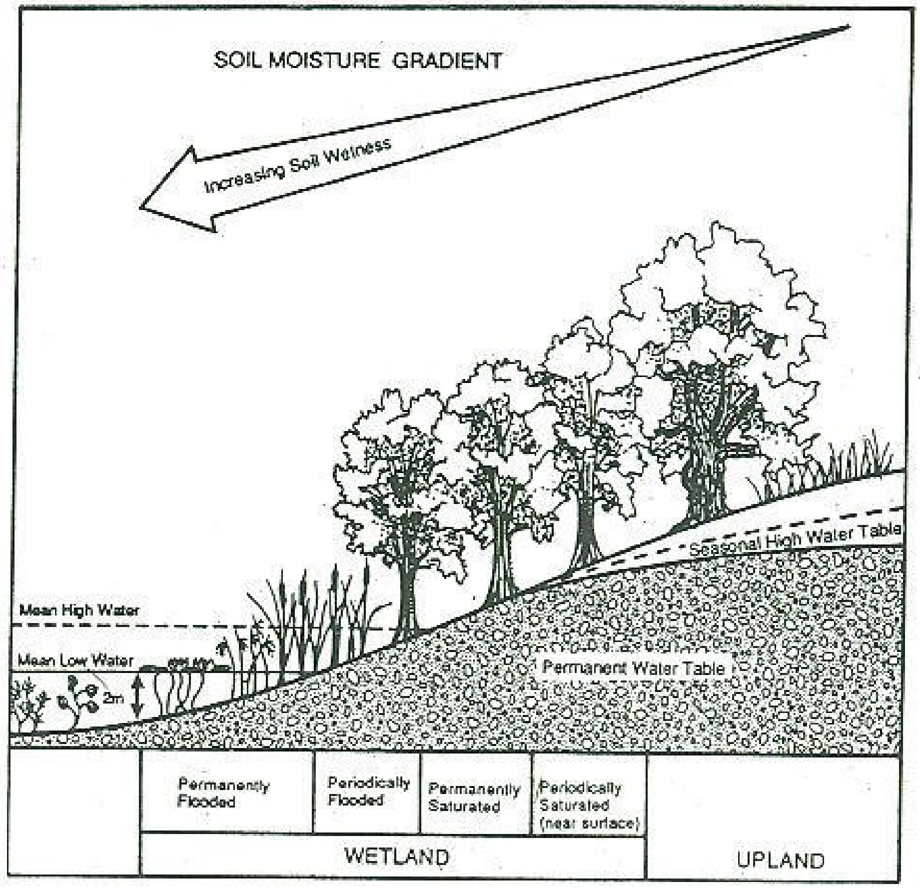


Fig. 2. Conceptually, wetlands occupy a low and intermediate position on the soil moisture continuum between deepwater habitats and uplands. From this standpoints, wetlands are no more ecotones than the variety of terrestrial habitats that exists along this continuum between deserts and wetlands. Since this diagram is conceptual, one must recognize that most North American wetlands do not occur between dryland and deepwater habitats, but are located in places with seasonal high water tables and essentially surrounded by upland, except for a shallow stream.

for extended periods during the year. From this standpoint, wetlands are no more ecotones than other habitats that exist along the moisture continuum between deserts and deep water. Certain wetland types or portions of wetlands may indeed

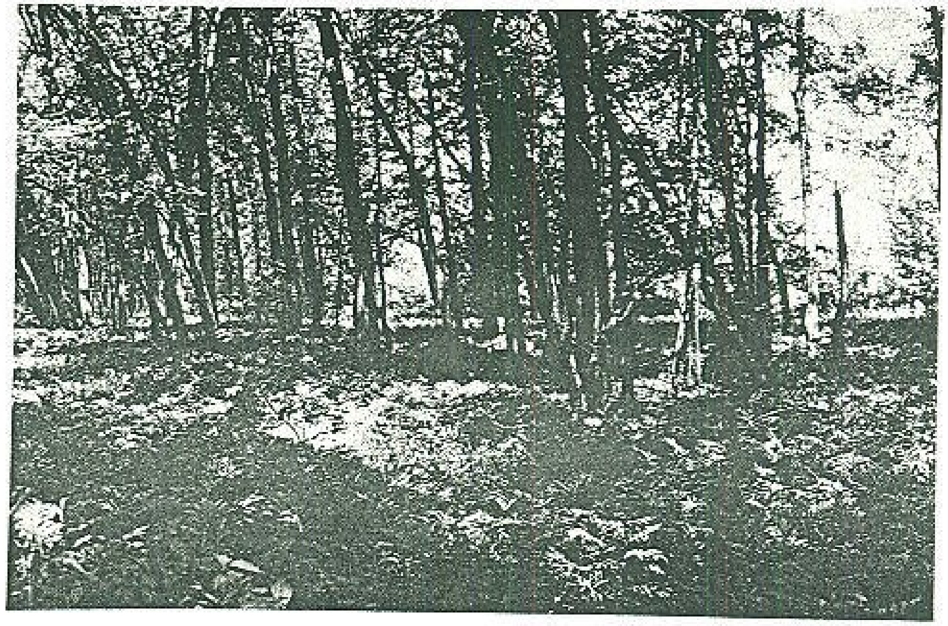
appear as transitional or ecotonal communities, yet all wetlands do not fit this simple categorization. The notion of wetlands as ecotones between land and water is a gross oversimplification of the nature of plant community dynamics. The variety of wetlands in the world resulting from differences in climate, hydrogeomorphology, soils, and other factors, plus the wealth of upland plant communities provide ample evidence that wetland plant communities no more exemplify ecotones than terrestrial communities.

NON-ECOTONAL WETLANDS

The majority of North American wetlands are not found between land and large waterbodies. Instead, they are essentially surrounded by upland except perhaps for a shallow stream, and therefore do not exemplify an ecotone between dryland and deep water. These wetland communities are usually distinctive, but do not typically contain mixtures of both aquatic and terrestrial species living together. They are generally characterized by obligate and/or facultative wetland plant species, while many may be dominated by facultative species with no affinity for wetland or upland habitats.

Looking beyond the macrophytic vegetation, significant differences occur at and below the soil surface of wetlands and nonwetlands. Soil types are distinctly different, with most wetlands typified by at least periodically anaerobic soils (e.g., organic soils or gleyed mineral soils with organic enriched surface layers). On the other hand, adjacent upland soils are better aerated mineral soils and adjacent deepwater habitat substrates of sands, silts and clays are often anoxic, but may lack comparable accumulations of organic matter. The differences in soil properties are so significant that they may be used to separate wetlands from nonwetlands in the United States (Federal Interagency Committee for Wetland Delineation 1989, Tiner and Veneman 1987).

Odum (1959) recognized that communities may not have ecotones and gave as a generic example, a transition community with characteristics of its own. I believe that many wetlands fit this type of categorization, although I prefer to consider them as "intermediate" communities between dryland and water, rather than "transitional" communities for reasons I will later discuss. Included among these wetlands in North America are the interior portions of large wetland complexes, the Florida Everglades, arctic and subarctic muskegs, many boreal bogs and fens, the majority of prairie pothole marshes, wet meadows, playas, vernal pools, seepage wetlands, forested wetlands in interstream divides along the Gulf-Atlantic Coastal Plain (including pocosins - "swamp-on-a-hill"), Carolina bay wetlands, and even certain floodplain wetlands that are effectively separated from adjacent rivers by natural levees (Fig. 3). Different vegetation patterns and soil properties of these wetlands typically reflect microsite variations in the frequency and duration of flooding and/or soil saturation, but not a water to land zonation, since a permanent waterbody is lacking in most of these wetland systems. The gradient is not a simple continuum based on elevation and its effect on flooding, as in the lakeshore marsh for example, but instead it is based on variable soil moisture resulting from a complex set of environmental factors including elevation, soil type, geomorphology



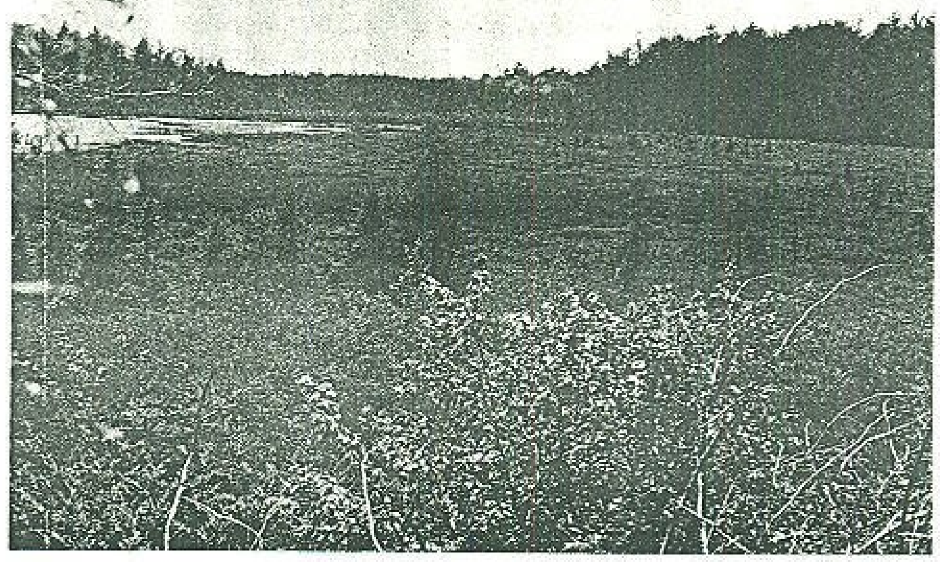


Fig. 3. Examples of non-ecotonal wetlands in North America: (a) floodplain swamp dominated by silver maple (*Acer saccharinum*), (b) lakeside bog dominated by ericaceous shrubs including leatherleaf (*Chamaedaphne calyculata*) and (c) isolated depressional forested wetland. These wetlands are not ecotones between water and dryland. ➡

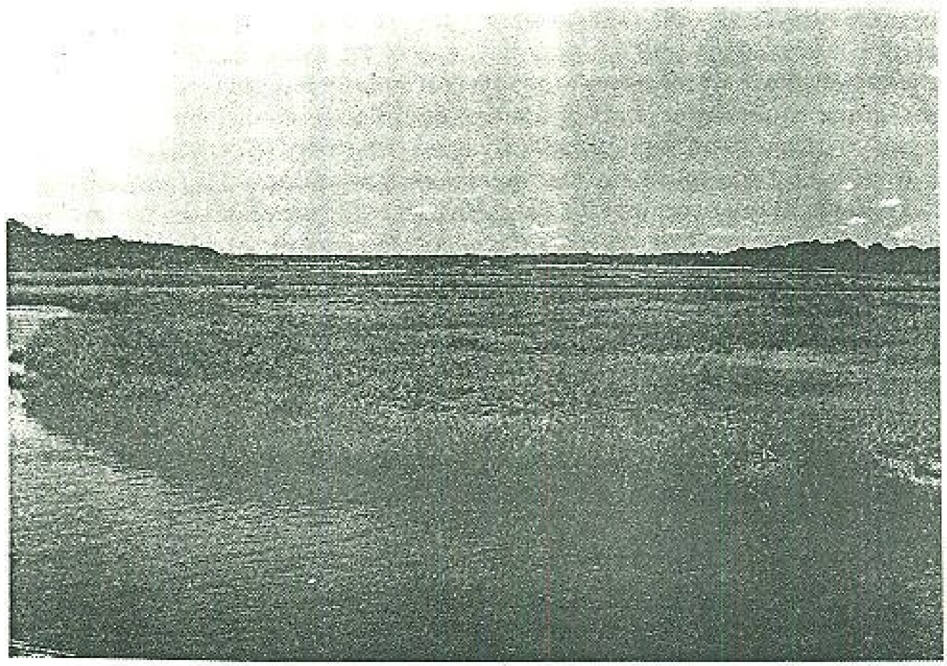


Fig. 4. Coastal marshes are another example of a non-ecotonal wetland. Although they occur between water and dryland, coastal marshes are not ecotones between them. Their vegetation is quite distinct from adjacent habitats and indicative of a highly salt-stressed environment. Only within coastal marshes and along their edges, particularly the marsh-upland border, may these wetlands possess ecotonal qualities.

and local hydrology. The change in vegetation patterns in wetlands within a given climatic region largely reflects differences in these important factors plus human intervention and the activity of other animals, such as beaver, muskrat, nutria, snow geese, and other herbivores.

Even coastal salt marshes lying between large estuarine waterbodies and dryland are not valid examples of an ecotone between land and water. In New England, these marshes develop peaty substrates unlike the bottom substrate of adjacent waters. This difference is as abrupt as the macrophytic vegetation (Fig. 4). The salt marsh community does not contain any significant macrophytic species of adjacent habitats, with few exceptions. Most of these exceptions occur at the edges of the salt marsh. For example, at the seaward edge of New England salt marshes, marine algae - rockweeds (*Ascophyllum nodosum* and *Fucus vesiculosus*) - may be found in the low marsh intermixed with smooth cordgrass (*Spartina alterniflora*). At the landward edge, switchgrass (*Panicum virgatum*) is a common border plant that grows in both wetlands and upland fields (Tiner 1987). The salt marsh-upland border zone has the highest plant diversity, while the marsh itself generally has low species diversity (Tiner 1987, 1993). This border zone has ecotone qualities of increased diversity and intermixing of macrophytic species from adjacent communities. The salt marsh proper, however, is characterized by plants that are mostly unique to salt marshes. These halophytic (salt-tolerant) species are specially adapted for life in saline soils and most do not grow in adjacent upland communities. Despite occurring between large bodies of water (e.g., estuarine bays and sounds) and dryland, salt marsh plant communities have little in common with adjacent communities and should not, therefore, be considered ecotones. The boundary between salt marshes and adjacent upland forests is abrupt due to significant change in elevation that precludes tidal flooding with salt water on all but perhaps the rarest of occasions. Salinity is an extremely effective limiting factor for plant growth and the relatively few species that are adapted for life in saline soils have extensive areas available for colonization both in coastal areas and in inland arid and semiarid regions where salts also concentrate in the soil. Besides the marsh edges, ecotones may occur within coastal marshes. Chabreck (1988) recognized two types of ecotones in coastal marshes: (1) the broad intertidal region representing different marsh types varying with salinity and (2) the zones between different marsh types (e.g., brackish marsh from intermediate or oligohaline marsh).

Generally speaking, the greater the change in hydrology (the frequency and duration of flooding and/or soil saturation) between adjacent communities, the more distinctive the difference in their plant composition. Where slopes adjacent to any wetland are steep, vegetation changes are abrupt and no transitional plant community develops. This commonly occurs in recently glaciated regions where many depressional wetlands exist in former kettleholes. It may even be relevant to artificially created ponds. These ponds often have a margin of cattails (*Typha* spp.) or other obligate wetland emergent plants in the shallow water zone. These distinct depressional wetlands have no transitional zone on the landward side - the adjacent plant community is cropland or pasture with vegetation completely different from the marsh. The extreme difference in the hydrology between the adjacent communities is reflected in the vegetation patterns. Is this an ecotone between land

and water as Clarke (1954) suggested? Yes, if "land" is broadly defined as any surface not permanently flooded, but no, if "land" is defined as upland (dryland). There is no zone of tension or transition between upland and the pond, and the cattail marsh would still exist in all probability if a parking lot replaced the cropland or pasture community. Depending on the size of the marsh and the permanence of water, the lower part of the wetland may be ecotonal, but it would be an ecotone between aquatic communities (e.g., aquatic beds) and wetland communities and not simply between water and land, unless one defines "land" in its broadest sense. Such definition of "land" probably was partly respon-sible for describing wetlands as transitional habitats.

CYCLICAL WETLANDS

While most wetlands probably experience fluctuating water levels and many may appear to be "dryland", at least at the surface during a significant part of the growing season in North America, there are certain wetland types that are dry for years - an event that may drastically change the vegetation pattern. These wetlands may be called "cyclical wetlands". A cyclical wetland is one where the plant community changes back and forth between one dominated by wetland species to one dominated by terrestrial species based on drastic hydrologic changes due to the natural variation in the hydrologic cycle, to fire in permafrost regions, or to other events which alter the hydrology of the wetland on a periodic (relatively short-term), but not permanent basis. Cyclical wetlands are probably most common and characteristic of arid and semiarid regions where severe droughts occur. These wetlands provide an interesting perspective on the issue of wetlands as ecotones because the nature of plant community can change dramatically in a relatively short period of time. Given these dynamics, are these wetlands ecotones between land and water or simply communities in flux?

Since the concept of ecotones implies that a transitional community lies between two distinct plant communities, consider the case for prairie pothole wetlands of North America. Where a prairie pothole contains a near permanent pond at its center, the outlying wetland communities appear ecotonal between water and land. Yet many potholes lack an open waterbody and therefore their communities should not be considered ecotonal between deep water and land, although the wetland area itself is under tension due to changing hydrologic conditions. During prolonged droughts, annual and perennial terrestrial species may predominate the temporarily flooded wetlands, while during wet years, obligate wetland species may characterize these isolated basins. Consequently, the appearance of "wetland plant communities" is cyclical, so these wetlands may be considered cyclical from both the vegetative and hydrologic standpoints. Despite the dynamics in vegetation and hydrology, the soil retains hydric properties indicative of wetlands and therefore can be used to distinguish these wetlands during droughts. Virtually all prairie pothole wetlands and probably playas in the Southwest have dynamic plant communities due to the regional (arid and semiarid) climates. While those that have permanent water in the center of their basins may be considered as ecotones

between land and water, most should not, since they are not juxtaposed between land and water.

Another type of cyclical wetland occurs in the arctic and subarctic where severe fire melts the near-surface part of the underlying permafrost, increasing the depth to the permafrost layer, and thereby improves drainage for some time. Within a period of 30 years or more, the permafrost layer is gradually restored to its former level (near the surface), thereby impeding drainage and bringing about the return of the black spruce wetland (Ping et al. 1990). These wetlands do not occur between land and water and are not ecotones from that standpoint. Moreover, hydrologic change is so drastic that it may be debatable whether the area is or should be considered wetland during the time of recovery. However, it is clear that the ultimate pathway of change leads to a return to wetland conditions within a few decades, at a minimum. It therefore, seems prudent to consider these sites as cyclical wetlands.

Should cyclical wetlands be considered ecotones? I think not since they are dynamic plant communities either in state of near constant flux due to the regional climate or in the process of recovering from a perturbation (e.g. fire). They are not a tension zone between two established adjacent communities. The ecotone concept should not be applied to these cyclical communities, it is better reserved to truly transitional habitats between two distinct communities.

ARE WETLANDS REALLY TRANSITIONS BETWEEN WATER AND DRYLAND?

One of the reasons for the traditional notion of considering wetlands as ecotones and transitional habitats could be a belief that all wetlands would eventually become uplands. Gates' models of hydrarch succession for the Douglas Lake region of Michigan show a progression of communities from aquatic bed communities to marsh fen communities to shrub wetlands to forested wetlands to the climax - "dry land" (Gates 1926). If wetlands were part of the evolutionary pathway from open water to uplands, there would be some reason to consider them as possible ecotones or transitional habitats in a generic sense. Although plant communities may be extremely dynamic within some wetlands, wetlands do not typically evolve into uplands, unless the hydrology is modified by man, by a climatic change, or by other catastrophic events (e.g. mudslide, volcanic eruption, or earthquake). Several scientists have supported this position (Nichols 1915, Heinselman 1970, and Niering 1989). Wetlands are relatively stable spatially in the absence of these significant hydrologic changes. For example, Damman (1987) believes that many North American peatlands will remain in their present state since they are in equilibrium with the local climate and that their vegetation pattern will change little, unless the hydrology is altered. Thus, wetlands are generally long lived features on the landscape, although their vegetation may change due to fire, droughts, heavy grazing, and other factors.

Today more uplands are probably becoming wetlands due to natural processes than the reverse. For example, rising sea level is inundating low-lying areas adjacent to salt marshes and permitting the salt marsh to migrate landward converting upland to wetland or previously nontidal forested wetland to salt marsh.

Rising sea levels following the last glaciation have drowned river valleys, forming extensive coastal wetlands and estuaries, such as Chesapeake Bay. In addition such processes alter local hydrology by increasing water tables thereby promoting the development of freshwater wetlands as well. In boreal regions, paludification processes facilitated by the growth habit of peat mosses (*Sphagnum* spp.) result in the "bogging" or "swamping" of uplands adjacent to existing bogs (Crum 1988, Skoropanov 1968). The landscape underlying peatlands in the former Lake Agassiz basin in Minnesota provides direct testimony to this process (Heinselman 1970). Man and beaver also play an important role in wetland creation. In the arid west of the U.S., irrigation projects have increased local water tables causing an increase in wetlands (marshes and wet meadows) at the expense of uplands. Beaver dams have transformed many uplands to wetlands throughout North America.

Besides major climatic changes and tectonic activity, natural processes do not convert significant acreage of wetlands to uplands in the short term. Glacial rebound may change wetlands to uplands by changing elevations and local hydrology, as has been reported for Arctic Canada (Tarnocai and Zoltai 1988). Desertification with its migrating dune fields could and probably does convert wetlands to uplands in arid regions of the world, but in North America, it is not a significant process.

The most significant process changing wetlands to uplands in North America is human action. Filling, drainage, channelization, freshwater diversion, and regulating river flows are responsible for converting vast acreage of wetlands to drylands. In the U.S., over half of the nation's original wetlands have been destroyed, mostly due to human activities (Tiner 1984, Dahl 1990). Many riparian cottonwood forests in the Southwest represent former wetlands that are no longer flooded sufficiently to be considered wetlands due to river flow alteration.

The examples provided above should amply demonstrate that the ultimate fate of most wetlands is not to become uplands through natural processes. Using hydrarch succession models to suggest that wetlands themselves are ecotones between land and water is inappropriate and invalid. Moreover, wetlands should not be viewed simply as transitional habitats, since most wetlands are relatively stable spatially, although the nature of the plant community may change markedly over time due to many factors.

CONCLUSION

While the lower and upper edges of many wetlands do represent ecotones between the wetland and an adjacent waterbody or upland, the majority of wetlands, including many distinct wetland types, are not ecotonal between dryland and water (aquatic communities). These wetlands simply do not occur along a waterbody and they cannot be considered transitional between water and land in the strict sense. Most wetlands possess distinct associations of plant species and diagnostic soil properties that clearly separate them from adjacent dryland communities. Moreover, there are many more examples of uplands becoming wetlands due to natural events than vice versa. Based on these conditions, we must question the validity of generically considering wetlands as ecotones between land and water. In my

opinion the ecotone concept has been too broadly applied to wetlands in a way that oversimplified the issue by ignoring the high variability among wetlands, the lack of a permanent waterbody by many wetlands, and the distinctness of wetlands versus other habitats in terms of plants and/or soils. Moreover, the concept of ecotones seems best applied to individual plant communities, allowing for the recognition of ecotones within wetland complexes, between wetlands and non-wetland communities, and between adjacent upland communities.

Future papers and publications dealing with wetlands should be sensitive to the issues discussed and should, at a minimum, qualify the application of the concept of ecotones for wetlands and refrain from referring to all wetlands as ecotones or even as transitional habitats. The position of wetlands between "land" and "water" would be presented in other ways, mainly by emphasizing the soil moisture continuum. Wetlands should be considered as relatively distinct communities associated with hydric soils. While conceptually, wetlands may occur along the soil moisture continuum between mesic terrestrial habitats and aquatic systems, in reality most are wet places on the landscape surrounded by uplands. This position of wetlands is more intermediate than transitional. The latter implies that wetlands are in a state of transition from a former waterbody (deepwater habitat) to an upland habitat which is not true for many wetlands. Since most wetlands are relatively stable spatially and their transitional nature is more internal as reflected by the plant community dynamics within individual wetlands, wetlands themselves should not be categorically viewed as transitional communities between land and water. Finally, wetlands are no more ecotones than the other habitats occurring along the soil moisture continuum between deserts and deep water.

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