# Four general principles for the management and conservation of wetlands in large lakes: The role of water levels, nutrients, competitive hierarchies and centrifugal organization

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## Abstract

The most important factor in shoreline wetlands is variation in water depth. Superimposed upon this are gradients of soil fertility, ranging from sandy, open shorelines to sheltered, fertile bays. The use of both transplant and pot experiments shows that competitive hierarchies rapidly arise in wetland vegetation and that species are sorted along exposure and depth gradients according to their relative competitive abilities. These patterns can be summarized in the centrifugal organization model, in which competitive dominants occupy preferred core habitats and where different species and vegetation types are then arrayed outward along different constraint gradients (Wisheu & Keddy 1992). Knowledge of these general patterns provides an essential tool for managing lakes and reservoirs in order to maintain and enhance biological diversity.

## WETLANDS AND SHORELINE GRADIENTS

The shorelines of lakes and rivers provide large areas of wetland vegetation. These wetlands include all four major kinds of wetlands; swamps, marshes, fens and bogs. Because plant and animal species, vegetation and the wetland types are so variable, it is often difficult to consider all of these together. Far too often one encounters specialist publications on plants of a particular reservoir, such as a bog, fen, marsh, mire, reed swamp or aquatic community; these fragmented treatments distract attention from the general principles involved in the management of lakes and reservoirs. Furthermore, as so much focus on lake and reservoir management is placed upon fish, limnology too often, takes precedence over plant ecology. The large expanses of wetland vegetation therefore are largely ignored or treated in passing as 'aquatic plants'. Our objective here is to try to pull together all these disparate vegetation types, species and physiographic types and present four general principles necessary for managing them.

From one perspective, referring to shorelines as a whole may appear unwise as shorelines appear to have little in common with one another because one can find almost any type of wetland, from an ombrotrophic peat bog to a sandy bay along a shoreline. However, all types of wetlands are, in fact, controlled by only a short list of environmental factors: water levels, soil fertility, disturbance, salinity, grazing and burial. This is true whether one is talking about the largest tropical floodplain complex in the world, the Amazon basin (Lowe-McConnell 1975, 1986; Goulding 1980; Junk 1983, 1986) or small temperate zone lakes (Pearsall 1920; Spence 1964; Bernatowiscz & Zachwieja 1966; Keddy 1981, 1983, 1984). In fact, irrespective of location, a shoreline is merely a gradient that stretches a wetland out along several gradients, acting not unlike a prism.

From another perspective, shorelines are unique, in that they are subject to frequent changes in water level, waves and ice scour. In general, these kinds of natural disturbances lead to a high biological diversity and thus, shorelines may support many kinds of unusual or rare species. Well-studied examples include the furbish lousewort on the eroding banks of rivers in north-eastern North America, the rich Atlantic coastal plain communities along the shorelines of
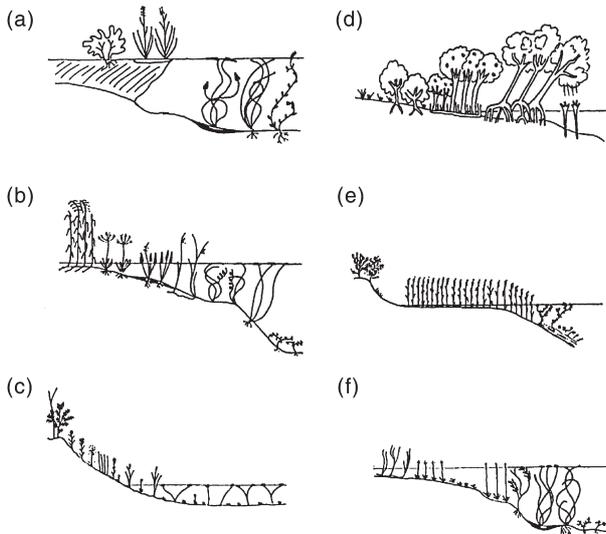
**Fig. 1.** Some examples of plant zonation. (a) A bog (after Dansereau 1959); (b) St Lawrence River (after Dansereau 1959); (c) Wilson's Lake, Nova Scotia (after Wisheu & Keddy 1989b); (d) a mangrove swamp of the Caribbean (after Bacon 1978); (e) the eastern shore of Lake Kisajno, north-eastern Poland, a typical small-lake phyto littoral (after Bernatowiscz & Zachwieja 1966); (f) a sandy shoreline (after Dansereau 1959).

the Great Lakes and the eastern seaboard of North America. In these habitats, shorelines appear to generate extra high levels of biological diversity.

In this paper, we want to combine these two approaches to explore how to manage shorelines to maintain the different types of wetlands found along them and, in particular, to protect or create the unusual features that promote high species diversity. We believe that a commonsense application of a few general principles will provide practical guidelines for the management of both lakes and reservoirs.

## FOUR ESSENTIAL PRINCIPLES
### Water level fluctuations

While all wetland vegetation is associated with flooded soils, the duration of flooding is largely responsible for different vegetation types. This leads to conspicuous zonation on shorelines. That is, as different species tolerate different degrees of flooding, the range of flooding regimes creates distinct vegetation types (Fig. 1). This is the first source of botanical variation generated on shorelines. It is so conspicuous that far too many ecologists seem content to draw a profile of the vegetation and conclude that they have completed their study of the shoreline.

Zonation is a dynamic, not static, property of shorelines. Let us consider two limiting cases to frame the discussion and clarify thinking. If water levels were entirely stable, the result would be a two-zoned system (Fig. 2). There would be aquatic communities with some emergent species below the water, while above the shoreline, there would be woody plants. If water levels fluctuated widely and wildly, they would
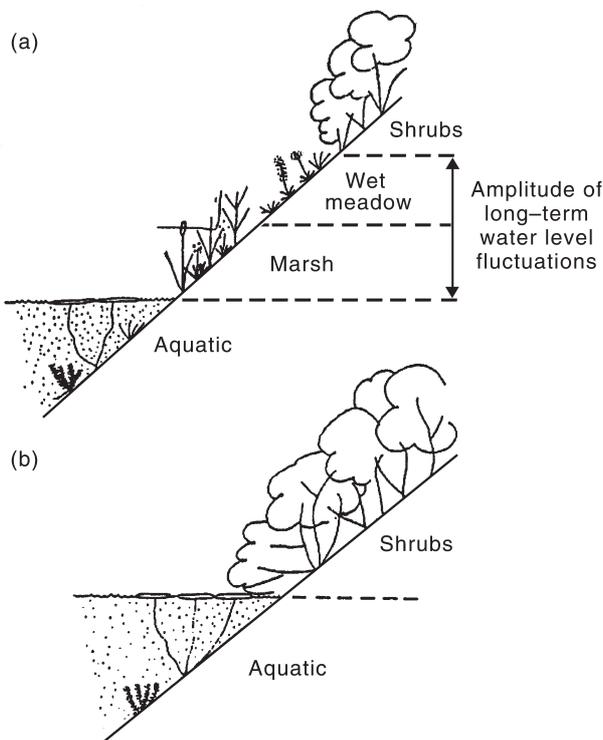


**Fig. 2.** Constriction of water level fluctuations reduces wetland habitats from (a) four zones to (b) two zones (Keddy 1991).
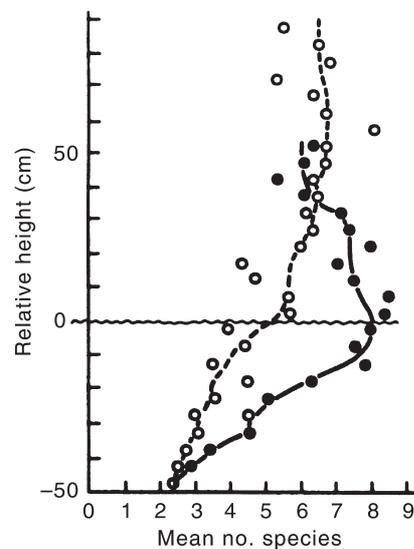


**Fig. 3.** Relationship between the mean number of species (0.025 m²) and the August water level for (●) sheltered and (○) exposed shores in a Nova Scotia lake (modified from Keddy 1984).

frequently exceed the natural tolerance limits of most species, thus producing shorelines that are devoid of plants, or dominated by only a few weedy species.

Somewhere within these two extreme situations lies the regime that promotes maximum plant diversity. Year to year fluctuations are an important factor for generating plant diversity. High-water periods kill shrubs that dominate the upper shore, whereas low water periods allow many other species to regenerate from buried seeds. If mean water levels change from one year to the next, one can then transform the two-phase system to a four-phase system (Fig. 2). In this case, the simple practice of changing water levels from one year to the next doubles the number of vegetation types. Moreover, it more than doubles the number of plant species, because new vegetation types such as emergent marsh and wet meadow generally support large numbers of plant species. If we plot the number of species against the water depth on such a shoreline, the peak of diversity where water levels vary from year to year is obvious (Fig. 3).

How much year to year change is enough? This probably varies with climate, but our research on the Great Lakes suggest that changes over many metres are required; in smaller inland lakes, this probably drops to less than 1 m. Superimposed upon year to year variation is the variation that occurs within a year. This is probably less important for producing rich wetland plant communities, but some seasonal water fall is natural and is generally found on species-rich shorelines. Dropping water levels by approximately 0.5 m during the growth season is probably a good first estimate. Let us now briefly introduce two models that have an immediate practical application to the management of lakes and reservoirs. Both are discussed in more detail by Keddy (2000).

## Predictive model for changes in shoreline wetlands

The Great Lakes are among the largest bodies of fresh water in the world (Table 1). The water levels of these lakes have changed over both geological and historical time scales (Fig. 4) so there is now a rich array of wetland types (Table 2). Rich, wet, meadow flora are particularly well developed on gently sloping sandy shorelines (Reznicek & Catling 1989). The Great Lakes wetlands provide an important habitat for fish, waterfowl and rare plant species (Smith *et al.* 1991). Large areas of these wetlands have been drained and humans have also reduced the amplitude of water level fluctuations in them. More recently, there was added pressure to control them further. Figure 5 was used to provide preliminary estimates of the probable effects on wetland areas. The objective was to predict the upper

**Table 1.** Large rivers and lakes provide extensive areas of shoreline with zoned plant and animal communities (modified from Czaya 1983)

|  | Country | Average annual discharge at mouth (m$^3$ s$^{-1}$) |
|---|---|---|
| Ten largest rivers in the world |  |  |
| Amazon | Brazil | 180 000 |
| Congo | Zaire/Angola | 42 000 |
| Yangtze Kiang | China | 35 000 |
| Orinoco | Venezuela | 28 000 |
| Brahmaputra | Bangladesh | 20 000 |
| Yenisei | USSR | 19 600 |
| Rio de la Plata | Argentina/Uruguay | 19 500 |
| Mississippi–Missouri | USA | 17 545 |
| Lena | USSR | 16 400 |
| Mekong | Vietnam | 15 900 |
| Ten largest Lakes of the world |  | Surface area (km$^2$) |
| Caspian Sea | USSR | 371 000 |
| Lake Superior | USA/Canada | 83 300 |
| Lake Victoria | Uganda/Kenya/Tanzania | 68 800 |
| Lake Aral | USSR | 66 458 |
| Lake Huron | USA/Canada | 59 570 |
| Michigan | USA | 57 016 |
| Lake Tanganyika | Zaire/Burundi/Zamibia/Tanzania | 34 000 |
| Great Bear Lake | Canada | 31 792 |
| Lake Baikal | USSR | 31 500 |
| Lake Malawi | Malawi/Mozambique | 30 500 |

boundary of wet meadows as well as the lower boundary of the marsh.

To model the landward edge of the wet meadow, it was necessary to consider the dieback and recolonization by woody plants. Two assumptions were made according to an exponential model. The first was that the dieback of woody plants was directly related to high water levels during the growth season and the second was the reinvasion of woody plants. This allowed predictions of the lower limit of woody plants from projected water levels (Fig. 5). The lag times of 15 or 20 years, as opposed to 18 years, made little difference.

To model the lower boundary of the marsh, the assumption that marsh plants moved down-slope the same year that water levels fell was required; this would most likely be the result of the germination of buried seeds. As water levels rose, the wetland plants would dieback over several years

(Fig. 5, bottom line). The lag times of 2 or 4 years, as opposed to 3 years, made little difference.

The area between these lines is the area of wet meadow and marsh, as a function of time. For example, the great areas of wetlands that occurred during the low-water period of the mid-1930s is clearly visible. This model was then used for projected water level scenarios to forecast the effects on wet meadow and marsh areas in the Great Lakes. If further reductions in amplitude occurred, the model would have predicted losses approximating 30% of the wetlands in Lake Ontario alone.

## Descriptive model for frequency and intensity of flooding

Two of the most important components of flooding are frequency and intensity. These can be plotted on orthogonal
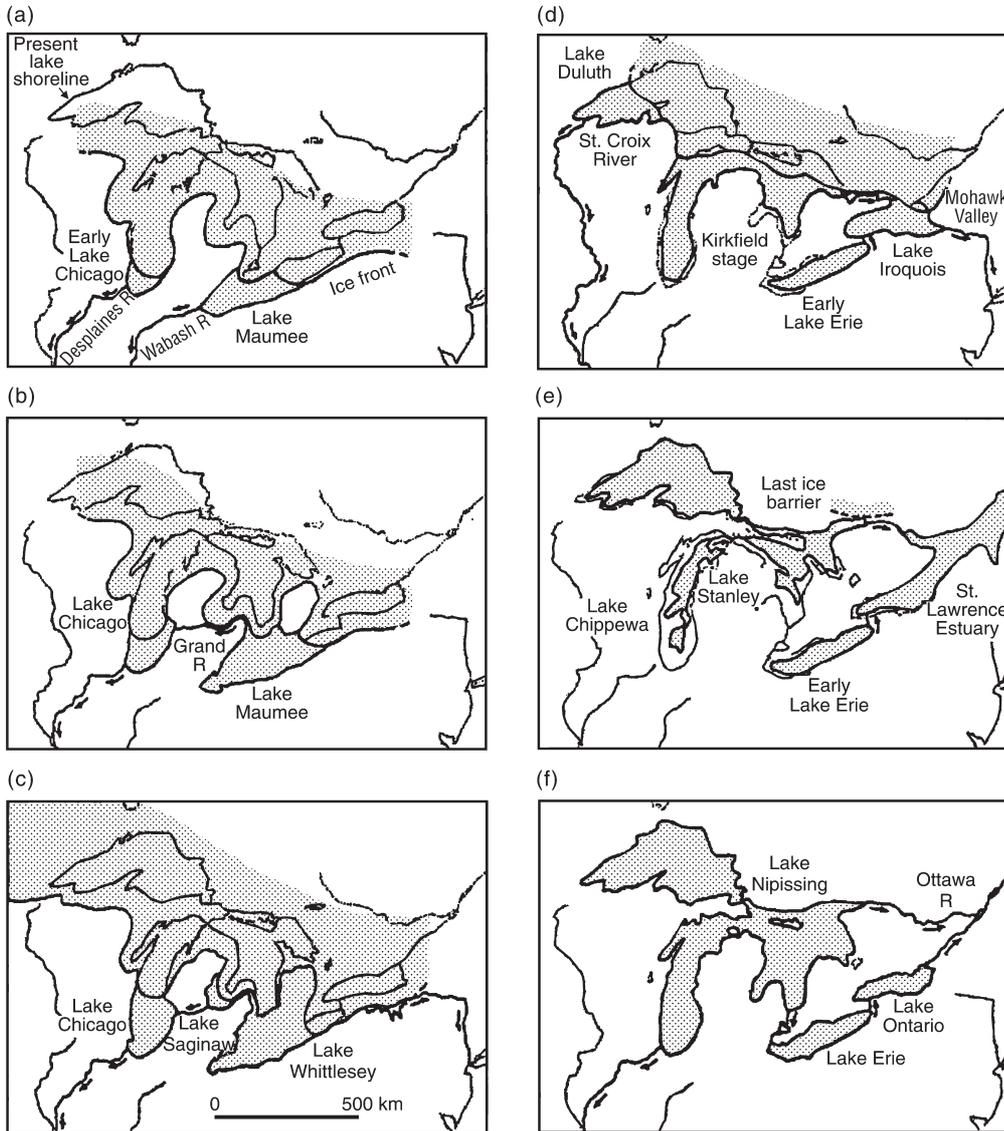


**Fig. 4.** Changes in the water levels of the Great Lakes over millennia. (a) Glacial retreat (Woodfordian Substage), (b) Glacial retreat (continued), (c) Port Huron glacial advance (Late Woodfordian Substage), (d) Glacial retreat (Post-Valderan), (e) Glacial retreat (Final) and (f) Post-Glacial Great Lakes (from Strahler 1971).

axes to represent all possible pair-wise combinations. We can then plot, for many sites, the frequency of flooding against the depth of flooding, or perhaps more conveniently, the frequency of flooding and amplitude of water level changes. There are several important properties we could then plot on these axes. One could plot the many reservoirs or wetlands of the world in order to explore different patterns. Are there for example, certain combinations that are rare and other combinations that are common? One *could* also plot important properties such as productivity or wildlife diversity and explore how they respond to differing water level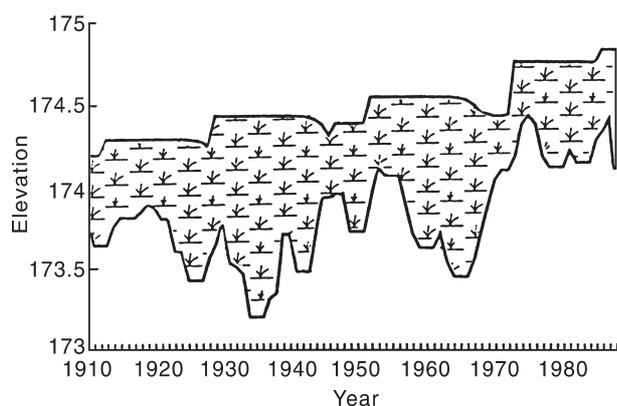s. Unfortunately, the required data on water levels are scattered through a broad literature describing individual cases and also buried in reams of unpublished reports. Futhermore, the axes are not often comparable. As a first step in this direction, Fig. 6 shows such a plot for a few lakes and identifies a corridor of high plant-species richness. This is based upon a set of lakes in eastern North America and there is currently no way to know how well we can extrapolate beyond this geographical region or to other properties.

## Fertility

Those shorelines exposed to waves and ice scour have silt and clay constantly eroded and exported from them, so these



**Fig. 5.** A simple simulation model showing response of wetland vegetation to changes in water levels (elevation in metres) in the Great Lakes (modified from Painter & Keddy 1992). The upper line is the woody plant boundary (18 years), while the lower line is the herbaceous plant boundary (3 years). Note that the area of wet meadow varies with water level history.
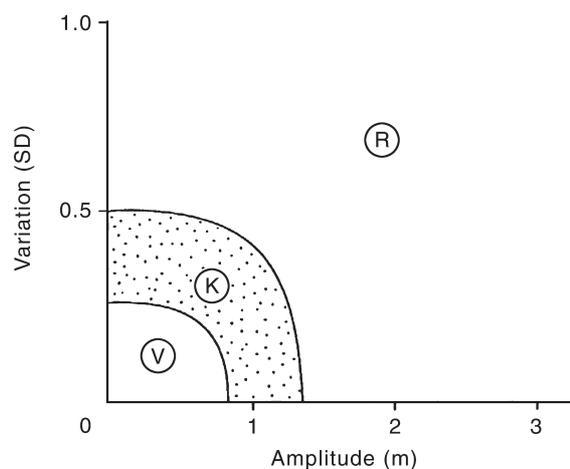


**Fig. 6.** A corridor of (▓) high species richness is associated with among year water level amplitudes of roughly 1 m and SD of roughly 0.5 m. The letters within circles indicate three representative lakes from Nova Scotia: V, Vaughan; K, Kejimkujik; R, Rossignal. (Hill *et al.*, 1998).

**Table 2.** Characteristics of wetlands in the Great Lakes ( Smith *et al.* 1991)

| | | | Lakes | | |
|---|---|---|---|---|---|
| | St Lawrence River | Lake Ontario | Lakes Erie and St Clair | Lake Huron | Georgian Bay |
| No. wetlands | 27 | 64 | 28 | 13 | 10 |
| Area of wetlands (ha) | 3511 | 11 555 | 19 306* | 1274 | 1829 |
| Marsh[†] | 91.2 | 79.1 | 83.9 | 5.1 | 73.3 |
| Swamp[†] | 8.8 | 20.3 | 16.1 | 27.8 | 24.6 |
| Fen[†] | | 0.2 | | 16.7 | 2.1 |
| Bog[†] | | 0.1 | | | |
| Palustrine and isolated[†] | 0.7 | 2.4 | 3.9 | 27 | 4.1 |
| Riverine[†] | 95.8 | 28.9 | 3.9 | 7 | 27.4 |
| Rivermouth[†] | 3.5 | 25.2 | 16.4 | 2.2 | |
| Lacustrine on bay[†] | | 27.5 | 13.8 | 5.2 | |
| Lacustrine[†] | | 16.6 | 61.3 | 58.6 | 68.5 |
| Organic soil[†] | 6.2 | 45.4 | 50.3 | 31.9 | 0 |
| Mineral soil[†] | 89.6 | 53.7 | 49.7 | 68.1 | 100 |
| No. vegetation communities | 9.1 | 9.6 | 6.8 | 32.2 | 11.8 |

*Walpole Island marshes account for at least another $10\,000 \times 10^4\,m^{-2}$. [†]Represents percentages of components.

areas tend to be infertile and support only distinctive plant species. In contrast, silt and clay are deposited in bays and these areas tend to be dominated by large clonal dominants with dense canopies. Exposure gradients are therefore an important feature in producing different plant communities around the margin of a water body. The greater the array of exposure types on a shoreline, the greater the array of vegetation types and plant species will be (Pearsall 1920; Spence 1964; Bernatowiscz & Zachwieja 1966; Keddy 1981, 1983, 1984). This is easily illustrated by using the biomass of plant communities as a measure of their location along the exposure gradient. Figure 7 plots the number of plant species and the number of rare plant species against the biomass of shoreline wetlands. The diversity of plant species is highest in intermediate levels of biomass (exposure) and the number of rare species is greatest on the sites with the lowest levels of biomass (highest levels of exposure).

Eutrophication will, however, reduce the length to this gradient and slowly cause more areas of shoreline to converge on the high biomass vegetation type. In one experiment we created 12 different shoreline types in NIOL containers. These included sand, gravel, cobbles, stable and fluctuating
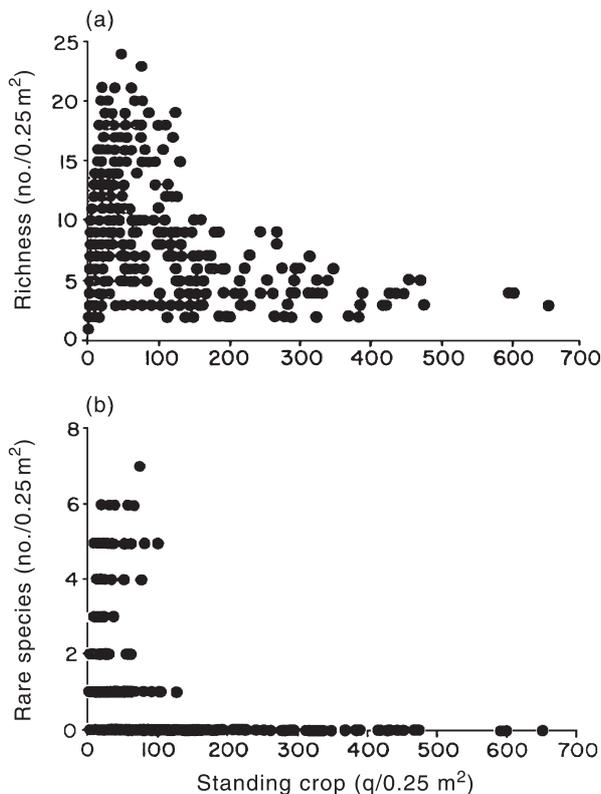
water levels. Each were replicated 10-fold. Half of these shoreline types received additional nitrogen, phosphorus and potassium fertilizer and in every case, the number of plant species was lower in the fertilized plant communities (Fig. 8).

## Competitive hierarchies

Over the last few decades, it has become apparent that most plant communities are organized into competitive hierarchies. That is, a small number of strong competitors tend to make up most of the biomass on a shoreline whereas larger numbers of weak competitors use the remaining space. Furthermore, increasing the soil fertility increases the ability of these few species to dominate a site and exclude neighbours. A comparison between the dominance achieved by *Typha* or *Phragmites* in fertile soils with the rich array of plant types in interdunal meadows, wet prairies or fens can be made. The distribution of species along shorelines is controlled by hierarchies of competitive ability. The stronger competitors occupy the fertile sites and exclude the weaker competitors to infertile areas. In one study, the competitive ability of seven plant species measured in an experiment was able to predict their field distribution along a shoreline; the large leafy plants occupied the fertile sites whereas small rosette species were excluded to the sandy shores (Wilson & Keddy 1986). We have repeated this study with a much larger sample of species and found the same result (Gaudet & Keddy 1995). This merges with the work on fertility, as it is well-established that fertilization enhances the competitive performance of the large leafy species. The more eutrophic a site is, the greater the likelihood of dominance by a few aggressive shoreline species such as *Typha*, *Phragmites* or *Phalaris*.

## Centrifugal organization

The same species usually prosper in the fertile and sheltered sites around a lake, but different species can occur at other sites, depending on the constraints. Shallowly sloping sands may develop fens, gravel shorelines may have isoetid plants, wet prairies may occur where fire or water level fluctuations kill woody plants, pannes may develop between alkaline sand dunes, and so on. The benign ends of many gradients are similar enough that we can describe them as a 'core' habitat that can be dominated by the same species. At the peripheral end of each axis, however, species with specific adaptations to particular sources of adversity occur. This pattern is termed centrifugal organization (Fig. 9). Many peripheral habitats radiate outwards from the single, central core habitat.

On shorelines, the core habitat has low disturbance and high fertility and is dominated by large leafy species



**Fig. 7.** Plant species richness along gradients of standing crop (a) for 401 0.25 m² quadrats in eastern North America (b) the same quadrats, but with nationally rare species only (reprinted with permission from Moore *et al.* 1989).

capable of forming dense canopies. In north-eastern North America, *Typha* dominates the core region. In other climatic regions, herbaceous perennials in the genera *Papyrus*, *Phragmites*, *Phalaris*, *Calamagrostis* or *Rhynchospora* may play a similar role. Outside the core, different constraints create radiating axes, along which different groups of species and vegetation types are arrayed. Along an axis of soil phosphorus, for example, that is highest in a fertile embayment and lowest at an infertile open shoreline, the community composition changes from a high biomass *Typha*-dominated wetland to a sparsely vegetated shoreline that is dominated by isoetid and insectivorous species (Moore *et al.* 1989), two groups of plants indicative of infertile conditions (Boston 1986; Givnish 1988). Furthermore, the shortage of phosphorus, as opposed to nitrogen, allows for rather different plant communities to arise (Verhoeven *et al.* 1993, 1996).

Gradients of nutrient concentrations, however, are only some of the many gradients that occur in wetlands. Others are gradients of disturbance and the species found along these gradients differ from those found along gradients of fertility. *Typha* would again occupy fertile, protected areas, but where ice scour or severe flooding occur, either reeds or annual species would be abundant (Day *et al.* 1988; Moore *et al.* 1989). The deeply buried rhizomes of reeds protect them from moderate ice scour while fast-growing annuals are able to set seed between periods of mud deposition (Grubb 1985; Day *et al.* 1988). Peripheral habitats that are formed by different kinds and combinations of infertility and disturbance, support distinctive flora that reflect differing environmental conditions (e.g. shoreline fens, Charlton & Hilts 1989; Yabe 1993; Yabe & Onimaru 1997); interdunal swales and sand spits (Willis 1963, Reznicek & Catling 1989); coastal plain wetlands (Keddy & Wisheu 1989); river banks (Brunton & Di Labio 1989; Nilsson *et al.* 1989) and flood plains (Salo *et al.* 1986; Duncan 1993)).

Our objective here is to introduce this model and stress its value in creating biologically diverse shorelines. The postulated mechanisms that produce this arrangement of vegetation and the tests of these postulates are discussed elsewhere (Keddy 1989, 1990; Wisheu & Keddy 1992; Gaudet & Keddy 1995; Keddy & Fraser 1999; Keddy, 2000).

## MANAGEMENT GUIDELINES

The following guidelines apply to all wetland types. The numbers given are drawn from temperate zone lakes and will have to be calibrated for other wetland types. Tropical floodplains, for example, may have much larger seasonal variation compared to temperate lakes:
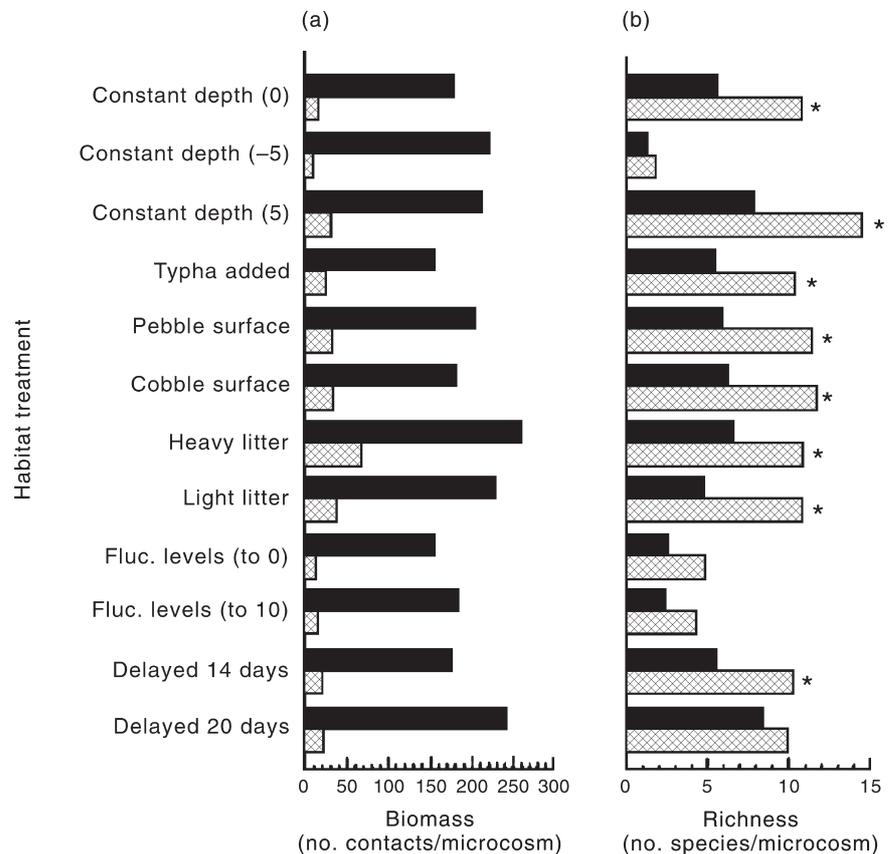


**Fig. 8.** Effect of fertilization on (a) biomass and (b) species richness of wetland plants in 12 artificially created habitats (Wisheu *et al.* 1990). (▨) Infertile plants, (■) fertile plants. *P = 0.001.
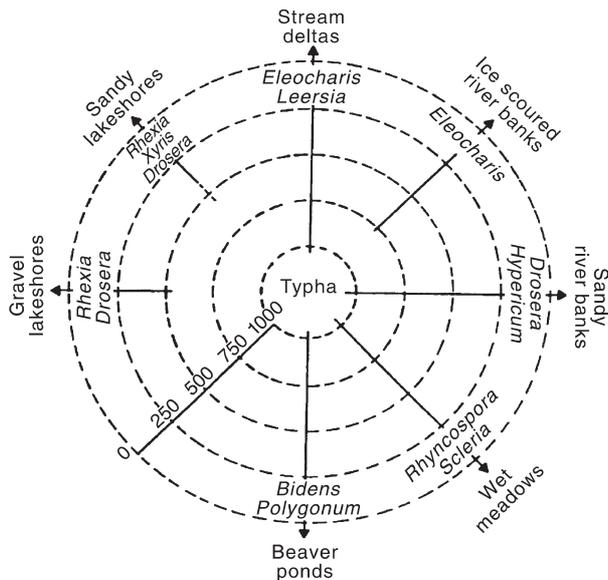

**Fig. 9.** When many gradients radiate outward from a shared core habitat, the pattern is termed centrifugal organization (Wisheu & Keddy 1992).

1.  Water levels should vary from year to year. A 10-year cycle with changes of 1–4 m is probably typical of smaller lakes, with greater fluctuations found in larger lakes. The highest water levels will determine the area of herbaceous wetlands by setting the lower limit of trees and shrubs.

2.  Within years, high water levels in spring will further retard the invasion of herbaceous wetlands by shrubs and trees.

3.  During the growth season, water levels should fall approximately 0.5–1.0 m.

4.  The gradient(s) from infertile to fertile sites greatly increase the number of plant communities that can arise.

5.  The more kinds of infertile and otherwise constrained habitats available, the more kinds of plants can coexist in a lake, reservoir or wetland.

6.  Eutrophication usually reduces the number of plant species at individual sites, as well as reducing the total number found in a lake, reservoir or wetland.

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