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GREAT LAKES VEGETATION DYNAMICS: THE ROLE OF FLUCTUATING WATER LEVELS AND BURIED SEEDS

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ABSTRACT. The objective of this study was to review the relationship between fluctuating water levels and shoreline vegetation dynamics in the Great Lakes. Low water periods allow many plant species and vegetation types to regenerate from buried seeds. A review of published seed bank densities shows that some lakeshores have densities of buried seeds greater than 10^4 *seeds* m^{-2}*, an order of magnitude greater than densities reported from prairie marshes. High water periods kill dominant species (e.g.,* Typha *sp.), thereby creating gaps which other species can colonize during low water periods. High water also kills woody plants, thereby extending marshes landward. Fluctuating water levels therefore increase the area of shoreline vegetation, and the diversity of vegetation types and plant species. Any stabilization of water levels would likely reduce marsh area, vegetation diversity, and plant species diversity. Four basic shoreline vegetation types (forest and shrub thickets, wet meadow, marsh, and aquatic) can be recognized; both wet meadow and marsh largely result from fluctuating water levels.*

ADDITIONAL INDEX WORDS: Wetlands, coastal marshes, vegetation establishment.

> "This rise and fall of Walden [Pond] at long intervals serves this use at least; the water standing at this great height for a year or more, though it makes it difficult to walk round it, kills the shrubs and trees which have sprung up about its edge since the last rise. . . . and, falling again, leaves an unobstructed shore; for, unlike many ponds and all waters which are subject to a daily tide, its shore is cleanest when the water is lowest. . . . By this fluctuation the pond asserts its title to a shore, and thus the shore is shorn, and the trees cannot hold it by right of possession."
>
> H. D. Thoreau, 1854

INTRODUCTION

Since Thoreau's observation was made, there has been little improvement in our understanding of shoreline vegetation and its dynamic interaction with water levels. The objective of this paper is to review what is known about water levels and shoreline vegetation in the Great Lakes, and produce a qualitative model to describe the effects of fluctuating water levels. Since few published papers provide quantitative data on changes in lakeshore vegetation with water level, and fewer still discuss the Great Lakes vegetation specifically, we have reviewed the known effects of water level fluctuations on vegetation in other North American wetlands, and sought some general principles which could likely be applied to Great Lakes shorelines. These were supplemented with some descriptive papers on the flora of shoreline marshes (e.g., Dore and Gillett 1955, Hayes 1964, Stuckey 1975, Bristow *et al.* 1977; Jaworski *et al.* 1979, Fahselt and Maun 1980) to provide at least some qualitative observations on the effect of water level fluctuations on plant species composition. First we will discuss the dynamics of shoreline vegetation with changing water levels, and present our qualitative model. We will then discuss the flora associated with different vegetation types.

PART I: WATER LEVEL FLUCTUATIONS AND VEGETATION

Marsh vegetation dynamics have received much more attention (e.g., Harris and Marshall 1963, van der Valk and Davis 1978 and 1979, van der Valk 1981, Smith and Kadlec 1983) than lakeshore vegetation dynamics (Keddy and Reznicek 1982, Nicholson and Keddy 1983). Therefore, we have had to extrapolate from the former as well as the latter. The usefulness of such extrapolation is partly dependent upon the degree of similarity between marshes and lakeshores. Lakeshore vegetation may be little different from a typical marsh when it occurs in sheltered, gently sloping bays. But the steeper the shoreline becomes, the narrower the wetland becomes and at some point along this gradient lakeshores will become very different from marshes. Lakeshore vegetation patterns have recently been reviewed by Hutchinson (1975) and Spence (1982). Unlike marshes, lakeshores have strong environmental gradients parallel to the waterline as waves sort material from highly exposed shores to sheltered shores (Hutchinson 1975, Spence 1982, Davidson-Arnott and Pollard 1980, Keddy 1982 and 1984). As well, lakeshores are often exposed to erosion from water. In such cases, the upper shorelines are eroded, and deposition occurs in the deeper water. Bernatowicz and Zachwieja (1966) have distinguished 10 types of littoral zones, considering primarily the effects of erosion on different substrate types. While lakeshores therefore exhibit processes not found in prairie marshes, the two wetland types may be quite similar when the lakeshore wetland occurs in a gently-sloping sheltered bay.

Because seasonal (or within-year) water-level fluctuations are super-imposed upon long-term (or among-year) fluctuations, we will first consider the effects of long-term fluctuations. As a typical example of water level changes, Figure 1 shows the August water levels at Port Stanley on Lake Erie over a 53-year period. The present distributions and abundance of shoreline species will be determined by past as well as present water levels. How far into the past, or with what weighting, we do not know. The extreme highs and lows will produce the most rapid vegetation change; we will consider low periods first.

Low Water Periods

During low water periods, several changes can be expected. Soil chemistry may change dramatically as soils become less anoxic (Ponnamperuma 1972). Some plant species will change their growth form to accommodate dryer conditions (Sculthorpe 1967, Hutchinson 1975) but the vegetation will usually change dramatically as species intolerant of drying die and are replaced by species emerging from reserves of buried seeds. Much emphasis has been placed on documenting this regeneration from buried seeds (e.g., Kadlec 1962, Harris and Marshall 1963, Salisbury 1970, van der Valk and Davis 1976 and 1978 and 1979, van der Valk 1981, Keddy and Reznicek 1982, Smith and Kadlec 1983). Table 1 shows the density of seeds in soil samples from different North American wetlands (see Fig. 2 for the locations of these wetlands).

While densities of buried seeds are high in most wetland vegetation types, they appear to increase from prairie marshes to coastal marshes to lakeshores (Table 1). The only lake studied (Matchedash Lake) has a very rich flora on gently-sloping sand and gravel shorelines. Since low water periods allow many species to replenish reserves of buried seeds, the high densities of buried seeds might be attributed to frequent low water levels in Matchedash Lake. Given the regular occurrence of low water periods in the Great Lakes, comparable data would be most interesting.

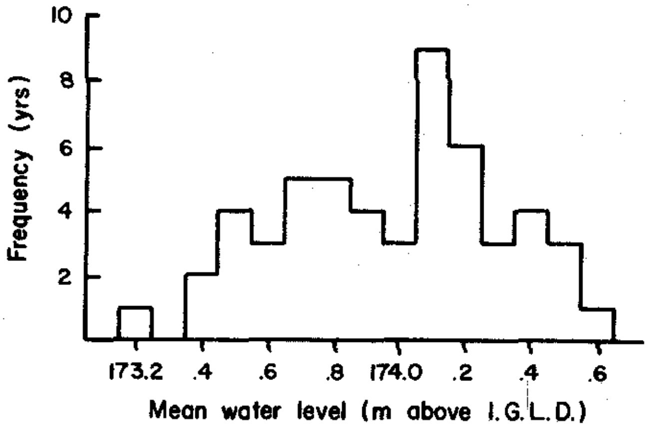

FIG. 1. Year-to-year variation in August mean monthly water level in Lake Erie, (Port Stanley; 1927–1980 except 1978; data from Monthly and Yearly Mean Water Levels 1980, published by Marine Environmental Data Services, Department of Fisheries and Oceans, Ottawa, 1983).

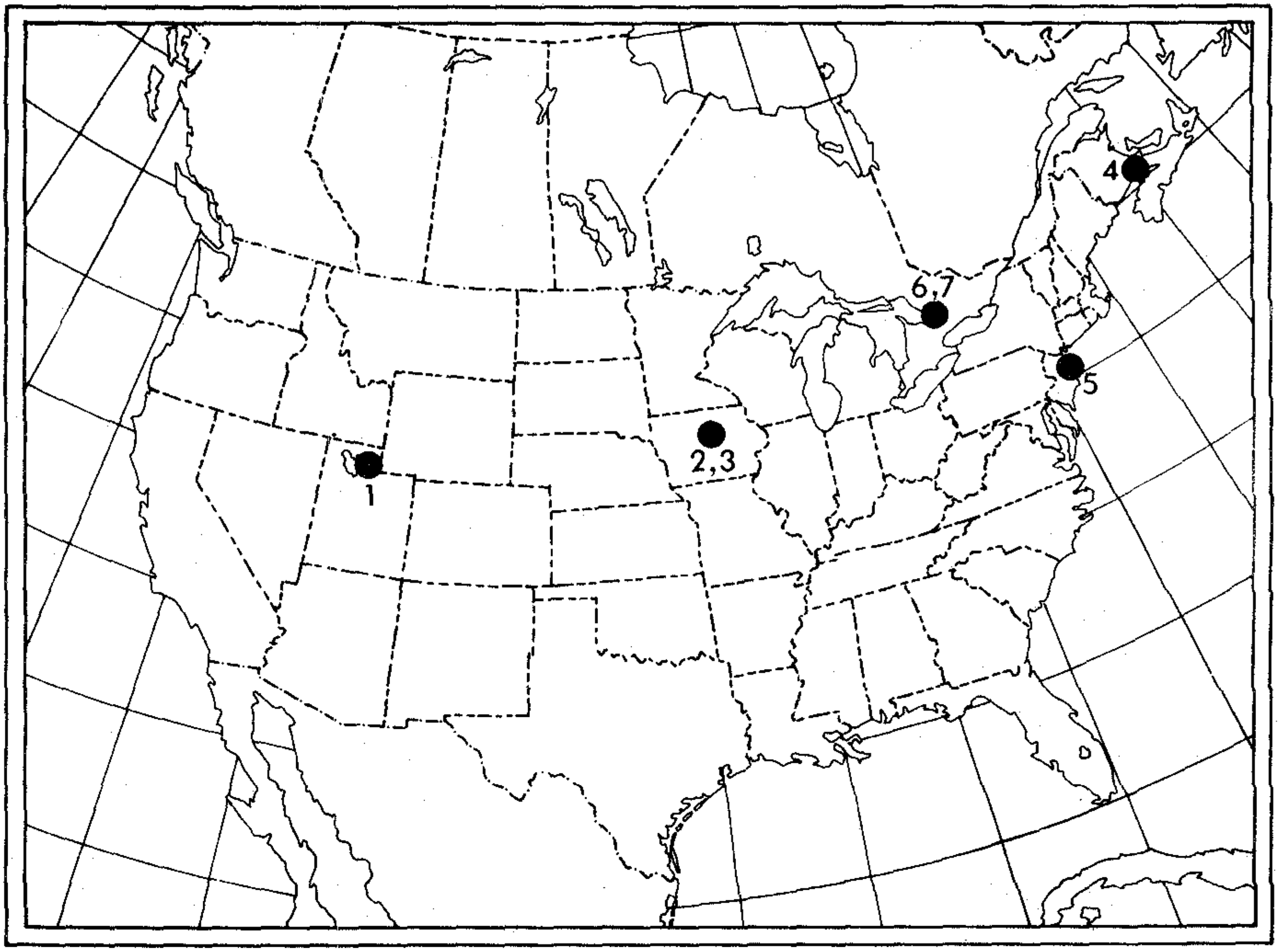

FIG. 2. Location of seed bank studies used in compiling Table 1 and 2. Numbers refer to those in Table 1.

The data in Table 1 also suggest that seedling densities are highest in the littoral zone. Pederson and van der Valk (1984) have also found seed concentrations to be highest in the transition between aquatic and terrestrial vegetation in marshes. Perhaps these intermediate depths have the appropriate combination of submersed and emersed periods for seeds to accumulate.

Many genera found in seed banks are common on the shorelines of the Great Lakes. Table 2 lists genera which could be expected to occur in samples from Great Lakes marshes.

Although the densities of buried seeds may be high, samples are often dominated by only a few species. Figure 3 shows the relative abundances of seedlings from six water depths on the shoreline of Matchedash Lake. The dominant species at all depths was *Hypericum majus*, except for 0 cm where it was *Panicum implicatum*. Many species were present as less than five individuals.

Seeds on lakeshores may be shallowly buried. The only data from a lakeshore (Nicholson and Keddy 1983) revealed that more than 80% of buried seeds occurred within the top 2 cm of the soil. In contrast, studies in marshes have found viable seeds to be relatively common at depths of 12 cm or more (Leck and Graveline 1979, van der Valk and Davis 1979, Moore and Wein in press). Moore and Wein (in press) propose the use of fire during a drawdown in order to remove accumulated organic matter and expose seeds buried deeply in the substrate. The available data from lakeshores suggests that fire could have much greater effects on shorelines, and might, if the seeds were buried in a shallow organic layer, entirely eliminate the seed bank.

High Water Levels

Rising water levels will change soils from oxic to anoxic (Ponnamperuma 1972). Organic matter and

TABLE 1. Comparison of freshwater wetland seed banks, using data from moist (not flooded) germination treatments. Van der Valk and Davis (1979) was excluded because flooded and moist conditions could not be separated in their tables; Haag (1983) was excluded because only flooded conditions were used.

	Sample unit				
Study	Surface area (cm^2)	Depth (cm)	Number	Site	Seedlings m^{-2}
PRAIRIE MARSHES					
1 Smith and Kadlec 1983[1]	400	4	25	*Typha* spp.	2,682
				Scirpus acutus	6,536
				S. maritimus	2,194
				Phragmites australis	2,398
				Distichlis spicata	850
				Open water	70
2 van der Valk and Davis 1978[2]	~225	~4–5	12	Open water	3,549
				Scirpus validus	7,246
				Sparganium eurycarpum	2,175
				Typha glauca	5,447
				Scirpus fluviatilis	2,247
				Carex spp.	3,254
3 van der Valk and Davis 1976[3]	~230	~4–5[4]	27	Open water	2,900
			15	*Typha glauca*	3,016
			3	Wet meadow	826
			3	*Scirpus fluviatilis*	319
FRESHWATER COASTAL MARSHES					
4 Moore and Wein 1985[5]	125	12	10	*Typha latifolia*	14,768
				Former hay field	7,232
				Myrica gale	4,496
5 Leck and Graveline 1979[6]	100	10	10	Streambank	11,295
				Mixed annuals	6,405
				Ambrosia	9,810
				Typha	13,670
				Zizania	12,955
LAKESHORE					
6 Nicholson and Keddy 1983[7]	7.5	10	49	Lakeshore, 75 cm water	38,259
7 Keddy and Reznicek 1982[8]	7	5	75	Waterline	1,862
				30 cm below water line	7,543
				60 cm below water line	19,798
				90 cm below water line	18,696
				120 cm below water line	7,467
				150 cm below water line	5,168

[1] Table 1.

[2] Table 2.

[3] Table 1, using highest density for each site type we multiplied by 14.5 to obtain no./m2.

[4] Based on van der Valk and Davis 1978.

[5] Table 1, spring samples.

[6] Data from text (p. 1009) which had been extrapolated from Table 1 to include the depths 2-4 and 6-8 cm.

[7] Table 1, 0 to 10 cm depths only used to avoid gaps in core beyond this depth.

[8] Recalculated from original data.

TABLE 2. Genera with widespread occurrence in wetland seedbanks[1], based on species germinating during moist treatments (i.e., germinating during conditions simulating low water periods).

	Vegetation type		
Genus	Prairie Marshes[2]	Freshwater Coastal Marshes[3]	Lakeshores[4]
Bidens	√	√	√
Carex	√		√
Cuscuta	√	√	
Cyperus	√	√	
Echinochloa	√	√	
Galium	√	√	
Hypericum		√	√
Impatiens	√	√	
Juncus		√	√
Leersia	√		√
Ludwigia		√	√
Lycopus	√		√
Panicum	√	√	√
Polygonum	√	√	√
Sagittaria	√	√	
Scirpus	√	√	√
Spirea		√	√
Typha	√	√	
Viola		√	√

[1] 80 genera were recorded in these studies. Many were restricted to a single study (43,*) or a single vegetation type (18). Only widespread genera occurring in at least two vegetation types are listed here. Other genera recorded were:

prairie marshes: *Alisma, Amaranthus, Asclepias*, Berula*, Brachyactis*, Chenopodium, Cicuta*, Cirsium*, Distichlis*, Eleocharis, Epilobium*, Eragrostis*, Glyceria*, Iris*, Mentha*, Mimulus*, Penthorum*, Phragmites*, Polypogon*, Populus*, Potamogeton*, Ranunculus*, Rorippa, Rumex, Salicornia*, Scutellaria*, Sium, Solanum*, Sparganium, Stachys*, Urtica*;

freshwater coastal marshes: *Acnida*, Ambrosia*, Callitriche*, Gratiola*, Hibiscus*, Lythrum*, Mikania*, Peltandra*, Pilea*, Potentilla, Veronica*, Zizania**;

lakeshore: *Agrostis, Calamagrostis*, Chamaedaphne, Cladium, Drosera, Dulichium*, Eriocaulon, Gnaphalium*, Linum*, Lysimachia*, Muhlenbergia, Myrica*, Rhexia, Rhynochospora, Rubus*, Solidago*, Triadenum*, Xyris**.

[2] Smith and Kadlec (1983); van der Valk and Davis (1978, 1976).

[3] Moore and Wein (in press) genera list may not be complete; Leck and Graveline (1979).

[4] Nicholson and Keddy (1983); Keddy and Reznicek (1982).

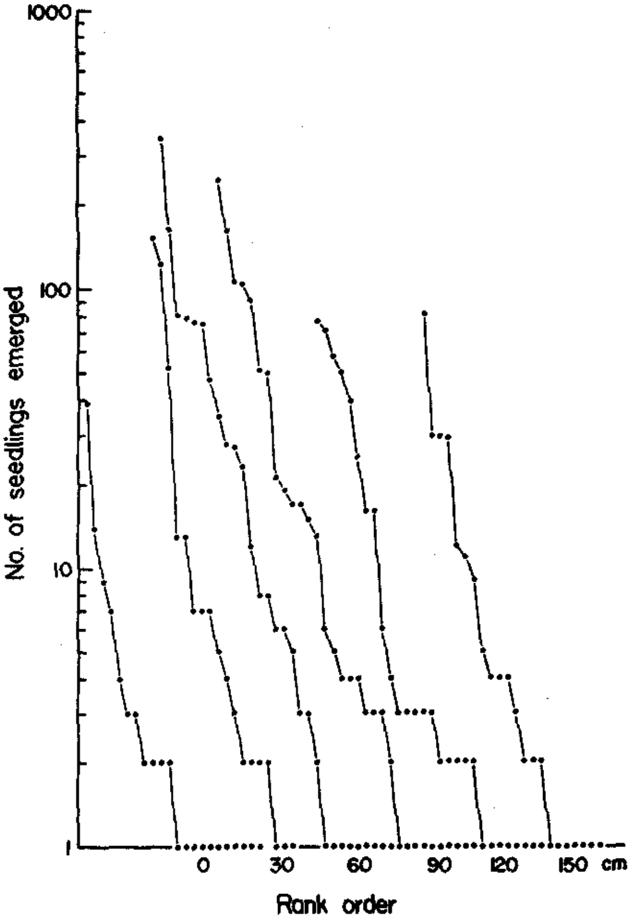

FIG. 3. Relative abundances of seedlings from samples representing six depths on the shoreline of Matchedash Lake. 0 cm marks the water depth when the samples were taken, but falling water levels could expose all depths. For each depth, species abundances are arranged left to right in order of declining abundance.

fine particles (e.g., silt and clay) may be removed by water circulation (Jaworski *et al.* 1979). Simultaneously, mud flat species disappear (e.g., Salisbury 1970, van der Valk 1981). Emergent species will propagate vegetatively under shallow water, but will gradually die out under deeper water (Harris and Marshall 1963, van der Valk and Davis 1978). Figure 4 shows the survival rates of two emergents after flooding to three different water depths. Farney and Bookhout (1982) described how high water levels in Lake Erie converted emergent vegetation to open water. Even cattails (*Typha* spp.), which covered more than 20 percent of their study area, were eliminated. Other common cover types, such as *Hibiscus palustris* and *Leersia oryzoides*, also disappeared. Jaworski *et al.* (1979) provided many similar examples from Lakes Michigan, Huron, St. Clair, and Erie. High water periods therefore eliminate one group of marsh species, and allow them to be temporarily replaced by floating-leaved and submerged species more tolerant of flooding. The causes of the death

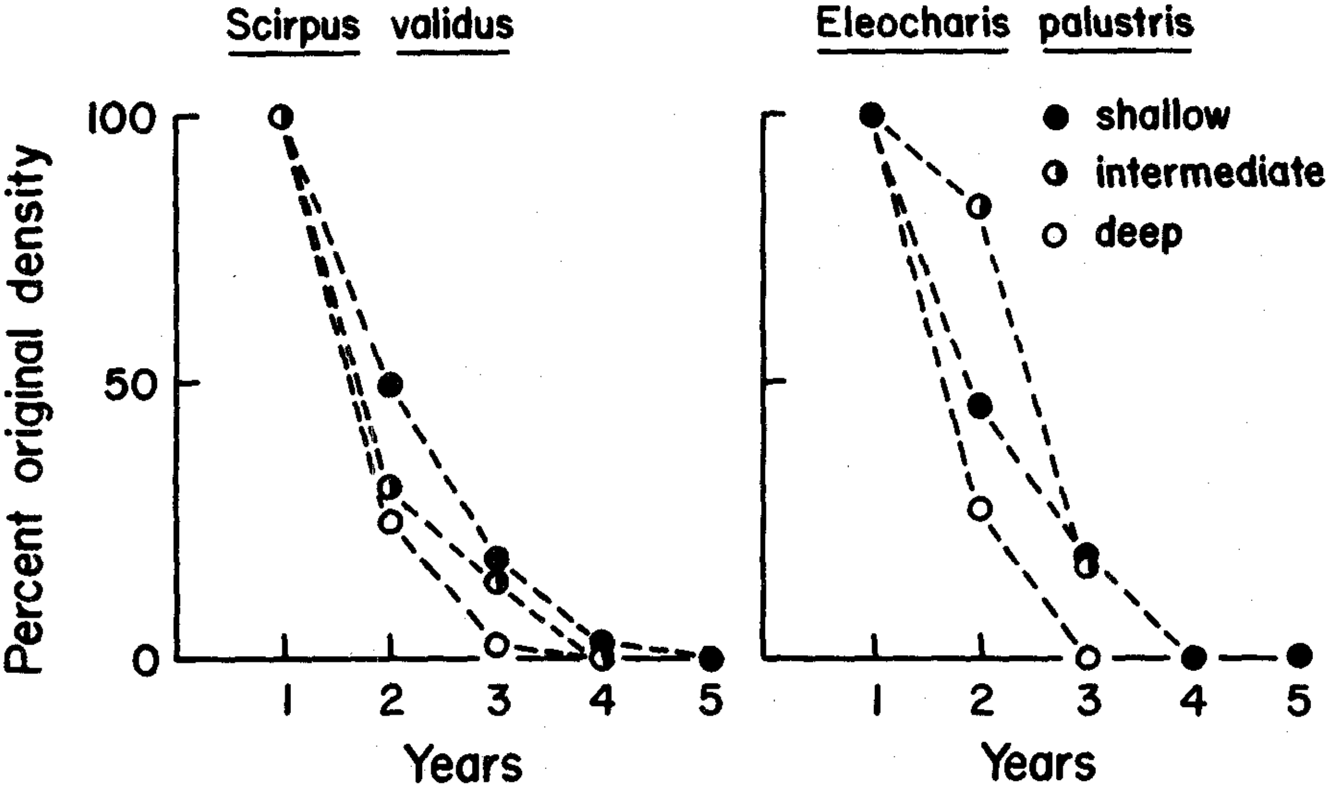

FIG. 4. The effect of flooding to three different water depths on the survival of two emergent wetlands plants (drawn from Table III in Harris and Marshall 1963). Summer water depths coded as follows: Shallow, 0–25 cm; intermediate, 25–38 cm, deep, > 38 cm. In contrast, Carex *spp. increased in the shallow treatments, while dying at intermediate and deep.* Typha *spp. increased in the shallow and died off only in the deep.*

of emergents are unclear. Some species which are intolerant of flooding produce toxic ethanol during anoxic conditions; species more tolerant of flooding possess an alternative pathway which leads to the accumulation of the far less toxic malate (McManmon and Crawford 1971, Barclay and Crawford 1982). In prairie marshes, muskrat damage and disease may also contribute to the death of emergents during high water periods (van der Valk and Davis 1978).

High water levels have a second important effect on lakeshore marshes: the elimination of trees and shrubs. Woody plants may determine the upper limits of herbaceous species on shorelines (Keddy 1983). A canopy from shrubs severely curtails growth of herbaceous shoreline plants (Sharp and Keddy 1985). High water levels, by eliminating woody plants, may increase the area occupied by herbaceous wetlands species (e.g., Keddy and Reznicek 1982). An observation consistent with this proposal is that in small lakes with stable water levels, the shrub zone frequently occurs right to the water line, leaving only a narrow zone of emergents.

Several studies have erroneously implied and/or concluded that high water levels have a negative impact on shoreline vegetation, based simply on the observation that "marsh" area temporarily decreases during high water years (e.g., Jaworski *et al.* 1979, Lyon and Drobney 1984). These arguments have been rebutted elsewhere (Reznicek and Keddy, in press). High water levels should actually increase marsh area by eliminating woody plants. They should also increase marsh diversity by killing dominant species such as *Typha* sp.

Seasonal Fluctuations and Strand Vegetation

Water levels fluctuate on many time scales. Seasonal fluctuations (Fig. 5) are likely to have effects that are very different from fluctuations with a period of a decade or longer. In the latter case, population responses can occur, with some species surviving only as buried seeds, and others tempo-

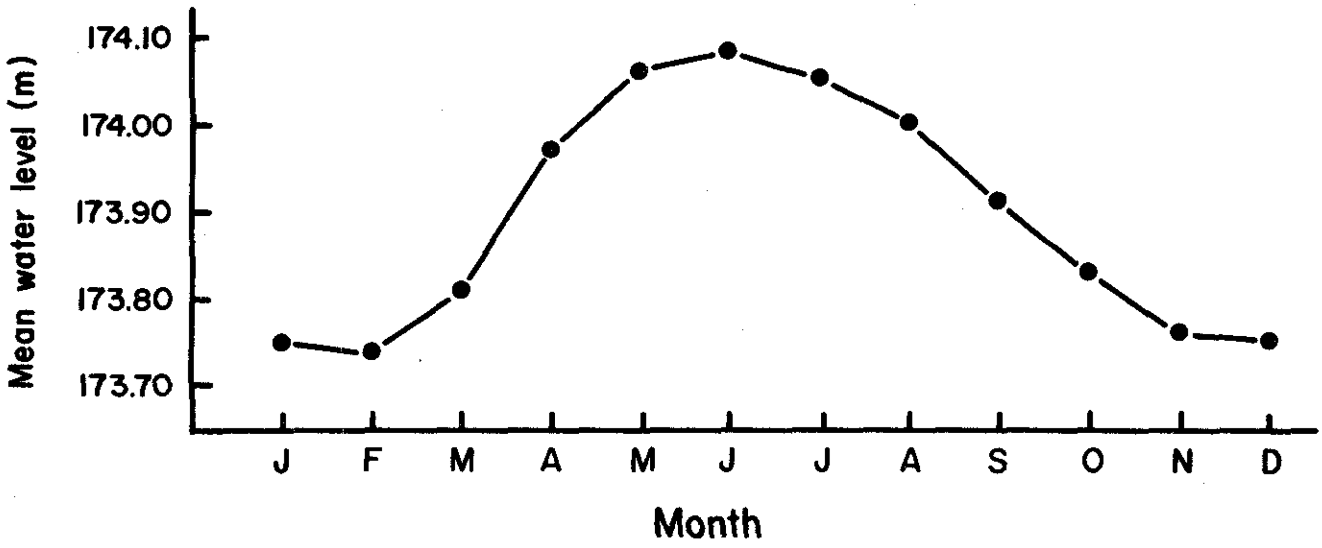

FIG. 5. Seasonal (within year) fluctuations in water level at Port Stanley on Lake Erie, averaging data from 1927-1980 (except 1978). Source of data as in Figure 1 caption.

rarily exploiting the existing conditions. With seasonal fluctuations, population responses are possible only for annuals which complete their life cycle rapidly. As the water level falls, different annuals will germinate and temporarily exploit favorable sites. In contrast, perennial species must be able to survive the entire range of conditions encountered during seasonal fluctuations in order to occupy a site during the growing season. Thus, they may produce different shoot morphologies as the season progresses (Sculthorpe 1967, Hutchinson 1975), and have different metabolic pathways for surviving anoxic periods (McManmon and Crawford 1971, Barclay and Crawford 1982). The annuals can escape seasonal fluctuations; the perennials must tolerate them. Seasonal fluctuations may increase species diversity. Stuckey (1975) observed at Put-in-Bay, Lake Erie, that "The greatest diversity of vegetation zones and greatest diversity of species within zones occur in that part of the marsh where the water level fluctuated the most throughout the season." He recognized 12 "dominant vegetation zones," seven of which were associated with fluctuating water levels.

At the very least, seasonal fluctuations in water level increase the annual component of the vegetation. For perennial species which can germinate only on exposed mud flats, the seasonal low may supplement or accentuate regeneration phases provided by long term fluctuations. Lastly, since many wetlands species are apparently intolerant of continual submergence (e.g., Harris and Marshall 1963, van der Valk and Davis 1978), seasonal lows may allow shoreline species to occur deeper into the lake.

Water Level Fluctuations: A Natural Disturbance

Water level fluctuations are a natural form of disturbance in lakes. The role of natural disturbance in promoting vegetation diversity has been discussed by Grubb (1977), Connell (1978), Huston (1979), White (1979), and Grime (1979).

Disturbance has several quantifiable components including intensity and frequency. We do not yet know what intensity (amplitude) or frequency of disturbance from fluctuating water levels will maximize species diversity. Some combinations of high intensity and frequency have a negative impact on shoreline vegetation, as illustrated by the sparse vegetation of the margins of some

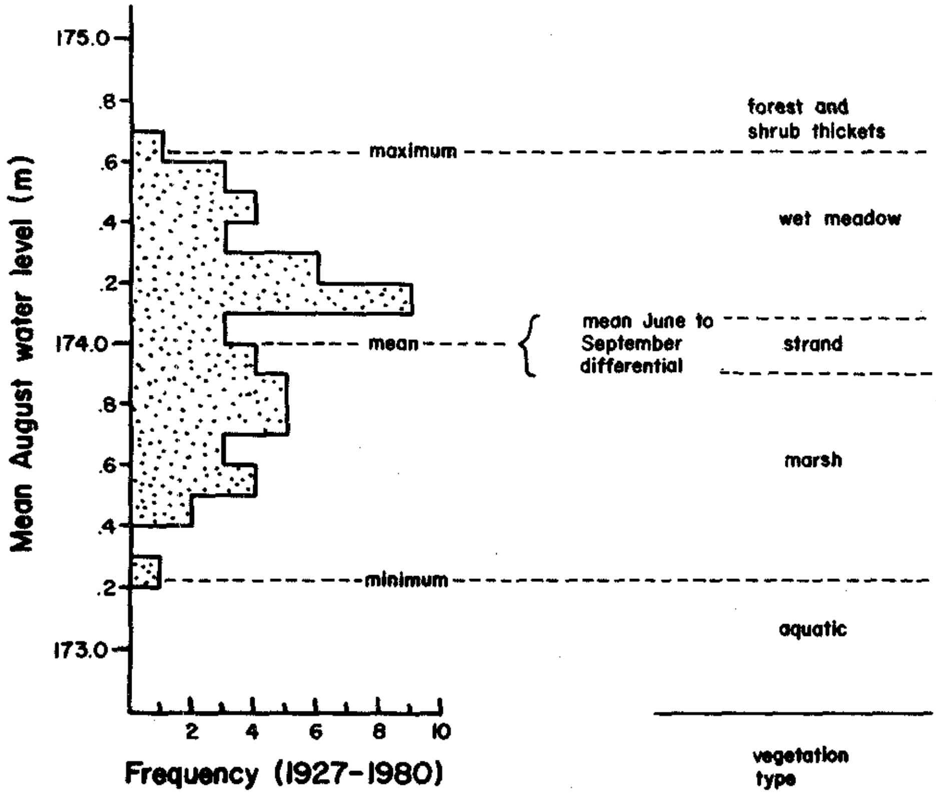

FIG. 6. Proposed relationship between water levels and vegetation types on the Great Lakes shorelines. The water level data represent Lake Erie 1927–1980, minimum 1934, maximum 1973. The boundaries between the vegetation types will shift as waterline levels change; the strand, composed of short-lived ruderals, tracks the water with a width resulting from the fall in water levels from June to September. Other environmental factors such as slope, substrate type, wave action, water chemistry, and fire will influence the species composition within each vegetation type.

hydroelectric reservoirs. Stabilizing water levels (reducing the intensity and frequency of disturbance) would also be expected to cause major changes in wetlands, particularly (1) the loss of species which regenerate during low water periods, and (2) increased dominance by woody plants and *Typha* spp.

A Model of Water Levels and Shoreline Vegetation in the Great Lakes

A model outlining the relationships of Great Lakes wetland vegetation types to water level fluctuations is depicted in Figure 6. This model is simplistic in that it considers only the role of water level fluctuations in determining wetland vegetation types. Topography, substrate type, wave action, latitude, water quality, fire, water currents, exposure, and length of time since the last high or low water phase are not considered. Although the model thus is not refined enough to predict the occurrence of communities or species associations, we offer it as a useful conceptual framework for interpreting the large-scale cyclic processes of vegetation in Great Lakes wetlands.

The following discussion summarizes the hypothesized dynamics of the wetland types described earlier. Only strand vegetation is omitted, since it results primarily from various kinds of disturbance near the water line.

The upper part of the shore is dominated by woody species intolerant of flooding. They form forest and shrub thickets.

Wet meadow vegetation develops between the maximum high and present water level. The dynamics of this vegetation are probably similar to the dynamics of vegetation on shores of smaller lakes with fluctuating water levels (Keddy and Reznicek 1982). During high water phases, these communities are narrow in width or even totally flooded. Woody plants that have invaded since the last high water level are killed, as are many herbaceous species. When water levels recede, wet meadow species re-establish from buried seeds and from individuals which survived on the upper fringes of the wet meadow zone. (We have used August water level data in Figure 6, but it is likely that higher water levels in June set the lower limits of woody plants; thus the upper limit of meadow species is probably higher than we have indicated).

Between the present water line and the extreme minimum water level is the zone in which shallow marsh vegetation is best developed. The emergent aquatics can survive permanent flooding, but many require occasional low water levels to expose the lake bottom in order for seedlings to establish. Thus periodic seed recruitment of species can only occur above the extreme low water line, although some emergent aquatics can spread vegetatively into water deeper than the minimum low water line. While the frequency of flooding thus determines whether wet meadow or marsh forms, both of these vegetation types appear to require fluctuating water levels for herbaceous species to regenerate from buried seeds.

Below the minimum low water level is the zone where aquatic vegetation survives continuously. In the shallower levels of the zone, emergent aquatics may invade during low water, although they will be eliminated again when water levels rise.

In the terminology proposed by Jeglum *et al.* (1974), our forest and shrub thicket zone would include treed fen, thicket swamp, and hardwood swamp. The wet meadow zone would include meadow marsh and graminoid fen, and the marsh zone would include deep marsh and shallow marsh. Jaworski *et al.* (1979) presented some profiles which illustrate these zones in different wetlands.

An excellent starting point for future studies on water level fluctuations and shoreline vegetation would be van der Valk's (1981) proposals. He presents a model where determination of three life history features (life span, propagule longevity, and establishment requirements) is sufficient to predict the fate of individual wetland species during different water levels. By combining the three life history features, van der Valk recognizes 12 basic life history types. The wetland environment can then be treated as a sieve which permits the establishment of only certain life history types at any given time. To apply van der Valk's model to an actual wetland, one must determine the potential flora of the wetland, and the life history type of each species. The potential flora includes all species growing in the wetland at a given time, plus all additional species represented by buried seeds.

PART II: SHORELINE VEGETATION AND FLORA

Vegetation

Reliable information on the vegetation of Great Lakes wetlands is scattered and scanty. A large number of unpublished marsh management reports and vegetation surveys exist (see reviews by Whitlow and Harris 1979, Triplett *et al.* 1980), but they usually suffer from at least one of the following problems:

(1) They were designed for the study of one or more animal species, and thus only plant species considered important for the animal species are considered.

(2) They were not carried out by knowledgeable botanists. Thus some of the identifications of plant species are clearly wrong, and many others are questionable. This situation is complicated by the taxonomic difficulties in major plant groups encountered (e.g., *Carex, Juncus, Potamogeton*).

(3) They are unpublished or published in nonreferred journals, and are therefore difficult to locate and evaluate.

(4) The methodologies used are rarely explained in detail and these methodologies may vary significantly from one report to the next.

We have therefore recognized only four broad shoreline vegetation types: wet meadow, strand, marsh, and aquatic (Fig. 6). Each vegetation type has a specific physiognomy, relationship to water levels, and life form of dominant species. Auclair *et al.* (1976a,b) have studied vegetation-environment relationships in some similar vegetation types.

Wet Meadow

Wet meadows occur wherever slope and substrate conditions are not too steep or rocky. They are poorly developed on Lake Superior, but a very characteristic feature of the shores of Lakes Huron and Michigan. Where slopes are very gentle, shoreline wet meadows can cover vast areas. Fens occur when the wet meadows have extensive calcareous seepage. They are similar to wet meadows physiognomically and floristically although often more species rich. Wet meadows and fens support more species than other wetland communities, and contain more than half of the species recorded from Great Lakes wetlands. A single shoreline fen much less than 1 hectare in area, near Methodist Point, Georgian Bay, Ontario, contained 96 species (Reznicek, unpublished data). Dominant species in wet meadows may include *Calamagrostis canadensis, Carex lanuginosa, C. lasiocarpa, C. sterilis, C. stricta, Cladium mariscoides, Deschampsia cespitosa, Equisetum variegatum, Eleocharis elliptica, Juncus balticus, Potentilla fruticosa, Scirpus acutus, S. americanus, S. cespitosus, Solidago ohioensis,* and *Spartina pectinata*. Many other species are also capable of dominating local areas.

Strand

This vegetation occurs at or just above the waterline where seasonal water level fluctuations and waves cause erosion and deposition. This repeated disturbance produces a zone dominated by annuals in the genera *Bidens, Cakile, Cyperus, Eleocharis, Juncus, Panicum, Polygonum,* and *Xanthium.*

Marsh

In marshes, emergent species are prominant. Some emergents can occur in water as deep as approximately 1.5 m, although best development normally occurs in shallower water. In most areas, the major dominant is *Typha* sp. Locally, *Decodon verticillatus, Eleocharis smallii, Phragmites australis, Pontederia cordata, Sagittaria latifolia, Scirpus acutus, S. fluviatilis,* and *Sparganium eurycarpum* can also dominate extensive areas. In shallow water, (less than 15 cm deep) *Carex aquatilis, C. atherodes, Leersia oryzoides, Lythrum salicaria,* and *Phalaris arundinacea,* as well as some other less important species, may dominate.

Aquatic

The submersed and floating-leaved aquatic plants are the least well known of all the Great Lakes wetland species. They occur in shallow water in openings in marshes, as an occasional "understory" to emergent aquatic vegetation, and in water deeper than the maximum depth tolerated by emergent species. The maximum depth to which aquatics occur is uncertain, but it is at least 8 m (Meyer *et al.* 1943, Voss 1972) under ideal conditions. Species capable of dominating large areas are numerous. Among the most important are *Ceratophyllum demersum, Elodea canadensis, Heteranthera dubia, Megalodonta beckii, Myriophyllum* spp., *Najas flexilis, Nymphaea odorata, Nuphar variegatum, Potamogeton* spp., *Ranunculus aquatilis* (s.l.), *Utricularia vulgaris*, and *Vallisneria americana.*

Flora and Phytogeography

Floristic information covering Great Lakes wetlands is also scanty. Reliable floristic surveys are available only for a few local areas and thus the information presented here is based mainly on our own field experience. The flora is quite rich, with about 400–450 species of vascular plants regularly occurring in Great Lakes wetlands. The most important genera (based on 10 or more species represented) are *Carex* (approximately 50 spp.), *Cyperus* (approximately 10 spp.), *Eleocharis* (approximately 12 spp.), *Juncus* (approximately 15 spp.), *Polygonum* (approximately 10 spp.), *Potamogeton* (approximately 22 spp.), and *Scirpus* (approximately 13 spp.).

The flora of Great Lakes wetlands comprises several floristic elements. The extensive wetlands on Lake Erie are especially rich in southern species found only rarely or not at all on the other Great Lakes. Examples of species capable of forming extensive stands and dominating communities include *Hibiscus palustris, Nelumbo lutea,* and *Nuphar advena*. Other rarer species include *Boltonia asteroides, Hibiscus laevis, Sagittaria montevidensis,* and *Senecio glabellus.*

The wetlands of the southern Great Lakes also have a rich wet prairie element in the flora. This element is especially prominent in the Saint Clair River delta marshes (Hayes 1964). Species representing this element are *Helianthus* spp., *Platanthera leucophaea, Pycnanthemum* spp., *Solidago riddelli, Veronia* spp., and *Veronicastrum virginicum.*

The fens and wet meadows of the northern portions of Lakes Huron, Michigan, and Superior have many boreal, subarctic, and (on Lake Superior) arctic species (Given and Soper 1981). Examples include *Carex capillaris, Pinguicula vulgaris, Selaginella selaginoides,* and *Scirpus cespitosus.*

Many aquatic and wetland plants are very widespread; a few, such as *Ceratophyllum demersum,* are essentially cosmopolitan. Thus, other Great Lakes wetland species are distributed throughout the entire region.

CONCLUSION

The existing shoreline vegetation of the Great Lakes depends upon regular fluctuation in water levels. Fluctuating water levels not only increase the area of shoreline vegetation, but increase the diversity of vegetation types and plant species. High water periods prevent woody vegetation and terrestrial species from occupying sites close to the water, and temporarily change the vegetation from wet meadow to emergent species, or from emergent species to floating-leaved and submersed species. High water periods also kill dominant species such as cattails (*Typha* sp.) which might otherwise form extensive monocultures. Low water periods allow many mud flat annuals, meadow and emergent marsh species to regenerate from buried seeds. It appears that buried seed reserves on lakeshores have higher densities than marshes, and are more shallow. Any stabilization of water levels would likely reduce marsh area, vegetation diversity, and plant species diversity.

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