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Implications of hydrologic variability on the succession of plants in Great Lakes wetlands

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Primary succession of plant communities directed toward a climax is not a typical occurrence in wetlands because these ecological systems are inherently dependent on hydrology, and temporal hydrologic variability often causes reversals or setbacks in succession. Wetlands of the Great Lakes provide good examples for demonstrating the implications of hydrology in driving successional processes and for illustrating potential misinterpretations of apparent successional sequences. Most Great Lakes coastal wetlands follow cyclic patterns in which emergent communities are reduced in area or eliminated by high lake levels and then regenerated from the seed bank during low lake levels. Thus, succession never proceeds for long. Wetlands also develop in ridge and swale terrains in many large embayments of the Great Lakes. These formations contain sequences of wetlands of similar origin but different age that can be several thousand years old, with older wetlands always further from the lake. Analyses of plant communities across a sequence of wetlands at the south end of Lake Michigan showed an apparent successional pattern from submersed to floating to emergent plants as water depth decreased with wetland age. However, paleoecological analyses showed that the observed vegetation changes were driven largely by disturbances associated with increased human settlement in the area. Climate-induced hydrologic changes were also shown to have greater effects on plant-community change than autogenic processes. Other terms, such as zonation, maturation, fluctuations, continuum concept, functional guilds, centrifugal organization, pulse stability, and hump-back models provide additional means of describing organization and changes in vegetation; some of them overlap with succession in describing vegetation processes in Great Lakes wetlands, but each must be used in the proper context with regard to short- and long-term hydrologic variability.

Keywords: community changes, levels

Introduction

Succession is a basic concept of ecology, but it is not without controversy. Since the early work of Cowles (1899) on dune plant communities at the south end of Lake Michigan and the development of differing models of succession by Clements (1916) and Gleason (1917), succession of plant communities has had a long history of conflicting interpretation. Clements' autogenic model viewed succession as linear changes in recognizable and characteristic plant communities

directed toward a mature climax community, with changes being driven from within the plant communities. Gleason's allogenic model viewed succession more broadly as any change in the relative abundance of species in the plant cover of an area or in its floristic composition over time, with changes being driven by environmental factors outside the plant communities. The two views have been examined by many others in both terrestrial and aquatic habitats (e.g., Pearsall, 1920; Wilson, 1935; Whittaker, 1953; Walker, 1970). In wetlands, it is likely that autogenic and

allogenic mechanisms can both contribute to vegetation change in specific settings; however, the key role of hydrology in causing wetlands to be wet makes the allogenic model much more prevalent. The classic paper by van der Valk (1981) introduced a Gleasonian model for succession in wetlands that incorporated hydrologic changes as the driving mechanism for succession, with life history traits of plant species found in the seed bank determining which species persist and which species are extirpated when hydrologic conditions change. In this paper, I shall adhere to van der Valk's (1981) modified definition of allogenic succession: 'whenever one or more new species becomes established, when one or more species already present is extirpated, or when both occur simultaneously in a wetland.'

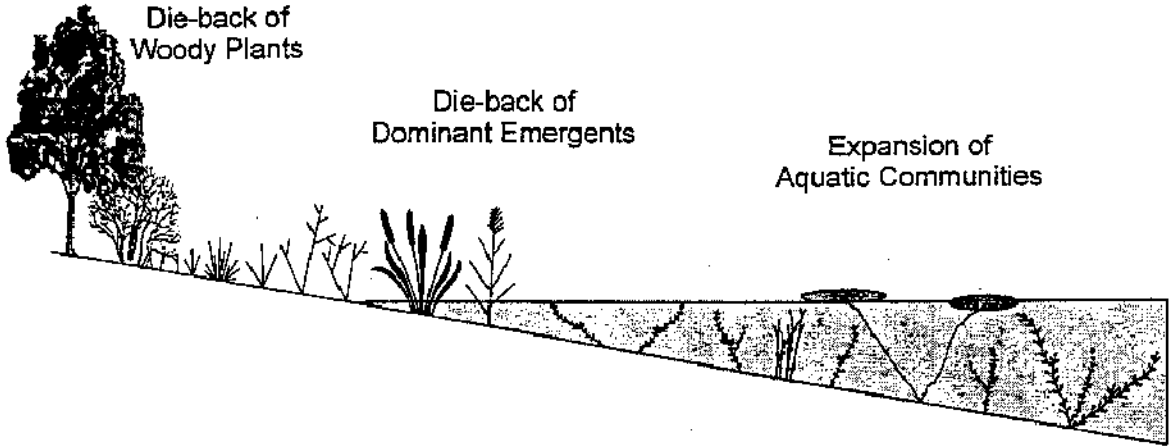
Settling on a definition of succession does not end the potential for confusion among ecological terms. A variety of other ecological models have been offered to describe spatial and temporal variation in wetland plant communities, including functional guilds (Keddy, 1992; Boutin and Keddy, 1993), centrifugal organization (Wisheu and Keddy, 1992), pulse stability (Odum, 1971), and the 'hump-back' model of greatest species richness at moderate standing crop (Grime, 1979; Moore and Keddy, 1989; Moore et al., 1989). In addition, some patterns and changes in plant communities can be misinterpreted as succession. Common examples are zonation patterns in wetlands that relate to water depth or moisture gradients, maturation or year-to-year increases in biomass of individual plants within a community without loss or replacement of species, and fluctuations, which are strictly quantitative changes in vegetation without species change (van der Valk, 1982; Keddy, 2000). Alternatively, the continuum concept (Whittaker, 1967) suggests that individual plant communities do not exist, but instead, a gradient of subassociations overlaps across an environmental gradient in accordance with the environmental tolerances of individual species. In wetlands, however, such subassociations seem to be clustered (Keddy, 1983; Shipley and Keddy, 1987). Finally, we arrive at 'hydrarch succession', which arose from the work of Shelford (1911, 1913) in dune ponds at the south end of Lake Michigan between the dune systems studied by Cowles (1899) and was later invoked by many others (e.g., Pearsall, 1920; Gates, 1926; Wilson, 1935). This term suggests that Clementsian autogenic succession occurs in aquatic ecosystems and ultimately results in conversion to upland and climax upland plant communities. In this paper, I will address the applicability of hydrarch succession in Great Lakes wetlands in

view of other concepts about vegetation change, with a particular emphasis on the implications of hydrologic variability.

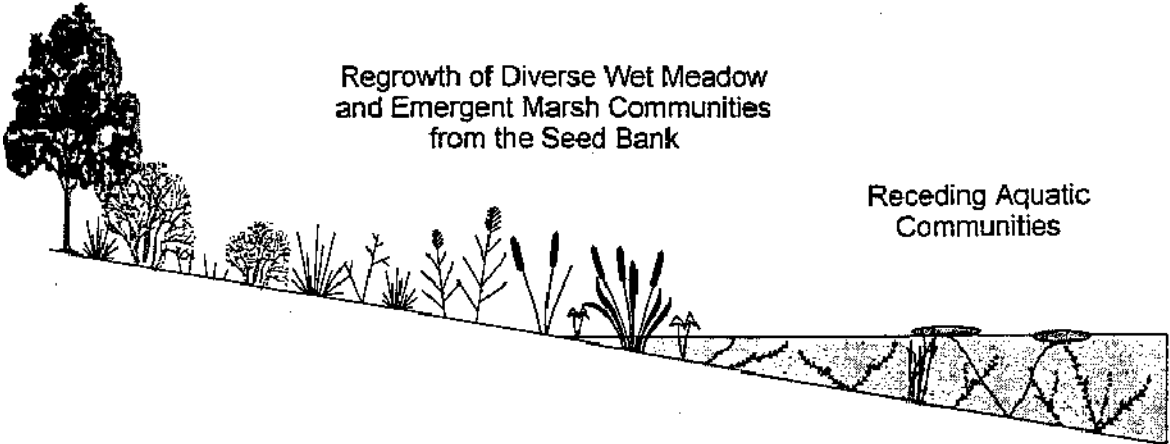
Patterns of lake-level change

Water-level changes in the Great Lakes are caused by a combination of seasonal and longer-term weather conditions and climate changes that affect water volume. They occur at frequencies varying from seasons to years, decades, and centuries, as well as varying magnitudes, timing, and duration, each with different effects on vegetation. Seiches and barometric pressure changes can also create localized changes in water levels that last for only hours. Lake levels have been systematically recorded by the U.S. and Canadian governments since 1860. Wind-driven seiches with amplitudes of 10 to 30 cm are common across most Great Lakes and larger embayments within the lakes (e.g., Saginaw Bay of Lake Huron, Chequamegon Bay of Lake Superior), but seiches with amplitudes of over 3 m have been recorded in Lake Erie. Seasonal and annual data show cycles of low winter levels and high summer levels that vary in magnitude by lake. The peak lake levels generally occur during multi-year periods of high lake stages; lower lake levels occur during the intervening periods (Figure 1). Water-level changes have also been recorded in the late Holocene geologic record as sequences of beach ridges of similar origin but different age (chronosequences) that formed during repeated occurrences of high lake levels, with intervening low levels. Baedke and Thompson (2000) used the elevations of foreshore deposits in these ridges coupled with radiocarbon dates from the wetlands between the ridges to develop a 4700-year lake-level record for lakes Michigan and Huron (same lake hydrologically). The record shows a quasi-periodic behavior, with short-term fluctuations with a range of 0.5 to 0.6 m that occur about every 30 to 33 years and longer-term fluctuations with a range of 0.8 to 0.9 m that occur about every 150 to 160 years. A preliminary record for Lake Superior shows that similar patterns occurred there while lakes Superior, Michigan, and Huron were joined as one lake (Johnston et al., 2004). It appears that Lake Superior has taken on its own lake-level pattern following its split from the other lakes. The variety of water-level fluctuation described above demonstrates that, under a natural hydrologic regime, wetland plant communities in the Great Lakes developed and are maintained in a hydrologic environment with great variability.

Year 1 - High Water Levels



Year 2 - Receding Water Levels



Year 3 - Low Water Levels

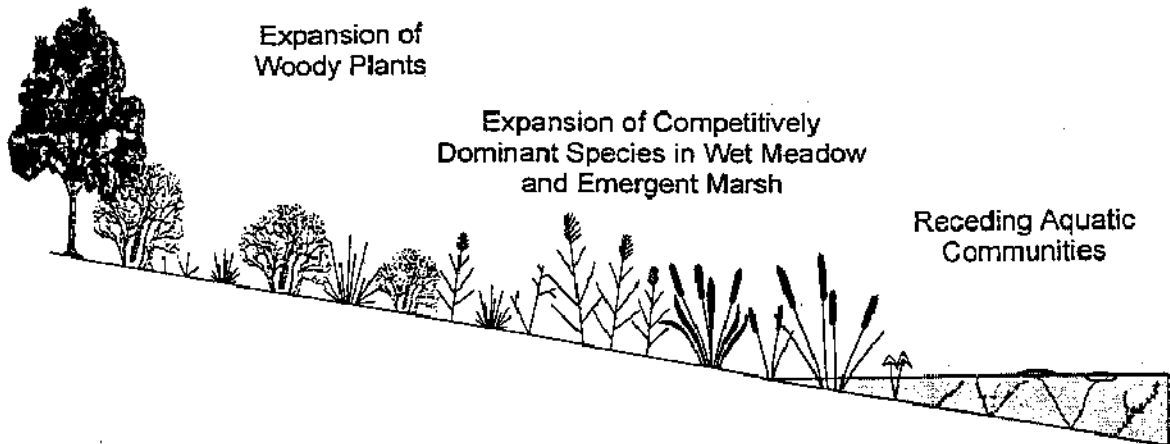


Figure 2. Simplified diagram of the effects of water-level fluctuations on coastal wetland plant communities of the Great Lakes (Maynard and Wilcox, 1997).

of new seedlings is due to the distribution of seeds in the sediments. In ensuing years, the distribution of full-grown plants is due to seedling survival through competitive interactions. However, if one species is favored in early colonization, its density may be great enough that it can maintain dominance of an area (site preemption).

The different plant communities that develop in a Great Lakes wetland may shift from one location to another in response to changes in water depth. The water-depth history largely determines the species composition of a particular site at a given point in time, with the plant communities generally corresponding to zones that are a) almost never covered with water, b) occasionally covered with water, c) covered/uncovered on a short-term basis, d) often covered with water, and e) almost always covered with water (Keddy and Reznicek, 1986). Future water-level changes couple with seed bank composition to determine future species composition.

Long-term records of plant community changes in Great Lakes wetlands

Chronosequences of wetlands, formed sequentially by similar processes in adjacent locations through time, provide opportune locations to study long-term changes in wetlands that are also often associated with hydrologic changes. Examples include oxbow lakes (van der Valk and Bliss, 1971) and ridge and swale terrains of ocean and Great Lakes coasts. In embayments along the Great Lakes coast, these wetlands occur in strand plains composed of beach ridges. Individual beach ridges form during repeated periods of high lake levels and are created in the final stages of lake-level rise when the rise begins to slow to its maximum elevation (Thompson and Baedke, 1995). The beach ridge grows in height and width during the subsequent lake-level fall. The wetlands form in swales between ridges where the water table is at, near, or above the swale surface. Ground-water flow toward the lake is often focused as a result of the morphometry of the embayment, thereby assisting in wetland development. Each succeeding beach ridge and accompanying wetland forms lakeward from earlier ridges. The resulting terrain contains a chronosequence of wetlands decreasing in age with proximity to the lake.

Shelford (1911, 1913) studied differences in fish and invertebrate communities in such a chronosequence of wetlands at the south end of Lake Michigan, which

formed linear rows of dune ponds, and related their distributions across ponds of differing ages to successional changes in the habitat provided by plants, which were assumed to be autogenic. Wilcox and Simonin (1987) later used a stratified-random sampling design to study plant communities in five ponds in each of five pond rows in this chronosequence (Figure 3), along with differences in water depth, sediment depth, water chemistry, and sediment chemistry. A detrended correspondence analysis ordination separated the plant communities of ponds according to age, with two outliers that can be explained by large numbers of shallow sampling sites in those ponds (Figure 4). The most common taxa in the youngest ponds were submersed aquatics *Chara* spp., *Najas flexilis* (Willd.) Rostk. & Schmidt, and *Potamogeton gramineus* L. Submersed species were joined by floating leaf taxa such as *Nymphaea tuberosa* Paine, *Nuphar advena* (Ait.) Ait. f., and *Nuphar variegatum* Engelm. in the next row of ponds and emergent taxa such as *Calamagrostis canadensis* (Michx.) Nutt., *Typha angustifolia* L., and *Typha x glauca* Godron in the third row. Emergent taxa such as *Calamagrostis*, *Typha*, *Polygonum coccineum* Muhl., *Sagittaria latifolia* Willd., and *Scirpus acutus* Muhl. became yet more prominent in the fourth and fifth rows, while some of the submersed taxa decreased or were not sampled at all. As pond rows increased in age, sediment depths increased and water depths decreased. Water chemistry did not seem to be correlated with plant community differences across pond rows. Percent organic matter and nutrient concentrations in sediments were generally greater and sediment pH lower in older ponds; although these differences could affect distributions of plant species (Gaudet and Keddy, 1995), Wilcox and Simonin (1987) were not able to show causation.

Differences in plant communities in these dune ponds might be interpreted as evidence for hydrarch succession; the vegetation changes that occurred in increasingly older ponds might also be expected to occur in an individual pond as it ages. However, Wilcox and Simonin (1987) opted to explain the differences across pond rows as a response to disturbance history. Sand mining, timber harvesting, surrounding residential and industrial development, three railroad corridors through the study site, and fire history associated with timber harvesting and the railroads were cited as potential causes of increased nutrient availability and increased sedimentation rates that hastened shallowing of water depth and conversion of plant communities from submersed to emergent species.

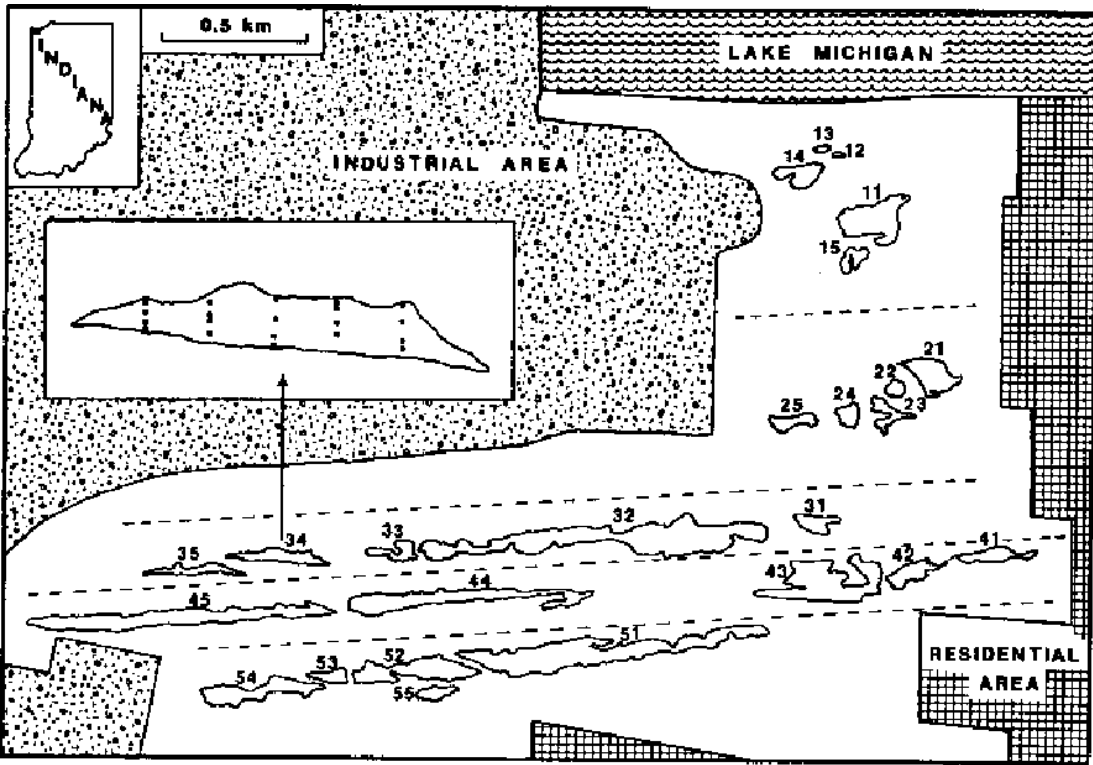


Figure 3. Map of the Miller Woods study area showing numbered study ponds, surrounding development, and schematic diagram of sampling design (Wilcox and Simonin, 1987).

A follow-up paleoecological study by Jackson et al. (1988) confirmed the role of human disturbance in shaping the role of modern plant communities in these dune ponds. Plant macrofossils and pollen in a sediment core taken from one of the oldest ponds were studied to test the hypothesis that the differences in plant communities among rows of ponds represented a hydrarch successional sequence. The 3000-yr record showed a brief colonization period and then early development of a diverse assemblage of submersed (*Najas*, *Chara*, *Nitella*), floating (*Brasenia*, *Nuphar*), and emergent macrophytes (*Cyperus*, *Eleocharis*, *Polygonum*, *Bidens*, *Leersia*, *Scirpus*, *Dulichium*, *Eupatorium*, *Zizania*, *Carex*). Although fluctuations in abundance of these taxa occurred during the ensuing 2500 or more years, major increases in *Typha*, *Sparganium*, *Cephalanthus*, *Glyceria*, and *Equisetum* did not occur until about 150 years BP. At that time, many of the previously characteristic taxa also decreased in abundance. The 150 yr BP horizon marks the rise in *Ambrosia* pollen associated with regional land clearance by European settlers and corresponding decreases in tree pollen.

Jackson et al. (1988) concluded that, following the initial succession-related colonization, there was no in-

dication of successional change in plant communities from 3000 to 150 years BP. When changes began to occur following European settlement, they were considered to be a response to human disturbance via alteration of hydrology or increases in nutrients, dissolved and particulate organic matter, and particulate mineral matter related to the land-clearance activities described by Wilcox and Simonin (1987). The changes in vegetation were rapid and controlled by allogenic rather than autogenic processes. Thus, inference of a hydrarch successional sequence from the chronosequence of dune ponds as proposed by Shelford (1911, 1913) was discredited. The array of ponds not only differed in age and degree of successional development but also in disturbance history. This allogenic influence increased sedimentation deposition and caused water depths in older ponds to decrease more rapidly than would have occurred under the sole autogenic influence of accumulating plant detritus. Chronosequences may display the appearances of successional development of plant communities; however, Jackson et al. (1988) recommended that the evidence must be evaluated in each case.

Singer et al. (1996) later conducted paleoecological analyses on cores from a pond in this chronosequence

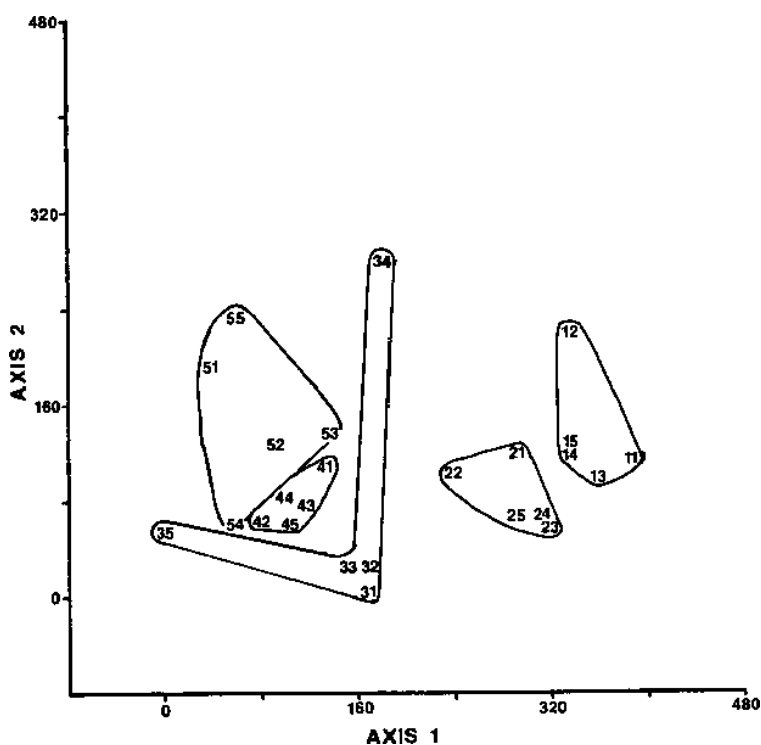


Figure 4. Two dimensional plot of DCA ordination of the importance value \times pond matrix from Miller Woods explaining 93.6% of the variance. Points are plotted as pond numbers (Wilcox and Simonin, 1987).

that is further removed from Lake Michigan (>10,000 years old). They demonstrated that wetland plant communities shifted from primarily submersed taxa of open water such as *Najas* and *Chara* to shallow marsh that included floating-leaf taxa (*Brasenia*, *Nuphar*) and emergent taxa often characteristic of drawdown conditions (e.g., *Cyperus*, *Eleocharis*, *Rhynchospora*). However, the assemblage of plant taxa suggested that periodic fluctuations of water levels occurred throughout the history of the wetland, and the fluctuations corresponded to past climatic events. Although the autogenic process of sedimentation gradually made the wetland more shallow, the changes in plant communities were shown to be driven by climate-induced hydrologic changes rather than autogenic changes alone. As found in the study by Jackson et al. (1988), yet another shift in vegetation occurred when European settlement began about 150 years BP, likely the result of human alteration of hydrology and adjacent land uses.

Hydrologic variability, succession, and overlap of terminology

If hydrologic variability constrains successional processes in Great Lakes wetlands through short- or

long-term flooding and drawdown cycles, how do the resultant plant communities comply with other concepts of organization and changes within communities? Other factors come into play.

In lake-connected wetlands, when high water levels are followed by low levels, germination of seeds and propagules in the exposed sediment can initiate the formation of **functional guilds** or groups (Keddy, 1992; Boutin and Keddy, 1993). For example, in the first year, ruderals would proliferate, with obligate annuals such as *Cyperus* and *Bidens* dying after one year and facultative annuals such as *Lycopus* and *Verbena* persisting. Interstitial taxa with a compact growth form and shallow rooting might also get a good start, and matrix taxa with vigorous clonal spread, such as *Typha* and *Scirpus*, would gain a foothold. However, if water levels rose again in the second year, the dynamics could change. On a sloping wetland surface, all ruderals might be lost in the second year at the lower end of the depth gradient, and the matrix species would sort out according to tolerance of water depth. At the upper end of the depth gradient, facultative annuals might persist, along with interstitial species and those matrix species that can tolerate drier soils in ensuing years. The resulting array of plant species might demonstrate a

clear **zonation** pattern, with zonation depicting the relative tolerances of water depth or soil moisture (van der Valk, 1982; Keddy, 2000). Alternatively, the distribution of species along the depth gradient might be more integrated and perceived as a **continuum** (Whittaker, 1967). In either case, the forcing factor is allogenic, not autogenic. The scenario described is common in the Great Lakes, where hydrologic variability is an important natural process and short-term fluctuations of 0.5 to 0.6 m have been shown to occur about every 30 to 33 years (lakes Michigan and Huron; Baedke and Thompson, 2000).

If lake levels in the example above remained relatively stable for several years, **fluctuations** or quantitative changes in vegetation without loss or gain of species might occur (van der Valk, 1982). Alternatively, clonal dominant matrix taxa such as *Typha*, or perhaps invasive species such as *Phragmites australis* (Cav.) Trin., *Lythrum salicaria* L., or *Phalaris arundinacea* L., would likely out-compete other plants and temporarily form the core habitat described by Wisheu and Keddy (1992) in their model of **centrifugal organization**. Since many of these clonal dominant taxa sustain a large standing crop, a reduced species richness in that vegetation type would match the prediction of the **hump-backed model** (Grime, 1979; Moore and Keddy, 1989). Year-to-year increases in biomass of individual plants might also be considered **maturation** (van der Valk, 1982). The competition-based change in vegetation to *Typha* can be described as autogenic, but it would still be driven by the allogenic dynamics of hydrology. Vegetation changes would begin anew when high lake levels returned as a result of climate-driven increases in water supply (Baedke and Thompson, 2000).

Despite the short-term changes in vegetation, the basic character of most undisturbed wetlands that are hydrologically connected to the Great Lakes should remain the same when viewed over longer time periods because the wetlands are in dynamic equilibrium with the environment. The short-term changes in extant vegetation caused by periodic hydrologic pulses are mediated by the seed bank; thus, Great Lakes wetlands could be considered to display **pulse stability** (Odum, 1971).

Chronosequences of wetlands between ridges on strand plains, as described in the previous section, are not subject to the same water-level dynamics as lake-connected wetlands. Hydrologic variability is more likely controlled by longer-term climatic variability, such as the 150- to 160-year or longer patterns observed in lakes Michigan and Huron (Baedke and Thompson, 2000). Autogenic processes would therefore have more

time to cause temporary changes in vegetation (Singer et al., 1996). However, if strong ground-water supplies are available, as in the younger ponds in the southern Lake Michigan site (Doss, 1993), there could be a reduced hydrologic response to regional climate changes, and autogenic basin-shallowing would become the major driving force for vegetation change, albeit extremely slow to non-existent (Jackson et al., 1988).

At the longer time-scale of the strand plain wetlands, functional guilds may still be used to describe plant species, but they are not an effective means for describing vegetation change, nor are zonation patterns, the continuum concept, fluctuations, and maturation. Centrifugal organization (Wisheu and Keddy, 1992) becomes a more meaningful tool for prediction of vegetation changes across environmental gradients, and pulse stability (Odum, 1971) takes on its true meaning.

Finally, the term **hydrarch succession** should be revisited. According to van der Valk's (1981) definition of succession cited previously, there is little question that succession occurs in Great Lakes wetlands. However, hydrologic variability dictates that allogenic processes overwhelm autogenic processes, which can persist for short time periods only. It is highly unlikely that autogenic succession can result in conversion to upland and climax upland plant communities in Great Lakes wetlands. As stated by Niering (1989) and also quoted by Mitsch and Gosselink (2000),

'Traditional successional concepts have limited usefulness when applied to wetland dynamics. Wetlands typically remain wet over time exhibiting a wetland aspect rather than succeeding to upland vegetation. Changes that occur may not necessarily be directional or orderly and are often not predictable on the long term. Fluctuating hydrologic conditions are the major factor controlling the vegetation pattern. The role of allogenic factors, including chance and coincidence, must be given new emphasis. Cyclic changes should be expected as water levels fluctuate. Catastrophic events such as floods and droughts also play a significant role in both modifying yet perpetuating these systems.'

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