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APPLIED WETLAND SCIENCE

The Twin Limit Marsh Model: A Non-equilibrium Approach to Predicting Marsh Vegetation on Shorelines and in Floodplains

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Abstract

Vast areas of wetland occur on shorelines of ponds, lakes, and rivers. These wetlands are divided into vegetation zones, including aquatic vegetation, marsh, and swamp. Here, we provide a simple, mechanistic, and non-equilibrium model that explains the occurrence of marsh as a function of past flood pulses. Marshes are sandwiched between two limits, both of which fluctuate with time. The lower limit is set by the tolerance of marsh plants to continuous flooding. The upper limit is set by competion with woody plants, which are killed by extreme high water events. The twin limit marsh model (TLMM) requires long-term water-level records and two biological inputs: duration of flooding required to drown marsh plants (f) and the duration of dewatering required for woody plants to reinvade once water levels drop (s). In the temperate zone, we suggest that f is ~4 yr and s is ~30 yr. We illustrate the model for the marshes of Lakes Erie and Ontario. High water years that kill woody plants, followed by low water years, produce large expanses of marsh. The regulation of lakes and rivers generally has negative effects on marsh area and diversity. The TLMM can be calibrated for other climates or ecoregions.

Keywords Marsh · Shoreline · Floodplain · Flood pulse · Drowning · Succession · Wet meadow · Water-level fluctuations

Introduction

The zonation of ecological communities along shoreline elevation gradients is a well-known characteristic of wetlands. For example, the Cowardin classification system (Cowardin et al. 1979) recognizes four vegetation zones along river floodplains: aquatic bed, emergent wetland, scrub/shrub wetland, and forested wetland. It is easy to assume that such zonation is at equilibrium with recent flood duration and controlled simply by the flood tolerance of individual species. Experimental studies, however, show that other biological interactions produce zonation, and while lower limits of species may be mostly set by flood tolerance, the upper limits of species are determined in part by competition (Grace and Wetzel 1981; Pennings and Callaway 1992; Keddy 2010), particularly from canopy-forming woody plants (Keddy and Reznicek 1986). Moreover, the observed vegetation patterns may not be at equilibrium with present conditions but, instead, may be caused by past conditions, with various lag times. For example, in prairie wetlands, there is a five-year lag between the onset of flooding and the conversion of emergent marsh to open water (Harris and Marshall 1963). Thus, the correlation between present water levels and vegetation zones does not represent simple cause and effect. Lag effects may be particularly important in rivers, lakes, and ponds having large changes in water level among years, where a year of high water may be followed by several years of lower water. The present-day zonation of these wetlands would then reflect the effects of floods that occurred in the past, just as present-day patterns in forests reflect the effects of previous fires and wind storms.

Our objective in this paper is to provide a simple mechanistic model that can describe and, more importantly, predict the effects of flood pulses on the extent of shoreline and floodplain marshes. We include both herbaceous emergent wetland and wet meadows in our definition of marsh. The model

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Botanical nomenclature: https://www.itis.gov

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focusses only on the upper and lower elevational limits of marsh vegetation, that is, the critical flood regimes at which marsh converts to another vegetation type (woody vegetation and aquatic vegetation, respectively). Hence, we call it the Twin Limit Marsh Model (TLMM). The model incorporates basic information on wetland ecology and incorporates non-equilibrium mechanisms, that is to say, it does not implicitly assume that current or recent water levels necessarily explain current vegetation patterns. Using the typology of Pielou (1977), the model can be described as deductive (rule-based), analytical, and deterministic, with discrete time steps. It can be run with simple spreadsheet software. Painter and Keddy (1992) first developed a similar model to forecast changes in wetland area in the Great Lakes of North America, given proposed scenarios of water-level control. However, the model coding has been lost, and the summary report is not readily available, being an unpublished pdf file in the library at the Canada Center for Inland Waters. Yet, the principles still apply. We have resurrected this model with the original objective: to provide a series of simple assembly rules for modelling wetland vegetation response to changes in water level on shorelines and in floodplains. Several other quantitative models exist to predict non-tidal marsh vegetation (Poiani and Johnson 1993; Coops et al. 2004; Johnson et al. 2005; Hudon et al. 2006; Wilcox and Xie 2007; Wei and Chow-Fraser 2008; Hebb et al. 2013). Our model is distinct from other models by together (1) incorporating non-equilibrium lag effects as the vegetation follows water-level forcing, (2) modelling total marsh area, not separate marsh vegetation types, (3) being simple and consequently widely applicable, only requiring the calibration of two simple parameters in different biomes, and (4) being mechanistic, allowing users to understand the biology behind the model. As an example of potential applications, we use the shoreline marshes along the Great Lakes of North America, where extreme high and low water levels may be separated by decades (Quinn and Sellinger 2006; NOAA 2019); it is between these two extremes that most emergent marsh and wet meadows occur (Keddy and Reznicek 1986; Wilcox and Xie 2007; Keddy 2010; Wilcox 2012b). However, we wish to emphasize that our aim is to build a general model that is applicable to marshes globally, from the subarctic to the tropics.

We need general models like this to guide the global conservation and management of wetlands. For instance, one of the factors causing the global loss of wetlands is the reduction of extreme flood pulses as a result of the construction of dams on rivers (Rosenberg et al. 1995; Middleton 2002; Nilsson et al. 2005; Keddy 2010; Merritt 2013). The reduction in flood pulses not only leads to loss of wetlands, but also to declines in wetland biodiversity, as wetland zonation is reduced and species-rich habitats like wet meadows are invaded by larger clonal graminoids and woody plants (Keddy and Fraser 2000; Keddy 2010). Global examples of how dams affect downstream riparian wetlands include the construction of canals and levees in the Everglades (Davis and Ogden 1997), flow diversions in the semi-arid regions of the Rocky Mountains (Caskey et al. 2015), the construction of the Ataturk dam upstream from the Mesopotamian wetlands (Partow 2001), or the newly proposed hydroelectric Project C on the Peace River, British Columbia (Report of the Joint Review Panel 2014). To emphasize how dams can disrupt the hydrology of the Mesopotamian wetlands downstream (Partow 2001), the Ataturk dam, just one of many on the Euphrates, itself has a reservoir capacity greater than the total annual flow of the Euphrates River!

The Lower Limit of Marsh

The Biology Behind the Model

We first need to quantify how the lower elevational limits of marshes respond to changing water levels. When falling water levels expose new areas of substrate, marshes rapidly re-establish from buried seeds because of their large seed banks. This process is well-documented in prairie marshes (van der Valk and Davis 1978; van der Valk 1981; Poiani and Johnson 1989) and is now understood to be a widespread phenomenon in shoreline wetlands (Keddy and Reznicek 1986; Keddy 2010). Annuals may dominate in the first year, but they are mostly replaced by perennials in subsequent years. Our first rule is therefore that one year of dewatering and drawdown during the growing season is sufficient to produce marsh on newly-exposed sediments. Falling water levels consequently expand marsh area over the short term.

When water levels rise, how much flooding is necessary to kill herbaceous marsh plants? We know from laboratory experiments that flooding puts stress on marsh plants and can reduce growth rates by up to 50% (Laing 1940). We know from comparative studies that some marsh plants can tolerate anoxia for only a few weeks, while others could survive and even extend their growing shoots after several months of anoxia (Braendle and Crawford 1987; Fraser and Karnezis 2005). We also know from field experiments that increased flooding causes reduced growth in an array of common marsh plants (Campbell et al. 2016). Fewer studies, however, specify how long flooding duration is needed to kill marsh plants by drowning. Here are four studies, representing increasing spatial and temporal scales of evidence. (1) Campbell et al. (2016) ran a carefully controlled field experiment with ten emergent marsh species, each planted in monoculture, along a flooding gradient in a constructed pond over four years. After three years, there was virtually complete mortality across all species when subjected to flooding for 100% of the growing season. In this experiment, some species, such as *Pontederia cordata,* died when flooded for as little as 50% of the growing season. (2) A larger field experiment was conducted in ten 5-ha cells built in the Delta Marsh on the edge of Lake Manitoba, Canada, in which water levels were both lowered and raised (van der Valk et al. 1994; van der Valk 2005). One main observation was "*As has previously been observed in other prairie wetlands, 2 years of high water resulted in the extirpation of most of the emergents…*" (van der Valk 2005, p. 182). In his summary, he states: "*prolonged periods (2 or more years) of high water (1 m or more above the mean water level) per se will eliminate emergent species.*" (p. 182). The presence of muskrats accelerated this process. Two dominant clonal species, *Phragmites australis* and *Typha* X *glauca* were most resilient, but still declined to 25% of the pre-flooding cover by the second year of flooding (van der Valk et al. 1994). (3) A classic study reported on water level manipulations of thousands of hectares of the Agassiz National Refuge in Minnesota, USA, where water levels were first lowered, and then the area was re-flooded (Harris and Marshall 1963). There was full mortality after 4–5 years of flooding for species including *Schoenoplectus tabernaemontani* and *Eleocharis palustris* (Fig. 1). Deeper flooding led to faster rates of decline. (4) The most extensive study examined changes in 71 shallow marsh wetlands in Saskatchewan, Canada over a ten year period (Millar 1973). Millar concluded "*2 or more years of continuous flooding were required to eliminate emergent cover completely and convert the wetland to open water.*" Species that were reduced by flooding included *Persicaria amphibia*, *Carex atherodes*, *Scolochloa festucacea*, and *Eleocharis palustris*.

Across the different ecological regions, different sample designs, and different species, there is strong agreement that three years of flooding is sufficient to eliminate many marsh plants. Our rule is therefore that marsh plants tolerate one year of continuous flooding during the growing season, but, erring on the conservative side, are killed by four years of such conditions. It is reasonable to assume that this decline is exponential, since, while many plants appear tolerant to the initial months of flooding, progressively longer periods of flooding have cumulative effects. This exponential shape is evident from the data in Harris and Marshall (1963; Fig. 1).

We do not specify the depth of flooding. Once the ground surface is covered by water, hypoxia rapidly develops in soils. If the water is raised high enough to cover shoots, the impacts on plants will be greater, since the shoots would not be able to transport atmospheric oxygen down to roots through aerenchyma. Many young shoots would be fully submersed earlier in the growing season, which is the critical period when shoot and leaf extension occurs, and so even shallow flooding would have an impact. However, owing to natural seasonal variation within most wetlands, and particularly lakeshores and floodplains, the simpler criterion of being continuously flooded (without using a specified depth) is likely sufficient.

Modelling the Lower Limits of the Marsh

The model requires only long-term records of water levels. During falling water levels, the model assumes that marsh will colonize the newly-exposed sediments within a year. For rising water levels, we include one biological term, flooding tolerance f, which is the number of years it takes for flooding to kill marsh plants and create open water or aquatic vegetation. This is biological information, and as reviewed above, the literature suggests a figure of about 4 years. We also include one site-specific term, d_t, denoting the duration of flooding at a specified elevation, which is determined from the water-level history of the site. These terms describe the relative marsh decline from flooding, c_d.

If d_t has been longer than f, no marsh remains (Fig. 2). This will often be the case along rivers, lakes, or reservoirs in which the water level has been kept relatively stable. The model does not deal with whether these areas now have submersed aquatic plants or have reverted to open water. We are concerned only with the fate of the marsh. In those cases where d_t is less than f, that is on the left side of the graphs, our task is to calculate

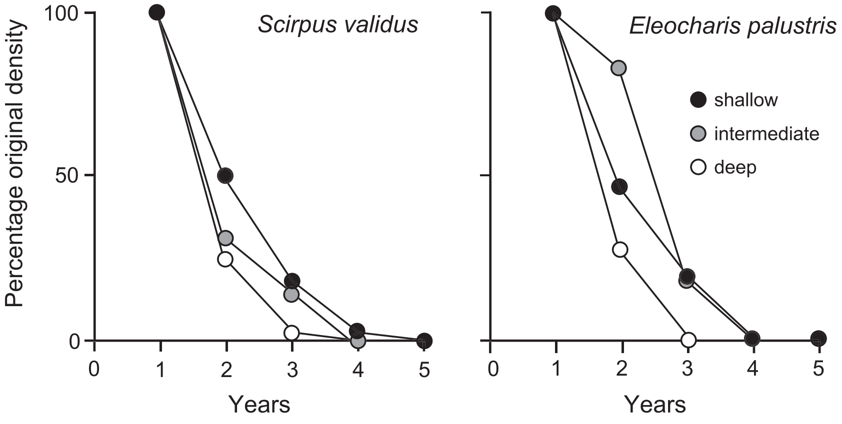


Fig. 1 The effects of flooding to three different water depths on the survival of two emergent plant species. All plants were dead within five years, often in as little as three. Data from Harris and Marshall (1963)

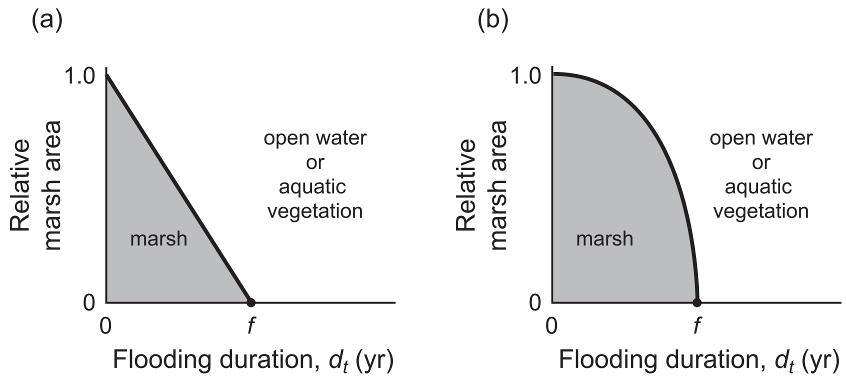


Fig. 2 General view of marsh ecology: the area of marsh is at maximum when flooding begins, and then declines from drowning, (a) linear decline or (b) exponential decline

what proportion of the initial marsh area remains as time passes. Maximum marsh area occurs in the first year as flooding begins, and marsh area then declines to zero as time passes, with time passage measured by $(d_t - f)$. It is useful to scale the time elapsed by f, hence $(d_t - f)/f$. A linear representation of the reality (Fig. 2a) captures the essence of the mechanism but is overly simplified. The rate of marsh loss is likely exponential (Fig. 2b), so it is slow at first but then accelerates as the effects of hypoxia become lethal.

To accommodate this exponential decline in marsh area due to flooding, we assume that the logarithm of marsh area varies with $(d_t - f)/f$. However, since the log of zero is undefined, we add a constant, c_{min}. Thus, our non-linear model for conversion of marsh to open water gives the relative marsh decline, c_d, as $-\log_{10}c_{min}((d_t - f)/f)$, from c_{min} to 1 (Fig. 3a). When back-transformed, this rate is appropriately exponential (Fig. 3b). The smaller the value of c_{min}, the stronger the exponential rate of marsh decline. For simplicity, we use a value of 0.01 for c_{min}, so the marsh decline occurs over two orders of magnitude, but this can be adjusted. Since an exponential curve, by definition, does not reach zero on the y axis, but reaches c_{min}, we need a scaling adjustment,$(1 - c_d)/(1 - c_{min})$. With this ratio, we are able to plot the relative marsh area remaining as a function of flood duration (Fig. 3c).

The Upper Limit of Marsh

The Biology Behind the Model

Now we consider how the same fluctuating water levels expand or contract the upper elevation limit of the marsh. Let us begin with marsh expansion at this upper limit. When water levels rise, woody plants that occur around the upper edge of emergent marsh and wet meadow will drown. Most temperate woody plants are killed by just one year of continuous flooding, but a few can survive for as long as 2 to 3 years (Crawford 1982; Kozlowski 1984; see Table 1). Once the trees or shrubs are killed, the canopy is lost, and marsh or wet meadow can re-establish from existing plants that were present in the swamp understory, by dispersal of vegetative propagules and turions, by clonal growth from adjoining marsh, and by germination of buried seeds. Germination from buried seeds may be the most important mechanism (e.g., van der Valk and Davis 1978; van der Valk 1981; Keddy and Reznicek 1986; Keddy 2010, Table 4.1), but since most marsh plants require dewatering for germination, this process will not normally begin until the flood pulse that killed the forest canopy has passed. Most flood pulses in floodplains pass within a few months, but in some circumstances, high water periods may last several years. For simplicity, the model allows marsh to

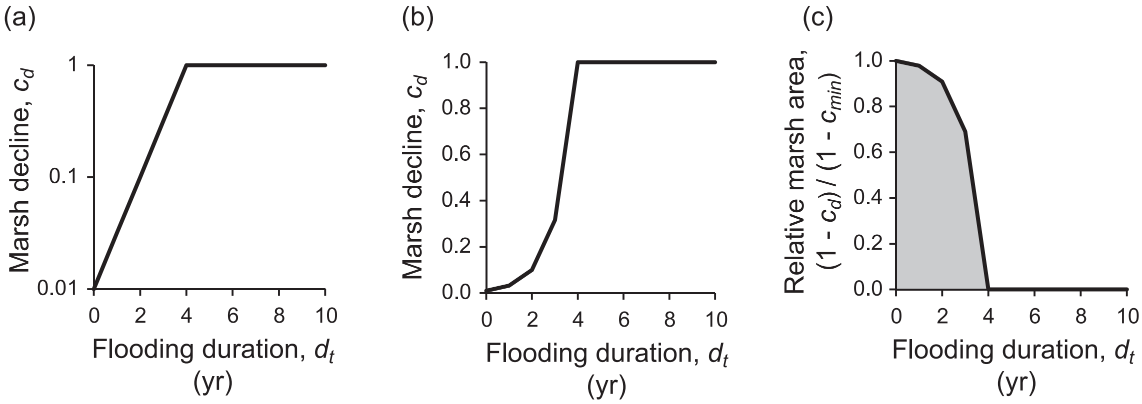


Fig. 3 Model output leading to description of marsh area (shaded) as a function of time since flooding, (a) the effects of flooding increase with time on a log scale, (b) back-transformed to show the exponential mortality, (c) the area of marsh as a function of the duration of flooding

Table 1 The relative survival time under inundation of some flood-tolerant trees (Crawford 1982)

Species	Survival time (yr)
Quercus lyrata	3
Q. nuttalii	3
Q. phellos	2
Q. nigra	2
Q. palustris	2
Q. macrocarpa	2
Acer saccharinum	2
A. rubrum	2
Diospyros virginiana	2
Fraxinus pennsylvanica	2
Gleditsia triacanthos	2
Populus deltoides	2
Carya aquatica	2
Salix interior	2
Cephalanthus occidentalis	2
Nyssa aquatica	2
Taxodium distichum	2
Celtis laevigata	2
Quercus falcata	1
Acer negundo	0.5
Crataegus mollis	0.5
Platanus occidentalis	0.5
Pinus contorta	0.3

re-establish one year after flooding of woody vegetation. Forested elevations, then, are converted to marsh after there is a flood pulse that lasts a least one growing season.

If, however, the water levels after a pulse remain low and the site is dewatered for multiple years, the marsh vegetation can be reconverted back to swamp forest or terrestrial vegetation. There are at least three separate potential mechanisms for loss of marsh plants and return to upland vegetation. Each likely requires a longer period of time. (1) Marsh plants can die from desiccation, when soils become drier than their physiological tolerances. (2) They can die from competition with terrestrial herbaceous plants that invade from adjoining habitats. (3) Finally, and most importantly, they could die when taller woody plants shade and replace herbaceous wetland vegetation. It is this latter process that is most relevant to our model.

Just how long does it take for early successional trees and shrubs to form a canopy once water levels drop? The data are surprisingly scarce. Many of the observational and experimental data from wetlands (e.g., (Harris and Marshall 1963; van der Valk 1994; van der Valk 2005) are primarily concerned about changes between kinds of marsh, or between marsh and open water, and hence do not address situations where conditions are dry enough or long enough to convert (or reconvert) to cover by woody plants. Let us look at a few examples of data involving woody plants.

In Minnesota prairie wetlands, Harris and Marshall (1963, p. 366) describe a drawdown lasting five years. During the fourth year, the summer was very dry. "*Willow became particularly noticeable. In the fall the pool was dry and looked like a field overgrown with willows about 3 feet high*" which had the appearance of "*low brushy "jungle."*." In the following year, which was also dry, "*many portions of the pool bottom were exposed for a fifth year. In these areas rapid growth of willow occurred. Plants that had been 24-30 inches high in June reached 60-72 inches by fall. In June individual roots were represented by only single or double stems, but by September clumps of five to ten stems completely covered areas of over 3 square feet each.*" They also note that in these conditions, poplar seedlings "*became conspicuous*." They add that "*In spite of the severe competition of the willows, the various emergents still persisted in favourable locations*". Presumably, the "*favourable locations*" were wetter areas at lower contours where water had accumulated creating "*islands of meadow*" within the willows.

Here is an example of woody plant invasion after a drawdown of a managed dyked marsh on the southwest shore of Lake Erie, within the Ottawa National Wildlife Refuge. The substrate is highly productive soil of the former Great Black Swamp, and cottonwood (*Populus deltoides*) is an important woody species. Ron Huffman (pers. comm. 2017) offers a limiting case for our model, a situation with rapid invasion by trees:

> *In a scenario of a drawdown with adjacent mature cottonwood trees, and wetland soil being exposed just as cottonwood is seeding, then establishment can be rapid under good climatic conditions. If the drawdown is extended into a second growing season, then greater than 50% canopy cover with tree heights over 6' tall is possible, and happened in a half acre area or so in one of our units 2 years ago during construction.*

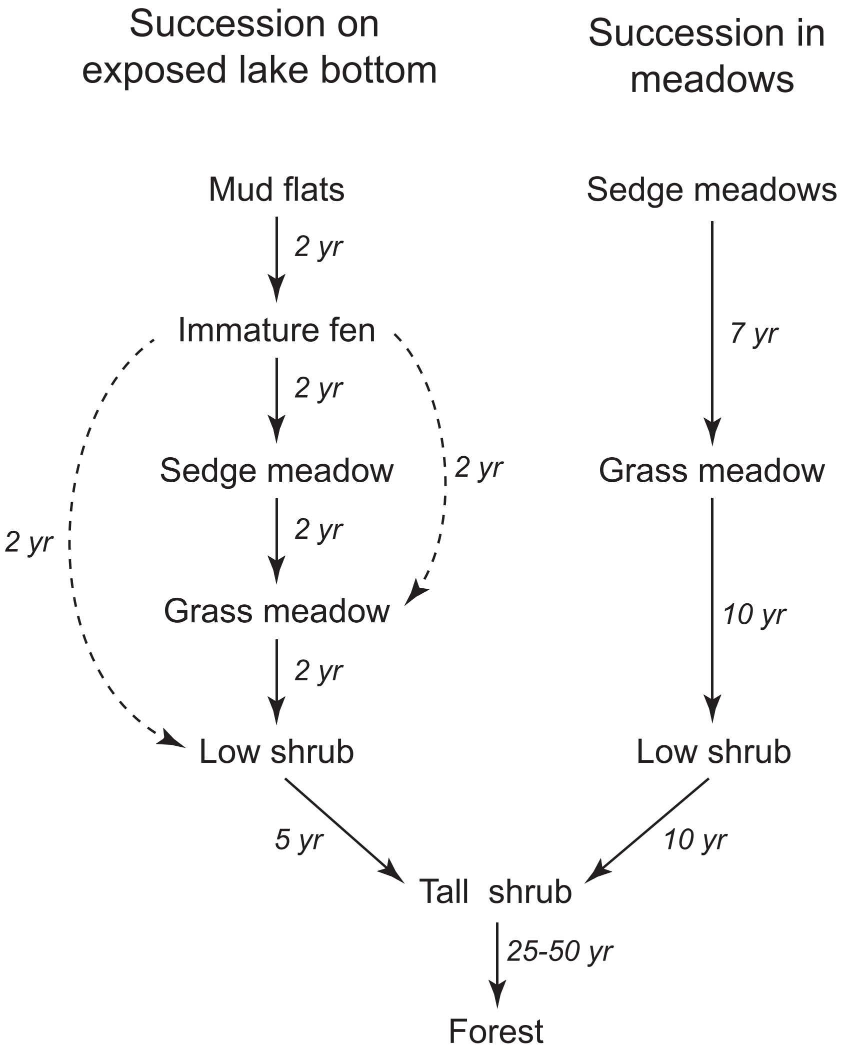
Huffman also reports that dogwood (*Cornus* spp.) establishment is slower and not typically encountered. They are rapidly killed by reflooding, whereas buttonbush (*Cephalanthus occidentalis*) is more likely to regenerate, and once established, more able to persist during flooding. Similar anecdotal accounts exist of rapid cottonwood and willow (*Salix*) colonization on bare sediments following dewatering in a western Lake Erie marsh restoration (Wilcox and Whillans 1999).

One classic, long-term study of woody plant invasion comes from a floodplain wetland. The Peace-Athabasca delta provided a kind of natural experiment where flood pulses on the Peace-Athabasca River were abruptly reduced by the W.A.C. Bennett Dam, completed in 1968. Field observations on changes in vegetation were used to construct a simulation model (Townsend 1972), in which woody plants rapidly invade sedge meadows, converting them to tall shrubs within 30 years (Fig. 4 right) and into forests within another 25–50 years. In areas that were mud flats (Fig. 4 left), the process was considered to be more rapid, with conversion to tall shrubs within nine years.

Another general source of evidence is the establishment of vegetation on newly-deposited sediments in rivers. The chronosequence of vegetation along floodplains has been well-studied (Merritt 2013). Along the Beatton River in northeast British Columbia (Nanson and Beach 1977), newly-exposed sediment was colonized by balsam poplar (*Populus balsamifera*). The density of poplar rapidly increased within the first 30 years, along with shrub species, principally alder (*Alnus incana*) or willow (*Salix* spp.). Maximum poplar density was reached within 40 to 50 years. Further south, Johnson (1994) studied rates of poplar-willow invasion along the Platte River in Nebraska, where flows have been reduced by dams and irrigation upstream. Historical records and photographs suggest that woodland began to expand into the floodplain about 1900, and that by 1930 large areas of the channel had become woodland. An overview of restoration possibilities along the Rhine River in the Netherlands gives a time of 30–50 years for the development of climax poplar and willow floodplain forests (Duel et al. 2001). Since we are focussed not on when the climax forest occurs, but simply when woody plants replace herbaceous species, this time period of 20–50 years is clearly an upper limit, just as the estimate of two years for cottonwood invasion provides a lower limit.

One other source of evidence comes from the body of data on how fast abandoned agricultural fields convert to forest in terrestrial situations. We consider this a reasonable analogue to shorelines and floodplains, at higher elevations during low water periods, when the upper reaches of shorelines can be relatively dry, although herbicide residues and higher nutrient levels in abandoned agricultural fields may extend the time for woody plant encroachment. One study

Fig. 4 Simulated changes in the vegetation in the Peace–Athabasca delta, Canada, after the construction of the W. A. C. Bennett Dam reduced spring flooding. From Townsend (1972)



from New York gives 50 years for woody plants to invade abandoned agricultural land, with 70 years for typical forest trees (Copenheaver 2008). Further south, a mere 20 years may be long enough for neotropical forest to establish in abandoned fields (Guariguata and Ostertag 2001). Further north, a century may be required for primary succession to boreal forest (Bormann and Sidle 1990). A review of old field succession in North America (Wright and Fridley 2010) concluded that most fields will be 50% covered by woody plants within 50 years, some in as few as a decade. The time required was greater at higher latitudes (Fig. 5). In this set of studies, there were already herbaceous plants established in these fields, and established herbaceous plants may delay the establishment of woody plants by means of competition, or enhance it through facilitation (Connell and Slatyer 1977). Indeed, the more rapid progression from mud flat to shrubs in the Peace-Athabasca floodplain is consistent with the view that established clones of sedges and grasses may delay wetland succession by about a decade. Based on such data, we suggest an interim figure of 30 years for the transition from marsh to woody vegetation after dewatering in temperate climates. This figure is consistent with our own observations over many years and locations but remains to be ground-truthed and may be considerably less in some circumstances.

What is the shape of the function for woody plant invasion? The simplest model for conversion to forest would again be linear. A short lag might be included, since many species of trees do not have buried seed banks (Grime 2001), but rather disperse in space from established individuals nearby, as do the wind-dispersed seed of willows and poplar. However, an exponential model is more likely, reflecting the biological reality of slow establishment of tree seedlings, followed by more rapid closing of the canopy once a sufficient number of shrubs and trees has established.

Modelling the Upper Limits of the Marsh

Our modeling of the upper marsh limit is analogous to our modelling of the lower marsh limit and again requires only records of long-term water levels. For rising water levels, the model assumes that marsh plants establish the year after a flood pulse of one growing season kills the woody plants, mostly through germination of buried seeds, but also possibly from vegetative expansion. For falling water levels, we need to describe the loss in marsh area from invasion by woody plants, which overtop and shade out the emergent marsh plants. We include one biological term, *s*, which is the number of years it takes for a site to become closed canopy woody vegetation after it is dewatered. This number is biological

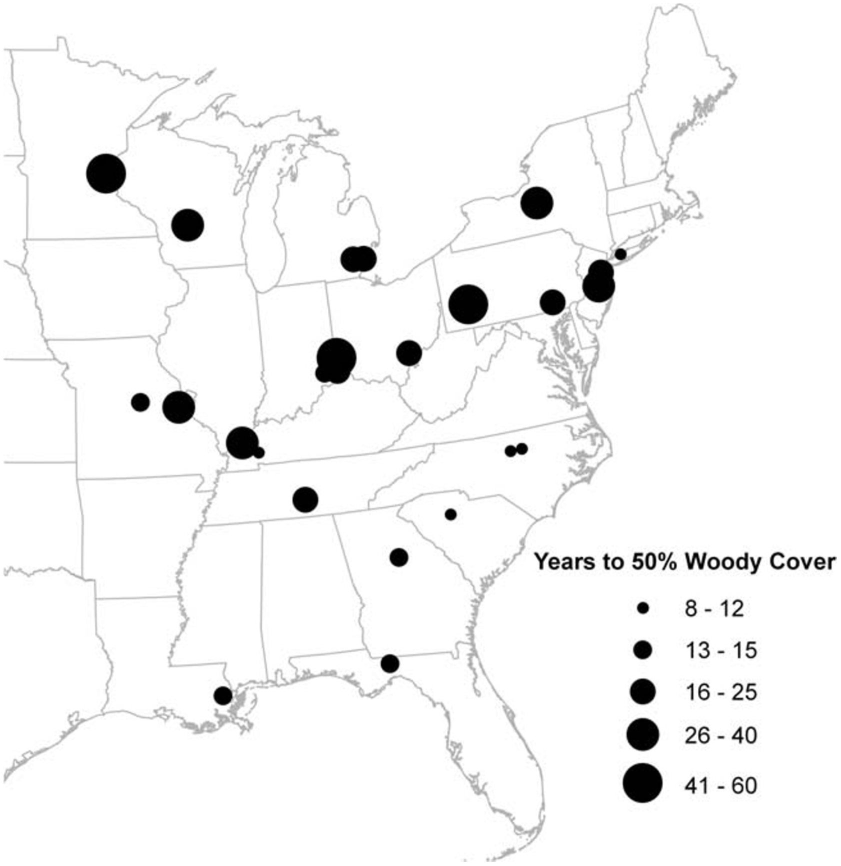


Fig. 5 The number of years after abandonment until old fields are dominated by woody vegetation (measured as 50% woody cover). From Wright and Fridley (2010)

information, and as reviewed above, the literature suggests a general figure of approximately 30 years. It should be groundtruthed in a region; it might be extracted from habitat management data, or measured using dendrochronology and historic aerial photography. We again include one site-specific term, x_t, denoting how many years the site has been dewatered and has been subject to succession by woody plants, determined from the water level history of the site. These terms describe the relative marsh decline caused by the succession of a canopy of woody vegetation, w_x.

If x_t has been longer than s, no marsh remains (Fig. 6). That is, in our general case, with s equal to 30 years, sites dewatered for more than 30 years will succeed to a closed canopy of woody vegetation and have no marsh remaining. This will often be the case in floodplains or on shorelines where water levels have been controlled. In those cases where x_t is less than s, that is on the left side of the graphs, our task again is to calculate what proportion of the initial marsh area remains as time passes. Maximum marsh area occurs in the first year after dewatering, and marsh area then declines to zero as time passes, with time passage measured by $x_t - s$. It is useful again to scale the time elapsed by s, hence, $(x_t - s)/s$. A linear representation of this change (Fig. 6a) is simple, with regard to fundamental mechanisms, but once again, the rate of loss of marsh is likely exponential (Fig. 6b), probably slow at first, and then accelerating as woody plants arrive, establish, spread, and form a canopy.

To accommodate this exponential decline in marsh area due to woody plant encroachment, we assume that it is the logarithm of marsh area that varies with $(x_t - s)/s$. We again need to add a constant, which we call w_{min}. Thus, our nonlinear model for conversion of marsh to woodland gives the relative marsh decline as $-\log_{10} w_{min}(x_t - s)/s$, from w_{min} to 1 (Fig. 7a). As before, when back-transformed, this rate is exponential (Fig. 7b). The value assigned to w_{min} is a measure of the rate of invasion of marshes by woody plants. Given that the literature was barely able to give realistic values of s, it is unlikely that we yet know real values for w_{min}. For simplicity, we use a value of 0.001 for w_{min}, but this is easily adjusted. We further need to scale the remaining marsh appropriately, so we use the scaling adjustment $(1 - w_x)/(1 - w_{min})$, which allows us to plot the relative loss of marsh as a function of the duration of dewatering (Fig. 7c).

Two Examples: Lake Erie and Lake Ontario

Our aim is to be able to apply this model to any watershed or any lake. Here, we provide two well-known examples from the Great Lakes of North America to illustrate the model: the undyked marshes of Lake Erie and Lake Ontario, the first having no water-level control and the second with modest control.

Lake Erie is a large lake with published water-level records extending back to 1860. It still has extensive undyked marshes, such as at Long Point on the north shore, which has a rich wetland flora that has been well-described and linked to water-level fluctuations (Reznicek and Catling 1989). This lake has also been used as an example of how water-level fluctuations create wetland vegetation (Keddy and Reznicek 1986). We applied the model using September mean water levels in Lake Erie as recorded in Cleveland, Ohio since 1860 (NOAA 2019). We used September levels to capture the maximally exposed area during the summer growing season, a period when plant canopies are at their maximum, and during which germination can occur. Figure 8a shows water levels in Lake Erie, and the response of the lower limit of marsh, in this case with $f = 4$ (four years of drowning removes marsh). Figure 8b shows the same water levels, and the response of the upper limit of marsh with $s = 15$ (fifteen years for a canopy of woody plants). We used this lower time frame of 15 years, instead of 30 years in our general case, to reflect the nutrient-rich conditions of the marshes in the lower Great Lakes, but again, its value must be ground-truthed. Figure 8c shows both the lower and upper limits of marsh. Figure 8d shows the span of elevation between the marsh upper limit (MUL) and the marsh lower limit (MLL), as the marsh tracks, approximately, and with lags, the changing water levels. This is the relative marsh area, or the marsh expanse—the range of elevations for

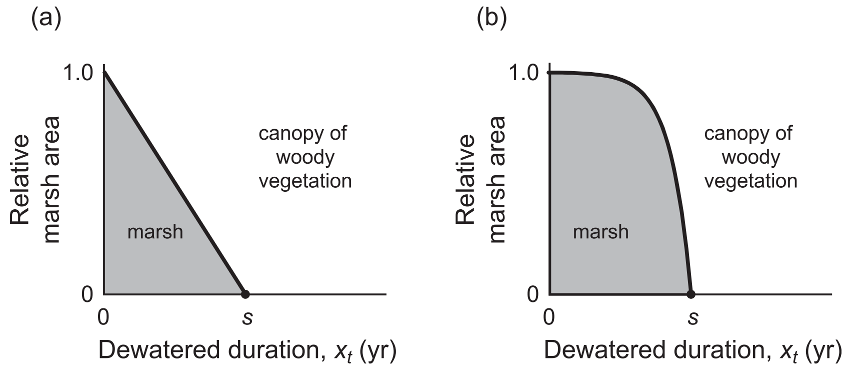


Fig. 6 General view of marsh ecology: the area of marsh is at maximum in the year after dewatering, and then declines with woody plant invasion and canopy formation, (a) linear decline, (b) exponential decline

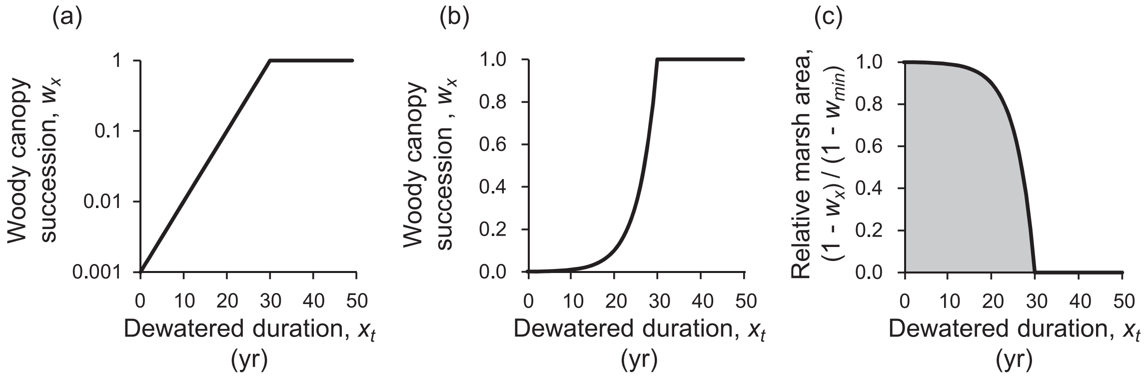


Fig. 7 Model output leading to description of marsh area (shaded) as a function of time since dewatering, (a) woody plants increase in cover on a log scale, (b) back-transformed to show the exponential nature of succession and marsh decline, (c) the relative area of marsh as a function of duration of dewatering

marsh. It is not marsh area, since we have not included the site-specific topography and bathymetry associated with each elevation. Given that many lakes and rivers have extensive areas of shoreline with relatively gentle slope, relatively small differences between MUL and MLL can correspond to vast changes in marsh area.

This model applied to Lake Erie shows an important general lesson—that the expanse of marsh is controlled predominantly by occasional high water periods that re-set the upper level of marsh vegetation, and that years following these occasional highs, with falling water levels, can be expected to have significantly larger expanses of marsh, as has been found elsewhere (Wilcox and Nichols 2008; Wilcox 2012a). This is the case in 1935. Conversely, time periods in which water levels are relatively stable, or slowly rising, will have years with less marsh, as is the case in 1900. This suggests that the expanse of marsh on shorelines is relatively sensitive to rates of woody plant succession in the landscape. If the rate of succession is faster than in this example ($s < 15$), as found in some impounded marshes along Lake Erie after drawdown (Ron Huffman, pers. comm.), the upper line in Figure 8b will be reduced.

Now let us turn to Lake Ontario, which has had its water levels partially controlled as a result of the construction of the Moses-Saunders Dam in 1958, downstream from the lake outlet, for power generation and to aid navigation of the St. Lawrence River. There are water-level records from Oswego, New York since 1870 (NOAA 2019). If we again use the September water levels, and the same model parameters as for Lake Erie ($f = 4$, $s = 15$ years), the marsh expanse, that is the difference in elevation between the marsh upper limit (MUL) and the marsh lower limit (MLL), would have been even wider than in Lake Erie prior to the construction of the dam (Fig. 9). However, after the construction of the dam, water-level fluctuations in Lake Ontario were much reduced, which produced a lower range of water-level fluctuations and, consequently, narrower upper and lower limits for marsh than in Lake Erie.

Discussion

Structural Assumptions of the Model

We have opted for the simplest possible model structure, requiring water levels and two biological parameters, with the one proviso that it must allow for non-linear responses to changes in the environment. We suspect that this simplicity is sufficient to capture the underlying behaviour of marshes. We remind readers that there is always a trade-off between simplicity and transparency, but that in general, simpler models are to be preferred (Leary 1985; Starfield and Bleloch 1991). Very large models also require large computers; our simple spreadsheet model can be used by anyone with a modest computer. We acknowledge that numerical refinements are possible.

Biological Assumptions of the Model

We assume that marshes rapidly re-establish from buried seeds when flooding is followed by dewatering (van der Valk and Davis 1978; van der Valk 1981). In a few cases, the seedbank may be small, which may retard marsh establishment. However, even in open water areas adjacent to marshes, seed banks still exceed 130 to 1300 seeds m^{-2} (van der Valk 1981; Poiani and Johnson 1989).

We also assume that woody plants are killed by continuous flooding for as little as 1–2 years (Crawford 1982; Kozlowski 1984). However, we acknowledge our experience is mainly in the temperate zone and that flood tolerances may be different in other biomes, such as those in Amazonian floodplains (Valle Ferreira and Stohlgren 1999; Parolin 2009).

There are two parameters built into the model: how long marshes persist under continuous flooding, *f*, and how long it takes for woody plants to re-invade after an elevation is dewatered, *s*. We have provided our justification for suggesting 4 years, and 30 years, respectively, as interim values, but

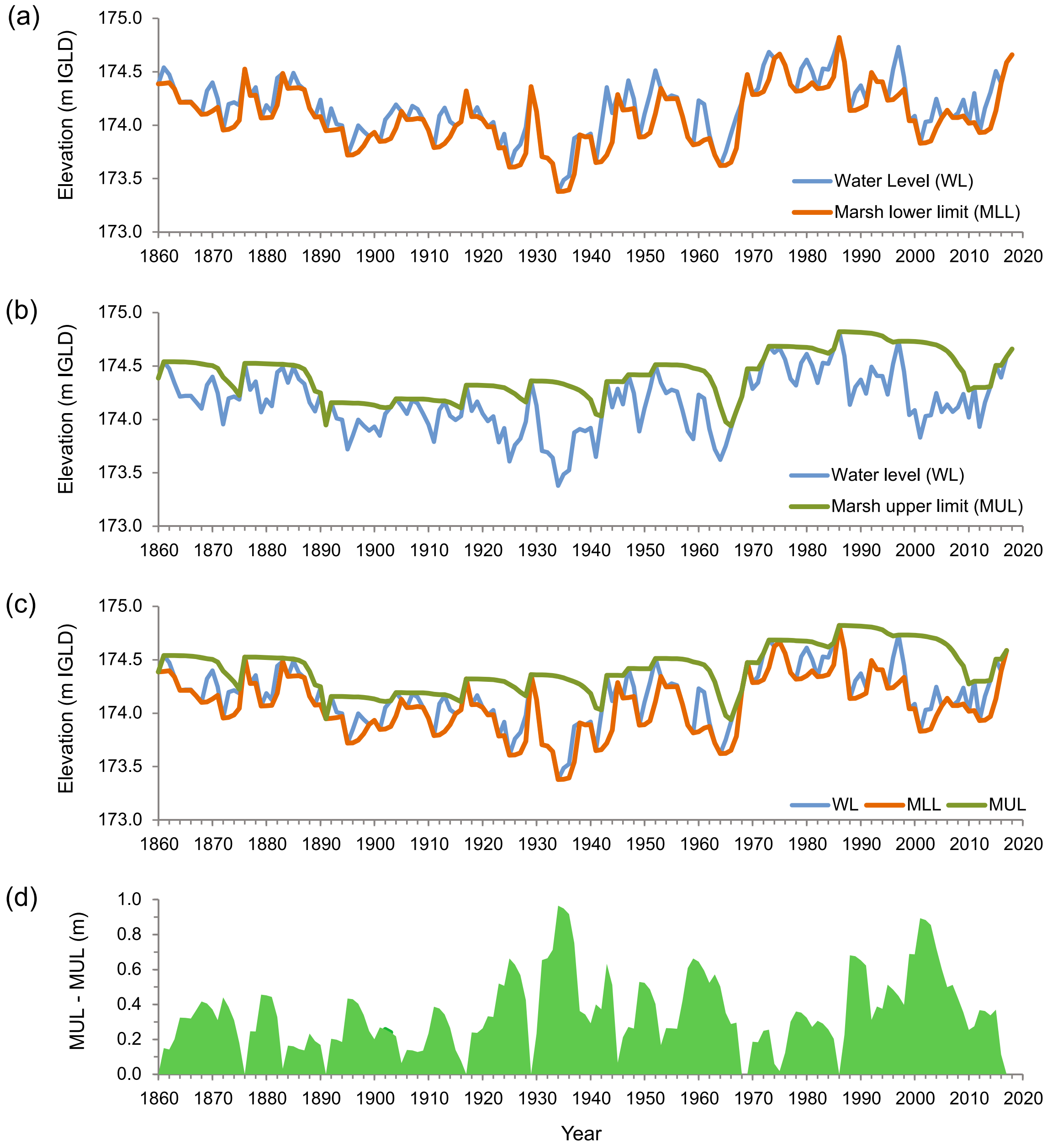


Fig. 8 The Lake Erie example showing how water levels (WL) can determine (a) the marsh lower limit (MLL), (b) the marsh upper limit (MUL), (c) both upper and lower limits together and (d) the span of elevations between MLL and MUL over which marsh occurred, extracted from Fig. 8c. (IGLD = International Great Lakes Datum 1985, September mean water level data from Cleveland, OH since 1860 (NOAA 2019), with *f* = 4 and *s* = 15)

these must be ground-truthed in different biomes. We have used a lower s value of only 15 years for the examples in Figs. 8 and 9. It would be useful for ecologists to compile a set of *f* and *s* values for different regions of Earth. Eventually, we envisage a table of *f* and *s* values at the scale of ecodistricts or ecoregions (Olson et al. 2001).

We recognize that situations may occur where marsh plants persist for longer periods than our interim value of *f* = 4 years of flooding, as would be the case if the vegetation is buoyant, producing floating mats (Sasser et al. 1996; Mallison et al. 2001). For instance, *Pontederia cordata*, which does not survive extensive flooding when rooted in non-floating substrates (Campbell et al. 2016), is commonly found in floating mats (Mallison et al. 2001).

Our model also assumes that woody vegetation acts to delimit the upper boundary of marsh. However, this may not universally be the case. In some arid biomes, woody plants may not grow in adjoining terrestrial landscapes; here competition between herbaceous plants will delimit the marsh from upland vegetation. In some areas, human activities like farming may remove adjoining woody vegetation (Mirck and Schroeder 2013).

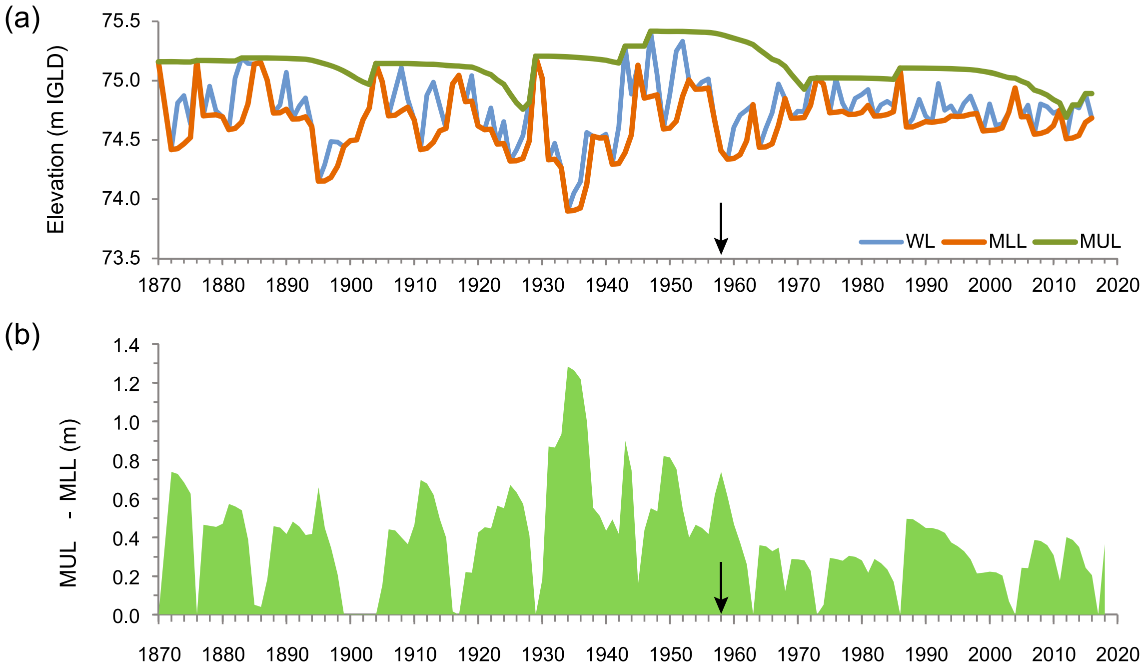


Fig. 9 The Lake Ontario example showing how water levels (WL) can determine (a) the marsh lower limit (MLL) and marsh upper limit (MUL) and (b) the span between MUL and MLL over which marsh occurred. (IGLD = International Great Lakes Datum 1985, September mean water level data form Oswego, NY since 1870 (NOAA 2019), *f* = 4 and *s* = 15). The arrow indicates the beginning of water level control

Finally, this model focuses on water levels, which are the predominant factor controlling wetland vegetation (Keddy 2010). Other secondary factors will, of course, also control marsh area, including fertility, disturbance (e.g., fire, ice, wave exposure), herbivory, and burial (Keddy 2010). Although we have focussed on systems driven by occasional large flood pulses, we appreciate that in watersheds with multiple dams and other anthropogenic modifications, various complicated flood regimes could arise. How lag effects, drowning, and succession might affect marsh area in each specific watershed is a problem we leave as an open question for other researchers to explore.

Extending the Model

Our model focusses explicitly on freshwater marshes, including herbaceous emergent vegetation and wet meadows. In a typical shoreline profile, with typical wetland zonation, there would be additional wetland vegetation on either side of the marsh. The TLMM does not address these adjoining vegetation zones, but let us briefly consider each, in turn.

Above the upper limit of marsh, one would expect a zone of swamp—a wetland dominated by flood-tolerant woody plants, either trees or shrubs. Like marsh plants, the regeneration of most woody plants from seed requires a period of dewatering (Penfound 1952; Parolin 2009). As with marsh plants, the duration and frequency of flooding will determine the presence of particular woody species. Near the lower limit of the swamp, woody plants may be flooded annually for much of the growing season, while near the upper limit of swamp, woody plants may be flooded only once a decade (e.g., Kellison et al. 1998). With data on the duration of flooding that converts terrestrial forest to swamp, one could extend the TLMM to predict the extent of the swamp zone, with an added algorithm that describes the upper limit of swamp probably being set by the occasional flood pulses that drown terrestrial trees. This might be an important exercise, since it is possible that the construction of dams on many lakes and rivers may have reduced flooding and caused a significant loss of swamp forests around the world (Nilsson et al. 2005). It may be a simple task to extend this model in boreal or temperate ecoregions, given the lower diversity of flood-tolerant tree and shrub species. However, nearer the equator, the diversity of flood-tolerant woody species is high. For instance, along the Amazon, there are more than a thousand species of flood-tolerant trees, and some may be flooded for up to nine months out of the year (Valle Ferreira and Stohlgren 1999; Parolin 2009).

Below the lower limit of the marsh, there would usually be aquatic vegetation. Aquatic plants have the greatest flood tolerance among wetland plants and may have floating leaves or submersed foliage (Sculthorpe 1967). Such plants can withstand continuous flooding for many years. Many are tolerant of extreme hypoxia (Laing 1940) and some can transport oxygen from surface leaves into submersed rhizomes (Dacey 1980). Most, if not all, can reproduce sexually in standing water, although they usually also have the capacity for asexual reproduction by means of turions and rhizomes. Water lilies, such as *Nymphaea* spp. and *Nuphar* spp., are two classic examples. The lower limits of aquatic plants are determined by multiple factors, including water clarity, plankton abundance, waves, and herbivory. It might eventually be possible to create an algorithm for the lower end of the aquatic zone and add it to the model as well.

Could this model be extended to tidal wetlands? In tidal wetlands, the added complications include storm surges and salinity (Keddy 2010; Kearney et al. 2019). If and when such storm surges and/or salinity pulses kill woody plants, then a similar dynamic may arise, with the upper elevation of tidal marsh area being controlled by the interaction between occasional flood pulses followed by woody plant succession.

The Importance of Wet Meadows on Shorelines and Floodplains: An Overlooked Type of Wetland

There is a particular type of marsh vegetation that we think deserves added mention, as it likely contain species that are good indicators of the active, non-equilibrium relationships between water levels and plant diversity. These are ‘wet meadows’ or ‘marsh meadows.’ They often have high plant diversity and many rare species. Wet meadows occur near the upper edge of marshes, near the transition zone to woody vegetation. Hence, wet meadow plant species will generally be less flood-tolerant than emergent marsh plants but more drought-tolerant. Wet meadow plants are particularly sensitive to reductions in water-level fluctuations because of the consequent encroachment of woody vegetation and emergent marsh. Two example species that occur in wet meadows along rivers are *Pedicularis furbishiae* and *Sabatia kennedyana*, the former being endangered in the United States of America and the latter being endangered in Canada.

Plant diversity is high in wet meadows, but it rapidly declines with increasing biomass. In studies of wet meadows from eastern North America, high plant diversity occurred only at low biomass, the critical limit being biomass less than 400 g/m^2 (Moore and Keddy 1989; Moore et al. 1989; Wisheu and Keddy 1989). For instance, low biomass wet meadows sometimes had more than 20 species in a quadrat measuring only one quarter square meter, and such quadrats sometimes included 6 or 7 rare plant species (Wisheu and Keddy 1989). In quadrats with higher biomass, a few species of larger clonal graminoids dominate the vegetation, such as *Calamagrostis canadensis*, *Schoenoplectus americanus*, and *Carex aquatilis*. Similar patterns of higher plant diversity and rare species in low productivity wetlands are well-documented in European wetlands (Ellenberg 1985) and in English fens (Wheeler and Giller 1982). This pattern is true for grasslands overall (Grime 1973).

Why, in wet meadows, does lower biomass vegetation have high plant diversity? It seems reasonable to conclude that high diversity and low biomass vegetation in wet meadows is the result of early successional processes and low competition, occurring shortly after flood-pulse disturbances, before graminoids become dominant, and before woody plants finally replace those graminoids. This is consistent with general models that describe how plant diversity is controlled by the balance between rates of natural disturbance and rates of recovery from that disturbance (Huston 1979). Thus, while our TLMM model deals primarily with the outright loss of marshes that occurs with the removal of flood pulses, it is also important to consider a secondary effect, that reduced flood pulses will also change the species composition of the remaining marshes. Compositional changes may be more problematic when clonal invasive species such as *Phragmites australis* or *Typha angustifolia* are present (Tulbure et al. 2007; Wilcox et al. 2008).

Conclusion

There is considerable evidence that loss of wetlands can be caused by reduction in flood pulses, and that this problem is global in scale. This arises because the zonation commonly observed on shorelines is not necessarily in equilibrium with current water levels but likely shows substantial lag effects. When the lag effects are lost, marsh area declines. While all marshes are susceptible, it may be the upper elevations of marshes known as ‘wet meadows’ that are particularly at risk, since occasional flood peaks no longer remove encroaching woody plants from shorelines. This may provide a context for understanding why species including *Pedicularis furbishiae* and *Sabatia kennedyana* are now endangered. That is, these two species, like the proverbial canary in the coal mine, may illustrate a much broader problem in shoreline wetlands overall. The Twin Limits Marsh Model provides mechanistic insight into why this problem has arisen and may serve as a tool for forecasting the impacts of proposals to further alter flood pulses in lakes and rivers.

Acknowledgments We thank Scott Painter for first translating the ideas of Keddy and Reznicek (1986) into simple rules that could be used for ecological prediction. We also appreciate early work by Paul Catling and Tony Reznicek that document the extremely high plant diversity of Great Lakes shorelines, as illustrated by work such as *The Flora of Long Point*. We appreciate Ron Huffman’s detailed letter on woody plants in the Ottawa National Wildlife Refuge on Lake Erie. This project was completed without grant support, and without salary, for either of the authors.

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