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Small Changes in Flooding Have Large Consequences: Experimental Data from Ten Wetland Plants

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Abstract Flooding regime is a major determinant of vegetation composition in wetlands. Flooding regimes are also commonly altered by human activity. We used an experimentally-created elevation gradient on mineral soil to measure the responses of ten common marsh species to flood regimes ranging from 0 to 100 % of the growing season. We asked three questions. (1) What are the minimum and maximum tolerances of these ten species to a flood duration gradient? (2) Is there one duration of flooding that is physiologically optimal for a majority of the species? (3) How sensitive are these species to minor changes in flood duration? We found that the number of species, the cover and the aboveground biomass were highest when flood duration was less than a third of the growing season. All species showed a pattern of inclusive fundamental niches for flooding duration, with a preference for shorter periods of flooding, for less than a third of the growing season. Narrow-leaved graminoids became relatively more common with longer flooding duration. This study challenges our notions of the fundamental niches of these wetland emergent plants. Other factors beyond flooding tolerance must be acting to structure wetland communities along wetland depth gradients.

Keywords Emergent plants · Flooding · Flood plains · Hydrology · Inclusive niches · *Cladium jamaicense*

Introduction

The duration of flooding is one of the most fundamental factors controlling wetland communities ((Keddy 2010; Mitsch & Gosselink 2007); Table 1). Plant zonation is widely-observed along these flooding gradients, and copiously described. Typically, we attribute this zonation to differences in flood tolerance, particularly differences in ability to tolerate hypoxic rooting conditions (Kozłowski 1984b; Mendelssohn et al. 1981; Ponnampereuma 1972; Reddy & DeLaune 2008; Sculthorpe 1967). However, such physiological interpretations tend to minimize the possible impacts of other factors affecting plant zonation along flooding gradients, including herbivory, fire, competition, mutualism and even drought. Our understanding of the effects of flooding should compare the physiological tolerances of wetland plants in the absence of these other effects, but these mechanistic data are generally not available.

The duration of flooding is also being changed systematically throughout the biosphere (Dynesius & Nilsson 1994; Nilsson et al. 2005; Poff et al. 2007), with multiple, widespread, but poorly understood consequences to wetlands (Fraser & Keddy 2005; Keddy 2010; Kuiper et al. 2014). These changes in the flooding of wetlands may be caused by water control structures like dams and levees (Kajak 1993; Keddy 2010; Middleton 2002; Shaffer & Gosselink 2005), or they may have more diffuse human causes, through the construction of road networks (Forman et al. 2002), ditching and channelization (Blann et al. 2009; Fisher et al. 1996), management of forest cover (Chang 2012) or manipulation of animal populations, either herbivores such as beaver

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Table 1 Some attributes of freshwater wetlands and wetland plants that change with flood duration, with selected references

Ecological scale	Attribute	References
Landscape/community	Area occupied by wetland plants	(Keddy 2010; Mitsch & Gosselink 2007)
	Species composition of wetland plants	(Keddy 2010; Mitsch & Gosselink 2007; Reyes et al. 2000)
	Competitive interactions among wetland plants	(Grace & Wetzel 1981; Shipley et al. 1991)
	Invasion by terrestrial plants	(Keddy 2010; Johnson 1994)
	Methane production	(Matthews & Fung 1987; Mitsch & Gosselink 2007)
	Salinity (primarily coastal areas)	(Gosselink et al. 1998; Turner 1997)
Population/individual	Sexual versus asexual reproduction	(Sculthorpe 1967; van der Valk 1981; Webb et al. 2012)
	Primary production	(Mendelssohn et al. 1981; Mitsch & Gosselink 2007)
	Leaf and stem morphology	(Sculthorpe 1967; Webb et al. 2012; Hutchinson 1975)
	Allocation to aerenchyma	(Hutchinson 1975; Sculthorpe 1967)
	Aerobic versus anaerobic respiration	(Mendelssohn et al. 1981; Sculthorpe 1967)
	Gas flow	(Kozłowski 1984a; Kozłowski 1984b; Sorrell and Hawes 2010)

(Naiman et al. 1988) or top predators such as alligators (Keddy et al. 2007).

What are the actual consequences of these shifts in flooding regimes for wetland plants? Evidence comes mainly from two types of sources (for review see Webb et al. 2012). The first source tends to be descriptions of changes in composition in wetlands after the construction of dams and levees. Global examples include boreal rivers in Sweden (Jansson et al. 2000), the Yamuna River in India (Chauhan & Gopal 2005) and the Murray River in Australia (Robertson et al. 2001), while North American examples include the Mackenzie River (Rosenberg & Barton 1986), the Mississippi River (Shaffer & Gosselink 2005), and the Platte River (Johnson 1994). Similar large scale changes in vegetation composition are found in non-riverine wetland types where flow and pulsing has been altered, ranging from temperate marshes along the shorelines of the Great Lakes (Keddy & Reznicek 1986) to subtropical marshes of the Everglades (Newman et al. 1996). All of these examples show similar trends—major changes in plant composition after flow and flooding patterns are altered. The second major source of evidence is from fine scale experimental studies of one or a few species, usually in containers, which generally show that increased duration of flooding reduces plant growth (Howard & Mendelssohn 1995; Kozłowski 1984a). In between these extremes, there lies a considerable area of unanswered questions.

One important class of data sets has been poorly represented: the relative flood tolerance for large sets of plant species measured under controlled conditions. Comparative data from controlled experiments are essential for understanding wetlands and for building mechanistic

models. Few data sets on flooding tolerances have been collected across larger numbers of species, mostly for seedlings of marsh and wet meadow species in North American and Europe (Banach et al. 2009; Fraser & Karnezis 2005). The scarcity of such data for wetland taxa may be ascribed to several causes. First, it is easiest to describe field distributions, much harder to manipulate them. Second, the experimental effort increases with the number of species, so most studies focus upon a single species, and therefore do not provide a comparative context for interpreting the ecological significance of the patterns found. Third, when flooding is experimentally manipulated, only a few selected flood regimes are usually created. Fourth, when flooding is experimentally manipulated, water levels are normally fixed at standard levels, whereas fluctuating water levels that are more typical of natural wetlands are not included. Hence, while we have a growing list of single species experimentally grown under one or a few flood regimes, broader comparisons have been strictly limited.

Our objective in this study was to investigate the multi-year comparative response of ten wetland species grown experimentally along a flooding gradient extending from 0 to 100 % flooding during the growing season. This approach allows comparisons of physiological tolerances when other factors such as fire, herbivory and competition are kept minimal. The species we used are common across southeastern North America, and in some cases, can produce large areas of relatively homogeneous vegetation—particularly in the case of *Cladium jamaicense*, *Panicum hemitomon*, as well as with *Schoenoplectus americanus*, *Peltandra virginica* and *Pontederia cordata*. Yet our knowledge of the comparative ecology of these species is limited. We asked three questions. (1) What are the minimum and maximum tolerances of these ten common species to a flood duration gradient when they are grown in monoculture? (2) Is

there one duration of flooding that is physiologically optimal for a majority of the species? (3) How sensitive are these species to minor changes in flood duration?

Methods

The experiment took place on the campus of the Southeastern Louisiana University (30° 31.4' N, 90° 28.4' W; 11 m elevation) between 2002 and 2005. Mean annual temperature is 19.3 °C, with January and July means of 9.5 and 27.6 °C, respectively, and a mean annual precipitation of 159.1 cm (1981–2010 normals, Hammond 5E, LA, 10 km E; NCEI 2015). Annual temperature and precipitation from 2002 to 2005 were within one standard deviation of the normals, except for 2003 which received 193.6 cm of rain (NCEI 2015).

We built a 60 m by 50 m (ca 0.3 ha) pond during summer 2002, with the south and east shorelines smoothly graded to a 33 % slope. We spread a layer of topsoil ~10 cm thick over the smoothed surface. We then constructed 75 narrow lanes perpendicular to the shoreline of the artificial pond. Each lane extended 3.66 m along the slope. The typical lane was 0.5 m wide, separated from adjoining lanes by two 4 m × 25 cm × 8 cm planks joined side to side lengthwise to form a T-shape in cross-section. The one plank that lay parallel to the soil surface provided a walkway between lanes, while the plank buried at a right angle to the walkway to a depth of 25 cm provided a barrier to rhizomes spreading between lanes. The walkway plank between every second lane also ensured sufficient space between lanes. We grouped lanes into five blocks of ten lanes and randomly assigned one of the 10 species to a lane within the blocks. We divided each lane into an elevation gradient with ten even levels, delimited by cross-piece steps on the walkways. We transplanted species into each lane at 0.25 m intervals during the summer 2002, forming monocultures within lanes along a continuous elevation gradient (Fig. 1). The lowermost level was continuously flooded during the growing season, while the uppermost level remained unflooded for the duration of the experiment (Fig. 2). Since most wetlands have natural water level fluctuations that correspond to seasonal or storm events (Keddy 2010), we artificially manipulated water levels in a cyclic fashion over the eight remaining levels of the elevation gradient. Over a period of 8 weeks, we progressively raised water levels by stages in eight steps. In the typical year, this meant three pulses of flooding during the growing season. The resulting water level gradient can be translated into the following categories, corresponding approximately to 0, 11, 22, 33, 44, 55, 67, 78, 89, and 100 % flooding during the growing season. At the end of the growing season in October, we left water levels permanently low until the following spring. On occasion tropical storms or hurricanes altered water levels, but the normal cycle was reestablished after a few days. In late August 2005, a large oak fell into the



Fig. 1 Photograph of the experimental wetland, showing lanes of monocultures of plants grown on a shoreline graded to a 33 % slope (photo credit: Randy Bergeron)

experiment during Hurricane Katrina, destroying three of the lanes in one block and our capability to manipulate the water level.

We selected 10 herbaceous emergent species for the experiment (Table 2). All are classified as obligate wetland species in the Atlantic and Gulf coastal plains (<http://plants.usda.gov>), so occur over 99 % of the time in wetlands (Tiner 1991). In selecting the species, we focused first upon two ecological properties: (1) wide geographical distribution, as determined by floras such as Godfrey and Wooten (1979); and (2) local abundance as determined by field experience, augmented with advice from local ecologists and sources such as Penfound and Hathaway (1938) and Chabreck (1972). We did not include annuals to avoid replanting, nor woody plants, since they were likely to grow too large given the size of the experiment. We purchased species from Louisiana Growers (Amite, LA). We acclimated most of them near the study area for ~6 months and then transplanted them from 1-l containers into the lanes from June–November 2002. *Sagittaria lancifolia* and *Pontederia cordata* were transplanted with bare roots. We

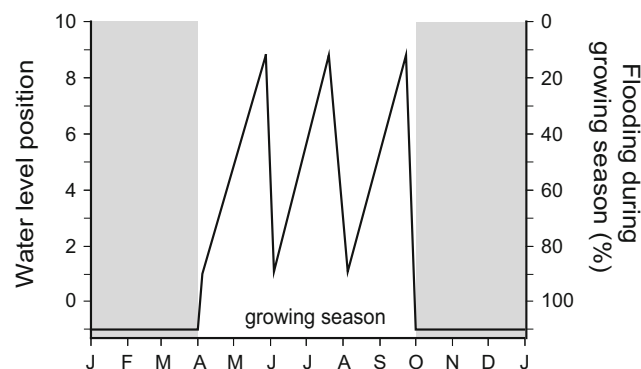


Fig. 2 Flooding regime in the experimental wetland in the 2005 season. The water level position refers to the step intervals within lanes (see Fig. 1). Water levels were cycled during the growing season from the start of April through October to create a gradient duplicating natural floods typical of heavy summer rainfall. Water levels were maintained below the experimental plots from November through March

Table 2 Species used in the experiment and their characteristics. Nomenclature follows the Integrated Taxonomic Information System (<http://www.itis.gov/>)

Species	Family	Growth Habit
<i>Acorus calamus</i> L.	Acoraceae	Short-rhizomatous perennial forb
<i>Cladium jamaicense</i> Crantz	Cyperaceae	Short-rhizomatous perennial Graminoid
<i>Juncus effusus</i> L.	Juncaceae	Bunch-forming perennial graminoid
<i>Panicum hemitomon</i> J.A. Schultes	Poaceae	Rhizomatous perennial graminoid
<i>Peltandra virginica</i> (L.) Schott	Araceae	Bunch-forming perennial forb
<i>Pontederia cordata</i> L.	Pontederiaceae	Short-rhizomatous perennial forb
<i>Rhynchospora inundata</i> (Oakes) Fern.	Cyperaceae	Rhizomatous perennial graminoid
<i>Sagittaria lancifolia</i> L.	Alismataceae	Rhizomatous perennial forb
<i>Saururus cernuus</i> L.	Saururaceae	Rhizomatous perennial forb
<i>Schoenoplectus americanus</i> (Pers.) Volk. Ex Schinz & R. Keller	Cyperaceae	Rhizomatous perennial graminoid

All species are classified as obligate wetland species in the Atlantic and Gulf Coastal Plain of North America according to the PLANTS database (<http://plants.usda.gov>)

weeded the lanes periodically to remove non-target species. Only *Panicum hemitomon* spread via rhizomes to neighboring lanes, but these occasional shoots were periodically weeded. Species were free to move up or down the slope within lanes. The effects of herbivores on the experimental species were minimal throughout the study.

To document the consequences of flooding on soil oxidation, we measured redox potential at 3 cm and 15 cm depths in one randomly chosen lane of each block on October 7 2004. This was later in the growing season, when only levels 8–10 were submerged. We used welded platinum tipped electrodes (Faulkner et al. 1989), with a saturated calomel reference electrode to obtain the actual redox potential value (Patrick et al. 1996).

We determined the presence of species and visually estimated their percent cover at each of the ten levels within a lane (0.5 m × 0.25 m) between October and November, for one growing season prior to flooding (2002) and for three growing seasons after flooding was initiated (2003–2005). In November 2005, we harvested the aboveground biomass, sorted by species and elevation, dried it to a constant weight at 80 °C and weighed it. During the last growing season, heavy rain from Hurricane Katrina temporarily raised water levels, but these changes were short term and did not visually impact biomass or plant distributions.

We addressed our three questions on flooding tolerances using four metrics for each species and lane, based on the biomass data collected in 2005. We determined the maximum and minimum flooding durations at which species survived in a lane, the flooding duration at which peak biomass occurred and the range of flooding from the difference in maximum and minimum flooding tolerance within each lane. We analyzed these four metrics using analyses of variance. We considered species as a fixed factor and block as a random factor; we did not include an interaction term in the model. We evaluated assumptions of normality and homogeneity of variance with

residual plots and used Tukey's test to determine *post hoc* significance among treatments. We set the type I error rate at 0.05. We used locally weighted scatterplot smoothing (LOWESS) with zero stiffness to determine best fit lines. All analyses conducted using STATISTICA®, version 10.

Results

Our flooding regimes created a strong redox potential gradient, with a rapid transition from aerobic to anaerobic soil conditions at the pond's water line (Fig. 3).

Survival across all these emergent wetland species and over the 3 years was highest if the flooding did not exceed 22 % of the growing season (Fig. 4a), and was almost as high if the species were not flooded at all. Beyond 22 % flooding, survival decreased almost linearly each year. The effect intensified after the second season, with less than one species on average surviving at 89 % flooding duration by the fall 2004 and 2005, and none surviving in the 100 % flooding treatment

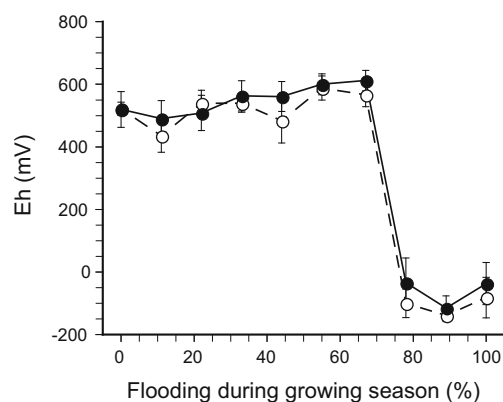


Fig. 3 Redox potential (Eh) of substrate at 3 cm (closed symbols) and 15 cm below the surface (open symbols) on October 7, 2004, when the water level was set just below the 67 % flooding duration level (mean ± SE, $n = 5$)

by the fall 2004. In a similar fashion, the mean plant cover peaked when flooding was between 11 and 33 % during the growing season over all 3 years (Fig. 4b); the non-flooded plants had just 3-5 % lower cover than those flooded for 33 % of the growing season. Cover declined steadily when flooding exceeded 33 % during the growing season; there was hardly any cover by 78 % flooding and none by 100 % flooding duration. At the end of the experiment in November 2005, mean biomass was generally similar from 0 to 33 % flooding, and then declined to low levels by 78 % flooding of the growing season (Fig. 4c).

Our intention was to create dry enough conditions upslope to kill at least some species. But all species survived with mean minimum flooding tolerances of 0 to 7 %. When species are examined separately, they did not differ in their minimum flooding tolerance (Tables 3 and 4; Fig. 5). The story is different at the wet end of the gradient. Here there were major differences in maximum flooding tolerance. Both *Sagittaria lancifolia* and *Peltandra virginica* tolerated maximum flooding duration of less than a quarter of the growing season on average. *Pontederia cordata* was nearly as sensitive and survived only in areas flooded for roughly a third or less of the growing season. *Acorus calamus* and *Rhynchospora inundata* were slightly more tolerant, with maximum flooding duration of a third to a half of the growing season. *Juncus effusus*, *Saururus cernuus*, *Schoenoplectus americanus*, *Panicum hemitomon* were tolerant to flooding of half to two thirds of the growing season and had wider niche breadth. *Cladium jamaicense* was the most tolerant, able to tolerate no flooding conditions, all the way to a flooding duration of over 80 % of the growing season. The story for the range of flooding was essentially the same as that for the maximum flooding tolerance ($r=0.97$).

When we examine the mean flooding duration at which peak biomass occurred (Tables 3 and 4; Fig. 5), both *Cladium jamaicense* and *Juncus effusus* had peak biomass under almost non-flooded conditions (5.5 and 8.8 % mean flooding respectively). However, most species had peak biomass at intermediate flooding regimes of 16 to 24 % flooding during the growing season, and biomass decreased with shorter or longer flood duration. *Schoenoplectus americanus* and *Panicum hemitomon* preferred the more flooded conditions, and attained peak biomass under 35 and 42 % mean flooding, respectively. There was no correlation between the mean flooding duration at which peak biomass occurred and the mean minimum flooding tolerance ($r=-0.28$) or maximum flooding tolerance for these species ($r=0.02$).

Discussion

Changes in water levels within and among years are a feature of most wetlands. Our study provided a standard gradient to allow us to focus upon interspecific differences among a

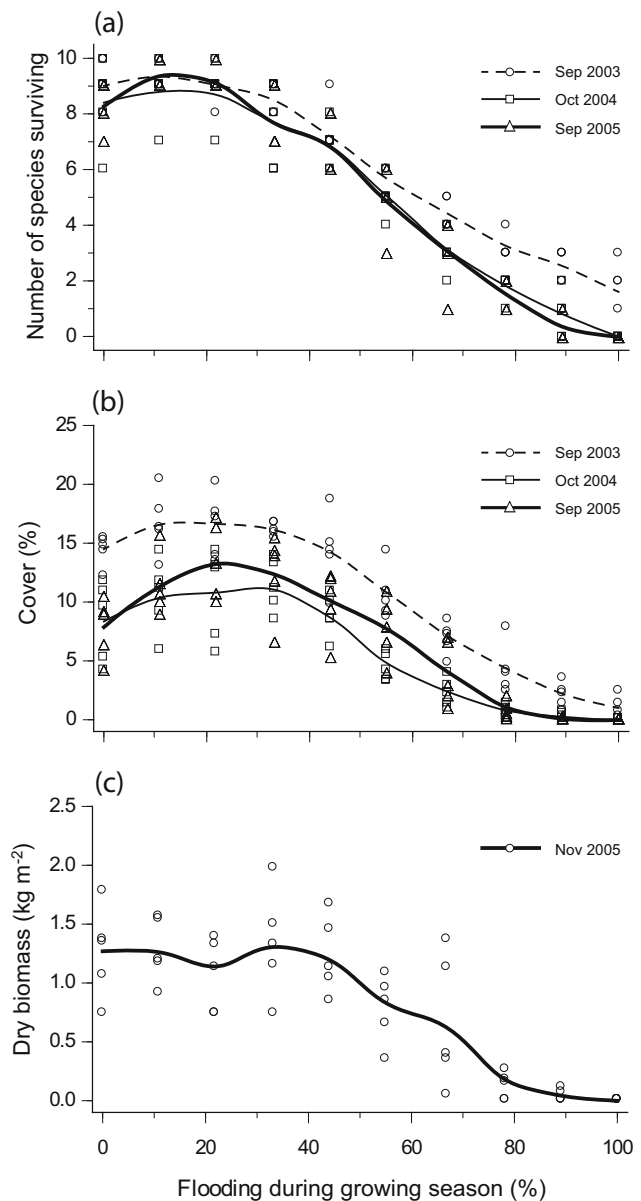


Fig. 4 Scatterplots of the **a** number of surviving species, **b** mean cover and **c** mean biomass along the flooding duration gradient over 3 years, with locally weighted scatterplot smoothing lines. The ten experimental wetland plants were each grown in monoculture, and the number of species, mean cover and mean biomass were determined within separate experimental blocks

group of common wetland plant species. The field distributions of wetland plants, of course, reflect the consequences of multiple ecological factors including flood duration, soil characteristics, rates of sedimentation, interspecific competition, and tolerance to fire and grazing (Keddy 2010; Mitsch & Gosselink 2007). We removed many of these unknown factors to document the comparative effects of flooding per se upon a set of common wetland species grown in mineral soil. This set of comparative data can be thought of as the physiological tolerances upon which other factors such as competition and herbivory are then superimposed (Ernst 1978).

Table 3 Analyses of variance of the flooding tolerance of the ten wetland species grown in monoculture based on biomass, as harvested in 2005, after 3 years of growth

Source	df	Minimum			Maximum			Peak biomass			Range		
		MS	F	P	MS	F	P	MS	F	P	MS	F	P
Block	4	25.2	0.62	0.65	142	0.77	0.55	153	1.08	0.38	228	0.79	0.54
Species	9	40.5	1.01	0.46	1775	9.62	<0.0001	607	4.3	0.0012	2119	7.29	<0.0001
Error	30	40.3			184			141			291		

Separate analyses were conducted for the minimum and maximum flooding duration tolerated, the flooding duration at which peak biomass occurred and the range of flooding duration. Significant differences are shown in bold ($P < 0.05$)

We asked three questions in this study. We first asked what the minimum and maximum tolerances are of these ‘obligate’ wetland emergent plants to a flood duration gradient when they are grown in monoculture. Our intention in designing this experiment was to create drier conditions at the upper end of the gradient to eliminate them. However, all the species survived under non-flooded conditions. Biomass for most species was reduced when they were not flooded, but several, including *Cladium jamaicense* and *Juncus effusus*, thrived. Sufficient soil moisture must have been present under the zero-flooding treatment to limit a strong drought effect, either from summer rains or soil water diffusing up the slope. However, our redox measurements show that soil flooding occurred close to the pond’s water line, so the no-flooding treatments would not have experienced soil flooding. Our experimental design prevented any competition from terrestrial or facultative wetland species plants, perhaps allowing our ‘obligate’ wetland plants to survive under non-flooded conditions. The upper edges of flooding gradients normally support a larger number of less flood-tolerant, facultative wetland or terrestrial species, including woody plants (Keddy 2010;

Kozłowski 1984a; Timoney & Argus 2006). Competition with these more terrestrial plants may be driving these common wetland species down the shoreline into flooded environments. If this is generally true, it may be that competition from upland plants is what makes these species ‘obligate’ wetland plants (Keddy 1989; Keddy 2010). That is, flooded conditions provide a refugium, and so one might suggest that ‘obligated’ is a more accurate characterization of their wetland preference instead of ‘obligate’.

Another general observation is the greater amount of variation in maximum flooding tolerances among species. As flood duration increased, fewer species were present. There was a consistent shift from broad-leaved species towards narrow-leaved species. Only graminoids (*Cladium jamaicense*, *Panicum hemitomon*, *Schoenoplectus americanus*, *Juncus effusus*) and one broad-leaved species (*Saururus cernuus*) persisted when flooding exceeded half the growing season, and no species was able to tolerate continuous flooding during the growing season. Longer flooding regimes may provide an explanation for the nearly monospecific stands of graminoids sometimes seen in floodplains, in coastal marshes and in areas

Table 4 Flooding tolerance parameters of the ten wetland species (mean ± SE) when grown in monoculture after 3 years, with the minimum flooding duration tolerated, the maximum flooding duration

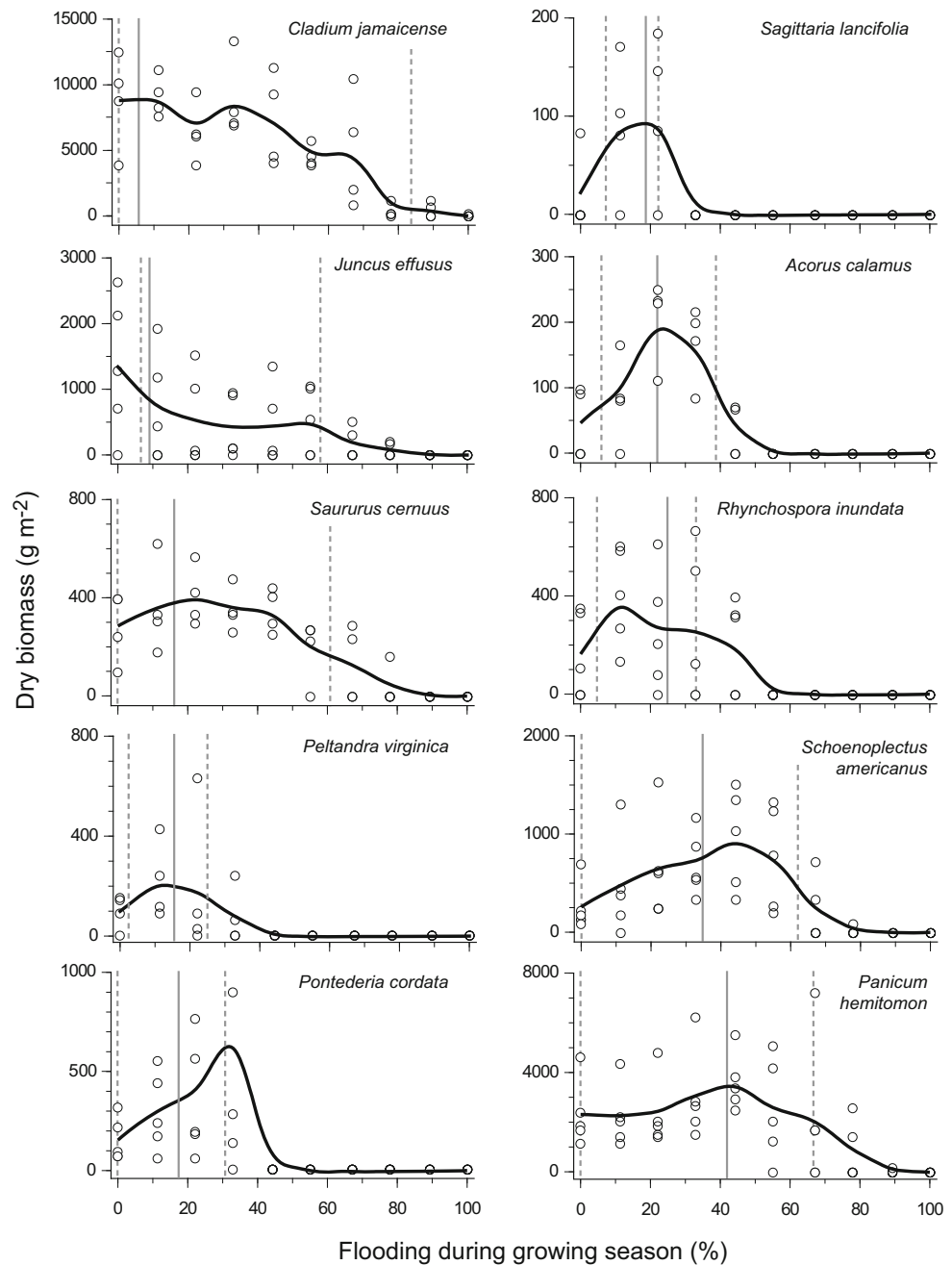
tolerated, the flooding level at which peak biomass occurred and the range of flooding. Flooding duration is expressed as the percent of the growing season under flooded conditions

Species	n	Minimum			Maximum			Peak biomass			Range		
		Mean	SE	Group	Mean	SE	Group	Mean	SE	Group	Mean	SE	Group
<i>Cladium jamaicense</i>	4	0	0	a	83.5	7.1	e	5.5	3.2	a	83.5	7.1	e
<i>Juncus effusus</i>	5	6.6	6.6	a	57.6	9.0	bcde	8.8	6.4	a	51.0	14.4	abcde
<i>Saururus cernuus</i>	4	0	0	a	61.0	7.4	bcde	16.5	3.2	ab	61.0	7.4	bcde
<i>Peltandra virginica</i>	4	2.8	2.8	a	24.8	5.3	a	16.5	9.5	ab	22.0	6.4	ab
<i>Pontederia cordata</i>	5	0	0	a	30.8	2.2	ab	17.6	6.6	ab	28.6	2.7	abc
<i>Sagittaria lancifolia</i>	3	7.3	3.7	a	22.0	0.0	a	18.3	3.7	ab	14.7	3.7	a
<i>Acorus calamus</i>	4	5.5	3.2	a	38.5	3.2	abcd	22.0	0.0	ab	33.0	6.4	abcd
<i>Rhynchospora inundata</i>	5	4.4	2.7	a	33.0	7.0	abc	24.2	6.4	ab	28.6	8.2	abc
<i>Schoenoplectus americanus</i>	5	0	0	a	62.0	4.6	cde	35.2	6.4	b	62.0	4.6	cde
<i>Panicum hemitomon</i>	5	0	0	a	66.6	8.0	de	41.8	2.2	b	66.6	8.0	de

Species are ordered by the mean flooding level of peak biomass

Groups show significant differences based on Tukey’s *post-hoc* tests ($P < 0.05$)

Fig. 5 Scatterplots of the biomass of ten wetland species grown in monoculture along a flooding duration gradient after 3 years, with locally weighted scatterplot smoothing lines. The right and left grey dotted lines show the mean minimum and mean maximum flooding duration tolerated by the species. The central solid gray line is the mean flooding duration at which peak biomass occurred. Species are ordered by the mean flooding duration for peak biomass



with sheet flow such as the Everglades (Chabreck 1972; Newman et al. 1996).

In our second question, we asked if there was one duration of flooding that is physiologically optimal for a majority of the species. The majority had peak biomass when flooding was relatively short, from 8 to 24 % of the growing season, on average. *Schoenoplectus americanus* and *Panicum hemitomon* preferred the most flooded conditions, but they still grew best if flooded for only 35 and 42 % of the growing season, respectively. The number of plant species, the plant cover and the overall biomass also showed that these species shared physiological preference for relatively short periods of

flooding, a third or less of the growing season. It is clear that these emergent plants show an inclusive structure for their fundamental niche (Keddy 2010), with a preference towards shorter duration of flooding.

Finally, we asked how sensitive these emergent wetland species are to minor changes in flood duration. About half of the species had narrow fundamental niches, as measured by their ranges of tolerance to flooding. Increases in flooding of >25–33 % of the growing season would have major changes in plant composition for these species. For example, a shift in flood duration from 25 to 33 % of the growing season would eliminate *Sagittaria lancifolia* and a shift from 33 to 44 %

flooding would almost eliminate four common wetland plants, *Peltandra virginica*, *Acorus calamus*, *Pontederia cordata* and *Rhynchospora inundata*. The other five species had wider fundamental niche breadth in flood duration and were less sensitive to small scale shifts in flooding duration.

This study was explicitly not designed to test a mechanistic or physiological explanation for the observed patterns, apart from removing obvious factors such as variation in soil type and interspecific competition. Yet the patterns, such as the relative lack of tolerance to flooding in species such as *Pondetaria cordata*, *Peltandra virginica*, *Sagittaria lancifolia* and *Acorus calamus*, or the preference of all the study species for short duration flooding, challenged our pre-conceptions about the ecology of these 'obligate' wetland species. Several hypotheses might be offered to account for this result.

The first 'explanation' might be that there is nothing to explain. Our perception of *Peltandra virginica*, *Pontederia cordata*, and *Sagittaria lancifolia* as highly flood-tolerant species may be incorrect. *Sagittaria lancifolia* appears to be one of the less flood tolerant species of native *Sagittaria*; it rarely grows as an emergent unlike, say, *Sagittaria latifolia*, but often occurs in wet meadows and marshes where dry periods alternate with wet, such as coastal tidal marshes (Grace & Ford 1996). One might conclude that most of these species are in fact species of wet meadows rather than species found in standing water, and their restriction to areas flooded for less than a third of the growing season is therefore reasonable and consistent with current knowledge. The preference of emergent species for low degrees of flooding is in agreement with other studies. Two comparative studies of seedlings of marsh and wet meadow species show higher survivorship and biomass in non-flooded treatments (Banach et al. 2009; Fraser & Karnezis 2005), findings that are generally consistent with van der Valk's model for mud-flat regeneration of wetland plants during low water (van der Valk 1981). Physiological studies of gas flow show that adult emergent species generally prefer less flooding (Sorrell & Hawes 2010). A systematic review of the flooding tolerances of wetland species also concluded that there is generally better performance under low flooding conditions (Webb et al. 2012). These patterns suggest that additional factors cause the zonation of species seen along water depth gradients; competition is likely involved, with stronger competitors occupying the less flooded conditions (Geho et al. 2007; Grace & Wetzel 1981).

Alternatively, one might hypothesize that the absence of one or multiple factors in our study modified the relative flood tolerance of some species. First, our plants may have had excessive light. For instance, in our experience, *Peltandra virginica* and *Saururus cernuus* often occur in wetter sites beneath a tree canopy, so with more shade than in our study. Second, our experiment may have produced intense hypoxia. The roots of neighboring plants might normally assist in oxidizing the substrate during periods of standing water (Bertness

& Hacker 1994; Bertness & Yeh 1994), and without this facilitation, conditions may have become too harsh for our plant species. Third, smaller isolated plants may be less tolerant of flooding than large patches or clones. Groups of shoots, even when not linked by rhizomes, may collectively oxidize the substrate, an interspecific mutualism similar to that described for shrubs benefiting neighboring plants. In the case of clonal plants, the foregoing mechanism may occur, and in addition, the lateral movement of oxygen through rhizomes among stems of differing ages may reduce hypoxia (e.g., Armstrong et al. 1996). It is also possible that plant height was a factor, since taller plants, such as *Cladium jamaicense*, would have had longer periods of direct access to the atmosphere for oxygen transport to rhizomes. Fourth, the substrate of many shorelines and wetlands are more organic than those used in this experiment. Pearsall (1920) first suggested that plant zonation on shorelines might be more affected by soil type than water depth. Sorrell and Hawes (Sorrell & Hawes 2010) showed that sediment characteristics affect flooding tolerances among species. Willis and Hester (Willis & Hester 2004) report that *Panicum hemitomom* had significantly higher productivity in mineral than organic soils.

It is also possible that fluctuating water levels, while closer to reality, may have produced some unexpected consequences. In particular, the periodicity of flooding may have reduced the formation of aerenchyma, and thereby reduced the capacity to withstand flooding. This pattern is consistent with one we have observed in some reservoirs, where wetland plants are relatively uncommon, and the occasional low water periods provide conditions for ephemeral species (e.g., Hill & Keddy 1992; Hill et al. 1998). While this possibility offers a mechanism and is consistent with patterns seen in the field, it does not explain the lack of occurrence of these species at the lowest water levels where flooding was continuous or near-continuous.

The fluctuation in water levels may have had another impact—it might have provided conditions that increased the flood tolerance of *Cladium jamaicense* and *Panicum hemitomom* relative to the other species in the experiment. These two species may be able to grow rapidly during short periods of drawdown. As noted above, their relatively tall growth form may allow them to emerge from the water and continue to oxidize the rooting zone even when partially flooded, thereby reducing the duration of hypoxic soil conditions, and the apparent duration of the flooding. The interconnection of rhizomes may allow also transport of oxygen from higher elevations to lower elevations.

There is an alternative hypothesis with opposite predictions—that the fluctuations in water level increased sensitivity to flooding, by preventing physiological and morphological acclimation to flooding. There is equally the possibility that these two effects cancelled each other out, and therefore document the relative flood tolerances of these important and widespread native plants.

Overall, we suggest that future experiments on flood tolerance will need to include fluctuating as well as standing water. The consequences of long periods of flooded conditions with short dry periods during the growing season, and short periods of flooding with long dry periods, might be particularly worthy of evaluation.

Conclusions

Our results provide comparative information on the flood tolerances of ten species that are widespread in wetlands across southeastern North America, including wetlands of the Mississippi River Delta and the Everglades. Our data show that most cannot tolerate continuous flooding, and show maximum growth of biomass when flooded for less than one-third of the growing season. Our results document that even apparently minor changes in flood regime can cause significant mortality and significant changes in plant species composition.

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