

The Roles of Competition and Facilitation in Producing Zonation Along an Experimental Flooding Gradient: A Tale of Two Tails with Ten Freshwater Marsh Plants

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Independent

Research Article

Keywords: freshwater marsh, emergent macrophytes, flooding stress, competition, facilitation, Stress Gradient Hypothesis.

Posted Date: September 20th, 2021

DOI: <https://doi.org/10.21203/rs.3.rs-874951/v1>

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Version of Record: A version of this preprint was published at Wetlands on January 1st, 2022. See the published version at <https://doi.org/10.1007/s13157-021-01524-4>.

Abstract

Plant zonation is conspicuous in wetlands. The cause is frequently assumed to be the direct physiological effects of physical factors (termed ‘stress’), however many experiments show that competition and facilitation also cause zonation patterns. We conducted a field experiment with freshwater marsh emergent plants to test the causes of zonation along a single stress gradient: flooding duration. We constructed an experimental wetland with ten flooding levels to ensure that the environmental conditions represented the full range of potential flooding levels, from never flooded to continually flooded. We planted ten common marsh plants with varied ecology along the flooding duration gradient. We grew them alone and in mixture for three years and measured changes in the minimum and maximum limits, the mode and the range of distribution, and interaction importance. The mode of distribution did not shift, whether species were grown alone or with neighbours. We found strong effects of competition under low flooding stress. We found no effects from facilitation under high flooding stress. Flooding duration alone controlled the lower limits of plants. The effects of competition were intense enough to eliminate half of the species within three growing seasons. Our experiment showed that competition and physical stresses, but not facilitation, controls the zonation of emergent macrophytes along a flooding duration gradient, at least in freshwater wetlands. Models guiding wetland restoration need to include competition as well as flood duration as causal factors, but not facilitation.

Introduction

The zonation of plants along wetland gradients is widespread and well-described (Keddy 2010). Shoreline gradients have been compared to a prism that sorts plant communities into different functional groups and species. The simplest explanation is also the oldest: that changes in species composition along a gradient are a direct consequence of changes in physical stresses, such as flooding or salinity, that act directly upon plant growth (e.g., Penfound and Hathaway 1938; Chabreck 1972). (By ‘stress’, we follow the definition of Grime (1989) as the “external constraints limiting the rates of resource acquisition, growth or reproduction of organisms”). Field and lab experiments, however, have repeatedly shown that species interact along these same physical stress gradients through competition, facilitation and even herbivory (e.g., Pennings and Callaway 1992; Bertness and Hacker 1994; Grace and Ford 1996), and these interactions contribute to plant zonation. The Stress Gradient Hypothesis (SGH) summarizes these interactions and theorizes that competition among plants is important in habitats with low environmental stress, while facilitation is more important where high physical stress or high consumer pressure prevail (Bertness and Callaway 1994). The SGH has broad support (He et al. 2013).

Terrestrial plants segregate along hydrological gradients because of edaphic constraints (Silvertown et al. 2015). In wetlands, these edaphic constraints are extreme; the principal stress to plants is the duration of flooding (Reddy and DeLaune 2008; Nakamura and Noguchi 2020). Upon flooding, soil organisms deplete oxygen supplies. Soils become rapidly anoxic, then increasingly reduced as flooding duration extends. Low redox conditions not only interfere with root respiration, but also change substrate chemistry and nutrient cycling and even produce toxic compounds in the rooting zone, such as hydrogen

sulphide and reduced forms of manganese and iron (Pezeshki 2001; Reddy and DeLaune 2008; Lamers et al. 2013). Flooding directly reduces plant survival and growth (Pezeshki 2001; Garssen et al. 2015) and has secondary effects for soil nutrient content and nutrient uptake. Many wetland species escape hypoxia through anatomical or physiological mechanisms, such as the production of aerenchyma which brings oxygen to the flooded roots, while other species cease growth and become quiescent (Nakamura and Noguchi 2020). Additional stresses may accompany flooding, related to the mechanical impacts of submersion and wave action, the chemistry of the water itself, and changes in light quality with water depth (Sculthorpe 1967; Spence 1982).

There is strong evidence that competition affects the distribution of plants along flooding stress gradients, especially under less flooded conditions. Here are four examples. In an early experiment, Ellenberg (1953) grew six species of grass along a moisture gradient and concluded that all of them could grow along the entire gradient in monoculture, but that wetland species are displaced into wetter sites. Grace and Wetzel (1981) grew two common species of cattail (*Typha* spp.) along a flooding gradient and reported that *T. latifolia* displaces *T. angustifolia* into deeper water. Lenssen et al. (1999) used removal experiments to test for competition effects in wet meadows in the Netherlands, concluding that “species richness of freshwater shorelines is controlled by abiotic factors in the frequently flooded zone and by plant interactions at higher elevations”. More recently, in tidal brackish marsh, Schile et al. (2017) found that competition among emergent macrophytes increased under less flooded conditions.

Facilitation among plants has also been encountered along flooding stress gradients. Several studies in New England salt marshes demonstrated that saltmarsh rush (*Juncus gerardii*) facilitates the growth of other plant species less tolerant to hypoxic conditions and higher salinity levels found in more flooded salt marsh (Bertness and Hacker 1994; Bertness and Yeh 1994; Hacker and Bertness 1995; 1999). Emergent macrophytes also facilitate the establishment of mangrove seedlings in coastal wetlands (McKee et al. 2007). The mechanism appears to be oxygen leakage from the roots of flood-tolerant plants that raises soil redox potential (Armstrong 1964; McKee et al. 1988; Hacker and Bertness 1995; Callaway and King 1996; McKee et al. 2007; Silliman et al. 2015), which allows less flood-tolerant plants to survive more flooded conditions. However, stress gradients in salt marshes are complicated because they combine at least two causal stresses: flooding and salinity. The flooding gradient is further complicated by tidal fluctuation. Guo and Pennings (2012) also reported facilitation in saltmarsh sites with high flooding and salinity, but they could not tease these stresses apart.

The mechanisms that cause zonation are not only theoretical questions. They have important consequences for the management and restoration of wetland communities. Consider wetland models used in the Everglades (Sklar et al. 2005) and in coastal restoration in Louisiana (Visser et al. 2004). Both regions have suffered wetland losses and are now threatened by rising sea levels. Both models also assume direct control from physical factors, principally flooding, nutrients and salinity. If, however, the upper elevational limits of species are also controlled by competition, and the lower elevational limits by facilitation, then models linking vegetation to flooding may be unreliable. Or consider efforts to harness the process of facilitation among plants along wetland flooding gradients to promote coastal restoration

(Silliman et al. 2015; Renzi et al. 2019). If incorrect, wetland restoration projects may be based upon false assumptions of causation.

We set up an experiment to explicitly test which mechanisms control zonation in freshwater marshes using a controlled gradient of flooding duration stress. We emphasize that we focussed upon a single causal factor: flooding duration. We tested alternative hypotheses for species distribution along the flooding gradient: (1) no effects of neighbours (direct physiological responses to the flooding), (2) competition and (3) facilitation. To maximize generality, we used ten marsh species, many of which have wide geographical distributions in North America (Table 1). The United States has a pool of more than 2000 obligate wetland species (USACE 2018), and it is not uncommon to find ten of them growing along natural flooding gradients (Chabreck 1972; Keddy 2010). Our species included dominant graminoids, such as sawgrass (*Cladium jamaicense*) and bulrush *Schoenoplectus americanus*), but it also included presumed interstitial species (sensu Boutin and Keddy 1993) with clumped or short rhizomatous growth form, such as arrow arum (*Peltandra virginica*) and pickerelweed (*Pontederia cordata*).

Table 1
Species used in the experiment.

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

Our main intention was to experimentally test for overall patterns among all ten species. However, ecologists still often think about competition or facilitation as occurring between pairs of species. We

therefore added three pairwise comparisons to provide information about interactions among different functional types of emergent macrophytes: dominant and interstitial species (Boutin and Keddy 1993).

Materials And Methods

The experiment took place between 2002 and 2005 in a 0.3 ha experimental wetland on the campus of Southeastern Louisiana University ($30^{\circ} 31.4' N$, $90^{\circ} 28.4' W$; 11 m elevation; Campbell et al. 2016). Mean annual temperature was $19.3^{\circ}C$, with January and July means of $9.5^{\circ}C$ and $27.6^{\circ}C$, respectively, and mean annual precipitation was 159.1 cm (1981–2010 normals, Hammond 5E, LA, 10 km E; NCEI 2020). From 2002 to 2005, annual temperature and precipitation were within one standard deviation of these normals, except for 2003, which received 193.6 cm of rain.

We smoothly graded the northeast and southeast shorelines to a 33% slope (Fig. 1). We built 75 0.5 m wide lanes with lumber, perpendicular to the shoreline, grouped into five blocks. Each lane extended 3.66 m along the slope into the pond and was separated from adjoining lanes by two 4 m by 25 cm by 8 cm planks and wooden walkways. Since many wetlands along the Gulf Coastal plain arise in floodplain sediments deposited by rivers, and also occur in loess landscapes, we aimed for relatively fertile conditions, and therefore also spread a ~10 cm layer of topsoil, bringing the surface ~5 cm below the timber framework. We divided each lane into 0.5 by 0.25 m cells along the elevation gradient into which we planted plants.

We selected ten species of herbaceous perennial emergent plants classified as obligate wetland species in the Atlantic and Gulf coastal plains (USACE 2018; Table 1), so they occur over 99% of the time in wetlands. These species have wide geographical distributions and are also abundant locally in wetlands (Penfound and Hathaway 1938; Chabreck 1972). We purchased plants from Louisiana Growers (Amite, LA) in 1 L containers or as bare root seedlings (*Sagittaria lancifolia* and *Pontederia cordata*) and planted them from June–November 2002 into each cell. We planted them as (1) monocultures (ten species, $n = 5$); (2) mixtures with all ten species planted in each cell, with two multi-species mixture treatments per block ($n = 10$) and (3) three mixtures of two species ($n = 5$). For pairs, we chose (i) *Cladium/Panicum*, two graminoids that we judged to be likely ecological dominants; (ii) *Peltandra/Pontederia*, two clump-forming species that we judged were likely interstitial species (sensu Boutin and Keddy 1993); and (iii) *Panicum/Pontederia*, a mixture of a presumed dominant and a presumed interstitial species.

All plants remained non-flooded until spring 2003 to allow them to establish. We weeded the lanes periodically to remove non-planted species.

We began flooding cycles in April 2003. The lowermost cell was continuously flooded during the growing season, while the uppermost cell remained unflooded. We artificially manipulated water levels over the eight remaining cells in a cyclic fashion along the elevation gradient by progressively raising water levels by stages, each stage lasting approximately one week. In a typical year, this meant three flooding pulses over the growing season. Cells consequently received 0, 11, 22, 33, 44, 55, 67, 78, 89, and 100 percent

flooding over approximately 6.5 months during the growing season. 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 (Campbell et al. 2016). At the end of the growing season in October, we left water levels permanently low until the following spring. On occasion, large precipitation events altered water levels, but the normal cycle was re-established after a few days. The experimental pond had low fetch (< 60 m), so there was no wave erosion associated with our flooding gradient. In late August 2005, a large oak fell into the experiment during Hurricane Katrina, destroying three of the lanes in one block and our ability to manipulate the water level, so we ended the experiment in the autumn 2005.

To avoid destructive sampling, we visually estimated the cover of each species in each cell prior to flooding (November 2002) and for three growing seasons after flooding was initiated (September 2003, October 2004, September 2005). In November 2005, we harvested the aboveground biomass, sorted by species and elevation, dried it to a constant mass at 80°C and weighed it.

We analysed the data with R (version 4.0.2) using linear or generalized linear mixed-effects models with the packages *lme4* and *glmmTMB* (Bates et al. 2015; Brooks et al. 2017). We evaluated competing models with AIC and checked residuals using DHARMA (Hartig 2020; code available in Supplemental Materials).

We first examined the number of surviving species along the flooding gradient for each year separately. We compared the number of surviving species per block in the ten monoculture lanes grouped together against the two mixture lanes as a function of the presence and absence of neighbours, with the extent of flooding as a repeated measure. We used a generalized Poisson distribution because of problems of over or under dispersion.

We then evaluated the changes in distribution of species with flooding using four metrics, based on our data for cover in each cell in autumn 2003, 2004 and 2005: (i) the minimum and (ii) the maximum flooding limit at which species survived in a lane, (iii) the range of flooding from the difference in maximum and minimum flooding tolerance, and (iv) the mode of the flooding distribution at which peak cover occurred. We minimally rescaled these variables, so they fell just above 0 and below 1 (Smithson and Verkuilen 2006), and we tested the overall effect of neighbours on each of these rescaled metrics, with the presence/absence of neighbours as the main effect and year as a repeated measure within lanes, while ignoring the identity of species. If a species did not survive in mixture, we removed the species from this overall test, leaving ten species in 2003, eight in 2004 and only five in 2005. We evaluated models with a beta distribution with or without zero augmentation and with constant or variable dispersion (Douma and Weedon 2019). We then examined for effects of the presence and absence of neighbours and species on these metrics, separated by year because of the decreasing survival of species in the mixture plots, with blocks as the random factor, and with the same beta distribution models. We used Tukey tests to examine post hoc differences.

To further evaluate the importance of competition versus facilitation along the flooding gradient, we also determined the additive interaction importance index ($Nlmp_A$; Diaz-Sierra et al. 2017) using the final biomass data. $Nlmp_A$ is a standardized and symmetric index that examines the difference of a species' performance between mixtures and monocultures, relative to the species' best performance. The largest biomass per cell across all blocks was used as to determine a species' best performance. We analysed $Nlmp_A$ separately for each species against flooding levels, with block as a random variable.

The analysis of the two species mixtures was similar. We could not conduct analyses of survival because of problems of model convergence or lack of variance at many flooding levels. We analysed the flooding statistics (minimum, maximum, range and mode) for each pairing by the presence or absence of neighbours, species and year within lanes, again using beta distributions. We also again calculated and analysed $Nlmp_A$ along the flooding gradient.

Results

When grown alone, all species were able to survive in at least one of the elevations along the gradient over the entire three-year duration of the experiment (Online Supplementary Figs S1-S2). Growth generally declined with flooding, but all species were able to tolerate flooding between 11 and 44 percent of the growing season. The highest number of species occurred at the elevation with slight flooding – less than 22 percent of the growing season. When grown in mixture, the species distributions were visually different, and several species did not survive past the first or second flooding season.

Growing with many neighbours: Survival

In the autumn 2002, before we flooded the experiment, all ten species survived evenly in cells across the elevation gradient when grown in monoculture (Fig. 2a). Slightly but significantly fewer species survived when grown in multi-species mixture (8.2 species on average; $P=0.0002$), but they also survived evenly along the elevation gradient ($P=0.82$), without any interaction ($P=0.11$; Online Supplementary Table S1; Fig. 2b).

In autumn 2003, after just one growing season of flooding, survival decreased along the flooding gradient, but it depended on whether plants were grown with neighbours or not ($P=0.0013$). When grown in monoculture, 8.6 species on average survived when they were flooded for 33% or less of the growing season, and survival declined with increasing flooding duration. When species were grown in multi-species mixtures, at most 4.8 species on average survived, again declining with more flooding duration.

In autumn 2004, after two growing seasons, survival differed strongly between monoculture and mixture lanes ($P<0.0001$) and generally decreased with greater flooding ($P<0.0001$), without an interaction ($P=0.11$). In monoculture, survival was like 2003, except that no species survived 100% flooding. In mixture, species survival at elevations with 44% or less flooding declined to 3.1 species on average. *Rhynchospora* and *Schoenoplectus* completely disappeared in mixture, and *Sagittaria* and *Pontederia* barely survived.

By autumn 2005, the third year, survival again declined when species were grown in mixture ($P < 0.0001$) and under more flooded conditions ($P < 0.0001$), and again without an interaction ($P = 0.12$). The most species, 2.9 species on average, survived in cells with no flooding. *Acorus*, *Sagittaria* and *Pontederia* almost or completely disappeared in mixture, leaving only five species. *Cladium* and *Panicum* dominated, *Saururus* survived in all mixture lanes, and *Juncus* and *Peltandra* barely survived in a few mixture lanes.

In summary, across all species, species mortality increased with flood duration. After only three years, just five of our original ten species survived when grown in mixture. At this point, the experimental wetland was dominated by just three species: *Cladium*, *Panicum* and *Saururus*.

Growing with many neighbours: Overall test

Growing with neighbours had a strong effect on the minimum flooding limit (upper end of the gradient) when species identity is not considered ($P < 0.0001$; Online Supplementary Table S2). In monoculture, these wetland plants were able to grow in nearly unflooded conditions at high elevations along our gradient (average 2% flooding), but, when grown in mixture, their minimum limit shifted toward deeper water (average 12% flooding; Fig. 3a). There was no difference among years ($P = 0.99$) and no statistical interaction ($P = 0.62$).

In contrast, if we look at the other end of the gradient, the maximum flooding limit (lower end of the gradient), growing with neighbours had no overall effect across species ($P = 0.29$, Fig. 3b). The overall maximum flooding limit changed among years ($P < 0.0001$), dropping from 55% average flooding in 2003 to 52% average flooding in 2004 and 2005, but again with no statistical interaction ($P = 0.08$).

Because of the significant effect on minimum flooding limit but no effect on maximum flooding limit, species grew over a narrower range of flooding conditions when they grew in mixture than when they grew in monoculture ($P = 0.012$), but only in 2003 (Tukey $P = 0.032$) and not in 2004 or 2005 (Tukey $P > 0.42$).

Now consider the mode, the point along the flooding gradient at which the greatest percent cover occurred. Despite the shifts in minimum flooding limits, the overall mode did not change when plants were grown with neighbours ($P = 0.45$) and remained at an average of 31% flooding. The mode did not shift across years ($P = 0.41$), nor was there a statistical interaction ($P = 0.75$).

In summary, there is an overall pattern of competition at the minimum limit of plants where less flooding occurred, that is, at the higher elevations, but there is no evidence of competition or facilitation at the maximum limit where more flooding occurred.

Growing with many neighbours: By year and species

Results in 2003: ten species surviving in mixture. Growing with neighbours strongly affected the minimum flooding limit in 2003 ($P < 0.001$; Online Supplementary Table S3; Fig. 4), as with the overall test. All ten species had a similar minimum limit in nearly unflooded conditions ($P = 0.97$), and there was no interaction indicating any different behaviour among species when they were growing with neighbours

or not ($P=0.82$). Growing with neighbours again had no effect on the maximum flooding limit ($P=0.77$), as with the overall test. The maximum limit differed strongly among species ($P<0.0001$), as would be expected, but now a strong interaction occurred ($P<0.0001$): *Cladium*, *Juncus* and *Schoenoplectus* had their maximum limit strongly reduced when grown with neighbours (Tukey $P<0.001$), as well as *Sagittaria* (Tukey $P=0.03$), unlike other species (Tukey $P>0.07$). The range differed among species ($P<0.0001$), as to be expected, and although growing with neighbours had only a small effect ($P=0.03$), an interaction occurred ($P<0.0001$): the range of *Cladium*, *Juncus* and *Schoenoplectus* contracted strongly when growing in mixture (Tukey $P<0.0001$), while *Acorus* and *Peltandra* contracted less (Tukey $P<0.03$). The mode of species distribution along the flooding gradient was not affected by growing with neighbours ($P=0.71$), although it differed substantially among species ($P<0.0001$), with no interaction ($P=0.19$). Each species, as one might expect, had different modes for flooding tolerance, but there was no general shift up or downslope attributable to the growing with neighbours. When ordered by their mode of distribution in monoculture, *Sagittaria* and *Rhynchospora* grew best with the least flooding, while *Juncus*, *Pontederia* and *Acorus* grew best at elevations with the most flooding (Fig. 4).

Results in 2004: eight species in mixture. The same patterns in the overall test were again evident in 2004. Growing with neighbours again reduced the minimum flooding limits of the surviving species ($P<0.0001$; Online Supplementary Table S3 and Fig. S3), but now there was a significant interaction among species ($P=0.0009$): *Panicum*, *Cladium* and *Sagittaria* did not show any difference in their minimum limit whether they were grown with neighbours or not (Tukey $P>0.07$), but the other species did, especially *Juncus*, *Peltandra* and *Pontederia* (Tukey $P<0.004$). The maximum limit of flooding was again not affected by growing with neighbours ($P=0.71$), and again differed among species ($P<0.0001$), but an interaction occurred ($P=0.0065$): the maximum flooding limit of *Cladium* and *Saururus* reduced when grown with neighbours (Tukey $P<0.004$), while for the other species it did not (Tukey $P>0.15$). Growing with neighbours contracted the range of flooding tolerance ($P=0.0019$), but again an interaction occurred ($P<0.0001$): only *Cladium* and *Saururus* contracted their range when grown with neighbours (Tukey $P<0.004$), and the other species did not (Tukey $P>0.15$). The mode of species distribution was not affected by growing with neighbours ($P=0.80$), but once again an interaction occurred ($P=0.0004$): the mode for *Cladium* shifted to less flooded conditions when grown with neighbours (Tukey $P=0.0002$), whereas the mode of *Juncus* shifted to more flooded conditions (Tukey $P=0.004$), while the modes of the other species were unaffected.

Results in 2005: five species in mixture. Growing with neighbours still reduced the minimum flooding limits ($P=0.006$), and there was no interaction ($P=0.10$; Online Supplementary Table S3 and Fig. S3). Growing with neighbours also reduced the maximum limit ($P=0.003$), but a borderline interaction occurred ($P=0.04$), in which *Cladium* and *Saururus* showed a reduced maximum limit when grown with neighbours (Tukey $P<0.004$), but *Panicum*, *Juncus* and *Peltandra* did not. The range consequently also contracted when plants were grown with neighbours ($P=0.006$). The mode did not shift as result of growing with neighbours, but the mode again showed an interaction ($P=0.0007$): the mode of *Saururus* shifted to less flooded conditions as a result of growing with neighbours (Tukey $P=0.0012$), whereas *Juncus* had an almost significant shift to more flooded conditions (Tukey $P=0.058$), while the modes of

other species were not affected. In summary, after three years, with only five species surviving, of which only three are dominant, competition still determines the minimum flooding limit, while the physiological tolerances of plants determine the maximum limit. Still, after three years, there was no evidence of facilitation.

Growing with many neighbours: $NImp_A$ index

The $NImp_A$ index based on final biomass showed significant competition along the flooding gradient for *Sagittaria*, *Rhynchospora*, *Saururus*, *Cladium*, *Schoenoplectus*, *Juncus*, *Peltandra* and *Acorus* ($NImp_A < 0$; Online Supplemental Table S4 and Fig. S4). None of these species showed facilitation, although several had reduced competition importance in more flooded conditions. The other two species, *Panicum* and *Peltandra* showed no significant intercept and no regression trend, suggesting that neither competition nor facilitation were important factors controlling their distribution along this flooding gradient after three years.

Growing in species pairs

Our three pairings provide additional information on growing with neighbours, depending on whether they were presumed dominants or interstitial species (Online Supplementary Figs S5, S6).

Panicum - Cladium

For the two presumed dominant graminoids, survival was high in monoculture until over 89% flooding in 2003 and until 66% flooding in 2004 and 2005, but when they grew together, survival decreased beginning at 11% flooding and continued to decrease gradually with increased flooding, across all years (Fig. 5a). Both species had a minimum limit under no flooding and growing with neighbours had no effect on their minimum limit even after three years ($P=0.24$; Fig. 6a; Online Supplementary Table S5, Fig. S7). However, the maximum limit of *Cladium* was again reduced substantially when growing with neighbours, as in the ten species mixture, while *Panicum* was unaffected (interaction $P<0.0001$). The range of *Cladium* was consequently reduced, but *Panicum* was unaffected (interaction $P<0.0001$). For the mode, *Cladium* now moved toward less flooded conditions and *Panicum* toward more flooded conditions when grown with neighbours (interaction $P=0.0006$). Competition now determines the maximum flooding limit and not the minimum limit. However, by the end of the experiment, the $NImp_A$ index still showed significant competition for *Cladium* under less flooded conditions, becoming more neutral with increasing flooding depth, as in the ten species mixture (Online Supplementary Table S6, Fig. S8). *Panicum* again showed predominantly neutral interactions, with no trend along the flooding gradient.

Peltandra - Pontederia: For the two presumed interstitial species, survival was the same when grown in monoculture as compared to when grown in mixture, across all years (Fig. 5b). The minimum flooding limit was not affected by competition ($P>0.14$; Fig. 6b). However, *Peltandra* significantly increased its

maximum flooding limit, and consequently its range when grown with *Pontederia*, an indication of potential facilitation, but *Pontederia* was not affected (maximum: interaction $P=0.047$; range: interaction $P=0.039$). The mode of both was unaffected by growing with neighbours. By the end of the experiment, the $NImp_A$ index showed that competition was important or neutral for *Pontederia* but with no significant trend with flooding, while for *Peltandra*, interaction importance ranged from competitive to facilitative, but again with little trend along the flooding gradient (Online Supplemental Table S6, Fig. S8).

Panicum - Pontederia

When we paired *Panicum*, a presumed competitive dominant, with *Pontederia*, a presumed interstitial species, *Pontederia* only survived in mixture with *Panicum* in two lanes by autumn 2003 and none survived through 2004 and 2005 (Fig. 5c). Insufficient data were available to analyse for changes in flooding distributions between these species. The $NImp_A$ index showed a clear increase in competition importance for *Pontederia* with increased flooding, but no trend for *Panicum* (Online Supplemental Table S6, Fig. S8).

Discussion

The primary objective of this experiment was to test for effects of competition and facilitation upon plant zonation along a gradient of flooding stress, and only flooding stress, without interference from other environmental stresses. We examined the entire length of the flooding gradient, with ten even interval steps from no flooding to complete flooding, thereby avoiding the pitfalls of experiments along natural stress gradients such as partial gradients, unequal step levels of stress, or insufficiently extreme stresses (He and Bertness 2014). The multiple flooding levels also allowed us to test the shape of interaction importance along the flooding gradient relationship. We used adult transplants of ten different species of wetland emergent macrophytes with varying morphology and ecology and wide distribution, to maximize generality, and we ran the experiment for three years.

The experiment was designed to evaluate the generality of previous work on competition along gradients and to evaluate the SGH hypothesis, which hypothesizes an important role for facilitation (Bertness and Callaway 1994; He et al. 2013). When ten species are considered simultaneously, the resulting zonation along the flooding gradient was determined by one-sided competition: the upper limits of species along the gradient were affected by multispecies competition, while the lower limits were determined by physiological tolerances to the physical stress of flooding. Furthermore, the mode of their distribution did not change. Our results are consistent with field experiments showing that competition among wetlands plants is relatively strong in habitats with low flooding stress (Ellenberg 1953; Pielou and Routledge 1976; Grace and Wetzel 1981; Shipley et al. 1991; Pennings and Callaway 1992; Lenssen et al. 1999; Budelsky and Galatowitsch 2000; Pennings et al. 2003; Guo and Pennings 2012; Schile et al. 2017). This result is

also consistent with the view that many wetland plants are stress tolerators (Keddy 2010), although to different degrees. That is, these wetland species could grow under less flooded conditions, if not for competition with plants that are better suited to unflooded conditions. The mode of distribution for our species was also stable whether grown alone or with neighbours. This is consistent with Bartelheimer and Poschlod (2016), who demonstrated that species optima do not change along hydrological gradients, whether grown alone or with neighbours. However, our results are not consistent with the Stress Gradient Hypothesis, which predicts that facilitation among plants should become evident as conditions become increasingly more flooded and stressful. Instead, the tolerance of flooding alone controlled the lower limits of plants.

This observed pattern of one-sided competition was not universal: some differences among species depending upon time and location. When the experimental wetland became a mixture of only a few competitively dominant species, as happened by the third year of the experiment, a flipped version of one-sided competition occurred with competition determining species distribution at the more flooded, supposedly more stressful end of the gradient. The same pattern was observed in the pair-wise mixture containing the *Cladium* and *Panicum* pairing. In this light, the most dominant species – *Panicum hemitomon* – does not appear to follow the same rules as the others, being able to outcompete other wetland plants even under more flooded, and supposedly more stressed conditions. We return to this apparent exception below.

Even when we evaluated the data by year and by species, there was scant evidence for facilitation. The mode of *Juncus* did shift to more flooded conditions in 2004 when grown with neighbours, with a borderline shift again in 2005. As well, *Peltandra* expanded its range toward more flooded conditions when grown in a pair with *Pontederia*. But the $NImp_A$ index did not show evidence for facilitation under more flooded conditions, although it did show reduced competition for *Juncus* and a few other species.

The SGH predicts slightly different outcomes depending on whether the stress is a resource or not and whether the beneficiary and benefactor species have competitive or stress-tolerant strategies (Maestre et al. 2009). Although flooding could be a resource gradient because soil oxygen is a resource, flooding may be more appropriately considered as a non-resource gradient because it rapidly shifts all root and soil metabolic processes. In this case, Maestre et al. (2009) theorize that facilitation is expected at high stress levels, among all functional types, but our results suggests that this does not occur at high flooding stress.

Could there be something about a flooding stress gradient that hinders facilitation under more flooded conditions? The transport of oxygen in aerenchyma to the roots and into the surrounding substrate seems like a reasonable mechanism for facilitation in flooded locations (e.g., Hacker and Bertness 1995; Callaway and King 1996; McKee et al. 2007). This transport would increase soil redox potential, thereby allowing less flood-tolerant neighbouring species to survive. There may however be other stresses acting along with low oxygen, such as phytotoxic compounds found under and low redox conditions (Pezeshki 2001; Reddy and DeLaune 2008; Lamers et al. 2013), which may prohibit facilitation.

There is a limitation to further generalizations regarding zonation, and this is the result of one life form being absent from this experiment: woody plants. It is frequently observed in wetland zonation patterns that there is a transition from herbaceous plants to woody plants at higher elevations (Keddy and Campbell 2020). Analyses of zonation patterns show that many wetland plants reach their upper limits at the lower limits of shrubs on shorelines (Pielou and Routledge 1976; Keddy 1983), and experimental removals of woody plants have been shown to allow herbaceous plants to expand landward (Keddy 1989). Hence, in future flooding gradient experiments, it may be useful to include woody species with herbaceous species. One-sided effects or even facilitation might be more obvious when competitive interactions include different life forms.

In a similar way, the experiment did not include floating-leaved species such as *Brasenia schreberi* and *Nymphaea odorata*, species which can form dense floating canopies in shallow water. Future experiments might look for competition and facilitation between emergent macrophytes and floating-leaved species. In a full range of shoreline habitats and a full range of life forms, it is possible that emergent macrophytes might be excluded from drier locations by one-sided competition from woody plants, and excluded from shallow water by one-sided competition from floating-leaved plants. If this is the case, then our observations on *Panicum hemitomon*, which is partially floating, might suggest that it was the functional equivalent of a floating-leaved aquatic in the experiment – setting lower distributional limits by competition. Until we have more experiments between emergent wetland plants and floating-leaved plants, this possibility remains hypothetical.

We did include *a priori* two different functional types of emergent macrophytes: matrix species and interstitial species (Boutin and Keddy 1993) This distinction arises in mostly herbaceous plant communities, where, it is proposed, some species form the vegetation matrix within which the interstitial species are then embedded (Grubb 1986); matrix species often have clonal spread and usually produce dense stands of whereas the interstitial species survive in various kinds of gaps created within the matrix species. In our experiment the interstitial species (*Sagittaria*, *Peltandra* and *Pontederia*) were strongly affected by the presence of the matrix species (*Cladium* and *Panicum*). Thus, one might reinterpret the observed patterns in our experiment in the following way: the matrix species may be predominantly controlled by the direct effects of flooding, and by competition with one another. The interstitial species are then controlled mostly by the effects of competition with matrix species.

Finally, our results also suggest two cautions for related to coastal wetland restoration initiatives, especially given expected sea level rise. Successful restoration requires ecologists to rank the causal factors that produce different ecosystems and then to manipulate the most important of these causal factors to produce desired outcomes (Keddy 2017; Keddy and Laughlin in press). It is therefore vital, in both theory and practice, to determine which causal factors have the greatest impact on a particular ecosystem. That is, while it is true that many causal factors will likely have some measurable effects upon any particular ecological community, it is also true that only a small number of these causal factors will have large effects. In this context, our experiment suggests two consequences for coastal wetland restoration. (1) Models for wetland restoration that consider only abiotic stresses may be inadequate for

forecasting future states of wetland vegetation. Instead, our experiment concurs with many other studies that suggest that competition acts on a nested niche structure along the flooding gradient to produce the observed patterns of wetland vegetation (e.g., Ellenberg 1953; Grace and Wetzel 1981; Shipley et al. 1991; Lenssen et al. 1999). Hence, conceptual models for coastal wetland restoration in areas such as the Everglades (Sklar et al. 2005) or Louisiana (Visser et al. 2004) need to include competitive interactions to accurately forecast future vegetation composition and vegetation responses to changing climate, flood frequencies and sea levels. (2) Our results also suggest caution in proposing that facilitation along flooding gradients is an important causal factor can be harnessed in wetland restoration (Silliman et al. 2015; Renzi et al. 2019). Although there is ample evidence that facilitation does occur among selected species in saline wetlands, it does not appear that facilitation among plants is strong and universal along pure flooding gradients.

Declarations

Funding: Initial funding for the experiment was provided by National Science Foundation grant DEB-0129024. Thereafter, costs of analysis and manuscript preparation were borne by the co-authors, who, like Thoreau, had neither salary nor grant support.

Conflicts of interest/Competing interests: None.

Availability of data and material: Data used in the production of this manuscript are available at DOI: <https://doi.org/10.6084/m9.figshare.12937031.v1>

Code availability: R code for statistical analyses is available in Supplemental Materials.

Author contributions: PK conceived and designed the experiment. DC helped to set up the experiment and collect the data. DC analyzed the data and produced the figures. DC and PK co-wrote the manuscript. Both authors contributed critically to this draft and gave final approval for publication.

Ethics approval: Not applicable.

Consent to participate: Not applicable.

Consent to publish: Not applicable.

References

1. Armstrong W. 1964. Oxygen diffusion from the roots of some British bog plants. *Nature* 204:801-802. <https://doi.org/10.1038/204801b0>
2. Bartelheimer M, Poschlod P. 2016. Ellenberg's water table experiment put to the test: species optima along a hydrological gradient. *Oecologia* 181:1163-1172. <https://doi.org/10.1007/s00442-016-3624-3>

3. Bates D, Maechler M, Bolker B, Walker S. 2015. Fitting linear mixed-effects models using lme4. *J Stat Softw* 67:1-48. <https://doi.org/10.18637/jss.v067.i01>
4. Bertness MD, Callaway R. 1994. Positive interactions in communities. *Trends Ecol Evol* 9:191-193. [https://doi.org/10.1016/0169-5347\(94\)90088-4](https://doi.org/10.1016/0169-5347(94)90088-4)
5. Bertness MD, Hacker SD. 1994. Physical stress and positive associations among marsh plants. *Am Nat* 144:363-372. <https://doi.org/10.1086/285681>
6. Bertness MD, Yeh SM. 1994. Cooperative and competitive interactions in the recruitment of marsh elders. *Ecology* 75:2416-2429. <https://doi.org/10.2307/1940895>
7. Boutin C, Keddy PA. 1993. A functional classification of wetland plants. *J Veg Sci* 4:591-600. <https://doi.org/10.2307/3236124>
8. Brooks ME, Kristensen K, van Benthem KJ, Magnusson A, Berg CW, Nielsen A, Skaug HJ, Machler M, Bolker BM. 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R J* 9:378-400. <https://doi.org/10.32614/rj-2017-066>
9. Budelsky RA, Galatowitsch SM. 2000. Effects of water regime and competition on the establishment of a native sedge in restored wetlands. *J Appl Ecol* 37:971-985. <https://doi.org/10.1046/j.1365-2664.2000.00540.x>
10. Callaway RM, King L. 1996. Temperature-driven variation in substrate oxygenation and the balance of competition and facilitation. *Ecology* 77:1189-1195. <https://doi.org/10.2307/2265588>
11. Campbell D, Keddy PA, Broussard M, McFalls-Smith TB. 2016. Small changes in flooding have large consequences: experimental data from ten wetland plants. *Wetlands* 36:457-466. <https://doi.org/10.1007/s13157-016-0754-7>
12. Chabreck RH. 1972. Vegetation, water and soil characteristics of the Louisiana coastal region. Louisiana State University Agricultural Experiment Station, Baton Rouge
13. Diaz-Sierra R, Verwijmeren M, Rietkerk M, de Dios VR, Baudena M. 2017. A new family of standardized and symmetric indices for measuring the intensity and importance of plant neighbour effects. *Methods Ecol Evol* 8:580-591. <https://doi.org/10.1111/2041-210x.12706>
14. Douma JC, Weedon JT. 2019. Analysing continuous proportions in ecology and evolution: a practical introduction to beta and Dirichlet regression. *Methods Ecol Evol* 10:1412-1430. <https://doi.org/10.1111/2041-210x.13234>
15. Ellenberg H. 1953. Physiologisches und ökologisches verhalten derselben Pflanzenarten. *Ber Deutsch Bot Ges* 65:350-361. <https://doi.org/10.1111/j.1438-8677.1953.tb00671.x>
16. Garssen AG, Baattrup-Pedersen A, Voesenek L, Verhoeven JTA, Soons MB. 2015. Riparian plant community responses to increased flooding: a meta-analysis. *Global Change Biol* 21:2881-2890. <https://doi.org/10.1111/gcb.12921>
17. Grace JB, Ford MA. 1996. The potential impact of herbivores on the susceptibility of the marsh plant *Sagittaria lancifolia* to saltwater intrusion in coastal wetlands. *Estuaries* 19:13-20. <https://doi.org/10.2307/1352647>

18. Grace JB, Wetzel RG. 1981. Habitat partitioning and competitive displacement in cattails (*Typha*): experimental field studies. *Am Nat* 118:463-474. <https://doi.org/10.1086/283841>
19. Grime JP. 1989. The stress debate: symptom of impending synthesis? *Biol J Linn Soc* 37:3-17. <https://doi.org/10.1111/j.1095-8312.1989.tb02002.x>
20. Grubb PJ. 1986. Problems posed by sparse and patchily distributed species in species-rich plant communities. p. 207-225. In Diamond J, Case TJ (eds.), *Community Ecology*. Harper and Row, New York
21. Guo HY, Pennings SC. 2012. Mechanisms mediating plant distributions across estuarine landscapes in a low-latitude tidal estuary. *Ecology* 93:90-100. <https://doi.org/10.1890/11-0487.1>
22. Hacker SD, Bertness MD. 1995. Morphological and physiological consequences of a positive plant interaction. *Ecology* 76:2165-2175. <https://doi.org/10.2307/1941690>
23. Hacker SD, Bertness MD. 1999. Experimental evidence for factors maintaining plant species diversity in a New England salt marsh. *Ecology* 80:2064-2073. [https://doi.org/10.1890/0012-9658\(1999\)080\[2064%3AEEFFMP\]2.0.CO%3B2](https://doi.org/10.1890/0012-9658(1999)080[2064%3AEEFFMP]2.0.CO%3B2)
24. Hartig F. 2020. DHARMA: Residual diagnostics for hierarchical (multi-level/mixed) regression models. <https://cran.r-project.org/web/packages/DHARMA/vignettes/DHARMA.html>
25. He Q, Bertness MD. 2014. Extreme stresses, niches, and positive species interactions along stress gradients. *Ecology* 95:1437-1443. <https://doi.org/10.1890/13-2226.1>
26. He Q, Bertness MD, Altieri AH. 2013. Global shifts towards positive species interactions with increasing environmental stress. *Ecol Lett* 16:695-706. <https://doi.org/10.1111/ele.12080>
27. Keddy PA. 1983. Shoreline vegetation in Axe Lake, Ontario: effects of exposure on zonation patterns. *Ecology* 64:331-344. <https://doi.org/10.2307/1937080>
28. Keddy PA. 1989. Effects of competition from shrubs on herbaceous wetland plants: a 4-year experiment. *Can J Bot* 67:708-716. <https://doi.org/10.1139/b89-094>
29. Keddy PA. 2010. *Wetland ecology, principles and conservation* (2nd ed.). Cambridge University Press, Cambridge. <https://doi.org/10.1017/CBO9780511778179>
30. Keddy PA. 2017. Restoration of freshwater wetlands. p. 243-260. In Allison SK, Murphy SD (eds.), *Routledge Handbook of Ecological and Environmental Restoration*. Routledge, New York. <https://doi.org/10.4324/9781315685977>
31. Keddy PA, Campbell D. 2020. The Twin Limit Marsh Model: a non-equilibrium approach to predicting marsh vegetation on shorelines and in floodplains. *Wetlands* 40:667-680. <https://doi.org/10.1007/s13157-019-01229-9>
32. Keddy PA, Laughlin DC. in press. A framework for community ecology: species pools, filters and traits. Cambridge University Press, Cambridge
33. Lamers LPM, Govers LL, Janssen ICJM, Geurts JJM, Van der Welle MEW, Van Katwijk MM, Van der Heide T, Roelofs JGM, Smolders AJP. 2013. Sulfide as a soil phytotoxin-a review. *Front Plant Sci* 4. <https://doi.org/10.3389/fpls.2013.00268>

34. Lenssen J, Menting F, van der Putten WH, Blom K. 1999. Control of plant species richness and zonation of functional groups along a freshwater flooding gradient. *Oikos* 86:523-534. <https://doi.org/10.2307/3546656>
35. Maestre FT, Callaway RM, Valladares F, Lortie CJ. 2009. Refining the stress-gradient hypothesis for competition and facilitation in plant communities. *J Ecol* 97:199-205. <https://doi.org/10.1111/j.1365-2745.2008.01476.x>
36. McKee KL, Mendelsohn IA, Hester MW. 1988. Reexamination of pore water sulfide concentrations and redox potentials near the aerial roots of *Rhizophora mangle* and *Avicennia germinans*. *Am J Bot* 75:1352-1359. <https://doi.org/10.2307/2444458>
37. McKee KL, Rooth JE, Feller IC. 2007. Mangrove recruitment after forest disturbance is facilitated by herbaceous species in the Caribbean. *Ecol Appl* 17:1678-1693. <https://doi.org/10.1890/06-1614.1>
38. Nakamura M, Noguchi K. 2020. Tolerant mechanisms to O₂ deficiency under submergence conditions in plants. *J Plant Res* 133:343-371. <https://doi.org/10.1007/s10265-020-01176-1>
39. NCEI. 2020. Climate Data Online. National Centers for Environmental Information Asheville, NC. accessed May 22, 2015, <http://www.ncdc.noaa.gov/cdo-web/>
40. Penfound WT, Hathaway ES. 1938. Plant communities in the marshlands of southeastern Louisiana. *Ecol Monogr* 8:1-56. <https://doi.org/10.2307/1943020>
41. Pennings SC, Callaway RM. 1992. Salt marsh zonation: the relative importance of competition and physical factors. *Ecology* 73:681-690. <https://doi.org/10.2307/1940774>
42. Pennings SC, Selig ER, Houser LT, Bertness MD. 2003. Geographic variation in positive and negative interactions among salt marsh plants. *Ecology* 84:1527-1538. [https://doi.org/10.1890/0012-9658\(2003\)084\[1527:Gvipan\]2.0.Co;2](https://doi.org/10.1890/0012-9658(2003)084[1527:Gvipan]2.0.Co;2)
43. Pezeshki SR. 2001. Wetland plant responses to soil flooding. *Environ Exp Bot* 46:299-312. [https://doi.org/10.1016/s0098-8472\(01\)00107-1](https://doi.org/10.1016/s0098-8472(01)00107-1)
44. Pielou EC, Routledge RD. 1976. Salt marsh vegetation latitudinal gradients in the zonation patterns. *Oecologia* 24:311-321. <https://doi.org/10.1007/bf00381137>
45. Reddy KR, DeLaune RD. 2008. Biogeochemistry of wetlands: science and applications CRC Press, Boca Raton. <https://doi.org/10.1201/9780203491454>
46. Renzi JJ, He Q, Silliman BR. 2019. Harnessing positive species interactions to enhance coastal wetland restoration. *Front Ecol Evol* 7:14. <https://doi.org/10.3389/fevo.2019.00131>
47. Schile LM, Callaway JC, Suding KN, Kelly NM. 2017. Can community structure track sea-level rise? Stress and competitive controls in tidal wetlands. *Ecol Evol* 7:1276-1285. <https://doi.org/https://doi.org/10.1002/ece3.2758>
48. Sculthorpe CD. 1967. The biology of aquatic vascular plants. Edward Arnold, London
49. Shipley B, Keddy PA, Lefkovitch LP. 1991. Mechanisms producing plant zonation along a water depth gradient: a comparison with the exposure gradient. *Can J Bot* 69:1420-1424. <https://doi.org/10.1139/b91-184>

50. Silliman BR, Schrack E, He Q, Cope R, Santoni A, van der Heide T, Jacobi R, Jacobi M, van de Koppel J. 2015. Facilitation shifts paradigms and can amplify coastal restoration efforts. PNAS 112:14295-14300. <https://doi.org/10.1073/pnas.1515297112>
51. Silvertown J, Araya Y, Gowing D. 2015. Hydrological niches in terrestrial plant communities: a review. J Ecol 103:93-108. <https://doi.org/10.1111/1365-2745.12332>
52. Sklar FH, Chimney MJ, Newman S, McCormick P, Gawlik D, Miao SL, McVoy C, Said W, Newman J, Coronado C, Crozier G, Korvela M, Rutcher K. 2005. The ecological-societal underpinnings of Everglades restoration. Front Ecol Environ 3:161-169. <https://doi.org/10.2307/3868544>
53. Smithson M, Verkuilen J. 2006. A better lemon squeezer? Maximum-likelihood regression with beta-distributed dependent variables. Psychol Methods 11:54-71.
<https://doi.org/http://dx.doi.org/10.1037/1082-989X.11.1.54>
54. Spence DHN. 1982. The zonation of plants in freshwater lakes Adv Ecol Res 12:37-125.
[https://doi.org/10.1016/s0065-2504\(08\)60077-x](https://doi.org/10.1016/s0065-2504(08)60077-x)
55. USACE. 2018. National Wetland Plant List, version 3.4. U.S. Army Corps of Engineers, Engineer Research and Development Center, Cold Regions Research and Engineering Laboratory, Hanover, NH.
<http://wetland-plants.usace.army.mil/>
56. Visser J, Steyer G, Shaffer G, Hoeppner S, Hester MW, Reyes E, Keddy P, Mendelsohn I, Sasser C, Swarzenski C. 2004. Chapter C.9 Habitat switching module. and State of Louisiana Ecosystem Restoration Study Louisiana Coastal Area (LCA), Louisiana. US Army Corps of Engineers New Orleans

Figures



Figure 1

Photograph of the experimental wetland graded to a 33 % slope in a pond with water level controls, showing lanes of experimental plantings along the flooding gradient (photo: Randy Bergeron).

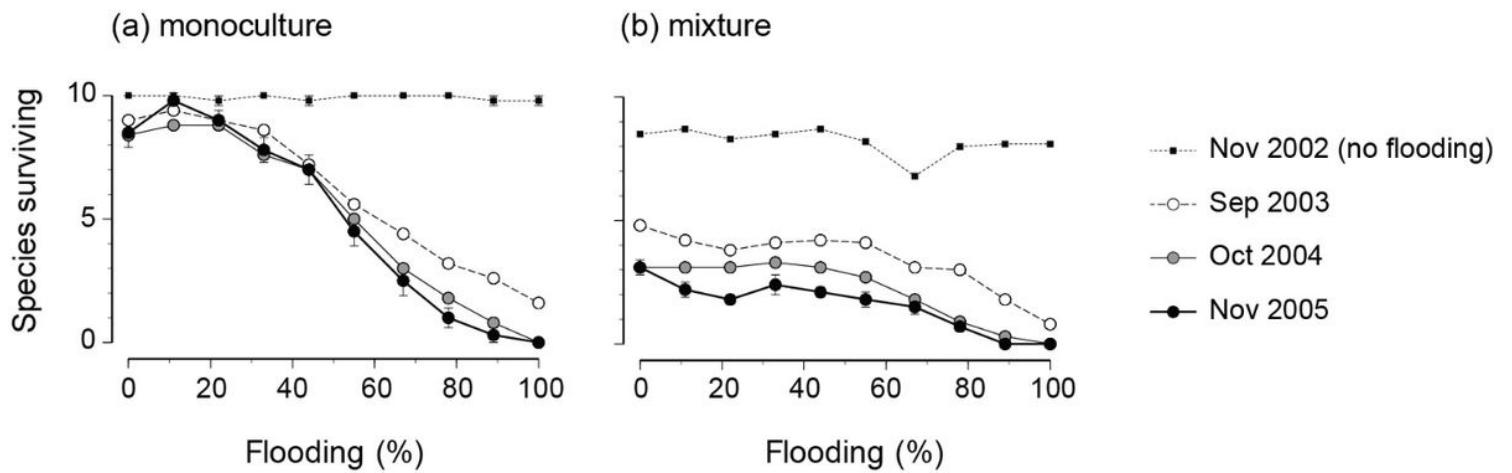


Figure 2

Survival of the ten marsh species in (a) monoculture or (b) multi-species mixture along the flooding gradient in the autumn of 2002 (pre-flooding), 2003, 2004 and 2005 (mean \pm SE). The flooding gradient is expressed as the percent of the growing season days that are flooded.

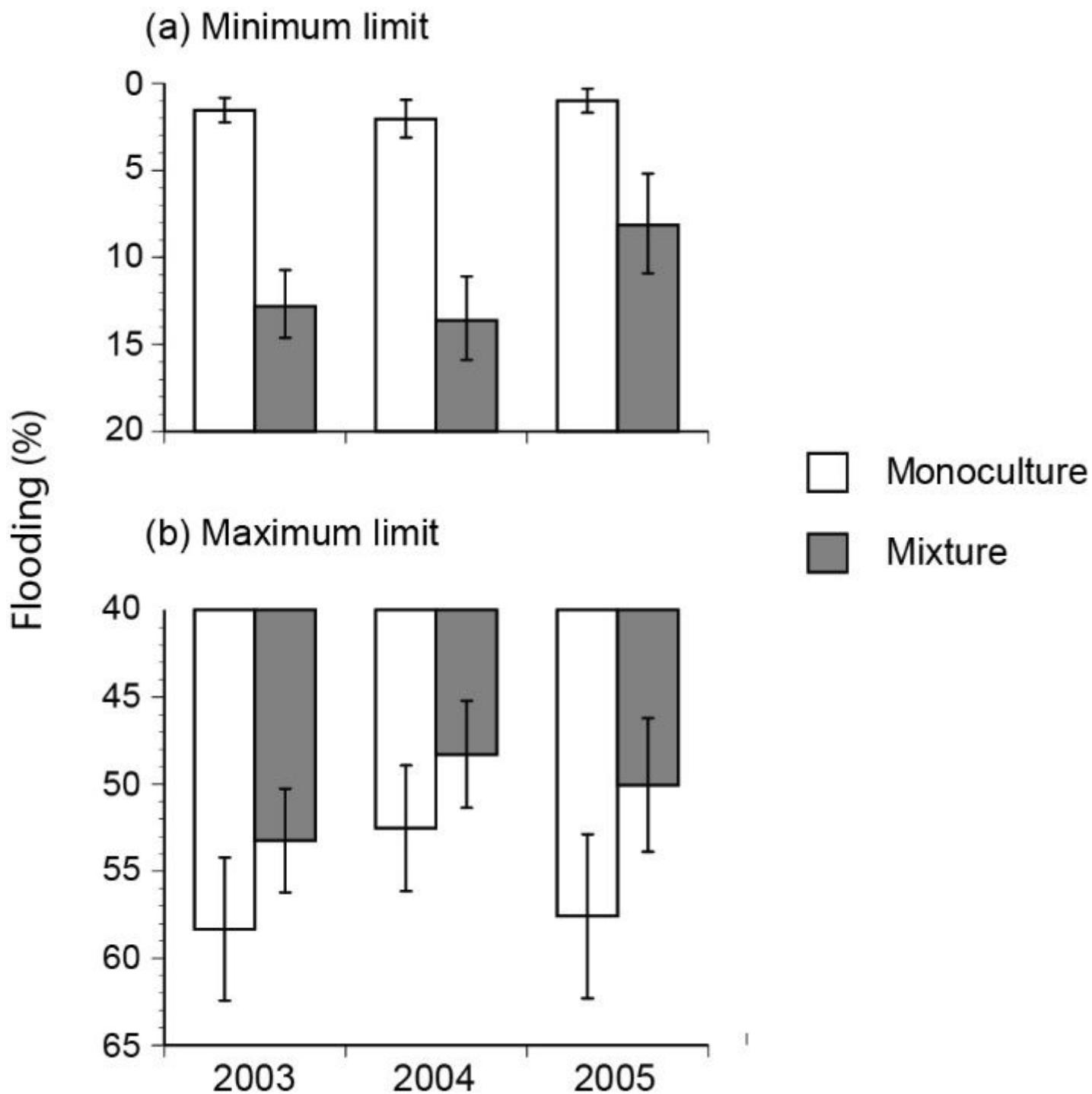


Figure 3

Bar graphs combining all species showing (a) minimum limit (upper end of gradient) and (b) maximum limit (lower end of gradient) for marsh plant distributions along the flooding gradient grown either in monoculture or in multi-species mixtures (mean \pm SE, based on 10 species in 2003, 8 in 2004 and 5 in 2005).

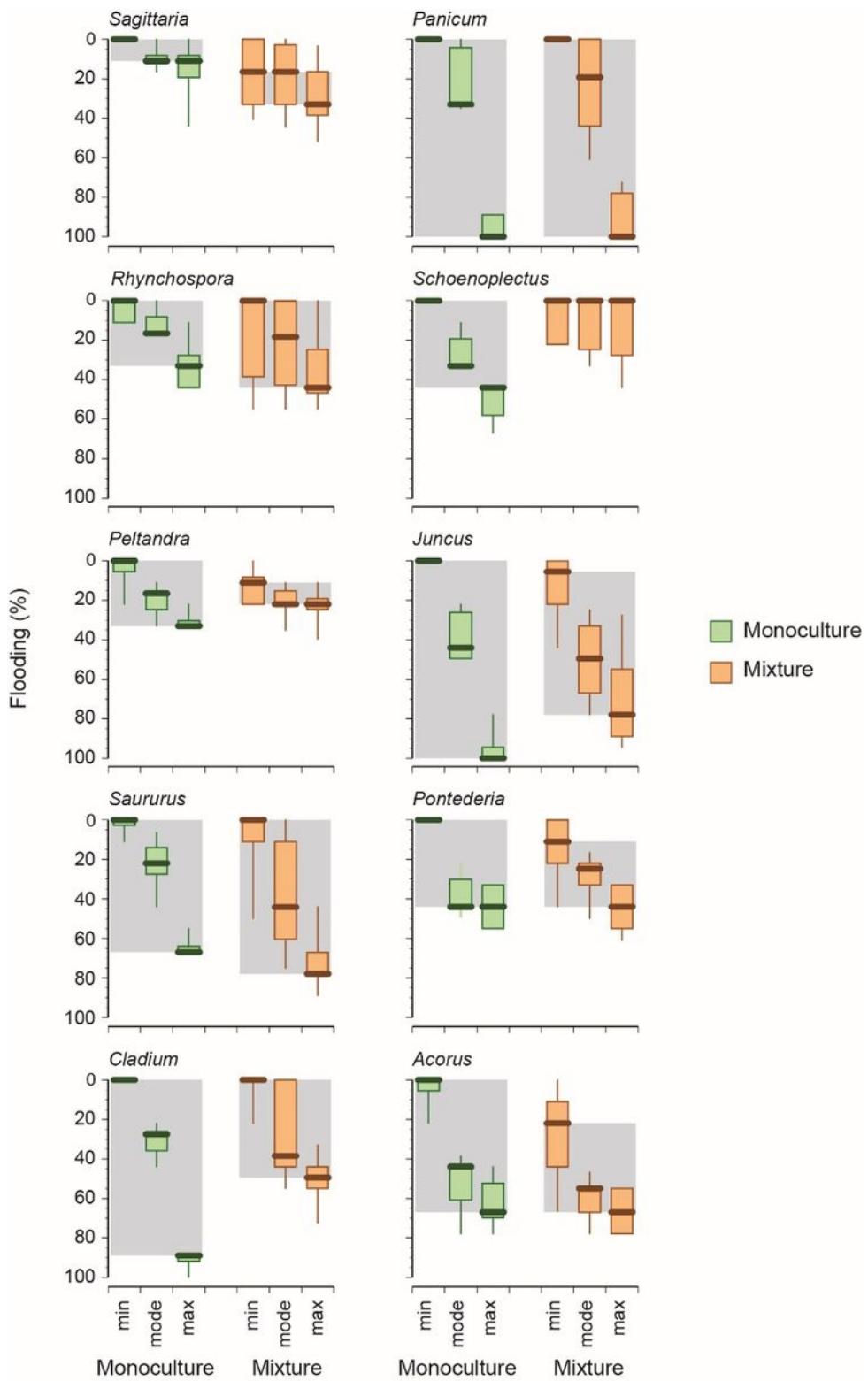


Figure 4

Box plots of the minimum limit, mode of the distribution and maximum limit along the experimental flooding gradient for the ten marsh species when grown in monoculture (green) and in multi-species mixture (orange) in the autumn of 2003. The background grey shading shows the range from the median minimum limit to the median maximum limit. Species are ordered by their mode of distribution of flooding when grown in monoculture.

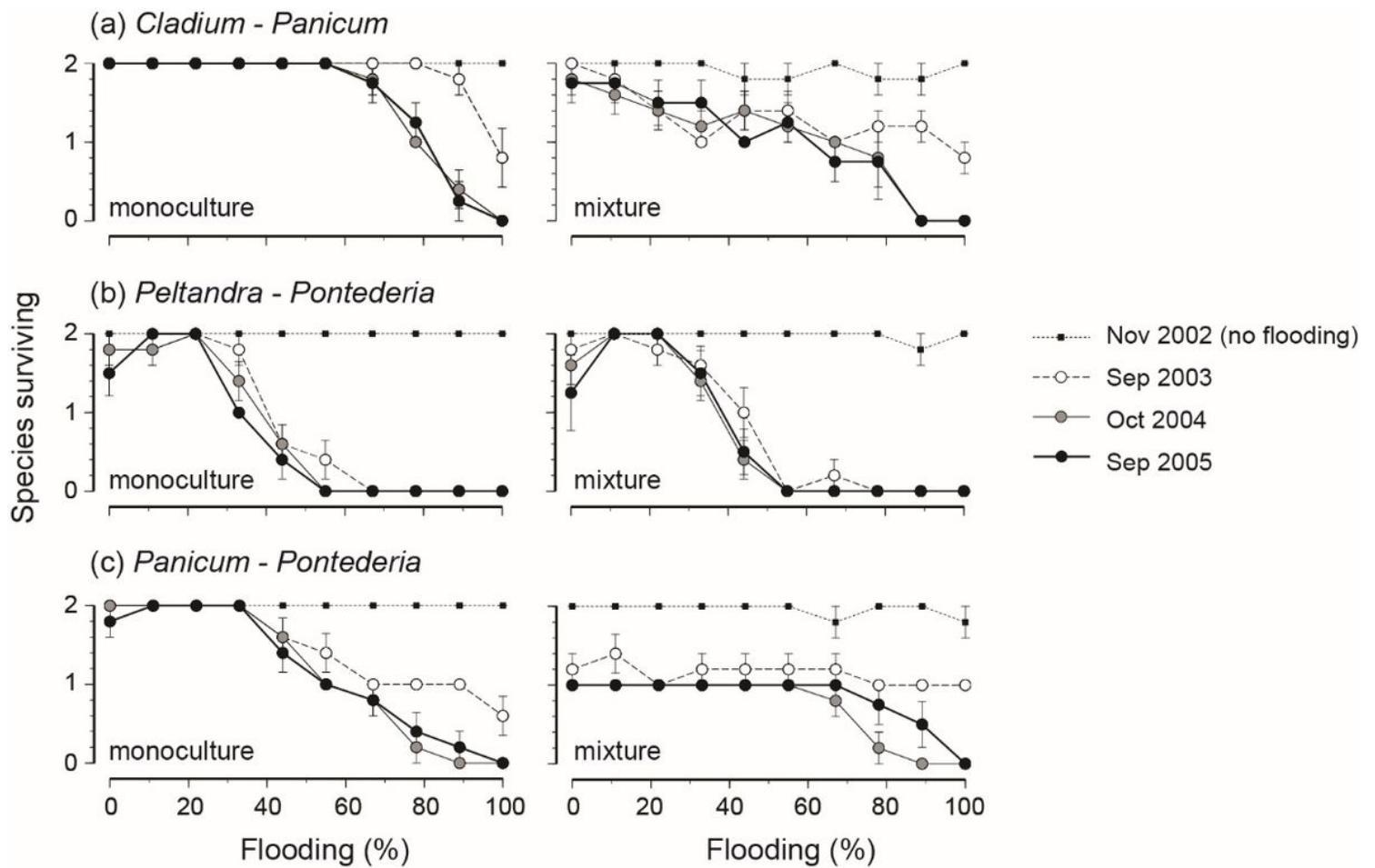
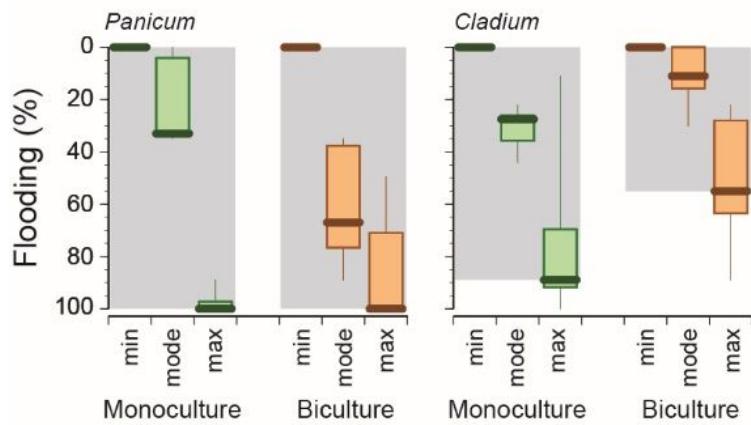


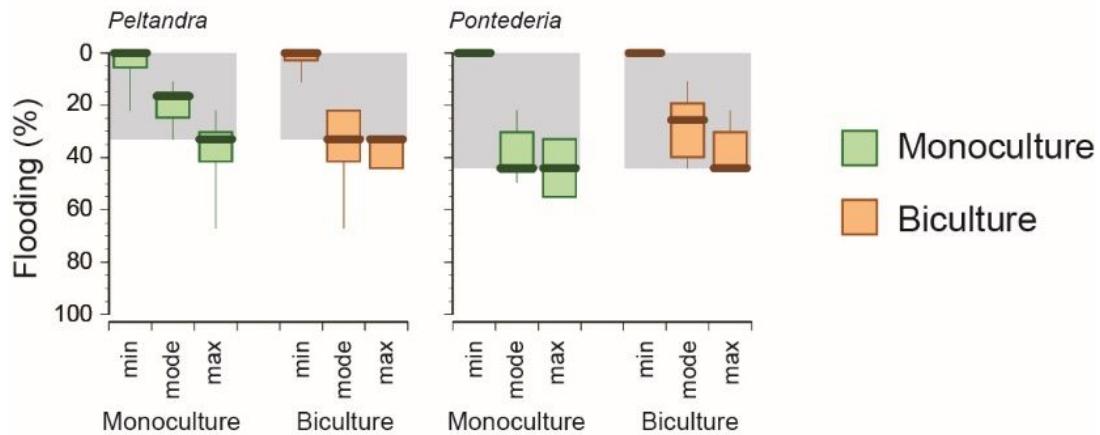
Figure 5

Survival of (a) *Cladium/Panicum*, (b) *Pontederia/Peltandra* and (c) *Panicum/Pontederia* when grown in monoculture or two species mixture along the flooding gradient in the autumn of 2002 (pre-flooding), 2003, 2004 and 2005 (mean \pm SE).

(a) *Cladium - Panicum*



(b) *Peltandra - Pontederia*



(c) *Panicum - Pontederia*

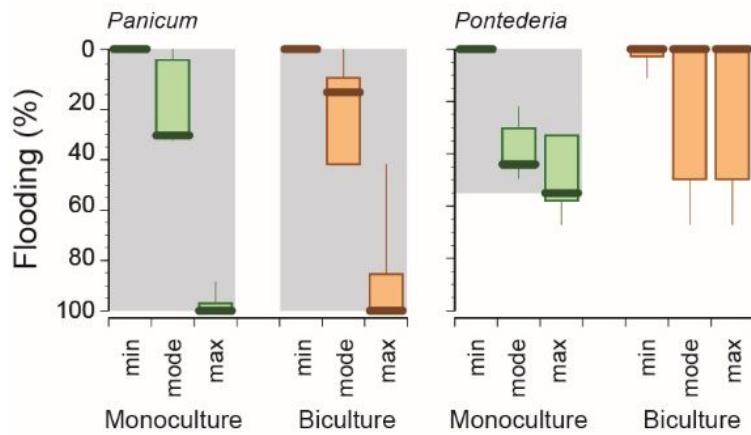


Figure 6

Box plots of the minimum limit, the mode of distribution and the maximum limit along the experimental flooding gradient in the autumn of 2003 for (a) *Cladium/Panicum*, (b) *Pontederia/Peltandra* and (c) *Panicum/Pontederia* when grown in monoculture and in two species mixture.

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