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Impact of Flood Duration on Germination Success of Paraná River Delta (Argentina) Plants

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Abstract
The hydrological regime determines the structure and diversity of wetland vegetation, and it has been considered as the most relevant determinant for the plant communities in the Paraná River Delta. However, experimental validations explaining the causes of the distribution patterns are scarce. The objective of this article is to determine the effect of flood duration on wetland species germination. For that purpose, the seeds of four species from contrasting hydrogeomorphological environments, three ligneous species and one herbaceous species, were sowed. The 24 germination trays were watered weekly, and undergone four flood duration treatments: zero, one, seven and 13-day flood period every two weeks. We found that the longer the flood duration, the greater the reduction on germination for ligneous species, and the opposite was observed for the herbaceous species. The odds of germination in the longer duration treatment, versus control treatment, can be reduced up to 99% for ligneous species, and can be increased 900% for herbaceous species. Germination in the studied species performed as expected in their natural environments, although the ligneous species showed a broader niche, indicating that other mechanisms are also necessary to understand the distribution of these species. The results provide experimental evidence that flood duration impacts on germination and species composition of wetland species and provide tools for the prediction of anthropic impacts and the ecological restoration of wetlands.

Keywords Freshwater tidal wetland · Hydrological regime · *Terminalia australis* · *Erythrina crista-galli* · *Sesbania virgata* · *Schoenoplectus californicus*

Resumen
El régimen hidrológico determina la estructura y diversidad de la vegetación de humedal y ha sido reconocido como el condicionante más relevante de las comunidades de plantas del delta del río Paraná. Sin embargo, existe una escasez de validaciones experimentales que permitan explicar las causas de los patrones de distribución encontrados. El objetivo del trabajo fue analizar el efecto de la duración de la inundación sobre la germinación de especies de humedal. Para ello se sembraron semillas de cuatro especies, tres leñosas y una herbácea, características de ambientes hidrogeomorfológicos contrastantes. Las 24 bandejas de germinación fueron regadas semanalmente y se sometieron a cuatro tratamientos de duración de inundación: cero, uno, siete y 13 días de inundación cada dos semanas. Se observó una disminución de la germinación a mayor duración de inundación para las especies leñosas y lo contrario para la herbácea. El odds de germinar en el tratamiento de mayor duración, respecto al del control, puede disminuir hasta 99% para las leñosas y aumentar 900% para la herbácea. La germinación de las especies estudiadas respondió según lo esperado a los ambientes donde se desarrollan naturalmente, aunque las especies leñosas mostraron un nicho más amplio indicando que otros mecanismos son también necesarios para entender la distribución de estas especies. Los resultados aportan evidencias experimentales a favor de que la duración de la inundación impacta en la germinación y composición de especies de humedal y aportan herramientas para la predicción de impactos antrópicos y la restauración ecológica de humedales.

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Introduction

The hydrological regime influences the structure and diversity of wetland vegetation, even in the finest spatial scales (Raulings et al. 2010). Duration, frequency, and depth of flooding have been identified as major determinants for the type of plant community that emerges and establishes in a place (Casanova and Brock 2000). In riparian environments, flooding may provide new alluvium for germination, destroy pre-existing vegetation, determine whether seedlings will survive to maturity, and disperse propagules to colonization sites (Bendix and Hupp 2000). In effect, the selection pressure produced by the hydrological regime in the establishment of plants from seed entails evident ecological and evolutionary consequences (Leck and Brock 2000). Flooding produces anaerobiosis, and while some species were documented as able to germinate in such conditions, oxygen is fundamental for plant germination (Zhou et al. 2020). While the seed bank could be a factor in controlling the abundances of species to emerge, the hydrological regime determines which species would become established by stimulating or suppressing the germination of the diverse species (Webb et al. 2006).

The hydrological regime has been recognized as the most relevant determining factor for the Paraná River Delta wetland macromosaic vegetation. In his original description of the vegetal communities, Burkart (1957) noted that the factor impacting vegetation during river flooding is not so much water levels as the flood duration, and the presence or absence of stagnant flood water. Also, Malvárez (1997) concluded that inundability, as well as the origin of the flooding, are the main factors in structuring communities and region species distribution, and in the cases in which anaerobiosis conditions are prevalent, tolerant species are reduced to a few, creating virtually monospecific communities. Accordingly, Kandus et al. (2003) stated that species differential presence corresponds to two main gradients of variance: water permanence and the water source and its hydrodynamics.

The results obtained by Kalesnik et al. (2011) also show that the variables related to the hydrological regime, along with the modifications of landscape elements, could allow to explain vegetation patterns of levee forests, and even invasion patterns by invasive tree species. More recently, Morandeira and Kandus (2016) found a significant association among the effects of flooding frequency, topographic position, and landscape units on herbaceous species functional types. Nonetheless, so far, these regional patterns have not been subject to any experimental validation that could explain, at least partially, its causes.

The hydrological regime from the Paraná River Delta region is subject to a main West–East gradient, with a decreasing influence from the Paraná River and a growing influence of the Río de la Plata River; in short, an axis of "fluvial-tidal" influence (Malvárez 1997; Durante and Di Bella 2020). The fluvial influence is defined by the seasonal floods of the Paraná and Uruguay rivers, and the tidal influence, by the daily tides from the Río de la Plata River, which could be significantly increased by wind circulation (Baigún et al. 2008). Due to these variations, the topographic position and the form of deltaic islands determine the frequency and duration of the flooding to which the different species are subject, shaping a prominent environmental heterogeneity with a characteristic and distinctive vegetation (Kandus et al. 1999, 2006). Among the species that characterize the hydrogeomorphological environments of the Lower Paraná River Delta are *Terminalia australis* Cambess. (Combretaceae), a tree from the levee forests; *Erythrina crista-galli* L. (Fabaceae), an arboreal species in intermediate topographic positions; *Sesbania virgata* (Cav.) Pers. (Fabaceae), a bush in environments lower than levees, and adjacent to creeks; and *Schoenoplectus californicus* (C.A.Mey.) Soják (Cyperaceae), an equisetoid herbaceous plant in lower topographic positions (Fig. 1).

The objective of this study was to analyze the impact of flood duration on wetland species germination. We hypothetize that the flood regime impacts the germination in various species and its response corresponds with the hydrogeomorphological environments they inhabit. Therefore, the prediction was that germinations would be maximum under the following conditions: under short flood durations for *T. australis*, under intermediate durations for *E. crista-galli* and *S. virgata*, and under prolonged durations for *S. californicus*.

Methods

The four species under study were selected because they are characteristic of contrasting hydrogeomorphological environments and because they have a hydrocorous dispersion (Kandus et al. 2006, Kalesnik and Sirolli 2011). All of them reproduce by seeds although *S. californicus* can also multiply by division of rhizomes (Quintana et al. 2012). Although they can be recorded in almost the entire Paraná River Delta, *T. australis*, *E. crista-galli* and *S. californicus* are more abundant in the Lower Paraná River Delta and *S. virgata* in the Upper Paraná River Delta (Burkart 1957).

The fruits of the species under study were collected between March and June of 2018, in the creeks from the Third Section of Paraná River Delta islands (central latitude and longitude coordinates: -34.10, -58.47). The islands of this sector, the Lower Paraná River Delta, are characterized by being basin-shaped and presenting a high edge called "albardón" (levee), only reached by large and brief floods, and a low and swampy interior (Burkart 1957). The fruits were stored in

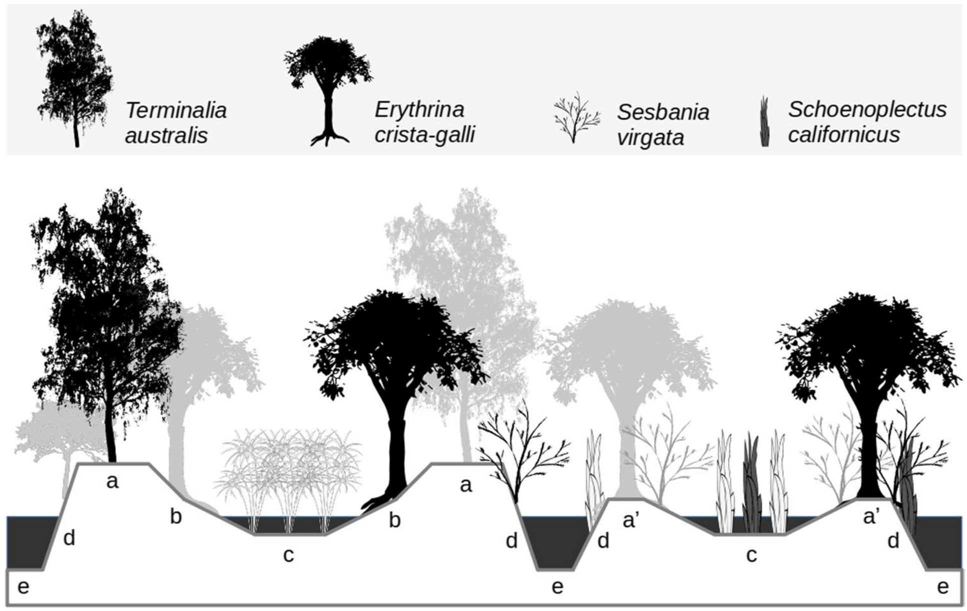


Fig. 1 Topographic and geomorphological settings of the four studied species in Lower Paraná River Delta: levee (**a**), mid-slope (**b**), center of the island (**c**), riverbank (**d**), watercourse (**e**), low levee (a'). The drawing is a simplification, including a newly formed island (right) and an older island (left)

paper envelopes, in a dark storage room at room temperature d umidity until the beginning of the experiment. Before planting, the seeds of *E. crista-galli, S. virgata* y *T. australis* were mechanically scarified to break the dormancy (Silva et al. 2006; de Menezes Silva et al. 2011). The germination was carried out on 24 multi-cell plastic trays. Each cell was perforated at its base, and their dimensions were a diameter of 4 cm on the upper part and a depth of 6 cm. Each one of them was filled with 4 cm of sand, and assigned to a species regularly and alternately, resulting in 19 cells per species and tray. The seeds were sowed in the sandy substratum at 1 cm depth, two per cell for *S. californicus* (N = 38 seeds per tray) and one per cell for the rest of the species (N = 19 seeds per tray).

The flood treatments were generated in the following way: the multi-cell trays were inserted in buckets of 30 by 45 by 10 cm with adjustable drain. The buckets were arranged even over a table in a greenhouse in the experimental campus of Ciudad Universitaria, belonging to the University of Buenos Aires (Argentina). Once every two weeks, the buckets were filled with water until the water level surpassed the sand level in 0.5 cm. The buckets were drained based on the following scheme: "Zero day" treatment (T0), without flooding; "One day" treatment (T1), draining after 24 h of flooding; "Seven day" treatment (T7), draining after 7 days of flooding; "13 day" treatment (T13), draining after 13 days of flooding. Every tray was watered weekly until reaching the soil field capacity.

The experiment was carried out between September 5th and December 20th, 2018. The seeds from the four species were sowed at the same time. The first germinating species, *E. crista-galli* y *S. virgata*, reached stabilization in the curve of germination accumulation after six weeks; for that reason, it was decided to establish the duration of the experiment in 6 weeks after the first germination for all the species. The environmental conditions of light, temperature and humidity during the experiment were natural, with absolute minimum, average and absolute maximum for September to December months being 7.0, 19.4 and 31.6 °C respectively. The buckets were rotated on a weekly basis to homogenize the conditions for all experimental units. Data from all cells was logged weekly, and seeds were counted as germinated only if the emergence of any part of the seedling was observed. Upon completion of the experiment, the seedlings were removed, dried in a heater at 50 °C for 24 h, and weighted in an analytical balance. For each tray, the dry weight per seedling at the end of the experiment was the sum of the dry weight of all the emerged seedlings divided by the total number of emerged seedlings in each tray. For each germinated seedling, the germination time was the difference between the germination and sowing dates. The germination time per tray was the average germination time of all the germinated seedlings in each tray.

For the statistical analysis, it was assumed that the Proportion of germinated seed response variable (number of germinated seeds in relation to the total number of sowed seeds per tray), followed a binomial distribution, and it was modeled with generalized linear models using the *glm* package from the software RStudio (R Core Team 2021). The explanatory variables were Species and Flood duration treatment. The latter was treated as a qualitative variable (four levels: T0, T1, T7, and T13) since the models that took the variable as a quantitative variable did not fulfill the linearity in the response. The assumption of the absence of underdispersion or overdispersion was analyzed with the *DHARMa* package (Florian Hartig 2021). The overdispersion was significant, consequently, the data was modeled taking the germination tray as a random variable using the *glmmTMB* package (Brooks et al. 2017). A lack of significant normality was not detected in the residues for said variable, neither when they were graphically analyzed (qqplot) nor with a Shapiro–Wilk test. The model with interaction between species and treatment showed a lower AIC value than the model without interaction and those models considering only one of the two variables. Post-hoc Tukey contrast tests were made using the *emmeans* package (Lenth 2021). Regarding the Dry weight per seedling variable at the end of the experiment, a normal distribution was assumed, and it was modeled using linear models with the *lm* package from the aforementioned software. Significant lack of normality and lack of homoscedasticity were detected, consequently the data was modeled with the *gls* function from the *nlme* package (Pinheiro et al. 2022). Variance modeling function *varIdent* showed a lower AIC value than the other two functions analyzed (*varPower* and *varExp*). Post-hoc Tukey contrast tests were made using the same package. The significance threshold for all the tests was 0.05.

Results

The cumulative number of germinated seeds over time is shown in Fig. 2. The effect of flood duration differed based on the species, showing a significant interaction between these two variables (flood duration and species, $p<0.05$, type II Wald chi-square). The greater the flood duration, the greater the germination decrease for ligneous species; and the opposite was observed for the herbaceous species (Fig. 3). Analyzing the simple effects, flood duration impacted the germination of the four wetland species under study ($p<0.05$, Tukey). On the contrary, only one significant effect of this variable was observed at the end of the study on the dry weight per seedling in one of the species (*E. crista-galli*, $p<0.05$, Fisher). The time the seeds needed to germinate was (average ± standard deviation) 70 ± 8, 17 ± 7, 17 ± 7 y 56 ± 11 days respectively for *T. australis*, *E. crista-galli*, *S. virgata,* and *S. californicus*.

For the species *T. australis*, 89 seeds germinated, which represents a germination success rate of 20% compared to sowed seeds (Fig. 2). The germination was the highest when they received zero and one day-flood treatment every two weeks and it dropped significatively in the other two more prolonged flood times ($p<0.05$, Tukey) (Fig. 3). The model indicates that the probability of germinating versus the probability of not germinating (odds) with a 13-day flood regime every two weeks (T13) drops, in average, 99% compared to the non-flood regime (T0) (Table 1). The dry weight per seedling at the end of the study ranged from 16 to 27 mg, without significant differences among treatments ($p>0.05$, Fisher).

The germination success rate of *Erythrina crista-galli* was 52%, considering the four treatments applied (238 germinated seeds). The germination was the highest in the non-flood treatment, without differences for one and seven day-flood treatments, and the lowest in the more prolonged flooding ($p<0.05$, Tukey, Fig. 3). The odds of germination with a regime like T13 drops in average 95% compared to T0 (Table 1). Mean dry weight per seedling at the time of the extraction was 1632, 2510, 1973 and 348 mg respectively for T0, T1, T7 and T13, with significant differences between the longer flooding time and the rest ($p<0.05$, Tukey).

For the species *Sesbania virgata*, a total of 252 seeds germinated, that is, a germination success rate of 55%. A reduction in the germination on longer flood durations was observed, with rates ranging from 78 to 9% ($p<0.05$, Tukey, Fig. 3). The model indicates that the odds of germination with a very long flood regime (T13) can decrease, in average, up to 97% compared to the non-flood regime (T0) (Table 1). The dry weight per seedling at the end of the study ranged between 29 and 44 mg without differences among treatments ($p>0.05$, Fisher).

The seeds of *Schoenoplectus californicus* had a germination success rate of 4% (37 seeds). In contrast to the other three species, the germination increased significatively with a longer flood duration, with rates ranging from 1 to 9% ($p<0.05$, Tukey, Fig. 3). With the 13-day flood regime every two weeks, the odds of germination increase, in average, 900% compared to the non-flood regime (Table 1). The dry weight per seedling at the extraction ranged between 1 and 2 mg, without differences among treatments ($p>0.05$, Fisher).

Discussion

The flood regime had an impact by decreasing or increasing the percentage of germination differentially according to the species. Consequently, this process allows to explain, in part, the vegetation patterns from Paraná River Delta (Burkart 1957). Particularly, in the conditions of the study, without a water deficit due to supplementary irrigation, the longer the duration of the flooding, the biggest inhibitory effect in the germination percentage of ligneous species, and the opposite was true for the herbaceous species. This pattern experimentally underpinned the descriptions by Malvárez (1997), who stated that if the flooding period extends in time, the water in the soil brings to prolonged saturation conditions and a reduced aeration, causing a reduction in the number of tolerant species and in the complexity of communities. In seed bank studies subject to prolonged flooding, lowered community richness dominated by herbaceous species have been reported (Casanova and Brock 2000). Herbaceous species not only

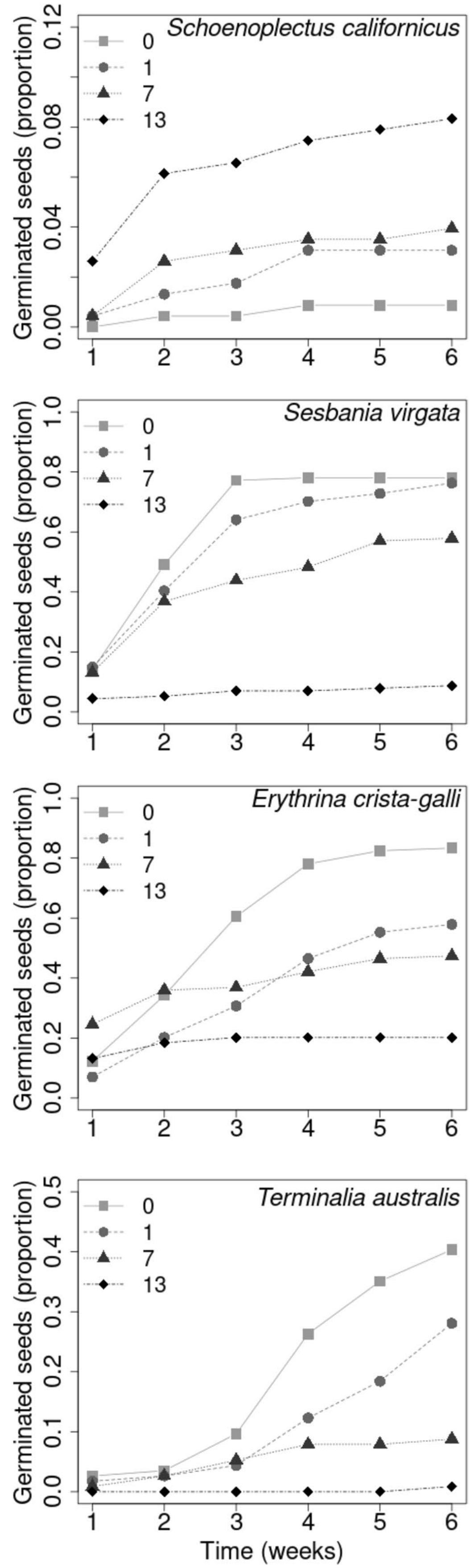


Fig. 2 Proportion of germinated seeds over time in the four studied wetland species. The four flood duration treatments of this study are indicated in days every two weeks, using different series. The time axis covers six weeks starting at the first germinations, which occurred on different dates for each species. N = 228 sowed seeds per treatment for *Schoenoplectus californicus*, and 114 for the other three species. Y-axis maximum value is variable for a better visualization

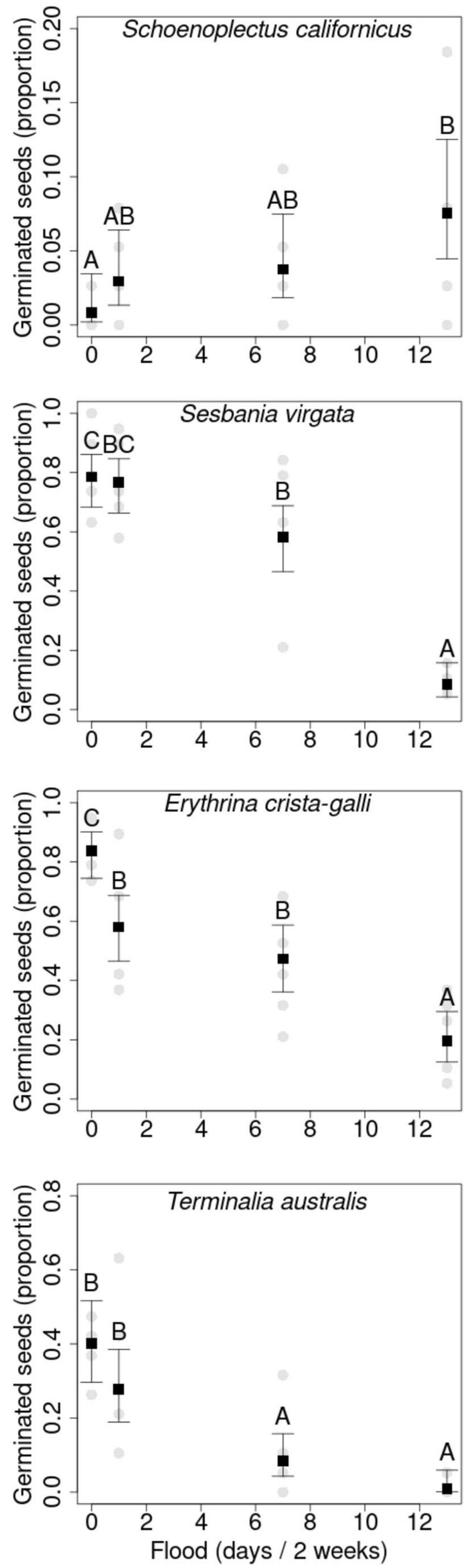
show a higher germination rate than ligneous species under longer durations of flooding, but also have better asexual reproduction mechanisms, straightening the predominance of herbaceous dominant communities with little or no representation of ligneous species (Barrett et al. 2010).

Under flooded conditions, most of the seeds absorb water and their coats break, benefiting the germination, although, by contrast, continued soaking results in seed death (Cronk and Fennessy 2001). In this study, water absorption was facilitated by the scarification made to the ligneous species seeds and it wasn't a limiting factor, as it could occur in nature (Baskin and Baskin 2014). Additionally, this fact would allow to explain the better recruitment of the herbaceous species under more prolonged flooded conditions, since said species hadn't been scarified. Accordingly, the results of this study agree with Stone et al. (2020), who found differential seedling emergence among trees, shrubs, and herbaceous species under different flood durations.

Once germinated, the dry weight of each seedling at the end of the study wasn't significatively impacted by flood duration. Various studies on seed banks have found dry weight reductions under a longer flood duration, considering the sum of germinated seedlings (Casanova and Brock 2000). In agreement, experiments about wetland seedling survival have also shown dry weight reductions under flooded conditions (Fraser and Karnezis 2005). Consequently, the results of this study indicate that, in a context without water deficit, the dry weight developed in the first two months post-germination would be determined by the number of germinating and surviving seedlings rather than by a differential growth depending on flood duration. Therefore, the results show that the determination of dry weight found by weighing the dry mass of all individuals, even though less exact than seedling count, is suitable for comparing treatments like those applied to this study.

In three out of the four studied species, experiments have been conducted to assess their response to flooding, and it has been concluded that they are plants with a high tolerance to flooding. In these conditions, *E. crista-galli* develops a metabolism with a high level of tolerance to flooded conditions, activating the fermentation pathway and increasing the activity of antioxidant enzymes (Ferreira Larré et al. 2016). Likewise, *S. virgata* can survive in flooded soils for more than 56 days, developing metabolic and anatomic adaptations, such as the increase of intercellular space, defoliation, and the drop of biomass (Davanso-Fabro et al. 1998;

Fig. 3 Proportion of germinated seeds based on the flood duration treatment, in days every two weeks, at the end of the study. The observed values per tray are indicated with grey circles, the predicted values are indicated with black squares, and their confidence interval is 95%, based on a generalized linear model. N = 6 trays per treatment. The different letters indicate significant differences among treatments for each species using post hoc Tukey comparisons. Y-axis maximum value is variable for a better visualization



Zanandrea et al. 2009). Our results show that these two species germinate to a significant extent, even under flooded conditions during half of the time. Besides, *S. californicus* has been broadly reported as a tolerant species to flooding, even when compared to other common herbaceous species in wetland ecosystems (Sloey et al. 2015, 2016). Our results show that these adaptations to flooding include early stages of development, such as germination, and they allow us to understand that flooding is an essential factor in the installation of this species on new substrates. Finally, germination studies for *T. australis* weren't found, however, our results show that even though it is tolerant to brief flooding periods, its germination declines fast when the flood is prolonged.

The germination of the species under study responds as expected to the flooding duration, if the hydrological regimes associated with the natural topographic positions are considered (Burkart 1957; Malvárez 1997; Kandus et al. 2003; Kalesnik et al. 2011; Sirolli et al. 2021). Nevertheless, in this study it was observed that the ligneous species have a niche that extends to flood values lower and higher than expected, according to their realized niche (Hutchinson 1957). Consequently, as usually happens, other mechanisms such as competence, available nutrients, water quality, sediment texture, etc. are needed to understand the distribution of these species in the studied area. For example, this study results show that *E. crista-galli*, a species forming monospecific forests in floodable soils, could thrive in topographically higher environments, like the levees where *T. australis* and other tree species grow, but its abundance is low in the levees, and its population structure pattern is nomadic or remnant (Sirolli et al. 2021). On the contrary, *S. californicus* is always under flooded conditions, and it is not a part of land communities. The results of this study reveal that this selection occurs from the plant germination.

In a context of lack of knowledge regarding hydrological regime and wetland plants, this study provides experimental evidence supporting flood duration impact on germination and, in consequence, on wetland species composition just as Webb et al. (2012) have stated. It is important to note that this study was limited to a flooding intensity of a few centimeters and to a biweekly flooding frequency; by modifying these variables, the impact of duration could be different, since the three variables act simultaneously (Mitsch and Gosselink 2015). Therefore, the decrease in germination shown in this study with the increase of flood duration

Table 1 Post-hoc Tukey contrasts among treatments for the four studied species. The flood days every two weeks were indicated with the numbers 0, 1, 7, and 13, based on each of the four treatments. Significant differences are listed in bold (p < 0.05)

Contrast	Odds ratio	SE	Lower CL	Upper CL	P value
Terminalia australis					
0 / 1	1.75	0.60	0.72	4.28	3.60E-01
0 / 7	**7.32**	**3.13**	**2.38**	**22.49**	**7.65E-05**
0 / 13	**80.07**	**83.32**	**5.22**	**1229.12**	**3.82E-04**
1 / 7	**4.18**	**1.82**	**1.33**	**13.11**	**8.27E-03**
1 / 13	**45.71**	**47.72**	**2.95**	**707.84**	**2.50E-03**
7 / 13	10.95	11.77	0.65	184.02	1.25E-01
Erythrina crista-galli					
0 / 1	**3.73**	**1.37**	**1.42**	**9.79**	**3.34E-03**
0 / 7	**5.75**	**2.11**	**2.19**	**15.09**	**5.06E-05**
0 / 13	**21.11**	**8.32**	**7.50**	**59.39**	**1.29E-10**
1 / 7	1.54	0.51	0.65	3.65	5.51E-01
1 / 13	**5.67**	**2.02**	**2.22**	**14.46**	**3.43E-05**
7 / 13	**3.67**	**1.31**	**1.44**	**9.34**	**2.56E-03**
Sesbania virgata					
0 / 1	1.11	0.41	0.42	2.92	9.92E-01
0 / 7	**2.63**	**0.93**	**1.05**	**6.63**	**3.61E-02**
0 / 13	**39.82**	**17.76**	**12.35**	**128.38**	**0.00E + 00**
1 / 7	**2.38**	**0.83**	**0.95**	**5.92**	**6.96E-02**
1 / 13	**35.92**	**15.90**	**11.24**	**114.81**	**0.00E + 00**
7 / 13	**15.11**	**6.47**	**4.91**	**46.50**	**7.83E-08**
Schoenoplectus californicus					
0 / 1	0.28	0.23	0.03	2.45	4.16E-01
0 / 7	0.22	0.18	0.03	1.82	2.42E-01
0 / 13	**0.10**	**0.08**	**0.01**	**0.79**	**2.27E-02**
1 / 7	0.78	0.43	0.19	3.28	9.69E-01
1 / 13	0.37	0.18	0.10	1.36	1.97E-01
7 / 13	0.48	0.22	0.14	1.60	3.81E-01

should be analyzed in a context of frequent flooding, typical of Paraná River Delta front and other wetlands affected by lunar and/or wind tides. Finally, the results of this study help to predict the impact of wetland loss, or the changes in wetland hydrological regime, on the vegetation, and serve as tools for the management and the ecological restoration of these environments (look deeper into these issues at, for example, Davidson 2014; Sica et al. 2016; Finlayson et al. 2018; An and Verhoeven 2019).

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Author Contributions All authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by Horacio Sirolli, Andriy Bazylenko and Mariano Ernesto Ramello. The first draft of the manuscript was written by Horacio Sirolli and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Data Availability The datasets generated during the current study are available from the corresponding author on reasonable request.

Declarations

Competing Interests The authors have no relevant financial or non-financial interests to disclose.

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