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Effects of Seasonal Inundation on Riparian Plant Growth and Reproduction

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ABSTRACT

Timing and duration of flooding influence plant maintenance and reproduction, but the extent to which these factors affect different plant species and functional groups (terrestrial vs. riparian) remains unclear. Our study aimed to determine broad patterns of resilience of these functional groups to seasonal inundation. We conducted an experiment testing four riparian and four terrestrial plant species exposed to three inundation treatments (no inundation, 1 week, 4 weeks) in both spring and summer. In spring, long inundation often reduced the survival and growth of the terrestrial grasses, while riparian species showed high survival and stable growth across treatments. Flowering and seed production in both terrestrial and riparian species were often delayed or reduced by spring inundation. In summer, terrestrial grasses exhibited reduced survival and growth with inundation, while riparian species performed best with short inundation. Flowering in most species began earlier than the summer treatments, making the effects of summer inundation on flowering less clear. However, summer inundation promoted reproduction in the riparian species *Juncus amabilis*. Seed viability showed no clear patterns with treatments for most species in either season. Our findings suggest that spring inundation mimicking natural flows may support riparian plant communities by reducing terrestrial plant growth. Riparian species were also more resilient to summer inundation than terrestrial grasses, potentially benefiting from brief flooding. In regulated rivers, environmental flows in spring and short events in summer are likely to promote riparian over terrestrial plants.

1 | Introduction

River regulation alters the magnitude, frequency, duration, and timing of inundation, subjecting riparian vegetation to hydrological regimes that differ substantially from natural conditions (Ye et al. 2018; Poff et al. 1997). Such changes can affect plant survival, growth, and reproduction, impacting riparian plant diversity (Nilsson et al. 1991; Bejarano et al. 2018). Degraded vegetation in regulated systems requires enhanced plant growth and recruitment under favorable conditions to recover, reestablish, and maintain bank stability. However, promoting these responses necessitates a deeper understanding of how plants, particularly different functional groups, respond to seasonal inundation.

Riparian and terrestrial plant species exhibit varying tolerances to inundation, influencing their distribution and persistence along riverbanks (Main et al. 2022; Vivian et al. 2020; Fraaije et al. 2015; Tonkin et al. 2020). While many riparian plants can thrive in saturated soil or partially flooded conditions, their survival may be reduced when fully submerged for extended periods (Vivian et al. 2014). Riparian

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species are generally better adapted to fluctuating water levels, with morphological adaptations such as aerenchyma formation and petiole elongation facilitating survival during inundation (Blom and Voesenek 1996; Voesenek et al. 2004; Garssen et al. 2015) and an ability to recover after prolonged flooding through regeneration mechanisms (Catford and Jansson 2014). In contrast, most terrestrial species lack these adaptations, making them vulnerable to inundation (Vivian et al. 2020; Casanova 2011; Blom and Voesenek 1996). Despite these broad distinctions, certain terrestrial species demonstrate resilience through mechanisms such as rapid root growth or dormancy (Nabben et al. 1999; Ram et al. 2002; He et al. 1999). Understanding how these functional groups respond to inundation can provide critical insights for managing riparian vegetation in regulated river systems.

The duration and timing of inundation are critical factors shaping plant growth, reproduction, and community composition along rivers. Prolonged inundation often hinders seedling establishment and can shift community dynamics by favoring flood-tolerant species (Casanova and Brock 2000; Greet et al. 2013). While riparian species exhibit resilience through mechanisms like vegetative propagation and underwater photosynthesis, terrestrial species are typically more vulnerable to sustained flooding due to their limited physiological adaptations (Blom and Voesenek 1996; Vivian et al. 2020). However, inundation can disrupt key reproductive stages of both riparian and terrestrial plant species. For instance, flooding may delay flowering and reduce seed production by interfering with physiological signals such as oxygen availability and hormone regulation (e.g., ethylene and abscisic acid) (Zhou et al. 2020). In some cases, flowering may be postponed entirely to subsequent years (Van Der Sman et al. 1993).

The timing of inundation is also important because plants are often less tolerant of inundation in warmer seasons (Vivian et al. 2020; Kitanović et al. 2023). Suitably timed floods can enhance seed dispersal and recruitment opportunities (Dawson et al. 2017), while inappropriately timed inundation risks causing reproductive failure (Garssen et al. 2015; Main et al. 2022). Despite this, much remains unclear about how seasonal inundation specifically impacts different stages of plant reproduction, such as flowering, seed production, and seed viability. Furthermore, studies often focus on either plant growth responses or reproductive outputs, rarely integrating the two to provide a holistic view of plant performance under variable inundation scenarios. Few experimental studies simulate the natural timing and duration of floods across plant functional groups in controlled environments, limiting our understanding of how effects differ, particularly during critical reproductive stages.

Environmental flow management aims to balance ecological and human water demands by restoring hydrological patterns that support riparian plant communities. However, implementing effective flow interventions requires an understanding of how inundation timing and duration affect plant survival, growth, and reproduction across functional groups (Poff et al. 1997). Experimental studies that simulate seasonal inundation are essential to identify thresholds and mechanisms that determine plant responses (Webb et al. 2012). By examining both spring and summer inundation effects, our study addresses these gaps, investigating how seasonal timing and varying inundation durations influence plant survival, growth, and reproductive success across functional groups. This information is vital for developing flow strategies that mitigate the negative impacts of river regulation and improve the effectiveness of environmental flow management.

We conducted a nursery experiment manipulating inundation timing (spring or summer) and duration (no inundation, 1 week, or 4 weeks) across two distinct plant functional groups, riparian plants and terrestrial grasses, focusing on plant growth and reproductive output. We hypothesized that (1) terrestrial grasses would show greater declines in growth and reproduction in response to inundation compared to riparian species, especially during summer; (2) longer inundation durations would delay flowering in spring for both groups but primarily affect riparian plants in summer due to earlier flowering in terrestrial species; and (3) reproductive output, including seed production and viability, would decline with long inundation, especially in terrestrial grasses during spring and riparian species during summer. By focusing on survival, growth, flowering, seed production, and seed viability at the functional group level, our study seeks to uncover broad patterns of resilience and vulnerability to inform the management of environmental flows.

2 | Methods

We conducted a nursery experiment during austral spring and summer 2022/23 at the University of Melbourne, Burnley Campus, to determine the responses of terrestrial and riparian plant species to inundation duration and timing.

2.1 | Study Species

Eight native, perennial plant species were chosen representing different inundation tolerances and included both riparian (*Carex appressa*, *Cyperus lucidus*, *Juncus amabilis*, *Eleocharis acuta*; a mix of sedge and rush species) and terrestrial (*Bothriochloa macra*, *Microlaena stipoides*, *Poa labillardierei*, *Rytidosperma caespitosum*; all grasses) species (Figure 1). Individual plants that were of similar height (~20 cm), age (3–4 months), and expected to flower in the coming spring/summer were selected (Table 1).

The terrestrial species selected for this experiment exhibit varying tolerance levels to complete inundation. *Poa labillardierei*, for example, is a terrestrial damp species, and while considered generally intolerant of flooding, it can germinate on saturated soils (Casanova 2011) and can survive up to 8 weeks of flooding during summer and autumn (Kitanović et al. 2023; Vivian et al. 2020). In contrast, the survival and growth of *Rytidosperma caespitosum*, a terrestrial dry species, is more quickly and severely impacted by inundation (Vivian et al. 2020). The cover of *Microlaena stipoides*, another terrestrial damp species, reduced following a major flood event, indicating that prolonged inundation negatively affects its survival and growth (Greet et al. 2015). *Bothriochloa macra*, a C4 species with high drought tolerance

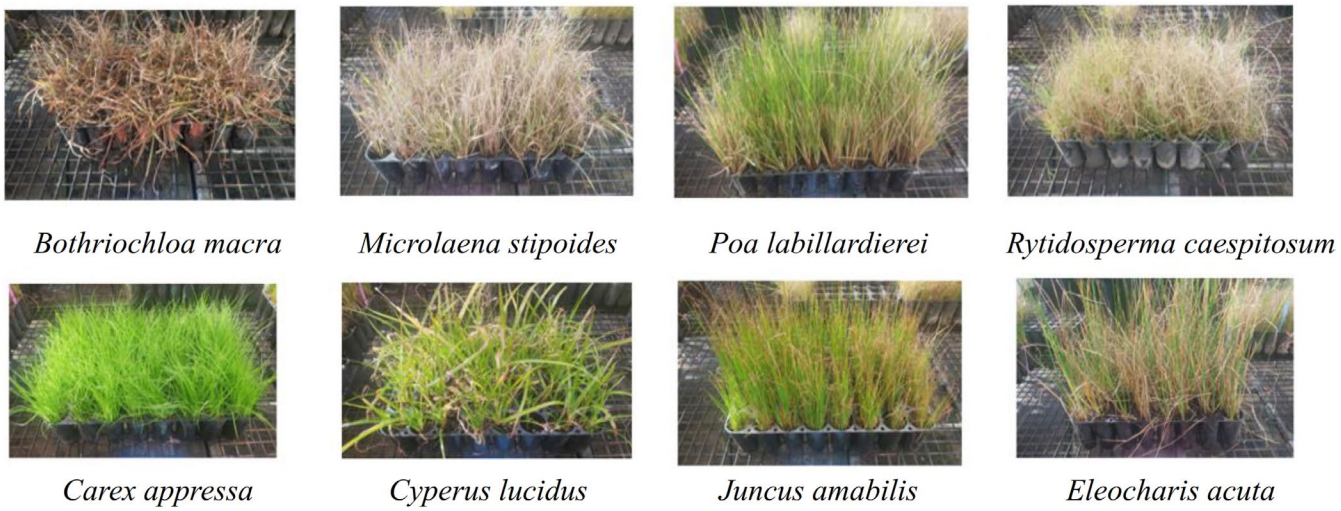


FIGURE 1 | The eight perennial plant species included in the inundation experiment. All plants were sourced from a commercial plant nursery. The top row comprises terrestrial grass species, while the bottom row comprises riparian plant species, a mix of rush and sedge species (Table 1). [Color figure can be viewed at wileyonlinelibrary.com]

TABLE 1 | Attributes of the eight perennial plant species used in the inundation experiment. All species are common to riparian zones in south-eastern Australia.

Species name	Common name	Growth form	Expected inundation tolerance	Average initial height (cm)	Flowering time[a]
Bothriochloa macra	Red grass	Grass	Intolerant	9	Early summer–mid autumn Late winter–early spring
Microlaena stipoides	Weeping grass	Grass	Intolerant	12	Early spring–early autumn
Poa labillardierei	Common Tussock grass	Grass	Tolerant	25	Mid spring–late summer
Rytidosperma caespitosum	Common wallaby grass	Grass	Intolerant	18	Mid spring–mid summer
Carex appressa	Tall sedge	Sedge	Tolerant	16	Early spring–late spring
Cyperus lucidus	Leafy flat sedge	Sedge	Tolerant	18	Early spring–late summer
Juncus amabilis	Gentle rush	Rush	Tolerant	30	Early summer–mid autumn
Eleocharis acuta	Common spike rush	Rush	Tolerant	26	Early spring–late summer

[a]Source: VicFlora (2024).

and an adaptation to well-drained soils, is likely intolerant of prolonged inundation (Stone et al. 2020), although specific studies on its inundation tolerance are limited.

The riparian species used in this study, a mix of rushes and sedges, are amphibious fluctuation tolerator species commonly occurring on lower riverbanks (Pereira et al., 2021). These species have been demonstrated to increase in cover in response to 6-week inundation, both in spring and summer (Greet et al. 2013).

2.2 | Plant Preparation

Plants were sourced from a commercial plant nursery as tube stock. The plants were transplanted into 1.4 L round black



(A) (B) (C)

FIGURE 2 | Photographs of (A) plants growing inside the glasshouse; (B) tank layout under the polytunnel ($n = 18$ tanks); and (C) pot arrangement within each tank ($n = 3$ plants per species per tank). [Color figure can be viewed at wileyonlinelibrary.com]

plastic pots with approximately 3 cm of pine bark in the bottom and filled to 2 cm from the top with a 7:1 sand:topsoil growing media. All plants were kept in a glasshouse for 4 weeks to acclimatize prior to experiment commencement with automatic irrigation for 2 min twice per day, keeping the pot media moist (Figure 2A). Plants were fertilized with Pete's Professional liquid fertilizer (0.5 g/L, N:P:K of 20:8.7:16.6) 2 weeks after transplanting. Established plants of a similar size were selected for the inundation experiment.

2.3 | Experimental Setup

The experiment commenced at the start of austral spring (September 2022) and continued until the end of austral summer (February 2023), a total of 27 weeks. Eighteen tanks approximately 100 cm in height and 95 cm in diameter were used for the experiment. Tanks were located in an outdoor polytunnel with a translucent plastic roof and no walls (Figure 2B).

Three inundation durations were used in the experiment: (1) no inundation, (2) 1 week inundation (short inundation treatment), and (3) 4 weeks inundation (long inundation treatment), applied in either of two seasons (spring and summer), resulting in six different treatments (Figure 3). Each tank was randomly allocated to one of the six treatments, with three tanks per treatment. Three replicate plants of each species were randomly allocated to each tank. Plants were placed on a platform inside each tank positioned halfway up the tank (Figure 2C). Automatic pendant loggers were mounted in each tank below the water surface to record water temperature and light levels hourly. The average daily maximum water temperatures were 20.6°C in spring and 26.5°C in summer during the experiment period.

2.4 | Plant Measurements

2.4.1 | Plant Biomass

At the start of the experiment, six plants of each species were harvested for initial biomass measurement (plant dry weight). To measure the initial biomass, plant roots were washed clean of soil, above-ground plant parts (stem and leaves) and roots were separated, dried for 72 h at 80°C, and weighed. A similar procedure was performed at the completion of the experiment for all remaining plants to determine their final shoot and root biomass, and biomass change was calculated by comparing values with average initial biomass as an indicator of plant growth.

2.4.2 | Plant Survival and Flowering

At weekly intervals, plant survival (yes/no), flowering (yes/no), and the number of flower heads were recorded. When green leaf material was no longer visible, plants were recorded as dead.

2.4.3 | Seed Production

Prior to seed setting, meshed bags were placed around flower heads and used to collect plant seeds. Seeds released into the bags were then collected and stored in a sealed container in a cool and dry place. Seeds collected from multiple seed heads from the same plant were pooled to create a single seedlot for each plant. The number of seeds and weight of collected seeds from each plant were measured. As *Juncus amabilis* produces many tiny seeds that are difficult to count individually, the total weight of the collected seeds in each plant was obtained, and the number of seeds in 0.0001 g was counted and used to determine the total seed quantity.

2.4.4 | Seed Viability

Collected seeds were used to test for viability. From each plant, up to 25 seeds were sown in a Petri dish with moistened filter paper. Petri dishes were sealed with Parafilm to prevent desiccation and incubated at a constant temperature of 25°C with 8 h light/16 h dark (SER 2023). Weekly observations were made to count the number of germinated seeds over a two-month period. The moisture level of the filter paper was monitored, and water was added as needed.

2.5 | Data Analysis

Statistical analysis was conducted on plant survival, growth, survival, biomass, flowering, seed production, and seed viability

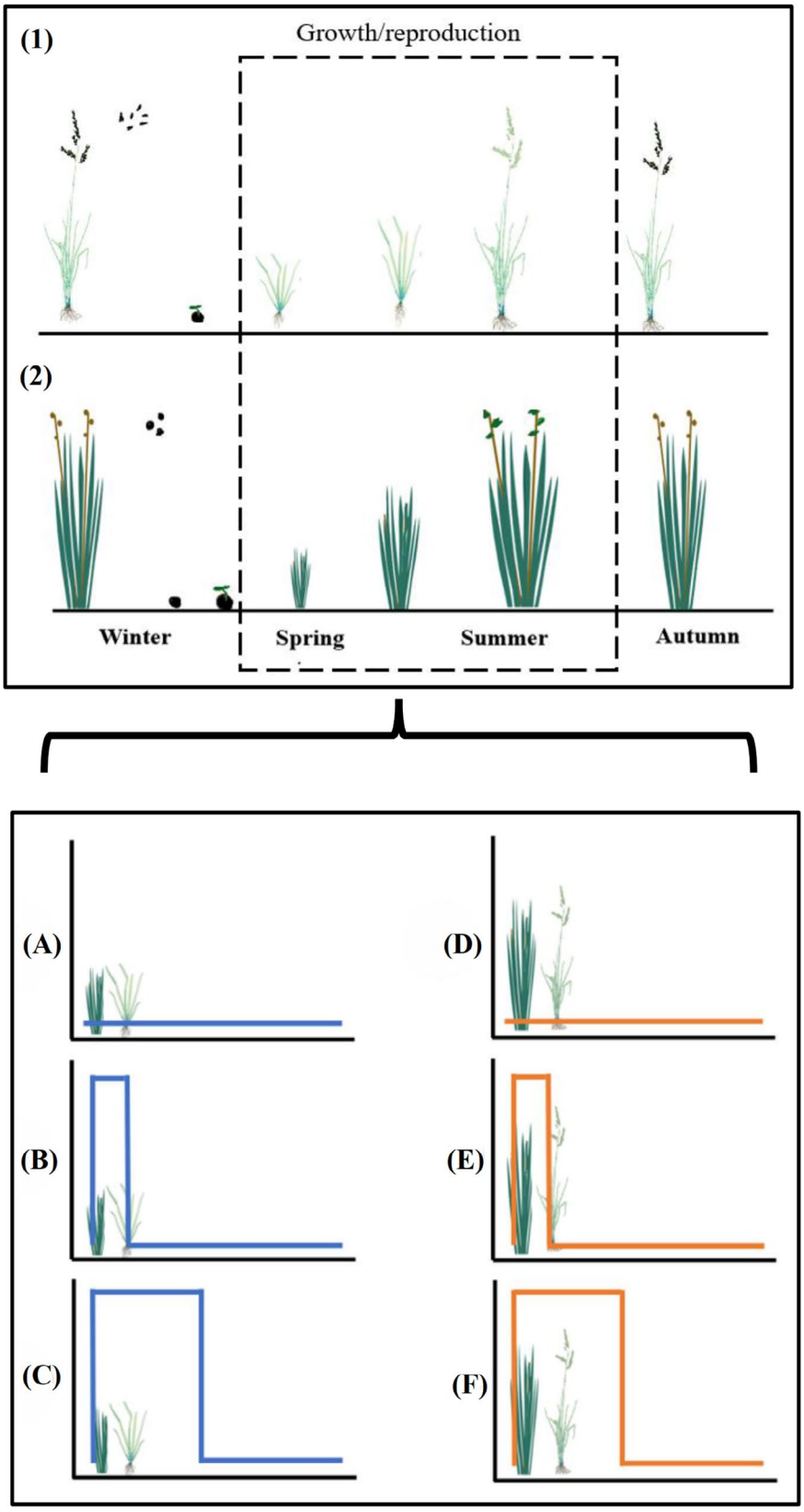


FIGURE 3 | A conceptual diagram illustrating the six experimental treatments applied in spring (blue) and summer (orange). The treatments are (A) spring no inundation (plants not inundated at any stage), (B) spring short inundation (plants fully inundated for 1 week during early spring), (C) spring long inundation (plants fully inundated for 4 weeks during early spring), (D) summer no inundation (plants not inundated at any stage), (E) summer short inundation (plants fully inundated for 1 week during early summer), and (F) summer long inundation (plants fully inundated for 4 weeks during early summer). The diagram also represents the life history stages of (1) a typical perennial grass and (2) a riparian plant, highlighting their growth and reproductive stages considered in this experiment. Perennial grasses generally tend to flower earlier compared to riparian plants. [Color figure can be viewed at wileyonlinelibrary.com]

variables to evaluate treatment effects using R version 4.3.2 (R Core Team 2023). Individual plants ($n = 9$ per species per treatment) were the experimental unit for analysis.

Plant survival rates were evaluated as the proportion of plants surviving at each week for each species in each treatment. Kaplan–Meier models were used to test whether survival curves differed significantly between experimental treatments for each species using the *survival* package (Therneau and Grambsch 2000).

To evaluate the effect of the different treatments on plant growth (change in total plant biomass), linear mixed-effects models were used with each of the eight species modeled separately. Models were fitted using the lmer function from the *lme4* package (Bates et al. 2015). The models included treatment as a fixed effect and tank as a random effect to account for potential variability between experimental tanks. Post hoc pairwise comparisons between treatments were conducted using the *emmeans* package (Lenth 2024). Estimated marginal means were computed for each treatment level, and Tukey's pairwise contrasts were examined to identify significant differences between treatments. The resulting *p*-values, estimated marginal means, and standard errors were used to interpret the differences in biomass response between treatment groups.

To assess flowering proportion, seed production, and seed viability, generalized linear mixed-effects models were fitted using the *glmmTMB* package (Brooks et al. 2017). Flowering proportions and seed viability, both proportion data, were analyzed with a beta distribution, while seed production (counts of seed heads per plant and seeds per seed head) was analyzed with a Poisson distribution. For flowering and seed viability, small constants were added to handle zeros and scaling, respectively. All analyses were conducted separately for spring and summer to account for seasonal variation, with post hoc pairwise comparisons performed using the *emmeans* package (Lenth 2024) to estimate marginal means and identify significant treatment effects ($p < 0.05$). Tukey's adjustment was applied for multiple comparisons where appropriate.

3 | Results

3.1 | Plant Survival

In the spring treatments, all plants survived except for *R. caespitosum* (88% survival) and *M. stipoides* (22% survival) in the spring long inundation treatment (Figure 4A). In summer, while most terrestrial grasses in the no inundation and short inundation treatment survived, several plants across all terrestrial grass species were killed by long inundation, with significant reductions in survival for *B. macra* ($p = 0.04$) and *R. caespitosum* ($p < 0.001$) (Figure 4B). All riparian plants survived short and long inundation in both spring and summer.

3.2 | Plant Growth

Riparian plants generally exhibited greater overall biomass growth compared to terrestrial grasses, regardless of the treatment (Figure 5). Terrestrial grasses tended to grow more in the absence of inundation in both spring and summer and appeared to be more sensitive to long inundation, particularly in summer. *B. macra* was generally less sensitive to short inundation than the other grass species, particularly in summer when it grew equally well under the short inundation and no inundation treatments. However, most comparisons between treatments for the terrestrial grasses were not significant, except that long inundation significantly reduced the biomass of *M. stipoides* ($p = 0.008$) and *P. labillardieri* ($p = 0.075$) compared to no inundation in spring.

Similar to terrestrial species, riparian species tended to grow less with inundation in spring (Figure 5). In contrast, riparian plants tended to grow best with short inundation in summer. However, variability in the biomass increases meant that there were no significant differences between treatments.

3.3 | Plant Flowering

Among the eight species, flowering was observed in six species, with *C. appressa* and *C. lucidus* not flowering during the experiment in any treatment. For the terrestrial grass species, *B. macra*, *P. labillardierei*, and *R. caespitosum*, short and long inundation in spring delayed the onset of flowering (Figure 6). Moreover, the proportion of flowering in all terrestrial species tended to decrease with spring long inundation, with *P. labillardierei* flowering significantly reduced ($p = 0.012$, Table S1). Similarly, *R. caespitosum* flowering was reduced with spring long inundation ($p = 0.025$) but was increased with spring short inundation ($p = 0.012$, Table S1). Among riparian species, the onset of flowering was delayed only in *E. acuta* with long inundation (Figure 6). However, the proportion of flowering plants for both *J. amabilis* and *E. acuta* was reduced with inundation, particularly *E. acuta* with short inundation ($p = 0.010$, Table S1).

In summer, the flowering of *P. labillardierei*, *R. caespitosum*, *M. stipoides*, and *E. acuta* commenced earlier than the treatments, with no clear evidence of the impact of the treatments on the proportion of flowering plants afterward (Figure 6). The terrestrial grass *B. macra* tended to flower less after long inundation, while the riparian species *J. amabilis* flowered earlier and in greater abundance following inundation. However, summer inundation had no significant effects on the proportion of flowering plants.

3.4 | Reproductive Output

3.4.1 | Number of Seed Heads

In spring, terrestrial grasses tended to produce more seed heads in the no inundation treatment (Figure 7A), with long inundation significantly reducing seed head production in *R. caespitosum* ($p = 0.001$, Table S2) compared to the short inundation treatment, and *B. macra* exhibiting a significant reduction in seed head production in response to short inundation ($p = 0.031$, Table S2).

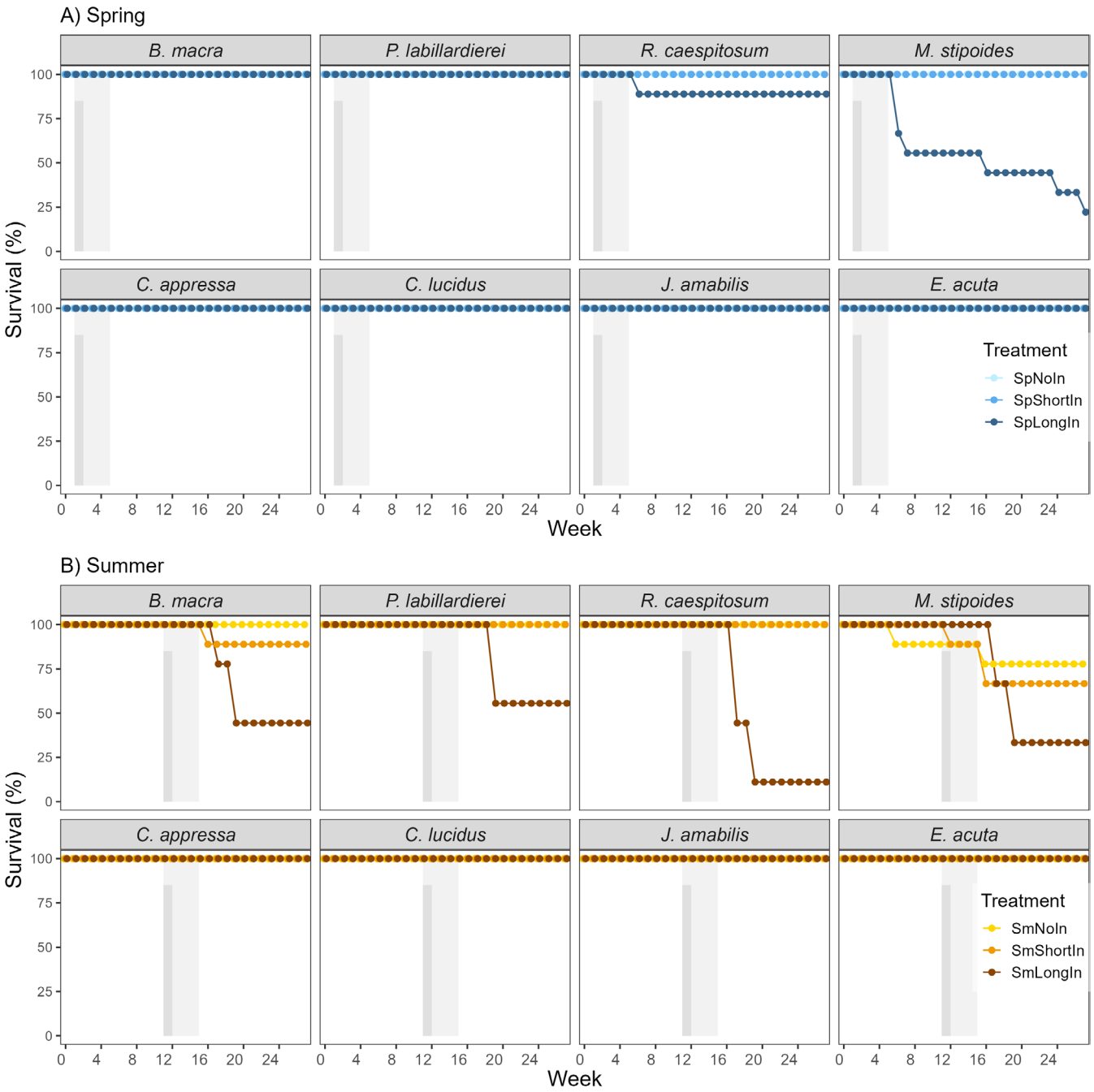


FIGURE 4 | Survival rates of plants by species during the experiment for the different treatments (NoIn = no inundation, ShortIn = short inundation, LongIn = long inundation) in (A) spring (Sp) and (B) summer (Sm). Dark grey shading in each panel indicates the short inundation period and light grey shading indicates the long inundation period. [Color figure can be viewed at wileyonlinelibrary.com]

For the riparian species *J. amabilis* and *E. acuta*, seed head production also tended to be greater without inundation, with *E. acuta* exhibiting a significant reduction in seed head production in response to short inundation ($p = 0.040$, Table S2).

In summer, *B. macra* seed head production appeared to be unaffected by short inundation but was reduced by long inundation (Figure 4). In contrast, *J. amabilis* seemed to benefit from inundation, with higher seed head counts in the inundation treatments compared to no inundation; however, these differences were not significant (Figure 7B).

3.4.2 | Number of Seeds per Seed Head

In spring, all terrestrial species produced the highest median number of seeds per seed head without inundation and produced more seeds in response to short inundation compared to long inundation. *R. caespitosum* seed production was significantly reduced by long inundation compared to short inundation ($p < 0.001$, Table S3). Riparian species *J. amabilis* followed a similar trend to the terrestrial grasses, while *E. acuta* produced similar numbers of seeds per seed head across the treatments (Figure 8A).

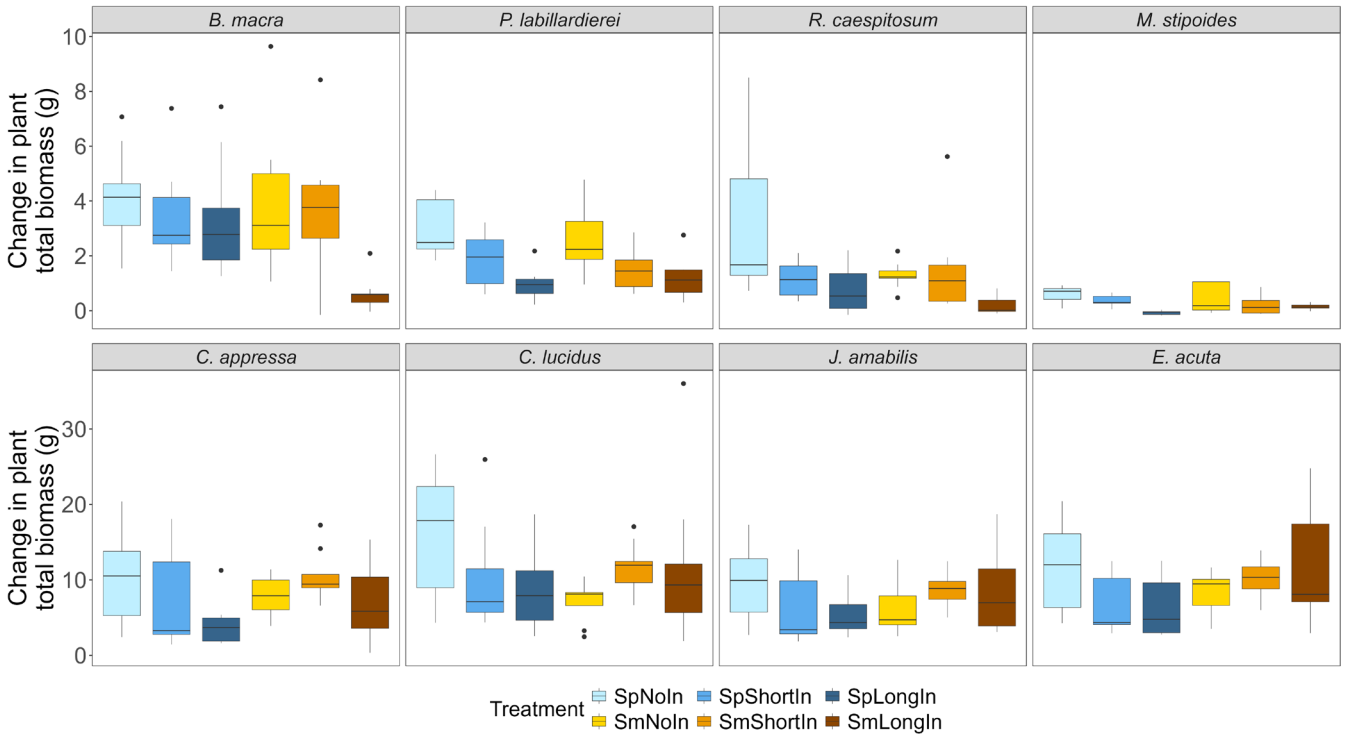


FIGURE 5 | Change in plant biomass by species during the experiment for the different treatments (NoIn = no inundation, ShortIn = short inundation, LongIn = long inundation) in spring (Sp) and summer (Sm). N.B. different y-axes values in the top (terrestrial plants) and bottom (riparian plants) rows. [Color figure can be viewed at wileyonlinelibrary.com]

In summer, *B. macra* showed a nonsignificant reduction in seed production under short-duration inundation, while long-duration inundation resulted in a more substantial reduction. In contrast, *J. amabilis* produced a higher number of seeds per seed head in response to long inundation, while the no inundation treatment resulted in almost no seed production, although this difference was not statistically significant (Figure 8B, Table S3).

3.5 | Seed Viability

In spring, seed viability was variable across plants but did not differ between treatments for most species (Figure 9A), with the exception of *R. caespitosum*, which had significantly higher viability in plants exposed to short inundation compared to long inundation ($p = 0.006$, Table S4). In summer, there were no clear patterns in seed viability between treatments for either *B. macra* or *J. amabilis* (Figure 9B).

4 | Discussion

Terrestrial grasses generally exhibited higher survival and growth in the absence of inundation across both spring and summer, whereas long inundation, especially in summer, significantly reduced terrestrial plant survival and performance. In contrast, riparian plants demonstrated resilience under both short and long inundation treatments, with some species even benefiting from short inundation in summer through enhanced growth and reproductive output. While flowering and seed production in both terrestrial and riparian species were often delayed or reduced by inundation in spring, summer inundation effects were unclear for terrestrial but positive for riparian species.

4.1 | Impact of Inundation on Plant Survival and Growth

Our findings align with previous studies showing that terrestrial plant survival and biomass decline with inundation. These reductions are often more pronounced during warmer seasons, when the increased metabolic demands of plants reduce their tolerance to flooding (Van Eck et al. 2005; Van Eck et al. 2006; Vivian et al. 2020; Main et al. 2022). In our experiment, the growth and survival of a few terrestrial species declined after 4 weeks of inundation in spring, and the survival of all species declined after 4 weeks of inundation in summer. This is consistent with previous studies that indicate that terrestrial plants demonstrate greater tolerance to inundation in cooler compared to warmer conditions (Kitanović et al. 2023; Main et al. 2022; Van Eck et al. 2006). These responses can be species-specific, with terrestrial species capable of mobilizing and metabolizing carbohydrates during inundation able to survive longer, regardless of the season (Van Eck et al. 2005). Nonetheless, flood-intolerant terrestrial species, regardless of season, may lack the physiological mechanisms necessary for accessing carbohydrates under prolonged inundation stress (Laan and Blom 1990; Crawford 2003). It is important to note, however, that inundation tolerance varies among the terrestrial grasses studied (Table 1), with *Poa labillardierei* exhibiting greater tolerance than the others. These species-specific differences likely contribute to the variation we observed and

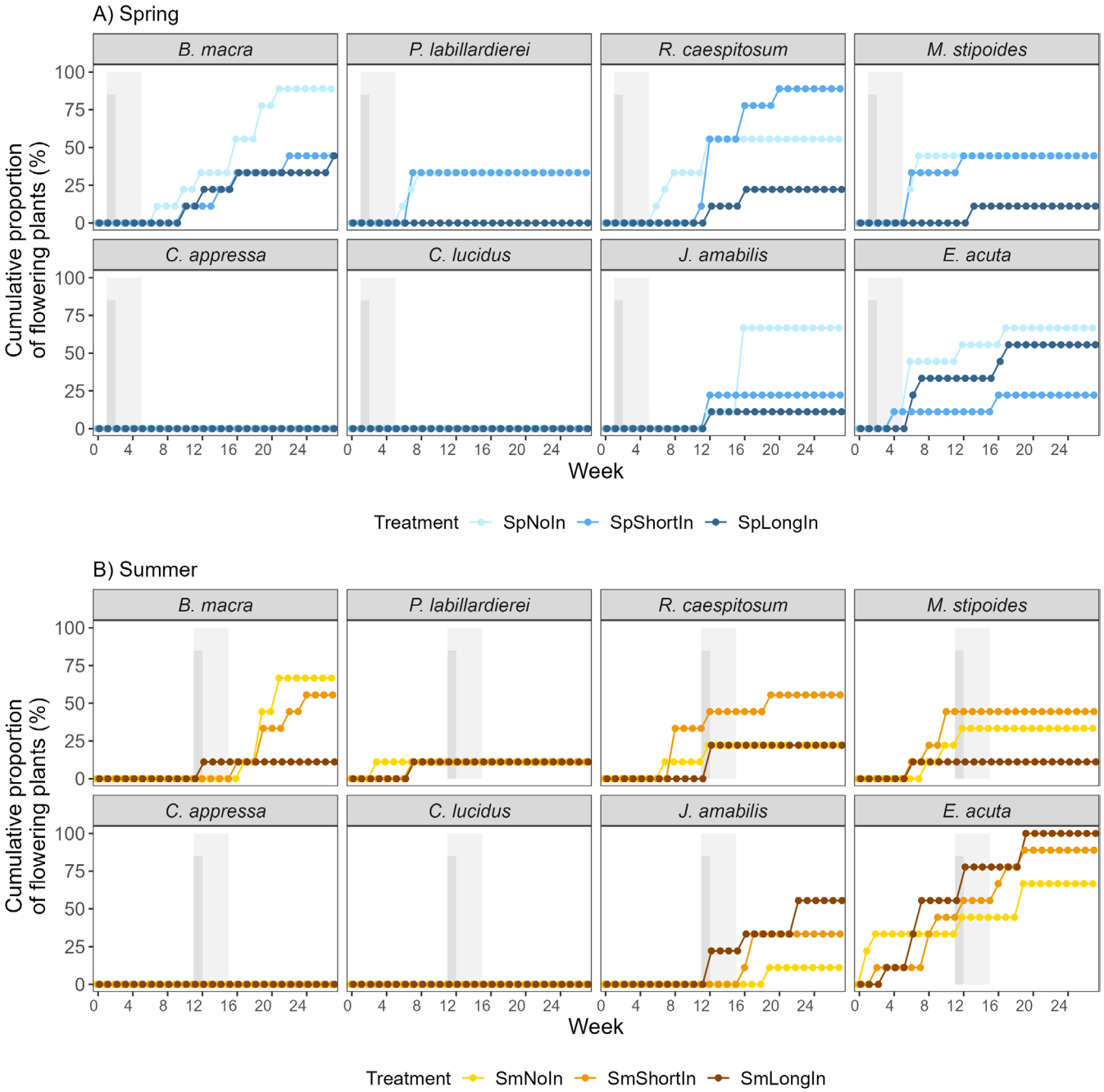


FIGURE 6 | Cumulative proportions of flowering plants by species during the experiment in response to the different treatments (NoIn = no inundation, ShortIn = short inundation, LongIn = long inundation) in (A) spring (Sp) and (B) summer (Sm). Dark grey shading in each panel indicates the short inundation period and light grey shading indicates the long inundation period. [Color figure can be viewed at wileyonlinelibrary.com]

indicate that outcomes could differ if alternative terrestrial species were tested.

In contrast, riparian species in our study demonstrated high survival rates and no substantial biomass reduction under either short or long inundation in both spring and summer. This is consistent with previous studies that show riparian plants generally tolerate or respond well to temporary inundation (Greet et al. 2013; Greet et al. 2015). This is likely to be because such species have adaptations, such as aerenchyma tissue and the ability to elongate their stems, which enable efficient internal oxygen transport, reducing hypoxic stress during temporary inundation (Jackson and Armstrong 1999; Blom and Voesenek 1996). Among our study species, *J. amabilis* and *E. acuta* exhibited rapid stem elongation in response to long inundation in both seasons. This elongation of stems or leaves is a well-documented adaptive strategy of wetland plants that allows them to reconnect with light and air, improving oxygen and carbohydrate supply that are critical for sustaining plant functions under inundation stress (Rijnders et al. 2000; Banach et al. 2009).

4.2 | Impact of Inundation on Plant Reproduction

Our terrestrial study species showed notable sensitivity to spring inundation, with flowering delayed or reduced under

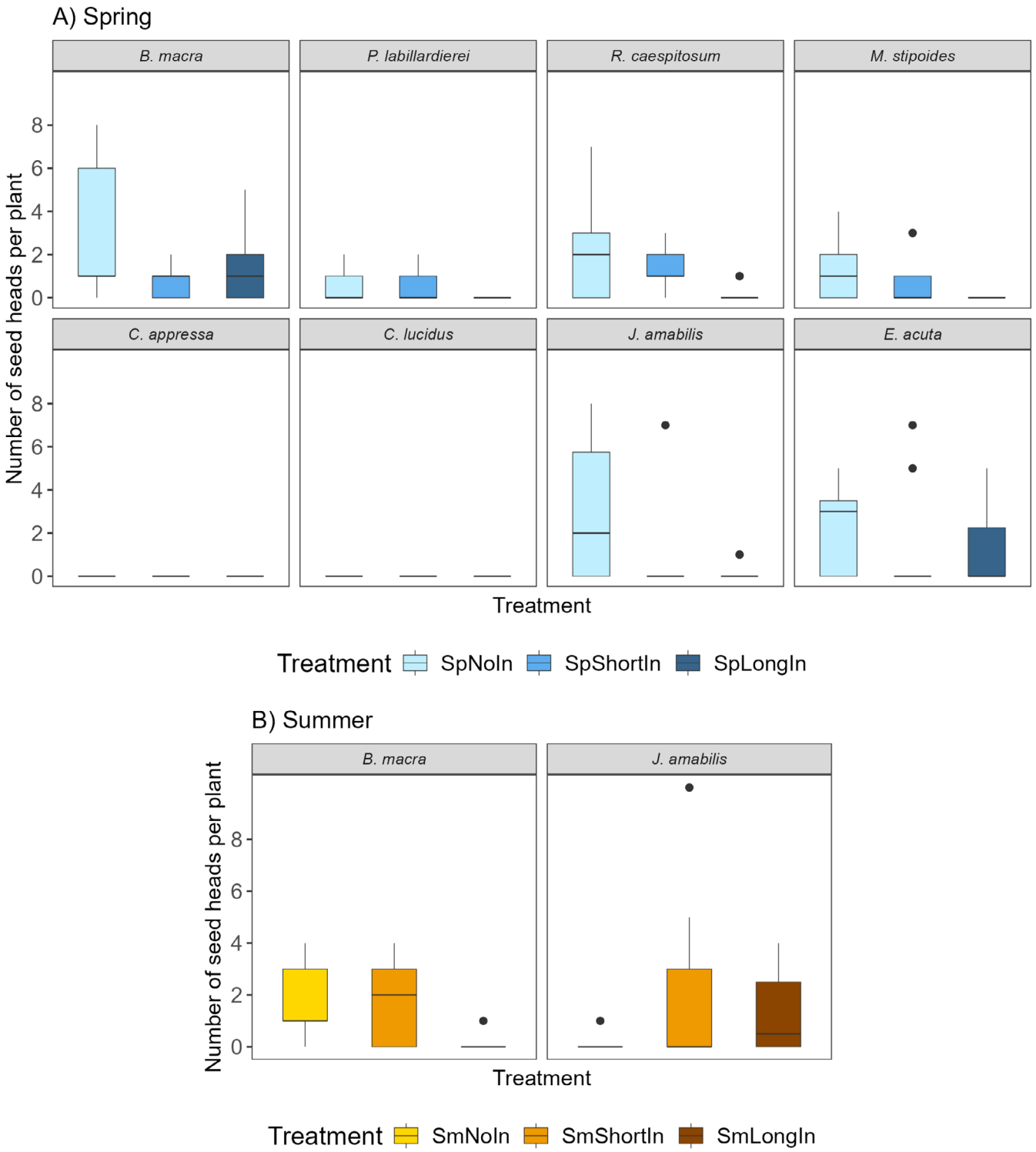


FIGURE 7 | Number of seed heads produced per plant for each species under different inundation treatments (NoIn = no inundation, ShortIn = short inundation, LongIn = long inundation) in (A) spring (Sp) and (B) summer (Sm). *C. appressa* and *C. lucidus* did not flower during the experimental period. Only *B. macra* and *J. amabilis* are shown for summer, as these were the only species that flowered following the treatments. The y-axis is scaled consistently to better highlight the variation across species. [Color figure can be viewed at wileyonlinelibrary.com]

both short and long inundation treatments. This aligns with other observations of reduced flowering in terrestrial plants following inundation (Sman et al. 1992; Greet et al. 2013), which is likely driven by their inability to morphologically or physiologically adapt to flooding. As inundation restricts air access, it blocks the energy production necessary for reproductive processes, thus limiting flowering and seed head production in these species (Robe and Griffiths 1998). Studies indicate that plant reproductive success in wetland habitats often correlates with biomass, as more robust growth can enhance the allocation of resources to reproductive structures (Warwick and Brock 2003). In our study, terrestrial plants

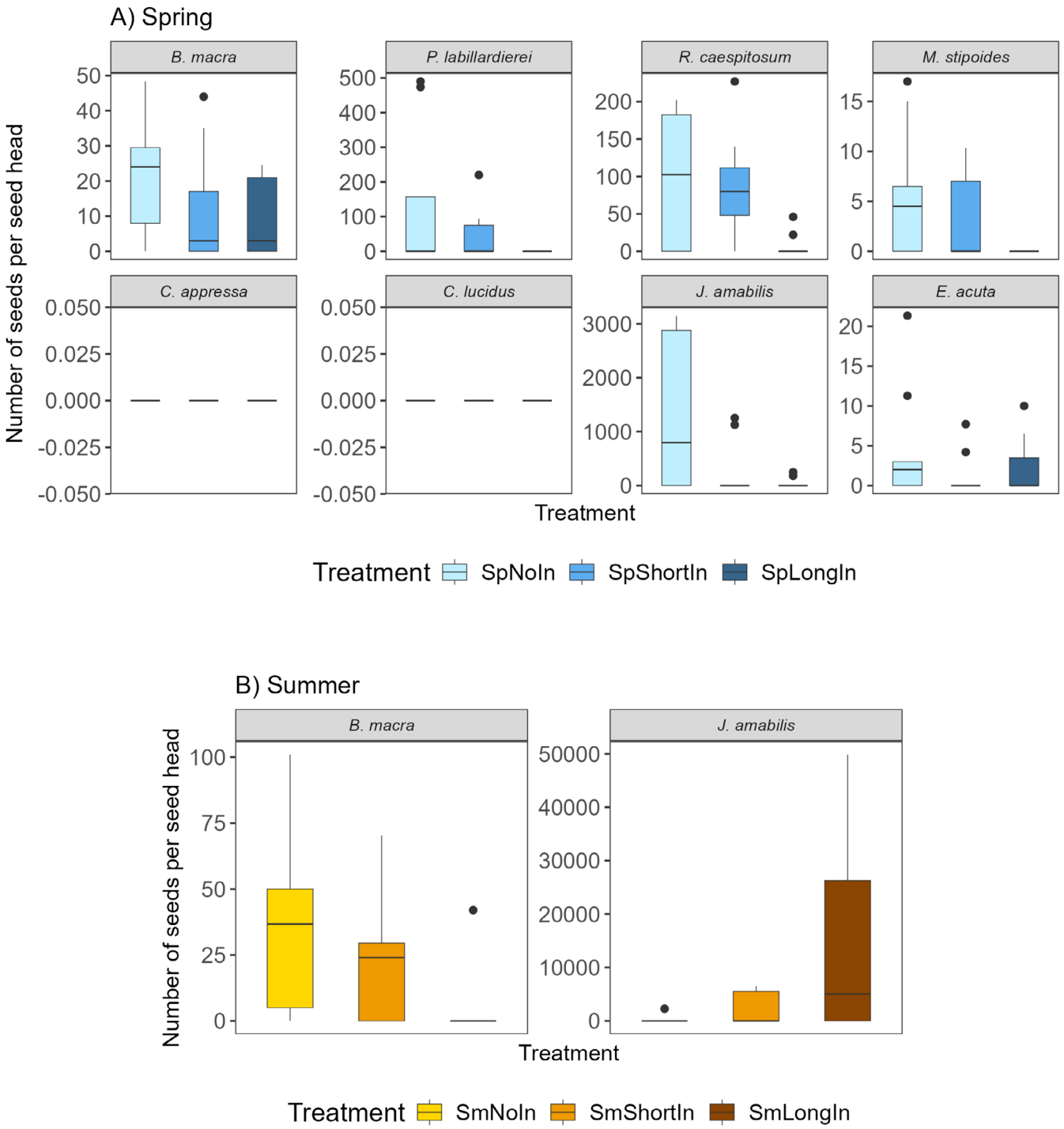


FIGURE 8 | Number of seeds produced per seed head for each species under different inundation treatments (NoIn = no inundation, ShortIn = short inundation, LongIn = long inundation) in (A) spring (Sp) and (B) summer (Sm). *C. appressa* and *C. lucidus* did not flower during the experimental period. Only *B. macra* and *J. amabilis* are shown for summer, as these were the only species that flowered following the treatments. The y-axis is scaled freely given the large variation between species. [Color figure can be viewed at wileyonlinelibrary.com]

subjected to inundation exhibited reduced growth, which likely limited the resources available for flowering and seed production. Collectively, our results indicate that terrestrial grasses probably lack the morphological adaptations and resource allocation strategies to sustain growth and reproduction under inundation, reducing their competitive advantage in regularly inundated environments.

In contrast, riparian species such as *J. amabilis* and *E. acuta* demonstrated greater reproductive output in response to summer inundation. In our study, *J. amabilis* responded to inundation by advancing flowering onset and producing a greater number of flowerheads. This aligns with findings by Mony et al. (2010), who observed that riparian species often enhance their allocation to reproductive structures during partial inundation.

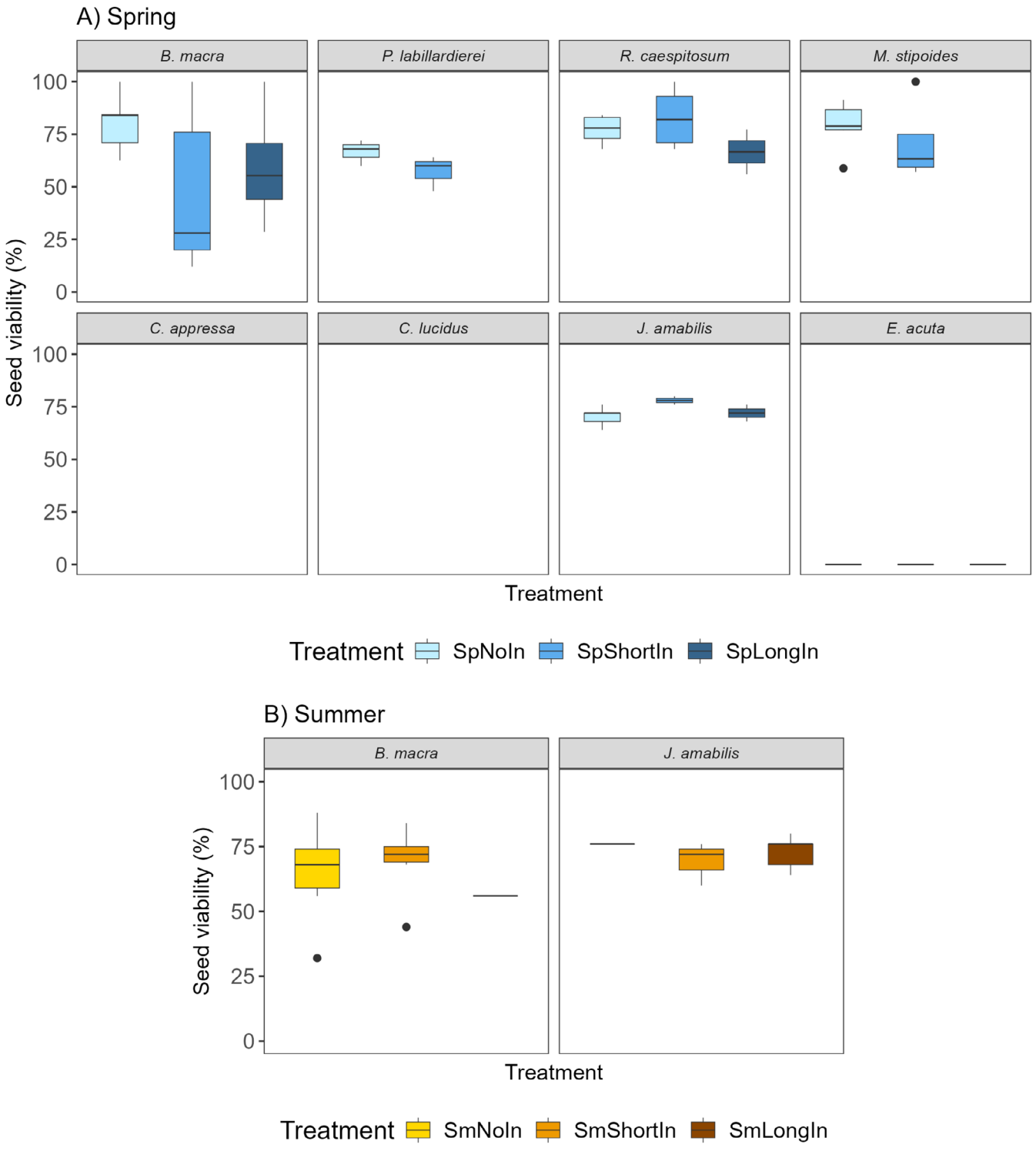


FIGURE 9 | Seed viability for each species under different inundation treatments (NoIn = no inundation, ShortIn = short inundation, LongIn = long inundation) in (A) spring (Sp) and (B) summer (Sm). *C. appressa* and *C. lucidus* did not flower during the experimental period and none of the *E. acuta* germinated. Only *B. macra* and *J. amabilis* are shown for summer, as these were the only species that flowered following the treatments. [Color figure can be viewed at wileyonlinelibrary.com]

Although their study focused on partial inundation, the similar reproductive advantages observed with periodic full inundation in our study suggest shared mechanisms, such as stem elongation, which enables plants to access light and air. Furthermore, inundation depth can positively influence reproductive timing in some riparian plants. For instance, Wang et al. (2014) found that increased water depths favored sexual reproduction in *Zizania latifolia*, with prolonged inundation advancing the onset and increasing flowering. Alternatively, *E. acuta* exhibited stable seed head production across treatments, indicating a tolerance mechanism that enables consistent reproduction despite variability in water levels. This stability highlights the

capacity of some riparian species to sustain reproduction under fluctuating hydrological regimes, such as via balancing ethylene production, concentration, and sensitivity, which are critical for adaptive growth and reproduction under partial inundation (Blom et al. 1990).

The contrasting flowering responses of terrestrial and riparian species to inundation likely reflect differences in phenology and physiological adaptations. Terrestrial grasses flower mostly in spring, so inundation at this time can delay or suppress reproduction. In contrast, riparian species, such as *Eleocharis acuta* and *Juncus amabilis*, often flower in summer and are adapted to tolerate temporary flooding, so summer inundation aligns with and can enhance their flowering.

4.3 | Implications of Findings for Riverine Ecology and Management of Regulated Rivers

Our findings highlight that targeted short-duration spring inundations can be highly beneficial for managing vegetation in regulated rivers. These flows provide essential moisture for terrestrial and riparian seedling establishment without significantly impacting plant survival (Bejarano et al. 2018; Nilsson and Svedmark 2002). Early spring inundation, if kept short in duration, is likely to support a balanced vegetation composition by promoting the maintenance of both terrestrial and riparian plants. Additionally, long-duration spring events can help limit the encroachment of terrestrial species on lower banks, given they are more sensitive to inundation while having negligible effects on riparian plants. Importantly, spring flows that overlap with early flowering stages may stimulate reproductive success in riparian plants by providing favorable hydrological conditions for flowering and seed set.

In summer, flow management strategies must consider the impact of inundation on terrestrial species, which are very susceptible to water stress and reproductive disruption during warmer months. Summer flows could therefore be used to reduce the abundance or health of undesirable terrestrial species; however, this will not influence annual species that have already senesced by this time (Tonkin et al. 2020). Alternatively, short flow events in summer could promote the flourishing of riparian plant species. For example, the growth and reproductive output of rush species such as *Juncus amabilis* are likely to be increased following short inundation events in summer. Short, intermittent summer flow events could help sustain riparian plant species while suppressing terrestrial plant encroachment, providing there is sufficient air exposure between inundation periods to enable growth and seed production. In drier regions, controlled summer inundations may prevent the establishment of abundant exotic terrestrial species, while in wetter regions, where flood-tolerant exotics are common, additional measures such as targeted removal of exotics and replanting of native vegetation may be necessary to maintain ecological integrity (Tonkin et al. 2020).

Our findings suggest that targeted spring inundations of longer duration and short summer inundations could favor riparian vegetation while controlling terrestrial species, helping to sustain the ecological health of river systems. As our study simulated inundation under still water conditions, care should be taken when extrapolating to natural flood events, in which other factors such as flow, shear stress, and erosion may become important.

5 | Conclusion

Inundation timing and duration are critical for managing vegetation in regulated rivers. In spring, long inundation reduced the survival and growth of terrestrial grasses but had minimal impact on riparian plants, indicating that spring flows mimicking natural regimes can suppress terrestrial encroachment and support riparian vegetation. However, delays or reductions in flowering and seed production across both groups underscore the need to align inundation with key reproductive stages. In summer, riparian species demonstrated greater resilience to short inundation, maintaining growth and reproduction, while terrestrial grasses showed reduced survival and performance. These findings suggest that environmental flows in spring and short events in summer are likely to promote riparian vegetation in regulated rivers.

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Data Availability Statement

All relevant data and code for analyses are available via the Open Science Framework (https://osf.io/xwqe4/).

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Table S1:** Conditional model estimates and estimated marginal means (EMMs) for the effects of treatments on flowering proportions of the species. Significant effects ($p < 0.05$) are indicated with bold text. Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05. **Table S2:**. Conditional model estimates and estimated marginal means (EMMs) for the effects of treatments on the number of seed heads produced by the species. Significant effects ($p < 0.05$) are indicated with bold text. Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05. **Table S3:**. Conditional model estimates and estimated marginal means (EMMs) for the effects of treatments on the number of seeds per head produced by the species. Significant effects ($p < 0.05$) are indicated with bold text. Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05. **Table S4:**. Conditional model estimates and estimated marginal means (EMMs) for the effects of treatments on the seed viability of the species. Significant effects ($p < 0.05$) are indicated with bold text. Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05.