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Salinity tolerance of flowering rush, *Butomus umbellatus*

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ABSTRACT

Flowering rush is an invasive aquatic plant in North America that has deleterious effects on native ecosystems. There are two cytotypes, a triploid and diploid, and multiple genotypes are contained within the diploid cytotype currently established in the United States. Despite its presence in river drainages connected to estuarine areas, documentation on the salinity tolerance of flowering rush is scarce. Currently, information is limited to anecdotal reports suggesting intolerance to saline conditions. A better understanding of the salinity tolerance of this species is essential to providing insight into its invasive range and better informing management efforts. The following study investigated the sprouting and growth of vegetative propagules from four genotypes of flowering rush when exposed to a range of salinities (0 to 35 parts per thousand [ppt]). Sprouting (experiment 1) and growth (experiment 2) were assessed through benchtop and mesocosm experiments, respectively. Sprouting varied among cytotypes, with triploids tolerating higher salinity levels than diploids. Diploid genotypes showed a decrease in sprouting at concentrations > 5 ppt, while triploid sprouting was equivalent to the control up to 15 ppt. Propagules remained viable following salinity exposures, indicating that populations can likely persist after high-saline events. In the growth study, there was no genotype effect but a significant salinity treatment effect. When averaged across genotypes, mean relative daily growth rate was significantly lower for all treatments when compared to the control, and no differences were detected among treatment at doses > 10 ppt. This study corroborates previous classification of this species as a glycophyte or intolerant to saline conditions.

Key words: cytotype, diploid, genotypic diversity, invasive, salinity, sprouting, triploid

INTRODUCTION

Flowering rush (*Butomus umbellatus* L.) is an invasive aquatic plant species that has become a major concern for freshwater ecosystems in North America. Native to Eurasia, this species was first reported along the St. Lawrence River in 1905 (Core 1941) but has since spread rapidly and aggressively through wetlands, shallow shorelines, and submersed habitats found in lakes, ponds, streams, and rivers across the northern United States and southern Canada (Hroudová and Zákravsky 1993, Gunderson et al. 2016). Flowering rush is perennial, known for its ability to outcompete native aquatic plant species, limit recreational water use, reduce water flow, and impact native flora and fauna (Boutwell 1990, Parkinson et al. 2010, Jacobs et al. 2011). Plants can be found growing as an emergent and submersed growth form, thus allowing it to invade sites up to 6 m in depth (Parsons et al. 2019). The emergent form can grow in moist soils or in water up to 1.5 m; it is characterized by rigid triangular leaves and produces large, umbrella-shaped clusters of pink flowers on a round stalk. The submersed form has thin, ribbon-like leaves and does not produce flowers (Boutwell 1990, Hroudová et al. 1996).

There are two established cytotypes in the United States: a triploid that is dominant in the western United States, and a diploid that is dominant in the eastern United States throughout the Great Lakes Region (Gunderson et al. 2016, Gaskin et al. 2021). Triploid flowering rush is sterile and does not produce viable seeds, thus relying solely on clonal reproduction via fragmentation of rhizomes and rhizome buds (Hroudová and Zákravsky 1993, Lui et al. 2004). Conversely, diploid populations can reproduce both sexually through seeds and clonally through bulbils. However, bulbils have been shown to be the primary mode of reproduction as seed is believed to play a minor role in the spread of flowering rush due to low recruitment (Lui et al. 2004).

A large portion of the available flowering rush literature focuses on either the diploid or triploid cytotype; however, studies comparing cytotypes and/or distinct genotypes are limited. Previous and current flowering rush research has documented differences in cytotype response to varying nutrient levels (Harms et al. 2021), disease susceptibility (Harms and DeRossettee 2019), competitiveness (Harms 2020), sprouting requirements (Sartain et al. 2024), and herbicide response (B. Sartain and N. Harms, unpub. data). Among the two cytotypes there are six distinct invasive genotypes of flowering rush in the United States: four diploid and two triploid (Gaskin et al. 2021). Within the United States, the distribution of flowering rush genotypes is largely segregated, and it is unknown whether this is the result of differing environmental tolerances or introduction patterns (Gaskin et al. 2021). Different genotypes reflect diverse evolutionary origins giving rise to variation in phenotypic and physiological traits thereby influencing seasonal growth rates, response to management, and overall invasiveness of a population (Soltis and Soltis 2000).

Salinity is a major abiotic factor affecting the growth rate, productivity, and distribution of aquatic macrophytes (Grewell et al. 2021). Salinity was shown to be a key factor in structuring

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TABLE 1. LOCALITIES FOR FLOWERING RUSH GENOTYPES COLLECTED FOR USE IN THESE STUDIES.

Genotype	Source population	Ploidy	Latitude	Longitude
1	Columbia River, Tri-Cities, WA	Triploid	47.8012N	117.5552W
3	Springbrook pond, IL	Diploid	41.72989N	88.20537W
4	Unity Island, NY	Diploid	42.93367N	78.90814W
5	Forest Lake, MN	Diploid	45.27235N	92.93743W

aquatic macrophyte assemblages in coastal habitats (Hyman et al. 2021, Tursi et al. 2023). Plants can be categorized based on their tolerance to salinity into two main groups: halophytes and glycophytes. The ability of a plant to thrive in saline conditions hinges on its capacity to control the accumulation of sodium ions and ionic balance maintenance in the cytoplasm, ensuring osmotic equilibrium (Flowers et al. 1977, Cheeseman 1988). Halophytes, or salt-tolerant plants, employ strategies to prevent intracellular sodium buildup such as compartmentalizing toxic ions into vacuoles (Flowers and Colmer 2008). In contrast, glycophytes are less adept at handling salinity stress. They either limit sodium absorption or store sodium in older tissues, like mature leaves (Cheeseman 1988). When exposed to high salinity levels, glycophytes struggle to regulate the influx of harmful sodium ions, leading to ion toxicity and eventual plant death (Zhu et al. 1997).

The United States Geological Survey classifies flowering rush as intolerant to brackish or saline conditions; however, peer-reviewed literature pertaining to the salinity tolerance of one or both cytotypes of invasive flowering rush is lacking (Cao et al. 2024). Both flowering rush cytotypes and multiple genotypes within the diploid cytotype are currently established and spreading throughout multiple river basins linked to estuarine habitats (Gaskin et al. 2021). Documentation of the osmotic tolerance of this species is essential to providing insight into this plant's invasive range to limit its spread and better inform management efforts. Therefore, the objective of this work is to evaluate sprouting and growth response of multiple flowering rush genotypes exposed to a range of salinity levels.

MATERIALS AND METHODS

Two experimental trials were conducted at the U.S. Army Corps of Engineers Engineer Research and Development Center (ERDC), Vicksburg, MS (32.318N; 90.878W) to investigate the influence of salinity on the sprouting of vegetative propagules and growth of four genotypes of flowering rush (Table 1). Parent plants of each flowering rush genotype were grown from culture stocks maintained at a common garden at ERDC to ensure adequate quantities of bulbils and rhizome segments were available for studies.

Experiment 1: Sprouting

A completely randomized factorial design was used, consisting of two factors: genotype (four levels: one triploid genotype, G1, and three diploid genotypes: G3, G4, G5) and salinity (seven levels: 0, 5, 10, 15, 20, 25, and 35 parts per thousand [ppt]), with each treatment combination replicated five times. By including a range across all ecologically relevant salinity levels, a better understand of the full spectrum of flowering rush's response to salinity can be determined. Rhizome bulbils (700 per diploid genotype/2,100 total) and rhizome segments approximately 5 cm in length with at least one rhizome bud (700 total triploid genotype) were harvested, arranged evenly across a moist paper towel, placed in labeled 3.7 L polyethylene plastic bags, and refrigerated at 4 C for 10 wk to simulate a cold stratification period (Sartain et al. 2024). After cold storage, propagules were placed into clear Petri dishes arranged in a temperature (24 ± 1 C) and light (14:10 light:dark) controlled environmental growth chamber at ERDC. Each Petri dish (experimental unit) contained 20 bulbils or rhizome segments and 130 ml of the specified salinity solution, which was premixed in 19 L buckets using deionized water and Instant Ocean® Sea Salt.[1] Salinity levels were monitored biweekly using a HI98319 Marine Salinity Tester[2] and maintained within ± 1 ppt of the designated salinity level. Sprouting was assessed every 2 days for a duration of 45 days (6.5 wk) after planting. Sprouting was determined by the presence of an emergent green shoot ≥ 3 mm in total length. Upon sprouting, the date, propagule width (mm), length (mm), and wet weight (g) were recorded. Sprouted propagules were subsequently removed from the Petri dish to avoid recounts. At the conclusion of the 45-day observation period, propagules that failed to sprout in salinity treatments were transferred to freshwater and observed for 2 wk to assess viability (data not subjected to statistical analysis).

A one-way analysis of variance (ANOVA) was performed in RStudio version 4.2.2[3] for each genotype with final mean germination as the response variable and salinity treatment as the fixed factor. Tukey's HSD was performed to identify significant differences across salinity levels for each genotype. To compare the median effective dose (LC_{50}) values across each genotype, a four-parameter log-logistic model was fitted for each genotype's sprouting data using the "drc" package in RStudio version 4.2.2[3] (R Core Team 2022). The LC_{50} values were estimated for each model using the "ED" function, which provides the dose at which sprouting was reduced by 50%. To determine if sprouting time varied among genotypes, data within each salinity treatment for each genotype were subjected to a time-to-event analysis where sprouting was the event of interest. Utilizing a time-to-event analysis offers the advantage of assessing the distribution of sprouting times for individual propagules, rather than relying solely on cumulative sprouting rates (Sartain et al. 2024, Onofri et al. 2010, McNair et al. 2012, Pérez and Kettner 2013). This approach enables comparisons regarding both the timing and rate of sprouting, rather than focusing solely on final sprouting proportions. The time-to-event assessment for each *B. umbellatus* genotype involved using a Kaplan-Meier estimator of survivor function and log-rank test ($P \leq 0.05$) in SigmaPlot®, Version 14.0 software.[4] The Kaplan-Meier is a nonparametric method that accommodates censored (nonsprouted propagules) and noncensored (sprouted propagules) data, making it suitable for estimating survivor functions in sprouting datasets (Onofri et al. 2010, McNair et al. 2012, Pérez and Kettner 2013). Log-rank tests enable the comparison of sprouting curves across different experimental treatments (Bland and Altman 2004). In cases where significant difference between curves was observed, a Holm-Sidak all-pairwise multiple comparison analysis ($P \leq 0.05$) was used to isolate the genotype(s) that significantly differed from the others.

Experiment 2: Growth

Propagules from four genotypes of flowering rush (one triploid, three diploid) were floated in fresh water until sprouted. Once sprouted, propagules were placed in 32 cell seed-start trays filled with sand, then amended with 1 g kg^{-1} slow-release fertilizer[5] and freshwater until leaf height reached 15 cm. Plants were removed from trays, rinsed, and weighed prior to placing in experimental mesocosms. Excess water was removed by blotting with a paper towel prior to weighing. Four pretreatment plants of each genotype were harvested and dried for use in calculating estimated pretreatment dry weights of each experimental plant. After obtaining wet weights, plants were placed in 3.3 L (12 by 11.5 by 11.5 cm) pot with Black Kow Topsoil[6] amended with 4 g kg^{-1} of slow-release fertilizer.[5] Fourteen 1,330 L fiberglass tanks were used in the experiment with two tanks designated to each of the seven salinity treatments (0, 5, 10, 15, 20, 25, and 35 parts per thousand [ppt]). Four plants per genotype were placed in each tank (16 total per tank). Mesocosm water was premixed using municipal water and Instant Ocean® Sea Salt[1] at predetermined salinity levels prior to adding plants. Water level was maintained at 15 cm to encourage emergent growth. Salinity level was monitored biweekly using a handheld salinity meter[2] and maintained within ± 1 ppt of the experimental salinity level. A Tunze Osmolator 3155[7] automatic top-off system was utilized on each tank to pump freshwater in as water evaporated to maintain salinity and water levels for the duration of the experiment. Mean ambient water temperature for the duration of this study was 18.1 ± 0.8 C.

Plants were observed for 56 days following planting in mesocosms. At 56 days after planting, above and below ground material were combined, rinsed, separated, and dried in a forced air-dry oven set at 60 C for 1 wk. Above and below ground biomass was combined and weighed (mg) for use in calculating growth rate. Daily growth rate was calculated for each individual plant using an absolute growth rate equation (Hunt 1990):

$$\text{Growth rate} = \frac{Dw_2 - Dw_1}{T_2 - T_1},$$

where dry weight 1 (DW_1) is the calculated pretreatment dry weight at time 1 ($T_1 = 0$ days) and dry weight 2 (DW_2) is the dry weight at time 2 ($T_2 = 56$ days). DW1 was calculated using the mean percent water loss from pretreatment plants and multiplying wet weights of each experimental plant by the calculated water-loss percentage. Estimated water weight was then subtracted from initial wet weights of experimental plants to obtain the DW1 calculations. Data were analyzed with a two-way ANOVA ($\alpha = 0.05$), where growth rate as the response variable and genotype and treatment as fixed factors. A Tukey's post-hoc test was performed to isolate significant differences. Statistical analysis was performed in RStudio version 4.2.2.[3]

RESULTS AND DISCUSSION

Cumulative mean sprouting of vegetative propagules for each genotype was highest in the 0 ppt treatment (Figure 1). Cumulative sprouting of triploid propagules was not reduced until salinity reached 20 ppt (Figure 1). In contrast, sprouting of diploid bulbils decreased compared to the control when exposed to 10 ppt salinity (Figure 1). Triploid rhizome segment sprouting remained consistent at salinities up to 15 ppt, while diploid bulbils decreased in sprouting at salinities > 5 ppt. Cumulative mean sprouting of triploid G1 rhizomes decreased from 70% at 20 ppt to 0.05% at 35 ppt. In contrast, minimal sprouting of diploid bulbils was observed, and no differences were detected between treatments ≥ 20 ppt for all diploid genotypes. The estimated LC_{50} values differed among genotypes (Figure 2). G3 exhibited the lowest LC_{50} (9.2, 95% CI: 7.1 to 11.2), indicating greater sensitivity to salinity. In contrast, G1 had the highest LC_{50} (23.2, 95% CI: 21.6 to 24.7), demonstrating increased tolerance. G4 and G5 showed overlapping LC_{50} (13.1 and 13.3, respectively), suggesting no difference between them. G1 rhizome segments germinated significantly faster than diploid bulbils in all treatments except 35 ppt (Figure 3; Table 2). All genotypes showed significantly different sprouting rates at 10 ppt with G1 having the highest and G3 having the lowest rates. A viability assessment of salinity exposed bulbils and rhizome segments that failed to germinate during the study period indicated that upon reintroduction to freshwater 85% of diploid bulbils and 50% of triploid rhizome segments successfully sprouted (data not shown).

When averaged across salinity treatments, no significant differences were detected among genotypes ($P = 0.237$) for calculated mean daily growth rates at the conclusion of the study. However, when pooled across genotype a significant salinity treatment effect ($P < 0.001$) was detected (Figure 4). All salinity treatments negatively impacted plant growth compared to control treatments. The 0 ppt control treatment resulted in the greatest mean daily growth rate (58.7 ± 4.3 mg day 1) whereas growth rate decreased by approximately 49% (30.0 ± 4.3 mg day 1) in plants exposed to 5 ppt salinity. Compared to the control, flowering rush mean daily growth rate was reduced > 95% in response to saline conditions ≥ 10 ppt.

Plant distribution patterns are often largely explained by temperature and precipitation patterns (Woodward and Williams 1987). Variables related to cold temperatures and precipitation seem to drive the distribution of flowering rush in both its native and invasive range (Banerjee et al. 2020); however, an understanding of this species' response to other environmental gradients, such as salinity, can

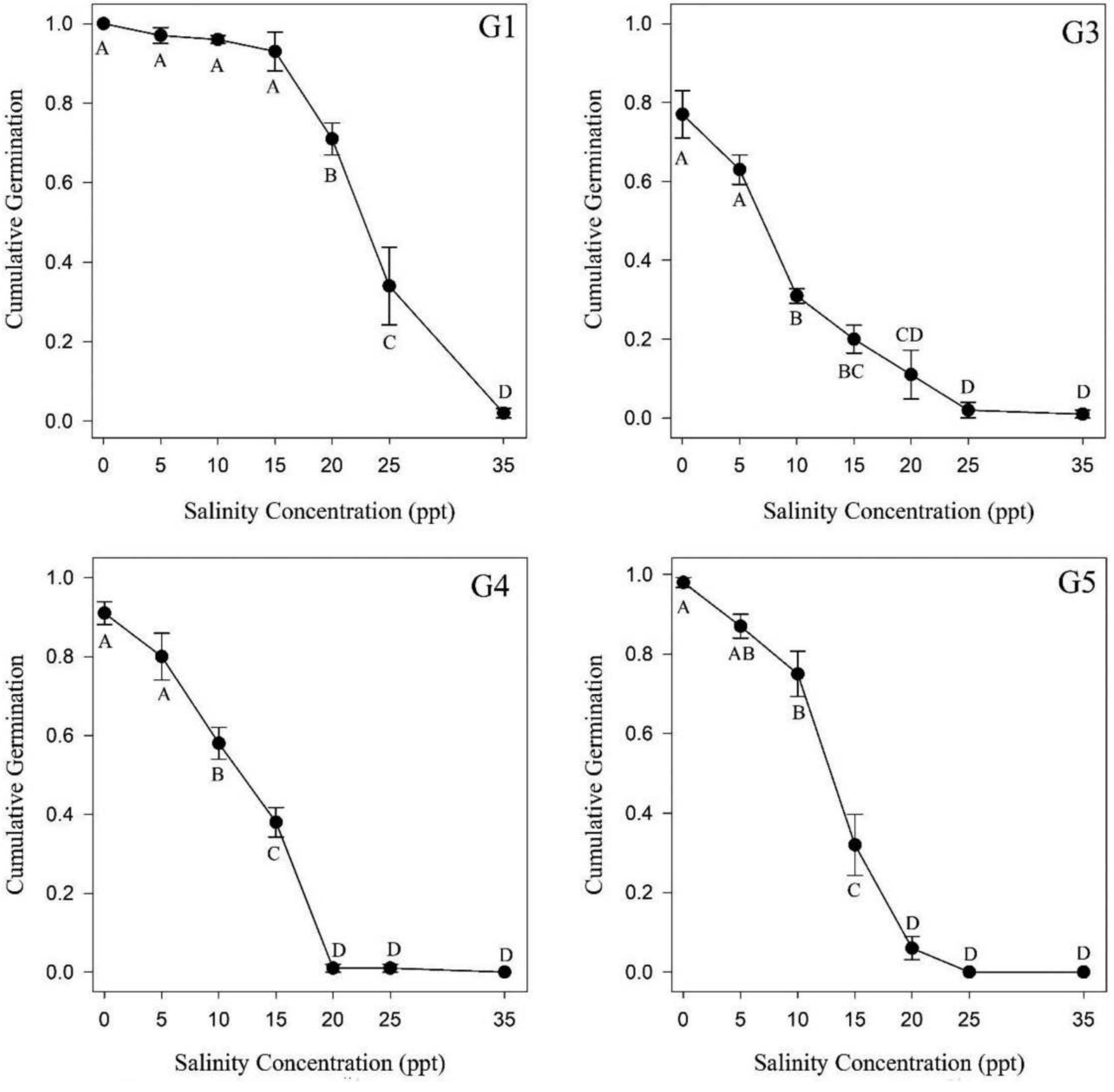

Figure 1. Germination of flowering rush genotypes across salinity treatments. Letters denote significant differences ($P < 0.05$) in germination response to salinity treatment.

support future predictions about where it is likely to occur and inform management efforts in at-risk areas.

In the sprouting study, we observed variability in response of propagules to salinity. G1 rhizome bud sprouting was greater than all diploid genotypes across salinity treatments; however, this could be an artifact of propagule type. Given that the triploid genotype does not produce bulbils, the rhizome segments utilized allowed for the internal rhizome structures to be directly exposed to the saline solutions. When initially added to the salinity treatments, accumulation of salts into the rhizome tissues was apparent by a decrease in salt concentration in dishes containing triploid rhizomes. While an increase in salinity is expected due to evaporation, the observed decrease can be attributed to uptake of ions into rhizomatous tissues to maintain osmotic balance in cells.

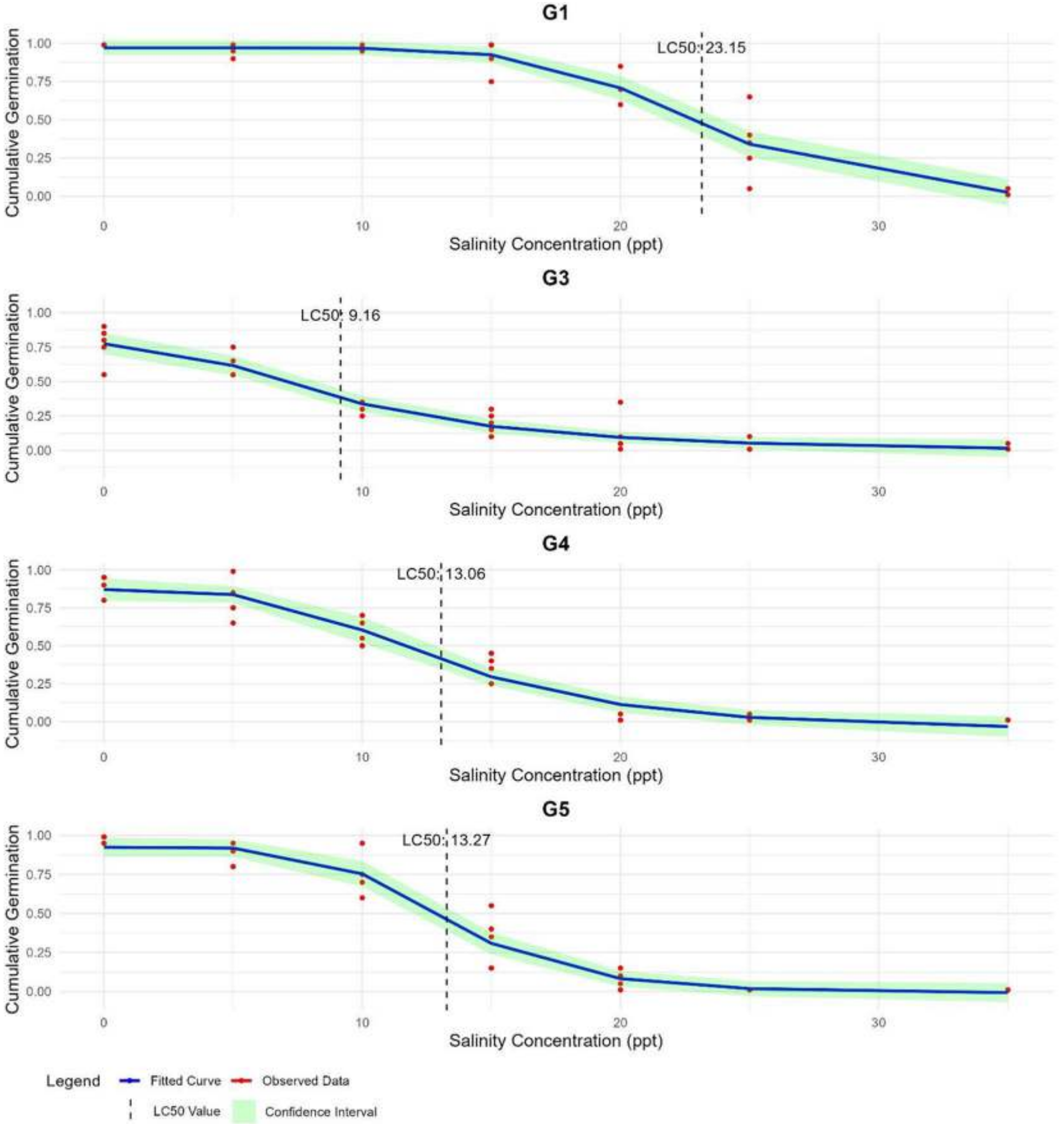

Figure 2. Fitted log-logistic dose-response regression for each genotype. LC_{50} values for each genotype are marked.

Saline conditions cause a reduction in available water, which typically delays or inhibits sprouting (Reguera et al. 2020). Delayed sprouting was apparent when comparing diploid and triploid sprouting rates. For instance, at 10 ppt, G1 sprouting reached nearly 75% after 10 days, while diploids showed less than 10% after 10 days. A high proportion of propagules exposed to salinity remained viable, which could allow dispersal into coastal habitats following tidal fluctuations.

The growth of flowering rush was severely impacted by salinity. Complete necrosis of above ground tissue was documented as early as 14 days after exposure to 35 ppt salinity levels. Plants exposed to the minimum salinity (5 ppt) still maintained green leaves at the end of the 56-day observation period; however, growth rates were reduced by nearly 50% in comparison to the control. One of the most apparent effects of salinity stress in plants is necrosis of leaves (Munns and Tester 2008). As plants undergo prolonged salinity stress, the chlorosis and necrosis of photosynthetic tissue (e.g., leaves) becomes one of the most pronounced symptoms (Munns and Tester 2008). If saline conditions persist, stomatal closure and the loss of leaves reduce photosynthetic capacity and plant growth and ultimately lead to plant death (Munns and Tester 2008).

These studies highlight several key findings. First and foremost, flowering rush propagules can remain viable after exposure to saline solutions of 35 ppt. This suggests a potential pathway for invasion into coastal habitats following high-water events such as storm surge or flooding. This underscores the importance of identifying such events as possible means of dispersal and implementing appropriate management strategies. Second, there is observed variation in sprouting rates between diploid and triploid genotypes; however, this could be a result of propagule type and requires further investigation (e.g., whether diploid

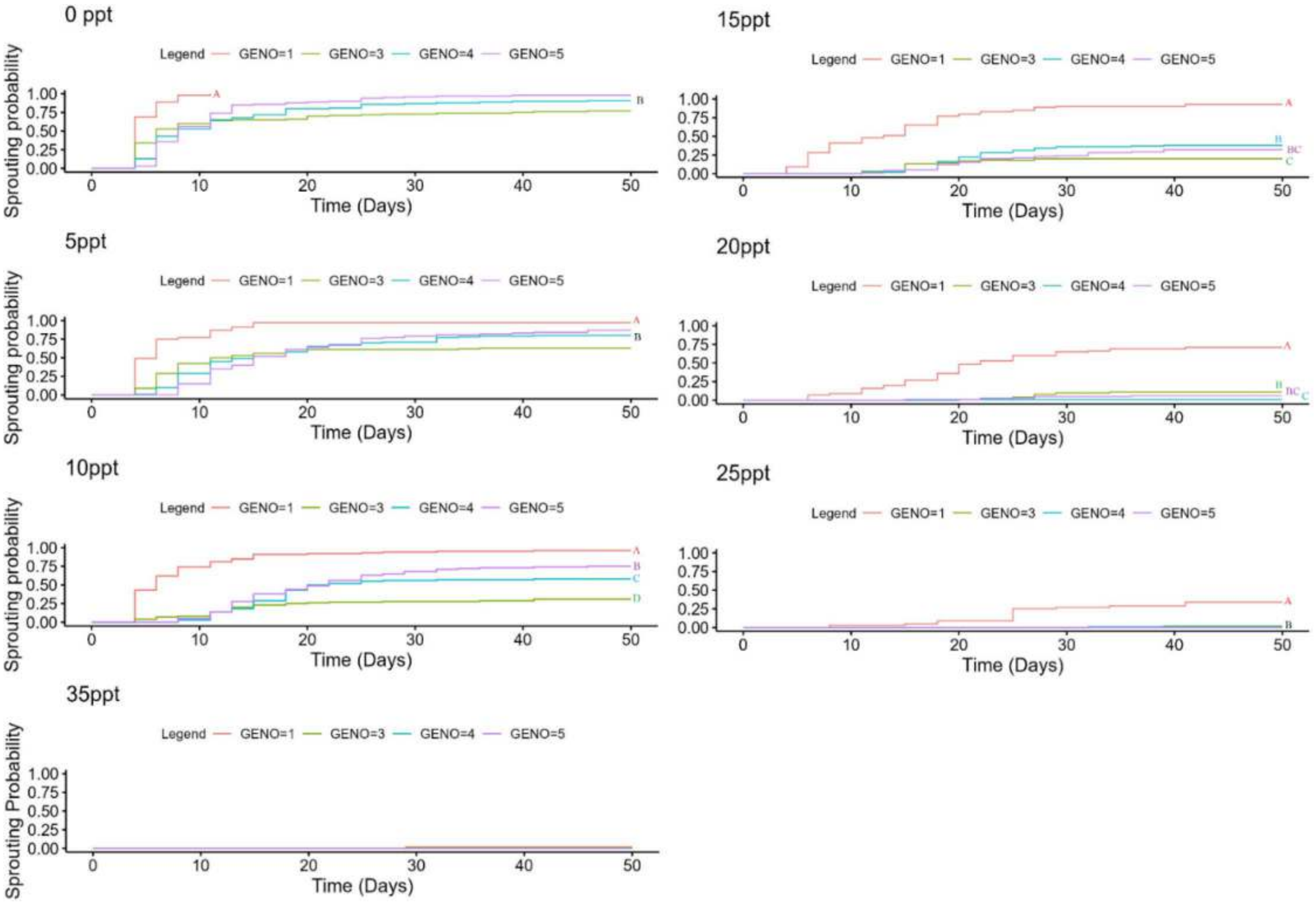

Figure 3. Kaplan-Meier survival curves generated for each genotype at each treatment level. Letters denote significant ($P < 0.05$) differences between genotypes.

rhizomes respond similarly to triploid rhizomes when exposed to salinity). Third, growth is significantly affected by salinity, with severe impacts observed even at relatively low levels (5 ppt). Above 10 ppt growth rates across genotypes remained consistent and minimal (> 95% compared to the control). Given that flowering rush propagules remained viable following extended exposure to salinity levels, dispersal into coastal habitats should be monitored. The possibility of flowering rush invading and establishing in estuarine areas seems improbable because of the observed reduction in growth at all salinity levels. Future investigation into tidal influence (e.g., fluctuating salinity levels) could provide valuable insight regarding possible establishment of flowering rush in estuarine areas.

Table 2. Results of log-rank test for bulbil sprouting curves in each salinity treatment. A Holm-Sidak test ($P \leq 0.05$) was used to isolate the genotypes that significantly differ.

	All genotypes			G1 and G3		G1 and G4		G1 and G5		G3 and G4		G3 and G5		G4 and G5	
Treatment	χ^2	df	P	χ^2	P	χ^2	P	χ^2	P	χ^2	P	χ^2	P	χ^2	P
0 ppt	130.887	3	< 0.001	54.3	< 0.001	88.821	< 0.001	105.677	< 0.001	1.112	0.292	3.854	0.142	2.518	0.212
5 ppt	140.784	3	< 0.001	60.257	< 0.001	74.919	< 0.001	86.343	< 0.001	0.973	0.543	1.693	0.475	0.064	0.8
10 ppt	244.796	3	< 0.001	132.963	< 0.001	110.282	< 0.001	84.461	< 0.001	11.485	0.0014	31.858	< 0.001	4.327	0.038
15 ppt	253.544	3	<0.001	129.438	< 0.001	104.593	< 0.001	119.933	< 0.001	6.312	0.036	2.807	0.179	0.993	0.319
20 ppt	241.127	3	< 0.001	84.259	< 0.001	111.605	< 0.001	96.086	< 0.001	8.728	0.009	1.541	0.214	3.648	0.109
25 ppt	105.761	3	< 0.001	34.999	< 0.001	37.486	< 0.001	40.959	< 0.001	0.334	0.563	2.01	0.399	1	0.534
35 ppt	3.685	3	0.298	—	—	—	—	—	—	—	—	—	—	—	—

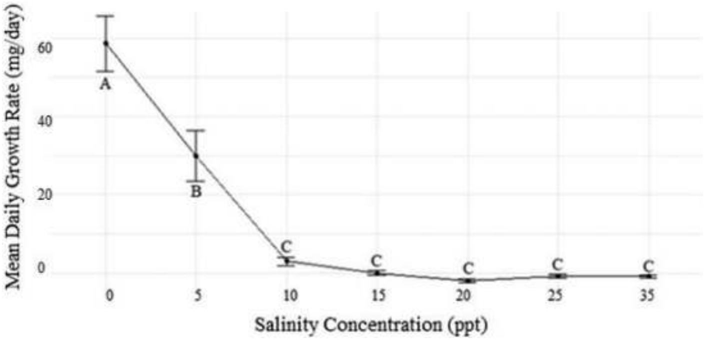

Figure 4. Growth rate of flowering rush genotypes. Letters denote significant differences ($P < 0.05$) between treatment.

SOURCES OF MATERIALS

[1]Instant Ocean® Sea Salt, Instant Ocean Spectrum Brands, Blacksburg, VA 24060.

[2]HI98319 Marine Salinity Tester, Hanna Instruments Inc., Smithfield, RI 02917.

[3]RStudio version 4.2.2, R Foundation for Statistical Computing, Vienna, Austria.

[4]SigmaPlot®, version 14.0, Systat Software, San Jose, CA 95110.

[5]Osmocote 14-14-14, Florikan, Bowling Green, FL 33834.

[6]Black Kow Top Soil, Black Gold Compost Company, Oxford, FL 34484.

[7]Tunze Osmolator 3155, Tunze USA LLC, Buda, TX 78610.

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