Chemical control of torpedograss and common reed under altered salinity conditions

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ABSTRACT

Environmental conditions, such as salinity, flooding, and drought, can affect morphological and physiological features of plants, including leaf traits, biomass allocation, and growth rate. Changes in these features can impact herbicide absorption and translocation. This may present management challenges for species that grow in a variety of environmental conditions, such as torpedograss (*Panicum repens* L.) and common reed [*Phragmites australis* (Cav.) Trin ex. Steud]. To understand how salinity affects herbicide efficacy, plants of each species were grown in freshwater (0.7 ppt) or saline (15 ppt) conditions in a greenhouse and evaluated for growth characteristics after 2 wk. Torpedograss showed reductions in height, leaf number, stem number, biomass, and growth rate under high-salinity conditions. Common reed stem numbers were lower under freshwater conditions, but no other differences were observed. Plants were then treated with either imazapyr (0.14, 0.28, 0.56, and 1.12 kg ae ha^{-1}) or glyphosate (0.56, 1.12, 2.24, and 4.48 kg ae ha^{-1}) (four replications per treatment, plus a nontreated control, per salinity regime). Injury and aboveground biomass were measured 30 days after treatment (DAT), and above- and belowground biomass 60 DAT. Saline conditions reduced glyphosate and imazapyr efficacy on torpedograss, likely due to plant responses to salinity such as lower leaf number, leaf area, and growth rate. Observed differences in injury and biomass were more pronounced at the lower herbicide application rates, particularly for plants treated with glyphosate. The effects of salinity on herbicide efficacy for common reed were not significant.

Key words: glyphosate, imazapyr, *Panicum repens* L., *Phragmites australis* (Cav.) Trin. ex Steud, storm surge.

INTRODUCTION

Coastal wetlands are unique ecosystems that are particularly vulnerable to plant invasions due to disturbances such as erosion and major storms (Tobler et al. 2006; Pathikonda et al. 2010). As these wetlands become increasingly fragmented due to sea level rise, the impacts of invasive plants are likely to intensify (Tobler et al. 2006). A number of invasive plant species are found in coastal wetlands of Florida, including the rhizomatous perennial grasses torpedograss and common reed.

Torpedograss is a C4 species native to tropical and subtropical regions of Europe, Asia, and Africa (Hossain et al. 1999). In addition to being a major weed in crops and turf, torpedograss is an aggressive invader of aquatic habitats such as lake shores, wet prairies, and both freshwater and brackish marshes (Hossain et al. 1999; Smith et al. 1999). Common reed is a C3 species that has aggressively invaded salt marshes and freshwater wetlands across North America (Amsberry et al. 2000; Saltonstall 2002; Brisson et al. 2010). This species is globally distributed and separated into lineages based on geographic origin; lineages are further divided into haplotypes based on sequences of chloroplast DNA (Saltonstall 2002, 2003; Kettenring et al. 2012). The Gulf Coast lineage (Haplotype I, hereafter referred to as the Gulf Coast type) is often considered to be native to the Gulf Coast region of the United States, although recent genetic testing suggests that it may be a hybrid between the South American reed grass (*Phragmites mauritianus* Kunth) and common reed (Lambertini et al. 2012). Regardless of origin, the Gulf Coast type has become aggressive in disturbed wetlands in Florida and requires frequent management to maintain access to waterways (CJ Greene, personal communication, June 2015).

In the coastal wetlands that these species inhabit, salinity is an important environmental factor that fluctuates throughout the year due to seasonal precipitation patterns, natural disturbances, and water management practices (Montague and Ley 1993; Michener et al. 1997). For example, a strong seasonal variation in salinity occurs in Florida due to natural precipitation patterns (wet summers and dry winters), and salinity has been reported to fluctuate between 2 and 15 ppt throughout the year in some southeastern coastal marshes (Mulholland et al. 1997; Doering et al. 2001; Van Zandt and Mopper 2002; Pathikonda et al. 2010). Coastal wetlands are also susceptible to sudden increases in salinity due to severe weather events such as hurricanes and tropical storms. Storm surges from hurricanes can force large quantities of salt water into brackish and freshwater systems, in some cases raising salinity levels for more than a year, resulting in long-term impacts on plant communities (Connor 1994; McLeod et al. 1996; Michener et al. 1997; Mopper et al. 2004; Tobler et al. 2006; Pathikonda et al. 2010; Herbert et al. 2015).

It has been well documented that environmental factors, such as temperature, light, and water availability, can alter

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TABLE 1. Torpedograss height, stem number, growth rate, leaf number, leaf area, specific leaf area (SLA), above and belowground biomass, and the ratio of belowground to aboveground biomass (below : above) after 2 wk of growth under freshwater (0.7 ppt) or saline (15 ppt) salinity treatments.

Plant Trait	Freshwater	Saline
Height (cm)	77.21 ± 1.36 (a)[1]	66.07 ± 1.17 (b)
Stem number	19.08 ± 0.51 (a)	15.74 ± 0.53 (b)
Growth rate (cm day^{-1})	2.27 ± 0.05 (a)	1.78 ± 0.05 (b)
Leaf number	110.11 ± 3.15 (a)	75.38 ± 2.49 (b)
Leaf area (cm^2)	10.21 ± 0.27 (a)	7.73 ± 0.31 (b)
SLA (cm^2 g^{-1})	313.67 ± 7.92 (a)	311.70 ± 12.34 (a)
Aboveground biomass (g)	5.19 ± 0.52 (a)	3.76 ± 0.52 (a)
Belowground biomass (g)	1.39 ± 0.13 (a)	1.33 ± 0.18 (a)
Below : above	0.28 ± 0.02 (b)	0.36 ± 0.01 (a)

[1]Means with standard errors ($n = 80$) are displayed for plant traits; means within a row followed by the same letter are not significantly different ($P < 0.05$).

TABLE 2. Common reed height, stem number, growth rate, leaf number, leaf area, specific leaf area (SLA), above and belowground biomass, and the ratio of belowground to aboveground biomass (below : above) after 2 wk of growth under freshwater (0.7 ppt) or saltwater (15 ppt) salinity treatments.

Plant Trait	Fresh	Saline
Height (cm)	81.11 ± 1.65 (a)[1]	81.23 ± 1.61(a)
Stem number	1.58 ± 0.07 (b)	1.88 ± 0.06 (a)
Growth rate (cm day^{-1})	2.88 ± 0.07 (a)	1.71 ± 0.05 (a)
Leaf number	12.84 ± 0.45 (a)	14.13 ± 0.43 (a)
Leaf area (cm^2)	17.34 ± 0.73 (a)	15.41 ± 0.52 (a)
SLA (cm^2 g^{-1})	227.91 ± 4.77 (a)	235.28 ± 2.96 (a)
Aboveground biomass (g)	1.77 ± 0.15 (a)	1.67 ± 0.10 (a)
Belowground biomass (g)	2.58 ± 0.18 (a)	2.62 ± 0.20 (a)
Below : above	1.52 ± 0.12 (a)	1.66 ± 0.17 (a)

[1]Means with standard errors ($n = 80$) are displayed for plant traits; means within a row followed by the same letter are not significantly different ($P < 0.05$).

plant response to herbicide treatments (McWhorter and Azlin 1978; Johnson and Young 2002; Thompson and Nissen 2002; Prince et al. 2019). For example, if a change in environmental conditions affects leaf characteristics (e.g., cuticle thickness or leaf area), uptake of foliar applied herbicides may be altered (Devine et al. 1993). Similarly, conditions that result in lowered photosynthetic rates may limit translocation of systemic herbicides (Devine et al. 1993). Increases in salinity can affect morphological and physiological traits of plants, leaf area, and biomass accumulation (Parida and Das 2005); it is possible that these plant responses may impact herbicide efficacy.

Given that sudden salinity changes in coastal wetlands are common due to stormwater surge, water management practices, and natural seasonal fluctuations, it is important to understand how salinity affects herbicide efficacy in wetland plants. Pool (2005) found that efficacy of certain herbicides (such as atrazine) was slightly reduced on seashore paspalum (*Paspalum vaginatum* O. Swartz) that had been irrigated with saltwater. Therefore, it is possible that salinity may affect herbicide efficacy for common reed and torpedograss as well. Here we conducted a greenhouse experiment to investigate the effects of salinity on the response of common reed and torpedograss to two commonly used herbicides, glyphosate and imazapyr. We hypothesized that increases in salinity would reduce herbicide efficacy due to morphological changes in leaf characteristics and other traits. We also hypothesized that this effect would be greater in torpedograss than in common reed, because it is less salt tolerant than common reed and therefore likely to experience greater morphological and physiological changes in response to increased salinity.

MATERIALS AND METHODS

Plant material and greenhouse conditions

Rhizome segments of the Gulf Coast type of common reed were collected from Lake Jesup, FL, USA, in May 2015; leaf tissue samples were assayed using the PCR-RFLP described by Saltonstall (2003) to determine the haplotype. Torpedograss rhizomes were collected from South Lake, FL, in May 2017. Rhizome segments (two or three nodes in length) of each species were planted in commercial potting soil[1] with slow-release fertilizer[2] and grown under greenhouse conditions. After 2 wk, 80 plants per species were selected for uniformity based on height and shoot number and transplanted in 3.8-L pots filled with commercial potting soil. Pots were placed in 25-cm-diameter plastic saucers filled with 660 ml of half-strength Hoagland's fertilizer solution (Hoagland and Arnon 1938). After 2 wk, plant height (cm) was measured to the end of the highest fully extended leaf on the tallest stem. Salinity treatments were then initiated.

Salinity treatments

Forty plants per species were maintained on either half-strength Hoagland's solution with no salt added (0.7 ppt) or half-strength Hoagland's solution adjusted to 15 ppt using Instant Ocean Sea Salt.[3] This salinity level was chosen to reflect brackish conditions. Salinity was read using a conductivity meter.[4] Pots were filled with freshwater or saline solution and allowed to drain five times. The plastic saucers were then filled with 660 ml of freshwater or saline fertilizer solution. Saucers were refilled three times per week, with the solution completely replaced once per week. Plant height, stem number, and leaf number were recorded 2 wk after initiation of salinity treatments. Growth rates (GR) were calculated using the following equation:

$$GR = \frac{H_2 - H_1}{T},$$

where H_1 is plant height prior to initiation of salinity treatments, H_2 is plant height 2 wk after initiation of salinity treatments, and T is the length of time between the two height measurements in days. The second tallest fully extended leaf on each plant was harvested and used for leaf area measurements using a leaf area meter.[5] The harvested leaves were then oven dried at 60 C for 72 hr and weighed. Specific leaf area (SLA) was then calculated using the following equation:

$$SLA = \frac{A}{W},$$

where A is leaf area (cm^2) and W is oven-dried leaf weight (g). Four plants per treatment were also destructively
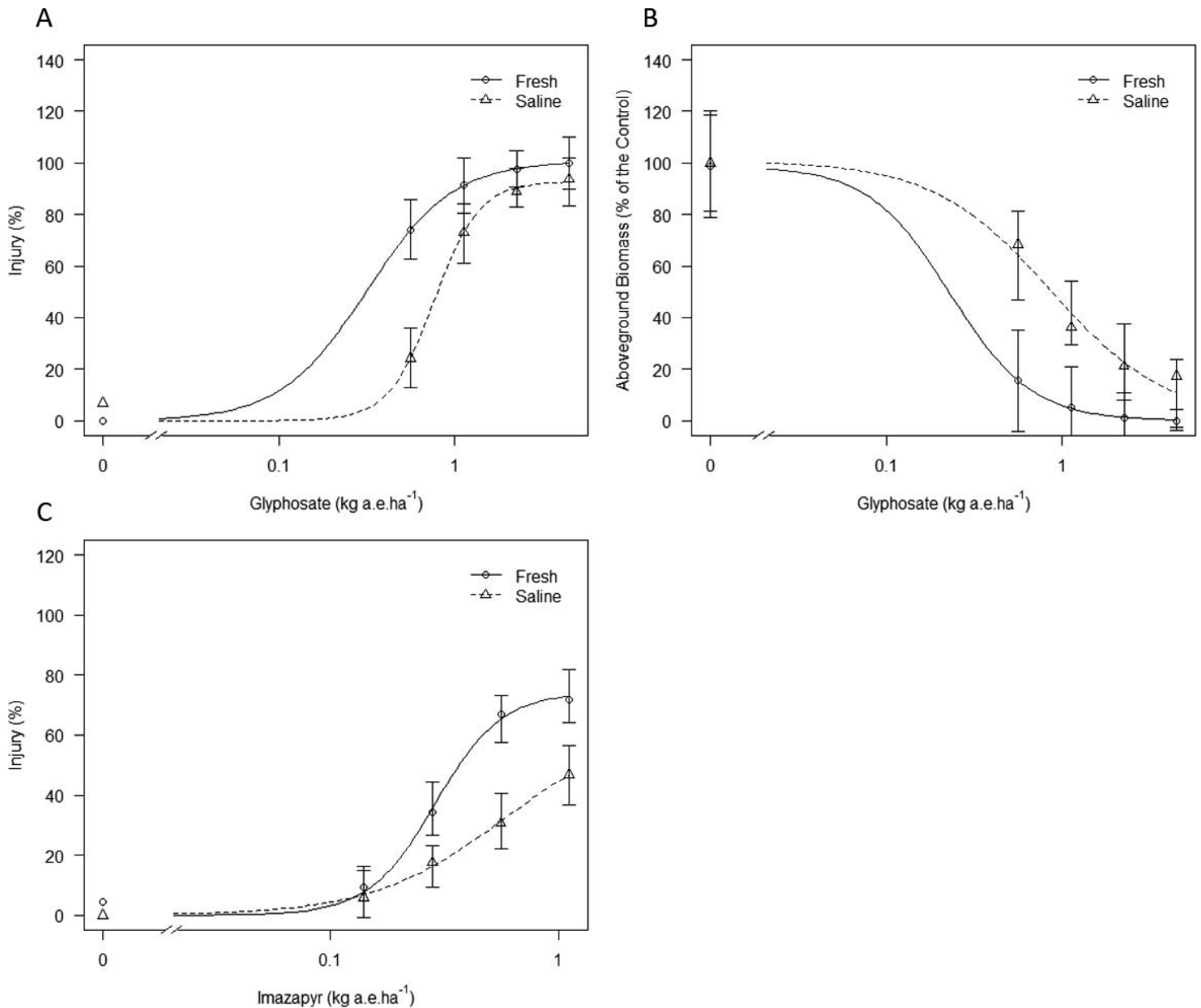
Figure 1. Dose response curves for torpedograss 30 days after treatment (DAT) with glyphosate or imazapyr under freshwater (0.7 ppt) or saline (15 ppt) conditions. Curves were generated for (A) injury estimations of plants treated with glyphosate, (B) aboveground biomass (expressed as a percent of the untreated controls) of plants treated with glyphosate, and (C) injury estimations of plants treated with imazapyr. All data series were fitted to a three-parameter log-logistic model $\left(Y = \frac{d}{1+\exp(b(\log x - \log e))}\right)$. Freshwater treatment: solid line, open circle; saline treatment: broken line, open triangle. Symbols are means ($n = 8$) of observed injury or biomass; error bars are $\pm$ model-based standard errors.

harvested 2 wk after initiation of salinity treatments to determine the oven-dried weight of above- and below-ground biomass; belowground biomass included all rhizomes and roots and was first rinsed to remove soil and debris. The ratio of belowground to aboveground biomass was then calculated using oven-dried values.

Herbicide application

Immediately following these initial measurements (2 wk after initiation of salinity treatments), foliar herbicide applications were made using a CO_2-pressurized backpack sprayer (241 kPa) with a four-nozzle[6,7] boom calibrated to deliver 187 L ha^{-1}. Glyphosate[8] was applied at rates of 0.56, 1.12, 2.24, and 4.48 kg ae ha^{-1}, and imazapyr[9] was applied at rates of 0.14, 0.28, 0.56, and 1.12 kg ae ha^{-1}. A nonionic surfactant[10] (0.25% v v^{-1}) was included in all herbicide solutions. Herbicide applications were made from lowest to highest rate for each active ingredient, and equipment was thoroughly rinsed between active ingredients to prevent cross-contamination. There were four plants per herbicide application rate, plus an untreated control, per salinity treatment. One plant was considered to be one experimental unit. Injury (%) was recorded 30 days after treatment

(DAT), and aboveground biomass was harvested and weighed. Plants were maintained as previously described for an additional 30 days to allow for recovery, at which point aboveground and belowground biomass were harvested and weighed. All biomass samples were oven dried at 60 C for 72 hr prior to measurement.

Experimental design and data analysis

There were two experimental runs: the first was initiated in June 2017 and the second in June 2018. Plants were maintained in greenhouse conditions under ambient light (13-hr photoperiod). The experiment had a completely randomized 2 × 5 factorial design, with salinity and herbicide application rate as factors; data were analyzed separately for each species and active ingredient. The positioning of plants in the greenhouse was rerandomized every week to prevent bench effects. There was no significant run effect ($P > 0.05$), so data were pooled across experimental runs. Data from the initial measurements were analyzed using one-way analysis of variance (ANOVA) in R (version 3.5.0) (R Core Team 2018) to determine the effect of salinity on plant traits. Fisher's Least Significant Difference (LSD) test was conducted using the *agricolae* package (de Mendiburu 2017) in R to determine mean separation at $\alpha = 0.05$. Residuals were tested for model assumptions of normality and homogeneity of variances; assumptions were met.

Injury estimates and biomass at 30 DAT and 60 DAT were analyzed using nonlinear regression models with the *drc* package in R (Ritz et al. 2015). Biomass data were expressed and analyzed as a percent of the untreated controls. All data series were fitted to a three-parameter log-logistic model:

$$Y = \frac{d}{1 + \exp\left(b(\log x - \log e)\right)}.$$

Lack-of-fit tests were performed to determine if the model was appropriate. When lack-of-fit tests showed the model was not appropriate, data were fitted to a three-parameter Weibull-2 model:

$$Y = d\exp\{1 - \exp[b(\log x - \log e)]\}$$

and again subjected to a lack-of-fit test. For all models, Y is the response (% injury or biomass), d is the upper limit, x is the herbicide application rate (kg ae ha^{-1}), e is value of x at the inflection point of the curve, and b is the slope of the curve at e (Ritz 2010). The upper limit d is an estimation of the injury or biomass of the control group (Ritz 2010). For the log-logistic model, e is also equivalent to the estimated herbicide application rate resulting in a 50% response in injury or biomass reduction (the effective dose, or ED_{50}, values). For the Weibull-2 model, e is not equal to the ED_{50} values, so they were calculated using the "ED" function in R. The "EDcomp" function in R was used to calculate relative potency values between plants grown in freshwater or saltwater. Relative potency (sometimes referred to as a selectivity index) represents the ratio of the ED_{50} values (freshwater : saline), and was used to here to determine the strength of the herbicide in freshwater over saltwater (Ritz
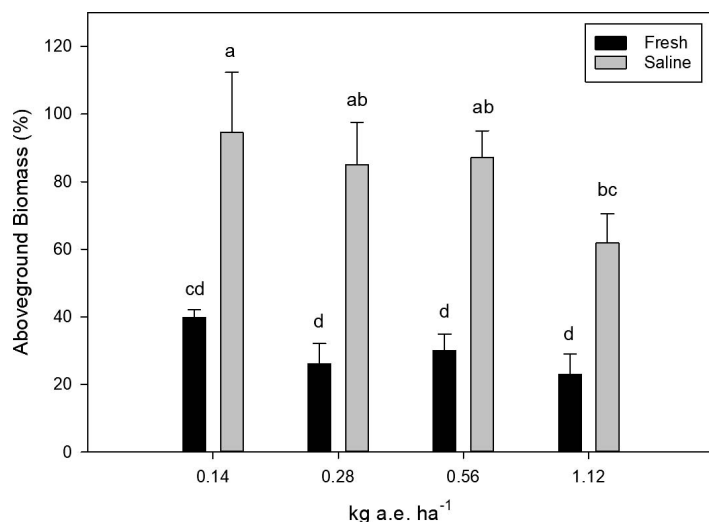

Figure 2. Aboveground biomass (expressed as a percent of the untreated controls) for torpedograss 30 days after treatment (DAT) with imazapyr. Means with the same letter are not significantly different according to Fisher's least significant difference (LSD) test at $P \leq 0.05$; $n = 8$.

et al. 2015). Fitted curves were plotted using the "plot.drc" function in R, which displays the averages and model-based standard errors (Ritz and Streibig 2016).

There were no appropriate nonlinear regression models for torpedograss biomass data 30 DAT with imazapyr and for biomass data of both species 60 DAT with imazapyr, as determined by a lack-of-fit test. Therefore, a two-way ANOVA was performed to determine the effects of herbicide application rate and salinity; Fisher's LSD was used to determine mean separation at $\alpha = 0.05$. Residuals were tested for model assumptions of normality and homogeneity of variances; assumptions were met.

RESULTS AND DISCUSSION

Initial response to salinity treatments

Salinity affected many of the measured plant traits for torpedograss (Table 1). Plants grown in saline conditions (15 ppt) were roughly 11 cm shorter on average than those in the freshwater conditions (0.7 ppt), with a lower growth rate (by approximately 0.5 cm day^{-1}) and fewer stems and leaves. Leaf area was also lower under saline conditions by an average of 2.48 cm^2. There was no effect of salinity on specific leaf area, aboveground biomass, or belowground biomass, although the ratio of belowground to aboveground biomass was greater under saline conditions than freshwater conditions (0.36 compared to 0.28, respectively).

The observed responses of torpedograss to our high-salinity treatment are consistent with symptoms of salt stress in nonhalophytic plants. For example, one of the first responses of nonhalophytic plants to salinity is a reduction (and eventually cessation) of leaf expansion; this results in a lower leaf area than plants growing in fresh water (Parida and Das 2005). Leaf abscission can also occur, resulting in fewer leaves or even complete defoliation (Gomez-Cadenas
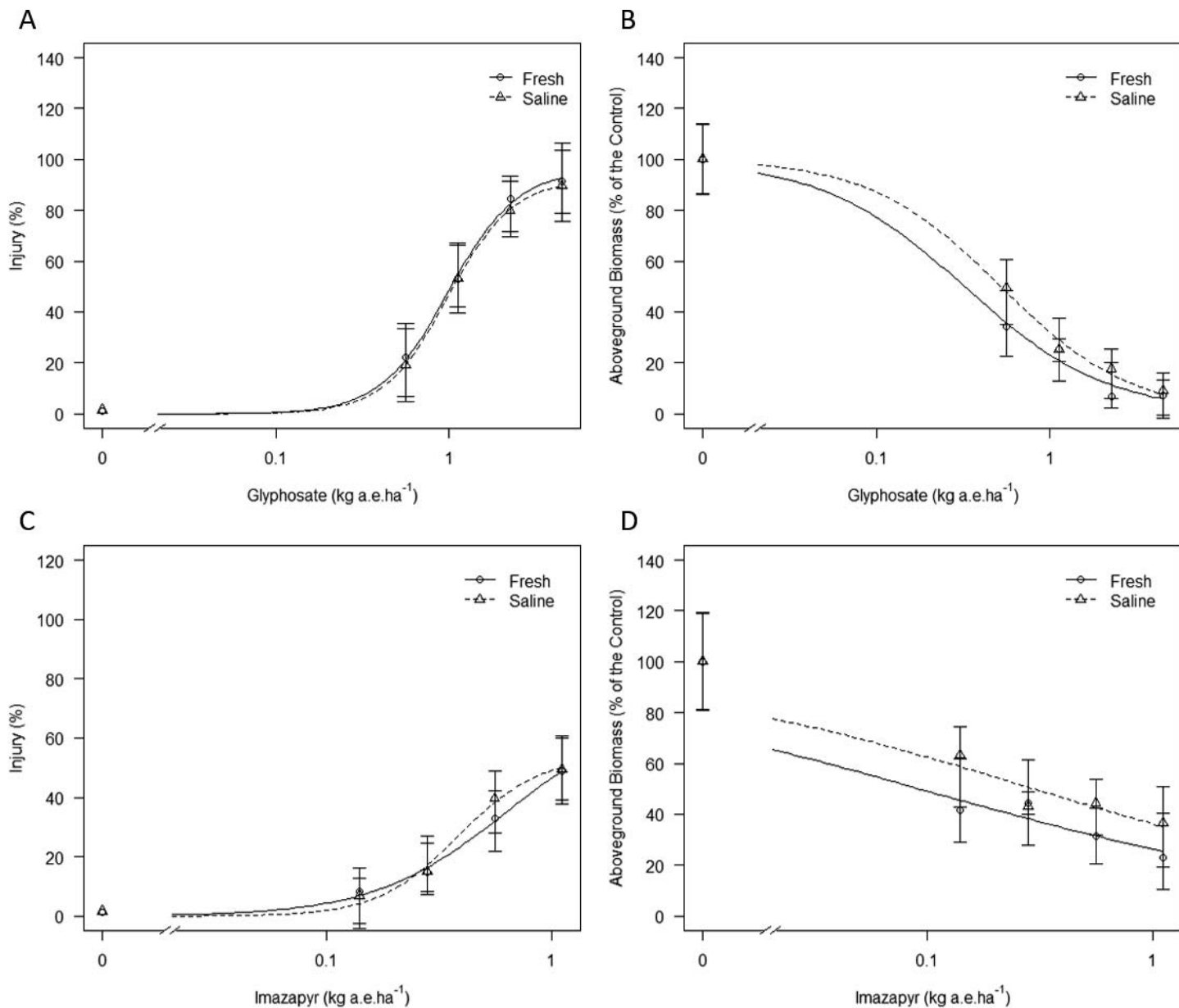
Figure 3. Dose response curves for common reed 30 days after treatment (DAT) with glyphosate or imazapyr under freshwater (0.7 ppt) or saline (15 ppt) conditions. Curves were generated for (A) injury estimations and (B) aboveground biomass (expressed as a percent of the untreated controls) of plants treated with glyphosate, as well as (C) injury estimations and (D) aboveground biomass (expressed as a percent of the untreated controls) of plants treated with imazapyr. All data series were fitted to a three-parameter log-logistic model $\left(Y = \frac{d}{1+\exp(b(\log x - \log e))} \right)$. Freshwater treatment: solid line, open circle; saline treatment: broken line, open triangle. Symbols are means ($n = 8$) of observed injury or biomass; error bars are $\pm$ model-based standard errors.

et al. 2003). We observed both of these responses in torpedograss in this study. This is in contrast to research by Pool (2005), who found that torpedograss was highly tolerant of salinity up to 30 ppt. However, authors in that study only measured visual injury, so it is possible that differences in plant height, biomass, etc., occurred and were not recorded. Differences with our study may also be due to ecotypic differentiation between source populations; our plants were collected from a freshwater lake, and it is possible that Pool (2005) sourced plants from a brackish system with greater tolerance. More research is needed to determine the extent of ecotypic differentiation in salt tolerance among torpedograss populations.

Salinity had a limited effect on the Gulf Coast type of common reed (Table 2); the only measured trait that was affected by salinity was stem number, which was greater in plants grown under saline compared to freshwater conditions (1.88 and 1.58 stems plant^{-1}, respectively). Other studies on common reed have noted that low levels of salinity (8 to 10 ppt) have a positive growth effect on certain haplotypes, stimulating photosynthesis, biomass production, stomatal conductance, and transpiration (Gorai et al.
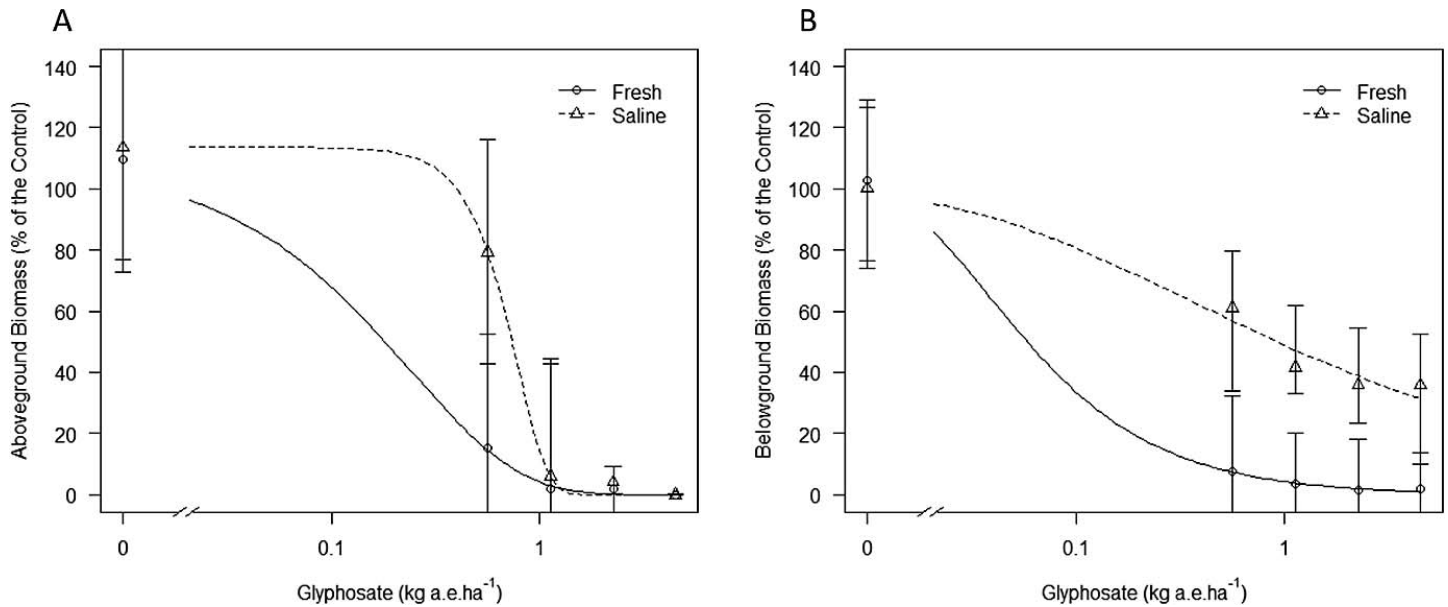
Figure 4. Dose response curves for torpedograss 60 days after treatment (DAT) with glyphosate under freshwater (0.7 ppt) or saline (15 ppt) conditions. Curves were generated for (A) aboveground biomass (expressed as a percent of the control) and (B) belowground biomass (expressed as a percent of the control). All data series were fitted to a three-parameter Weibull-2 model ($Y = d \; \exp\{1 - \exp[b(\log x - \log e)]\}$). Freshwater treatment: solid line, open circle; saline treatment: broken line, open triangle. Symbols are means ($n = 8$) of observed injury or biomass; error bars are $\pm$ model-based standard errors.

2010; Achenbach et al. 2013; Achenbach and Brix 2014). This may have been due to changes in leaf anatomy, such as higher chloroplast density (Munns and Tester 2008). It is possible that our salinity treatment of 15 ppt was low enough to have a stimulating effect as well, resulting in greater stem production. This may have implications for plant populations in areas of fluctuating salinity; if growth of the Gulf Coast type is stimulated by pulses of low to moderate levels of salinity, it may be able to expand its population at the expense of other, less tolerant, species following storm surges or seasonal fluctuations. Further research is needed to understand the effects of salinity on the Gulf Coast type of common reed.

Previous research on common reed has shown variable response of haplotypes to salinity (Vasquez et al. 2005; Achenbach et al. 2013). For example, the Eurasian type was found to be much more salt tolerant than two native North American haplotypes, facilitating its invasion into coastal salt marshes (Vasquez et al. 2005). To our knowledge, no studies have investigated the effects of salinity on the Gulf Coast type. However, Achenbach and Brix (2014) studied a closely related haplotype and found limited tolerance above 20 ppt salinity compared to other types. In this study, the Gulf Coast type showed high tolerance of 15 ppt salinity with limited response in measured plant traits.

Initial herbicide response

Efficacy of glyphosate and imazapyr on torpedograss was affected by salinity 30 DAT (Figure 1). For plants treated with low rates of glyphosate (< 1.12 kg ae ha^{-1}), injury was higher under the freshwater conditions (Figure 1A). However, there was no significant difference at higher application rates. Torpedograss was 0.41 ± 0.19 times as

sensitive to glyphosate under saline conditions than freshwater conditions, with ED$_{50}$ values of 0.76 ± 0.07 kg ae ha^{-1} and 0.32 ± 0.32 kg ae ha^{-1}, respectively. Plants treated with imazapyr had greater injury estimations in freshwater compared to saline conditions at the higher application rates (> 0.14 kg ae ha^{-1}) (Figure 1C). Torpedograss was approximately half as sensitive (0.5 ± 0.89) to imazapyr under saline conditions compared to freshwater conditions, with respective ED$_{50}$ values of 0.58 ± 0.52 kg ae ha^{-1} and 0.29 ± 0.03 kg ae ha^{-1}.

Plants treated with glyphosate also had higher aboveground biomass under the saline conditions compared to those under freshwater conditions, particularly at low application rates (< 2.24 kg ae ha^{-1}) (Figure 1B). Torpedograss was 0.27 ± 0.39 times as sensitive to glyphosate under saline conditions than freshwater conditions, with ED$_{50}$ values of 0.86 kg ae ha^{-1} and 0.23 kg ae ha^{-1}, respectively. We were unable to fit a dose response curve for aboveground biomass of plants treated with imazapyr, so data were subjected to an ANOVA to evaluate the effects of salinity and herbicide application rate (Figure 2). Plants grown in the freshwater conditions had lower aboveground biomass (as a percent of their untreated controls) compared to plants grown under saline conditions across all application rates. The effect of herbicide application rate was limited; no differences were seen in aboveground biomass between application rates for plants grown under freshwater conditions, and only a difference between the highest (1.12 kg ae ha^{-1}) and lowest (0.14 kg ae ha^{-1}) application rates for plants grown under saline conditions (Figure 2).

For common reed, there were limited effects of salinity on injury estimations or aboveground biomass for either herbicide (Figure 3). ED$_{50}$ values for injury of plants treated with glyphosate (Figure 3A) were identical for both salinity
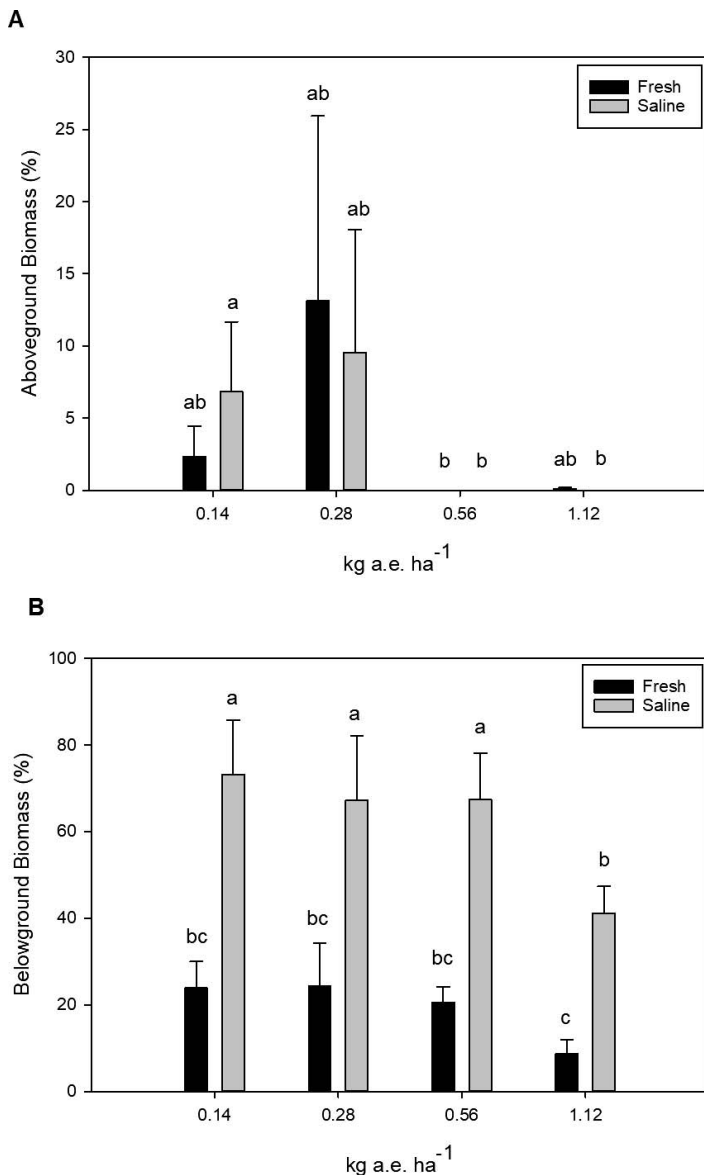
A

B

Figure 5. Mean (A) aboveground biomass and (B) belowground biomass for torpedograss 60 days after treatment (DAT) with imazapyr. Data are expressed as a percent of the untreated controls. Means with the same letter are not significantly different according to Fisher's least significant difference (LSD) test at $P \leq 0.05$; $n = 8$.

treatments (0.99 ± 0.17 kg ae ha^{-1}). Differences between salinity treatments were also minimal for aboveground biomass (Figure 3B); plants were 0.62 ± 0.33 times as sensitive to glyphosate under saline conditions than freshwater conditions, with respective ED$_{50}$ values of 0.52 ± 0.13 kg ae ha^{-1} and 0.32 ± 0.13 kg ae ha^{-1}.

Common reed treated with imazapyr was 1.62 ± 1.83 times as sensitive under freshwater conditions compared to saline conditions based on injury estimations, although variability was high and differences were nonsignificant (Figure 3C). ED$_{50}$ values were 0.38 ± 0.1 kg ae ha^{-1} and 0.62 ± 0.67 kg ae ha^{-1} for plants under saline and freshwater conditions, respectively. For aboveground biomass of plants treated with imazapyr (Figure 3D), common reed was 0.32 ±

0.4 times as sensitive under saline conditions compared to freshwater conditions; ED$_{50}$ values were 0.29 ± 0.18 kg ae ha^{-1} and 0.09 ± 0.1 kg ae ha^{-1} for plants grown under saline and freshwater conditions, respectively.

Efficacy of glyphosate and imazapyr was reduced by high salinity for torpedograss 30 DAT, while effects of salinity were limited for common reed. This differential response is likely linked to the morphological responses of plants to salinity that were observed prior to herbicide application; torpedograss displayed several responses to salinity that may affect herbicide efficacy, while common reed was minimally impacted by salinity treatments. For example, torpedograss had lower leaf area and leaf number under high-salinity conditions; plants with fewer, smaller leaves will intercept less foliar-applied herbicide, potentially limiting efficacy. This effect may not be as pronounced on imazapyr, which has residual soil activity and is readily adsorbed through plant roots (Shaner 2014). However, efficacy of both herbicides on torpedograss was affected by salinity in this study, suggesting that other factors may be responsible for observed effects. Photosynthetic rates are typically decreased by salinity in nonhalophytic plants (Parida and Das 2005); this can limit translocation of systemic herbicides such as glyphosate and imazapyr, possibly reducing efficacy. Although we did not measure photosynthesis directly, we did observe a lower growth rate and shorter plants under our high-salinity treatment which may have resulted from lowered photosynthetic rates. However, further research is needed to confirm this hypothesis.

Effects on regrowth

Aboveground biomass 60 DAT was greater for torpedograss under saline conditions at the lowest application rate of glyphosate (0.56 kg ae ha^{-1}), but not significantly so (Figure 4A). At higher application rates, there was no regrowth for plants under either salinity treatment. For aboveground biomass, torpedograss was 0.45 ± 1.41 times less sensitive under saline conditions than under freshwater conditions. ED$_{50}$ values were 0.54 ± 0.09 kg ae ha^{-1} and 0.24 ± 0.75 kg ae ha^{-1} for plants under saline and freshwater conditions, respectively. For belowground biomass, there was an effect of salinity across all but the highest glyphosate application rates; plants under the saline treatment had greater belowground biomass relative to their controls than those under the freshwater treatment (Figure 4B). Plants were 0.06 ± 0.54 times less sensitive to glyphosate under saline compared to freshwater conditions, with respective ED$_{50}$ values of 0.91 ± 0.7 kg ae ha^{-1} and 0.06 ± 0.49 kg ae ha^{-1}.

We were unable to fit a dose response curve for aboveground or belowground biomass of torpedograss treated with imazapyr, so data were subjected to an ANOVA to evaluate the effects of salinity and herbicide application rate (Figure 5). There was a significant effect of application rate on aboveground biomass, with lower biomass (as a percent of the untreated controls) produced by plants treated with high application rates (Figure 5A). There was no effect of salinity on aboveground biomass for torpedograss 60 DAT. For belowground biomass, there were
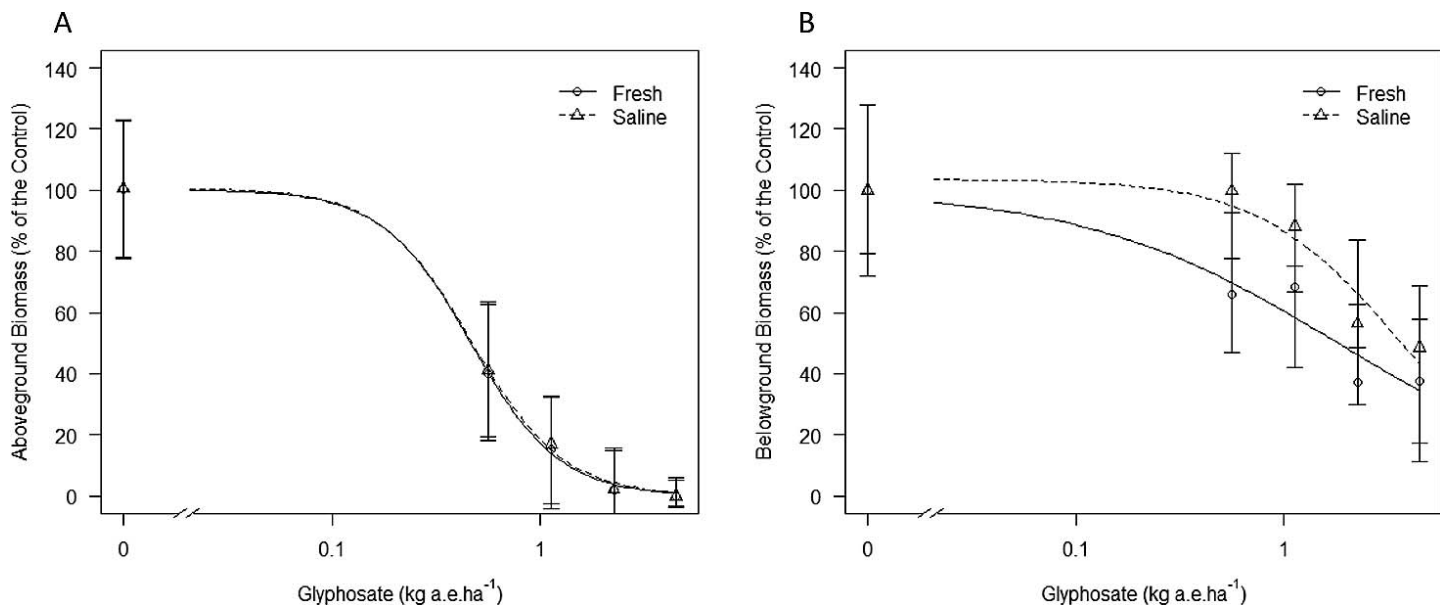
Figure 6. Dose response curves for common reed 60 days after treatment (DAT) with glyphosate under freshwater (0.7 ppt) or saline (15 ppt) conditions. Curves were generated for (A) aboveground biomass (expressed as a percent of the control) and (B) belowground biomass (expressed as a percent of the control). All data series were fitted to a three-parameter log-logistic model $\left(Y = \frac{d}{1+\exp(b(\log x - \log e))}\right)$. Freshwater treatment: solid line, open circle; saline treatment: broken line, open triangle. Symbols are means ($n = 8$) of observed injury or biomass; error bars are $\pm$ model-based standard errors.

significant effects of both salinity and herbicide application rate (Figure 5B). Plants grown under saline conditions had greater belowground biomass compared to their untreated controls compared to plants grown under freshwater conditions, and biomass was lower for plants treated with the highest imazapyr application rate (1.12 kg ae ha^{-1}).

The symptoms of salinity stress that were observed in torpedograss prior to herbicide application (i.e., the increased ratio of belowground to aboveground biomass and reductions in leaf traits) may have reduced rhizome mortality, resulting in greater belowground biomass 60 DAT in the high-salinity conditions. This may have management implications, as the rhizome system of torpedograss allows it to regenerate following herbicide applications. Although we did not observe an effect of salinity on aboveground biomass 60 DAT, it is possible that plants would have shown more regrowth under high-salinity conditions if the experiment had been extended an additional 30 days. More long-term research is needed to evaluate this.

For common reed, there was no effect of salinity on aboveground or belowground biomass across application rates for plants treated with glyphosate (Figure 6). ED$_{50}$ values for aboveground biomass were nearly identical between the salinity treatments (0.46 $\pm$ 0.14 kg ae ha^{-1} and 0.47 $\pm$ 0.14 kg ae ha^{-1} for freshwater and saline treatments, respectively). For belowground biomass, plants under the saline conditions were 0.52 $\pm$ 0.38 times less sensitive to glyphosate than those under freshwater conditions, although variability in ED$_{50}$ values was high (3.46 $\pm$ 1.28 kg ae ha^{-1} and 1.82 $\pm$ 1.07 kg ae ha^{-1} for saline and freshwater treatments, respectively). We were unable to fit a dose response curve for aboveground or belowground biomass of plants treated with imazapyr, so data were

subjected to an ANOVA to evaluate the effects of salinity and herbicide application rate (Figure 7). There were no effects of imazapyr application rate or salinity on either aboveground (Figure 7A) or belowground (Figure 7B) biomass of common reed.

Overall, our first hypothesis (that increases in salinity would reduce herbicide efficacy for torpedograss and common reed) was only partly supported by our data; efficacy of glyphosate and imazapyr was reduced under the saline treatment for torpedograss, but effects were minimal for common reed. However, this did fully support our second hypothesis, that the effects of salinity on herbicide efficacy would be greater for torpedograss than for common reed due to differences in their salinity tolerances. Although efficacy of glyphosate and imazapyr was affected by salinity for torpedograss, differences were most pronounced at the lowest application rates. Differences were limited at our highest application rates, which are similar to standard-use rates for torpedograss (standard-use rates of 4.25 kg ae ha^{-1} for glyphosate and 1.13 kg ae ha^{-1} for imazapyr, compared to rates of 4.48 kg ae ha^{-1} glyphosate and 1.12 kg ae ha^{-1} imazapyr used in this study). This indicates that salinity may have a limited impact on management in the field. We sought to replicate the effects of short-term salinity fluctuations and therefore exposed plants to a moderate level of salinity (15 ppt) for a relatively short amount of time prior to herbicide application. It is possible that we would have observed more pronounced effects at higher salinity levels or after longer exposure to the salinity treatments.

In addition, other factors may impact herbicide efficacy in the field that we did not evaluate in this study. For example, the salts that compose seawater can reduce efficacy of glyphosate (Nalewaja and Matyskiak 1991), and
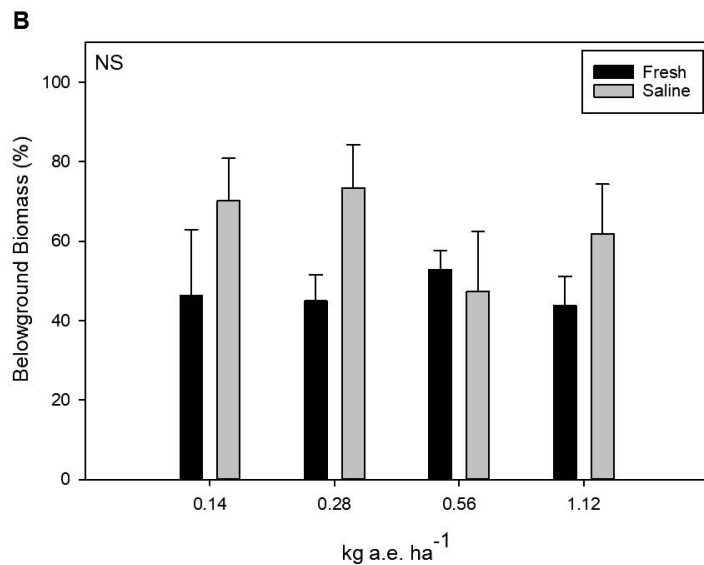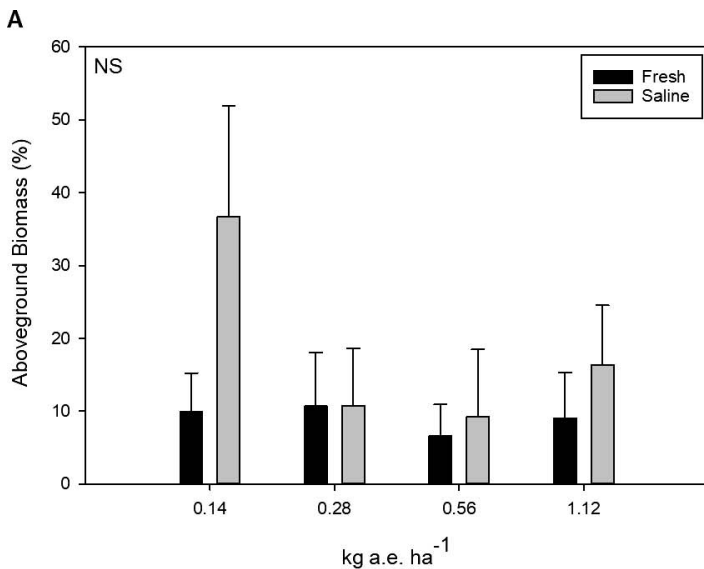
A

B

Figure 7. Mean (A) aboveground biomass and (B) belowground biomass for common reed 60 days after treatment (DAT) with imazapyr. Data are expressed as a percent of the untreated controls. Means with the same letter are not significantly different according to Fisher's least significant difference (LSD) test at $P \leq 0.05$; $n = 8$.

the leaves of plants in coastal areas are often coated with sea salt. For plants in tidal wetlands, drying time following tidal inundation may impact efficacy of certain herbicides (Patten 2002). More research is needed to evaluate the effects of salinity on herbicide efficacy in a field setting, as well as at different levels and durations of salinity exposure and in combination with flooding. In addition, the differences in response of torpedograss and common reed to herbicide applications under altered salinity regimes suggests that effects are species-specific; therefore, more research is needed to evaluate the effects of salinity on herbicide efficacy for other coastal invasive species and common reed haplotypes.

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ACKNOWLEDGEMENTS

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