Wetlands (2025) 45:19
https://doi.org/10.1007/s13157-025-01900-4

ORIGINAL RESEARCH ARTICLE

# Regional Variation in *Phragmites australis* Reproductive Traits and Seedling Performance in North America

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Received: 8 May 2024 / Accepted: 13 January 2025

## Abstract

Seedling recruitment is an important mode of establishment utilized by many invasive plants. In widespread invasive plants, regional variation in the rates of seedling recruitment can contribute to differences in invasion intensity across regions. In this study, we examined regional variation in reproductive traits and seedling performance in a cosmopolitan invasive wetland grass, *Phragmites australis*. We tested whether nitrogen levels and regions with different histories and intensities of invasion would affect reproductive traits and seedling performance. We sampled invasive *Phragmites* inflorescences from 34 populations across three regions in North America: The Northeast (old, most intense invasion), the Midwest (recent, intense invasion), and Southeast (recent, sparse invasion). We hypothesized that Northeast *Phragmites* populations would have the highest reproductive output and seedling performance, and that populations experiencing high nitrogen pollution would have higher reproductive output and seedling performance under high nitrogen conditions. We found that populations in the Northeast had the highest inflorescence mass, as expected. We also found that despite sparse distribution of *Phragmites* in the Southeast, populations from the Southeast displayed a high potential for sexual reproduction. However, increasing watershed-level nitrogen (kg/km$^2$) decreased percent seed germination in Southeastern populations, suggesting that Southeastern populations are sensitive to rising nitrogen levels. While elevated nitrogen improved seedling performance through increased belowground growth in Southeastern *Phragmites* seedlings, elevated nitrogen decreased belowground growth in Midwestern seedlings. These results suggest that the southeastern region of North America may be primed to become an emergent invasion front of *Phragmites*, warranting more research into the possible management of *Phragmites* spread in the region.

**Keywords** Biological invasions · *Phragmites australis* · Common reed · Nutrient pollution · Wetland invasion · Seedling recruitment

## Introduction

Plants with cosmopolitan distributions often exhibit regional phenotypic variation across a variety of growth and reproductive traits (Weber and Schmid 1998; García-Nogales et al. 2016; McAssey et al. 2016; Xiao et al. 2019; Leal-Saénz et al., 2020). Due to founder effects and inbreeding, invasive plants can often have lower genetic diversity than native range populations (reviewed in Hernández-Espinosa et al. 2022). However, as the range of invasive plants expands, rapid evolution of growth and defense related traits also increases (reviewed in Felker-Quinn et al. 2013). Regional variation in traits aiding in expansion, invasiveness, and competitive ability can lead to invasion hotspots. Invasive plants such as *Spartina alterniflora* and *Phytolacca americana* display latitudinal variation in growth traits such as plant height and the culm/stem density which may contribute to their invasiveness in Eurasia (Liu et al. 2016; Xiao et al. 2019). Understanding regional variation in the traits of invasive species can allow us to better understand variation in invasive success and ultimately inform region-specific management plans (Pyšek and Richardson 2007; Pyšek et al. 2009; Pyšek and Richardson 2010; Colautti and Barrett 2013; Xiao et al. 2019).

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Plant fecundity (the output of sexual reproductive propagules), germination, and early seedling performance are key traits that can determine invasiveness and that can exhibit regional variation. Fecundity traits can affect propagule pressure, which is one of the primary drivers in biological invasions (Colautti et al. 2006; Simberloff 2010). For example, *S. alterniflora* (Liu et al. 2020), *Ambrosia artimesiifolia* (Zhou et al. 2021), *Ambrosia trifida* (Hovick et al. 2018), *Phytolaca americana* (Xiao et al. 2019) exhibit regional variation in reproductive traits, which can lead to regional variation in seedling recruitment and differential rates of invasive expansion within the introduced range. Germination ability, seedling establishment, and survival have also been found to be important characteristics of invasive plants (Pyšek and Richardson 2007). The seedling stage represents a particularly vulnerable stage in a plant's life history, and a quick transition from relying on seed provisions to environmental sources of nutrients increases the chances of seedling survival (Leck et al. 2008; Silvertown 2008; Kettenring and Whigham 2018). Regional variation in germination and seedling performance has been observed across a variety of plant growth forms and in both native and invasive species, including native trees such as teak (*Tectona grandi*s, Jayasankar et al. 2003) and soapbark (*Quillaja saponaria*, Magni et al. 2019), native and invasive maples (*Acer spp.*, Lamarque et al. 2015), non-native black locust (*Robinia pseudoacacia*, Roman et al. 2022), non-native forbs (*Arabidopsis thaliana*, Samis et al. 2019) and native and invasive smooth cordgrass (*Spartina alterniflora*, Liu et al. 2020). One study also demonstrated that a species with higher seed provisioning in its invasive vs. native range, resulted in higher seedling performance in the invasive range (Hierro et al. 2013). Overall, understanding fecundity, germination, and early seedling performance across invasive ranges can help identify invasion hotspots and areas of potentially rapid expansion.

Global industrialization over the last 200 years has increased the rate of anthropogenic pollution resulting in excess deposition of nutrients into the environment (reviewed in Burkholder & Gilbert 2013). Anthropogenic nitrogen deposition is altering nitrogen dynamics in habitats worldwide, adding an additional layer of complexity to biological invasions (Canfield et al. 2010; Stevens et al. 2015). Increases in nitrogen can release plants from nutrient limitation and favor faster growing invasive plants that outcompete natives as seen with *Phalaris arundinacea* (Martina & Von Ende 2013) and *Molinia caerulea* (Tomassen et al. 2004). Wetlands often accumulate high concentrations of nitrogen from industrial and agricultural run-off and as a result can become areas of nitrogen saturation (Galloway et al. 2004; Withers et al. 2014; Fowler et al. 2015). This accumulation of nitrogen in wetlands may explain why wetlands are disproportionately affected by biological invasions as they make up 6% of Earth's landmass but are home to 24% of the world's most invasive plants (Zedler and Kercher 2004). Because anthropogenic pollution is often linked to biological invasions, understanding the nature of this relationship can inform current invasion dynamics and help us predict how they may change in the future.

Common reed, *Phragmites australis* (Cav.) Trin. ex Steud. is one of the most widespread plants on Earth and is found on every continent except Antarctica (Packer et al. 2017). In North America, the Eurasian lineage of *P. australis* (hereafter referred to as *Phragmites*) is rapidly becoming the most impactful invasive wetland plant (Chambers et al. 1999; Saltonstall 2002; Burdick and Konisky 2003; Buchsbaum et al. 2006; Lambertini et al. 2012a). Although some studies suggest evidence of multiple introductions of *Phragmites* into North America (Saltonstall et al. 2010; Meyerson and Cronin 2013), the earliest herbarium samples of *Phragmites* indicate that it was first introduced to the Mid-Atlantic region in the 19th century, and was first described in 1876, being found near ballast ground in Camden, New Jersey (Saltonstall 2002). *Phragmites* is now present across much of North America, but regional variation in distribution and invasion intensity exists (Saltonstall 2002; Kettenring et al. 2012). In the Northeast/Mid-Atlantic where the residence time of *Phragmites* is the longest, *Phragmites* invasion has rapidly spread across inland and coastal wetlands and has become a major threat to native wetland floral and faunal diversity (Chambers et al. 1999; Saltonstall 2002; Silliman and Bertness 2004; Buchsbaum et al. 2006; Kirk et al. 2011; Lazaran et al. 2013). In the Midwest, the invasion of Eurasian *Phragmites* is only a few decades old, but the spread and increase in *Phragmites* abundance has led to a decrease in native avian, nekton, and plant biodiversity and abundance (Lynch and Saltonstall 2002; Wilcox et al. 2003; Trebitz and Taylor 2007; Price et al. 2014; Whyte et al. 2015; Robichaud and Rooney 2017; Montgomery et al. 2020). *Phragmites* has also begun to colonize parts of the southwestern US (Meyerson et al. 2010; Lambert et al. 2016; Saltonstall et al. 2016) and has quickly become dominant in native wetlands in the Great Salt Lake in Utah (Kulmatiski et al. 2011; Long et al. 2017; EDDMapS 2024). However, the distribution of *Phragmites* in the Southeast and South-Central regions of the United States is rather sparse and patchy, and there have been few studies describing the ecological impact of *Phragmites* in this area (White et al. 2004; Meyerson et al. 2010; Hauber et al. 2011; EDDMapS 2024). One common garden study found that *Phragmites* growth tended to decrease with latitude, but flowering frequency tended to increase, suggesting that *Phragmites* fecundity may be even higher in southern populations (Mozdzer et al. 2016). Furthermore, environmental suitability modelling suggests that *Phragmites* is well-suited climatically to flourish in the Southeast and South-Central regions of the United States (Guo et al. 2013).

There is growing evidence that seedling recruitment is the primary mode of *Phragmites* establishment throughout much of North America. While *Phragmites* can disperse and establish new populations via vegetative propagules (rhizomes & culm fragments), these modes of dispersal are more stochastic and dependent on local hydrological conditions (Hudon et al. 2005; Meyerson et al. 2014). Studies suggest that the establishment of most new populations in the Northeast, Mid-Atlantic, and Midwest is through seedling recruitment (Brisson et al. 2010; Kirk et al. 2011; Albert et al. 2015; Kettenring et al. 2015; Fant et al. 2016). Once local genetic diversity is sufficient to overcome pollen limitation, *Phragmites* has a propensity for high sexual reproductive output (McCormick et al. 2010; Kettenring et al. 2011). *Phragmites* displays regional phenotypic variation in traits in both its invasive range (height, density, etc.) in North American and its native range in Eurasia as common garden studies demonstrate variation in growth traits across regional scales (Clevering et al. 2001; Achenbach et al. 2012; Eller and Brix 2012; Ren et al. 2020). Despite the importance of seedling recruitment in the establishment of new *Phragmites* populations in the Midwest (Fant et al. 2016), Northeast (Brisson et al. 2010; Kirk et al. 2011; Albert et al. 2015), and Mid-Atlantic (Kettenring and Whigham 2018), comparisons of *Phragmites* fecundity and seedling performance across regions have not been explored.

*Phragmites* thrives in high nitrogen environments, which often shifts competitive interactions in its favor when competing against native wetland plants (Minchinton and Bertness 2003; Rickey and Anderson 2004; Mozdzer et al. 2010; Mozdzer and Megonigal 2012). Elevated nitrogen can boost *Phragmites* fecundity by increasing the mass of individual inflorescences (Rickey and Anderson 2004), the number of inflorescences per plant, and the number of florets per inflorescence (Kettenring and Whigham 2009; Kettenring et al. 2011). Chronic nitrogen pollution may increase maternal seed provisioning and increase seed quality (seed viability, and seed mass) as seen across many commercial and wild grass species (Torres et al. 2009; Ronnenberg et al. 2011; Wang et al. 2022; but see Kettenring and Whigham 2009; Kettenring et al. 2011). Increased nitrogen availability promotes *Phragmites* seedling growth across a wide geographic sampling in Europe (Clevering 1999). In North America localized studies on the effects of nitrogen on *Phragmites* fecundity and seedling performance demonstrated that Mid-Atlantic and Midwestern populations had increased fecundity (inflorescence number/size and seed viability) (Rickey and Anderson 2004; Kettenring and Whigham 2009; Kettenring et al. 2011) and seedlings from Eastern Canada and the Mid-Atlantic have a positive growth response (higher overall biomass and plant height) (Saltonstall & Court Stevenson 2007; Kettenring and Whigham 2018) under elevated nitrogen.

While there has not been a continent-wide study of phenotypic trait variability in North America, there is ample evidence that genotypic variation and variation in intensity of invasion exists. In the Northeast and Mid-Atlantic (Chesapeake Bay), high levels of genetic diversity have been described in local *Phragmites* populations, most likely due to multiple introductions of *Phragmites* into the area (Belzile et al. 2010; Kettenring et al. 2012). Studies in the Midwest find higher genetic diversity in the introduced lineage compared to the native lineage (Tippery et al. 2020). This increase in genetic diversity is also correlated with the intensity of *Phragmites* invasion in the Midwest and the Atlantic, as *Phragmites* expansion in the Mid-Atlantic has increased by 25-fold over the last 40 years, and studies in the Saint Lawrence River and Rhode Island show that the introduced lineage has been expanding and dominating in native wetlands and estuaries (Lambert and Casagrande 2006; Belzile 2010; Kettenring et al. 2012). *Phragmites* invasion in North America is intensifying even in areas geographically distant from the Mid-Atlantic initial point of introduction, such as in the Great Salt Lake in Utah and southern Idaho which have only recently been invaded (Kulmatiski et al. 2011; Kettenring and Mock 2012; Long et al. 2017), in the upper Great Plains along the Platte River (Larson et al. 2011), and even into the southwestern United States (Meyerson et al. 2010; Lambert et al. 2016). Despite invasions intensifying in these geographically distant areas, Although the Gulf Coast appears to be a *Phragmites* hotspot, possessing multiple lineages of *Phragmites*, invasion of European *Phragmites* in the Southeast and South-Central region is rather sparse and the genetic diversity within the larger region is unknown (Lambertini et al. 2012b[b]). This suggests that *Phragmites* in North America is likely not monomorphic and regional phenotypic variation may exist.

Here we explored the effects of *Phragmites* region of origin (Northeast, Midwest, and Southeast) and local watershed nitrogen load on *Phragmites* fecundity and germination by conducting a survey of reproductive traits across 34 populations in its invaded range in North America. Because of *Phragmites'* tendency to establish and flourish in nutrient enriched habitats, we hypothesize that H1.1) *Phragmites* populations experiencing higher nitrogen loads will have greater inflorescence length, inflorescence mass, spikelet number, average seed mass, percent germination, and reproductive potential (defined as spikelet number * percent germination) than populations experiencing lower nitrogen loads. The high intensity of *Phragmites* invasion in the Northeast is due in some part to the high rates of seedling recruitment; thus, we also hypothesize that H1.2) populations from the Northeast will have greater inflorescence length, inflorescence mass, spikelet number, average seed mass, percent germination, and reproductive potential than populations from the Southeast and Midwest.

Since seedling recruitment is determined by both fecundity and seedling establishment, we also examined variation in seedling growth by region and in response to elevated nitrogen by performing a seedling growth experiment using seeds collected from the Northeast, Midwest, and Southeast and grown under ambient and elevated nitrogen. We hypothesize that based on regional patterns of *Phragmites* invasion modes and seedling response to nitrogen that H2.1) seedlings from the Northeast will have higher biomass, shoot height, and shoot number than seedlings from the Midwest and Southeast irrespective of nitrogen treatment, and that H2.2) elevated nitrogen will increase seedling growth, and this response will be more pronounced in populations with high local watershed nitrogen. In total, this research represents the first steps for investigating the regional variation in seedling recruitment in *Phragmites* and will help predict the capacity for invasive spread of *Phragmites* in the future.

## Methods

### Sample Collection

Inflorescences from 34 populations of *Phragmites* along a wide latitudinal and longitudinal gradient were collected between October - November 2021 (Fig. 1; Table S1). Populations sampled spanned 44° N (Quebec, Canada) to 31° N (Brunswick, Georgia, USA), and from 69° W (Cape Cod, Massachusetts, USA) to 87° W (Johnsonville, Tennessee, USA) (Fig. 1; Table S1). Sampling was conducted as follows: each collector would walk a 10 m transect from the edge of a *Phragmites* stand and collect a single randomly selected inflorescence every meter for a total of 10 inflorescences per site (total $N = 340$). Each inflorescence was subsequently laid out in the lab at room temperature for 48 h before being placed in an individual paper bag and then shipped and stored at room temperature at Tulane University before the start of processing in spring of 2022.

### Seed & Inflorescence Traits

The length of individual inflorescences from each population were measured from the base of the inflorescence where the first branches emerge (junction between first pedicel and rachis) to the tip of the last spikelet (Fig. S1). The mass of the inflorescence was obtained by measuring the full inflorescence and subtracting the mass of the seeds extracted from the inflorescence. An estimate of spikelet number per inflorescence for each sampled location was calculated by counting total spikelet number on two random inflorescences

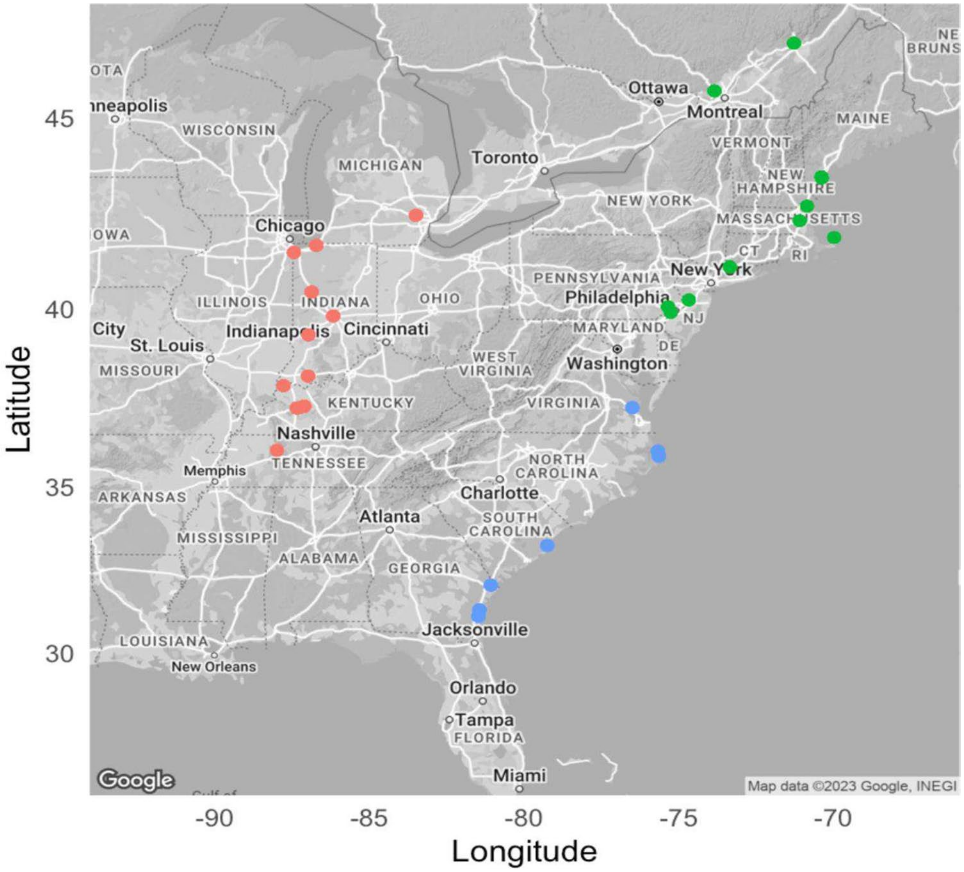

**Fig. 1** Location of *Phragmites*populations used for inflorescences collections in 2021. The points correspond to location of sites, the green points indicate populations designated as Northeast populations, blue points indicate populations designated as Southeast populations, and red points indicate populations designated as Midwest populations.

per population and using the relationship between average spikelet number and mass to estimate spikelet number for the other eight inflorescences from that same population (Fig. S1).

The caryopses (naked grass seeds) were extracted from each inflorescence by rubbing inflorescences against a 1 mm sieve followed by a 0.5 mm sieve. The chaff was blown off and only mature naked seeds were retained. A sample of 50 seeds was taken from each inflorescence and weighed on a microbalance (Mettler-Toledo; Columbus, OH, USA) to calculate mean seed mass.

Each 50-seed sample was plated on 1% agarose (50 seeds/ 90 mm diameter*15 mm height petri plate). The incidence of molding prior to germination is common and can often spread rapidly to surrounding seeds. To prevent mold from quickly taking over other seeds and influencing germination success all seeds were first sterilized using a modified version of the surface sterilization protocol from Shearin et al. (2018), consisting of a 3-minute 70% ethanol followed by a 3-minute 3% sodium hypochlorite wash on day 1, an overnight incubation at room temperature, and another round of surface sterilization on day 2 using a 5-minute ethanol wash followed by a 20-minute sodium hypochlorite wash. After the second surface sterilization wash, the seeds were placed in a growth chamber (Caron Scientific, Marietta, OH, USA) equipped with Phillips F54T5 841 HO EA ALTO 49 W fluorescent lights programmed to a 18/6 hour light cycle (500 μmol/m$^2$/s) and 30/15°C day: night temperature cycle. Petri dishes were checked daily for mold and all germinated seeds were counted after two weeks. Two weeks was determined to be sufficient as most seeds that would have germinated had already germinated within the first week, and after day 9 molding of ungerminated seeds was significant. Percent germination was calculated by counting germinated seeds per plate divided by 50. To estimate the possible reproductive output of *Phragmites* we created the metric, reproductive potential, which is the percent germination multiplied by the number of spikelets. Number of seeds was not used as a fecundity metric, as phenological differences between populations prevented us from collecting all the inflorescences before seed drop began.

## Seed Germination and Seedling Growth Experiment

Of the 34 populations sampled, we chose a subset of 24 populations (indicated in Table S1) to use in the seedling growth experiment, due to seed stock limitations. These 24 populations spanned a latitudinal range from Québec, Canada (N 46.832574°) to Brunswick, Georgia, USA (N 31.130608°) (Table S1). One seedling was grown from each of four randomly selected inflorescences collected from each of the 24 populations and was grown in two different nitrogen levels, an elevated N treatment (elevated N; 25 g.m$^2$.yr$^{-1}$) representative of a eutrophic tidal marsh ecosystem (Hopkinson and Giblin 2008) and an ambient N treatment (2g.m$^2$.yr$^{-1}$) representative of the mean nitrogen load found across all sites sampled according to the USGS SPARROW mapper (Ator 2020), totaling 192 pots (1 seedling * 4 inflorescences * 24 populations * 2 N treatments = 192 pots).

Seedlings for this experiment were germinated from a50-seed aliquot from four randomly selected inflorescences per population following the protocol described above. After one week, germinated seedlings were planted into square form pots (13.34 cm L x 13.34 cm W x 15.24 cm H) filled with Leafgro high humus soil conditioner (Leafgro, Maryland Environmental Service, Millersville, Maryland, USA). Pots were placed in flat trays (54.43 cm L x 27.79 cm W x 20 cm H), each holding up to 8 pots, at which time the trays were fertilized with either the elevated N treatment or the ambient N treatment. The programming for the growth chamber light and temperature regime was taken as the average day length in May (14/10 hour light cycle) and a 25/15°C day: night temperature cycle, representative of the mid-latitude (N 38°) climate. The amount of photosynthetically active radiation (PAR) at soil level was 250 umol/m2/s (for reference full sunlight ~ 2000 umol/m2/s). Trays were bottom watered to the lip of the tray twice per week and the corresponding N treatments were added to the trays every 2 weeks, at which time pots were rotated between trays receiving the same nitrogen treatment.

Seedling height and shoot number were collected throughout the growth experiment on days 7, 14, 28, and 42. Shoot number and shoot height within each pot were collected by counting the number of fully emergent shoots over 5 mm in height. On day 56 seedlings were clipped at the soil line and aboveground biomass was bagged in brown paper bags before being dried to constant mass at 50 °C. Belowground biomass was washed clean of soil using a 1 mm sieve to retain detached fine roots, before belowground biomass was dried to constant mass at 50 °C. A subset of the roots was stored for up to 7 days at 4 °C while root imaging was performed prior to drying. Root images were processed using the Rhizovision software (Seethepalli et al. 2020) to derive root length by root class (fine roots (< 1 mm in diameter), secondary roots (1–3 mm in diameter), and rhizome (> 3 mm in diameter)), specific root length, rooting depth, and root volume by root class.

## Nitrogen and Climate Data

Total nitrogen loads (kg/km$^2$) from the watershed corresponding to each site were obtained using datasets from the USGS SPARROW mapper (Ator 2020) which shows the annual nitrogen load in 2012. Mean growing season

(March-October of 2021) temperature and precipitation were extracted from the NOAA National Centers for Environmental Information climate monitoring data which displays temperature and precipitation on the county level. Climatic metrics were collected to estimate the relative influence of climate on the observed fecundity traits.

### Statistical Analysis

To test the effects of region (Northeast, Midwest, and Southeast) and watershed level nitrogen on each of our response variables in the field survey (inflorescence length, inflorescence mass, spikelet number, average seed mass, and germination rate) we compared multiple linear mixed effects models and generalized least square models using the "lme" and "gls" functions in the R package "nlme" version 3.1–149 (Pinheiro et al. 2023) in R studio version 1.3.1093 (R Core Team 2023). We first created a base model for backwards selection by including all fixed effects (region*watershed-level nitrogen + temperature + precipitation) in a model explaining variance in a particular response variable. Population was used as a random effect in all models. Backwards selection was performed, and best-fit models were selected using AIC. Because populations displayed a wide range of variation, we tested for heterogeneous variances across different populations using AIC. We then ran a type III ANOVA on the best model to determine the significance of each of the explanatory variables. We performed model validation by plotting fitted values against residuals, each of the fixed effects against residuals, and a histogram of the residuals alone. Because germination rates are proportions, we used binomial regression models using the "glm" function in R package "stat" version 4.0.3 (R Core Team 2023). Binomial regression models did not include the random effect and heterogeneous variances of population due to constraints of the "glm" function.

For the seedling growth experiment, the effect of watershed level nitrogen* region* nitrogen treatment were used as fixed effects in models of seedling growth response variables (total biomass, aboveground biomass, belowground biomass, aboveground: belowground biomass, SLA, total shoot height, shoot number, total root volume, total root length, specific root length, root depth, and the volume and length of each root class (fine roots (< 1 mm in diameter ), secondary roots (1–3 mm in diameter ), and rhizomes (> 3 mm in diameter ) using site as a random effect and heterogenous variances between sites in multiple linear mixed effects models described above. Tukey's HSD tests were performed on fixed effects to explore pairwise differences among factor levels, interpreting results based on compatibility intervals and estimates, reflecting "moderate evidence of impact" (Muff et al. 2022) on response variables rather than relying solely on p-value thresholds. The analysis was conducted using the 'lsmeans' function in the R package 'lsmeans' (Lenth et al. 2024) to extract least-square means, followed by the application of compact letter design via the 'cld' function in the R package 'multcomp' (Hothorn et al. 2008). In the case of interactions between fixed effects that have at least "moderate evidence of impact" (Muff et al. 2022), a new model was run combining the two fixed effects into a single factor so that the Tukey's test could be performed. For our results we present F-statistics and p-values in tables and use the language of evidence instead of arbitrary P-value cutoffs to describe evidence for our findings (Muff et al. 2022).

## Results

### Inflorescence and Seed Traits

There was moderate evidence that inflorescence mass was influenced by region (Table 1). Inflorescences from plants from the Northeast (3.68 mg ± 0.24 SE) had 22% and 7.6% more mass than inflorescences from plants from the Midwest (3.15 mg ± 0.20 SE) and Southeast (3.58 mg ± 0.27 SE), respectively, although the Tukey's HSD post-hoc test was unable to tease apart significant pairwise differences between regions (Fig. 2A). There was little to no evidence that local watershed nitrogen levels or region impacted inflorescence length and the number of spikelets on each inflorescence (Table 1; Fig. 2B-C).

There was little evidence that any of our explanatory variables had an impact on mean seed mass (Table 1). However, there was strong evidence that the effect of local watershed nitrogen on percent germination depended on region (watershed level nitrogen * region interaction) (Table 1) (region x watershed nitrogen interaction), such that there was an inverse relationship between watershed nitrogen levels and percent germination only in populations sourced from the Southeast ($R^2 = 0.406$) (Fig. 3). We observed moderate evidence that region impacted reproductive potential (Table 1), as plants from the Southeast (3623.99 ± 357.58 SE) had 33% higher reproductive potential than plants from the Northeast (2721.94 ± 219.38 SE) (Fig. 2F).

### Seedling Growth Traits

There was moderate evidence that the effect of nitrogen on total shoot height and shoot number after 42 days of growth was dependent on region (nitrogen treatment * region interaction) (Table 2). Tukey's HSD post-hoc test was unable to parse pairwise differences between treatment groups for total shoot height; however, Southeastern *Phragmites* responded positively to elevated nitrogen, with seedlings accumulating 22% more shoot height (2516.06 mm ± 252.96 SE) than seedlings grown under ambient conditions (2070.88

**Table 1** ANOVA degrees of freedom, F-value, and associated p-value from linear mixed effect models testing the effect of local watershed level nitrogen * region and environmental factors (precipitation and temperature) on inflorescence and seed traits collected from North American *Phragmites*in 2021

| | Inflorescence Mass | | | Inflorescence Length | | | Spikelet Number | | |
|---|---|---|---|---|---|---|---|---|---|
| | numDF | F-value | *p*-value | numDF | F-value | *p*-value | numDF | F-value | *p*-value |
| Nitrogen | 1 | 0.376 | 0.513 | 1 | 0.067 | 0.798 | 1 | 0.309 | 0.583 |
| Region | 2 | 3.704 | 0.038 | 2 | 0.288 | 0.752 | 2 | 2.215 | 0.130 |
| Region:Nitrogen | 2 | 2.211 | 0.129 | 2 | 0.265 | 0.769 | 2 | 0.419 | 0.662 |
| | **Mean Seed Mass** | | | **Percent germination** | | | **Reproductive potential** | | |
| | **numDF** | **F-value** | **p-value** | **numDF** | **Chi-squared** | **p-value** | **numDF** | **F-value** | **p-value** |
| Nitrogen | 2 | 1.889 | 0.309 | 2 | 12.424 | 0.001 | 2 | 3.995 | 0.205 |
| Region | 1 | 1.080 | 0.172 | 1 | 10.211 | 0.002 | 1 | 1.700 | 0.032 |
| Region:Nitrogen | 2 | 0.407 | 0.670 | 2 | 11.767 | 0.003 | 2 | 1.526 | 0.239 |

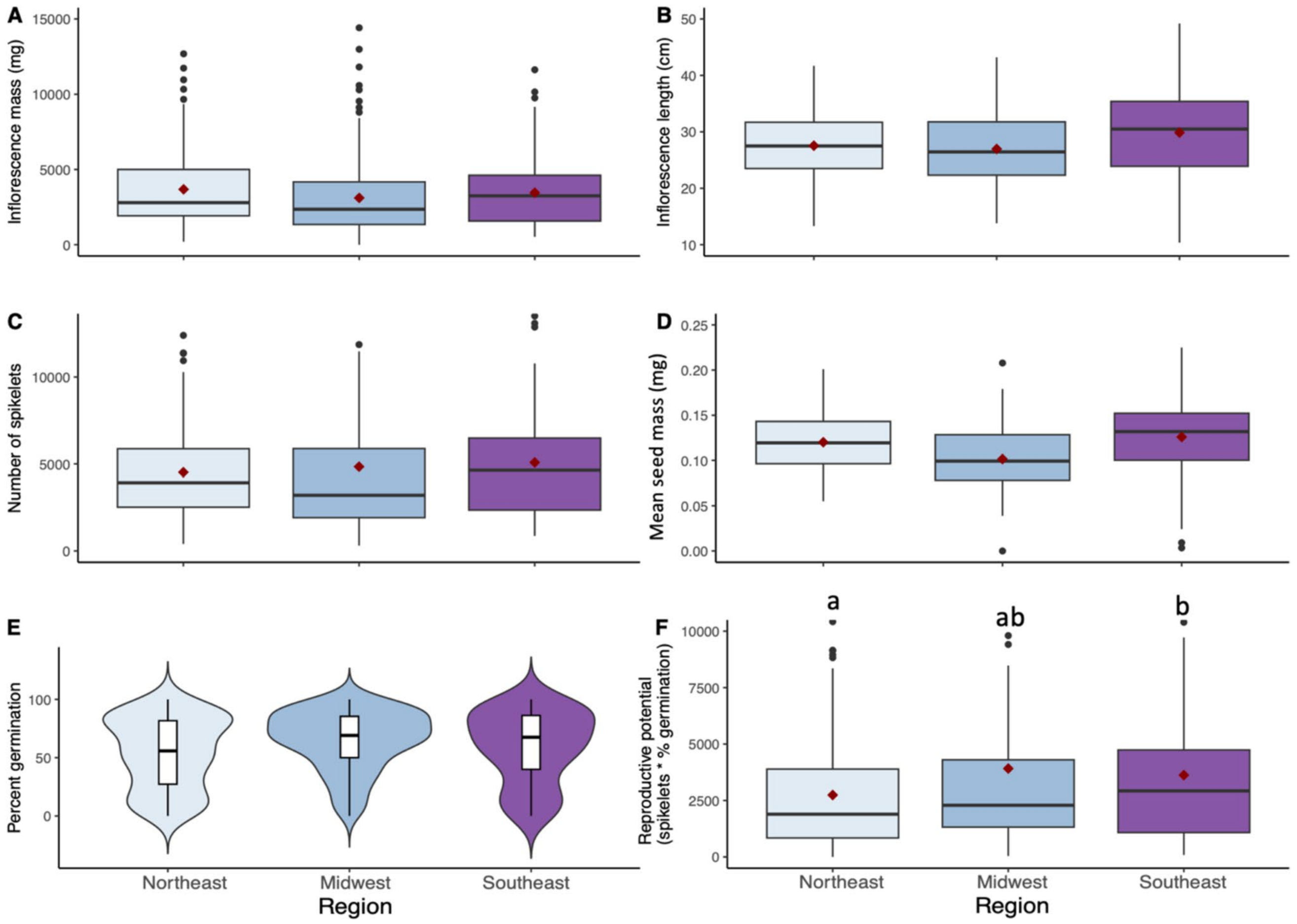

**Fig. 2** Mean of A) inflorescence mass, B) inflorescence length, C) number of spikelets, D) average seed mass, E) percent germination, and F) reproductive potential by region of origin (Northeast, Midwest, and Southeast). Letters represent Tukey's HSD test displayed in compact letter design (CLD) showing pairwise comparisons set to a p-value threshold of 0.05 comparing between each region. The dark red diamond within each boxplot (A-D, F) represents the mean value, the upper and lower hinges of each boxplot represent the 25th and 75th quantile, the middle line represents the median value, the whiskers represent the 5th and 95th percentile, and outliers are represented by black points. The box and whiskers in the violin plot represent the 10thquantile (lower whisker), 25th quartile (lower edge of box), midline (median), 75th quartile (top edge of box), and 90thquantile (top whisker).

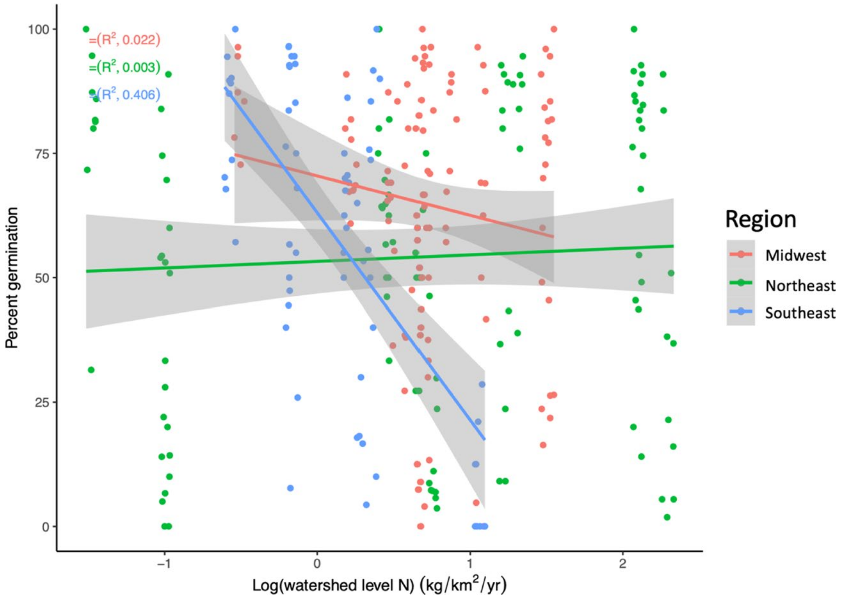

**Fig. 3** Effect of logarithm of watershed level nitrogen on percent germination across region of origin (Northeast, Midwest, and Southeast). Lines represent linear regression and grey area represents the 95% confidence interval.

mm ± 198.01 SE) (Fig. 4A). Conversely, seedlings from the Midwest had a negative response to elevated nitrogen, with seedlings grown under ambient nitrogen (2177.71 mm ± 136.034 SE) accumulating 12% more shoot height than seedlings grown under elevated nitrogen (1946.68 mm ± 97.58 SE) (Fig. 4A). There was moderate evidence that the effect on nitrogen on shoot number was affected by region (nitrogen treatment * region interaction), as seedlings from the Southeast grown in elevated N (5.94 ± 0.504 SE) had significantly more shoots (38%) than the same seedlings grown under ambient N (4.31 ± 0.35 SE), whereas elevated nitrogen did not affect shoot number for seedlings from Northeastern and Midwestern populations (Fig. 4B).

There was moderate evidence that the effect of nitrogen on total and belowground biomass also depended on region (nitrogen treatment * region interaction) (Table 2). Although Tukey's HSD post-hoc test was unable to resolve significant pairwise differences, there were notable patterns in total biomass between the treatment groups. Namely, Southeastern *Phragmites* seedlings grown under elevated nitrogen (2.49 g ± 0.33 SE) accumulated 31% more total biomass than seedlings grown under ambient conditions (1.90 g ± 0.23 SE) (Fig. 4C). The opposite pattern was observed in seedlings from the Midwest as seedlings grown under ambient nitrogen (1.90 g ± 0.18 SE) accumulated 16% more total biomass than seedlings grown under elevated nitrogen (1.648 g ± 0.128 SE) (Fig. 4C). The belowground biomass of seedlings from the Southeast grown under elevated nitrogen (0.69 g ± 0.10 SE) was 63% higher than that of Midwest seedlings under the same conditions (0.42 g ± 0.04 SE) (Fig. 4C). There was weak evidence that the effect of nitrogen on aboveground biomass also depended on region (Table 2); nitrogen only increased aboveground biomass of seedlings from the Southeast (Fig. 4C). There was also moderate evidence that the effect of nitrogen

**Table 2** ANOVA numerator degrees of freedom, F-value, and associated p-value from linear mixed effect models testing the effect of nitrogen * region on seedling growth traits and biomass collected from *Phragmites*seedling growth experiment

| | Total biomass | | | Aboveground biomass | | | Belowground biomass | | | Aboveground: Below-ground Biomass | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | DF | F-val | p-val | DF | F-val | p-val | DF | F-val | p-val | DF | F-val | p-val |
| Region | 2 | 1.053 | 0.367 | 2 | 0.900 | 0.422 | 2 | 1.247 | 0.308 | 2 | 2.700 | 0.090 |
| Nitrogen | 1 | 5.645 | 0.019 | 1 | 7.573 | 0.007 | 1 | 0.023 | 0.879 | 1 | 1.433 | 0.233 |
| Region:nitrogen | 2 | 3.456 | 0.034 | 2 | 2.500 | 0.086 | 2 | 3.625 | 0.029 | 2 | 4.072 | 0.019 |
| | **Specific Leaf Area** | | | **Total Shoot Height (day 42)** | | | **Shoot Number (day 42)** | | | | | |
| | **DF** | **F-val** | **p-val** | **DF** | **F-val** | **p-val** | **DF** | **F-val** | **p-val** | | | |
| Region | 2 | 0.509 | 0.608 | 2 | 0.401 | 0.674 | 2 | 0.026 | 0.975 | | | |
| Nitrogen | 1 | 1.092 | 0.298 | 1 | 2.619 | 0.108 | 1 | 5.878 | 0.017 | | | |
| Region:nitrogen | 2 | 0.023 | 0.977 | 2 | 3.444 | 0.034 | 2 | 3.976 | 0.021 | | | |

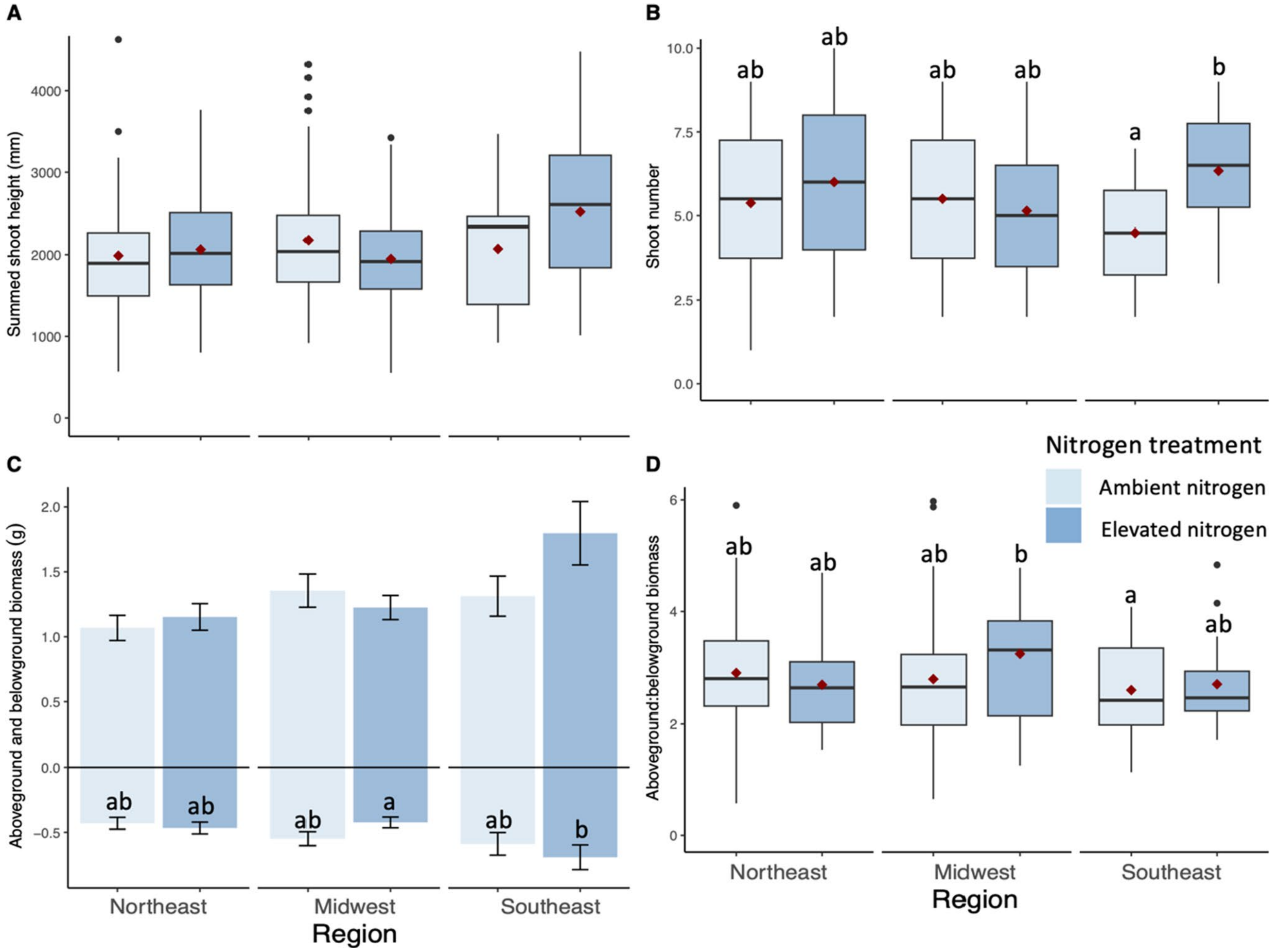

**Fig. 4** Mean of A) total shoot height at day 42, B) number of shoots at day 42, C) aboveground and belowground biomass, and D) aboveground: belowground biomass by region of origin (Northeast, Midwest, and Southeast) and nitrogen treatment (ambient and elevated nitrogen). Letters represent Tukey's HSD test displayed in compact letter design (CLD) set to a p-value threshold of 0.05 comparing between each region between each region*nitrogen treatment (significantly different letters indicated in red). In plot "C" CLD letter below the x-axis represent comparisons in belowground biomass, and error bars represent standard error. The dark red diamond within each boxplot represents the mean value, the upper and lower hinges of each boxplot represent the 25th and 75th quantile, the middle line represents the median value, the whiskers represent the 5th and 95th percentile, and outliers are represented by black points.

on aboveground: belowground biomass ratio was influenced by region ((nitrogen treatment * region interaction) (Table 2). Seedlings from the Southeast grown under ambient nitrogen (2.59 ± 0.24 SE) had 20% lower aboveground: belowground biomass ratio than seedlings from the Midwest grown under elevated nitrogen (3.24 ± 0.19 SE) (Fig. 4D). There was no evidence that watershed-level nitrogen had any effect on total ($F_{1,173} = 0.021$), aboveground ($F_{1,173} = 0.077$), or belowground ($F_{1,173} = 0.008$) biomass under elevated and ambient nitrogen.

We observed moderate evidence that specific root length and secondary root volume were influenced by region (Table 3). Seedlings from the Southeast region (10,936.18 $mm^3$ ± 1602.86 SE) had 68% higher secondary root volume than seedlings from the Midwest (6,527.24 $mm^3$ ± 500.90 SE) (Fig. 5A) and seedlings from the Northeast (28.56 mm/mg ± 1.54 SE) had 17% higher specific root length than seedlings from the Midwest (24.44 mm/mg ± 1.17 SE) (Fig. 5B).

## Discussion

### The Effects of Local Watershed Nitrogen on Seed Germination

We hypothesized that *Phragmites* populations experiencing higher watershed N loads would have higher fecundity and germination. However, we found that in general watershed-level nitrogen did not affect any of the inflorescence traits, average seed mass, or reproductive potential. We did find that watershed N only affected germination rates in the

**Table 3** ANOVA degrees of freedom, F-value, and associated p-value from linear mixed effect models testing the effect of nitrogen * region on root traits collected from *Phragmites* seedling growth experiment

| | Total Root Length | | | Fine Root Length | | |
|---|---|---|---|---|---|---|
| | numDF | F-value | *p*-value | numDF | F-value | *p*-value |
| Region | 2 | 3.162 | 0.063 | 2 | 3.131 | 0.065 |
| Nitrogen | 1 | 0.090 | 0.765 | 1 | 0.573 | 0.452 |
| Region:nitrogen | 2 | 0.731 | 0.485 | 2 | 0.898 | 0.413 |
| | **Secondary Root Length** | | | **Rhizome Length** | | |
| | **numDF** | **F-value** | **p-value** | **numDF** | **F-value** | **p-value** |
| Region | 2 | 3.030 | 0.070 | 2 | 1.919 | 0.172 |
| Nitrogen | 1 | 0.634 | 0.429 | 1 | 0.001 | 0.970 |
| Region:nitrogen | 2 | 0.217 | 0.806 | 2 | 0.679 | 0.511 |
| | **Total Root Volume** | | | **Fine Root Volume** | | |
| | **numDF** | **F-value** | **p-value** | **numDF** | **F-value** | **p-value** |
| Region | 2 | 2.696 | 0.091 | 2 | 2.669 | 0.093 |
| Nitrogen | 1 | 0.004 | 0.951 | 1 | 0.030 | 0.864 |
| Region:nitrogen | 2 | 0.451 | 0.639 | 2 | 0.977 | 0.382 |
| | **Secondary Root Volume** | | | **Rhizome Volume** | | |
| | **numDF** | **F-value** | **p-value** | **numDF** | **F-value** | **p-value** |
| Region | 2 | 3.624 | 0.045 | 2 | 1.587 | 0.228 |
| Nitrogen | 1 | 0.297 | 0.588 | 1 | 0.392 | 0.533 |
| Region:nitrogen | 2 | 0.444 | 0.644 | 2 | 2.229 | 0.116 |
| | **Specific Root Length** | | | **Root Depth** | | |
| | **numDF** | **F-value** | **p-value** | **numDF** | **F-value** | **p-value** |
| Region | 2 | 4.823 | 0.019 | 2 | 0.899 | 0.422 |
| Nitrogen | 1 | 1.586 | 0.212 | 1 | 1.061 | 0.307 |
| Region:nitrogen | 2 | 3.089 | 0.052 | 2 | 0.862 | 0.428 |

Southeast, where higher N decreased germination. While regional variation in germination success in other plant species has been observed (García-Nogales et al. 2016; Mohl et al. 2023), few studies have related variation in germination success to maternal nitrogen exposure. One study found that Powell amaranth (*Amaranthus powellii*), a noxious weed in croplands, experiences lower germination success in populations exposed to conventional (inorganic N) vs. organic (organic N) fertilization practices (Brainard et al. 2006). Another study found that in the yew species *Taxus baccata*, long-term maternal nitrogen fertilization reduced percent germination in offspring (Pers-Kamczyc and Suszka 2022). These studies contrast with what we observed in *Phragmites*, where *Phragmites* from more nutrient polluted regions (Northeast & Midwest) were less sensitive to local nitrogen levels than those from the historically less-polluted Southeast. Several experimental studies have shown that nitrogen fertilization decreased seed viability in *Succisa pratensis* (Vergeer et al. 2003), *Juniperus communis* (Gruwez et al. 2014), and a variety of subarctic plants (Milbau et al. 2017). Nitrate can increase seed viability (Ronnenberg et al. 2011; Baskin and Baskin 2014), but studies in other grass species have generally found no effect on seed viability (Wagner et al. 2001; Torres et al. 2009 Tullos & Cadenasso 2016). Notably, our *Phragmites* populations from the Southeast experienced on average lower watershed-level nitrogen (1.257 $g/m^2/yr$ ± 0.073) than those in the Northeast (3.145 $g/m^2/yr$ ± 0.335) or the Midwest (1.761 $g/m^2/yr$ ± 0.0908). The comparatively lower watershed-level nitrogen in the Southeast suggests that either the Southeast experiences lower levels of nitrogen pollution or that populations there are not adapted to high nitrogen levels. Like what has been observed in other grass species, localized studies in the Chesapeake found that elevated nitrogen had no effect on *Phragmites* seed viability (Kettenring et al. 2011). However, to our knowledge, studies on the effects of nitrogen pollution in other regions have not yet been explored. It is possible that low seed germination rates of Southeastern *Phragmites* populations established in nitrogen polluted areas may dampen its invasiveness in those areas, and this pattern warrants more research into whether nitrogen pollution is influencing *Phragmites* invasion dynamics across different regions.

## Regional Variation in Reproductive Traits

In line with our predictions, we found moderate evidence that inflorescences from the Northeast had higher mass than those from the Southeast and Midwest, even after accounting for weight of seeds. Increased inflorescence mass suggests that

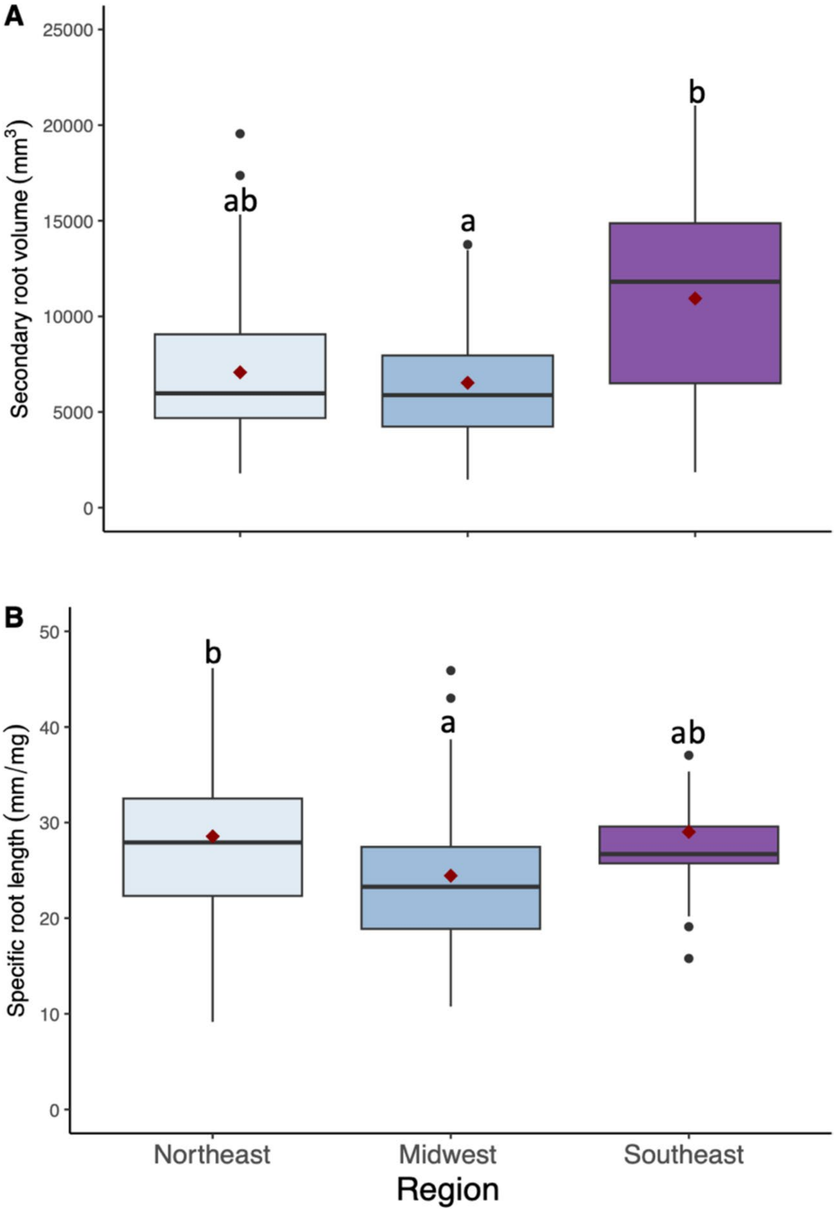

**Fig. 5** Mean of A) secondary root volume and B) specific root length by region of origin (Northeast, Midwest, and Southeast). Letters represent Tukey's HSD test displayed in compact letter design (CLD) showing significant pairwise comparisons between each region. The dark red diamond within each boxplot represents the mean value, the upper and lower hinges of each boxplot represent the 25th and 75th quantile, the middle line represents the median value, the whiskers represent the 5th and 95th percentile, and outliers are represented by black points.

the plants from the Northeast are investing more resources into reproduction than other regions (Mullins and Marks 1987). Considerable intraspecific variation in reproductive investment exists globally across various lineages of *Phragmites*, but the North American invasive *Phragmites* allocates more to reproduction than populations from Europe and Asia (Pyšek et al. 2019). The increased inflorescence mass of Northeast populations mirrors the wide distribution, high abundance, and impact on native floral and faunal diversity of *Phragmites* across in the Northeastern tidal wetlands (Saltonstall 2002; Burdick and Konisky 2003; Kiviat 2010; EDDMapS 2024). These results suggested that increased reproductive investment may be a mechanism contributing to *Phragmites* spread in the Northeast and warrants further research linking seedling recruitment and fecundity in the region.

While inflorescence mass varied regionally according to our hypothesis, seed traits (seed mass, germination, reproductive potential) did not demonstrate regional variation. The average seed mass from populations from the Northeast was the same as populations from the Midwest and Southeast. Furthermore, Northeast seeds had the lowest percent germination of any region, even considering the significant decrease in percent germination by Southeast populations with high levels of maternal N exposure. While regional variation in percent germination has not previously been studied in *Phragmites*, such variation has been observed in a variety of other invasive plant species. For example, invasive *Ambrosia artemisiifolia* in China exhibited lower germination in seeds from Northeastern latitude populations versus Southeast populations (Zhou et al. 2021). Invasive

*Spartina alterniflora* populations in China displayed the opposite pattern, with populations in Northeastern China exhibiting a higher percent germination than populations from the Southeast (Cheng et al. 2022). Thus, our results show that *Phragmites* populations from the Northeast invested more into inflorescences, but this investment did not translate into increased seed mass or germination. The reproductive potential of *Phragmites* from the Southeast was significantly higher than populations from the Northeast, which is opposite to our hypothesized patterns. These results suggest that seedling recruitment in the Southeast would be higher than in the Northeast. *Phragmites* habitat suitability modelling indicates that *Phragmites* can readily establish in the Southeast and South-Central regions of North America, yet the distribution of *Phragmites* in this region is sparse (Guo et al. 2013; EDDMapS 2024). Interestingly, a common garden study found that *Phragmites* grown in low-latitude climates tended to produce more inflorescences per plant, suggesting higher reproductive output in the South which is in-line with our findings (Mozdzer et al. 2016). Increased human activity (human population density, land use, and human access) can be responsible for nutrient pollution and is the strongest driver in the genetic structuring of *Phragmites* populations in North America (Guo et al. 2018). Human activity can increase disturbance and nutrient pollution, both of which have been linked to increased invasion in *Phragmites* (Chambers et al. 1999; Bertness et al. 2002; Minchinton and Bertness 2003; Silliman and Bertness 2004). Therefore, the spread of *Phragmites* may potentially be due to the history of industrialization in North America, which has historically lagged in the South (Bateman and Weiss 1975; Guo et al. 2018). Several studies show that weak Allee effects can limit the local spread of *Phragmites*, as local genetic diversity must accumulate for outcrossing to occur and produce viable seeds (McCormick et al. 2010; Kettenring et al. 2011). Although we were not able to accurately determine the number of seeds produced on each inflorescence due to variable seed drop, it is notable that populations from the Southeast had a fewer of seeds than the other regions we sampled. Because our reproductive potential metric only includes spikelet number x germination rate, and spikelets can have variable numbers of seeds, our metric misses important information on seed set which is where Allee effects would manifest. More research is warranted on the dynamics of reproduction and identifying potential limits in seedling recruitment in the Southeast, as we found the potential for high seedling recruitment.

## Regional Variation in Seedling Response to Nitrogen

We uncovered opposite belowground seedling responses to elevated nitrogen between *Phragmites* populations in the Southeast and Midwest. Elevated nitrogen boosted belowground biomass in seedlings from the Southeast while elevated nitrogen decreased belowground biomass in seedlings from the Midwest. This pattern may be driven by differences observed in secondary root volume, as seedlings from the Midwest had significantly lower root volume than plants from the Southeast. As a result of the inhibitory effects of elevated nitrogen on belowground growth in Midwestern seedlings, these seedlings had the highest aboveground to belowground biomass ratio observed in our study.

Ammonium ($NH_4$) and nitrate ($NO_3$) can act as signals for the proliferation or inhibition of lateral root growth, with both low N (Zhang et al. 2007) and high N (Zhang et al. 1999) thresholds for lateral root growth inhibition reported. Other studies have also demonstrated negative, neutral, and even positive relationships between sediment nitrogen levels and *Phragmites* belowground biomass, suggesting that there is considerable intraspecific variation in responses to nitrogen fertilization (Holdredge et al. 2010; Mozdzer and Megonigal 2012; Caplan et al. 2014; Chen et al. 2017; Gonzalez Mateu et al. 2021). These results suggest that the consequences of eutrophication on *Phragmites* belowground biomass may be very different among regions. Elevated nitrogen decreased the belowground biomass of the native wetland grass *Spartina alterniflora* and is hypothesized to cause tidal marsh collapse through increased tidal erosion in *Spartina*-dominated marsh (Deegan et al. 2012; Hanley et al. 2021). This phenomenon may very well be reflected in *Phragmites*, and if so, increased eutrophication in Midwestern (but not Northeastern or Southeastern) *Phragmites* dominated wetlands may lead to marsh destabilization. Increases in belowground biomass may also increase the priming of deep carbon pools as *Phragmites* can increase soil aeration through its aerenchyma tissue leading to higher rates of decomposition and subsidence (Bernal et al. 2017, 2023).

We found moderate evidence that the shoot number of *Phragmites* seedlings from the Southeast increased when grown under elevated nitrogen, which was not observed in the Northeast and Midwest. Although the expansion of *Phragmites* stands into adjacent wetland can be achieved through vegetative lateral expansion (Güsewell and Edwards 1999; Minchinton and Bertness 2003; Brisson et al. 2010), recent work has revealed that the advancing front of *Phragmites* stands can often be composed of multiple genets, highlighting the role of seedling recruitment in *Phragmites* patch expansion (Kettenring et al. 2016). Increased density in mature *Phragmites* stands correlates to lower native plant biomass and diversity (Holdredge and Bertness 2011; Elsey-Quirk and Leck 2021 but see Theuerkauf et al. 2017). Thus, increased shoot density of seedlings recruited near the edge of *Phragmites* stands may help in outcompeting native plants at the interface between native wetlands and invasive *Phragmites*. While seedling shoot density and biomass may not affect native plant communities as much as mature stands do, increased seedling vigor can help overcome seedling-stage mortality associated with flooding and competition and aid in successful establishment (Mauchamp et al. 2001; Saltonstall and Court Stevenson 2007).

Taken together, our results suggest that regional variation in seedling responses to nitrogen exists, as populations from the Southeast responded positively to increased nitrogen fertilization while Midwest populations showed the opposite pattern. Increased anthropogenic nutrient pollution may influence regions in different ways and potentially promote the invasion of populations in the Southeast more than in other regions.

### Study Limitations

While this study makes a lot of progress toward understanding regional variation in fecundity and seedling performance in *Phragmites*, there are some limitations to our methods that we acknowledge. Firstly, we experienced some logistical difficulties during the COVID-19 pandemic that reduced our scale and ability to collect inflorescences. Because of a university-wide travel restriction of within 50 miles of campus we had to rely on local volunteer collectors from universities and National Wildlife Refuges using provided sampling protocols. Collections of inflorescences at a consistent phenological stage (mature inflorescences before seed drop) was achieved through constant monitoring by local collectors, however some collections may have been performed during active seed dispersal, which is why spikelet counts were used as a proxy for seed counts to avoid variation in seed number due to seed dispersal.

We were unable to obtain soil and porewater samples from sampling locations due to logistical limitations of disseminating sampling materials, which led us to rely on the USGS SPARROW mapper (Ator 2020). Although the USGS SPARROW mapper is based on 2012 nutrient loading data and may not accurately reflect the nutrient loading experienced by sampling population plants in 2021. However, it does provide annual nutrient loading data that is more representative of cumulative nutrient loads experienced by local plants across an entire growing season as opposed to a point measurement at the end of the growing as provided by soil and porewater sampling.

## Conclusions

In summary, our evidence suggests that invasive *Phragmites* demonstrates a high degree of intraspecific variation in fecundity and seedling performance across North America. There was a disconnect between the relatively low abundance of *Phragmites* in the Southeast and the high reproductive potential and high growth potential under elevated nitrogen of Southeastern seedlings observed in this experiment. More research is needed to elucidate the mechanisms inhibiting Southeast *Phragmites* spread within the region. We also found regional variation in seedling responses to nitrogen, particularly in belowground biomass and shoot number, where populations from the Southeast responding positively to nitrogen fertilization and Midwest populations showed the opposite pattern. In the Southeast, increasing anthropogenic nutrient pollution may boost *Phragmites* belowground productivity and keep up with sea-level rise. However, the equilibrium between soil accretion through boosted growth and soil priming and increased decomposition must be explored to assess the net impacts. Southeastern *Phragmites* populations exhibit higher reproductive potential than populations from Northeast, a region where seedling recruitment is responsible for most of the spread. Combined with our findings that Southeastern *Phragmites* seedlings respond positively to nitrogen fertilization then the risk for the Southeast to become a potential invasion hotspot in the future warrants further investigation. This current study along with future research will help inform management on the importance of increasing vigilance towards early detection and eradication of new *Phragmites* populations to reduce local pollen donor sources combat the further spread of *Phragmites* into the Southeast.

**Supplementary Information** The online version contains supplementary material available at https://doi.org/10.1007/s13157-025-01900-4.

**Acknowledgements** Thank you to undergraduate researcher Julianna Fryman of Tulane University for her help in processing *Phragmites* inflorescences and the volunteer Terri J. Evans at the Smithsonian Institution Environmental Research Center in Edgewater, Maryland, for her help during the seedling growth experiment, and all of the collectors that helped in sourcing the inflorescences used in the study.

**Author contributions** S.L., K.C., M.K.M, T.J.M., and E.C.F. in conjunction designed the experiment. S.L. and volunteers helped with sampling of *P. australis* material. All procedures and data collection were performed by S.L. Guidance and assistance in data analysis was offered by E.C.F. Data analyses were performed by S.L. First draft was written by S.L. and all authors edited the manuscript.

**Funding** Funding was provided by Tulane University, the Smithsonian Institution Fellowship Program, and NSF Grant (NSF-DEB-2051602).

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

## Declarations

**Conflict of interest** None of the authors have any conflicts of interest or competing interests to report.

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