Effects of high- vs. low-intensity herbicide management on Phragmites australis propagule pressure in a brackish wetland of California

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Abstract

Brackish wetlands are vital habitats for migratory and endemic species in coastal areas, supporting nutrient cycling, flood management, and recreation. *Phragmites australis*, or common reed, is a relatively recent invader of brackish and freshwater ecosystems across North America. In California's Suisun Marsh—a 46,950-hectare network of public and private wetlands—*P. australis* has dramatically expanded over the past two decades. This expansion reduces habitat quality for waterfowl and other species, as dense stands displace native wetland plants. Herbicide-based management, primarily using glyphosate, has been employed in some areas of the marsh for over a decade, while other areas remain untreated or were only recently treated. To investigate the effects of management, we collected inflorescences from 11 high-intensity treatment parcels (≥ 9 years of spraying) and 9 low-intensity parcels (0–3 years). Random Forest classification identified large patches of *P. australis* across satellite imagery, allowing us to estimate propagule pressure as seeds per square meter. High-intensity parcels produced fewer seeds on average than low-intensity parcels, due largely to differences in the area occupied by *P. australis* ($t = -5.307$, $df = 313.93$, $p < 0.0001$). However, we found no significant differences in seed germination or herbicide resistance between the two groups ($t = 0.449$, $df = 101.95$, $p > 0.05$; $t = -1.52$, $df = 18$, $p > 0.05$). These findings highlight the effectiveness of consistent herbicide use in reducing *P. australis* seed output and emphasize the need for coordinated, watershed-scale strategies to prevent the establishment of new patches.

Introduction

Wetlands provide critical habitat to many migratory and endemic species, as well as essential nutrient cycling, flood control, and recreational ecosystem services (Bergstrom et al. 1990; Fennessy et al. 2008; Gokce 2019). Brackish and freshwater wetlands around the United States are becoming increasingly dominated by the perennial reed *Phragmites australis* (Cav.) Trin ex Steud (hereafter: *P. australis*) with varied management outcomes (Meyerson et al. 2009; Getsinger et al. 2013; Hazelton et al. 2014; Rohal et al. 2019; Conrad et al. 2023). The dense patches produced by *P. australis* have negative impacts on native plant biodiversity and nutrient dynamics, costing public and private interests more than $4.5 million (USD) annually in management costs (Martin & Blossey 2013; Hazelton et al. 2014; Uddin et al. 2017; Lindsay et al. 2022; Yuckin et al. 2023). Although native subspecies exist in North America, the predominant stands in recent decades are identified as the invasive Eurasian haplotype M (Saltonstall 2003; Lambert et al. 2016; Lindsay et al. 2022). While studies in other regions of North America and the world have clarified our understanding of *P. australis* expansion, its reproduction and management outcomes on the Pacific coast are obscure.

The brackish wetlands of Suisun Marsh in the Sacramento-San Joaquin Delta of California exemplify the expansion of invasive *P. australis* on the Pacific coast (Grossinger et al. 1998; Meyerson et al. 2009; Whitcraft et al. 2011; Grewell et al. 2014; Lambert et al. 2016; Conrad et al. 2023; Hagani et al. 2023). As one of the largest contiguous wetlands on the Pacific coast of North America, Suisun Marsh is managed heavily for waterfowl habitat, providing a large stopover area for migrant birds along the Pacific Flyway. Suisun Marsh also offers year-round critical habitat for endangered and endemic species such as the Delta Smelt (*Hypomesus transpacificus*), Salt-marsh Harvest Mouse (*Reithrodontomys raviventris*), and Ridgway's Rail (*Rallus obsoletus*) (Shapiro 1974; Sustaita et al. 2011; Takekawa et al. 2011; Smith et al. 2019; Hagani et al. 2023). Between 2000 and 2018, the 46,950-ha wetland experienced more than a 200% increase in *P. australis* cover despite the extensive efforts of land managers and the Suisun Resource Conservation District (SRCD), the agency responsible for managing control efforts of private landowners marsh-wide (Suisun RCD; Hagani et al. 2023). These efforts are principally herbicide-based, with mowing, disking, and burning as complementary or alternative methods (Conrad et al. 2023; Hagani et al. 2023). The patchwork of private, public, and non-profit land has resulted in a lack of uniformity in *P. australis* control across Suisun Marsh (Conrad et al. 2023; Hagani et al. 2023). Understanding how management outcomes differ between treatment regimes may inform cohesive future management in brackish wetlands.

Based on genetic and remote sensing analysis, non-native *P. australis* colonization in North America is thought to be primarily established sexually via wind-dispersed seeds followed by clonal patch expansion (McCormick et al. 2010; Hagani et al. 2023). Rhizomes are clonal underground stems that produce shoots and contribute to the expansion of individual patches, however, they do not increase genetic diversity and are less likely than viable seeds to initiate new patches (Baldwin et al. 2010; McCormick et al. 2010; Kettenring & Whigham 2018). Sexual propagation can increase genetic variation across and within stands of *P. australis*, a likely contributor to higher rates of seed viability in an invasive population of Chesapeake Bay due to cross-pollination (Kettenring et al. 2010; Kettenring et al. 2011; Hazelton et al. 2014). It is unclear whether the same relationship exists within the populations of *P. australis* in Suisun Marsh, but if so, it has the potential to create a positive feedback loop in which greater genetic variability increases seed viability, and vice versa.

Land managers continue to use herbicides for *P. australis* and other invasive species because of their efficacy on young shoots and new patches that drive rapid expansion (Mozdzer et al. 2008; Hazelton et al. 2014; Martin & Blossey 2013). More mature stems are damaged but do not always die from herbicide spraying. The damage endured by above-ground stems and leaves impacts the synthesis of essential amino acids via disruption of the shikimate pathway that limits energy and proteins available for seed production (Lacroix & Kurrasch 2023). Following decades of herbicide treatment with little abatement, remaining patches of *P. australis* in Suisun Marsh may have developed some resistance to the compounds being used due to intense selective pressure, as shown in other species (Sammons & Gaines 2014; Gaines et al. 2020). Based on our understanding of other tenacious populations of *P. australis*, we surmise that producing more viable seeds in areas of high patch density leads to rapid establishment and expansion of the *P. australis* haplotype M, which may also apply to Suisun Marsh. Here, we look to answer three main questions:

- How has past treatment impacted *P. australis* propagule pressure?
- How has past treatment impacted *P. australis* seed viability?
- Has the high-intensity treatment led to a detectable amount of herbicide resistance developing?

By answering these questions, we hope to better inform land managers' decision-making and contribute to more successful management outcomes in the future.

Methods

Study Area

Seeds were collected from public and private land parcels across Suisun Marsh (38.1475 N, 122.0053 W). The marsh consists mostly of managed wetland ponds protected from semi-diurnal tides by levees with some tidal wetlands and sloughs open to natural tidal influence. Salinity is generally highest in managed ponds, followed by canals, and then sloughs, with a mean salinity between 1 and 10 ppt (Schacter et al., 2021). Managed ponds are flooded and drained based on landowner needs, with most flooding occurring in September and early October to create habitat for the migratory season of many waterfowl. This is followed by a spring leaching cycle from February to May, after which managed ponds are dried up and invasive plant management is undertaken from July through September (Grewell et al. 2014; Conrad et al. 2023; Hagani et al. 2023).

Although 2,000–3,000 ha of managed land is being restored to tidal marsh to benefit these species, the vast majority is managed to support migrating and wintering waterfowl (Hagani et al. 2023). Herbicide treatments of *P. australis* with glyphosate-based products occur only in managed wetlands when ponds are dry to avoid impacts on non-target species. To cover large areas with some accuracy, most spraying is done aerially with helicopters or drones, but other methods of applying herbicide are also used (such as backpack sprayers). Mowing, disking, and burning are also employed on occasion, but we only took account of herbicide spraying in designating treatment areas as high- or low-intensity management because we did not have access to records on the prevalence of the other activities.

Seed Collection

Land parcels were selected for seed collection based on the years of glyphosate-based herbicide treatment as determined from historical data provided by SRCD, which has records of the acreage of spraying per parcel per year from 2000 to the present. Parcels with 9 or more years of herbicide spraying were classified as high-intensity treatment, while those parcels with 3 years or less of spraying were classified as low-intensity treatment. Five of the "low-intensity" treatment parcels had had no treatment at all during the period since 2000. Seeds were collected in late August 2022 from 11 sites of high-intensity treatment and 9 of low-intensity treatment, with multiple sites in some large parcels (Fig. 1). Five inflorescences were collected from 5 patches in each site for a total of 25 inflorescences per site and 250 inflorescences per treatment. All but one of the collection sites were in managed wetlands, while Joice Island (JI) is a tidal wetland that has never seen herbicide treatment.

During collection, a 0.5m x 0.5m quadrat was used to measure inflorescence density in 5 randomly selected areas across each patch. The long and short axes of each patch were measured to estimate each patch's area.

Propagule Pressure

Each inflorescence was weighed and stripped of all spikelets. Spikelets were then weighed separately from the stem. For each inflorescence, an aliquot of 60 spikelets was counted and weighed to estimate the mass of a single spikelet, and this value in turn was used to estimate the total number of spikelets on the inflorescence. Three spikelets from each inflorescence were also dissected to determine the average number of seeds per spikelet.

A raster file of *P. australis* cover in Suisun Marsh provided by the Random Forest classification of 2018 NAIP imagery was used to estimate the percentage of *P. australis* per m^2 of marsh in each parcel (Hagani et al. 2023). The propagule pressure of *P. australis* per m^2 of marsh was calculated as follows:

$$\frac{Seeds}{m^2\,marsh} = \frac{Seeds}{Spikelet} \times \frac{Spikelets}{Inflorescence} \times \frac{Inflorescences}{m^2\,P.\,australis} \times \frac{m^2\,P.\,australis}{m^2\,marsh}$$

Random Forest Classification

We used the classifications derived by Hagani et al. (2023) to estimate the area of *P. australis* per area of managed wetland in each land parcel. The classifications were built upon aerial imagery collected by the National Agricultural Imagery Program (NAIP) from 2003 to 2020. NAIP imagery includes three color bands (red, blue, and green) and a near-infrared band. In California, these images were collected every three years pre-2009 and every 2 years since. Eight classifications were generated within this timeframe: 2003, 2006, 2009, 2012, 2014, 2016, 2018, and 2020. For each classification year, representative *P. australis* patches were selected from the image and manually classified (Tadros et al. 2020) to use as training and validation data. Separate polygons were also manually selected to serve as "non-*P. australis*" data. Random forest classifiers (Breiman 2001; Cutler et al. 2007) were built in R Studio (Liaw and Wiener 2002; R Core Team 2021; R Studio Team 2021) using a random 70% of the training data, with the remaining 30% withheld for model evaluation (Paz-Kagan et al. 2019). Classifications were generated with the color bands, the near-infrared band, and an additional predictor variable for every year following 2003, which described the distance of every pixel from the nearest *P. australis* pixel classified on the previous image. For each classification year, five random forest models were run based on a different random selection of training and validation data, and accuracy metrics (User's accuracy, producer's accuracy, overall accuracy, and Kappa's statistic; Fielding and Bell 1997; Kraemer 2015) were averaged. The singular random forest classifier, which produced the best accuracy metrics, was then used to create a map of predicted *P. australis* each year in Suisun Marsh with the package "raster" in R (version 3.6–11; Hijmans and van Etten 2012). The final output of this process was a fine-scale (1-2m) wall-to-wall raster of Suisun Marsh with values of "1" to represent *P. australis* and "0" to represent non-*P. australis* for each classification year.

Seed Germination

Spikelets from each inflorescence were counted out in groups of 60 and then combined by patch so that each patch had 300 spikelets from 5 inflorescences in the germination trial. Spikelets were initially washed for two minutes in a deionized water bath with 10% by volume household bleach to prevent mold growth. Petri dishes of 150 mm were then filled halfway with autoclaved sand. Deionized water was added to moisten the sand, and any excess water was poured off. Filter paper was used to cover the sand and allowed to equilibrate to the moisture. The spikelets were spread onto the prepared Petri dishes in a layer 1 spikelet thick, after which the Petri dishes were sealed with parafilm. The seeds were then cold-stratified for 2 weeks at 4˚C in the dark according to the method of Kettenring et al. (2010). Once stratified, seeds were placed in an Intellus Control System growth chamber (Percival Scientific Inc., Perry, IA) set to an 11:9 h day/night cycle mimicking temperature fluctuations and daylight hours of Suisun Marsh in late spring and early summer, ramping linearly for 2 hours from 13˚C to 25˚C. The petri dishes were checked for germination and rotated every other day for 2 weeks. Germinated seeds were counted and removed. Germination was defined as the observation of a radicle emerging. After two weeks of germination trials, the ungerminated seeds were discarded.

Herbicide Resistance

Germinated seeds were grown in a greenhouse for 1.5 months in June and July 2022. Plants were kept at ambient temperature in Santa Clara, CA with ambient lighting. Plug trays were filled with potting soil and then placed into a larger tray kept flooded with water, whose salinity was managed to remain at 5.7 ppt, mimicking conditions found in Suisun Marsh. Plants were trimmed above the first healthy leaf to standardize for biomass and leaf area. The remaining leaf on each plant was then wiped with 2% glyphosate (Round-Up, Bayer Corporation, Whippany, NJ). *P. australis* plants were visually checked one week after herbicide application and damage was rated on a 0–5 scale, with 0 being no damage and 5 being total death (Ogg et al. 1991; Dear et al. 2003). We also took note of whether resprouts began growing from plants post-herbicide application.

Results

Propagule Pressure

The propagule pressure of *P. australis* was 17,986 seeds per m^2 of marsh, on average, in low-intensity treatment parcels and 8,178 seeds per m^2 of marsh, on average, in high-intensity treatment parcels, a 54.5% reduction in seed production ($t = -5.307$, $df = 313.93$, $p < 0.0001$). The difference results largely from the lower percentage of *P. australis* cover in land parcels classified as high-intensity treatment. Parcels subject to low-intensity treatment had 7.42% *P. australis* cover, on average, compared with 3.39% cover in parcels of high-intensity treatment. This was a 54.3% decrease in *P. australis* cover across the marsh from low- to high-intensity treatment land parcels, which includes 59 additional land parcels in Suisun marsh where seeds were not collected ($t = -3.23$, $df = 74$, $p < 0.05$). On average, inflorescences were similar in weight between the two treatment groups, with 1.1 g inflorescences, on average, in the low-intensity treatment parcels and 0.98 g in the high-intensity treatment parcels ($t = -1.036$, $df = 415.4$, $p > 0.05$). There was no significant difference in the number of seeds contained within each spikelet (~ 6 seeds/spikelet), nor stem density (~ 40 stems/m^2) between the high- and low-intensity herbicide treatments ($t = 1.051$, $df = 513.11$, $p = 0.4782$; $t = -1.2161$, $df = 441.93$, $p = 0.2245$).

Joice Island (JI) had the highest estimated propagule pressure with 44,212 seeds produced per m^2 of marsh (Fig. 2). This was the only tidal wetland site sampled that had never experienced herbicide treatments due to regulations on the use in tidally influenced areas. The sampled area had 9.33% *P. australis* cover and the mean weight of seed material per inflorescence was the greatest compared with all other sites at 1.89 g. The publicly managed Crescent Unit (CRU) had the lowest estimated propagule pressure with only 344 seeds per m^2 of marsh, attributable to smaller inflorescences (0.485 g) and low stem density (8.80 stems per m^2).

Seed Germination

Germination rates ranged from 0 to 35% which varied between patches of the same site. The mean germination rate was not significantly different between high- and low-intensity herbicide treatment sites with an average of 7.81% and 7.15% germinating, respectively (Fig. 3., $t = 0.349$, $df = 84.27$, $p > 0.05$). Seed viability ranged widely across all sites with the with East Lower Joice (ELJ), 11.1%; Mid Lower Joice, (MJL) 11.5%; North Lower Joice (NLJ), 17.1%; and Joice Island (JI), 22.9%) representing the highest percentages while other sites, such as Delta King (DK) and Grizzly Fairview (GFV) produced fewer viable seeds, on average, with 0.043% and 0.23% germinating, respectively.

Herbicide Resistance

The average damage rating of young plants grown from seeds collected in high- and low-intensity treatment sites was not significantly different, suggesting no difference in herbicide resistance ($t = -1.52$, $df = 18$, $p > 0.05$). There was also no difference in the percentage of resprouts between high- and low-intensity treatment plants that survived the glyphosate treatment ($t = 0.38$, $df = 18$, $p > 0.05$).

Discussion

Seed production was reduced in land parcels that experienced high-intensity herbicide spraying (≥ 9 years), with this reduction in propagule pressure primarily driven by decreased *P. australis* cover, though factors such as inflorescence weight and stem density also influenced overall production. The overall expansion of *P. australis* has been rapid over the past two decades, however, remote sensing analysis reveals that 61 land parcels across Suisun Marsh experienced a decrease in cover between 2003 and 2020, as reported by Hagani et al. (2023). The regular use of glyphosate-based herbicides to limit the establishment and expansion of *P. australis* patches is a likely contributor to the decrease in these land parcels, given our results. Successful control of *P.*

australis is less challenging for small, newly established “satellite” patches, whereas larger, established patches are more productive and difficult to control (Mozdzer et al. 2008; Kettenring et al. 2011; Hazelton et al. 2014; Martin & Blossey 2013). Therefore, land parcels that have been managed with herbicides for a longer duration may have prevented satellite patches from expanding their area via rhizome to become unmanageable. Corroborating our findings, another study evaluating the management outcomes of an introduced *P. australis* population in the Great Salt Lake found a marked reduction in seeds produced per m^2 following treatment with glyphosate and mowing at different times of the year (Rohal et al. 2019). Herbicide application was carried out in either early July or late August, the same period during which most management and maintenance operations are performed in Suisun Marsh.

Our results show that land managed with herbicides can still host considerable populations of *P. australis*, as Lower Joice Island has higher coverage than the mean of most other high-intensity treatment sites (Table 1). Despite their coverage, the majority of land parcels under both high- and low-intensity treatment produced an estimated hundreds or thousands of viable *P. australis* seeds per m^2 of marshland (Fig. 2). Consistent with previous research on the topic, this suggests that seed propagation is a notable contributor to new patch initiation (McCormick et al. 2010; Kettenring & Whigham 2018; Hagani et al. 2023). This presents continuous pressure as the dispersal of *P. australis* in managed land parcels is influenced by the number of unmanaged neighboring parcels (Hagani et al. 2023). Due to the long distances possible with wind dispersal, management is most effective at a watershed or regional scale, as is advocated for by other authors on the subject of *P. australis* control methods (Takekawa et al. 2011; Hazelton et al. 2014; Hagani et al. 2023).

Seed viability is a consequential element in the establishment of *P. australis*, and may be difficult to contend with in a noxious population, as our results showed no significant effect of glyphosate on seed germination rate (Fig. 3). Rohal et al. (2019) investigated the introduced Great Salt Lake population to quantify glyphosate impacts on seed viability which did not differ significantly from the control that received no treatment. Though not specifically looking at *P. australis*, Nurse et al. (2015) focused on the impacts of same-year glyphosate application on seed viability of Hairy cupgrass (*Eriochloa villosa*), an annual grass that can reduce crop yields in the Midwestern United States. They saw no changes in seed production, however, they reported a significant decrease in seed weight and germination rate. These results are the opposite of what we found in our results on *P. australis* production, though our focus was not same-year glyphosate application, but rather regular treatment over multiple years. Viable seed production can be controlled in some invasive species such as *E. villosa*, but our results support those of Rohal et al. (2019) that indicate lower susceptibility of *P. australis* to these effects.

While seed viability was not significantly impacted by the treatment regime in this case, the variability in viability across all sites regardless of treatment suggests other environmental or genetic factors. Influences affecting the viable seed production in *P. australis* are not fully understood, however, likely contributors to increased germination rates are genetic diversity and patch size (Kettenring et al. 2010; Kettenring et al. 2011). Thorough research of the introduced Chesapeake Bay population found slight positive relationships between both of these factors and seed viability. Future genetic analysis of patches with high and low seed viability may help illuminate the potential of positive feedbacks that result in more new patches of *P. australis*. Nutrient loads have also been evaluated as drivers of seed viability, and although a significant relationship was noted with inflorescence production per plant, the same was not true for viable seed production in the Chesapeake Bay.

Resistance to glyphosate in introduced populations of *P. australis* has yet to be investigated thoroughly, though the management implications of resistance are of utmost importance. Due to its prevalence as a weed control agent since the late 20th century, at least 24 species of weeds were documented to have developed some resistance in 2014, which has since reached 57 species as of 2023 (Sammons & Gaines 2014; Landau et al. 2023). The mechanism identified in resistance involves one to three point mutations in 5-enolpyruvylshikimate-3-phosphate synthase (EPSPS), which is essential in the shikimate pathway targeted by glyphosate herbicides (Sammons & Gaines 2014; García et al. 2019). The EPSPS mutation has not been identified in *P. australis*, but it was detected once during a small-scale investigation of *P. australis* resistance in a population of Indiana Dunes National Park, with inconclusive results (Nikkel et al. 2021). Future genetic analysis of populations in Suisun Marsh is vital to understanding the state of resistance.

It is clear from our findings that regular application of glyphosate is at least partially effective in controlling *P. australis* in Suisun Marsh by reducing cover. Still, many other factors are involved in the continued spread that have received little attention on the West Coast of North America. Even if cover is shown to decrease with continued herbicide application, the varied results in seed viability suggest that land managers are contending with uncontrolled environmental and genetic factors that heavily influence the success of new patches established via seed. Until our understanding of positive feedback and invasion mechanisms is clarified, management of *P. australis* will be most effective through combined, comprehensive, and contiguous control efforts across land parcels.

Declarations

Competing Interests

The authors have no competing financial or non-financial interests to disclose.

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Author Contributions

VM, MW, and GR contributed to the study conception and design, material preparation, data collection, and analysis. Herbicide resistance trials were primarily carried out by MW and VM. Remote sensing analysis was performed by JH. The first draft of the manuscript was written by GR and MW, and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Data Availability

The datasets generated and/or analysed during the current study are available in the *phrag* repository that is publicly available,

https://github.com/gaberodkey/phrag/tree/7528eb506bacc3199863d1f8d5e4b92868b4b311

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Figures

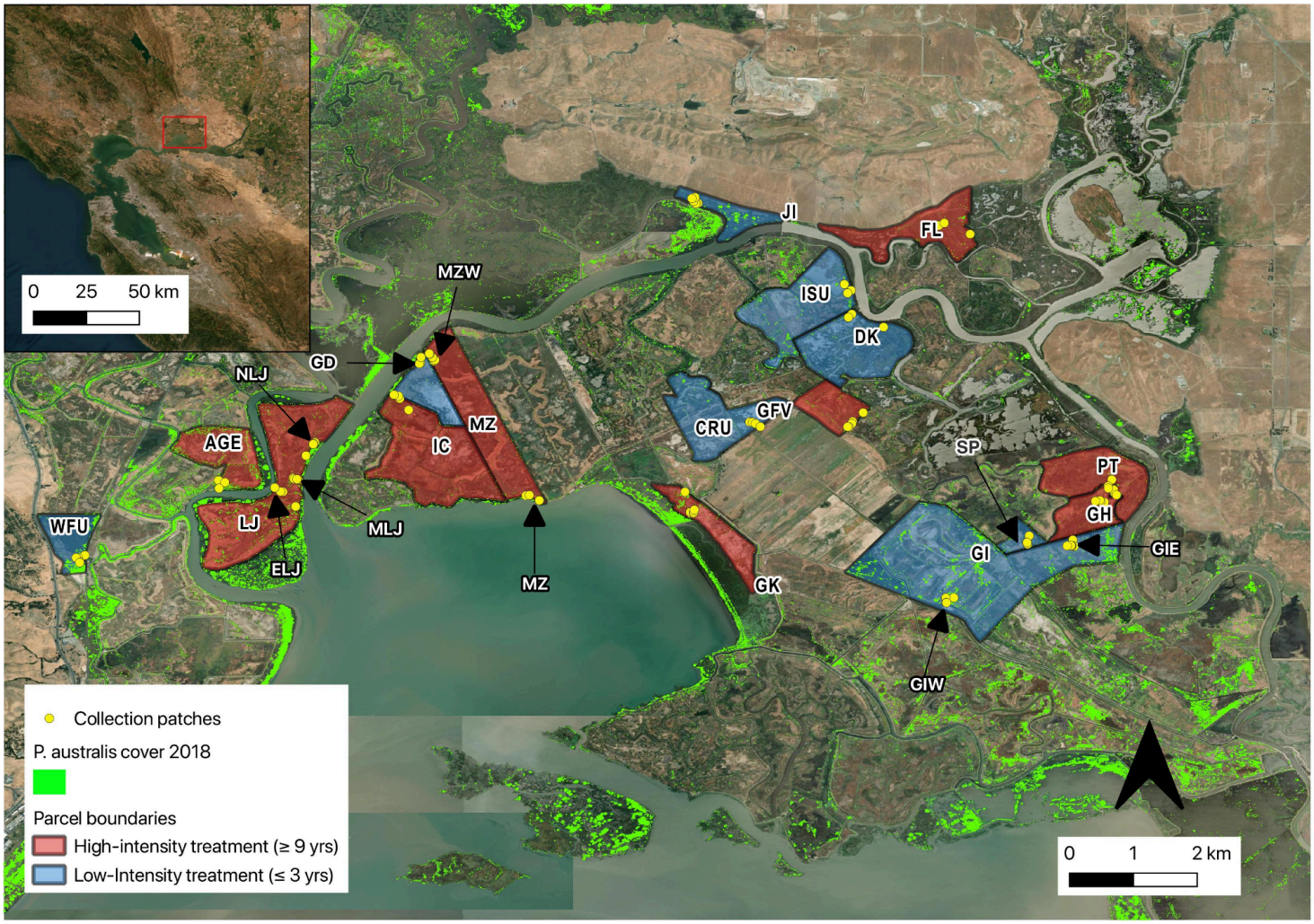

Figure 1

Areas of sample collection across Suisun Marsh. Labels bordered in white represent the entire land parcel; labels bordered in black represent sites within a single land parcel (LJ, MZ, GI). The red rectangle on the inset map represents the map area.

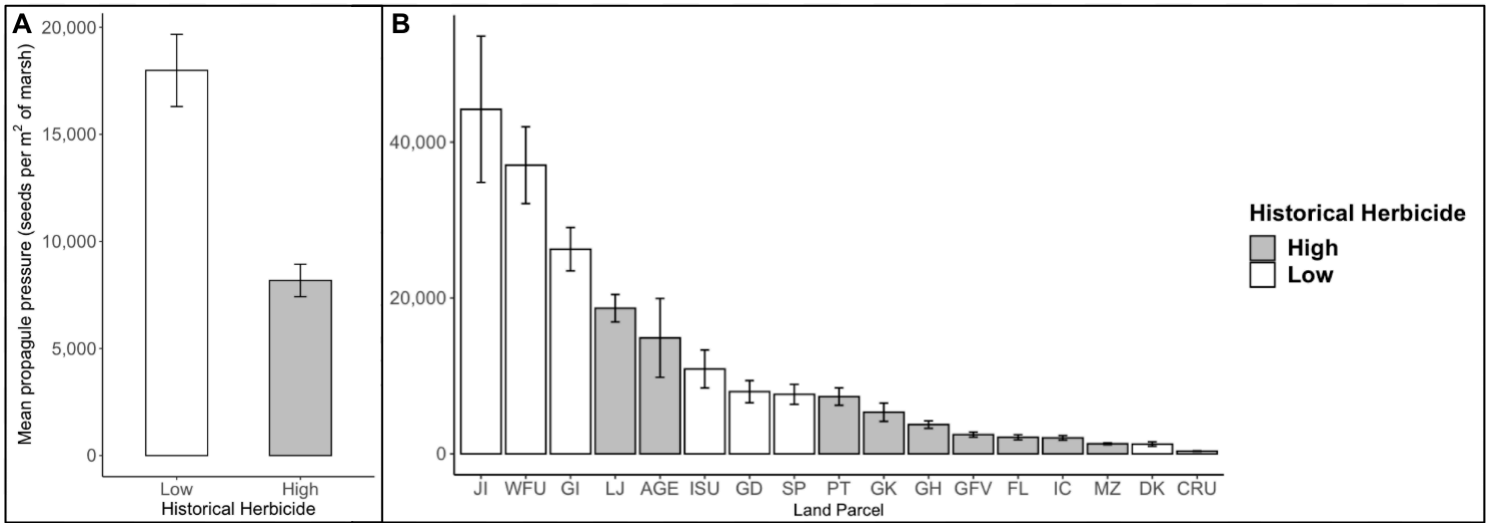

Figure 2

Production of *P. australis* seeds from high- and low-intensity herbicide treatment land parcels. A) Averages include all replicates within each treatment; n_{low} = 225, n_{high} = 294. B) Averages represent replicates from each land parcel; n = 5 for all land parcels, except n_{IC} = 4, $n_{GI, MZ}$ = 10, and n_{LJ} = 15. Error bars represent ±SEM.

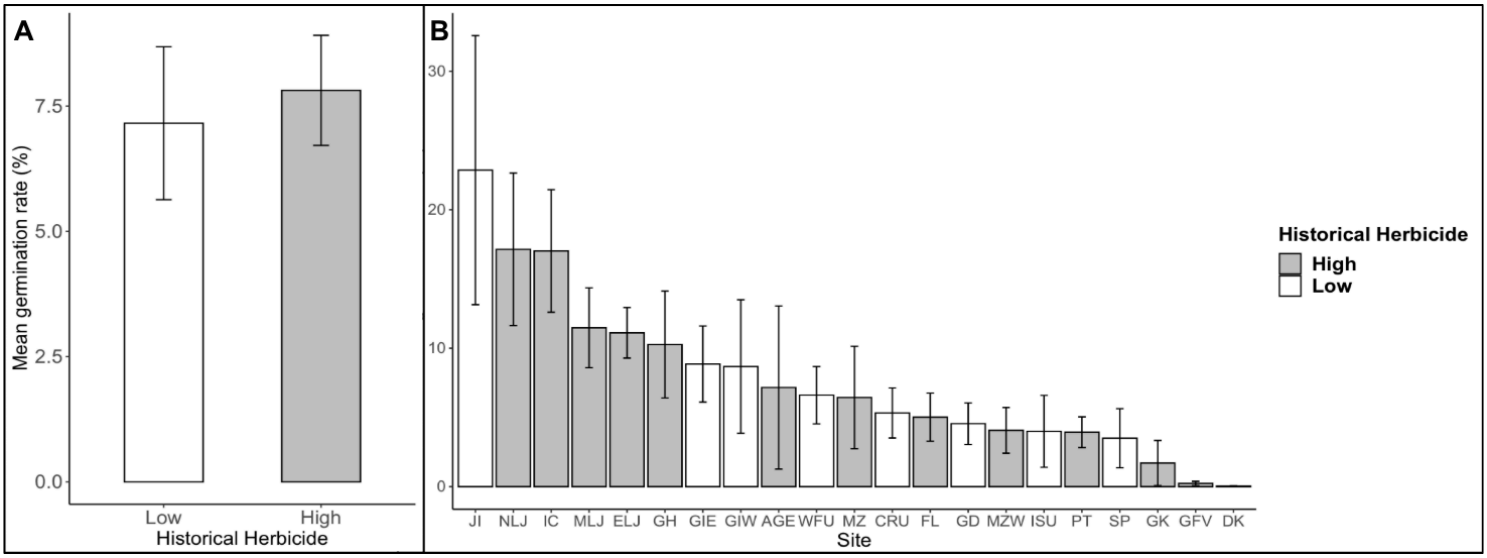

Figure 3

Germination rates of *P. australis* seeds from high- and low-intensity treatment land parcels. A) Averages represent replicates from each treatment; n_{low} = 54, n_{high} = 49. B) Averages represent replicates from each site; n = 5 for all sites, except n_{IC} = 4. Error bars represent ±SEM.