

## Research Article

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# Changing dominance of invasive common reed (*Phragmites australis*) and native plant colonization with variation in management, wildfires, and soils in a desert wetland

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## Abstract

Among the most widely distributed species globally, common reed [*Phragmites australis* (Cav.) Trin. ex Steud.] has generated extensive interest in invasive plant science and management because its introduced strains are highly invasive and often form monocultures that alter ecosystem properties. In desert wetlands in Las Vegas, NV, USA, where management goals included reducing hazardous *P. australis* fuels and increasing native plant diversity, we assessed variation in *P. australis* cover, the degree of native plant colonization, and soil seedbanks after *P. australis* management treatments (cutting, glyphosate–imazapyr herbicide) and wildfires across gradients in soil properties. Based on change in *P. australis* cover during six measurement events over 24 mo, 24 study sites formed three groups: (1) decreasing cover, where initially high *P. australis* cover (60% to 85%) decreased to <5% following multiple cutting or herbicide treatments; (2) sustaining low cover, where wildfire or clearing was associated with initially low *P. australis* cover which remained low (<30%) after multiple herbicide applications; and (3) sustaining high cover (45% to 100% initially and remaining at 30% to 100%), including sites unmanaged or treated/burned only once. High soil salinity correlated with low postmanagement *P. australis* cover. No native plants were detected in the sustaining high *P. australis* cover group, despite natives occurring in the seedbank. Where management reduced *P. australis* cover, minimal native plant colonization did occur. Secondary invasion by other non-native plants was nearly absent. Our results suggest that if *P. australis* can be initially cleared, multiple herbicide applications can persistently keep cover low, especially on drier, saline soils. Slow native plant colonization suggests that a phased approach may be useful to initially reduce *P. australis* cover, keep it low via repeated treatments, and actively revegetate sites with native species tailored to the moisture–salinity gradient across *P. australis*–invaded habitats.

## Introduction

The wetland-associated, tall grass common reed [*Phragmites australis* (Cav.) Trin. ex Steud.] is among the most widespread species on Earth, inhabiting all continents except Antarctica (Packer et al. 2017). With a complex genetic history, the species has high genetic variability and different genetic strains that vary in invasiveness among its native and introduced habitats (Eller et al. 2017). Introduced strains are in the category of the most-damaging invasive plants, by being highly invasive; having diverse mechanisms for spread (via both seed and clonal reproduction); forming monocultures; and being an ecosystem engineer that can change soil properties (e.g., forming thick litter layers), alter hydrology (e.g., slowing water flow in dense stands), and increase fire severity by producing abundant fuels (Engloner 2009). As a result, there is global interest in developing management strategies to reduce invasive populations of *P. australis* and increase native plants in diverse settings such as forested wetlands in Australia (Greet and King 2019), waterways in France (Errico et al. 2019), estuaries in South Africa (Russell and Kraaij 2008), created wetlands in Japan (Kimura and Tsuyuzaki 2011), and temperate (Zimmerman et al. 2018) and desert (Rohal et al. 2019) wetlands in the United States, among many others globally.

Two broad conclusions from the *P. australis* management literature are that (1) usually multiple treatment applications or combinations of different treatments are required to achieve control, with further research required to develop these management strategies in different environments across the variety of climates, soils, and plant community conditions invaded globally (e.g., Mal and Narine 2004; Quirion et al. 2018); and (2) the degree of native plant

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### Management Implications

Different trajectories in cover of invasive *Phragmites australis* (common reed) and native plant colonization occurred across variation in initial conditions, the number of management treatments (cutting, herbicide) or wildfires, and soil properties such as salinity. By 24 mo after our study began, 15 of 18 (83%) managed sites had *P. australis* cover  $\leq 16\%$ , compared with 80% to 100% cover on six unmanaged sites. Reducing *P. australis* cover and litter layers (which averaged 1-m thick on unmanaged sites) is important for meeting management goals of reducing hazardous fuels and providing open space for native plant colonization or active revegetation. After *P. australis* cover was reduced, secondary invasion by other non-native plants was minimal or absent. No colonization by native plants ever occurred on unmanaged sites, while some colonization occurred on managed sites by species such as narrowleaf willow (*Salix exigua* Nutt.), catclaw acacia [*Senegalia greggii* (A. Gray) Britton & Rose], and salt heliotrope (*Heliotropium curassavicum* L.). Active revegetation using saline-tolerant species may hasten native plant establishment on saline soil, where *P. australis* appeared to have lower resilience. More competitive natives may be suitable for moister or less saline soil, where *P. australis* was more resilient after treatments and wildfires. Our findings suggest that a multiphase approach may be useful to managing *P. australis* monocultures in desert wetlands. This could include taking advantage of initial wildfires (or potentially conducting prescribed fires) to cost-effectively clear *P. australis* biomass, applying herbicide multiple times to deter resprouting and reestablishment, and allowing native plants to colonize slowly with *P. australis* kept at low abundance or using active revegetation to hasten native plant establishment.

community establishment is highly variable following *P. australis* management (e.g., Güsewell 2003; Judd and Francoeur 2019). *Phragmites australis*'s diverse regeneration mechanisms, which can include seed dispersal, reproduction from soil seedbanks, rhizomes, stolons, and shoot nodes (Ailstock et al. 2001), coupled with its other traits (such as accumulation of dead mass and litter that can affect herbicide contact with live plant parts), often means that multiple applications of the same or different treatments in combination are needed to persistently reduce invasive populations (Breen et al. 2014; Monteiro et al. 1999; Rohal et al. 2019). There is a major role for invasive plant science to identify these effective treatment combinations in different settings, because effective treatments have varied among studies across the diverse management contexts of the global distribution of the species (Kimura and Tsuyuzaki 2011; Russell and Kraaij 2008; Zimmerman et al. 2018). Variations of mechanical cutting (e.g., mowing at different frequencies), herbicides, prescribed burning, managed flooding, grazing, and a variety of other treatments have shown promise for reducing *P. australis* (Hazelton et al. 2014; Packer et al. 2017; Rohal et al. 2019).

Management goals often include both reducing *P. australis* and stimulating native plant establishment, but dual achievement of these goals has varied in completeness among prior studies. This is illustrated in reviews of *P. australis* management, such as Hazelton et al. (2014), who concluded that little information on community-level recovery following removal of *P. australis* was available. Recently, examples of native plant responses to *P. australis* treatments have been highly variable, ranging from no increase in a floristic quality metric (Judd and Francoeur 2019), to other

non-native plants responding more positively than native plants (Robichaud and Rooney 2021), to native cover increasing but lacking recovery toward species composition typifying habitat not invaded by *P. australis* (Rohal et al. 2019), to native community composition converging with that typifying uninvaded habitat (Zimmerman et al. 2018). When *P. australis* is reduced, the degree of native plant colonization could depend on factors such as the abundance or composition of soil seedbanks or nearby vegetation (Rohal et al. 2023).

Relationships of *P. australis* management outcomes with site factors, such as soil properties, have also been noted as a potentially important but poorly understood variable in *P. australis* management (Rohal et al. 2023). As *P. australis* can invade a variety of wetland sites, ranging from freshwater to brackish or salt marsh, salinity can be a major factor in *P. australis* dynamics (Gorai et al. 2006). Although not considered a halophyte highly tolerant of salinity, *P. australis* nevertheless can invade saline soil but could have some life-history features compromised by salinity (Chambers et al. 2003). For example, salinity may reduce seed germination, making *P. australis* more reliant on clonal expansion (Bart and Hartman 2003).

We conducted our study to address uncertainties in *P. australis* management strategies, native plant recovery or secondary invasion during *P. australis* management, and potential associations of *P. australis* management outcomes with soil properties. Most *P. australis* research has occurred in temperate or Mediterranean climates, and we performed our study in a desert biome for which little *P. australis* ecology and management science is available (e.g., Rohal et al. 2021). The dearth of research in deserts is especially notable, as invasive strains of *P. australis* may have been expanding in deserts in recent decades (Kulmatiski et al. 2010). We asked: (1) How does *P. australis* cover change after different combinations of management treatments (cutting, herbicide) and wildfires? (2) To what degree do native or other non-native plants colonize during *P. australis* management and are these present in soil seedbanks? (3) Are soil properties, such as salinity, correlated with *P. australis* dynamics after treatments?

## Materials and Methods

### Study Area

The study area is the 85-ha Wetlands Nature Preserve (36.10°N, 115.02°W), within the 1,174-ha Clark County Wetlands Park, on the eastern edge of Las Vegas, NV, USA, in the Mojave Desert. The study area is adjacent to and on the south side of the Las Vegas Wash. The wash carries wastewater and runoff from the Las Vegas Valley to Lake Mead and had an average stream flow of  $10 \text{ m}^3 \text{ s}^{-1}$  in 2023 (Pabco Road Station, U.S. Geological Survey, Reston, VA, USA). Groundwater levels are typically within 1.5 m of the surface in our study area where *P. australis* occurs (Lato et al. 2006). Soils with *P. australis* in the study area are classified as fine-silty, mixed, superactive, thermic Typic Aquisalids (Land series) and fine-silty, carbonatic, thermic Typic Torrifluvents (Glencarb series). Both of these soils are derived from mixed alluvium, contain gypsum and carbonates, are moderately to very strongly saline (electrical conductivity 8 to 32+  $\text{dS m}^{-1}$ ), and are somewhat poorly to well drained (Lato et al. 2006). A weather station 1 km south of the study area recorded precipitation averaging 9.1  $\text{cm yr}^{-1}$  from 2006 through 2023 (Duck Creek Broadbent Station, Clark County Regional Flood Control District, Las Vegas, NV, USA). During the

years spanning our study, precipitation was 91% (2021), 45% (2022), and 81% (2023) of average.

Vegetation in our study area includes a mixture of native species that were planted since the early 2000s (e.g., Fremont cottonwood [*Populus fremontii* S. Watson] and Goodding's willow [*Salix gooddingii* C.R. Ball]) or recruited naturally (e.g., big saltbush [*Atriplex lentiformis* (Torr.) S. Watson]); infrequent and small (<1 ha) patches of non-native saltcedar (*Tamarix ramosissima* Ledeb.), which have been reduced by ongoing treatments since the early 2000s; and *P. australis* patches. The *P. australis* patches include a mixture of those thought to be at least 25 yr old and newer patches that have invaded open areas or become established and replaced patches of other vegetation after disturbances such as wildfires or floods (Whitney et al. 2015). A *P. australis* genetic investigation in the park concluded that the native strain and an invasive hybrid (between the native and introduced strains) occur along the Las Vegas Wash (Saltonstall et al. 2016). The *P. australis* in our study plots showed invasiveness (i.e., aggressive colonization) and formed a monoculture (Saltonstall et al. 2016). The invasiveness, low habitat diversity, disruption of water flow (Errico et al. 2019), and hazardous fuels of *P. australis* monocultures made them a priority for management and replacement with more diverse native vegetation.

### Phragmites australis Patches and Treatment and Wildfire History

We identified 24 *P. australis* patches of at least 0.05 ha based on a distribution map maintained by the park and our own field reconnaissance. Each patch was separated from other *P. australis* patches by other vegetation patches (mostly native species noted in the study area description) or public recreational trails (Figure 1).

Initial conditions varied among the *P. australis* patches in May 2021 when we began our study (Figure 1; Supplementary Table S1). Before May 2021, two of the patches were burned by wildfire in April 2020 and reburned (fueled by *P. australis* resprouts) in February 2021, while another two burned only in February 2021. Twelve of the patches were mechanically cut at ground level, with the cut material moved off site in November 2020, and four of these were then burned by wildfire in February 2021. Two additional cut patches had the cut *P. australis* material left spread on site in a layer (up to 1-m thick) intended to hinder resprouting. The Bureau of Land Management (Southern Nevada District) fuels-management program performed cutting using a T770 Compact Track Loader with a drum mulcher attachment (Bobcat, West Fargo, ND, USA) and a 299D2 Compact Track Loader with a disk mulcher (Caterpillar, Irving, TX, USA; and Diamond Mowers, Sioux Falls, SD, USA). The last six of the 24 patches were undisturbed in May 2021.

From these baseline conditions in May 2021 when we began our study, the diverse treatment and wildfire activity the 24 patches received over the next 2 yr enabled us to assess *P. australis* abundance change and native and non-native plant colonization across dynamic disturbances and management summarized in Supplementary Table S1. Of the six original undisturbed patches (i.e., no management or wildfires in May 2021), four remained undisturbed throughout our study to May 2023, when our study ended. The other two burned by wildfire in December 2021 but received no management throughout our study. The other 18 patches received one or more management treatments (with some also burned by wildfire) from May 2021 to May 2023. Fourteen of the patches received herbicide twice, in May 2021 and May 2022,

and another two patches received herbicide three times (May 2021 and 2022 and April 2023). Herbicide formulated for use around aquatic environments was applied via foliar spot spraying with backpack and vehicle-mounted tank sprayers by the National Park Service, Invasive Plant Management Team (Lake Mead National Recreation Area, Boulder City, NV, USA). A herbicide containing glyphosate under the aquatic formulation Rodeo® (Corteva Agriscience, Indianapolis, IN, USA) and imazapyr under the aquatic formulation Polaris® (Nufarm Americas, Alsip, IL, USA) was applied at a mix rate of 2% Rodeo®, 1% Polaris®, and 0.5% surfactant (Alligare, Opelika, AL, USA). This solution plus the water was sprayed per application at an average rate of 1,466 L ha<sup>-1</sup>, with a range of 335 to 9,020 L ha<sup>-1</sup> proportional to the coverage of *P. australis* (C Deuser, National Park Service Invasive Plant Management Team, Boulder City, NV, USA, personal communication). The last two managed patches received herbicide only once, in May 2021. In total, from 2020, representing conditions antecedent to our study, through the end of our study in May 2023, the number of times a patch was burned by wildfire or received a management treatment ranged from 0 to 5 among the 24 patches (Supplementary Table S1).

### Data Collection

Within each of the 24 *P. australis* patches and at least 3 m from the patch edge as a buffer, we randomly located a 10 m by 10 m (0.01 ha) plot. In each plot, we recorded the aerial cover of each vascular plant species (including *P. australis*) as 0.1%, 0.25%, 0.5%, 1% intervals for 1% to 10% cover, and 5% intervals for cover >10%, up to the maximum 100% cover a species could attain separately as live or dead cover. We recorded cover separately for live and standing dead plant parts. We also recorded the average height of *P. australis*. In eight equally spaced locations within each plot, we measured and averaged the depth of *P. australis* litter (in cm, and representing the undecomposed, Oi soil horizon) covering the ground surface and the aerial cover of litter (%), using the same cover classes as for live plants). Nomenclature and classification of species as native/non-native to the United States and by growth form (e.g., perennial forb) followed USDA-NRCS (2024). We sampled vegetation and litter on plots in May, August, and November 2021; in March and May 2022; and in May 2023.

During the initial sampling in May 2021, we collected 500 cm<sup>3</sup> of the 0- to 5-cm and 5- to 15-cm mineral soil from 2 m out of plots off the southwestern and northeastern corners of each plot and composited the samples per plot and per layer for analysis. We analyzed the samples for texture (hydrometer method), coarse fragment (>2-mm diameter) content by weight and volume, bulk density, and extract pH and electrical conductivity. In September 2022, we collected 200 cm<sup>3</sup> of the 0- to 5-cm mineral soil to measure gravimetric moisture (105 C oven drying for 24 h).

Approximately 2 m outside and encircling each plot, we used a metal soil corer (8-cm diameter, 5-cm deep) to collect eight subsamples (each 250 cm<sup>3</sup> and composited on a plot basis) of the 0- to 5-cm mineral soil seedbank (other propagules, such as emergence from rhizomes, were not detected during assays). We collected samples in May 2021 and again in August 2021, and we assayed these collections separately beginning within a week of sample collection. To process samples from each collection, we placed a 3-cm layer of sterilized sand into black, plastic nursery trays (28-cm wide by 54-cm long by 6-cm deep; Greenhouse Megastore, Sacramento, CA, USA). We then placed the 2,000-cm<sup>3</sup> composite sample of soil from each plot in a 1- to 2-cm-thick layer



**Figure 1.** Repeat photos from the same locations on three representative plots in each of three *Phragmites* cover groups in desert wetlands, Las Vegas, NV, USA. When we began our study in May 2021, the plot shown in the photo representative of the *Phragmites* decreasing cover group had 80% *Phragmites* cover that declined to 2% by May 2023 after two herbicide applications following cutting *Phragmites* in November 2020 and subsequent resprouting. The sustaining low plot began with <1% *Phragmites* cover in May 2021 (following a November 2020 cutting and February 2021 wildfire) that remained low (1%) in May 2023 after two herbicide applications. The sustaining high plot began with 100% *Phragmites* cover in May 2021 that remained high at 90% in May 2023. Photos in 2021 by SRA and in 2023 by SLP and KAK. Below the photos, the summary of management and wildfire history synthesizes information for all plots within each group (2× and 1-3× refer to the number of herbicide applications through time). Complete management and wildfire history and *Phragmites* cover for each plot is in Supplementary Table S1.

on top of the sterilized sand in the trays to optimize surface area for seedling emergence. After an initial watering to soil saturation, we covered trays with plastic humidity domes and randomly arranged the trays on a bench in a research greenhouse (University of Nevada Las Vegas). We then kept samples under natural lighting, randomly rearranged them on benches monthly, and watered them as necessary to keep soil moist during the emergence period. The emergence period was May through December 2021 (7 mo) for the May 2021 collection and from August 2021 through July 2022 (11 mo) for the August 2021 collection. We added 150 ml of 500 ppm of the germination stimulant gibberellic acid to samples after the first, second, and third months. Every 2 wk, we counted emerging seedlings by species and removed them from trays as they matured for identification.

### Statistical Analysis

Standing live ( $r = 0.58$ ,  $P < 0.001$ , 119 df) and dead ( $r = 0.49$ ,  $P < 0.001$ ) cover of *P. australis* both correlated with total (live + dead) standing cover of *P. australis* based on repeated-measures correlation on the 24 plots across the six measurement events (Marusich and Bakdash 2022). Based on this relationship, combined with the importance of both standing live and dead cover as fuel for wildfire and ecological effects such as shading across seasons (Ailstock et al. 2001), we used *P. australis* total cover for subsequent analyses.

We analyzed temporal change in *P. australis* total cover and related it to management and wildfire history and soil variables. After inputting a 24 plot by 6 measurement event (spanning May 2021 to May 2023) matrix containing *P. australis* total cover, we performed two complementary multivariate analyses in PC-ORD 7.07 (MjM Software Design, Gleneden Beach, OR, USA). We classified plots into groups displaying similar temporal variation in *P. australis* cover using cluster analysis (Euclidean distance, Ward's linkage method), followed by ordinating plots using principal

components analysis (correlation cross-products matrix). We input soil variables as a second matrix to screen them as correlates with *P. australis* cover in the ordination, and we summarized the number and type (mechanical or chemical) of management treatments and wildfire occurrences for each of three *P. australis* cover groups identified by the cluster analysis. Next, in SAS v. 9.4 (SAS Institute, Cary, NC, USA), we performed repeated-measures ANOVA to compare mean *P. australis* total cover, height, and litter cover and depth across measurement events within each *P. australis* cover group. We used autoregressive structure, and for models with  $P < 0.05$ , performed post hoc comparisons with Tukey tests (PROC GLIMMIX).

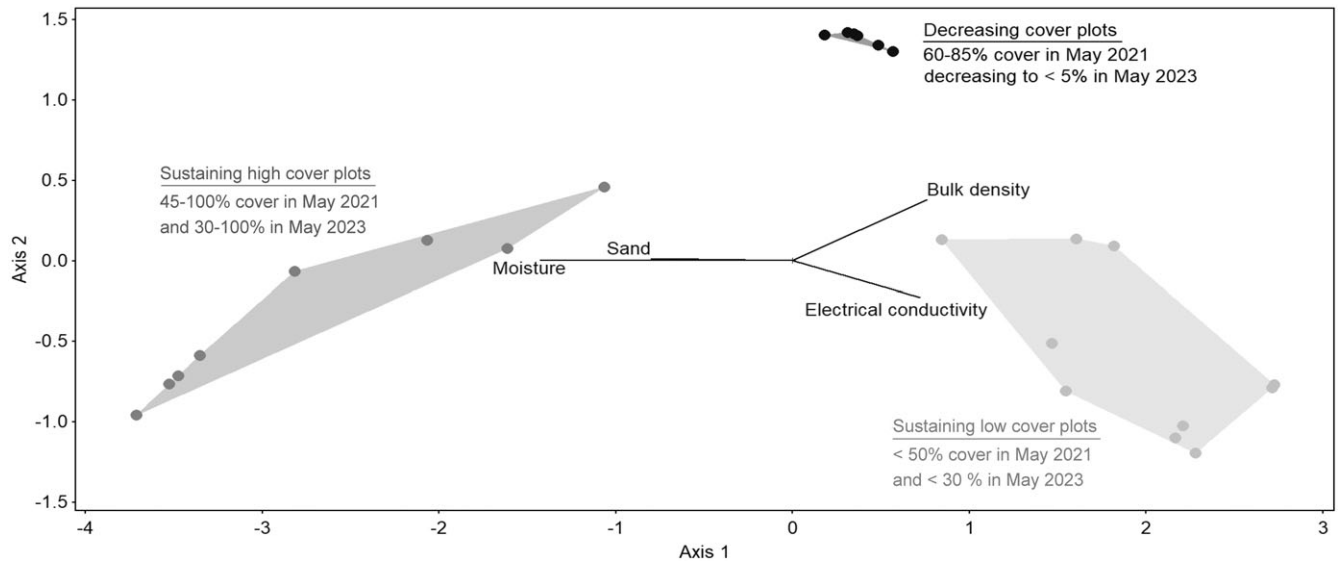
As native plants had low total cover (<5%, almost all live) among plots and were absent entirely from plots classified into a high *P. australis* cover group (hence, no variation to analyze), we assessed native species by calculating frequency (percentage of plots inhabited during at least one measurement event for each *P. australis* cover group). Similarly, we calculated frequency for non-native plants other than *P. australis* and mean seedbank density (seeds  $m^{-2}$  corresponding with a 0- to 5-cm sample depth) for native and non-native species.

## Results and Discussion

### *Phragmites australis* Cover Groups

Cluster analysis identified three groups of plots with similar temporal variation in total *P. australis* cover, and these groups separated distinctly in the ordination (Figures 1 and 2). We named these groups according to their temporal pattern across the six measurements between May 2021 and May 2023 in total *P. australis* cover: decreasing, sustaining low, and sustaining high.

Decreasing *P. australis* cover plots had high initial total cover of *P. australis* ( $76 \pm 4\%$ , mean  $\pm$  SEM) when our study began in May 2021, which included resprouting after cutting and removal of cut



**Figure 2.** Ordination of plots according to variation in *Phragmites* cover across six measurement events between May 2021 and May 2023 in desert wetlands, Las Vegas, NV, USA. Plots are symbolized based on their cluster analysis groupings of *Phragmites* cover and connected via convex hulls. Soil correlates with  $r^2 \geq 0.25$  are shown as vectors proportional to the strength of their correlation with distributions of plots in the ordination. All the soil variables were for the upper mineral soil layer (0–5 cm) except for sand, which was for the 5- to 15-cm depth. Statistics for the cluster analysis were 204,483 total sum of squares and 3.2% chaining. In the principal components ordination, axis 1 extracted 78% of the variance and axis 2 extracted 14% (92% cumulative).

material in November 2020. With successive herbicide applications in May 2021 and May 2022, however, *P. australis* total cover declined to <7% in 2022 and was nearly eliminated (1%) by the end of the study in May 2023 (Figure 3). Residual *P. australis* shoots remained  $\leq 0.5$ -m tall for the last year of the study (Figure 3). Although *P. australis* litter cover persisted, it always averaged  $\leq 6$ -cm deep (Figure 4).

Plots with sustaining low *P. australis* cover began in May 2021 with  $14 \pm 5\%$  total cover of *P. australis* following any of three scenarios of initial conditions. These scenarios of initial conditions included: wildfire in February 2021 and no management activities; cutting with material left on site in November 2020; or cutting in November 2020 in addition to wildfire in either or both April 2020 and February 2021. Throughout the rest of the study through May 2023, and encompassing one to three herbicide applications per plot, *P. australis* total cover always averaged less than 19% (Figure 3). As with the decreasing cover group, *P. australis* litter remained on plots only as a thin layer, always averaging <10-cm thick (Figure 4).

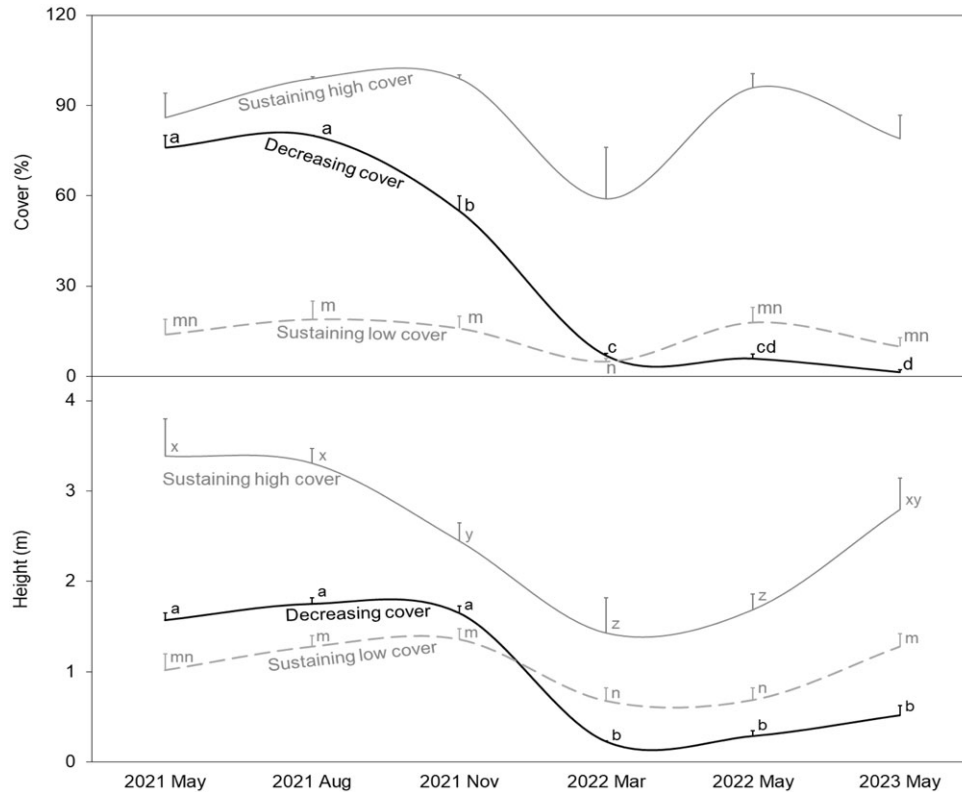
The sustaining high *P. australis* cover group began in May 2021 with  $86 \pm 8\%$  total cover of *P. australis* following either no management (six plots) or cutting and removal of biomass in November 2020 (two plots). Thereafter, cover remained high at 96% to 99%, only briefly dipping to 59% in early 2022 before rebounding for the rest of the study through May 2023 (Figure 3). Six of eight plots in this group received no management throughout the May 2021 to 2023 measurement period. The brief dip in average cover followed December 2021 or January 2022 wildfires that burned four plots, two of which then received a herbicide application in May 2022 but exhibited vigorous *P. australis* resprouting. Height of *P. australis* shoots averaged >3 m when our study began in May 2021 and remained 2.8-m tall in May 2023 within this group (Figure 3). Moreover, *P. australis* litter depth averaged 1-m thick in May 2021. Despite half the plots in this group burning once, litter on average still exceeded 0.5-m thick in May 2023 when our study ended (Figure 4).

### Native Plant Colonization, Secondary Invasion, and Soil Seedbanks

No native plants were recorded in vegetation during the study on plots in the sustaining high *P. australis* cover group (Table 1). This is consistent with studies from other regions finding that *P. australis* can form monocultures (Engloner 2009). Native plant colonization did occur on plots in the decreasing and sustaining low *P. australis* cover groups. Although their cover was low, native species colonizing plots where *P. australis* cover declined or remained low included: the trees *S. greggii* and *S. exigua*, the shrub willow baccharis (*Baccharis salicina* Torr. & A. Gray), and the perennial forbs Mojave thistle [*Cirsium mohavense* (Greene) Petr.], *H. curassavicum*, and yellow nightshade groundcherry (*Physalis crassifolia* Benth.).

These native colonizers were consistent with management objectives to convert *P. australis* monocultures to more diverse native species that could provide ecological functions important over time, as suggested by prior research. In a Mojave Desert study in southern California, for example, *C. mohavense* was a host plant for 25 genera of insects (Goeden and Ricker 1987). *Heliotropium curassavicum* produces abundant nectar and is utilized by butterflies (Wiesenborn and Pratt 2010). *Physalis crassifolia* is an important food plant for small mammals such as desert woodrats (*Neotoma lepida*; Cameron and Rainey 1972). The tree *S. greggii* is favored for nesting by birds, including in prior studies in the Las Vegas Valley (Austin 1970). In addition to providing wildlife habitat, the other native tree colonizing plots, *S. exigua*, can reduce pharmaceutical pollutants in water by sequestering them (Franks et al. 2019).

Throughout our study, secondary invasion by other non-native plants was limited to absent among plots, including after management activities and wildfires. Cover of non-native plants other than *P. australis* never exceeded 4% on any plot during any measurement. No non-native species occurred on more than one plot within any of the three *P. australis* cover groups (Table 1). The tree *T. ramosissima*, annual forb spiny sowthistle [*Sonchus asper* (L.) Hill], and the perennial forb broadleaved pepperweed (*Lepidium*



**Figure 3.** Mean ( $\pm 1$  standard error of the mean bars) vegetative cover and height of *Phragmites* across six measurement events within three *Phragmites* vegetative cover groups in desert wetlands, Las Vegas, NV, USA. Within a *Phragmites* cover group, if temporal variation was significant at  $P < 0.05$ , letters compare means through time (means not sharing a common letter differ at  $P < 0.05$ ). Statistics for repeated-measures ANOVA within *Phragmites* cover groups are as follows: decreasing,  $F(5, 25) = 5,218$ ,  $P < 0.001$  for *Phragmites* total cover, and  $F(5, 25) = 204$ ,  $P < 0.001$  for height; sustaining low,  $F(5, 45) = 3.0$ ,  $P = 0.020$  for *Phragmites* total cover, and  $F(5, 45) = 14$ ,  $P < 0.001$  for height; and sustaining high,  $F(5, 35) = 3.3$ ,  $P = 0.016$  for *Phragmites* total cover, and  $F(5, 35) = 12$ ,  $P < 0.001$  for height.

*latifolium* L.) were the only non-natives recorded in the vegetation, each occurring in one plot. Additionally, non-natives comprised only a small portion of the seeds in soil seedbanks: 17% in the decreasing, 3% in the sustaining low, and 2% in the sustaining high *P. australis* cover groups (Table 1). Of the two non-native species detected in the seedbank, one, red brome (*Bromus rubens* L.), is an upland species not detected in the wetlands vegetation and potentially unable to grow there (Jurand and Abella 2013). Although infrequent, *L. latifolium* was the only non-native in both the vegetation and seedbank and may represent the priority secondary invader of concern. *Lepidium latifolium* can reproduce via seed and vegetatively, is semi-tolerant of saline soil, and can form monocultures (Francis and Warwick 2007). The species can be controlled with flooding, herbicide, and, if at low density such as in our study, pulling, so long as rhizomes are extracted (Francis and Warwick 2007).

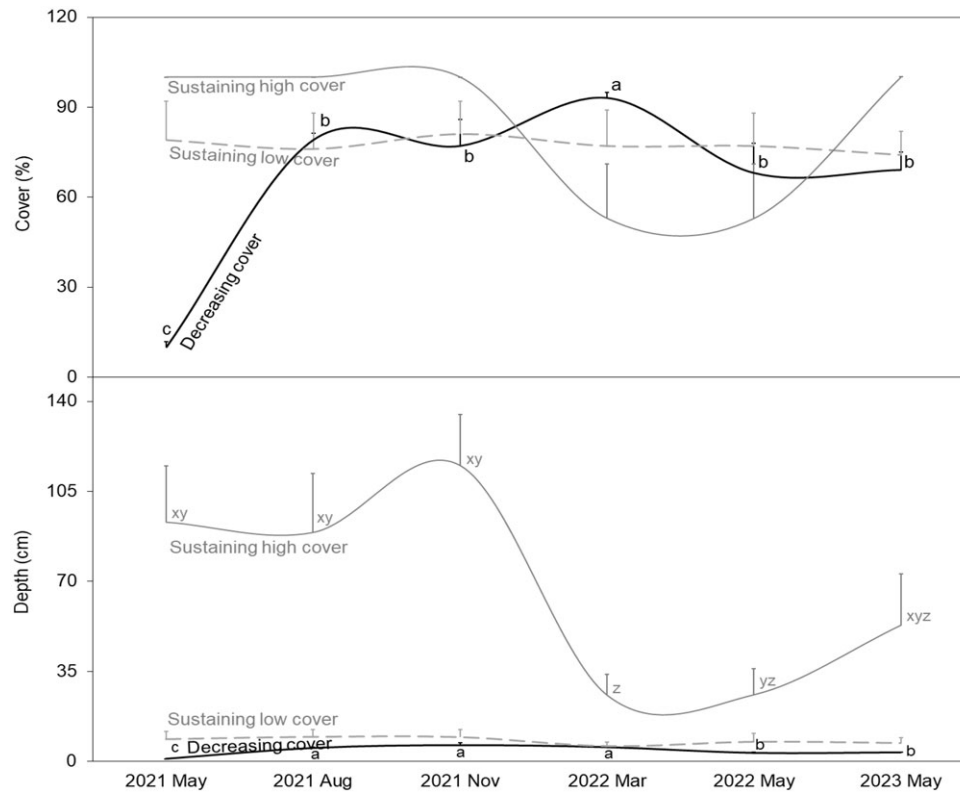
We detected only nine species in the soil seedbank, but it was dominated by natives in terms of species richness (78%, seven of nine species) and abundance (95% of seeds detected; Table 1). The native perennial forbs *H. curassavicum* and *P. crassifolia* occurred in both the seedbank and vegetation of plots, while several natives absent from the vegetation of plots (but present within the local flora of the study area) were in the seedbank (e.g., *B. salicina*, *Typha* spp.). Although no native species occurred in vegetation of the sustaining high *P. australis* cover group, native seedbank density was highest in this group. Native seedbank density in this group averaged 164 seeds  $m^{-2}$ , compared with 50 and 39 seeds  $m^{-2}$  in the decreasing and sustaining low *P. australis* cover groups. There could

be multiple processes for native seed retention within dense *P. australis* stands. For example, *P. australis* structure could slow winds, resulting in deposition of wind-blown seed, it could trap seed in thick litter layers, or it could inhibit seed germination via dense *P. australis* cover (Baldwin et al. 2010; Rohal et al. 2021).

We did not detect emergence of *P. australis* from the seedbank samples, and there could be several reasons for this. Much of the *P. australis* in our study area may be an invasive hybrid (Salstonstall et al. 2016). Including seed collections from around our study area, Williams et al. (2019) found that germination of the invasive hybrid's seed was low (9%). Germination overall across *P. australis* lineages and populations has been highly variable globally, ranging from almost no germination to 100% (Mal and Narine 2004). Viable seeds of *P. australis* can have minimal dormancy and thus may not form long-term seedbanks (Male and Narine 2004). Moreover, Greenwood and MacFarlane (2006) found that *P. australis* seeds decompose rapidly, which could also limit seedbank formation. Another factor limiting *P. australis* germination (and thus potential detection in seedbanks) could be the high salinity of our study area's soils, discussed in the next section.

### Soil Correlates

The county soil survey classified soil across our study area as saline (Lato et al. 2006), and our assay of soil samples from plots supported this classification. For surface (0 to 5 cm) soil, one plot was moderately saline (electrical conductivity of 7  $dS\ m^{-1}$ , within the 4 to 8  $dS\ m^{-1}$  moderately saline range), and the other 23 were strongly



**Figure 4.** Mean ( $\pm 1$  standard error of the mean error bars) *Phragmites* litter cover and depth across six measurement events within three *Phragmites* vegetative cover groups in desert wetlands, Las Vegas, NV, USA. Within a *Phragmites* group, if temporal variation was significant at  $P < 0.05$ , letters compare means through time (means not sharing a common letter differ at  $P < 0.05$ ). Note that the *Phragmites* groups are according to vegetative cover, not litter cover. Statistics for repeated-measures ANOVA within *Phragmites* vegetative cover groups are as follows: decreasing,  $F(5, 25) = 544$ ,  $P < 0.001$  for litter cover, and  $F(5, 25) = 65$ ,  $P < 0.001$  for litter depth; sustaining low,  $F(5, 45) = 1.1$ ,  $P = 0.369$  for litter cover, and  $F(5, 45) = 2.0$ ,  $P = 0.098$  for litter depth; and sustaining high,  $F(5, 35) = 105$ ,  $P < 0.001$  for litter cover, and  $F(5, 35) = 7.6$ ,  $P < 0.001$  for litter depth.

(8 to 16 dS  $m^{-1}$ ; 13 plots) or very strongly saline ( $>16$  dS  $m^{-1}$ ; 10 plots) according to soil salinity categories (Stavi et al. 2021). The maximum surface soil salinity we recorded, 64 dS  $m^{-1}$ , is 32 times higher than when growth of saline-sensitive plants is reported to be affected (Stavi et al. 2021). Our subsurface (5 to 15 cm) soil samples were less saline (2 to 11 dS  $m^{-1}$ ), but 17 of 24 plots (71%) were still at least moderately saline ( $>4$  dS  $m^{-1}$ ).

High soil salinity expressed as electrical conductivity was associated with sustaining low *P. australis* cover plots (Figure 2). Although *P. australis* can grow in brackish marshes and other saline habitats, it is sensitive to salinity and grows best in freshwater and nonsaline habitats (Packer et al. 2017). Increasing salinity in soil or water has reduced *P. australis* seed germination (Gorai et al. 2006; Greenwood and MacFarlane 2006). In fact, *P. australis* germination may be inhibited completely in very strongly saline soil (Chambers et al. 2003). Recruitment processes from seed in *P. australis* appear more sensitive to salinity than does vegetative reproduction. Bart and Hartman (2003) proposed a *P. australis* invasion model whereby the species can initially recruit on low-saline soil or from limited germination on saline soil, then expand across saline soil through clonal reproduction. The highly saline soils of our study area could be associated with lack of emergence of *P. australis* from the seedbank samples as well as the lower resilience of *P. australis* after it was reduced following management activities or wildfires on the most saline soils. We suggest that management activities for reducing *P. australis* could be most effective and persistent on the most saline soils.

Variation in salinity tolerance could also relate to native species occurrence in vegetation and seedbanks. In comparing salinity tolerance of 42 xeroriparian species in the American West, *S. greggii* was among the most tolerant of salinity for germination and growth, while *B. salicina* had low tolerance (Beauchamp et al. 2009). In our study, *S. greggii* was the most frequently occurring native in vegetation overall where *P. australis* cover was reduced or remained low. In contrast, *B. salicina* occurred in the seedbank but never in the vegetation, raising a question as to whether high salinity limited its establishment even where *P. australis* was reduced. If active revegetation is used to augment or hasten native plant colonization after *P. australis* is reduced, matching plant composition to the broad range of soil salinities we recorded could be important to revegetation success. Selecting the most salt-tolerant species from the local species pool, such as *S. greggii*, saltgrass [*Distichlis spicata* (L.) Greene], big saltbush [*Atriplex lentiformis* (Torr.) S. Watson], or *H. curassavicum*, may be important on the most saline soil.

Contrasting with salinity, high soil moisture was positively correlated with sustaining high *P. australis* cover plots (Figure 2). Although these plots contained the moistest soils in our study, standing water on the plots did not occur or was shallow ( $<3$ -cm deep) and infrequent. Prior studies in unmanaged wetlands have reported that *P. australis* often invades and grows best in soil of intermediate moisture that is neither on drier portions of the landscape nor in deep standing water (Chambers et al. 2003). For example, Baldwin et al. (2010) concluded that emergence of

**Table 1.** Occurrences of native and non-native plant species in the vegetation and soil seedbank across *Phragmites* cover groups (decreasing, sustaining low, or sustaining high *Phragmites* cover) in desert wetlands, Las Vegas, NV, USA.

Species <sup>a</sup>	<i>Phragmites</i> cover group					
	Decreasing		Low	High	Decreasing	
	Vegetation <sup>b</sup>		Seedbank <sup>c</sup>		High	
Native	% frequency		seeds m <sup>-2</sup>			
<i>Acacia greggii</i> (T)	33	10				
<i>Baccharis salicina</i> (S)					2	4
<i>Cirsium mohavense</i> (PF)	17					23
<i>Distichlis spicata</i> (PG)					2	
<i>Heliotropium curassavicum</i> (PF)	33				15	3
<i>Physalis crassifolia</i> (PF)	17				4	
<i>Pluchea odorata</i> (PF)					4	10
<i>Prosopis pubescens</i> Benth. (T)					2	5
<i>Salix exigua</i> (T)		30				23
<i>Typha</i> spp. (PF)					21	19
Non-native						111
<i>Bromus rubens</i> (AG)					6	
<i>Lepidium latifolium</i> (PF)	17	10			4	1
<i>Sonchus asper</i> (AF)	17					3
<i>Tamarix ramosissima</i> (T)				13		

<sup>a</sup>Plant growth forms are in parentheses: AF, annual forb; AG, annual grass; PF, perennial forb; PG, perennial grass; S, shrub; T, tree. Full botanical names for species in the table not listed in the text include sweetscent [*Pluchea odorata* (L.) Cass.] and screwbean mesquite (*Prosopis pubescens* Benth.).

<sup>b</sup>Percentage of plots (out of 6 for the decreasing, 10 for the low, and 8 for the high *Phragmites* cover groups) in which a species occurred during any of the six measurement events from May 2021 through May 2023. *Phragmites* occurred in all 24 plots.

<sup>c</sup>Based on samples of the 0- to 5-cm mineral soil collected in May and August 2021 (*Phragmites* was not detected in seedbank samples).

*P. australis* seedlings was prevented by continuous flooding with water 3.5-cm deep. Adult *P. australis* plants were more tolerant than seedlings to flooding and could adjust to fluctuations of up to 1.2 m in subsurface water levels before shoot growth appreciably declined (Hanslin et al. 2017). However, along with seedling establishment, clonal reproduction from rhizomes in adults can be hindered by continuous flooding (Smith 2005). This has stimulated recommendations that managed flooding be used for controlling *P. australis*, such as to deter resprouting after cutting or herbicide (or other disturbance such as wildfire) has initially reduced mature individuals (Rohal et al. 2019; Russell and Kraaij 2008). Managed flooding could be tested on suitable sites to examine potential effectiveness in soils in our study area, including identifying potentially effective flooding depth and duration.

### Potential for Phased Management Approaches

Combined with prior research, our results suggest several advantages of beginning *P. australis* management with clearing of *P. australis* live and dead biomass. Although *P. australis*'s own litter can inhibit recruitment and shoot growth (Granéli 1989), thick litter layers and dense standing dead material can hinder management effectiveness by limiting contact of herbicides with live plant parts, suppressing native plant colonization, and creating hazardous fuels (Breen et al. 2014). If *P. australis* biomass is not initially cleared, such as if only herbicide or cutting without biomass removal is used, litter decomposition rate could be a key consideration. Unfortunately, little information is available for *P. australis* litter decomposition rates in desert climates for nonaquatic habitats (Eid et al. 2014). It is also unclear how the extremely saline soils of our study area could affect decomposition, with one scenario being slow decomposition and persistence of *P. australis* litter for many years (sensu Wong et al. 2010). If not initially cleared, *P. australis* litter in our study was a dense thatch exceeding 1-m thick at 100% ground cover. Initial clearing of *P. australis* standing biomass and litter in our study occurred through cutting and transport off-site (which was

logistically difficult) or opportunistically by unplanned wildfires. Owing to high fire severity in dense *P. australis* stands, unplanned wildfires nearly completely consumed and cleared standing and downed *P. australis* biomass. These observations suggest potential for exploring prescribed fires to cost-effectively initially clear *P. australis* and facilitate subsequent management of *P. australis* resprouts.

Our results are consistent with a major conclusion in *P. australis* management literature that repeated treatments are needed to achieve control (Hazelton et al. 2014; Quirion et al. 2018). Plots in our study burned or treated just once quickly rebounded in *P. australis* cover, and the species appeared particularly resilient on moister and lower-salinity soil. Uncertainty remains in the *P. australis* literature regarding how many times treatments must be repeated or how many years of treatments are required to achieve persistent *P. australis* control (Hazelton et al. 2014). This could depend on factors such as how much top-killing may be needed to deplete *P. australis* energy reserves for resprouting and whether recruitment by seed rather than only clonal reproduction is occurring, as well as site factors such as soils and hydrology. In our study, high soil salinity correlated with *P. australis* cover remaining low on managed sites, suggesting that fewer treatments may be needed on saline soil to persistently reduce *P. australis*. Our results support those of Rohal et al. (2023) in suggesting that different management strategies may be applicable across the environmental gradients where *P. australis* occurs.

After initial reductions in *P. australis* cover and repeated *P. australis* treatments, further management phases could be considered and tested. The limited native plant colonization and soil seedbanks we recorded suggest opportunity for active revegetation to hasten and diversify native plant establishment after *P. australis* is reduced. On moister or less-saline soil where *P. australis* appeared more resilient, native species with potential to competitively suppress *P. australis* resprouts may be suitable as an initial native cover. On extremely saline soil, selecting native species most tolerant of salinity rather than primarily for their



competitive ability may be most appropriate. Coupling active revegetation of native species with maintenance management activities (e.g., managed flooding or fires) to keep *P. australis* cover low could be a next research step in identifying long-term strategies for converting *P. australis* monocultures to more diverse native species in desert wetlands.

**Supplementary material.** To view supplementary material for this article, please visit <https://doi.org/10.1017/inp.2024.21>

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