

This is a “preproof” accepted article for Invasive Plant Science and Management. This version may be subject to change in the production process, *and does not include access to supplementary material*. DOI: 10.1017/inp.2024.21

Short title: Managing *Phragmites australis*

Changing dominance of invasive *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, Nevada, 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 seed banks 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 months, 24 study sites formed three groups: 1) decreasing cover, where initially high *P. australis* cover (60-85%) 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 (45-100% initially and remaining 30-100%), including sites unmanaged or treated/burned only once. High soil salinity correlated with low post-management *P. australis* cover. No native plants were detected in the sustaining high *P. australis* cover group, despite natives occurring in the seed bank. 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.

Key words: Environmental gradient; initial conditions; Mojave Desert; salinity; secondary invasion; seed bank

Management Implications

Different trajectories in cover of invasive common reed (*Phragmites australis* (Cav.) Trin. ex Steud.) 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 months after our study began, 15 of 18 (83%) managed sites had *P. australis* cover \leq 16%, compared with 80-100% cover on six unmanaged sites. Reducing *P. australis* cover and litter layers (which averaged 1 m thick on unmanaged sites) is important to 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 (*Acacia greggii* Gray), 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 multi-phase 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.

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 U.S., 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 community establishment is highly variable following *P. australis* management (e.g., Güsewell 2003, Judd and Francoeur 2019). *Phragmites australis*' diverse regeneration mechanisms, which can include seed dispersal, reproduction from soil seed banks, 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 (Monteiro et al. 1999, Breen et al. 2014, 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 (Russell and Kraaij 2008, Kimura and Tsuyuzaki 2011, 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).

Often management goals include both reducing *P. australis* and stimulating native plant establishment, but dually achieving 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), other non-native plants responding more positively than native plants (Robichaud and Rooney 2021), 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 seed banks or nearby vegetation (Rohal et al. 2023).

Relationships of *P. australis* management outcomes with site factors, such as soil properties, has 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 (Kulmatski 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 seed banks? and 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 1174-ha Clark County Wetlands Park, on the eastern edge of Las Vegas, Nevada, 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 m³ s⁻¹ in 2023 (Pabco Road station; U.S. Geological Survey, Reston, Virginia, 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 Torrifuvents (Glencarb series). Both of these soils are derived from mixed alluvium, contain gypsum and carbonates, are moderately to very strongly saline (electrical conductivity 8-32+ 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 cm year⁻¹ from 2006 through 2023 (Duck Creek Broadbent station, Clark County Regional Flood Control District, Las Vegas, Nevada). 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. Wats.] 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 years 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 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 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 Company, West Fargo, North Dakota, USA) and a 299D2 Compact Track Loader with a disc mulcher (Caterpillar Inc., Irving, Texas, USA; and Diamond Mowers, Sioux Falls, South Dakota, 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 two years 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 nor 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, Nevada, USA). A herbicide containing glyphosate under the aquatic formulation Rodeo (Corteva Agriscience, Indianapolis, Indiana, USA) and imazapyr under the aquatic formulation Polaris (Nufarm Americas, Inc., Alsip, Illinois, USA) was applied at a mix rate of 2% Rodeo, 1% Polaris, and 0.5% surfactant (Alligare LLC, Opelika, Alabama, USA). This solution plus the water was sprayed per application at an average rate of 1466 L ha⁻¹, with a range of 335-9020 L ha⁻¹ proportional to the coverage of *P. australis* (C. Deuser, National Park Service Invasive Plant Management Team, Boulder City, Nevada, personal communication). The last two managed patches received herbicide only once, in May 2021. In total from 2020 representing antecedent conditions prior 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 × 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 1-10% cover, and 5% intervals for cover over 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 USA and by growth form (e.g., perennial forb) followed 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 cm³ of the 0-5 cm and 5-15 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 cm³ of the 0-5 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 in diameter and 5 cm deep) to collect 8 subsamples (each 250 cm³ and composited on a plot basis) of the 0-5 cm mineral soil seed bank (other propagules, such as emergence from rhizomes, was 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 × 54 cm long × 6 cm deep; Greenhouse Megastore, Sacramento, California, USA). We then placed the 2,000-cm³ composite sample of soil from each plot in a 1-2 cm thick layer 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 months) for the May 2021 collection and from August 2021 through July 2022 (11 months) 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 two weeks, 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 degrees of freedom) and dead ($r = 0.49$, $P < 0.001$) cover of *P. australis* were 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 \times 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, Oregon, 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 9.4 (SAS Institute, Cary, North Carolina, USA), we performed repeated measures analysis of variance 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 (% 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 seed bank density (seeds m⁻² corresponding with a 0-5 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 (Figure 1, 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 material in November 2020. With successive herbicide applications, however, in May 2021 and May 2022, *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 ≤ 0.5 m tall for the last year of the study (Figure 3). Although *P. australis* litter cover persisted, it always averaged ≤ 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 1-3 herbicide applications per plot, *P. australis* total cover always averaged below 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 (6 plots) or cutting and removal of biomass in November 2020 (2 plots). Thereafter, cover remained high at 96-99%, 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 2021-2023 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 over 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 Seed Banks

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 catclaw acacia (*Acacia greggii* Gray) and narrowleaf willow (*Salix exigua* Nutt.), the shrub willow baccharis (*Baccharis salicina* Torr. & A. Gray), and the perennial forbs Mojave thistle (*Cirsium mohavense* (Greene) Petr.), salt heliotrope (*Heliotropium curassavicum* L.), 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 *A. 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 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 seed banks: 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 seed bank, 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 seed bank 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 9 species in the soil seed bank, but it was dominated by natives in terms of species richness (78%, 7 of 9 species) and abundance (95% of seeds detected; Table 1). The native perennial forbs *H. curassavicum* and *P. crassifolia* occurred in both the seed bank 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 seed bank (e.g., *B. salicina*, *Typha* spp.). Although no native species occurred in vegetation of the sustaining high *P. australis* cover group, native seed bank density was highest in this group. Native seed bank 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 to result in deposition of wind-blown seed, trap seed in thick litter layers, or 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 seed bank samples, and there could be several possibilities 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 seed banks (Male and Narine 2004). Moreover, Greenwood and MacFarlane (2006) found that *P. australis* seeds decompose rapidly, which could also limit seed bank formation. Another factor limiting *P. australis* germination (and thus potential detection in seed banks) 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 (0-5 cm) soil, one plot was moderately saline (electrical conductivity of 7 dS m⁻¹, within the 4-8 dS m⁻¹ moderately saline range), and the other 23 were strongly (8-16 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× higher than when growth of saline-sensitive plants is reported to be affected (Stavi et al. 2021). Our sub-surface (5-15 cm) soil samples were less saline (2-11 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 non-saline 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 is 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 seed bank 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 seed banks. In comparing salinity tolerance of 42 xeroriparian species in the American West, *A. 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, *A. 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 seed bank 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 *A. 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 *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 (Russell and Kraaij 2008, Rohal et al. 2019). 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 *P. australis* 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 non-aquatic 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 down *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 *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, whether recruitment by seed rather than only clonal reproduction is occurring, and 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 seed banks 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.

Acknowledgments

We thank Liz Bickmore (Clark County Wetlands Park) for facilitating the study; Curt Deuser and Carlee Coleman (Invasive Plant Management Team, National Park Service) for providing records of herbicide treatments; Frank Rice and staff with the Bureau of Land Management (Southern Nevada District) for coordinating and performing cutting treatments; the Research Greenhouse in the Science and Engineering Building (University of Nevada Las Vegas) for providing space for the seed bank assay; and two anonymous reviewers for helpful comments on the manuscript.

Funding

This study was funded through a contract to Natural Resource Conservation LLC from Clark County Parks and Recreation, Clark County Wetlands Park. The California Fire Science Consortium provided further support via a partnership with the University of Nevada Las Vegas.

Competing Interests

The authors declare none.

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

Species ^a	<i>Phragmites</i> cover group					
	Decreasing	Low	High	Decreasing	Low	High
Native	Vegetation (% frequency) ^b			Seed bank (seeds m ⁻²) ^c		
<i>Acacia greggii</i> (T)	33	10				
<i>Baccharis salicina</i> (S)				2	4	23
<i>Cirsium mohavense</i> (PF)	17					
<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> (T)				2	5	23
<i>Salix exigua</i> (T)		30				
<i>Typha</i> spp. (PF)				21	19	111
Non-native						
<i>Bromus rubens</i> (AG)				6		
<i>Lepidium latifolium</i> (PF)	17	10		4	1	3
<i>Sonchus asper</i> (AF)	17					
<i>Tamarix ramosissima</i> (T)			13			

^aPlant growth forms are in parentheses: AF, annual forb; AG, annual grass; PF, perennial forb; PG, perennial grass; S, shrub; T, tree.

^bPercent 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.

^cBased on samples of the 0-5 cm mineral soil collected in May and August 2021 (*Phragmites* was not detected in seed bank samples).

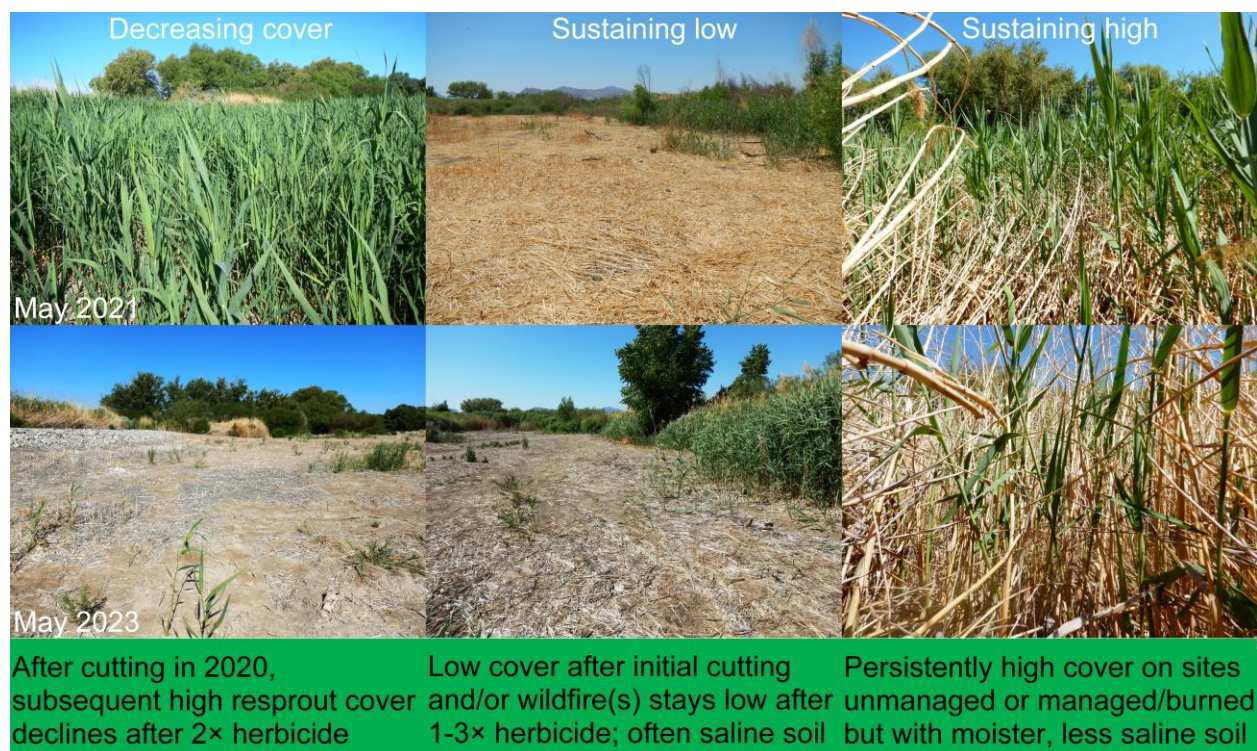


Figure 1. Repeat photos from the same locations on three representative plots in each of three *Phragmites* cover groups in desert wetlands, Las Vegas, Nevada, USA. When we began our study in May 2021, the plot shown in the photo representative of the *Phragmites* decreasing cover group had 80% *Phragmites* 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 S.R. Abella and in 2023 by S.L. Porter and K.A. Kline. Below the photos, the summary of management and wildfire history synthesizes information for all plots within each group (2× and 1-3× refers to the number of herbicide applications through time). Complete management and wildfire history and *Phragmites* cover for each plot is in Supplementary Table S1.

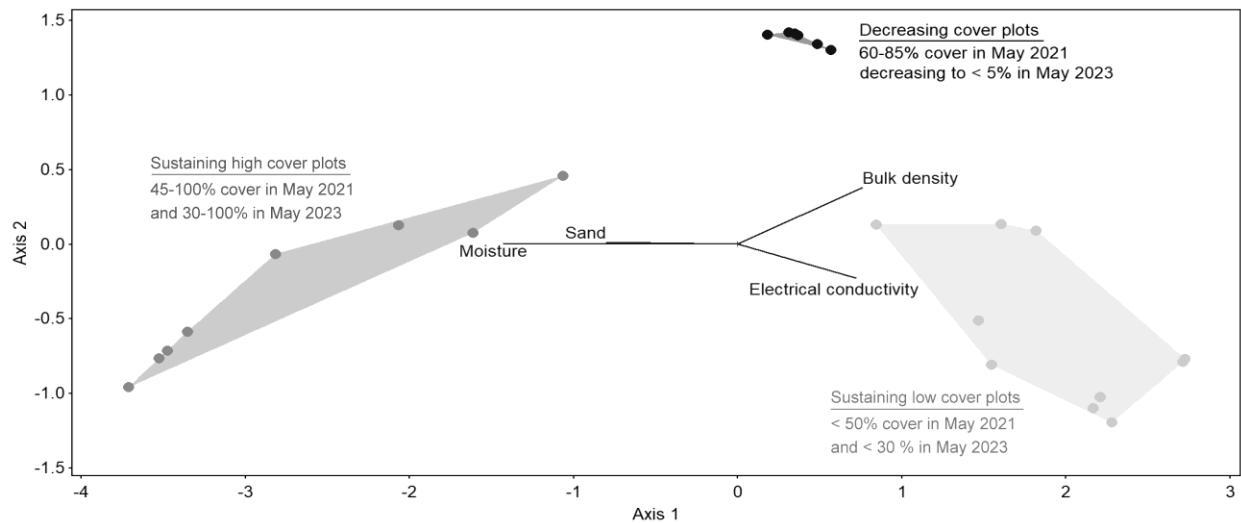


Figure 2. Ordination of plots according to variation in *Phragmites* cover across six measurement events between May 2021 and May 2023 in desert wetlands, Las Vegas, Nevada, USA. Plots are symbolized based on their cluster analysis groupings of *Phragmites* cover and connected via convex hulls. Soil 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 5-15 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 14% (92% cumulative).

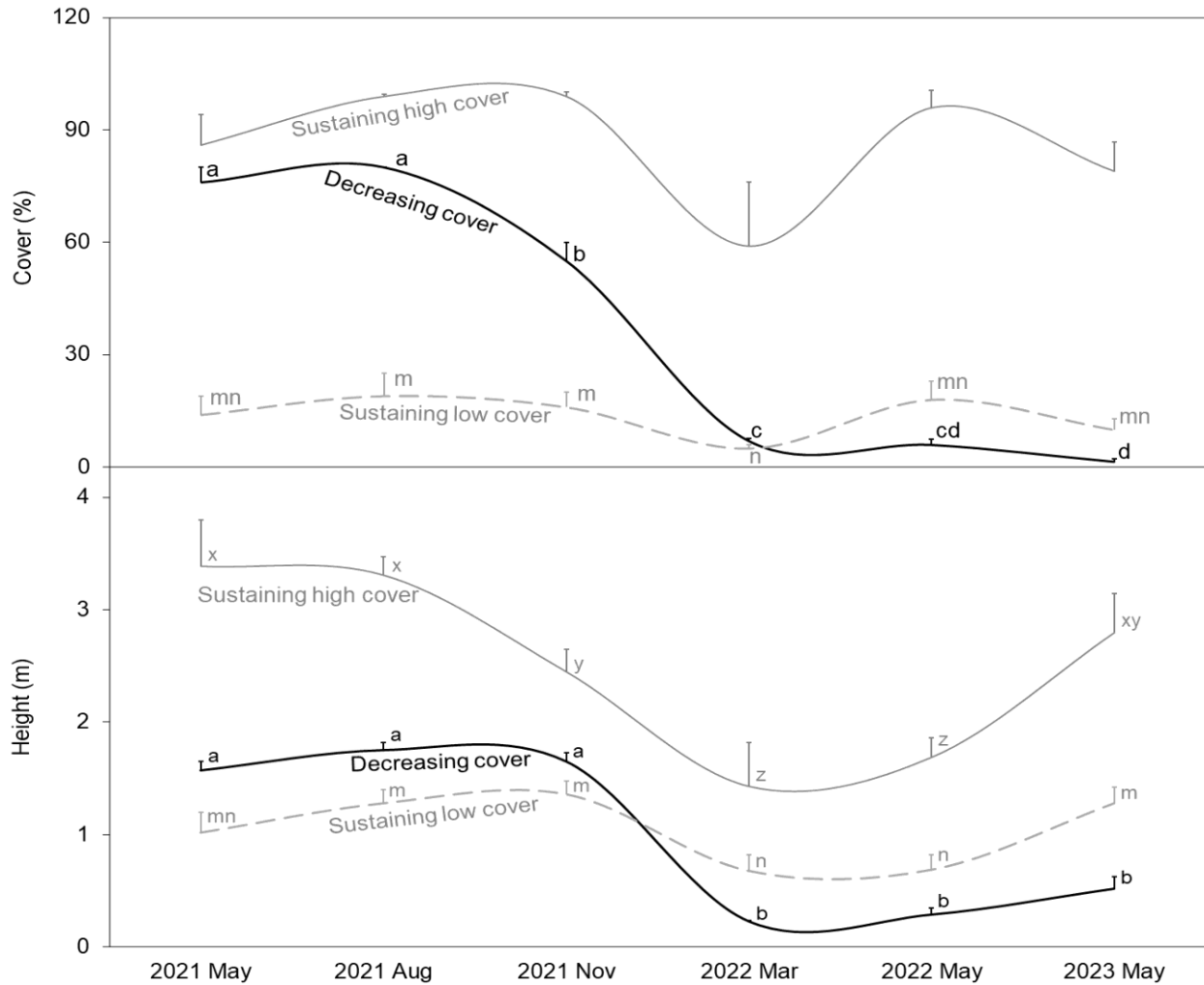


Figure 3. Mean (+ 1 SEM error bars) vegetative cover and height of *Phragmites* across six measurement events within three *Phragmites* vegetative cover groups in desert wetlands, Las Vegas, Nevada, USA. Within a *Phragmites* cover group if temporal variation was significant at $P < 0.05$, letters compare means through time (means not sharing a common letter differ at $P < 0.05$). Statistics for repeated measures analysis of variance 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.

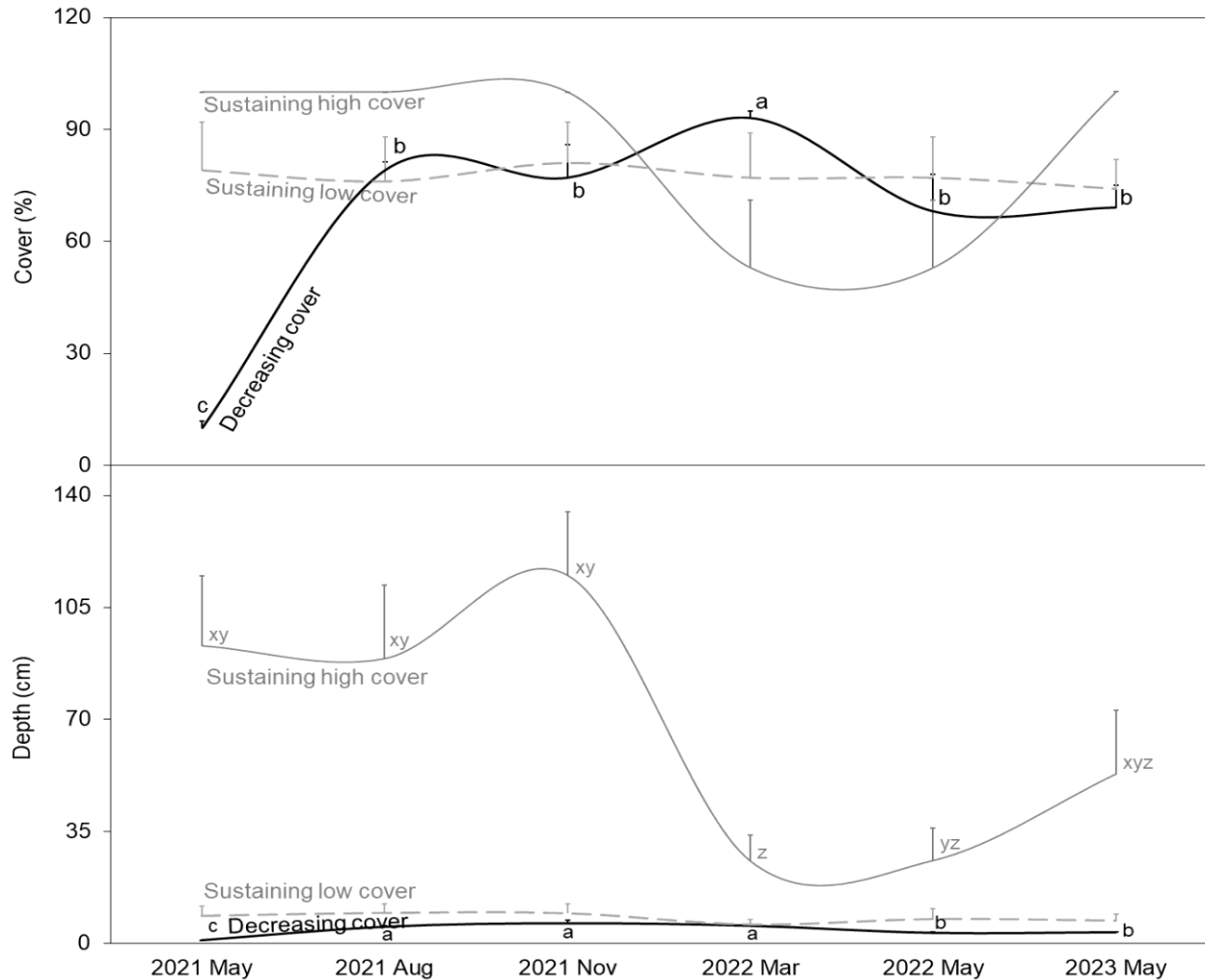


Figure 4. Mean (+ 1 SEM error bars) *Phragmites* litter cover and depth across six measurement events within three *Phragmites* vegetative cover groups in desert wetlands, Las Vegas, Nevada, USA. Within a *Phragmites* group if temporal variation was significant at $P < 0.05$, letters compare means through 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 analysis of variance 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.