ADVENTITIOUS ROOTS EFFECTS ON MANAGEMENT OF INVASIVE *PHRAGMITES AUSTRALIS* IN HIGH WATER

by

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Abstract:

The prevalence of invasive *Phragmites australis* (common reed), has threatened biodiversity and displaced native plant species throughout North America. Along shorelines, *Phragmites* survives in high water by growing above the water and transporting oxygen from above to below water. *Phragmites* plants may develop adventitious roots in response to high water, which could aid in dissolved oxygen uptake. Cut-to-drown management is a strategy whereby *Phragmites* stems are cut below the water to inhibit regrowth by depriving the plant of oxygen. This strategy can be effective, however adventitious roots could help the plants withstand cut-to-drown by providing oxygen access to the plants after they have been cut under water. Understanding the role of adventitious roots for *Phragmites* is vital for effective management strategies in the Great Lakes.

To examine the function of adventitious roots on *Phragmites*, we tested the effects of submergence, dissolved oxygen and presence of adventitious roots on below- and aboveground performance in a controlled greenhouse experiment. Plants receiving full cuts (cut at the soil line below water) and partial cuts (just below water) produced significantly less belowground biomass, new rhizome biomass and rhizosphere carbohydrates than controls. There was a significant negative effect of adventitious roots for rhizome biomass in the no cut treatment when the bubbler was present, but not when it was absent. Additionally, plants receiving partial cuts had significantly more new stems than no cuts and full cuts. The presence of adventitious roots produced a trend towards increased new stem growth when grown without bubblers.

Together, our results suggest that full cuts are most effective in controlling *Phragmites* partly due to the removal of adventitious roots. The effect of adventitious roots may depend on dissolved oxygen presence. This information could be incredibly valuable to land managers, increasing effectiveness of cut-to-drown management.

Acknowledgements:

I would like to acknowledge my co-advisor, Dr. Wesley Bickford, from the Great Lakes Science Center USGS for his tireless efforts and support of this project. His enthusiasm and expertise served as a constant source of inspiration and I could not have done it without him.

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Introduction:

Background:

The introduction of *Phragmites australis* (common reed) to the United States is thought to have occurred through various human-mediated pathways. Ballast water discharge from ships, often implicated in the introduction of non-native species, is one potential source of invasive *Phragmites* in North America (Smith et al., 2014). Additionally, unintentional introduction through contaminated seed stocks used for erosion control or wetland restoration projects is another plausible pathway (Kettenring et al., 2012). The intentional planting of *Phragmites* for ornamental purposes in gardens or landscapes may have contributed to its initial spread, as the non-native variety of *Phragmites* outcompetes native species (Meyerson et al., 2000). Historical land use practices, such as land clearing for agriculture or development, may also have created disturbed habitats conducive to the establishment and proliferation of invasive species, including *Phragmites* (Galatowitsch et al., 1999).

The surge in *Phragmites* along freshwater coastlines also coincides with Great Lakes water levels fluctuating in the late 1990s and early 2000s. The prolonged period of low water exposed vast stretches of shoreline and lake bottom, facilitating the expansion of *Phragmites* into that space in the absence of competition from established plants (Wilcox, 2012). Even when water levels rise, *Phragmites* continues to grow in water with their stems above the water level (Widin et al., 2023). It also adapts its rhizome architecture in response to water depth to optimize oxygen transport and support its growth and survival in aquatic environments (Weisner & Strand, 1996).

Impact of ***Phragmites***:

The increase in the prevalence of invasive *Phragmites australis* (common reed), has threatened biodiversity and displaced native plant species throughout North America (Galatowitsch et al., 1999). In Michigan, *Phragmites* invasion has been documented in various ecosystems, including wetlands, along highways, and in coastal areas (Doe & Smith, 2019). *Phragmites* poses a serious threat to biodiversity by outcompeting and displacing native plant species (Jones & Brown, 2016). This displacement disrupts local ecosystems, leading to habitat alterations that negatively impact various aquatic species (Johnson et al., 2019). Additionally, the accumulation of dead biomass in *Phragmites* stands increases the risk of fires, affecting both ecosystem health and public safety (Doe et al., 2020). In some areas, *Phragmites* is intentionally planted to remediate nutrient inputs (Yuckin & Rooney, 2019). However in most cases, *Phragmites* is managed to promote native wetland restoration and minimize its negative impacts. Efforts to control *Phragmites* are crucial to preserving biodiversity, maintaining ecosystem functionality, and safeguarding the economic and recreational value of affected areas.

Current management efforts:

Land managers commit significant resources to control the spread of invasive *Phragmites* due to the significant ecological disruptions caused by this aggressive plant species. From 2005-2009, over $4.6 million were spent by managers for *Phragmites* control each year in the United States (Martin & Blossey, 2013). Regionally, the United States has implemented coordinated programs to manage *Phragmites*, recognizing its widespread presence. For example, The Great Lakes *Phragmites* Collaborative has been instrumental in fostering collaboration among researchers, land managers, and policymakers to develop effective control strategies and share best practices (GLPC, 2021). Additionally, the Ontario *Phragmites* Working Group works to eradicate invasive *Phragmites* in Ontario and Canadian regions (OPWG, 2024). Continued research and management efforts are crucial to understand the current distribution of *Phragmites*, refine control methods, and inform policies that address the invasive species' impact on ecosystems.

Commonly used *Phragmites* management methods involve a combination of strategies, including a mix of mechanical approaches (such as mowing), controlled burning, and the application of herbicides (MDNR 2014; Hazelton et al. 2014). Although these management actions sometimes result in short-term reductions in cover, achieving long-term success necessitates implementing multiple years of treatments to prevent the subsequent re-invasion of *Phragmites* (Martin and Blossey 2013; Hazelton et al. 2014).

Issues with mechanical management:

One of the benefits of mechanical management of *Phragmites* is that it allows for targeted removal, focusing on specific areas of invasion (Nichols, 2020). Additionally, mechanical removal has instant, visible results. However, cutting/mowing *Phragmites* has a variety of issues. The first one is that it often focuses on removing aboveground biomass, leaving the extensive rhizome system in the soil to foster regrowth (Nichols, 2020). This strategy is also labor-intensive, especially for large or dense infestations. If not executed and removed properly, mechanical management can inadvertently spread

Phragmites fragments, leading to the colonization of new areas (Nichols, 2020). For expansive *Phragmites* infestations, mechanical methods alone may not be sufficient, and integrated approaches combining mechanical methods with other control measures may be necessary (Nichols, 2020). Additionally, mowing can be difficult in wet areas depending on the available equipment and tools (Tewksbury et al. 2002).

Issues with controlled burning management:

Controlled burning offers several advantages as a management strategy for *Phragmites*. Like mechanical management, it reduces the aboveground biomass of *Phragmites*, providing a means to open up the canopy and facilitate sunlight penetration to the soil. This reduction in biomass can create favorable conditions for the growth of native vegetation, aiding in the restoration of a more diverse plant community. From a resource perspective, controlled burning is often considered cost-effective, especially when dealing with large-scale *Phragmites* infestations, requiring fewer resources compared to manual removal or herbicide treatments (Kettenring & McCormick, 2018).

However, the use of controlled burning for *Phragmites* removal comes with certain drawbacks. Like mechanical management, the extensive rhizome system of *Phragmites* often survives underground, leading to potential regrowth (Kettenring & McCormick, 2018). Concerns about public acceptance and adequate funding for prescribed burns has also been a continuous struggle (Quinn-Davidson and Varner 2012).

Issues with herbicide management:

Herbicides provide a targeted and efficient method to control *Phragmites* infestations by suppressing its growth and preventing further spread (Meyerson et al., 2016). Herbicide applications are often cost-effective and can cover large areas efficiently, making them suitable for managing extensive *Phragmites* infestations, especially in marshes, wetlands, and coastal areas where the plant is known to proliferate rapidly (Gettys et al., 2006).

However, the use of chemical herbicides for *Phragmites* management also comes with inherent drawbacks. One significant concern is the potential non-target effects on other organisms within the ecosystem, including aquatic fauna and non-invasive plant species (Meyerson et al., 2016). The application of herbicides alters the composition of the surrounding habitat, negatively impacting microbial communities in both land and water (Pérez et at., 2007). Additionally, there is the risk of herbicide resistance developing in *Phragmites* populations over time, necessitating careful consideration of herbicide rotation and integrated pest management strategies (Marks et al., 2016). In specific regions, such as Canada, the approval of herbicides for use in aquatic environments is limited (Lombard et al. 2012; Hazelton et al. 2014; Sesin et al. 2021). Consequently, the enhancement of management outcomes could be achieved by including effective control strategies that do not rely on chemical herbicides.

Cut-to-drown management strategy:

The cut-to-drown management strategy is a non-herbicide approach for controlling invasive *Phragmites* in high water conditions that may overcome many limitations of current mechanical, burning and herbicide approaches. The technique involves *Phragmites* stems being cut either beneath the water surface or cut and subsequently subjected to manipulated water levels to submerge and drown the plant (Widin et al., 2023). When stems are severed beneath the water surface, the oxygen supply to the rhizomes is obstructed, thereby inhibiting the growth of the affected stem (Weisner & Granéli, 1989). *Phragmites* is sensitive to low oxygen transport to belowground parts of the plant and its maximum water depth penetration is likely to be negatively affected by eutrophication, which would lower oxygen availability (Weisner & Granéli, 1989). While the cut-to-drown method is widely used and found to be effective, especially in areas like Canada where herbicide use is highly regulated (Widin et al., 2023), it is still a topic of ongoing research at USGS to further develop best management practices.

Adventitious roots in *Phragmites*:

Despite the promise of cut-to-drown as a management strategy, it has been observed that under high water conditions, *Phragmites* generates aboveground adventitious roots (Widin et al., 2023). Adventitious roots, defined as roots originating on nodes above the ground and below the water, are known to develop in response to various stressors, with flooding constituting one such example (Widin et al., 2023). Although the precise rationale for the formation of adventitious roots remains unclear, researchers speculate that their development represents a survival strategy adopted by the plant to enhance its resilience under adverse conditions (Steffens, 2016). Adventitious roots may be an alternative way for *Phragmites* to get oxygen when the plant is growing below the water. Adventitious roots have been found to provide dissolved oxygen to other plants submerged in water, such as the invasive *Alternanthera philoxeroides* (Ayi et al., 2016). It is unknown if adventitious roots have the same effect for *Phragmites*.

Conceptual Model:

Understanding the system in which *Phragmites* grows in high water is essential to understand the potential function of adventitious roots.

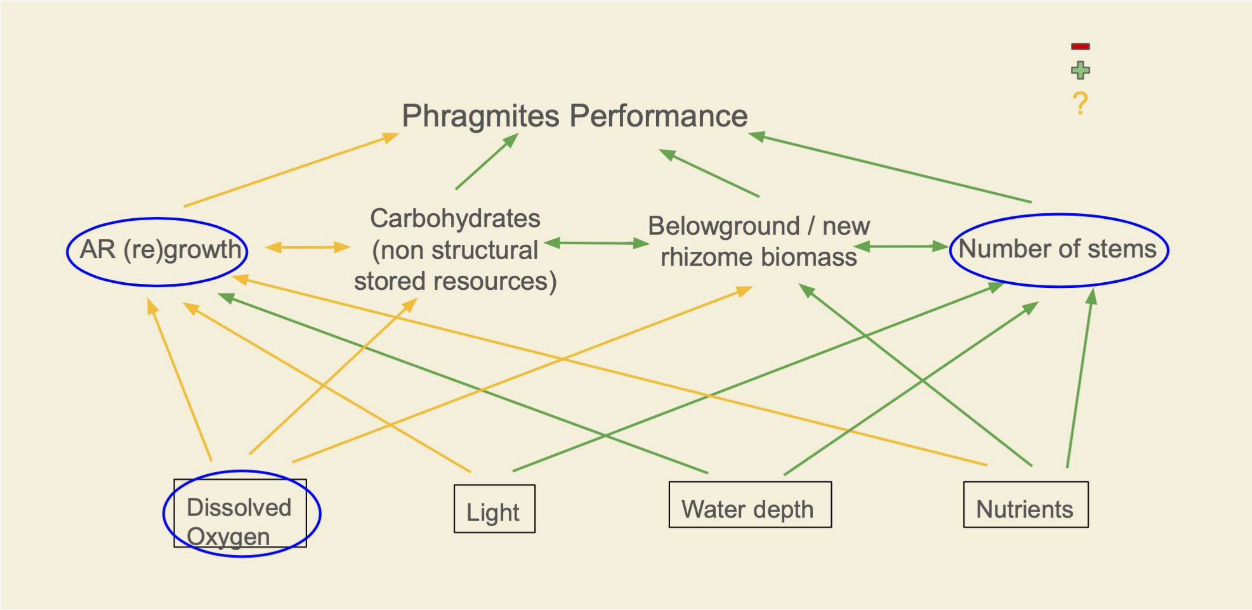

Figure 1: Conceptual model showing the relationships and interactions between environmental factors and performance measures of invasive *Phragmites* in high water conditions. Items circled in blue are the independent variables that were used to determine adventitious root impact on cut-to-drown management.

There are many environmental factors that influence the growth and success of *Phragmites* in high water including (but not limited to) dissolved oxygen, light, water depth and nutrients (Figure 1). These factors impact the number of aboveground stems of the plant (how the plant transports oxygen to belowground), the belowground biomass (roots and rhizomes that allow spreading), the new rhizome biomass (the rhizomes within the belowground biomass that were not established before the experiment began) and *possibly* adventitious root growth (VanDerZanden, 2024). The state of these performance measures determine the overall performance of the plant. However, the role of adventitious roots in overall performance is least well understood.

From a management perspective, it is crucial to understand the conditions that promote the growth of adventitious roots. The utilization of the cut-to-drown management approach, particularly in response to elevated water levels in the Great Lakes, stands as an opportune strategy for *Phragmites* management. However, a significant obstacle arises from the lack of information regarding the conditions governing the development of adventitious roots. If adventitious roots manifest in response to the cutting of stems below the water surface, then this could compromise the efficacy of the cut-to-drown management method. Knowledge on the role of adventitious roots for *Phragmites* in high water holds strategic importance for future cut-to-drown management projects. To inform management we sought to answer: What is the impact of adventitious roots on the effectiveness of cut-to-drown management? Specifically, what is the effect of adventitious roots on different measures of above-and belowground plant performance, and how is that effect impacted by dissolved oxygen and management cutting strategy? To answer these questions we directly manipulated available dissolved oxygen, adventitious roots, and the height at which plants were cut in a three-way factorial design.

Materials and Methods:

To address our research questions, we set up and conducted an experiment to study the growth and responses of *Phragmites*, under various treatment conditions. The experiment aimed to simulate different environmental conditions, including flooding and root manipulations, to understand their effects on plant growth and development. We did this by creating a 3x2x2 factorial design including the factors cutting (no cut, partial cut, full cut), adventitious roots (with, without) and dissolved oxygen (added, not added). This resulted in 12 unique treatments that were each replicated 9 times. The process encompassed several steps, including collecting rhizomes, preparing plants in the wet lab, potting them, assigning treatments, and monitoring their growth over time.

Rhizome Collection and Plant Preparation:

In May, 2023 we collected rhizomes from a field site, North Hydro Park in Ypsilanti, Michigan, to ensure consistency in genetic material (genetic uniformity within the population sharing similar environmental conditions). The collected rhizomes were processed at the Great Lakes Science Center in Ann Arbor, MI where they were sorted and cleaned to remove dirt and debris. They were then placed in a growth chamber set to 29℃ with a light schedule of 8hr:16hr dark:light to encourage plant growth.

Once the rhizomes sprouted (created a new stem at least 15 cm tall with roots), they were potted into soil-filled pots, labeled and transferred to the Great Lakes Science Center greenhouse, where they were watered regularly and allowed to settle and acclimate for 24 days.

Experiment Setup:

On June 5th, 2023 the individual potted plants were moved to Matthaei Botanical Gardens greenhouse and arranged in buckets, with each bucket representing a treatment condition (Figure 2). The buckets were filled with water to simulate flooding conditions and induce adventitious root growth. They grew in the buckets for two weeks to ensure the adventitious roots were established before beginning treatments.

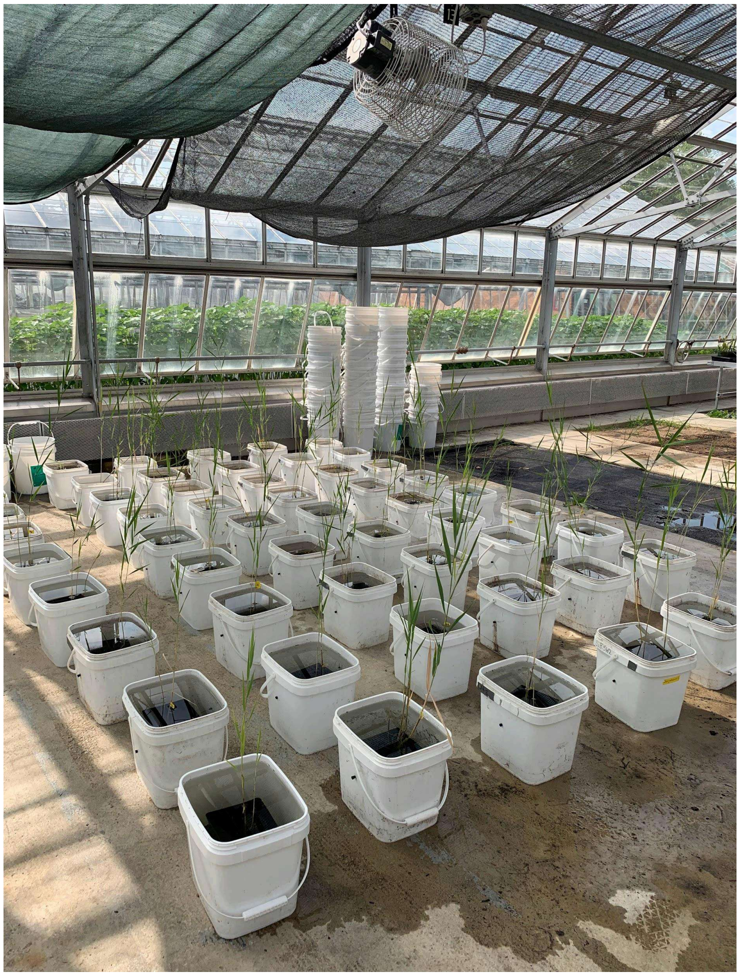

Figure 2: Replicated treatments spatially randomized spatialized in Matthaei Botanical Gardens Greenhouse.

Treatment Assignments:

Each plant was randomly assigned one of twelve treatment combinations, including variations in added dissolved oxygen, with or without adventitious roots, and cutting treatments.

1. Cutting treatments

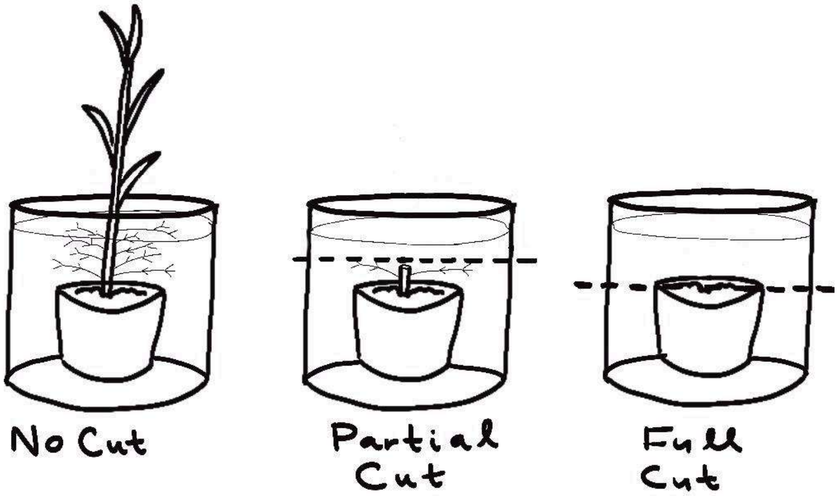

Figure 3: Three cut treatment options: no cut, partial cut and full cut.

To simulate the cut-to-drown management strategy, all of the plants were randomly assigned one of the three cut options: no cut (not cut at all), partial cut (cut below the water but above the soil leaving stem and some adventitious roots), or full cut (cutting at the soil line, not leaving any aboveground biomass; Figure 4). This treatment occurred twice during the season, one cut on day 1 and another on day 33.

2. Dissolved oxygen treatment

A 32W aerator (VH613), hereafter bubbler, was set up to transport additional oxygen to the replicates to simulate higher available dissolved oxygen (Figure 5). The bubbler was placed in the center of the area and rubber tubing was used to transport the air into the water of those with a bubbler treatment. Y splitters were used to have tubing and air go into each corresponding bucket. At the end of each piece of tubing, an air stone was inserted to create bubbles in the water. Control valves were also attached to the tubing for each bucket to keep the airflow the same throughout all of the buckets.

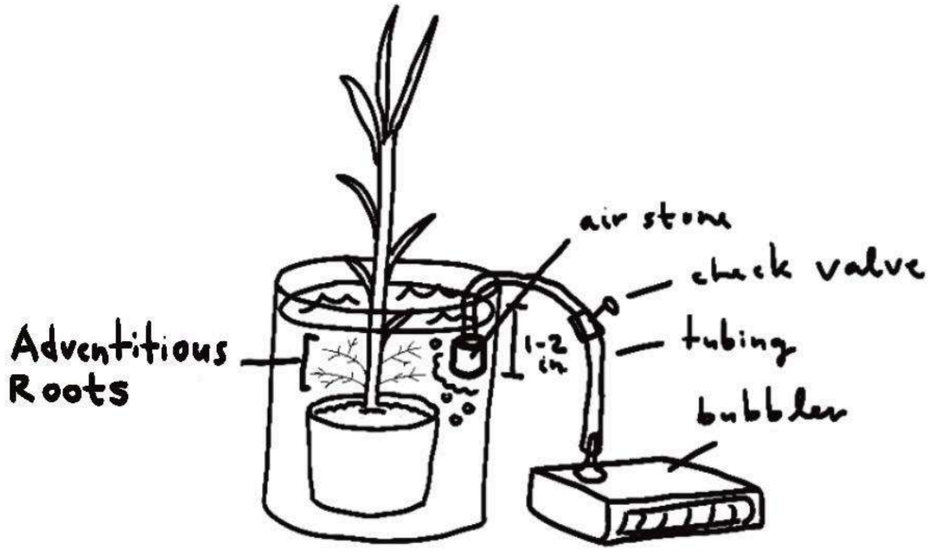

Figure 5. This figure shows the bubbler set up with one plant. The bubbler transfers air to the water in the bucket through the tubing and air stone attached at the end of the tube.

3. Adventitious root removal treatments

All treatments were randomly assigned either ’with adventitious roots ’ or ‘without adventitious roots’, meaning the treatment either kept the adventitious roots that grew or we removed them (Figure 6). Those that were assigned ‘without adventitious roots’ had the adventitious roots cut off as close to the stem as possible. Adventitious roots were checked every week during routine monitoring (Figure 7) and removed if they were present. On average roots regrew and were removed every 2-4 weeks. Those that were assigned ‘with adventitious roots’ had no adventitious root manipulation.

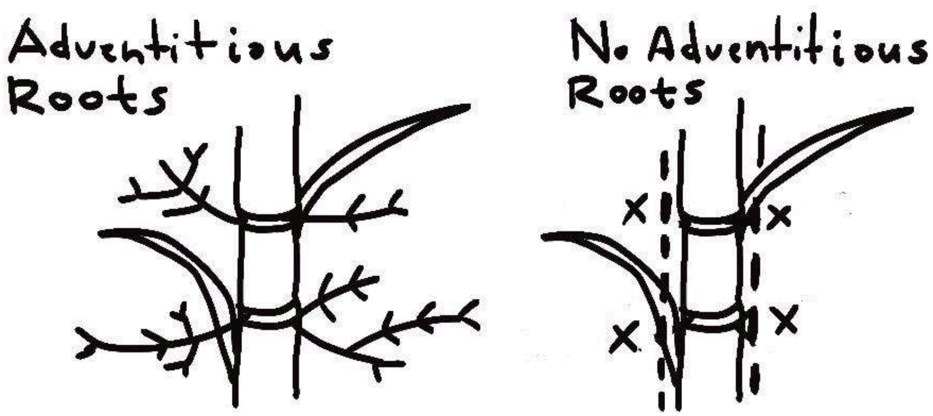

Figure 6: *Phragmites* with adventitious roots and without adventitious roots. The adventitious roots on the plant on the right are cut off close to the stem. Belowground rhizomes remain for both.

Figure 7: Adventitious root growth on plant sample during experiment in Matthaei Botanical Gardens greenhouse.

Monitoring and Data Collection:

The plants were monitored weekly for various response measures, including the number and height of stems, as well as the presence and type of adventitious roots. These roots were categorized as either feathering, characterized by smaller, hair-like branches extending from the main root, or non-feathering, consisting of a single root structure without additional hairs (or both). Additionally, three random adventitious root lengths were measured, along with the count of adventitious roots present on each node. Data collection occurred weekly to track the plants' response to the twelve different treatments over time. At the end of the experiment we collected samples to measure the aboveground, new rhizome and belowground biomasses.

Biomass assessment and carbohydrate analysis:

At the conclusion of the experiment on October 27th, 2023, the *Phragmites* plant samples in the greenhouse were harvested to assess their biomass and carbohydrate content. Plants were carefully uprooted from their pots, and the roots were washed to remove soil particles. Aboveground and belowground (rhizome and roots) biomass were separated into labeled paper bags for drying.

Plant tissues were dried to halt enzymatic activity and facilitate long-term storage. Initial drying was carried out for at least 90 minutes at 100°C to stop enzymatic processes. Subsequent drying occurred at 70°C for at least three days to remove moisture completely (Hellings and Gallagher 1992; Landhäusser et al. 2018). After drying, aboveground and belowground biomass were weighed separately to determine total dry biomass for each plant.

The rhizomes from each plant were ground into fine particles to increase the surface area for carbohydrate extraction. A vibrating ball mill grinder (HVBM-1200) was used for seven minutes per plant to achieve uniform grinding. Equipment used for grinding was thoroughly washed and dried between samples to prevent contamination.

Data analysis:

We analyzed the effect of the treatments on number of stems, belowground biomass, new rhizome biomass and non-structural carbohydrates using a separate

3-way ANOVA for each response variable, with dissolved oxygen treatment, cut treatment, and with or without adventitious root treatment as the independent variables. All analyses were run using RStudio version 2022.12.0+353.

Results:

Treatment effects on belowground growth and carbohydrates:

Cut treatment had a significant main effect on all final belowground biomass measures: total belowground biomass (F = 23.275, $p < 0.001$; Figure 8) and new rhizome biomass (F = 26.613, $p < 0.001$; Figure 9), as well as non-structural sugar carbohydrates (F = 52.1928, $p < 0.001$; Figure 10) Specifically for the biomass measures, plants that were not cut produced significantly more belowground/rhizome biomass than either the partial or full cut, which did not differ significantly from each other. For carbohydrates, the sugar content was significantly depleted the most in the full cuts, followed by partial cuts, with no cuts exhibiting the least depletion.

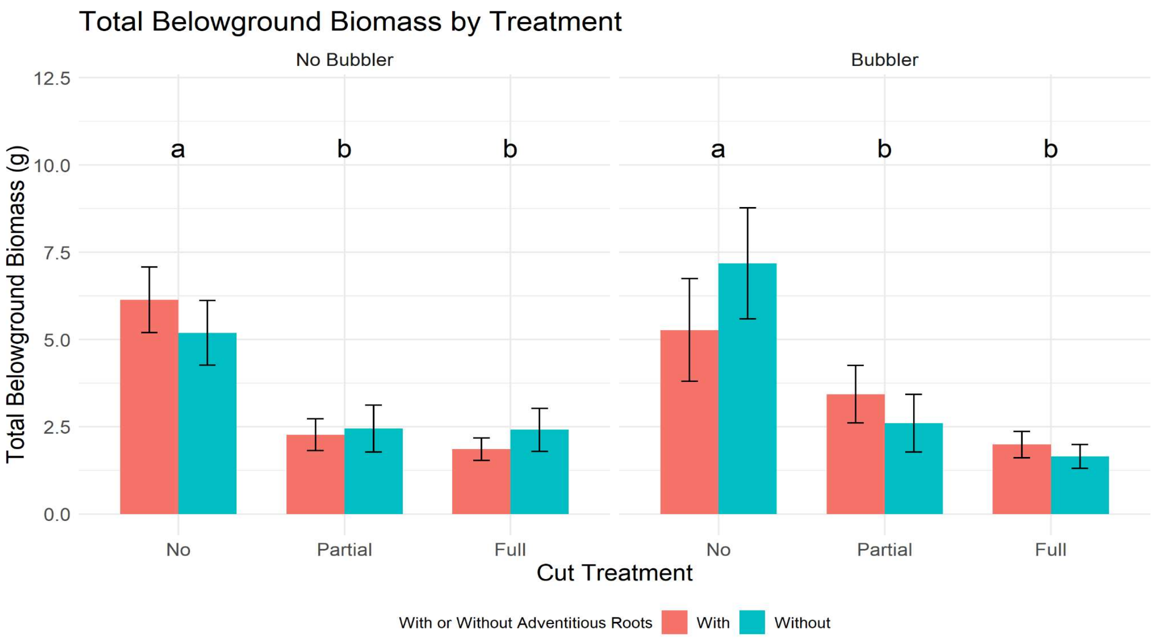

Figure 8: Belowground biomass in response to cut treatments (no cut, partial cut, full cut), bubbler treatments (bubbler, no bubber), and adventitious root treatments (with adventitious roots, without adventitious roots). Different letters denote significant differences among treatment combinations.

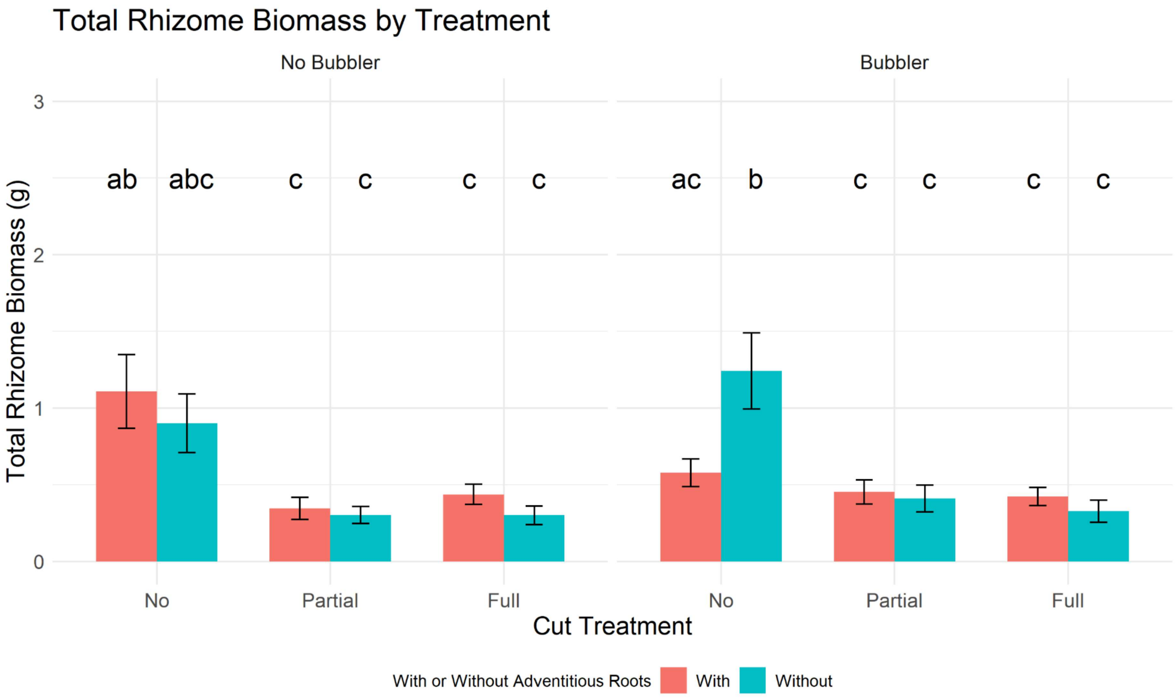

Figure 9: New rhizome biomass in response to cut treatments (no cut, partial cut, full cut), bubbler treatments (bubbler, no bubber), and adventitious root treatments (with adventitious roots, without adventitious roots). Different letters denote significant differences among treatment combinations.

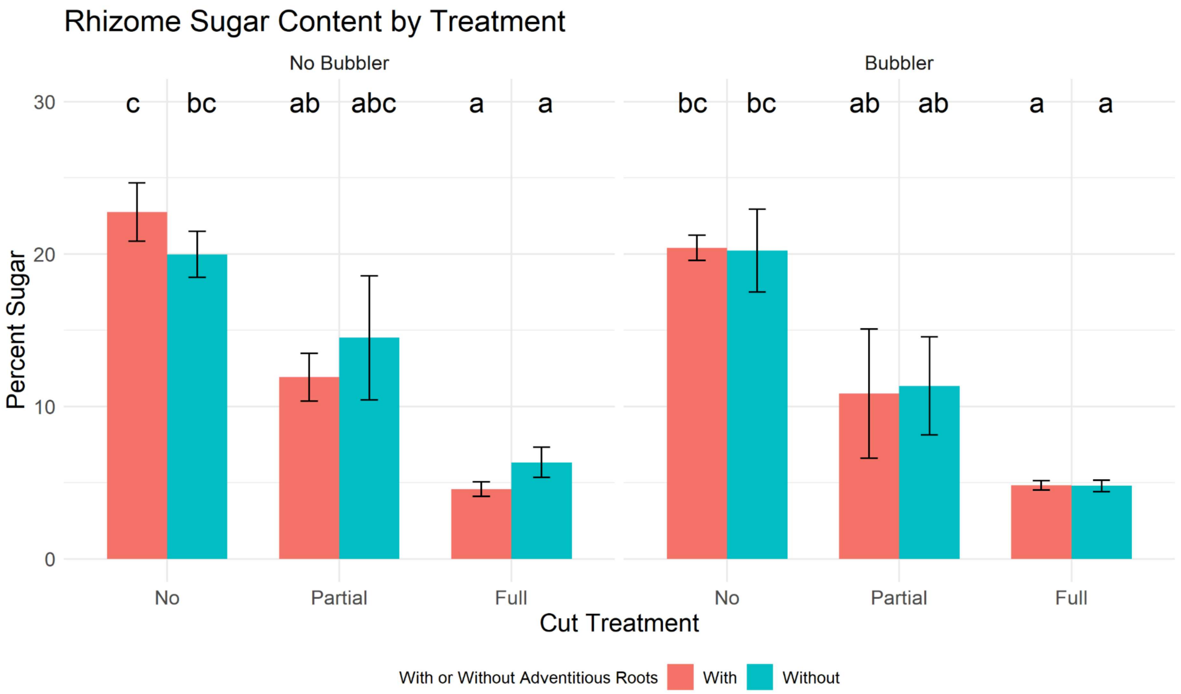

Figure 10: Non-structural carbohydrates (sugar content) in response to cut treatments (no cut, partial cut, full cut), bubbler treatments (bubbler, no bubber), and adventitious root treatments (with adventitious roots, without adventitious roots) on non-structural carbohydrates (sugar content). Different letters denote significant differences among treatment combinations.

Treatment effects on aboveground growth:

Cut treatment had a significant main effect on new stem growth (F = 93.384, $p < 0.001$; Figure 12). Cut treatments did significantly differ from each other in aboveground response (the cumulative number of stems produced over time) - with partial cuts sprouting significantly more stems compared to both no and full cut treatments (F =

53.437, p < 0.001; Figure 11). For new stem growth, partial cuts had significantly more new stems than no cuts and full cuts, which did not differ significantly from each other (with the exception for partial cuts with no bubbler or adventitious roots).

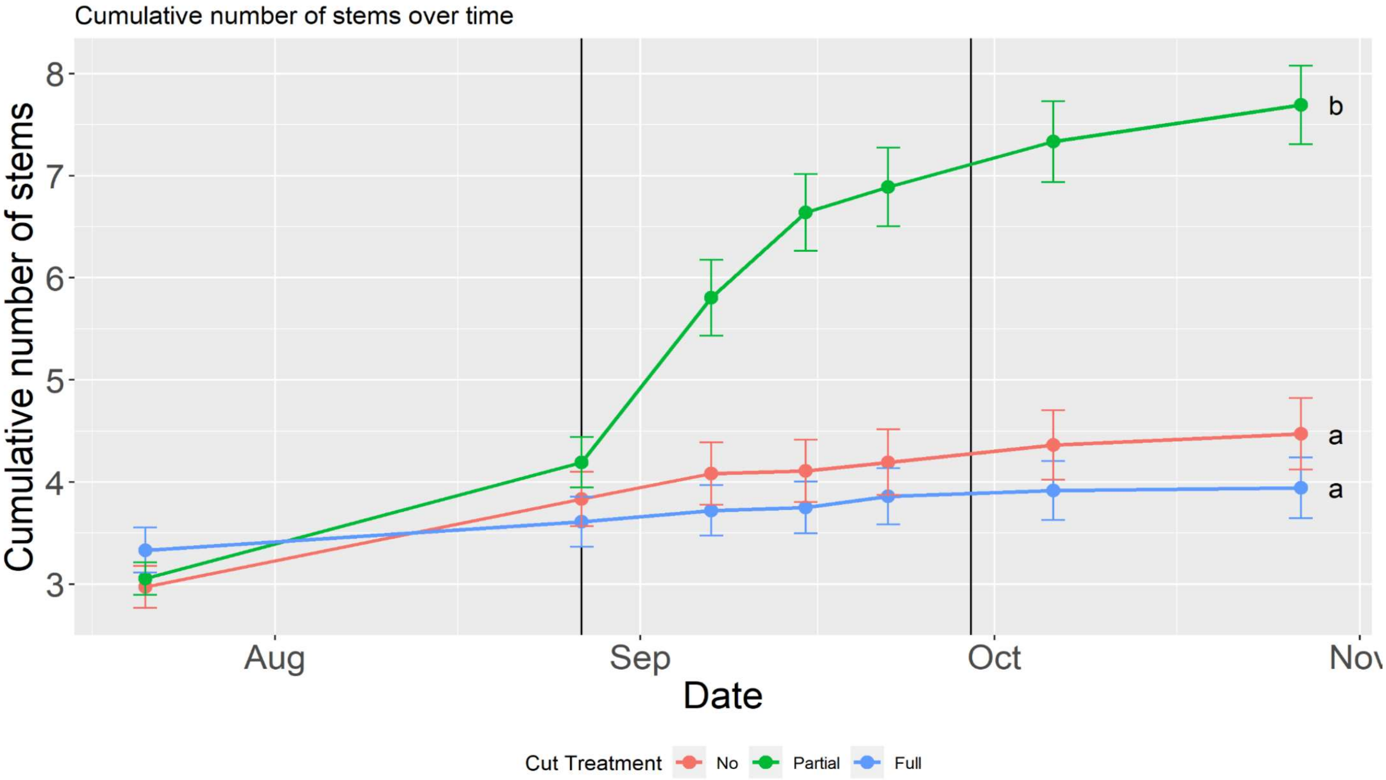

Figure 11: Cumulative number of stems over time by cut treatment (no cut, partial cut, full cut). Different letters denote significant differences among treatment combinations. Different letters denote significant differences among treatment combinations.

While the adventitious root and bubbler treatments did not have significant main effects on any response variable, there was a significant three-way interaction between bubbler, adventitious roots, and cut treatments for both new rhizome biomass (F = 3.547, p < 0.0327) and number of stems (F = 5.323, p < 0.005; Figure 12). For rhizome biomass, this interaction is reflected in the significant negative effect of adventitious roots for rhizome biomass in the no cut treatment when the bubbler was present, but not when it was absent (Figure 9). For stem growth, there was a trend toward the opposite, with adventitious roots increasing the number of stems more in the absence of bubblers (Figure 12).

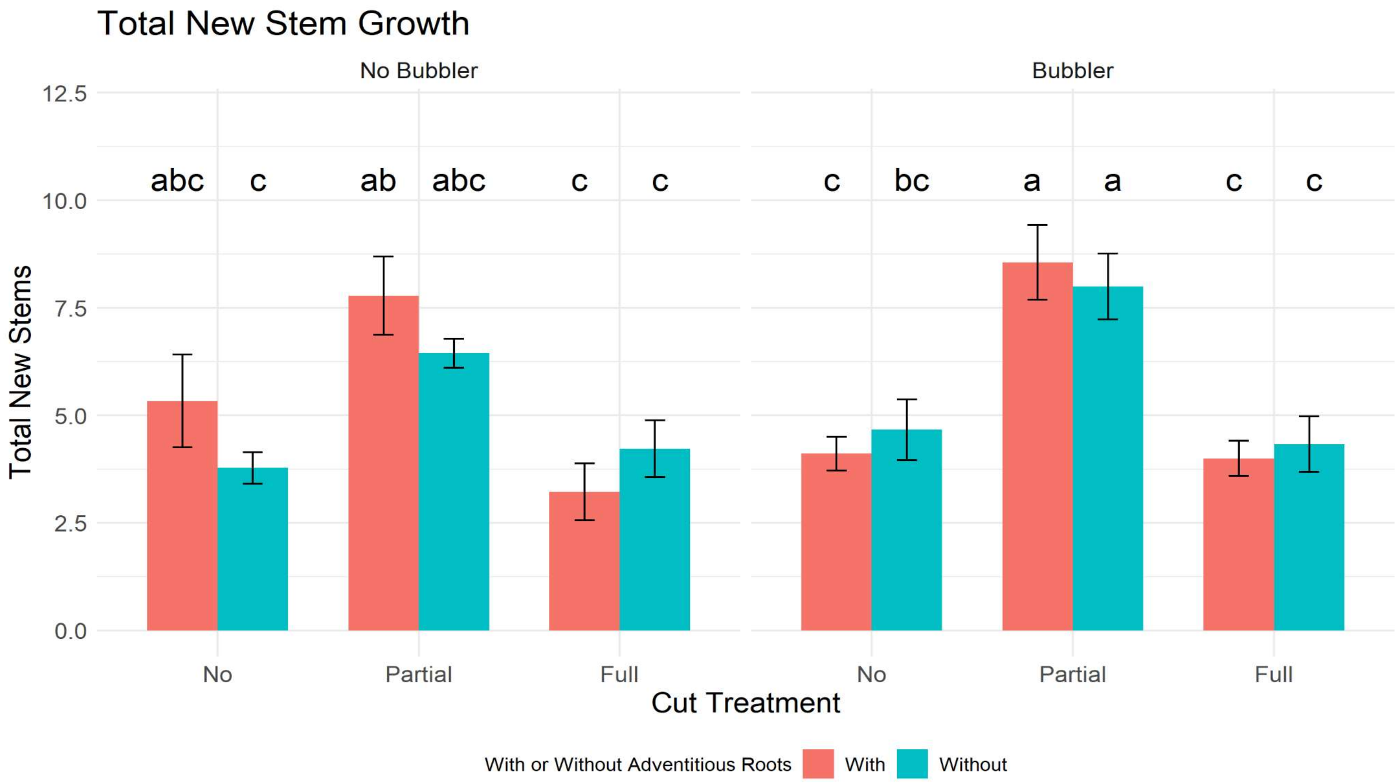

Figure 12: New stem growth in response to cut treatments (no cut, partial cut, full cut), bubbler treatments (bubbler, no bubber), and adventitious root treatments (with adventitious roots, without adventitious roots) on total new stem growth. Different letters denote significant differences among treatment combinations.

Discussion:

Consistent with the discoveries in Widin et al. (2023), our study demonstrates the effectiveness of cut-to-drown management in diminishing *Phragmites'* belowground growth and non-structural carbohydrate storage. As anticipated, we noted adverse effects of both complete submergence and cut-to-drown techniques on *Phragmites'* growth, ultimately resulting in rhizome mortality among the cut-to-drown plants. The results demonstrate that full cuts, where the entire aboveground portion of the plant, including adventitious roots, is removed, have the most significant impact on *Phragmites* growth.

Interestingly, the results show that the partial cuts had a higher aboveground regrowth response to cutting than full cuts and no cuts. Because partial cuts leave a portion of the stem remaining with adventitious root-forming nodes, this finding suggests that adventitious roots may have an influence on the plant's ability to regrow. Adventitious roots, by facilitating faster stem regrowth, effectively counteract the adverse effects of cutting-induced drowning. From a management perspective, our data suggests that full cuts (all the way to the soil surface) are likely to be most effective at controlling *Phragmites*. If partial cuts are the only feasible option for managers due to factors like equipment or uneven terrain (cannot conduct a full cut), it is necessary to conduct multiple cuts over the growing season to further deplete the carbohydrates and reduce the amount of regrowth over time.

Building upon previous research that showcases the regrowth potential of stems under total submergence conditions, Mauchamp et al. (2001) conducted a study demonstrating how submergence influenced stem length and biomass. Their findings highlight significant differences between partial (50% and 80%) and total submergence treatments. Specifically, partial submergence notably stimulated biomass accumulation and growth, while total submergence primarily reduced biomass production and growth in length, with a minor impact on stem numbers. Assuming their fully submerged stems had adventitious roots, this aligns with our findings, as adventitious roots enabled stems to regrow, thereby mitigating the impact of total submergence on stem numbers.

It is important to note that full cuts offer the most significant advantages to managers, even though partial cuts yield similar statistical outcomes for belowground biomass measurements. That is, the effects of cut treatments vary depending on whether the focus is on aboveground or belowground responses. Solely examining belowground biomass might suggest that any cut is effective. However, when assessing aboveground growth, it becomes evident that partial cuts lead to statistically higher stem growth compared to full cuts, which may compromise management outcomes.

Our observations reveal intriguing trends regarding stem regrowth in high and low dissolved oxygen conditions. In situations lacking a bubbler, no cuts with adventitious roots exhibited a trend towards increased stem regrowth. However, with the presence of a bubbler, the beneficial effect of adventitious roots on new stem growth seems to diminish. For new rhizome biomass, the removal of adventitious roots seems to increase new rhizome biomass in no cuts with a bubbler. This may be because the energy used to grow adventitious roots is reallocated to growing more rhizome biomass.

The dependence of adventitious roots on the presence of bubblers highlights the intricate interplay between oxygen availability and plant response. Our findings suggest adventitious roots might facilitate stem regrowth, particularly in oxygen-deprived environments where they serve as conduits for gas exchange. However, the presence of bubblers introduces oxygen into the system, potentially altering the necessity and efficacy of adventitious roots for stem regrowth. In environments with bubblers, where oxygen levels are presumably higher, the role of adventitious roots in facilitating stem regrowth may be diminished, as plants may rely less on them for oxygen uptake. This suggests that the effectiveness of adventitious roots in promoting stem regrowth is contingent upon oxygen availability.

The findings regarding the interplay between adventitious roots, oxygen availability, and stem regrowth contribute to our understanding of wetland ecology and invasive species management, aligning with existing literature while providing nuanced insights. Ayi et al., (2016) demonstrated that adventitious roots play a crucial role in facilitating oxygen uptake in invasive *Alternanthera philoxeroides*. Specifically, their research revealed a significant improvement in oxygen uptake when the plants retained their adventitious roots compared to instances where these roots were removed. Our observations on *Phragmites australis* align with Ayi et al.'s findings on *Alternanthera philoxeroides*, emphasizing the significance of adventitious roots in low oxygen conditions. This underscores their importance in plant resilience and adaptation to challenging environments. By confirming Ayi et al.'s results, we bolster the understanding of plant responses to submergence and oxygen availability in wetlands.

Though there are many causes of invasives' success, phenotypic plasticity allows invasive success (Gioria et al., 2023), especially for species that tolerate different hydrological conditions (Geng et al., 2007). Adventitious roots are an example of that type of plastic response to conditions. This plasticity allows the plants to rapidly adjust to changing hydrological conditions, facilitating their persistence and spread in diverse habitats. Understanding the dynamics of adventitious roots in response to management strategies like cut-to-drown is essential for developing more effective control measures against invasive *Phragmites* populations.

Implications for Management Strategies:

These findings have important implications for the development of management strategies for controlling *Phragmites* in wetland habitats. While single cutting events may provide temporary suppression of plant growth, they are unlikely to provide long-term control, especially if the single cut is a partial cut. That is because if adventitious roots help the plant regrow stems faster, they negate the drowning effects of cutting entirely. Our results suggest that management efforts should prioritize full cuts and consider implementing multiple cutting events throughout the growing season to effectively manage *Phragmites* populations and prevent regrowth. These full cuts will deplete the carbohydrates the most and remove adventitious roots that may be supplying dissolved oxygen to the plant. This is especially important when conditions would cause low oxygen (e.g. no water movement, warmer temperatures, etc.) because that is when adventitious roots may provide the greater advantage to *Phragmites* regrowth after being cut.

For management, understanding the interaction between adventitious roots and oxygen levels is crucial for optimizing restoration strategies. In environments with low oxygen levels, such as stagnant water bodies or heavily shaded areas, addressing the development of adventitious roots on partial cuts may be beneficial to reduce stem regrowth.

Limitations and Future Research:

It is important to acknowledge the limitations of our study, including the relatively short duration of the experiment and the focus on a limited number of cutting treatments. Future research should explore additional cutting strategies, as well as investigate the potential synergistic effects of cutting with other management techniques, such as herbicide application or controlled burns. Long-term monitoring of treated areas will also be valuable for assessing the persistence of treatment effects and evaluating the sustainability of management practices.

It is important to note that our experiment was conducted in a controlled greenhouse environment with young plants. Therefore, further research on a larger scale and in diverse field conditions is essential to validate the applicability of these findings to mature *Phragmites* stands. Nevertheless, our promising experimental outcomes align with observations made by land managers implementing cut-to-drown strategies in the field.

Other aquatic wetland plant species with similar structures and adventitious root growth are important to consider as well. Some examples of these include cattails

(Typha), Bulrushes (Schoenoplectus), and reed canarygrass (*Phalaris arundinacea*). Cattails, including both *Typha latifolia* and *Typha angustifolia*, are common wetland plants that can produce adventitious roots, especially in response to water level changes (Keddy, 2010). Bulrushes, such as *Schoenoplectus acutus* and *Schoenoplectus tabernaemontani*, exhibit rhizomatous growth and may develop adventitious roots in wetland environments (Sculthorpe, 1967). Reed canarygrass is another wetland grass species that may exhibit adventitious root growth in response to disturbances (Smith, 1987). Including these in a future study might enhance our overall understanding of adventitious roots in other invasive wetland plant species.

Conclusion:

In conclusion, our study reaffirms the efficacy of cut-to-drown management in curbing *Phragmites'* belowground growth and carbohydrate storage. We observed adverse effects of both complete submergence and cut-to-drown techniques on *Phragmites'* growth, with the latter resulting in rhizome mortality. Notably, full cuts, encompassing the removal of the entire aboveground portion including adventitious roots, exerted the most substantial impact on *Phragmites* growth by impeding resource allocation for growth and reproduction. Conversely, partial cuts exhibited robust regrowth responses, necessitating multiple cuts throughout the season. This suggests a notable influence of adventitious roots on regrowth dynamics, emphasizing the importance of considering cutting techniques in wetland management strategies.

Moreover, our findings shed light on the role of adventitious roots in response to varying oxygen availability. Our findings indicate that adventitious roots may aid in stem regrowth, especially in oxygen-deprived environments, where they function as channels for gas exchange. However in higher oxygen environments, the presence of adventitious roots appeared to have a diminished effect on promoting stem regrowth, as plants may rely less on them for oxygen uptake. This highlights the complex interplay between oxygen availability, adventitious roots, and plant response, underscoring the need for adaptive management strategies tailored to specific environmental conditions. Moving forward, our study underscores the significance of integrating knowledge on adventitious roots and oxygen dynamics into wetland management practices to achieve effective invasive species control and ecosystem restoration.

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