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Planted species influences soil phosphorus losses in a historically fertilized pasture system: A mesocosm study

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Abstract

The gradual accumulation of phosphorus from historical fertilization can contribute to the eutrophication of surface waters by increasing the potential for subsurface leaching losses. Grazing lands areas are a priority for concern, and phytoremediation efforts in grazing lands have prioritized grasses that may be used as forage for cattle. This study investigated the influence of three different forage species—*Paspalum notatum*, *Hemarthria altissima*, and *Cynodon nlemfuensis*—on the loss of phosphorus in leachate from surface soils. The experiment used a nested pot mesocosm design that allowed us to monitor leachate volume and concentration biweekly over the course of 3 months. Pots containing *P. notatum* plants leached significantly more phosphorus than pots containing *C. nlemfuensis* or empty pots with no plants growing in them, despite losing an equivalent amount of water. *H. altissima* lost equivalent amounts of phosphorus in leachate water, but each *H. altissima* plant removed approximately 33.6 mg of phosphorus, approximately 2.5× that removed by *P. notatum* (13.4 mg). *C. nlemfuensis* had lower average leachate phosphorus concentrations at each biweekly sampling than either plant species (*C. nlemfuensis-P. notatum*, $p_{adj} = 0.001$; *C. nlemfuensis-H. altissima*, $p_{adj} = 0.02$), averaging only 0.110 ppm in leachate relative to 0.175 ppm and 0.200 ppm in pots beneath *H. altissima* and *P. notatum*, respectively. This, combined with *C. nlemfuensis*' slightly higher-than-average aboveground P content and overall aboveground biomass expression suggest it is the best possible phytoremediation candidate. As even minor leachate P loads can be critically threatening to neighboring oligotrophic water bodies, if the conservation of downstream environments is the priority, the short-term threat of increased leachate must be considered. Further research is needed to explore the underlying mechanisms and field-scale implications of these findings.

KEYWORDS
agriculture, ecohydrology, Florida, legacy phosphorous, mesocosm, phytoremediation, water quality

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INTRODUCTION

Phosphorus (P) limits plant productivity in both terrestrial and aquatic ecosystems (Harpole et al., 2011). As a result, P fertilization is commonly used to grow crops or forage (Harpole et al., 2011). However, long-term excessive P fertilization can lead to the accumulation of "legacy" P in soils (Haygarth et al., 2014; Jarvie et al., 2013). This "legacy" P can be lost to surface water and poses a risk for eutrophication for years to decades after the excess inputs cease (Chen et al., 2018; Dodds et al., 2009; Wang et al., 2020). Even minimal losses can be devastating; dissolved P concentrations as low as ~ 0.02 ppm are considered sufficient for eutrophication in surface waters in agricultural regions of the Americas and around the world (Dodds et al., 2009; Gentry et al., 2007; Noe et al., 2001; Noe & Childers, 2007; Powers et al., 2016; Smith et al., 1999).

The Everglades of North America are paradigmatic of this crisis. Historically, the dominant source of P to the Everglades was rainfall; however, P loads in waters entering the Everglades have increased due to agriculture and urbanization (Childers et al., 2003; Noe et al., 2001). Annual P inputs have increased from historical levels of about 129 tons to modern inputs near 376 tons due to increased P loading from drained farms and ranchland (Davis & Ogden, 1996). Although a variety of human disturbances can lead to increased P in the soil in the region (Kohmann et al., 2021; Reddy et al., 1996), the strongest signal appears to be non point source cattle operations (Dunne et al., 2011; Reddy et al., 1996), and improved pastures and ranches with a history of fertilization are consistently thought to be among the highest contributors to downstream P load (Khare et al., 2021). As a consequence, grazing lands are increasingly prioritized in research designed to mitigate eutrophication (Khare et al., 2021; Reddy et al., 1996).

Given the danger of eutrophication (Canfield & Hoyer, 1988; Khare et al., 2021; Motew et al., 2017; Osmond et al., 2012), mitigation of P losses from these grazing land systems is desirable (Haygarth et al., 2014; Jarvie et al., 2013; Kleinman et al., 2011; Sharpley et al., 2015). One potential solution is phytoremediation, or cultivating and harvesting plants which accumulate P over the course of their life cycle. The use of vegetation harvest strips may be a particularly effective strategy for cattle systems, as reducing feed P imports by increasing on-farm forage production can be a cost-effective way to reach a neutral P balance (Kohmann et al., 2021). Phosphorus removal has been investigated for several warm-season forage grasses already. Sanderson et al. (2001) found that surface runoff passing through a switchgrass (*Panicum virgatum* L.) buffer strip, lost an average of 47% of its soluble reactive P by the time it had moved across the buffer strip. Similarly, the loss of manure P to soil P pools was mitigated by growing a mixed bermudagrass (*Cynodon dactylon* L.)–wheat (*Triticum aestivum* L.) pasture which could take up to 20% of the new P associated with manure (Sanderson & Jones, 1997).

Similar evidence does suggest that several perennial grasses (Newman, Agyin-Birikorang, Adjei, Scholberg, Silveira, Vendramini, Rechcigl, et al., 2009; Newman, Agyin-Birikorang, Adjei, Scholberg, Silveira, Vendramini, Rechcigl, & Sollenberger, 2009; Silveira et al., 2013) may reduce soil P levels in a Florida grazing land, potentially mitigating the risk of legacy P loss. However, in one experiment, the magnitude of decrease in soil P content exceeded the uptake of P in harvested plant tissue during the first year of the phytoremediation effort (Newman, Agyin-Birikorang, Adjei, Scholberg, Silveira, Vendramini, Rechcigl, et al., 2009; Newman, Agyin-Birikorang, Adjei, Scholberg, Silveira, Vendramini, Rechcigl, & Sollenberger, 2009). This loss was attributed to intense leaching of P associated with the low P-retention capacity of surface soils in Florida (Agyin-Birikorang et al., 2008; Alleoni et al., 2008; Noe et al., 2001; Obour et al., 2011; Reddy et al., 1996; Silveira & O'Connor, 2013). This result raises an important question for the management of soils in grazed lands. Perhaps unsurprisingly, it has already been shown that the solubility of P largely determines the magnitude of its loss in sandy Florida soils, as this may impact the rate at which it may leach (Agyin-Birikorang et al., 2008). As such, any possible plant influence that affects the solubility of P and consequently the P concentration of leachate will have a critical influence on ecosystem P losses (Figure 1). Moreover, the trade-off between long-term drawdown of soil P reserves and short-term acute damage caused by increases in leachate loss is particularly relevant to the Florida pasture ecosystem. Many soils across Florida appear to be low in surface P, yet consistently contribute P to downstream waterways, motivating focus on P retention.

Here we present the results of a three-month mesocosm experiment designed to test how three candidate grass species may impact P loss from surface soils. Leaching loads were calculated by multiplying leachate water P concentrations by leachate volume weekly and summing them at the end of the experiment. We designed our mesocosm experiment using the same species used in Newman, Agyin-Birikorang, Adjei, Scholberg, Silveira, Vendramini, Rechcigl, et al. (2009) and Newman, Agyin-Birikorang, Adjei, Scholberg, Silveira, Vendramini, Rechcigl, & Sollenberger (2009), *Paspalum notatum*, *Hemarthria altissima*, and *Cynodon nlemfuensis*. *H. altissima* and *C. nlemfuensis* are both warm-season perennial grasses known to tolerate perennially flooded wetlands (Sollenberger et al., 1989). Both *H. altissima* and *C. nlemfuensis* are stoloniferous and lack rhizomes. In Florida, *P. notatum* is grown on over

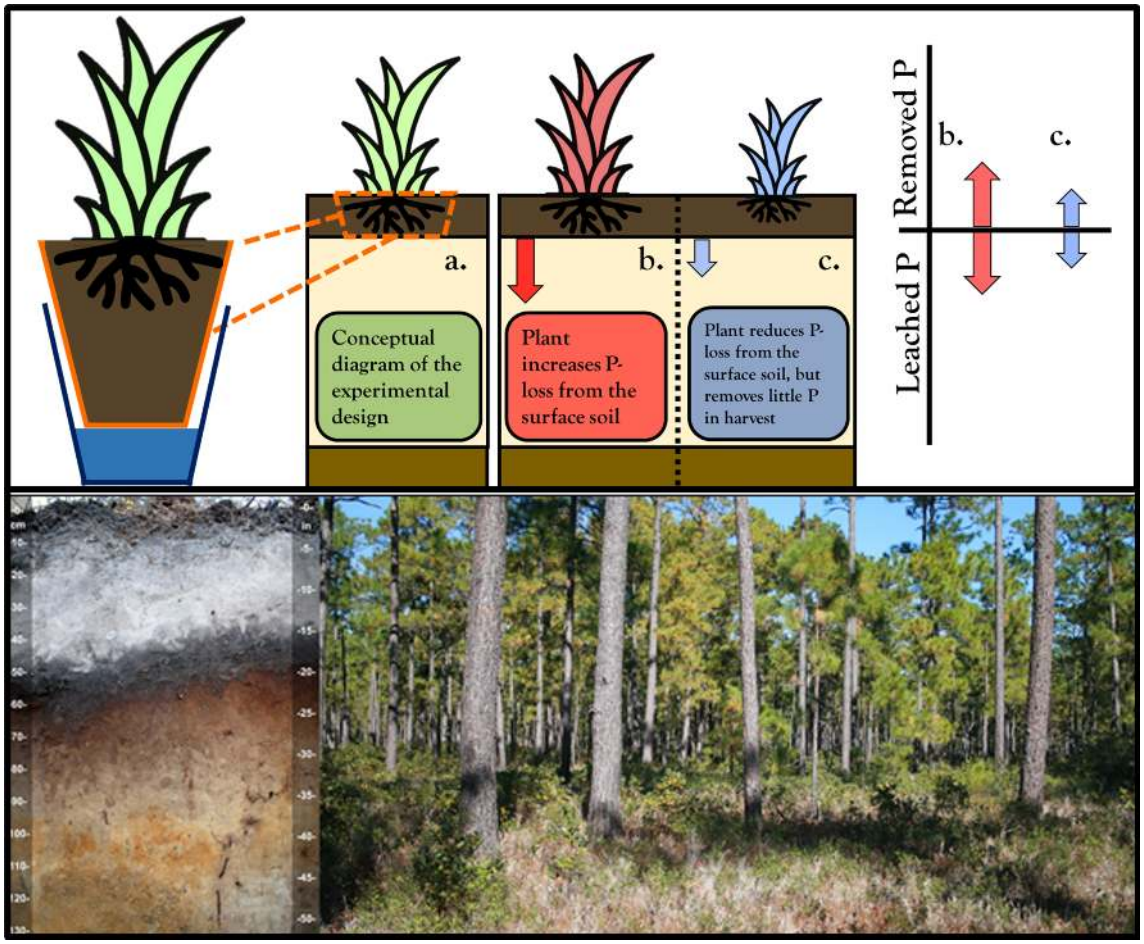


FIGURE 1 Conceptual figure that outlines the experiment and the unique nature of the Florida Spodosol ecosystem. Soils are highly stratified, with an extremely narrow dark *A* layer near the surface that extends between 4 and 10 cm into the soil profile. This is followed by an extremely depleted light-colored *E* horizon overlaying a reddish brown spodic horizon (also known as the *Bh* horizon). In scenario b, the planted species does draw up some P into aboveground harvestable tissue, removing and remediating P-loads in surface soils. However, in scenario b, this plant also inadvertently increases P loss from the surface soil, which may increase long-term risk, as P will leach to the spodic horizon, where it can be periodically remobilized during perennial flooding. In scenario c, the planted species reduces vertical P losses, mitigating leachate to the spodic horizon, but does not grow well in the P-deficient *A* layer, does not produce a large stock of "harvestable P," and thus may not be an optimal phytoremediation candidate for drawing down P in surface soils. The bottom half of the figure is a representative Myakka spodosol (the state soil of Florida). Note the clear formation of distinct soil layers. The right-hand side of this photo reflects the pine flatwood environment associated with the development of spodosols. The included photo by Unknown Author is licensed under CC BY (https://live.staticflickr.com/1327/5104788397_1bf0760ac7_b.jpg). The whiskers are the two lines extending from the box. One whisker goes from the minimum value to the lower quartile (the start of the box), and the other extends from the upper quartile (the end of the box) to the maximum value. Dots, where present, represent outliers that are greater than 1.5 times the interquartile range. That is, the whisker reaches the value that is the furthest from the centre while equal to or less than 1.5 times the interquartile range from the lower or upper 25th and 75th percentiles (the height of the box). This statement applies to all boxplots.

400,000 ha, making it the most planted perennial forage species in the state (Kalmbacher et al., 2005; Newman et al., 2007). *P. notatum* is rhizomatous and is often used for soil conservation and erosion control (Burton, 1948; Li et al., 2011). As such, we hypothesized that *P. notatum* would improve the retention of P in surface soils. Intensive management of all three forage grasses for hay production may be a viable option for remediating P-impacted soils, but their influence on surface soil P-loss remains unknown (Burton et al., 1997; Newman, Agyin-Birikorang, Adjei, Scholberg, Silveira, Vendramini, Rechcigl, et al., 2009).

METHODS

The experiment was conducted on the 4200-ha Buck Island Ranch, a division of Archbold Biological Station, in the headwaters of Lake Okeechobee in South Central Florida (27° 09′ N, 81° 12′ W). The climate is subtropical

with average rainfall of 1360 mm and minimum and maximum temperatures of 15.9 and 29.0°C, respectively (average of 30 years). Soils are sandy with a 15- to 25-cm organic layer, dominated by Alfisols and Spodosols. These soils are characterized by their low-P retention capacity in surface soils, high rates of vertical leaching, and presence of a dark spodic horizon at approximately a meter's depth (Figure 1). The local area was originally a seasonally inundated wetland–savanna mosaic adjoining the Kissimmee River floodplain. As such, the spodic horizon of these Spodosols is periodically submerged during perennial flooding, representing a source of P pollution that seriously threatens local waterways. Cattle ranching (free-range cow-calf operations) and agriculture (sugarcane, sod, and citrus) dominate the region.

The study was conducted in a shadehouse on site (permitting cross-ventilation and maintaining ambient relative humidity) with pots and leachate collection systems. Three forage grasses widely prevalent at Buck Island Ranch and used in subtropical rangelands worldwide were chosen as focal species: *P. notatum* (Bahia grass), *H. altissima* (Limpo grass), and *C. nlemfuensis* (Star grass). Ten replicates of each species were individually grown in plastic 3.8-L (1-gallon) pots filled with 10 kg of local soil. The soil was collected from 10 spots within pastures within a 1.6-km radius of the shadehouse. We focused on areas around the ranch that had been previously identified as hotspots of soil P (Qiu et al., 2024). Large roots were removed; soils from all 10 sampling spots were homogenized together to use as pot mix. Initial soil P and soil moisture were measured for all pots and were equivalent across all grass species and control pots (Appendix S1: Table S1). An automated irrigation system (RainBird, USA) was programed to water the pots three times per week for 5 min per watering event.

Plants were collected from local pastures/wetlands in the form of sprigs/stolons (cuttings with roots, stem, and few leaves), established in small pots for 2 weeks, then transplanted to 7.5-L experimental pots. In addition, 10 pots with only soil (no plants) were used as controls. An additional 7.5-L bucket was placed around each plant and control pot and served as a leachate collector. The airtight design served to both reduce evaporative losses from leachate containers and prevent the introduction of either rain or irrigation water (Appendix S1: Figure S1). The irrigation system was manually turned off during episodes of heavy rain to prevent leachate collectors from overflowing. Though particulate P loss is a critical issue when considering surface runoff, our principal interest is in the capacity of these plants to influence how the soil retains soluble P that will otherwise be vertically leached in fluid to the spodic horizon (Figure 1). To that end, a piece of ground fabric (Home Depot, USA) was placed over the drainage holes at the bottom of the internal pot to decrease large particle soil loss into collected leachate. This is an extremely crude representation of the soil matrix, which would similarly intercept large particle loss but allow for the leaching of dissolved P. Five soil cores (~120 g) were taken from each pot at the beginning of the experiment to determine initial soil P conditions by using Aqua Regia extraction of the ashed samples then analyzed using a spectrophotometer (BioTek Epoch 2). Our method, in brief, was to ash the material, converting all inorganic and organic P to Ortho P. Afterward, the use of an HCl extractant provided an "acid digest" ensuring all P from the plant or soil had been converted to a form that may be viewed with the spectrophotometer. Color development was via ascorbic acid (used for a higher range of P) or malachite green (in case of low P values). The ascorbic acid method involves the determination of total reactive P in a sample by reacting the orthophosphate in the sample with ascorbic acid and ammonium molybdate. The resultant compound has a blue color and the intensity of this color is then measured using a spectrophotometer at an absorbance of 880 nm. The intensity of the blue color is directly proportional to the amount of orthophosphate in the sample. We used a set of peach leaf standards (analytical lab grade NIST 1547, Sigma-Aldrich) included in every batch of foliar P to verify that our digestion was appropriate for plant materials. Peach standard total P should range from 0.129% to 0.145%; our sample reported 0.141%, 0.139%, and 0.143%, suggesting our protocol was effective. In order to ensure that our results were consistent, we also verified our spectrophotometric analysis against a series of stock dilutions of KH_2PO_4 dilutions. Our methodology builds on a history of soil and water P analyses, of which more detail can be found in the literature (D'Angelo et al., 2001).

The experiment was conducted for a total of 3 months, during which pots for controls and each grass species were randomly placed inside the shadehouse. A major concern of shadehouse experiments is the heterogenous climate conditions, particularly at the edges of the shadehouse. The top of the shadehouse had been removed prior to this experiment, so that the only protection from rain was a single layer of shade cloth that reduces radiation by ~50%. The shade cloth is not a complete protection against rainfall, and pots could have been exposed to rain inputs through the open sides of the shadehouse. To ensure homogeneity, pots were rearranged weekly in a random pattern to provide similar exposure to sunlight and wind/rain entering from the sides. Furthermore, periodic weeding was conducted on all pots to reduce competition to focal plant growth and untracked nutrient absorption.

Leachate collectors were monitored to ensure that there was no contact between leachate water and soil from the pots. Once immediately at the start of the experiment, and then biweekly, the leachate volume was measured to the nearest 10 mL using a graduated cylinder. A grab sample of

125 mL was collected and preserved using sulfuric acid to a pH value of 2.0. Then a persulfate digest was performed on the grab sample to determine the total P concentration by using a spectrophotometer (BioTek Epoch 2) (Pierzynski & Hodges, 2000). As with the plant samples, analysis is verified against a series of KH_2PO_4 dilutions. After each collection, the leachate collector bucket was washed out with tap water and acid washed. We also collected leachate from beneath pots that did not contain plants (i.e., the control pots). Total loss at each sampling interval was evaluated by multiplying the total P concentration by the total volume lost beneath the plant. To estimate total loss over the course of the experiment, the losses from each sampling interval were summed together. Leachate loss was evaluated relative to control pots to examine if pots containing certain species leached more or less than empty pots representative of bare ground.

At the end of the experiment, the entire plant was harvested from each pot. The plant was cut just above the soil boundary—representative of what would likely be harvested for hay by an average land manager. Belowground biomass was harvested as well, and the rhizosphere soil shaken free and washed from roots. In *P. notatum*, rhizomes were considered part of belowground biomass, not stems. Plant samples were dried in an oven for 48 h at 60°C. Samples were weighed before and after drying to determine water content and dry biomass. Dried samples were then ground and ashed. An HCL extraction and spectrophotometer were used to determine total P concentration in the ashed samples (Pierzynski & Hodges, 2000). We estimated the total amount of P that might be removed from surface soils, "P-harvest" (*H*), by estimating the total P in aboveground plant using aboveground biomass and concentration data, as belowground plant material would not be collected or used when making hay. In this way, we considered *H*, harvest, as equal to the mass of the harvested aboveground biomass from that plant in milligrams times the concentration of P (in micrograms per milligram) in the aboveground tissue.

$$H = \text{Biomass}_{\text{Above}}(\text{mg}) \times \text{TP}_{\text{Above}}\left(\frac{\mu\text{g}}{\text{mg}}\right). \quad (1)$$

In this way, we could estimate the relationship between total P removed in aboveground harvest and total leachate P loss over the course of the experiment as Harvest:Leachate Efficiency (HLE). HLE for a given plant is calculated as follows:

$$\text{HLE} = \frac{H}{L}, \quad (2)$$

where *L* is the total P lost in leachate (in milligrams) over the course of the experiment beneath that plant.

Data were analyzed using one-way regressions testing for species effects on P accumulation in hay and mitigation of P loss to leachate. We also used one-way regressions to evaluate whether the amount of P removed in aboveground biomass could be used to estimate the amount of P lost in leachate. Normality was assessed using a Shapiro–Wilk test, and normally distributed data were treated with ANOVA. Non-normal data were log- or square root-transformed where necessary to meet a normal distribution. When data were transformed, they were back-transformed before plotting to ease interpretation. When data transformation was insufficient to achieve a normal distribution, a Kruskal–Wallis test was used as a nonparametric alternative to ANOVA. All statistical data can be found in the Supplementary Material. Data were processed using the R statistical environment, R version 4.0.5 (R Core Team, 2021). Post hoc analysis to check for pairwise comparisons across species was done for each explanatory variable. For non-normally distributed data we used Dunn's test, and accordingly, the Bonferroni adjustment was used to reduce the risk of the family-wise error rate (Dinno, 2015). Similarly, we used Tukey's method to analyze pairwise contrasts in the normally distributed data (Keselman & Rogan, 1977).

RESULTS

There were no differences in initial soil conditions across pots. Each pot was filled with 10 kg of homogenized soil, with starting conditions of ~87.5 mg/kg of soil P, as measured by Aqua Regia extraction. There was no difference in initial soil weight, moisture, or P content across any of the three species or the control treatment (Appendix S1: Table S1). All differences in treatment effects were assumed to be due to the presence of plant species identity within the pot.

Plants had observable differences in aboveground biomass expression (Figure 2). In this mesocosm setting, *P. notatum* had less aboveground plant matter than either of the two species. When considering both the above- and belowground plant fractions, all species had approximately the same concentration of total P in tissue (Appendix S1: Figure S5). However, when above- and belowground fractions were considered separately, species-level differences emerged. While there was no difference in tissue P concentration belowground (Appendix S1: Figure S6), we observed that the aboveground tissue of *C. nlemfuensis* had slightly higher P concentration than *H. altissima* (Figure 3).

P harvest data were normally distributed, so we checked for the influence of species identity using a one-way ANOVA and a post hoc Tukey's pairwise

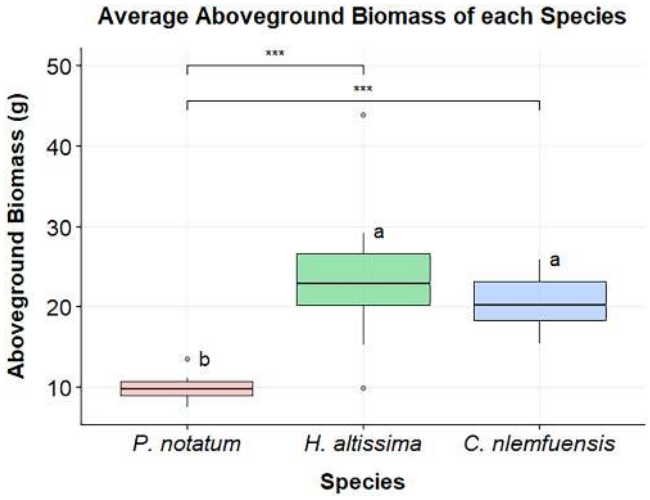


FIGURE 2 Aboveground biomass expression varies among the three species used in this mesocosm study. *Cynodon nlemfuensis* and *Hemarthria altissima* outgrew *Paspalum notatum* when considering their aboveground biomass. Aboveground biomass was prioritized in this experiment as it represents what a local land manager might harvest for hay production during a phytoremediation effort. Biomass data were log-transformed to meet assumptions of normality for a one-way ANOVA. Plots were made using the back-transformed means. Post hoc pairwise comparisons were done using Tukey's honestly significant difference (HSD) test. Significant pairwise comparisons are denoted by letters and asterisks (***$p < 0.0001$). On each box, the central mark indicates the median, and the bottom and top edges of the box indicate the 25th and 75th percentiles, respectively. There was no significant difference in aboveground biomass between *H. altissima* and *C. nlemfuensis*. The whiskers are the two lines extending from the box. One whisker goes from the minimum value to the lower quartile (the start of the box), and the other extends from the upper quartile (the end of the box) to the maximum value. Dots, where present, represent outliers that are greater than 1.5 times the interquartile range. That is, the whisker reaches the value that is the furthest from the centre while equal to or less than 1.5 times the interquartile range from the lower or upper 25th and 75th percentiles (the height of the box). This statement applies to all boxplots.

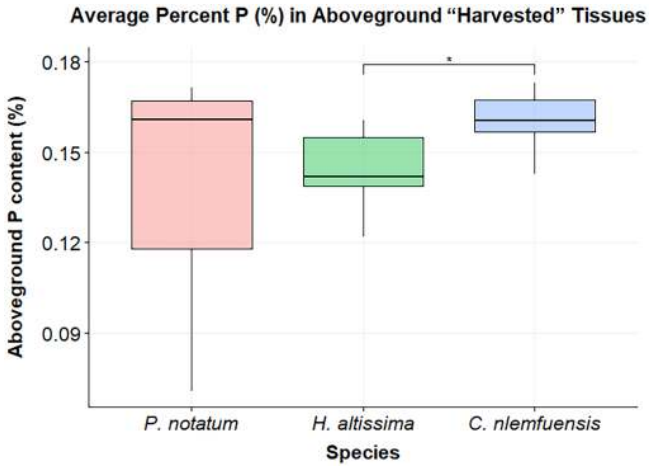


FIGURE 3 P content in aboveground "harvested" tissues representative of what may be collected by a land manager for hay. P content was consistent across species, although we did observe that *Cynodon nlemfuensis* had, on average, slightly higher P content than *Hemarthria altissima*. Data were not normally distributed, so a Kruskal–Wallis rank sum test was used in lieu of a one-way ANOVA. Post hoc pairwise comparison testing was done using a Dunn test, and p values were adjusted using the Bonferroni method ($p = p \times m$, where m is the total number of comparisons being made) to reduce the family-wise error rate and reduce the incidence of false positives. Significant pairwise comparisons (*$p < 0.05$) are plotted on the figure. On each box, the central mark indicates the median, and the bottom and top edges of the box indicate the 25th and 75th percentiles, respectively. The whiskers are the two lines extending from the box. One whisker goes from the minimum value to the lower quartile (the start of the box), and the other extends from the upper quartile (the end of the box) to the maximum value. Dots, where present, represent outliers that are greater than 1.5 times the interquartile range. That is, the whisker reaches the value that is the furthest from the centre while equal to or less than 1.5 times the interquartile range from the lower or upper 25th and 75th percentiles (the height of the box). This statement applies to all boxplots.

comparison (Figure 4). We found that both *C. nlemfuensis* and *H. altissima* had greater aboveground P removal potential than *P. notatum*, removing approximately three times as much P on a per-plant basis.

Pots did not vary significantly in the volume of leachate lost beneath them, and there was no significant difference in leachate volume among species (Appendix S1: Figure S4). Leachate water samples were tested for P content biweekly for the duration of the experiment. On average, water leached from pots containing *C. nlemfuensis* had lower overall P concentration than leachate beneath either *H. altissima* or *P. notatum* (Figure 5). As leachate volume did not vary among species (Appendix S1: Figure S4), pots containing *C. nlemfuensis* ultimately leached the least over the course of the experiment, leaching less total P than either *P. notatum* or *H. altissima* (Figure 6). Interestingly, when comparing the performance of planted pots against empty pots, we observed that pots containing *P. notatum* plants lost more P in leachate than control "empty" pots in which there was no plant-mediated influence (Figure 6). Though there was no difference in leachate volume loss between control and planted pots, we did note a nearly significant increase in leachate volume when comparing *P. notatum* to empty control pots ($p = 0.083$, Wilcoxon rank-sum test, data not shown).

Harvest (H) did not relate to the amount of P lost in leachate (adjusted $R^2 = 0.095$, $p > 0.05$) (Figures 4 and 6). Similarly, neither per-tissue P content nor aboveground

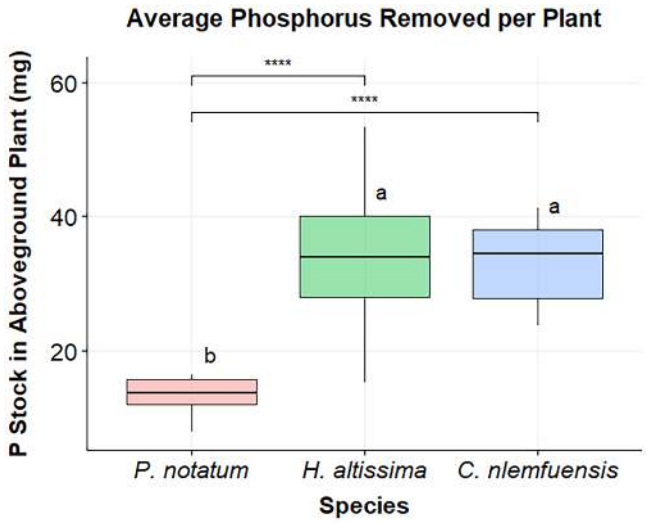


FIGURE 4 We combined the per-unit tissue P concentration data and the aboveground biomass data to estimate how much P might be removed on a per-plant basis during a vegetation harvest attempt. We used aboveground biomass and concentration data, as belowground plant material would not be collected or used when making hay. Harvest (*H*) data were normally distributed, so we checked for the influence of species identity using a one-way ANOVA and a post hoc Tukey's pairwise comparison. Total aboveground P stock varied across species, with *Paspalum notatum* removing considerably less P in aboveground biomass than either *Hemarthria altissima* or *Cynodon nlemfuensis*. Significant pairwise comparisons are denoted by letters and asterisks (****$p < 0.00001$) are plotted on the figure. On each box, the central mark indicates the median, and the bottom and top edges of the box indicate the 25th and 75th percentiles, respectively. There was no significant difference in total P harvest removed in harvested biomass between *H. altissima* and *C. nlemfuensis*. The whiskers are the two lines extending from the box. One whisker goes from the minimum value to the lower quartile (the start of the box), and the other extends from the upper quartile (the end of the box) to the maximum value. Dots, where present, represent outliers that are greater than 1.5 times the interquartile range. That is, the whisker reaches the value that is the furthest from the centre while equal to or less than 1.5 times the interquartile range from the lower or upper 25th and 75th percentiles (the height of the box). This statement applies to all boxplots.

biomass could be used to estimate leachate losses. HLE was higher in *C. nlemfuensis* than in either other plant (*C. nlemfuensis-H. altissima*, $p_{adj} < 0.001$; *C. nlemfuensis-P. notatum*, $p_{adj} < 0.00001$) (Figure 7). In both *H. altissima* and *C. nlemfuensis* individuals, leachate efficiency was higher when aboveground biomass was greater ($R^2 = 0.67$, $p < 0.01$; $R^2 = 0.58$, $p < 0.01$, respectively) (Appendix S1: Figure S2). However, there was no relationship between leachate efficiency and aboveground biomass in *P. notatum*.

To investigate our original hypothesis—that the large root structures associated with *P. notatum* may mitigate P leachate losses by improving soil water relations—we tested to see whether belowground biomass was related to leachate P. Overall, there was a weak but significant negative relationship between belowground biomass and leached P (adjusted $R^2 = 0.139$, $p = 0.03$) (Appendix S1: Figure S3). However, this was not obvious when examining intra-species interindividual variation.

DISCUSSION

This project used a mesocosm design to evaluate the potential of three grass species to remediate P leachate losses from perennially flooded pasture soils. We used species used in a previous vegetation harvest strip project (*P. notatum*, *H. altissima*, and *C. nlemfuensis*). Aboveground P removal was lowest in *P. notatum* (Figure 4), which we attributed to poor growth performance and reduced aboveground biomass expression (Figure 2). In general, aboveground biomass had a strong control over the projected per-plant P removal. There was little variation in plant P concentration among species, and although *C. nlemfuensis* did have slightly higher per-tissue P concentration than *H. altissima* (Figure 3), these differences did not have a large impact on projected removal (Figure 4). In terms of projected removal, both *C. nlemfuensis* and *H. altissima* removed an average of 33 mg of P on a per-plant basis, whereas *P. notatum* only removed an average of 13 mg (Appendix S1: Table S1). Importantly, despite soils being low in P (~100–140 mg/kg TP), the leachate collected beneath our mesocosms ranged from as low as 0.008 to as high as 0.975 mg/L. On average, leachate water was between 0.11 and 0.2 mg/L, well above federal thresholds (~0.08 mg/L; Khare et al., 2021) for P pollution even in the case of the best candidate.

As *P. notatum* is considered to improve soil–water relationships and is frequently implemented for erosion control, we anticipated that it would improve the retention of leachate water in surface soils and ultimately reduce P loads. Contrary to our expectations, P losses were greatest beneath *P. notatum* (Figure 6). In fact, control pots with no plants lost less P than pots containing *P. notatum* plants (Figure 6). This means that the presence of a *P. notatum* plant increased the loss of P from soils. While we cannot speak to the mechanism by which *P. notatum* increased the loss of P, there was no difference in leachate volume among pots, suggesting that the presence of a single plant did little to affect soil–water relationships from a purely hydrological standpoint. Instead, any variation in p loss is necessarily attributed to changes in the P concentration of leachate water or the contribution of mineral or organic P pools to the soluble P

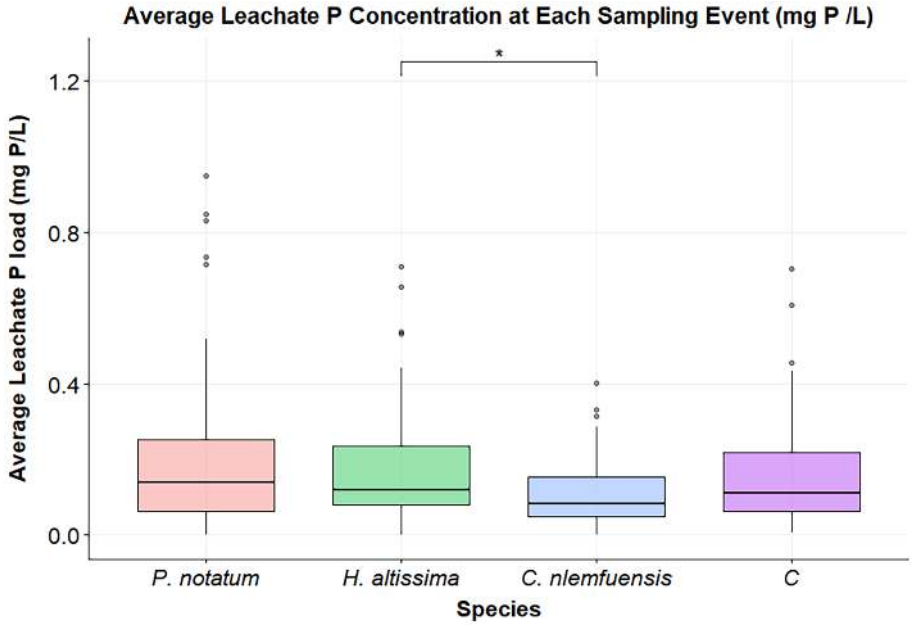


FIGURE 5 P content of leachate water was measured biweekly using a persulfate digest. Leachate concentration data were log-transformed to meet a normal distribution. A one-way ANOVA and a post hoc Tukey's pairwise comparison were used to examine the influence of species identity on P content in leachate. The average P content of leachate was lower in *Cynodon nlemfuensis* than in either of the other two plants. On each box, the central mark indicates the median, and the bottom and top edges of the box indicate the 25th and 75th percentiles, respectively. Significant pairwise comparisons are denoted by letters and asterisks (*$p < 0.01$; ****$p < 0.00001$). The whiskers are the two lines extending from the box. One whisker goes from the minimum value to the lower quartile (the start of the box), and the other extends from the upper quartile (the end of the box) to the maximum value. Dots, where present, represent outliers that are greater than 1.5 times the interquartile range. That is, the whisker reaches the value that is the furthest from the centre while equal to or less than 1.5 times the interquartile range from the lower or upper 25th and 75th percentiles (the height of the box). This statement applies to all boxplots.

pool. Accordingly, we found that leachate concentration was significantly different between species and leachate from beneath *P. notatum* was, on average, higher in P content than leachate from beneath *C. nlemfuensis* (Figure 5). Similarly, HLE was much lower for *P. notatum* than for either of the other species, and we estimated that *P. notatum* can remove, on average, approximately 5 mg of P each aboveground harvest for every mg leached from surface soils (Figure 7). Growing *H. altissima* and *C. nlemfuensis*, on the other hand, may yield between 14 and 17 mg of P in aboveground tissue for each milligram of loss (Figure 7; Appendix S1: Table S1).

As the P removed by *H. altissima* and *C. nlemfuensis* (~33.6 mg of P) aboveground biomass was approximately 2.5 times that of what was removed by *P. notatum* (13.4 mg of P), we anticipated that both *H. altissima* and *C. nlemfuensis* might each demonstrate commensurately improved leachate rates relative to *P. notatum*, but this was not necessarily the case. *C. nlemfuensis* did leach less P than *P. notatum* in leachate water, but *H. altissima* did not (Figure 4). This may in part be due to the wide variability of *H. altissima* individuals that were more widely variable in both aboveground harvest and loss than either *P. notatum* or *C. nlemfuensis* (Appendix S1: Table S1). HLE was higher overall in *H. altissima* than in *P. notatum*, but this was mainly due to improved harvest (Figure 4). In general, harvest (the amount of P removed in the whole plant aboveground biomass) could not be used to predict leachate loss, reinforcing that the total P removed in a harvested plant may not necessarily predict leachate rates. This potential mismatch (that P losses may be independent of P removal) merits further exploration. Contemporary explorations of these dynamics in field found that increasing the biomass production of *P. notatum* fields, the amount of P lost to groundwater could be reduced. Newman, Agyin-Birikorang, Adjei, Scholberg, Silveira, Vendramini, Rechcigl, et al. (2009) observed that *P. notatum* fields receiving nitrogen fertilization had increased aboveground P removal and correspondingly lower P concentrations in groundwater wells. Our results suggest the opposite, emphasizing that estimations of plant phytoremediation quality may be limited if we only consider the removal of P in aboveground tissue as a proxy for leachate.

When considering what other plant traits may influence leachate, we observed that *P. notatum* plants had

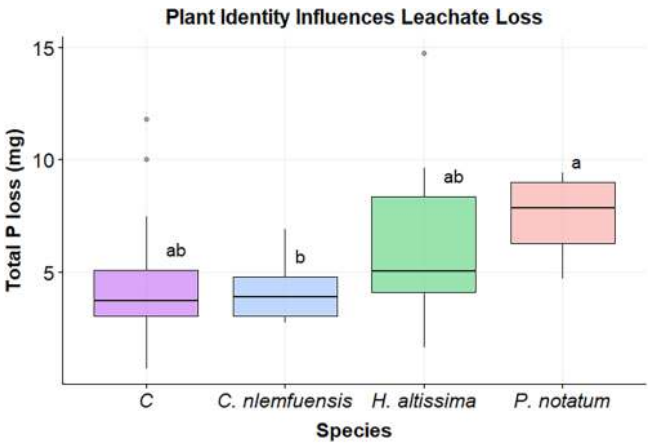


FIGURE 6 Total P loss in leachate was the summation of each biweekly loss estimate. At the end of the experiment, pots containing *Cynodon nlemfuensis* had leached the least, despite losing an equivalent volume of leachate water. Leachate data were not normally distributed, so they were transformed using a square root transformation to meet the necessary assumptions for ANOVA and Tukey's pairwise post hoc analysis. On each box, the central mark indicates the median, and the bottom and top edges of the box indicate the 25th and 75th percentiles, respectively. Significant pairwise comparisons are denoted by letters and asterisks (*$p < 0.05$; ***$p < 0.0001$). The whiskers are the two lines extending from the box. One whisker goes from the minimum value to the lower quartile (the start of the box), and the other extends from the upper quartile (the end of the box) to the maximum value. Dots, where present, represent outliers that are greater than 1.5 times the interquartile range. That is, the whisker reaches the value that is the furthest from the centre while equal to or less than 1.5 times the interquartile range from the lower or upper 25th and 75th percentiles (the height of the box). This statement applies to all boxplots.

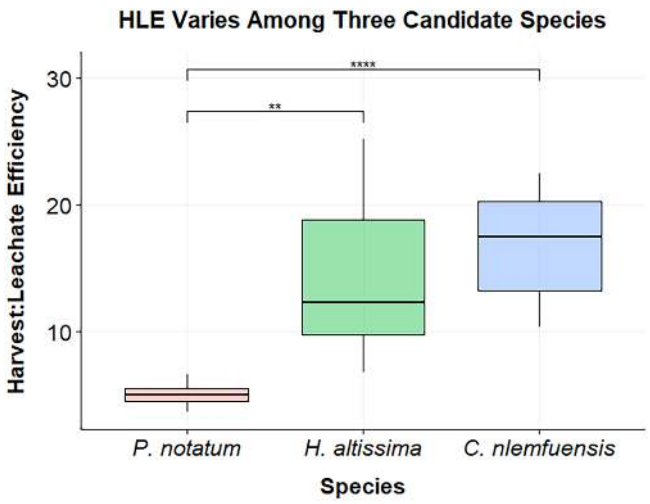


FIGURE 7 Harvest:Leachate Efficiency (HLE) was dramatically lower in *Paspalum notatum* than in the other two candidates. Data were not normally distributed and could not be transformed to meet a normal distribution, so a Kruskal–Wallis test by ranks was used. On each box, the central mark indicates the median, and the bottom and top edges of the box indicate the 25th and 75th percentiles, respectively. Significant pairwise comparisons are denoted by asterisks (**$p < 0.01$; ****$p < 0.00001$). The whiskers are the two lines extending from the box. One whisker goes from the minimum value to the lower quartile (the start of the box), and the other extends from the upper quartile (the end of the box) to the maximum value. Dots, where present, represent outliers that are greater than 1.5 times the interquartile range. That is, the whisker reaches the value that is the furthest from the centre while equal to or less than 1.5 times the interquartile range from the lower or upper 25th and 75th percentiles (the height of the box). This statement applies to all boxplots.

both higher leachate losses and larger belowground biomass expression than the other two species (Figure 6; Appendix S1: Figures S3 and S5). When all individuals were considered together as one population there was a weak but significant negative relationship between belowground biomass and total leachate losses, completely opposite to our hypothesis—that increased belowground biomass would reflect improved soil nutrient scavenging and better soil–water relations.

However, when considering variation among individuals of the same species, we did not find any relationship between belowground biomass and leachate P loss in any of the three species (Appendix S1: Figure S3). We interpret this to emphasize the influence of species-level differences influencing the solubility of soil P. It appears that it is not simply that larger roots predict increased loss, but rather that the presence of *P. notatum* plants in some way increases the fraction of P that can be lost in leachate, and that *P. notatum* plants happen to also have larger root networks (Figures 5 and 6). It is possible that the large rhizome and extensive root network beneath *P. notatum* could be creating channels for increased preferential flow through macropores created by roots, providing particulate P a more direct route into leachate with less potential for soil interception (Hooper & Vitousek, 1998; Liu et al., 2020; Smith et al., 2015). It is also possible that the increased release of root exudates from an extensive root network to solubilize soil P to increase bioavailability may indirectly increase the pool of soluble P and thereby the potential for leachate P loss (Roberts et al., 2020; Tran et al., 2020).

The influence of plants on surface soil P loss is particularly relevant when considering the Florida soil system (Reddy et al., 1996). The majority of Florida soils are Spodosols (Figure 1, bottom panel), characterized by coarse texture and intense leaching of minerals and nutrients into the subsoil (Graetz & Nair, 1995; Liao et al., 2019). In Spodosols, the surface soil has extremely poor P retention capacity and a high rate of vertical translocation of minerals (Yang et al., 2008). As a consequence, P in surface soils leaches downward, where it eventually accumulates in a black to reddish-brown spodic horizon that is

generally inaccessible to plants (Figure 1, bottom panel). Most agricultural soils in Florida were historically wetlands and remain poorly drained (Alleoni et al., 2008). When soils are perennially flooded, P released from the spodic horizon diffuses back up into the overlying surface soil, which, as mentioned, has extremely low capacity to retain P.

It was for this reason that we used a mesocosm design to study the loss of phosphorus from the surface layer, mimicking what may be lost to the eluvial layer. However, the use of a mesocosm design can add considerable uncertainty. The growth of a single plant may not reflect the actual in-field influence of a standing crop on surface soil water relationships. Furthermore, our design could not capture any possible influences of intercropping, even by weeds, as is sure to happen over the course of a normal hay-growing season. Plants share complex belowground networks with neighbors. The introduction of other neighboring plants, particularly forb species associated with influencing belowground nutrient balances, may lead to different results. The mesocosms also likely influence the soil environment, and higher soil temperatures associated with potted soils may have influenced root growth or the development of root-associated symbioses, both of which are crucial to the cycling of P. Moreover, the mesocosm itself has a unique hydrology, owing to its shape, and it is possible that the smooth interior of the perimeter allowed for some preferential flow that may not occur in the field. However, these conditions were the same for the entirety of the experimental setup, and while they may reflect a slightly different scenario than an in-field analysis, we are confident that the differences reported herein are due to plant-mediated influence.

Future work should focus on exploring this relationship at the field scale through the use of monitoring systems like lysimeters. Furthermore, belowground plant-fungal associations may also influence P solubility to improve uptake and improve P availability (Asghari et al., 2005; Asghari & Cavagnaro, 2011; Bender et al., 2015; Der Heijden & Marcel, 2010). Other work has suggested that these plant-fungal associations can vary in their strength and influence on leachate P, meaning they may be responsible for both increased loss beneath *P. notatum* and decreased loss beneath *C. nlemfuensis* (Köhl & van der Heijden, 2016; Verbruggen et al., 2012). We did not explore these plant-fungal interactions herein, but it is likely that they are important in highly disturbed and historically fertilized grazing lands given the interaction between nutrient availability and the need for these symbioses. It is our suggestion that future research include the collection of in-field samples of *P. notatum* to investigate if its associated microbiome may play a role in increasing the solubility of P.

CONCLUSION

Given our results, we suggest that *C. nlemfuensis* grown over a three-month period can be one strategy to reduce leachate P from historically fertilized ranchlands. It has the greatest HLE of the three candidates concerned, and has the unique property of reducing loss of P in leachate from the surface soil relative to the other two candidates. *P. notatum*, the predominant forage in Florida, was observed to increase the loss of P in leachate relative to both empty pots and pots growing other reference plants. The unique nature of the Florida Spodosol system places a particular emphasis on the importance of P loss from surface soils. In these perennially flooded systems, even a small fractional increase in P loss can be disastrous for the highly oligotrophic neighboring environments. If the conservation of downstream environments is the priority, this issue must be considered.

We did observe that in both *H. altissima* and *C. nlemfuensis* individuals, leachate efficiency was higher when aboveground biomass was greater. In general, aboveground biomass had the strongest control over per-plant P harvest. This suggests that efforts designed to increase aboveground biomass (like nitrogen fertilization) may further improve HLE and reduce loss, but this question remains unexplored in field.

Our results also suggest that current biophysical models for predicting nutrient losses may need to consider species-specific influences, instead of broad plant functional types. We posit that these conventional models may fail to accurately predict leachate loss beneath plants broadly used across subtropical grazing lands. Given the differences in leachate we observed in this study, this could result in underprediction of legacy P loss. However, given the challenges associated with a mesocosm study, these results should be replicated in the field to further understand the variable influences of planted cover on leachate P loss.

AUTHOR CONTRIBUTIONS

Elizabeth H. Boughton, Jiangxiao Qiu, and Jed P. Sparks designed the study and obtained funding. Amartya Saha, Haoyu Li, and Elizabeth H. Boughton conducted the study and lab processing in the field. Daniel F. Petticord analyzed the data, processed the results, and led the writing of the manuscript. All authors contributed to the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Petticord, 2024) are available from Zenodo: https://doi.org/10.5281/zenodo.12587023.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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