

Influence of Vegetation Type and Hydrology on Short-Term Nutrient Retention in Wetland Mesocosms

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Abstract

Wetland restoration is an increasingly used nature-based solution for nutrient mitigation in agricultural watersheds, often centered on the reestablishment of wetland hydrology and vegetation to restore pre-agricultural conditions. Understanding how each restoration component contributes to short-term nutrient retention is key to optimizing plans to meet multiple goals such as improving water quality and habitat. We used experimental mesocosms to quantify the nutrient retention capabilities of relevant vegetation types (unvegetated, emergent vegetation (EV) [*Leersia oryzoides*], and mixed tree plantings (TRP) [*Betula nigra* and *Taxodium distichum*]) and flood history (3-day vs. 3-week inundation cycles) often observed in agricultural floodplain wetlands in west Tennessee, USA. All treatments retained > 90% of NO_3^- and PO_4^{3-} after five days. Nitrate retention rates in EV were 38% and 32% higher compared to unvegetated or TRP, respectively. Phosphate retention was similar among treatments at 24 h following inundation, exceeding 75% reduction, which suggests sediment sorption was a dominant removal pathway. Nitrogen gas (N_2) production was similar across all treatments, averaging approximately $5.5 \text{ mg m}^{-2} \text{ h}^{-1}$, and nitrous oxide (N_2O) production was minimal (max = $0.20 \text{ mg m}^{-2} \text{ h}^{-1}$). Flood history had a minimal influence on nutrient retention and N_2O production and did not affect N_2 production. Although all treatments had high five-day removal, differences in early NO_3^- retention rates show vegetation type can be important in floodwater nitrogen retention for short-duration floods, or floods with shorter water residence time in the floodplain.

Introduction

In North America, intense agriculture within the Mississippi River Basin has caused substantial nutrient pollution in downstream water bodies. Floodplain wetlands along the Lower Mississippi River (LMR) tributary rivers and streams can mitigate some of the eutrophication caused by extensive fertilizer use, (Mitsch et al. 2005; Gordon et al. 2020) but significant LMR wetland loss over the past 200 years has likely significantly reduced their role in mitigating nutrient pollution. Wetland restorations are underway throughout the LMR, led by the US Department of Agriculture – Natural Resources Conservation Service's Agricultural Conservation Easement Program that restores former wetlands through vegetation and hydrology enhancements. Although improving water quality by filtering sediment and chemicals is often a restoration goal, the direct effects of specific restoration practices on nutrient retention potential are often uncertain (Faulkner et al. 2011). This project tested the individual effects of dominant vegetation types and varying inundation history in the LMR basin on nitrogen (N) and phosphorus (P) retention and denitrification potential.

Wetland restoration practices in this region often include planting tree saplings to redevelop bottomland hardwood ecosystems, adding shallow water areas that fill with emergent vegetation, and removing levees to improve hydrologic connectivity with streams (Hunter and Faulkner 2001; Mitsch and Gosselink 2015). The presence of trees and emergent vegetation can improve N and P retention during flooding through plant and soil microbe assimilation, increased water residence time promoting deposition of P-laden sediment, and alterations to the soil redox environment to support denitrification (Olde Venterink et al. 2006; Mitsch and Gosselink 2015; Brown et al. 2025). However, effects of these restorations on nutrient

retention during flooding are often unquantified, as it is difficult to isolate the retention by specific vegetation in situ.

Hydrologic restorations generally aim to reconnect isolated wetlands and rivers with their floodplain to trap and hold floodwater. Yet most of what is known about hydrology and nutrient retention reflects water residence time during the measurement period and less is known about how restoring a more natural long-term inundation regime shapes retention afterward. Increasing residence time generally improves N retention through greater denitrification potential and plant and microbial assimilation (Spieles and Mitsch 1999; Tong et al. 2019). Prolonged inundation can reduce P retention via the reductive dissolution of P-metal complexes under anoxic conditions (Reddy et al. 1999; Gu et al. 2018; Doyle et al. 2025), but it can also prevent P release after drawdown and reflooding by maintaining iron oxyhydroxides in their amorphous state, which sorbs more P than the crystalline forms that develop during drying (Baldwin 1996; Qiu and McComb 2002). Wetting and drying frequency matters as well. Rapid cycling can support N retention by creating a soil redox gradient that drives coupled nitrification-denitrification (Baldwin and Mitchell 2000), but frequent cycling can decrease P retention, since reflooding releases organically- and inorganically-bound P as osmotically shocked microbes lyse and rising anoxia resuspends colloidal-bound P (Schönbrunner et al. 2012; Gu et al. 2018).

This study used experimental mesocosms to determine whether NO_3^- and PO_4^{3-} retention and denitrification varied (1) among two wetland restoration vegetation types and an unvegetated control and (2) between two flood history regimes. Few studies have directly assessed how young tree plantings influence N and P dynamics or compared retention potential between these vegetation groups, and mesocosms are commonly used to isolate vegetation effects on N and P retention (Moore and Kröger 2011; Taylor et al. 2020; Jiang and Mitsch 2020). Emergent vegetation (EV) was represented by *Leersia oryzoides* and tree plantings (TRP) by *Betula nigra* and *Taxodium distichum* (approximately two-year old saplings), and inundation regimes consisted of long flood/shorter dry and short flood/longer dry cycles.

We expected vegetated mesocosms to enhance nutrient processing through two distinct pathways. The first is direct biotic assimilation. Plant uptake removes NO_3^- and PO_4^{3-} from the water column, and because plant P assimilation can be a significant wetland P sink (Gacia et al. 2019), we hypothesized that NO_3^- and PO_4^{3-} retention would be greatest where plant biomass was highest. The second is a carbon-supply pathway that operates independently of assimilation. Emergent vegetation like *L. oryzoides* supplies a stable source of organic carbon through leaf and root senescence, sustaining denitrifying microbial communities near the soil-water interface (Reddy et al. 1989; Kröger et al. 2007; Taylor et al. 2015). We therefore hypothesized that this senescence-derived carbon, rather than assimilation, would drive N_2 and N_2O production (a measure of incomplete denitrification). Because planted saplings likely have limited root development and lower biomass at that interface, reducing both direct assimilation and rhizosphere-mediated microbial processes, we expected both retention and denitrification to be greatest in vegetated mesocosms, with EV outperforming TRP (Tyler et al. 2012; Taylor et al. 2015, 2020). Unvegetated (UV) controls were expected to show the lowest retention and production rates, given the comparative absence of assimilatory pathways and rhizosphere-associated coupled nitrification-denitrification.

We further hypothesized that longer flood cycles would retain more NO_3^- than shorter cycles, since prolonged flooding establishes lower soil redox at the experiment's onset and enhances denitrification. The shorter cycle, with repeated drying and rewetting, was expected to reduce PO_4^{3-} retention compared to the longer flood cycle through processes such as crystallization of amorphous Fe hydroxides and P release from microbial mortality (Baldwin and Mitchell 2000; Qiu and McComb 2002; Chen et al. 2021). Finally, prolonged flooding was expected to yield higher N_2 and lower N_2O production than short-duration flooding, owing to its lower initial redox state.

Methods

Mesocosm Assembly

Thirty-six outdoor mesocosms were assembled at Tennessee Tech University's Shipley Farm following protocols established by Tyler et al. (2012) and Taylor et al. (2015). Each mesocosm consisted of a 379-L plastic tub (122 × 61 × 61 cm) fitted with plugged 0.64-cm surface and 3.81-cm subsurface drainage ports. Tubs were filled with approximately 30 cm of silica sand overlaid with 15 cm of wetland soil. Mesocosm soil (Falaya Silt Loam, collected < 0.6 m deep) was obtained from a stream restoration site adjacent to the Middle Fork Forked Deer River in west Tennessee, USA. Mesocosms were arranged in four rows of nine, with one supply tank per row. Approximately 0.9 kg of soil from a restored wetland in western Tennessee was added to each mesocosm to inoculate mesocosms with wetland microbial communities and accelerate their establishment. During simulated flooding, approximately 10 cm of water depth was maintained.

Treatment Assignment

One of six treatments was assigned to each mesocosm in a two-factor design (vegetation type × hydroperiod) using a random number generator. Vegetation treatments had three levels: UV, EV, and TRP. Species were selected to match those commonly planted during wetland restorations and by tolerance to prolonged root saturation. *Leersia oryzoides* was collected from the riparian area of Little Creek in Cookeville, Tennessee, USA (36.196383, -85.529292). Tree planting treatments contained two saplings of each species (four per mesocosm) purchased from a local nursery. Trees were planted equidistantly spaced, with conspecific saplings on the same side (Fig. 1). Hydrology treatments consisted of a short-duration cycle (3D: three days flooded, four days dry) and a long-duration cycle (3W: three weeks flooded, one week dry). Hydrologic treatments began once vegetation was established, approximately one month after planting (June 2022) and approximately two months prior to the start of the experiment.

Nutrient Enrichment and Sampling

From July 15 – September 9, 2022, mesocosms were subjected to hydrology treatments, ending with all mesocosms flooded. On September 9, mesocosms were drained overnight and reflooded on September 10 with dechlorinated municipal water (Cookeville, Tennessee, USA) enriched with sodium nitrate (NaNO_3) and

monopotassium phosphate (KH_2PO_4) to target concentrations of $10 \text{ mg L}^{-1} \text{ NO}_3^{-}\text{-N}$ and $1 \text{ mg L}^{-1} \text{ PO}_4^{3-}\text{-P}$. Target concentrations were chosen to initially saturate nutrient uptake and allow direct comparisons across treatments. Source water was stored in four 606-L dosing tanks (one per row) and manually mixed for five minutes prior to dosing. This process was repeated twice to fill all mesocosms. Paired water samples were collected from each tank at each filling to verify starting concentrations. No new water was added after initial flooding, and no precipitation occurred during the experiment.

Nutrient concentrations in each mesocosm were measured on day zero, within one hour after filling, and then every day for five days. Representative water samples were obtained by collecting from the left, middle, and right sides of each mesocosm and combining the three subsamples. Ten mL of water was collected from each section (30 mL total) using a 60-mL syringe fitted with a $0.45 \mu\text{m}$ membrane filter. Syringes were then pulled to create 10 mL of headspace, inverted 10 times to homogenize, and ejected into 20-mL scintillation vials. Samples were immediately placed on ice and frozen until analysis.

Nitrate, nitrite (NO_2^{-}), and PO_4^{3-} concentrations were determined via colorimetric analysis on a discrete analyzer (Seal AQ400). Nitrate and NO_2^{-} were measured using the sulfanilamide reaction method (EPA Method 353.2) with and without cadmium column reduction; NO_2^{-} was subtracted from $\text{NO}_3^{-} + \text{NO}_2^{-}$ values to yield $\text{NO}_3^{-}\text{-N}$. Phosphate was measured as soluble reactive phosphorus using the ascorbic acid method (EPA Method 365.1). Samples below the minimum detection limit were reported as half the MDL (Helsel 1990). Dissolved nutrient concentrations were converted to total surface water nutrient mass (mg mesocosm^{-1}) to correct for potential differences in water depth and volume across mesocosms (Eq. 1). Mesocosm surface was standardized to 0.74 m^2 . Mass was then converted from mg mesocosm^{-1} to $\text{mg m}^{-2} \text{ h}^{-1}$ by dividing nutrient mass by mesocosm soil surface area and multiplying by 24 (Eq. 2).

Equation 1:

$$\text{Nutrient Mass } (\text{mg meso.}^{-1}) = \text{Water Volume (L)} * \text{Nutrient Concentration } (\text{mg L}^{-1})$$

Equation 2:

$$\text{Nutrient mass } (\text{mg m}^{-2} \text{ h}^{-1}) = \frac{\text{Nutrient mass } (\text{mg meso.}^{-1})}{\text{Meso. Soil Surface Area } (\text{m}^2) * 24 \text{ (h)}}$$

Soil Organic Matter, Algal Biomass, and Nutrient Content

After final dissolved nutrient sampling on September 14 and overnight draining, soil samples for soil surface chlorophyll-a (chl-a) (attached algae), ash-free dry mass (AFDM, organic matter), total carbon (TC), total nitrogen (TN), and extractable phosphorus (P) were collected the following morning. For chl-a and AFDM sampling, mesocosm soil surfaces were partitioned into 25 grids (5×5 transects; Supplemental Fig. 1), and one grid per transect was randomly selected for sampling. Soil was then collected by pushing a

50-mL centrifuge tube (2.7 cm diameter) 1 cm deep into the soil (5.7 cm³ of soil per mesocosm). Soil nutrient samples (approximately 8 cm³) were collected from the top 10 cm of soil using a 2.54-cm hand auger in each of the three mesocosm zones where water samples were collected.

Soil AFDM was determined via the combustion method (Steinman and Lamberti 1996) and converted to percent organic matter. Chlorophyll-a subsamples were aggregated and analyzed using the Welschmeyer non-acidification method (Welschmeyer 1994) on a fluorometer (Turner Designs Trilogy, scaled to mg m⁻²). Soil nutrient subsamples were dried at 60°C for 72 h, homogenized, passed through a 2-mm sieve, and stored in 20-mL scintillation vials. Soil TN and TC were determined by catalytic combustion. Extractable P was determined via Mehlich-3 extraction followed by colorimetric analysis. All soil nutrient analyses were performed by Kansas State University Soil Testing Lab.

N₂ and N₂O Production

Dissolved N₂, oxygen (O₂) (representing soil oxygen demand), and N₂O flux were measured by incubating intact soil cores with N- and P-enriched water using a continuous flow-through system (Taylor et al. 2015; Brown et al. 2025). Following mesocosm draining and soil and algae sampling, one soil core (7.62 × 30.48 cm acrylic tubes driven ~ 15 cm deep with ~ 15 cm headspace) was collected from each mesocosm for UV and EV. For TRP, two cores were collected: one adjacent to each tree species to account for potential species-related differences in N₂ and N₂O production rates. Cores were then transported to the lab for incubation.

At the lab, cores were fitted with acrylic lids containing inflow and outflow tubing and incubated at 24°C in complete darkness to inhibit photosynthesis. Dechlorinated tap water enriched to 10 mg L⁻¹ NO₃⁻-N and 1 mg L⁻¹ PO₄³⁻-P was pumped through each core at 2 mL min⁻¹ (~ 6-h residence time). Triplicate water samples were collected from each core outflow at 12, 24, and 48 h into 12-mL exetainers, preserved with NaOH and ZnCl₂, and stored under water at 4°C until analysis. Three inflow lines not connected to a core were sampled to determine inflow nutrient concentrations.

Dissolved gas concentrations were measured using a Membrane-Inlet Mass Spectrometer (MIMS) fitted with a Secondary Electron Multiplier detector, with the argon ratio method applied to account for concentration changes due to physical processes (Speir et al. 2023). Concentrations were converted to areal flux rates (mg m⁻² h⁻¹) (Supplemental Equation S1), where positive values indicate net production in the water column and negative values indicate net removal. Triplicate flux rates per core and time point were averaged after excluding samples that deviated more than 90% from the group mean. A paired Wilcoxon test detected no difference in flux rates between cores collected near *T. distichum* and *B. nigra* in tree planting treatments, so values were averaged across both species to yield one value per mesocosm.

Statistical Analysis

Large differences in NO_3^- and PO_4^{3-} retention patterns required different statistical approaches for each nutrient. Nitrate content in the EV/3D flooded treatments was nearly zero by day three. To prevent fitting a linear slope to a logarithmic decay, we restricted NO_3^- analysis to day zero through three, when NO_3^- uptake rates were linear. Phosphate mass dropped rapidly in all treatments (> 75% on average) within 24 h of dosing, then slowed into a logarithmic decay consistent with concentration-dependent uptake kinetics. Because the rate of decline differed substantially between the first 24 h and the following days, we split the PO_4^{3-} data into two analyses. The first analysis used data from the initial 24 h only. Uptake rates were calculated by subtracting the day zero PO_4^{3-} mass from the day one mass. These raw rates were analyzed using a two-way ANOVA. The second analysis assessed trends in PO_4^{3-} flux using an ANCOVA on days two through five data, where the slower decline was approximately linear.

Nitrate, N_2 , and N_2O were modeled with generalized linear mixed models (GLMMs; Table 1). A GLMM with a random effect for mesocosm was originally used for PO_4^{3-} models but was dropped as its inclusion did not improve model fits. All models were validated visually with Q-Q and residual plots and fit in R (R Core Team 2022) using the nlme package (Pinheiro et al. 2022). Covariates were selected for their relevance to each response variable, informed by the literature and preliminary data exploration. Soil TN and extractable P were considered for the NO_3^- , N_2 , and N_2O models but omitted for multicollinearity with soil TC. Soil TC was retained for its role as an electron donor for denitrification and its influence on soil redox potential (Dodla et al. 2008; Reddy et al. 2022). Day one PO_4^{3-} mass was included in the PO_4^{3-} days two through five model to account for differences in starting mass among treatments.

Table 1

Model structure for each nutrient response. V = vegetation, H = hydrology, T = time (h); AR(1) = first-order autoregressive correlation structure.

Response	Model	Main effects	Interactions	Random effect
NO_3^-	GLMM	V, H, soil TC, chl-a, AFDM	$V \times H$, $V \times T$, $H \times T$, $V \times H \times T$	Mesocosm ID, AR(1) correlation structure
PO_4^{3-} (0–24 h)	ANOVA	V, H	$V \times H$	None
PO_4^{3-} (days 2–5)	ANCOVA	V, H, hour, soil TC, chl-a, AFDM, day 1 mass	$V \times H$, $V \times T$, $H \times T$, $V \times H \times T$	None
N_2	GLMM	V, H, O_2 , AFDM, chl-a, soil TC	$V \times H$, $V \times T$, $H \times T$, $\text{O}_2 \times T$, $V \times H \times T$	Mesocosm ID
N_2O	GLMM	V, H, O_2 , AFDM, chl-a, soil TC	$V \times H$, $V \times T$, $H \times T$, $\text{O}_2 \times T$, $V \times H \times T$	Mesocosm ID

Overall model significance was determined using an F-test (for NO_3^- , N_2 , and N_2O) or likelihood ratio test (for PO_4^{3-}) to compare against an intercept-only model ($\alpha = 0.05$). F-tests or chi-squared tests with type III sums of squares were then applied to the final model to test for differences in flux rates among treatments,

whether vegetation and hydrology interacted, and which covariates influenced mean NO_3^- and PO_4^{3-} flux and N_2 and N_2O production rates. Type III sums of squares were preferred due to an unbalanced sampling design for the PO_4^{3-} data due to a mesocosm leak resulting in the loss of one day five sample. Estimated marginal means and 95% confidence intervals for each factor were then calculated using the *emmeans* package (Lenth and Piaskowski 2017). Post-hoc pairwise comparisons were made using Tukey's HSD test.

Results

All treatments reduced dissolved NO_3^- and PO_4^{3-} content to near-zero after five days of inundation, though no treatment was best at reducing both nutrients. Phosphate mass was reduced faster than NO_3^- across all treatments, with substantial PO_4^{3-} reductions occurring during the first 24 hours following dosing. Unvegetated treatments were most efficient at reducing PO_4^{3-} content while EV was least efficient. In contrast, EV reduced NO_3^- most rapidly, lowering concentrations by more than 90% within three days for the EV/3D treatment. Vegetation type appeared to be the dominant factor influencing retention rates as hydrology was unrelated to retention for NO_3^- and PO_4^{3-} .

For the soil core incubations, N_2 and N_2O production rates were generally consistent across treatments. N_2 production rates were positive (i.e., net N_2 production) at every sampling timepoint, except for a single TRP/3D core in round one. Although N_2 production rates occasionally declined between rounds, these decreases were typically small. Nitrous oxide production rates were more variable, with all treatments having at least one core that both increased and decreased across sampling events. Neither vegetation nor hydrology treatments, alone or in combination, appeared to have a substantial effect on N_2 or N_2O production rates. Nitrous oxide flux ranged from 0.03 to 0.20 $\text{mg m}^{-2} \text{h}^{-1}$, suggesting that denitrification generally proceeded to completion with limited N_2O emissions.

Nitrate

All treatments steadily reduced NO_3^- content each day, reaching a > 90% reduction in initial NO_3^- mass by day five (Fig. 2). On average, EV treatments reached NO_3^- depletion, defined as a $\geq 99\%$ reduction initial nutrient mass, much faster than the other vegetation and hydrology combinations. By day two, EV/3D had reduced 86% of its initial NO_3^- mass, and both EV treatments achieved > 90% reduction by day three. Mean NO_3^- mass in all other treatments did not reach NO_3^- depletion until day four, with TRP/3W and UV/3W not reaching depletion until day five.

Type III tests of fixed effects identified several key associations between covariates and NO_3^- flux. An interaction between vegetation treatment and day was weakly associated with NO_3^- retention, indicating that retention rates varied among vegetation treatments (Supplemental Tables). There was no relationship between NO_3^- retention and hydrology or the three-way interaction among vegetation, hydrology, and day. Soil TC, chl-*a*, and AFDM were also unrelated to retention rates.

Analysis of marginal trends found that all combinations of vegetation and hydrologic treatment reduced NO_3^- over time, though statistically significant differences were only detected among vegetation treatments. Nitrate reductions were steepest (i.e., fastest uptake) for EV, followed by TRP and UV (Table 2, Fig. 3). Pairwise slope comparisons indicated that EV removed NO_3^- 38% faster than UV ($p = 0.003$) and 32% faster than TRP ($p = 0.010$). There was no difference between TRP and UV treatment rates.

Table 2
Estimated marginal slopes and 95% confidence intervals for NO₃⁻, PO₄³⁻ (days two – five), N₂, and N₂O, and raw mean 24-h PO₄³⁻ retention rates with 95% confidence intervals calculated using the t-distribution.

Treatment ¹	Estimate	Standard Error	95% Confidence Interval
<i>NO₃⁻ Retention Rates (mg m⁻² h⁻¹)</i>			
EV	-20.0	1.13	[-17.7, -22.2]
UV	-14.5	1.19	[-12.1, -16.8]
TRP	-15.1	1.13	[-12.9, -17.4]
3D	-17.7	0.95	[-15.8, -19.6]
3W	-15.4	0.92	[-13.5, -17.2]
<i>24-h PO₄³⁻ Arithmetic Mean Retention Rates (mg m⁻² h⁻¹)</i>			
EV	-5.4	0.34	[-6.1, -4.6]
UV	-6.6	0.25	[-7.1, -6.0]
TRP	-6.1	0.26	[-6.7, -5.5]
3D	-6.2	0.23	[-6.7, -5.7]
3W	-5.8	0.27	[-6.4, -5.2]
<i>Days two – five PO₄³⁻ Retention Rates (mg m⁻² h⁻¹)</i>			
EV/3D	-0.3	-0.8	[-0.4, -0.1]
EV/3W	-0.5	0.08	[-0.7, -0.4]
UV/3D	-0.2	0.09	[-0.3, 0.0]
UV/3W	-0.1	0.08	[-0.2, 0.1]
TRP/3D	-0.4	0.08	[-0.6, -0.2]
TRP/3W	-0.2	0.08	[-0.3, 0.0]
<i>N₂ Production Rates (mg m⁻² h⁻¹)</i>			
EV	5.8	0.50	[4.8, 6.8]
UV	5.6	0.50	[4.7, 6.6]
TRP	5.2	0.50	[4.3, 6.2]
3D	5.5	0.40	[4.8, 6.2]
3W	5.6	0.40	[4.9, 6.4]

Treatment ¹	Estimate	Standard Error	95% Confidence Interval
<i>N₂O Production Rates (mg m⁻² h⁻¹)</i>			
EV/3D	0.02	0.01	[-0.01, 0.05]
EV/3W	0.02	0.01	[-0.01, 0.04]
UV/3D	0.04	0.02	[0.01, 0.08]
UV/3W	0.01	0.01	[-0.02, 0.03]
TRP/3D	0.01	0.01	[-0.02, 0.04]
TRP/3W	0.02	0.01	[-0.01, 0.04]

¹ Treatment codes: EV = Emergent Vegetation, TrP = Tree Planting, EV = Unvegetated, 3W = 3 weeks flooded, 3D = 3 days flooded.

Phosphorus

All treatments rapidly reduced dissolved PO_4^{3-} in the overlying water, though removal rate and consistency varied by vegetation type. Unvegetated mesocosms showed the fastest initial removal and least replicate variability, while both vegetated treatments removed PO_4^{3-} more slowly with greater scatter. In EV, removal reached roughly 75 to 80% by day one but was highly variable, particularly under the 3W flood history. TRP followed a similar but more pronounced pattern, with about 70 to 75% removal by day one and a clear rise in water-column PO_4^{3-} mass at day two, most evident under the 3D condition. Across treatments, retention slowed markedly beyond 24 hours (Fig. 4) and occasionally reversed to release after day one, with some mesocosms releasing up to 31% of their initial PO_4^{3-} mass (EV/3D). These releases peaked on days two and three and were most pronounced in EV, which also showed the most variable daily PO_4^{3-} mass overall and UV the least. Beyond day three, any release was minimal (1 to 3% of initial mass), and all mesocosms held less than 4% of initial PO_4^{3-} mass by day four.

The 24 h PO_4^{3-} model was not a significantly better fit than the null ($\chi^2_{(5)} = 10.91$, $p = 0.0532$). Therefore, marginal means were not compared among treatments, and arithmetic means and confidence intervals indicated no differences among treatments. However, the PO_4^{3-} model for days two through five was significant ($\chi^2_{(14)} = 89.40$, $p < 0.001$) and identified strong associations between PO_4^{3-} retention rates and day one mass ($p = 0.018$), an interaction between vegetation and hydrology ($p = 0.007$), and a three-way interaction among vegetation, hydrology, and hour ($p = 0.018$). Marginally significant associations were detected between PO_4^{3-} retention rates and vegetation type ($p = 0.071$) and PO_4^{3-} and hour ($p = 0.069$). There was no significant main effect of hydrology treatment on retention rates.

When comparing vegetation levels by hydrology for the day two through five model, PO_4^{3-} retention rates in EV were 587% faster than UV and 187% faster than TRP in the 3W treatments ($p < 0.001$ and $= 0.012$,

respectively) (Fig. 5). There were no differences among vegetation levels for the 3D treatments. When comparing hydrology by vegetation level, retention rates were 81% faster for 3W than 3D treatments for EV ($p = 0.041$). For TRP, 3D treatments had 119% faster retention than 3W, though this difference was only marginally significant ($p = 0.059$) (Fig. 6). There were no differences between hydrology levels for UV.

N₂ Flux

All treatments produced N₂ on average at 12, 24, and 48 h incubation times, with N₂ loss only observed in one mesocosm (TRP/3D) at the 12 h incubation timepoint. Production rates in individual cores varied among treatments and across time points, ranging from -0.61 to $13.55 \text{ mg m}^{-2} \text{ h}^{-1}$ (EV/3D – 12 h and TRP/3D – 12 h, respectively). Within-core N₂ flux rates were non-monotonic across sampling events, with N₂ production rates occasionally decreasing between successive sampling events (Fig. 7). This pattern occurred most frequently in EV but was observed in all treatments. Across all treatments, any declines in N₂ flux between sampling events were generally minimal (median of all declines = $-0.21 \text{ mg m}^{-2} \text{ h}^{-1}$), except in a single core from EV/3D and one from TRP/3D, where N₂ production between 12 and 24 h declined by 1.21 and $3.44 \text{ mg m}^{-2} \text{ h}^{-1}$, respectively.

A Type III sums of squares test indicated that N₂ flux was strongly associated with dissolved O₂ flux, an interaction between dissolved O₂ flux and time, and was moderately associated with soil AFDM (Supplemental Tables). A $1 \text{ mg m}^{-2} \text{ h}^{-1}$ decrease in O₂ flux (i.e., oxygen consumption) was predicted to increase in N₂ flux by $0.18 \text{ mg m}^{-2} \text{ h}^{-1}$ on average. The effect of AFDM on N₂ flux was slightly larger, with a predicted average increase of $0.28 \text{ mg N}_2 \text{ m}^{-2} \text{ h}^{-1}$ per 1% increase in AFDM. No relationship between time and N₂ flux was detected, meaning there was no statistical evidence that N₂ rates changed across the 48-h sampling time points. Further, vegetation type, hydrology level, time, their interactions, and chl-a were unrelated to N₂ flux.

N₂O Flux

Nitrous oxide production rates in individual cores varied among treatments and across time points, ranging from -0.03 to $0.20 \text{ mg m}^{-2} \text{ h}^{-1}$ (HV/3D, 12 h and TRP/3W, 48 h, respectively). The most prominent pattern was a hydroperiod effect on N₂O magnitude. Production rates in the 3D cores were generally higher and more variable, while 3W cores were compressed near zero across all vegetation types (Fig. 8). Within the 3D hydroperiod, UV cores produced the highest initial rates and showed the steepest declines over time, whereas EV cores maintained more moderate, temporally stable fluxes. TRP cores were more variable, with one 3D core having the only negative flux at 12 h across all treatments. Beyond 12 h, flux directions became increasingly variable, with some cores shifting from decreasing N₂O production between 12 and 24 h to increasing between 24 and 48 h. Negative flux rates were observed most frequently in UV/3W and TRP/3W, though some cores produced N₂O across all sampling events. Within-treatment variability among individual cores was substantial, particularly under UV/3D and TRP/3D conditions.

A Type III sums of squares test found that N_2O flux was associated with the main effects of vegetation, hydrology, time, two-way interactions between vegetation and hydrology, vegetation and time, hydrology and time, and a three-way interaction among vegetation, hydrology and time (Supplemental Tables). The significant three-way interaction indicated that the trends in N_2O production over time for a given vegetation level depended on the corresponding hydrology level and vice versa. When comparing trends in N_2O production over time, the differences among treatments were limited, generally small and all model estimates except UV/3D overlapped zero (Table 2).

Discussion

The objective of this study was to quantify nutrient retention and denitrification rates under different vegetation and flood history regimes. We hypothesized that EV would have higher NO_3^- and PO_4^{3-} retention and N_2 and N_2O production than TRP, and rates would be greatest in the treatments that had been flooded longer prior to the experiment. Our first hypothesis was supported for NO_3^- retention, where EV strongly outperformed UV and TRP. However, our hypothesis was not supported for PO_4^{3-} , where retention rates were highest in UV treatments. Further, there were no differences in N_2 and N_2O production among treatments. Our flood history hypothesis was not supported, as hydrology treatment had no detectable effect on NO_3^- and PO_4^{3-} retention or N_2 production, and little ecologically meaningful impact on N_2O production. This lack of a hydrology effect was unexpected given the often-strong influence of flood frequency and duration on soil redox and nutrient dynamics (Baldwin and Mitchell 2000; Aldous et al. 2005; Morillas et al. 2013; Chen et al. 2021). Another unexpected finding was the speed with which EV reduced NO_3^- concentration in the water column, as well as the sharp decline in PO_4^{3-} within the first 24 h of dosing across all treatments. All vegetation-hydrology combinations reduced NO_3^- and PO_4^{3-} concentration to at or near depletion at the end of the experiment, indicating that all treatments can be effective N and P sinks during five days of inundation.

Dissolved Nutrients

Nitrate

All treatments reduced NO_3^- mass to near zero within five days of inundation, but removal was significantly faster in EV mesocosms than in TRP, regardless of hydrology. This is consistent with two prior LMR region mesocosm studies, in which *L. oryzoides* plantings achieved > 90% NO_3^- reduction within three days (Tyler et al. 2012; Taylor et al. 2015), and with evidence that EV removes water-column NO_3^- faster than vegetation-free controls in free water surface wetlands (Bastviken et al. 2009). Plant and microbial uptake are important direct and indirect N retention pathways in aquatic systems, particularly under low-flow conditions (Vymazal 2007; Taylor et al. 2015). In shallow or littoral areas, EV can support N removal by supplying labile carbon through leaf senescence, stimulating denitrification and N mineralization (Hefting et al. 2005; Korol et al. 2019).

Denitrification was likely the dominant N removal pathway across treatments, as indicated by high N_2 production ($> 5 \text{ mg m}^{-2} \text{ h}^{-1}$) and consistent with similar mesocosm studies (Tyler et al. 2012; Taylor et al. 2015). In EV, coupled nitrification-denitrification may have further enhanced removal. Roots create a redox gradient at the soil-water interface, maintaining aerobic microsites where nitrifying bacteria convert ammonium (NH_4^+) to NO_3^- that is then denitrified in adjacent anaerobic zones (Reddy et al. 1989; Eriksson and Weisner 1997). This provides a steady NO_3^- supply to denitrifiers beyond the initial dosing pulse. Plant shoots and roots also increase surface area for microbial colonization, supporting higher nitrification and denitrification rates (Eriksson and Weisner 1997, 1999; Bastviken et al. 2003). Plant assimilation likely contributed as well, though Matheson et al. (2002) found denitrification accounted for roughly 60% of dissolved NO_3^- removal in vegetated microcosms versus only 13% through assimilation. Together, denitrification and assimilation may explain why EV removed NO_3^- more efficiently than UV or TRP, which had little to no vegetation covering the soil between trees.

Phosphate

Dissolved PO_4^{3-} was rapidly removed from the water column across all vegetation and hydrology treatments, reaching nearly 100% removal by day five. Most removal occurred within the first 24 hours of dosing in all treatments, and the lack of effect of vegetation or hydrology during the first day suggests that physical processes were primarily responsible for the rapid removal of PO_4^{3-} . This is consistent with physicochemical adsorption of PO_4^{3-} onto reactive mineral surfaces, which is well established as a dominant short-term mechanism of inorganic P retention in flooded soils and sediments (Reddy et al. 1999, 2022). Though not quantified, our soil visually had high clay content. Clay can provide substantial reactive surface area in the form of iron (Fe) and aluminum (Al) oxyhydroxides and clay mineral edge sites, both of which exhibit strong affinity for dissolved PO_4^{3-} through ligand exchange reactions (Richardson 1985; Borggaard et al. 2005). Initial adsorption onto readily accessible surface sites occurs within minutes to hours, followed by a slower diffusion-limited phase as PO_4^{3-} migrates into micropores and interior binding sites over days to weeks (Zhang et al. 2012; Song et al. 2017; Reddy et al. 2022).

The fastest and most complete PO_4^{3-} removal occurred in UV mesocosms, reaching approximately 85% reduction within the first day and approaching 100% removal by day two to three under both hydrology treatments. Without vegetation, litter, or root-derived organic matter to compete for binding sites or impede diffusion, dissolved PO_4^{3-} may have had direct access to more reactive surface area of the clay-rich substrate. The tight clustering of observations in the non-vegetated treatments further supports a primarily abiotic removal mechanism, as physicochemical sorption is typically more predictable and less variable than biologically mediated pathways (Reddy et al. 1999).

Vegetated treatments had slower initial PO_4^{3-} removal and greater rebound behavior, likely reflecting several interacting processes. Root exudates and decomposing organic matter compete with PO_4^{3-} for sorption sites on Fe and Al oxyhydroxides, reducing the available reactive surface area (Borggaard et al. 2005; Zamuner et al. 2008). Root mats and litter layers can also create physical barriers that impede

diffusive transport of dissolved P to mineral surfaces. Perhaps most importantly, root-associated microbial communities rapidly consume oxygen in the rhizosphere (Fang et al. 2021; Lacroix et al. 2025), promoting the reductive dissolution of Fe(III) oxyhydroxides and the release of previously sorbed PO_4^{3-} (Moore Jr. and Reddy 1994; Reddy et al. 1999). The low variability and steady decrease in PO_4^{3-} mass in the unvegetated mesocosms is consistent with slower progression toward reducing conditions without root-mediated oxygen consumption and labile carbon inputs, allowing the Fe(III) sorbent phase to remain intact over the five-day observation period.

The absence of a hydrology effect on PO_4^{3-} retention, as well as on NO_3^- retention and N_2 production, was unexpected given the well-established influence of flood duration and frequency on nutrient dynamics (Baldwin and Mitchell 2000; Aldous et al. 2005; Bai et al. 2020). Two explanations may account for this null result. First, because mesocosms drained slowly and at variable rates, they were allowed to drain overnight prior to dosing, potentially re-oxygenating the upper soil layers and resetting any redox differences between 3D and 3W treatments. Second, studies linking flood regime to nutrient retention have often compared durations differing by months or seasons, and the temporal contrast in our experiment may have been too narrow to produce a detectable effect. If this experiment were repeated, dosing immediately following draining would help preserve treatment differences in soil redox conditions and clarify whether the absence of a hydrology effect is a methodological artifact.

The PO_4^{3-} differences among treatments in the 3W flooded group for the days two through five model likely reflect variation in day two PO_4^{3-} concentrations and the concentration-uptake relationship rather than true differences in inherent uptake efficiency. Day two and three PO_4^{3-} concentrations in UV and TRP were substantially lower than in EV, and likely had lower, concentration dependent uptake rates. A similar pattern is evident in the faster uptake rate for EV/3W compared to EV/3D, where concentrations were lower. The differences in uptake rates among vegetation levels, and hydrology treatments within EV, may be related to interactions between the rhizosphere and prolonged flooding. High soil water volume can reduce photosynthesis rates and decrease soil redox potential, limiting nutrient retention capacity (Pezeshki et al. 1989; DeLaune et al. 1998; Pierce et al. 2007), and continuous flooding has been shown to reduce growth rates and belowground biomass in *L. oryzoides* (Koontz and Pezeshki 2011; Koontz et al. 2013). These findings highlight how nutrient dynamics in EV can change with inundation history.

N_2 and N_2O Production

Denitrification was similar across all treatments, and the relatively high N_2 production rates suggest that denitrification was likely the dominant NO_3^- removal pathway in mesocosms. Nitrous oxide concentrations were low across all sampling time points (between -0.03 and $0.20 \text{ mg m}^{-2} \text{ h}^{-1}$), suggesting that denitrification mostly proceeded to completion. However, the finding that N_2 flux did not differ among vegetation treatments or across incubation timepoints was unexpected given the treatment-level differences in NO_3^- removal rates observed during the dosing experiment.

Despite the lack of treatment-level differences, N_2 production was significantly related to dissolved O_2 concentration, with decreases in O_2 associated with greater N_2 production. Dissolved O_2 decreased across incubation rounds, indicating progressive development or expansion of an anoxic zone. These results are consistent with studies demonstrating that decreases in O_2 increase denitrification rates (McKenney et al. 2001; Burgin and Groffman 2012). As source water NO_3^- concentration was maintained at 10 mg L^{-1} throughout incubations to prevent substrate limitation, the observed relationship between O_2 and N_2 flux reflects redox controls on denitrification rather than differences in NO_3^- availability.

The lack of differentiation among treatments after five days of flooding suggests the vegetation and flood history effects may not occur or may coalesce to a similar rate after prolonged (i.e., five days), constant inundation. Previous core incubations measuring N_2 flux in restored wetlands in this region show different flux rates in dry herbaceous vegetated areas, submerged vegetated, and mature bottomland forested wetlands during the first two days of flooding (Brown et al. 2025; Duwadi et al. 2026). However, because cores were collected after five days of submergence, the soil redox environment may have become homogenized across treatments, potentially obscuring differences that existed upon initial flooding. Submergence rapidly depletes soil O_2 , creating anoxic conditions that support denitrification (Rangasami et al. 2022), and because cores were collected and placed in incubation as soon as mesocosms drained, soils below the soil-water interface may have remained anoxic in all treatments. In situ incubations concurrent with initial flooding were attempted during development of the experimental setup but were unsuccessful due to persistent ebullition, which would have biased dissolved gas measurements. A comparison with field-based incubations conducted at the time of flooding would help determine whether these results reflect a true absence of treatment effects or an artifact of sampling timing.

Nitrogen gas flux was also significantly related to AFDM, though this association reflected within-treatment variability rather than treatment effects as AFDM content did not differ among treatments (Supplemental Tables). In contrast, neither bulk soil TC nor soil surface chl-a (benthic algae) was related to N_2 production. The lack of association with TC suggests that denitrification rates were more strongly linked to soil bioavailable carbon than to bulk or recalcitrant carbon pools, while the lack of association with chl-a indicates that algal biomass was not a key carbon source for denitrifiers within the cores. Increases in algal biomass have been found to stimulate denitrification by strengthening anoxic conditions in treatment wetlands (Cheng et al. 2022), but this effect may have been nullified by anoxic conditions at the start of incubations.

Hydrology had the strongest effect on N_2O production, with vegetation playing a limited secondary role. The suppression of N_2O rates in the 3W treatments is consistent with prolonged flooding lowering soil redox potential and facilitating complete denitrification to N_2 , an interpretation supported by the negative flux rates seen most often in UV/3W and TRP/3W, which indicate net N_2O consumption. The 3D treatment may have maintained a marginally more oxygenated soil-water interface, promoting incomplete denitrification and higher N_2O production, though differences among inundation histories were minimal. This pattern matches reports that frequent flooding raises N_2O emissions through alternation between oxic and anoxic redox states (Hernandez and Mitsch 2006; Jørgensen and Elberling 2012).

Within-treatment variability in N_2O among cores was substantial, particularly under UV/3D and TRP/3D. Spatial heterogeneity in denitrification is well-documented in wetland soils, where microbial hotspots vary over small spatial scales with localized organic C availability, O_2 diffusion, and NO_3^- supply (Groffman et al. 2009, McClain et al. 2003). The intact cores used here preserved this natural patchiness, likely producing the wide range of within-treatment responses and explaining why the model detected a significant three-way interaction while marginal mean comparisons revealed no differences. This variability is consistent with previous core incubations showing that N_2O production rates differ across dry and submerged herbaceous vegetation, bottomland hardwood forest, and sites spanning a gradient of inundation histories (Hernandez and Mitsch 2006; Audet et al. 2014; Brown et al. 2025). Although some cores reached notably higher rates (up to $0.20 \text{ mg m}^{-2} \text{ h}^{-1}$), all values fell within or below ranges reported in comparable studies (Hernandez and Mitsch 2006, Jørgensen et al. 2012, Okiti et al. 2025), and the very low marginal means suggest the ecological significance of this variation was minimal. Declining O_2 and corresponding N_2 production suggest N_2O production was likely low by day five of flooding, though little can be inferred about the early flooding period, when it was likely highest.

Conclusions

Our study found that vegetation type is a stronger driver of nutrient retention than flood history in experimental wetland mesocosms during a five-day long flood. Emergent vegetation had faster NO_3^- retention than young trees and bare soil, while UV treatments had the fastest PO_4^{3-} retention rates. Despite differences in initial uptake rates, all vegetation-hydrology combinations reduced both nutrients to near detection limits within five days of inundation. These findings suggest that wetland restoration designs incorporating a mosaic of UV areas and EV may optimize retention of both N and P during floods lasting less than 48 h, when differences among vegetation types are most pronounced. For longer flood events, the specific composition of wetland habitat becomes less consequential, as extended contact time between floodwater and soil appears sufficient to cause nutrient depletion regardless of vegetation cover. This has practical implications for wetland managers weighing the costs and complexity of vegetation establishment against expected flood durations at a given site.

A critical question raised by this study is what specific mechanisms drive the divergent retention patterns observed for NO_3^- and PO_4^{3-} among vegetation types, particularly given that N_2 and N_2O production rates did not differ substantially among treatments. This disconnect between NO_3^- uptake and N_2 flux suggests different soil and plant N storage pathways, and potentially, variable release in N during future floods. Stable isotope experiments would be beneficial to elucidating these retention pathways, and field-scale studies evaluating whether these mesocosm-derived patterns hold under variable flow conditions, heterogeneous soils, and natural flood regimes will further clarify how these short-term patterns contribute to seasonal and decadal nutrient retention trends as wetland restorations age.

Declarations

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Competing Interest

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

Author Contributions

All authors contributed to the study conception and design, along with material preparation and data collection. Data analysis was performed by Spencer Womble. The first draft of the manuscript was written by Spencer Womble. All authors reviewed and commented on previous versions of the manuscript. All authors have read and approved the final manuscript.

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Data Availability

The dataset generated and analyzed during this study are available in the online supplementary materials.

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Figures

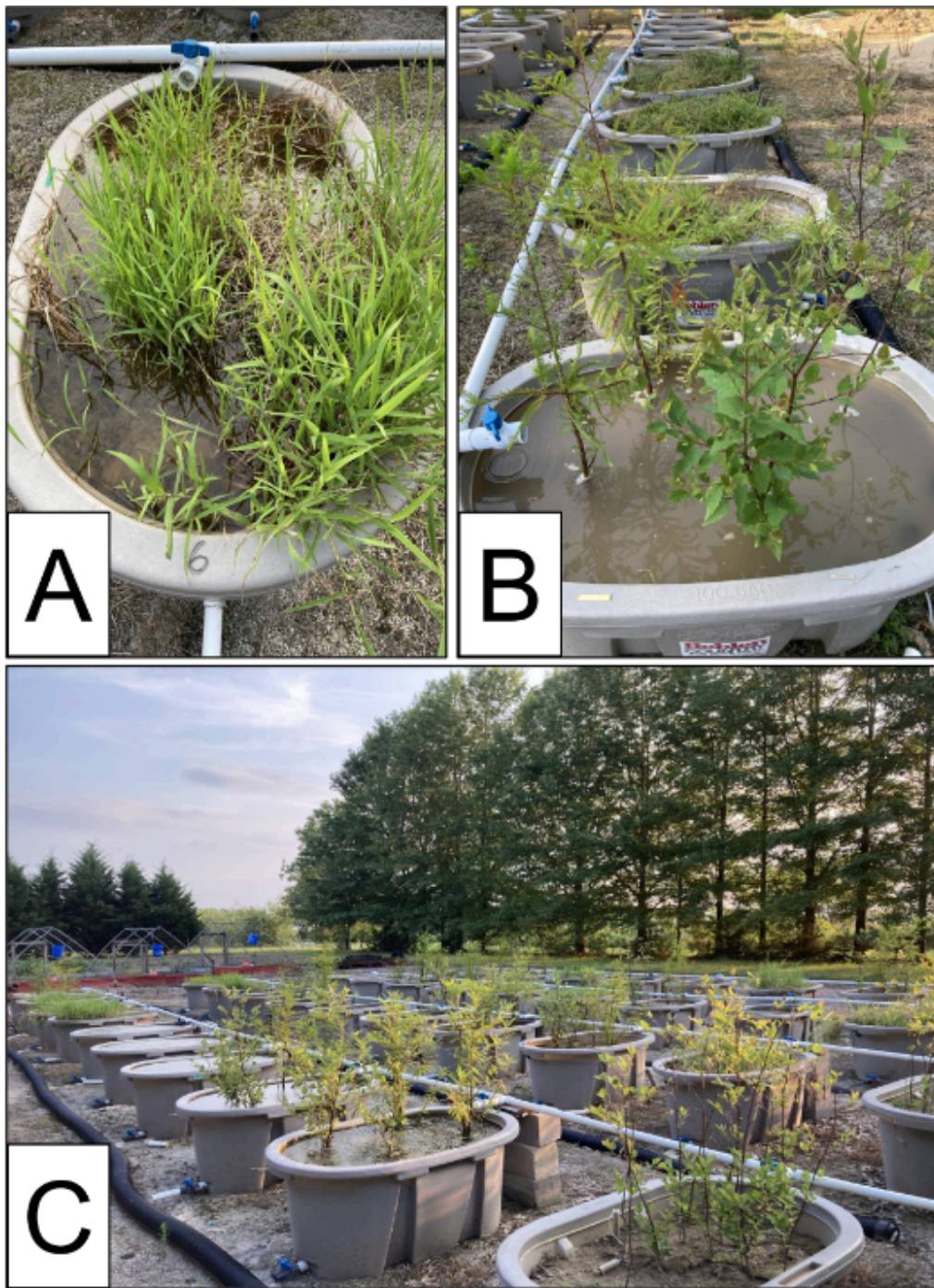


Figure 1

Typical emergent vegetation (A) and tree planting (B) treatments, and assembled mesocosms with assigned treatments (C). Note the nearest tub in the picture (C) was only used to maintain backup trees in case tree mortality. It was not used in the experiment, and no trees died during this study

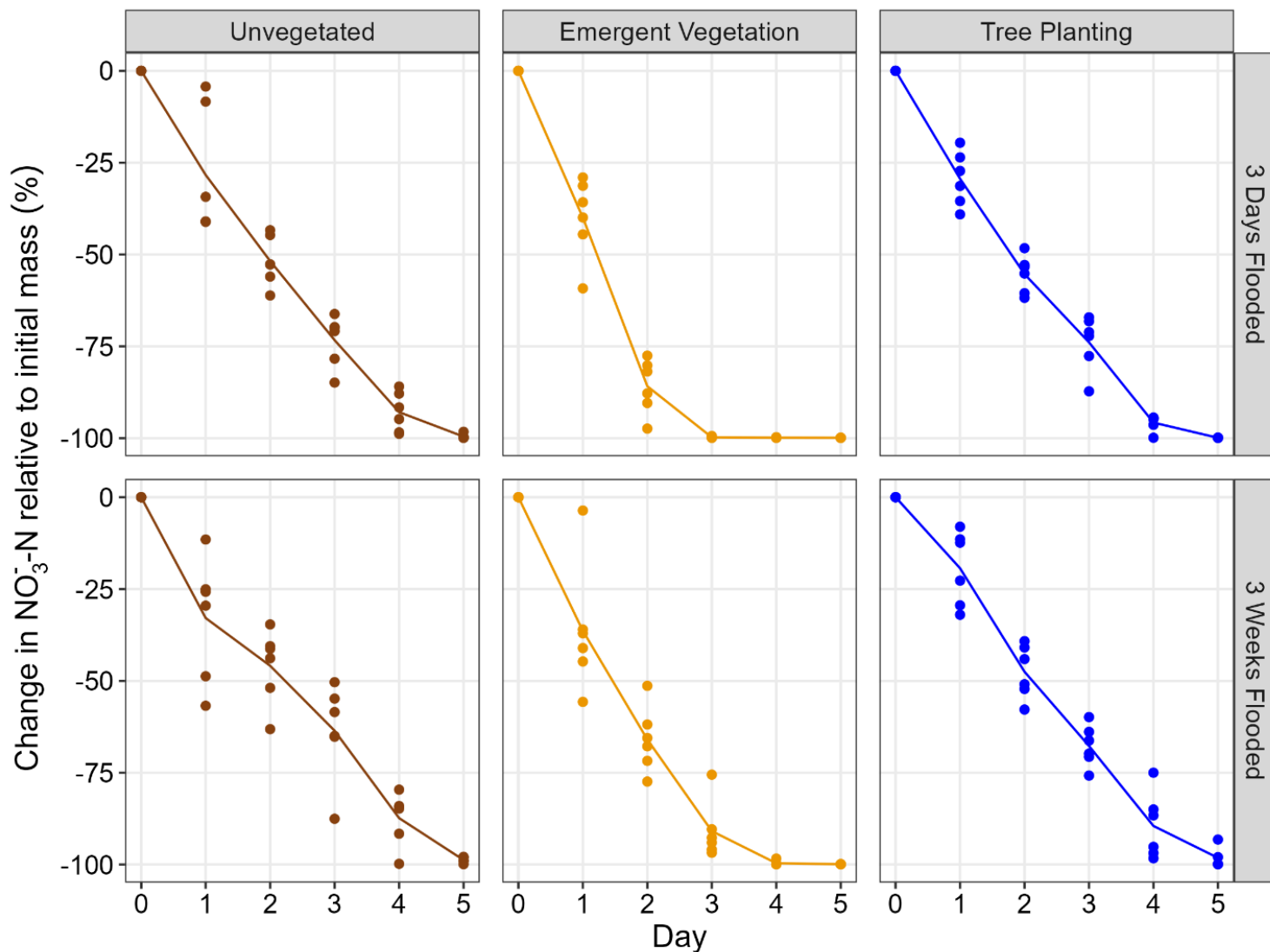


Figure 2

Percent reduction of initial NO_3^- content (mg mesocosm $^{-1}$) across days. Points are individual mesocosms. Lines show trends in treatment means across sampling days

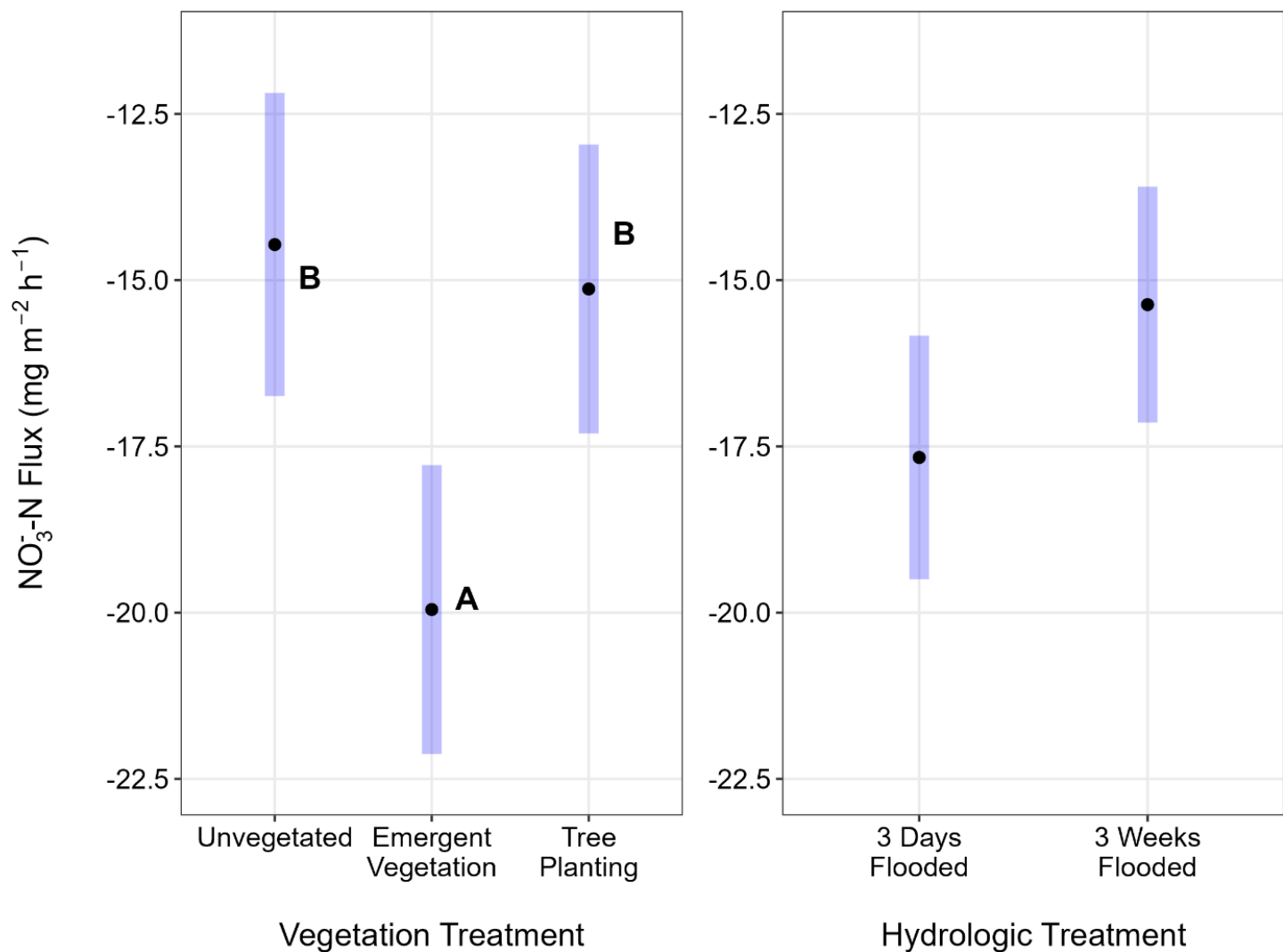


Figure 3

Nitrate flux rates by vegetation and hydrology treatment for data collected up through day three. Points indicate estimated marginal mean flux rates. Error bars show 95% confidence intervals. Different letters indicate treatments with significantly different retention rates at $\alpha = 0.05$. There were no differences between hydrologic treatment levels. Negative flux indicates nitrate removal from the water

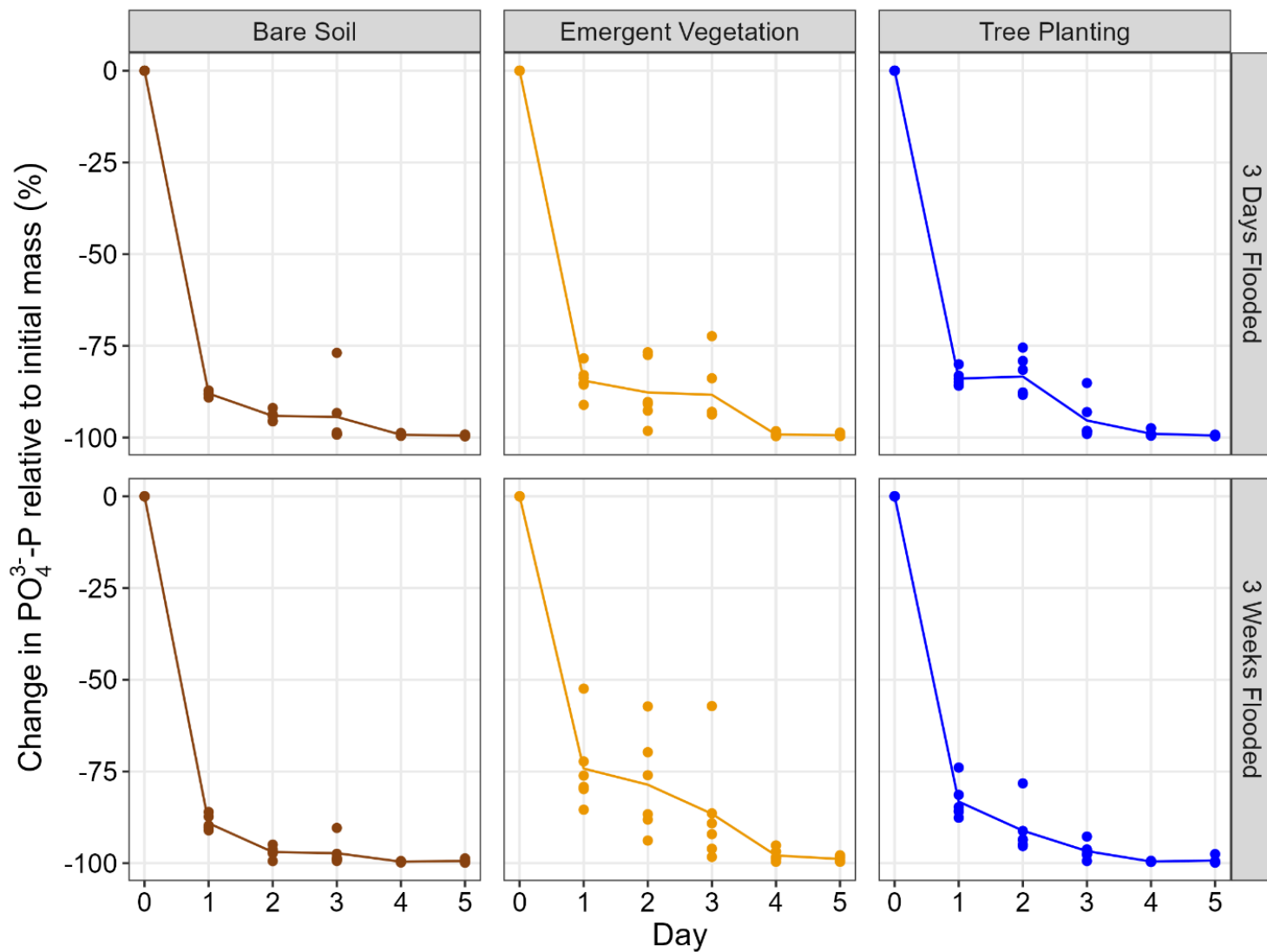


Figure 4

Percent reduction of initial $\text{PO}_4^{3-}\text{-P}$ content (mg mesocosm^{-1}) across days. Points are individual mesocosms. Lines show daily treatment means across sampling days

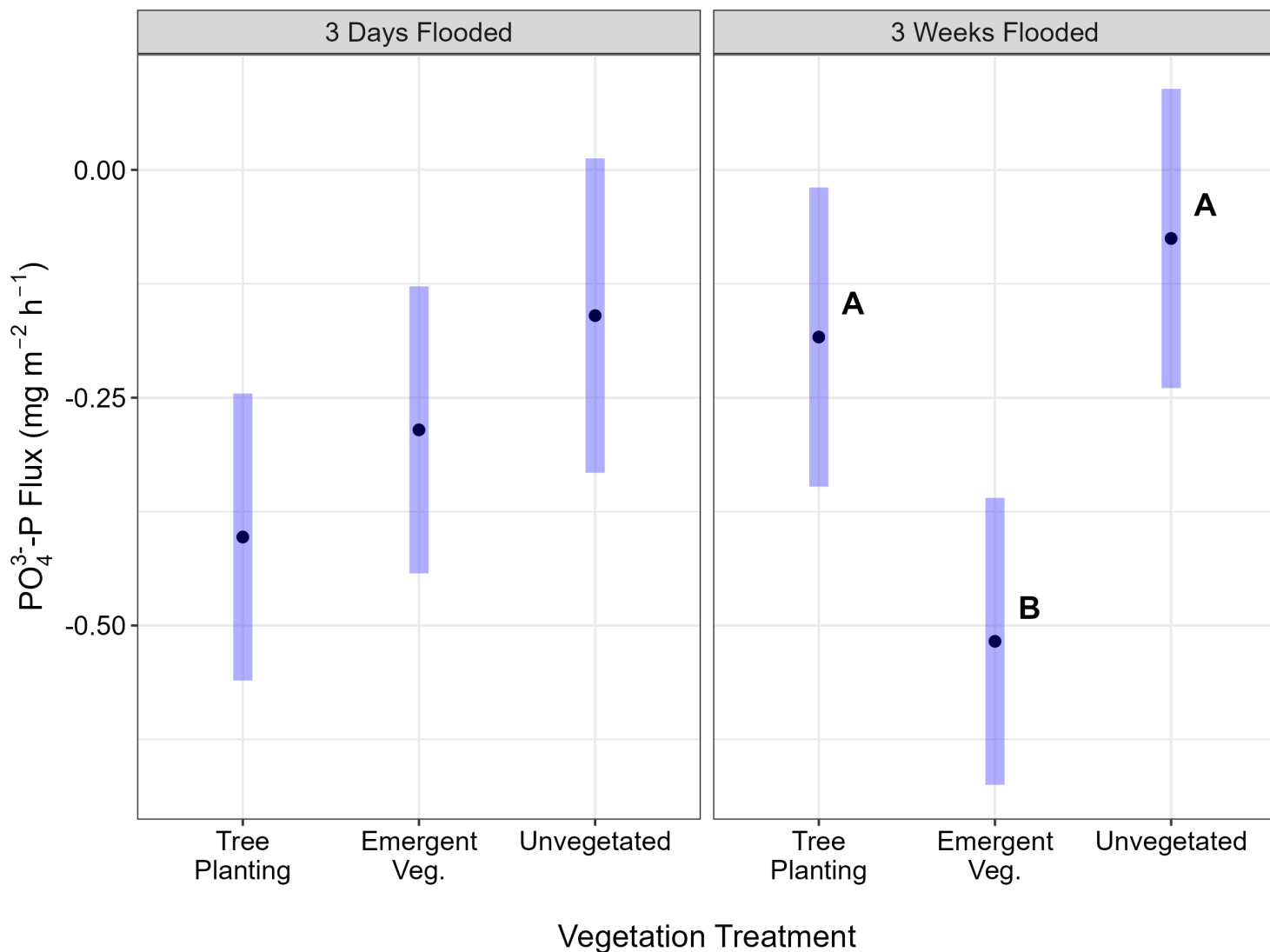


Figure 5

Phosphate flux rates for days two through five for each vegetation type grouped by hydrology level. Points indicated estimated marginal mean flux rates. Error bars show 95% confidence intervals. Different letters indicate treatments with significantly different retention rates at $\alpha = 0.05$. Negative flux indicates phosphate removal from the water

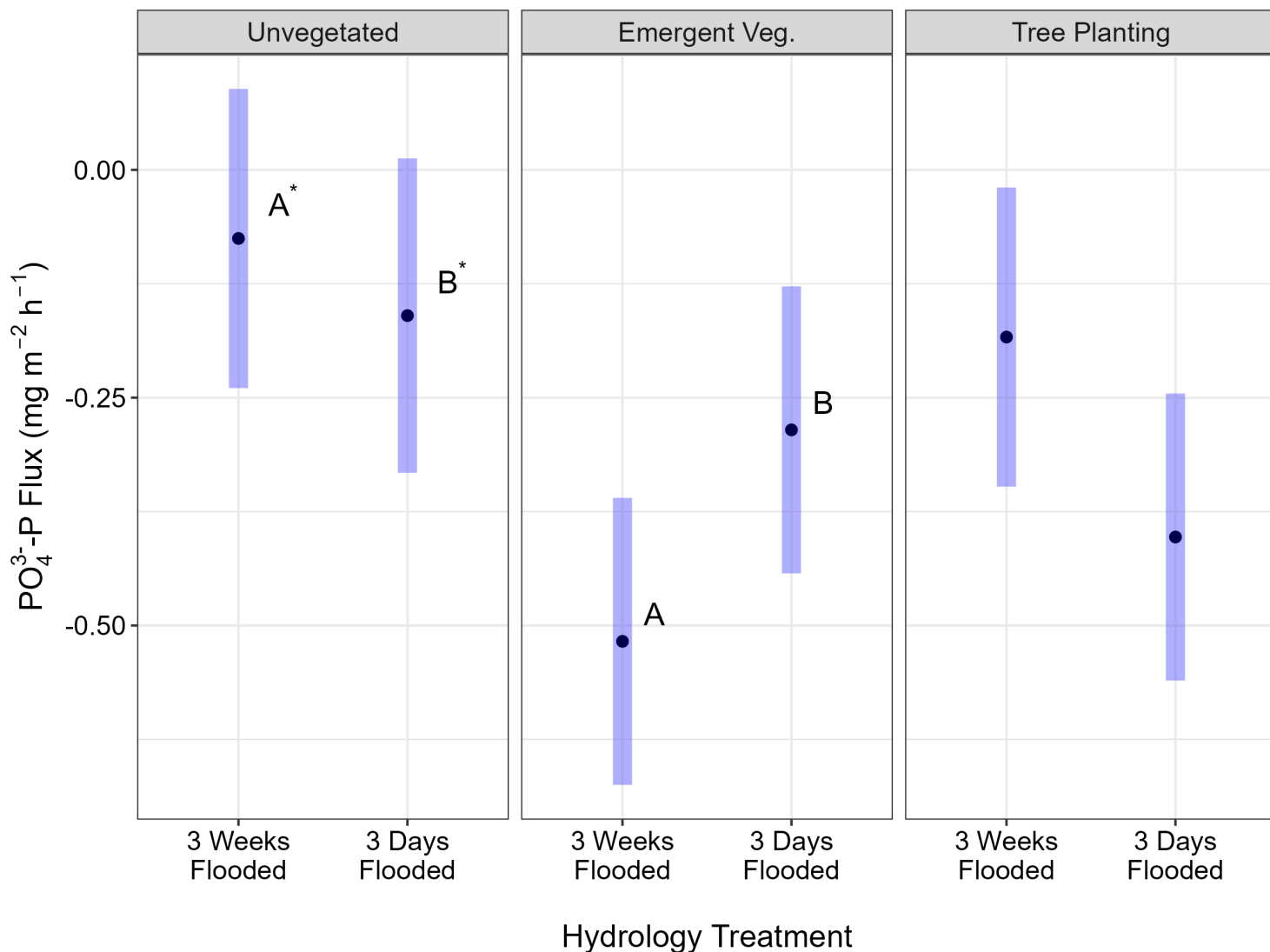


Figure 6

Phosphate flux rates for days two through five for each hydrology level group by vegetation type. Points indicated estimated marginal mean flux rates. Error bars show 95% confidence intervals. Different letters without stars indicate treatments with significantly different retention rates at $\alpha = 0.05$. Different letters with stars indicate a significant difference at $\alpha = 0.1$. Negative flux indicates phosphate removal from the water

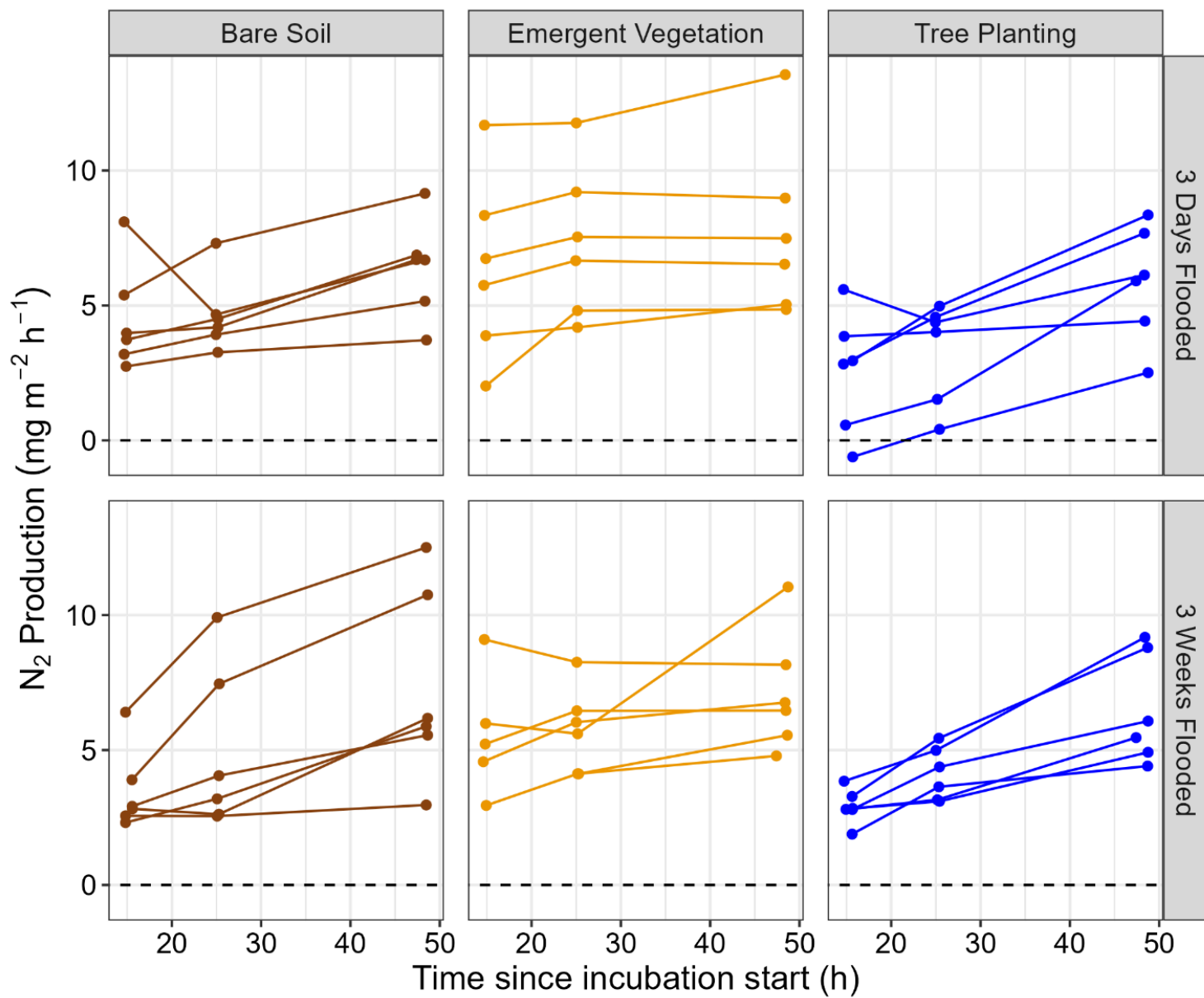


Figure 7

N_2 flux rates across sampling rounds for each vegetation and hydrology combination. Points represent individual cores at each sampling time point. Solid lines are used to highlight changes in N_2 production over time in each core. The dashed black line indicates zero

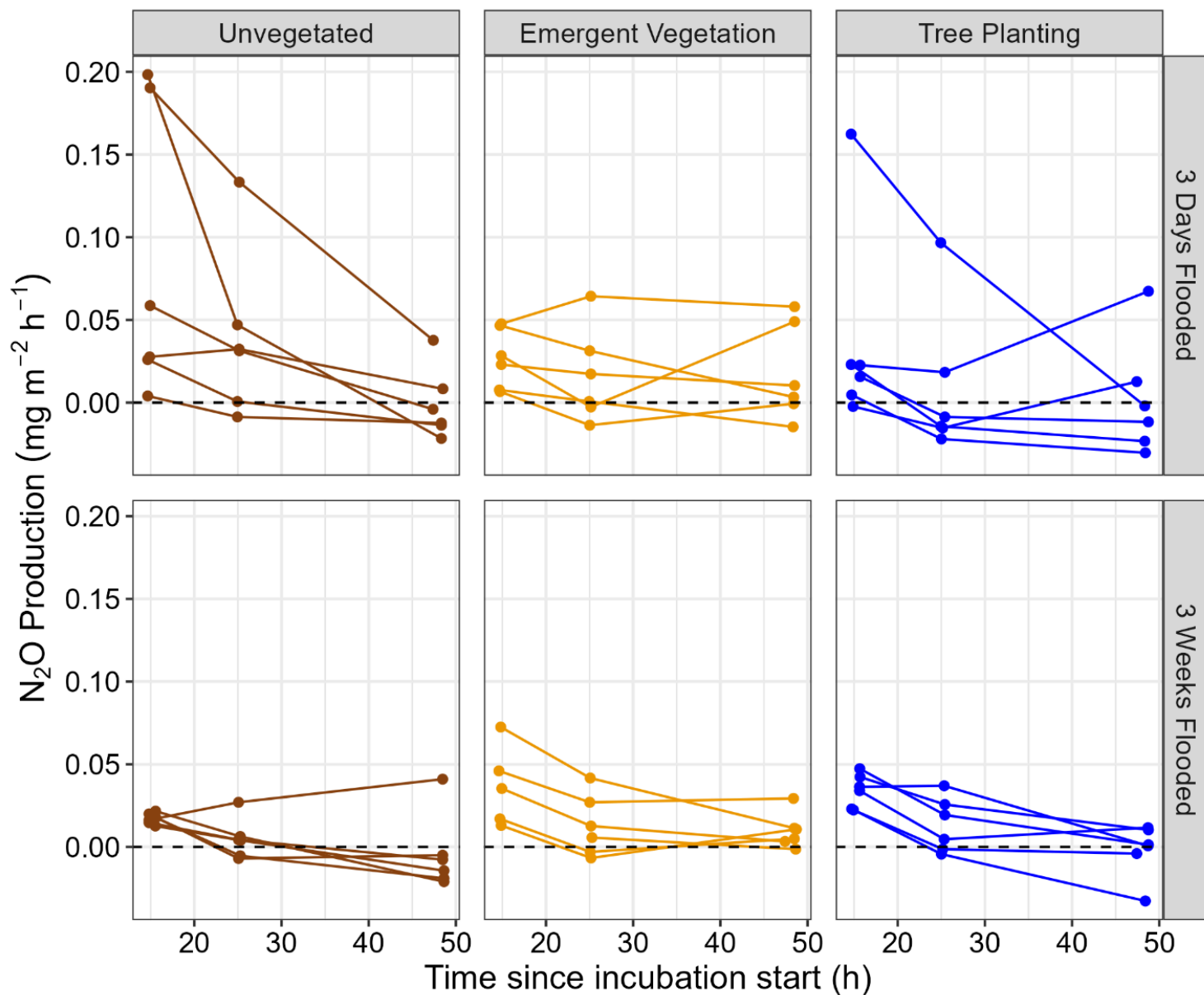


Figure 8

N_2O flux rates across sampling rounds for each vegetation and hydrology combination. Points represent individual cores at each sampling time point. Solid lines are used to highlight changes in N_2O production over time in each core. The dashed black line indicates zero

Supplementary Files

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