

**FACTORS INFLUENCING NUTRIENT RETENTION IN RESTORED FLOODPLAIN
WETLANDS IN WESTERN TENNESSEE AND KENTUCKY, USA**

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FACTORS INFLUENCING NUTRIENT RETENTION IN RESTORED FLOODPLAIN WETLANDS IN WESTERN TENNESSEE AND KENTUCKY, USA

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Doctor of Philosophy in Environmental Science

Floodplain wetlands function as important nutrient sinks which can improve downstream water quality by reducing nutrient export. In the lower Mississippi Alluvial Valley (LMAV), wetland loss and intense agricultural production throughout the Mississippi River Drainage has caused substantial nutrient pollution in the northern Gulf of Mexico. The Wetland Reserve Program (WRP)/Wetland Reserve Enhancement Partnership (WREP) program(s) within the U.S. Department of Agriculture were created to convert marginal croplands back to floodplain wetlands, in part to reduce nutrient export from agricultural watersheds. Using a combination of field, remote sensing, and experimental data, this dissertation evaluated restoration success by quantifying maximum nutrient retention potentials among various restored wetland habitat types throughout western Tennessee and Kentucky. Further, this dissertation investigated how vegetation, hydrology, and soil properties interact to influence nutrient cycling within these ecosystems. The results of these studies indicate that vegetation, hydrology, and soil properties can have distinct or combined effects on nutrient cycling rates during initial flooding. However, the strength of these relationships generally weakens as flood duration increases. Beyond 1 – 3 days of inundation, water residence time may become the primary factor regulating nutrient retention in these wetlands regardless of vegetation type, hydrologic regime, or soil properties. Further, increases in flood frequency appear to enhance nitrogen retention and closely correlate with select soil properties. These findings suggest that increasing wetland-floodplain connectivity and water residence time during floods may enhance nutrient retention and reduce or eliminate disparities among different restored wetland habitats.

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CERTIFICATE OF APPROVAL OF DISSERTATION

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by

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DEDICATION

This dissertation is dedicated to Robert Brown and Shrijana Duwadi for all we've been through and to my wife Kristin for all she's given me. Let's never do this again.

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CHAPTER 1: BACKGROUND INFORMATION

Much of Earth's freshwater has been degraded through agricultural runoff, with fertilizer applications and soil erosion substantially increasing the nutrient content of surface waters globally (Galloway & Cowling, 2002; V. H. Smith et al., 1999). High nutrient [nitrogen (N) and phosphorus (P)] input into aquatic ecosystems can degrade water quality and threaten biodiversity (Bini et al., 2014; Edmondson, 1994; V. H. Smith et al., 1999; Vonlanthen et al., 2012) through cultural eutrophication, the enriching of organic matter within an ecosystem due to nutrient pollution (Nixon et al., 1996). Cultural eutrophication can also alter biogeochemical cycles, change water pH, decrease dissolved oxygen content, and prompt the formation of nuisance algal blooms (Dale et al., 2008; Doney, 2010; Glibert, 2017; Kelly et al., 1990; Vitousek et al., 1997). Coastal areas are especially prone to eutrophication as they receive nutrient pollution runoff from entire basins or regions (Simpson et al., 2008).

In North America, intense agriculture within the Mississippi River watershed has caused substantial nutrient pollution throughout the basin and the Mississippi Delta. Expansive algal blooms now form seasonally in the northern Gulf of Mexico due to this nutrient enrichment (Dale et al., 2008). The influx of excess N and P into the Gulf of Mexico prompts rapid cellular division in certain algal species, resulting in a substantial increase in algal biomass. Once nutrients are depleted, algal cells begin to die and are decomposed by microbes. Cellular respiration by the decomposing microbes can deplete dissolved oxygen in the surrounding water column, and large areas of hypoxic (low-oxygenated, $< 2\text{mg/L}$) water known as "dead zones"

may form. Over the past 60 years, this seasonal (May – September) hypoxic zone has steadily increased in duration and size and is now the second largest annual hypoxic zone in the world, with the most recent 5-year average (2015 – 2020) size being 14,000 km² (U.S. Environmental Protection Agency, 2022). Hypoxic zones within the water column can decimate aquatic life and damage important commercial fisheries (Thronson & Quigg, 2008; Zimmerman & Nance, 2001). The economic and environmental devastation to coastal states in the Mississippi River Delta resulting from cultural eutrophication of the northern Gulf of Mexico have created an urgent need to reduce excessive N and P runoff within the Mississippi River basin.

Wetland Restoration by the National Resources Conservation Service

The lower Mississippi River Valley (LMRV) was historically comprised of bottomland hardwood forest interspersed with shallow riparian wetlands and oxbow lakes that created a large swamp-forest complex (Allen et al., 2001; Paul Keddy, 2000). These forest-wetland mosaics functioned as nutrient buffers for downstream waterbodies by trapping and storing excess nutrients from runoff in the surrounding watersheds but have been systematically logged, drained, and converted to cropland. An estimated 25% of original bottomland hardwood forest-floodplain wetland complexes within the LMRV remain intact and the remaining forest is severely fragmented (Twedt & Loesch, 2001). Loss of these wetland-forest complexes has greatly diminished the amount of N and P that may be retained by the landscape (U.S. Department of Agriculture & U.S. Environmental Protection Agency, 2015).

To reduce excess nutrient delivery to the Gulf of Mexico, former croplands within the LMRV are being converted back to floodplain wetlands by the National Resources Conservation Service (NRCS) within the U.S. Department of Agriculture (USDA). A financial incentive

policy called the Wetlands Reserve Program (WRP), renamed as the Wetland Reserve Enhancement Partnership (WREP) in 2018, has been established to encourage landowners to conserve floodplain wetlands located on their property. The program(s) pay landowners to enter croplands that were historically wetlands into long-term or permanent conservation easements wherein the land can no longer be used for commercial crop production or natural resource extraction. Under the WRP/WREP, NRCS may use a combination of methods (see Chapter Two) to restore, protect, or enhance ecosystem function and biodiversity (Jenkins et al., 2010).

Dissertation Objectives

Ecosystem restoration projects are rarely monitored and/or evaluated after initial restoration, especially over large spatial and temporal scales (Bash & Ryan, 2002; Cooke & Johnson, 2002; Wortley et al., 2013). This lack of monitoring may complicate or reduce the effectiveness of future restorations as there are few evaluations of restoration success (here defined as ecologically significant improvements in nutrient retention capabilities) (Block et al., 2001). Within the WRP/WREP program(s), the restoration strategies employed are predominantly focused on returning these wetlands to their historical pre-human degradation states, with the assumption that habitat restorations will also restore ecosystem functioning. However, the mechanisms responsible for healthy ecosystem functioning in undisturbed and restored wetlands are often unknown or unclear (Paul Keddy, 2000). The following chapters of this dissertation sought to identify the underlying ecological principals and relationships that enhance nutrient retention in WRP/WREP easements, and how retention potential differs among

various habitat restoration practices. Specifically, this dissertation sought to assess these aspects in the context of hydrologic disturbance.

CHAPTER 2: EFFECTS OF VEGETATION, HYDROLOGY, AND SOIL ON NITROGEN AND PHOSPHORUS RETENTION IN RESTORED FLOODPLAIN WETLANDS

Abstract

Croplands within the Mississippi Alluvial Valley are being converted back to wetlands to remove excess nutrients from floodwaters by restoring historical vegetation and hydrology. Quantifying nutrient retention potentials among restored habitats during flooding and determining which environmental factors influence retention rates will improve restoration outcomes. Nutrient retention potential was estimated for, and compared among, inundated shallow water (ISW), dry shallow water (DSW), tree planting (TP), natural regeneration (NR), and remnant forest (RF) habitats in 22 restored wetlands in western Tennessee and Kentucky. Soil properties and soil oxygen demand (SOD) were also measured as covariates for habitat comparisons. Paired soil cores were collected from each habitat for flow-through incubations and soil properties determination, respectively. Nutrient retention was measured after 6, 24, and 48 h of incubation. All habitats removed nitrate (NO_3^-) and phosphate (PO_4^{3-}) at each time point, with the greatest retention rates observed at 48 and 6 h, respectively. ISW habitats retained on average 101%, 117%, and 351% more NO_3^- at 6 h than NR, RF, and DSW, respectively. There were no statistical differences in NO_3^- retention beyond 6 h or at any time for PO_4^{3-} . Covariate influence varied by time point and nutrient species. Nitrate retention was positively correlated with soil moisture, SOD, total nitrogen, and soil phosphorus and negatively correlated with total carbon.

Phosphate retention was positively correlated with soil moisture and SOD and negatively correlated with soil phosphorus. These results suggest that all habitats are efficient at removing NO_3^- and PO_4^{3-} during a 48-h flood, but peak retention rates may be contingent upon flood duration and soil properties.

Introduction

Historical floodplain wetlands within the Mississippi River watershed are being restored, in part, to retain excess nitrogen (N) and phosphorus (P) from the surrounding landscape to reduce downstream nutrient export (S. Faulkner et al., 2011a; Hunter & Faulkner, 2001; Mitsch, Day, et al., 2005). However, without proper post-restoration monitoring, it is unclear how effective specific restoration strategies like revegetation and hydrologic manipulation are at meeting restoration goals (Bash & Ryan, 2002; S. Faulkner et al., 2011a; Taddeo & Dronova, 2018). Both the raw metrics of restoration success (i.e., nutrient removal rates) and the mechanisms determining the successes or failures to reach restoration goals must be considered to assess restoration success. Few studies have approached restoration monitoring from a wholistic perspective that considers hydrology, soil geomorphology, and habitat together (S. Faulkner et al., 2011a). The present study aimed to evaluate the effectiveness of restoration efforts by examining the interactions among hydrology and habitat, and their impact on nutrient retention. Additionally, it sought to determine the underlying mechanisms driving the success or failure of restoration practices by identifying correlations between nutrient retention or release rates with soil geomorphological features.

Overview of Nitrogen and Phosphorus Retention Pathways in Aquatic Ecosystems

Nitrogen Retention Pathways

Nitrogen in an aquatic ecosystem may be stored or removed through several pathways: sedimentation, biological uptake, denitrification, or export. Sedimentation is the absorption of labile N to suspended sediment particles in the water column that settle into stream substrate or wetland soil/sediment and can be a major source of N retention within floodplain wetlands (Olde Venterink et al., 2006). Biological uptake occurs when an organism (typically microbes or plants) removes N from either the sediment or water and incorporates it into its cell(s). Biological uptake is a dominant removal pathway for certain forms of N such as nitrate (NO_3^-), nitrite (NO_2^-), and ammonium (NH_4^+) (Grimm et al., 2003). Denitrification is the reduction of NO_3^- to nitrogen gas (N_2) by microbes that use NO_3^- as a final electron acceptor during organic matter respiration in the absence of oxygen (O_2). This is an important component of excess N reduction in aquatic systems as N_2 gas is transferred to the atmosphere and completely removed from the aquatic environment. Generally, denitrification is an anoxic process, meaning that the systematic reduction process of NO_3^- to NO_2^- to nitric oxide (NO) to nitrous oxide (N_2O) to N_2 primarily occurs in sediments devoid of O_2 . Under oxic conditions, certain species of microbes covert NH_4^+ to NO_2^- and then to NO_3^- through nitrification. Finally, any N that is not taken up biologically or stored in the sediment may be exported downstream as inorganic or organic N.

Phosphorus Retention Pathways

Sedimentation and biological uptake are the predominant pathways of P storage in aquatic ecosystems. Phosphorus readily binds to ferric iron (Fe_2O_3) under oxic conditions, and P

adsorption to iron-containing sediments often occurs quickly when O₂ availability is high (Dodds & Whiles, 2010); therefore, sediment transport and storage can greatly influence P export. Within floodplain wetlands, suspended sediment may become trapped as floodwaters recede. Suspended sediment, along with any sediment-bound P, then settles onto the (drying) soil or bottoms of impoundments. Sedimentation in wetlands has been found to remove a substantial amount of inorganic P from the water column during floods (Mitsch et al., 1995; Olde Venterink et al., 2006). Unbound inorganic P in the water column (mainly in the form of phosphate (PO₄³⁻)) or inorganic P bound in the sediment may also be removed from the water column via uptake by plants or microbes. However, as P does not have a gaseous state, any biologically-bound P will be released back into the environment upon the death of the organism. When sediments become anoxic, Fe₂O₃ and P dissociate, and P is released as PO₄³⁻ which may then be exported downstream during the next flood. While P retention and export in floodplain wetlands can be highly variable depending on the season (Bridgham et al., 2001; Johnston et al., 2001; X. Ye et al., 2014), wetlands still generally function as P sinks, as much of the imported sediment accretes and becomes trapped (Johnston, 1991).

Interactions Between Habitat and Hydrology on Nutrient Retention

Nutrient retention can vary among wetland habitat types, here defined as the combination of vegetation functional groups present and soil characteristics within a defined, relatively homogenous zone. Hydrology is one of the strongest environmental factors structuring habitats and regulating biogeochemical cycling in wetland ecosystems (Escalera-Vazquez & Zambrano, 2010; Paul Keddy, 2000; Y. Zhang et al., 2002). Habitat-hydrology interactions can greatly influence nutrient cycling rates (Hunter & Faulkner, 2001; Mitsch et al., 2015; Olde Venterink et

al., 2006) and create substantial variability in nutrient retention among and within wetlands (S. Faulkner et al., 2011a). The effects of these interactions are both caused, and are influenced by, multiple environmental characteristics such as soil structure and soil nutrient content that directly and indirectly affect nutrient retention potential (S. Faulkner et al., 2011a; Mitsch, Zhang, et al., 2005).

Soil Characteristics and Nutrient Retention

Soil Moisture

Soil moisture content can be a primary driver of soil nutrient flux rates. Increases in soil moisture can reduce carbon (C), N, and P storage due to a corresponding decrease in soil bulk density (Bai et al., 2010). High soil moisture content can also create an anerobic environment at the soil/sediment-water interface that facilitates denitrification (Marton et al., 2014; A. L. Peralta et al., 2010; Pinay et al., 2007), and increase N₂O, a potent greenhouse gas, emissions via incomplete denitrification (failure of NO₃⁻ to be completely reduced to N₂) (Zhu et al., 2018). Additionally, sudden changes in soil moisture can have strong temporal effects on nutrient cycling rates. For example, rapid increases in soil moisture from rain or flooding enhance denitrification rates, creating “hot moments” where rates rapidly increase for a short time (Sexstone et al., 1985).

Soil moisture gradients can also influence the distribution of microbial taxa and their nutrient cycling rates (Hu et al., 2019) within wetlands. Soil moisture can influence microbial community composition which affects nutrient availability to plant communities and root zone nutrient cycling dynamics (Brockett et al., 2012; Joris & Feyen, 2003). High soil water content

can also reduce soil redox state which enhances microbial uptake of dissolved and soil-bound nutrients in anoxic-dependent taxa.(Wang et al., 2015; Hu et al., 2019), and also promotes the high abundances of select denitrification genes (Nadeau et al., 2019).

Soil Nutrient Content

While soil moisture content is often a critical factor in determining nutrient retention rates in wetlands, other soil characteristics such as nutrient content and distribution also play a significant role (Hopkinson, 1992). Nutrient distribution in wetland soils along a flood zone gradient influences vegetation community structure and aboveground net primary production, with regularly flooded areas experiencing higher productivity due to enhanced nutrient delivery (Burke et al., 1999; Paul Keddy, 2000). Interactions among soil nutrients can also influence nutrient retention rates. For example, high soil C and NO_3^- content increases anerobic microbial biomass and activity following flooding, in turn increasing dissolved NO_3^- retention via assimilation and denitrification (Dong et al., 2009; Groffman et al., 1996; Jacks et al., 1994; Johnston, 1991; Jordan et al., 2007; Warneke et al., 2011). High soil total phosphorus (TP) content can also enhance denitrification and biological uptake by preventing P limitation in microbes (Kim et al., 2017; White & Reddy, 2003). Overall soil nutrient content can also influence PO_4^{3-} retention with high-nutrient soils releasing a higher amount of P during flooding compared to soils with low nutrient content (Bostic & White, 2007; Dunne et al., 2006a). However, the direct effects of soil nutrients on PO_4^{3-} cycling in wetlands are poorly understood, and further research is needed to determine the mechanistic effects of soil nutrient content on P retention.

Soil Structure

In addition to soil moisture and nutrient content, other physical soil properties influence wetland nutrient cycling. Soil bulk density, which reflects the relative amount of space between soil particles and pore water, can impact nutrient retention by altering the soil's physical and biological profile (McKee & Cherry, 2009; Mitsch & Gossilink, 2000; H. Wang et al., 2017). Higher bulk density reduces porosity and leads to a decline in denitrification rates as compact soils store less water and organic C (Bruland & Richardson, 2005b; Sakin & Tutar, 2011; Ullah & Faulkner, 2006). Additionally, high-bulk density soils often contain less organic C, leading to reduced P retention (Bruland & Richardson, 2006; Dunne et al., 2006b). High levels of soil organic C can indirectly enhance P retention by facilitating the binding of labile P to soil aluminum and iron (Axt & Walbridge, 1999; Darke & Walbridge, 2000; Hogan et al., 2004).

Soil pH is another key factor regulating wetland nutrient retention wetlands as pH influences plant and microbial community structure, above-ground nutrient storage, and microbially-mediated nutrient transformations (Devlin et al., 2000; Stevens et al., 1998; Yang et al., 2016). Soils that are more acidic tend to have greater P availability to plants (Penn & Camberato, 2019) whereas calcareous soils have less labile P due to the formation of P-containing metal complexes (e.g., calcium phosphate (Ca-P) and magnesium phosphide – (Mg-P)) (Ström et al., 2005). Further, increases in soil pH can increase N retention by enhancing dissimilatory nitrate reduction and denitrification rates (Devlin et al., 2000; Stevens et al., 1998).

Soil Redox Potential

Soil redox greatly influences N and P by regulating physical and biological responses to changing redox states (Braskerud et al., 2005; Grimm et al., 2003; Pett-Ridge et al., 2006). Anaerobic microbes, like denitrifying bacteria, are favored under reduced environments. As soil redox potential declines, respiration rates in anaerobic microbes increase, reducing labile N via increased denitrification and assimilation in these taxa (Hunting & van der Geest, 2011; Jayakumar et al., 2009). Following flooding, soils may transition from an oxic to an anoxic state, creating a redox gradient that supports coupled nitrification-denitrification (N fixation feeds denitrification until O₂ is depleted) at oxic-anoxic boundary. Coupled nitrification-denitrification can rapidly remove N from the soil via N₂ production. Conversely, P is often released under reduced soil conditions as Fe₂O₃ and P dissociate (Baldwin & Mitchell, 2000a; Qiu & McComb, 1995). Soil redox potential can be estimated by measuring soil O₂ demand (SOD), which represents the rate of O₂ consumption by plants and microbes (Evans & Murdock, 2018).

Need for Research on the Effects of Habitat Type, Hydrology, and Soil Geomorphology on Nutrient Retention

Given the complexity of wetland nutrient cycling and difficulty in predicting restoration outcomes, more research is needed to determine how habitat, hydrology, and soil geomorphology interact to influence nutrient retention. Evaluations of wetland restorations are lacking globally (Miller & Hobbs, 2007; Nilsson et al., 2016) and few studies have been conducted on WRP/WREP easements within the LMRV (S. Faulkner et al., 2011a). By investigating the effects of habitat, hydrology, and soil geomorphology on wetland nutrient cycling, we can more accurately predict nutrient retention outcomes for specific restoration

practices. This will help ensure that wetland restorations are as effective as possible in restoring and improving ecosystem functioning.

Objectives

Objectives: 1) Determine if NO_3^- and PO_4^{3-} flux rates (a measure of the rate at which a nutrient is retained or released within a given area over a defined period of time (reported as $\text{mg m}^{-2} \text{ h}^{-1}$)) differ among wetland habitats by incubating intact soil cores collected from restored floodplain wetlands 2) Correlate soil physical properties and nutrient content with NO_3^- and PO_4^{3-} flux to determine if these factors are associated with nutrient retention and release during a flood

Hypotheses

Hypothesis 1) Nitrate and PO_4^{3-} flux rates would differ among habitat types.

I predicted that dissolved N and P flux rates would differ among habitats, and differences would be a function of habitat type, soil characteristics, and SOD. Soil O_2 demand was predicted to correlate with increased NO_3^- retention and decreased PO_4^{3-} retention (presumably due to P release as soil O_2 was depleted) across all sampling time points during a 48-h simulated flood. Further, inundated shallow water habitats were predicted to have the greatest initial NO_3^- retention as prolonged inundation would have reduced the soil redox state prior to core collection, facilitating greater denitrification

rates. Conversely, inundated shallow water habitats were predicted to initially retain the least amount of PO_4^{3-} among the habitats due to this reduced soil redox environment prior to incubation.

Hypothesis 2) NO_3^- and PO_4^{3-} flux rates would correlate with soil characteristics.

I predicted that soil moisture and nutrient content would better correlate with nutrient flux rates compared to other soil characteristics. High soil moisture content was predicted to correlate with high NO_3^- retention and low PO_4^{3-} retention. Further, soil C and N were predicted to positively correlate with NO_3^- retention, presumably due to increased denitrification (Jacks et al., 1994; Johnston, 1991; Warneke et al., 2011). Additionally, soil P was predicted to negatively correlate with NO_3^- and PO_4^{3-} retention. Soils with high P content have been associated with decreases in denitrification rates (White & Reddy, 2003) and increased P release upon rewetting (Bostic & White, 2007; Dunne et al., 2006a).

Methods

Field Methods

Site Selection

Twenty-two WRP/WREP easements in western Tennessee and western Kentucky (Fig. 1.2) were sampled to determine NO_3^- and PO_4^{3-} retention among five restored floodplain wetland habitats: natural regeneration, remnant forest, inundated shallow water, dry shallow water, and

tree plantings. Sites were sampled from May through August of 2020 - 2022. All sites were located within a river floodplain and receive water from both overland flow and river flood water.

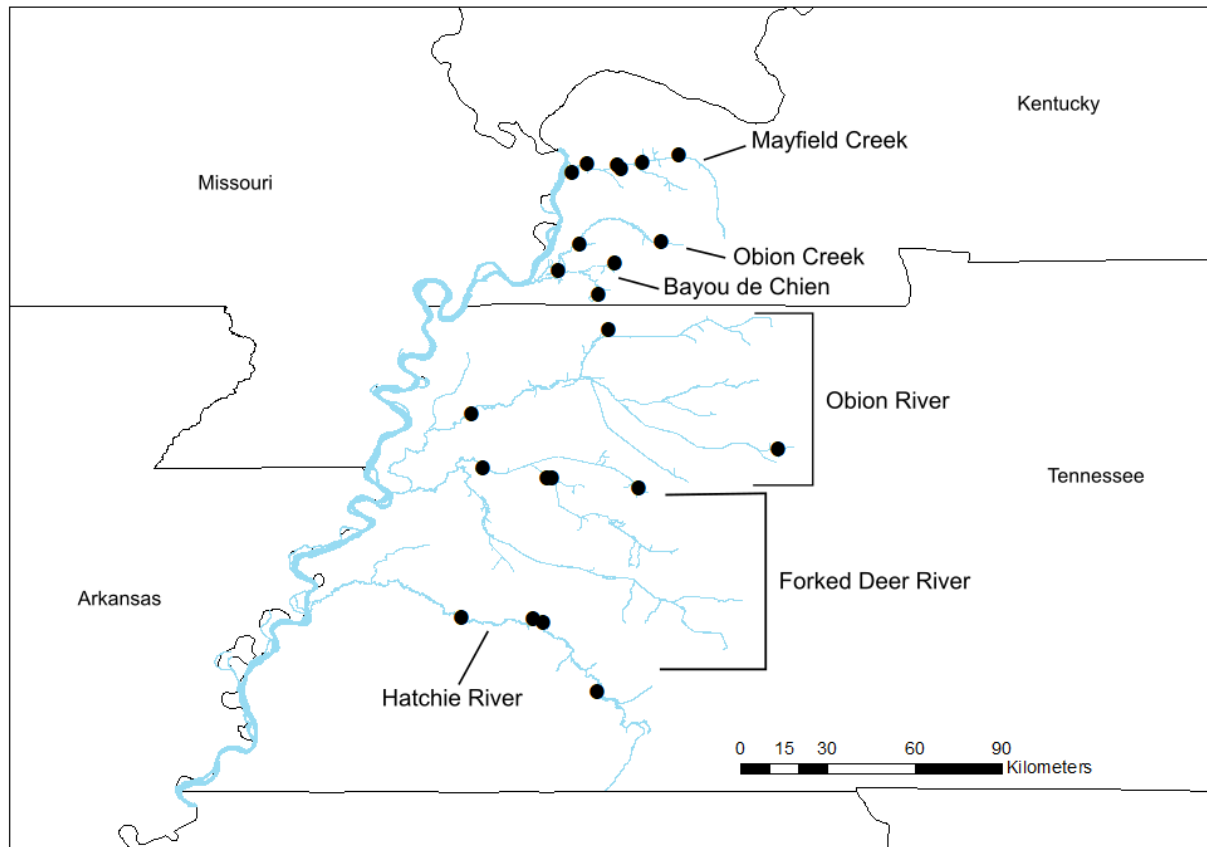


Figure 1.2 Map of WRP/WREP easements (black circles) included in the study.

Habitat Classifications

Restoration plans from NRCS, satellite imagery, and on-site visits were used to classify all major habitats present on a site (Fig. 2.2). Natural regeneration functioned as a catch-all

habitat designation as not all areas of a site fit into the other habitat categories. Areas were designated as natural regeneration habitats when specified as such in NRCS restoration plans, no habitats were listed for the area, or the area was a failed tree planting (most planted trees did not survive). Any inundated portions of a site that were not identified via NRCS documentation or satellite imagery as a natural or historical wetland were classified as inundated shallow water habitats. An area was classified as a dry shallow water habitat if it was excavated by NRCS to retain water but was dry during sampling or was a dry zone located at the periphery of an inundated shallow water habitat that showed signs of regular cycles of inundation such as lack of vegetation or cracked and compacted soil. Remnant forest habitats were defined as mature bottomland hardwood forests that were consistently present on all historical satellite images available from Google Earth imagery. Tree planting habitats were defined as any area where NRCS restoration plans indicated trees were planted and remained at high densities at the time of sampling.

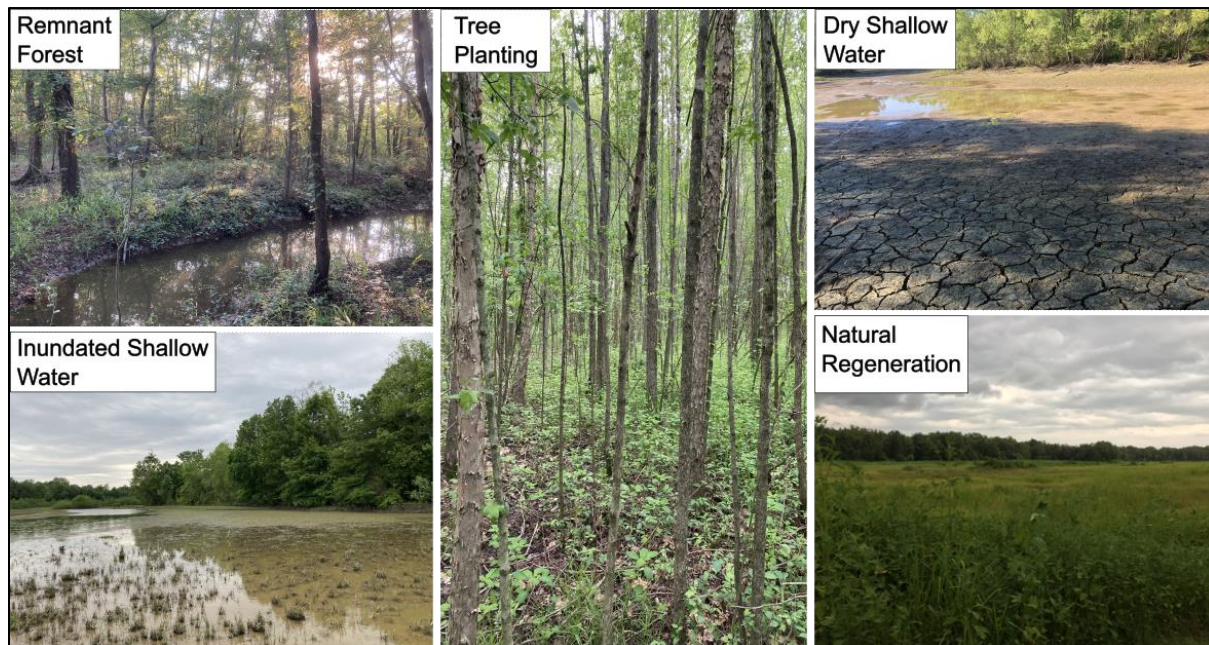


Figure 2.2 Examples of each habitat type sampled in the study.

Soil Core Distribution within a Site

Approximately 30 pairs of soil cores were collected from each site (60 total, 30 for incubation and 30 for soil properties determination). When possible, six cores were collected from each of the five habitats. This could not always be achieved due to access limitations and/or not all sites contained each habitat type. Therefore, the number of cores collected from each habitat on a site was variable and ranged from three to six cores per habitat. Cores were distributed within each habitat as evenly as possible to capture maximum within-habitat variability (Fig. 3.2). However, inundated shallow water habitats were only sampled along the water's edge as variable water depths and dangerous unconsolidated sediment/mud prevented uniform sampling.

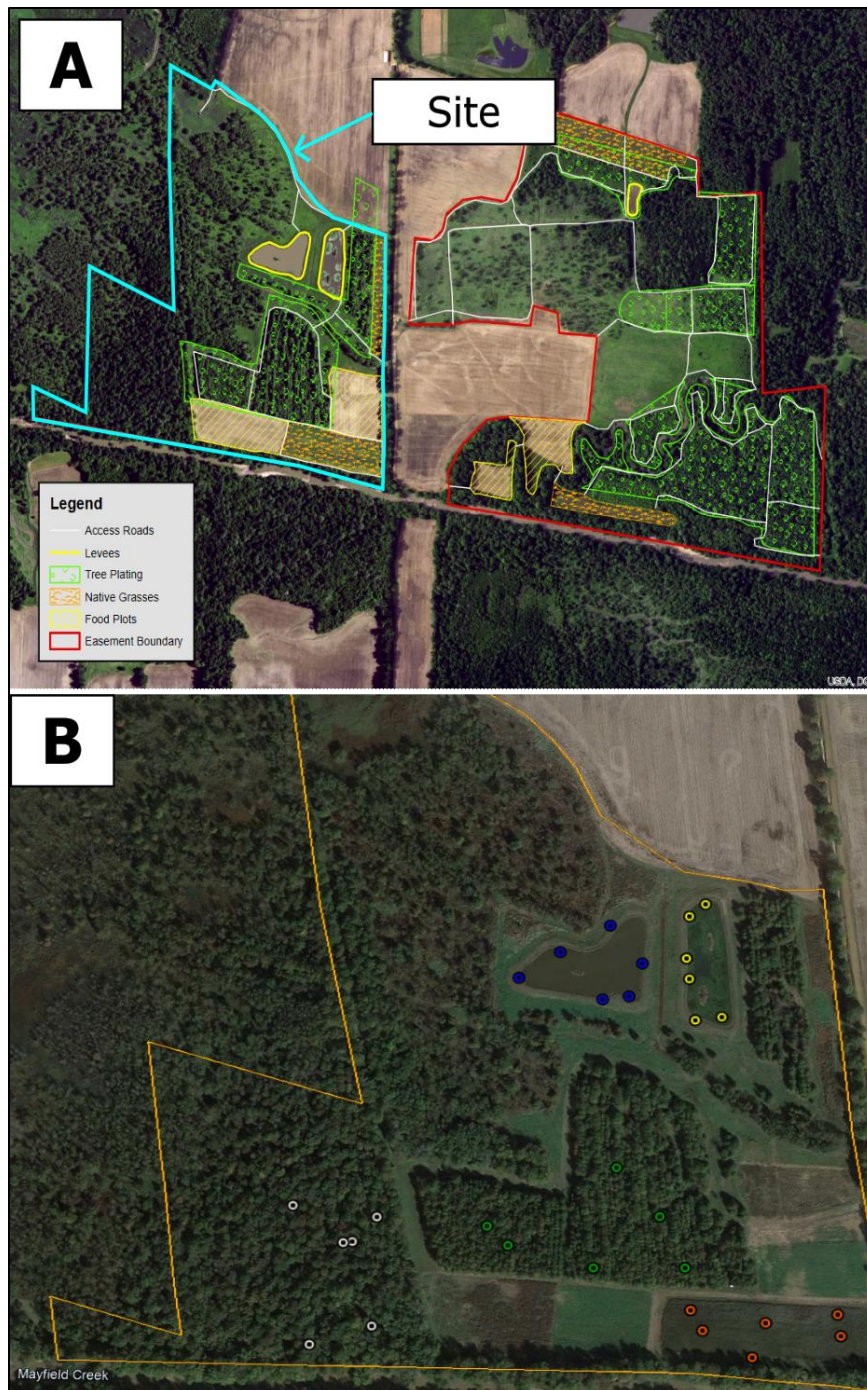


Figure 3.2 (A) An example of a NRCS site restoration plan for a WRP easement (restoration plan courtesy of NRCS), and **(B)** a typical restored wetland in western Tennessee with soil core collection locations (green pins = tree planting, blue pins = inundated shallow water, yellow pins = dry shallow water, white pins = remnant forest, orange pins = natural regeneration).

Soil Core Collection Protocols

A metal or PVC corer loaded with a 7.62 cm (width) by 30.48 cm (height) acrylic tube was driven into the soil or sediment to a depth of approximately 15 cm to collect roughly 584 cm³ of soil (Fig. 4.2). A sledgehammer was typically used to drive the metal corer into the soils. Cores collected from soft sediments were pushed into the sediment by hand whenever possible to minimize soil disturbance. For cores collected from inundated shallow water habitats, any empty space between the soil/sediment surface and the lid was filled with water from the collection location to minimize soil/sediment disturbance during transport to the lab. All cores were capped with a plastic lid upon collection. Core bottoms were sealed with a rubber cap and secured with a pipe strap to minimize atmospheric exchange and prevent water leakage during incubations (Fig. 5.2). Cores were immediately placed in a cooler with ice upon collection. Any overlaying water within the cores was siphoned out upon return to the lab.



Figure 4.2 Metal corer assembly

A secondary core was collected adjacent to the primary core at each sampling location following the collection procedures described above. Secondary cores were driven into the soil or sediment to a depth of at least 10 cm, and the top 5 cm was used to determine soil physical properties and nutrient content including moisture content, bulk density, pH, total C (TC), total N (TN), and extractable soil P at each sampling location.

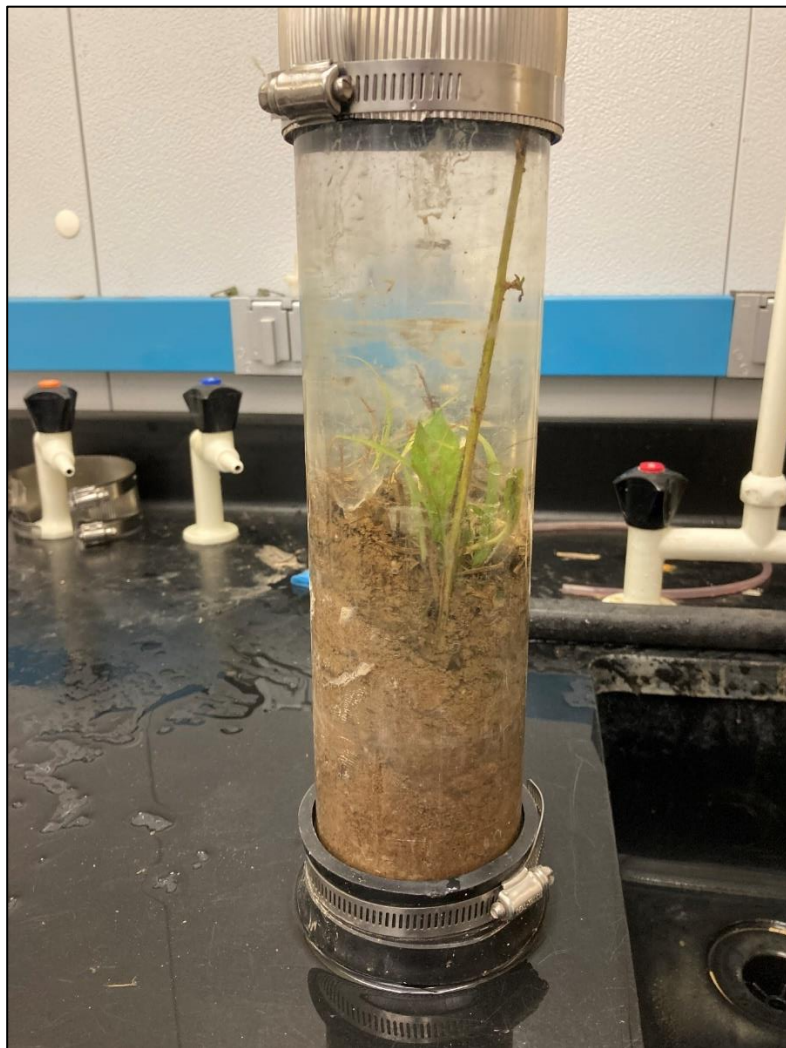


Figure 5.2 Image of a soil core.

Core Incubation Experimental Design

All primary core incubations began at 8:00am the morning after collection and lasted for 48 h total. Cores were incubated in a dark walk-in environmental chamber with ambient air temperature maintained at 24°C to simulate average regional summer air temperatures where cores were collected. Green-light head lamps were used during sample collection to reduce the potential for photosynthesis and associated oxygen bubble formation. Prior to incubation, cores

were sealed with acrylic tops containing inflow and outflow ports (1.0 mm diameter and 1.25 mm, respectively) (Fig. 6.2) adapted from Nifong et al. (2019). Masterflex L/S peristaltic pumps were used to pump water from a large cooler filled with laboratory-made water through each core (Fig. 7.2). Any water flowing out of the cores during non-sampling periods was discarded. Water flowed through all cores at a rate of approximately 2 mL min^{-1} to produce an approximately six-hour water residence time (the amount of time for water in the core to be completely replaced). Individual outflow rates for each core were measured at each sampling time point to account for potential differences in flow rates among the cores. Three lines of inflow tubing not connected to an incubation core were also sampled for dissolved NO_3^- , PO_4^{3-} , and O_2 . Dissolved nutrient and O_2 concentrations measured from these lines (referred to as inflow concentrations) were used to quantify NO_3^- , PO_4^{3-} , and dissolved O_2 concentrations flowing into each core. Measuring inflow concentrations was necessary to calculate the proportional change in nutrient or gas concentration attributed to a soil core.

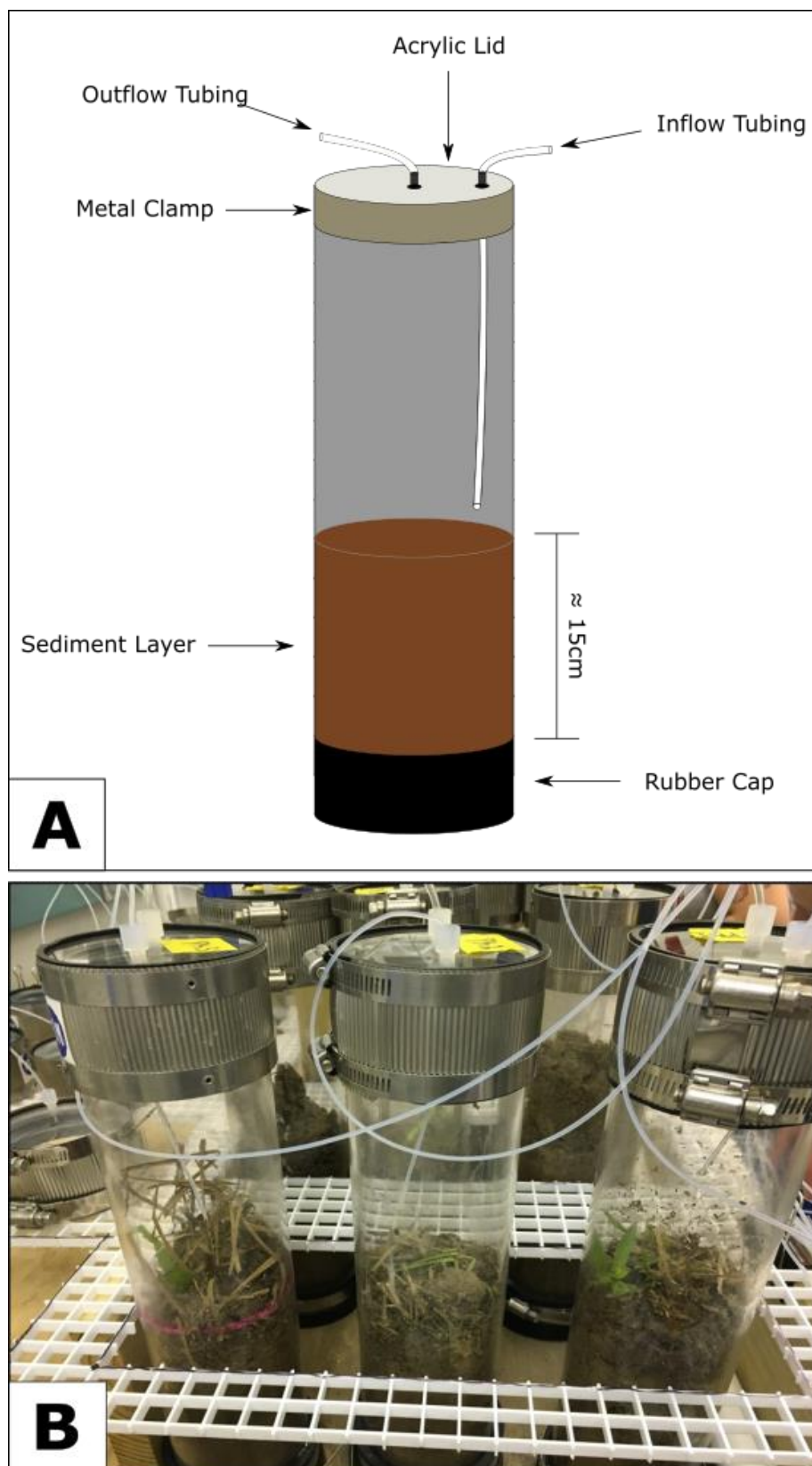


Figure 6.2 (A) Diagram of an incubation core and (B) image of incubation cores

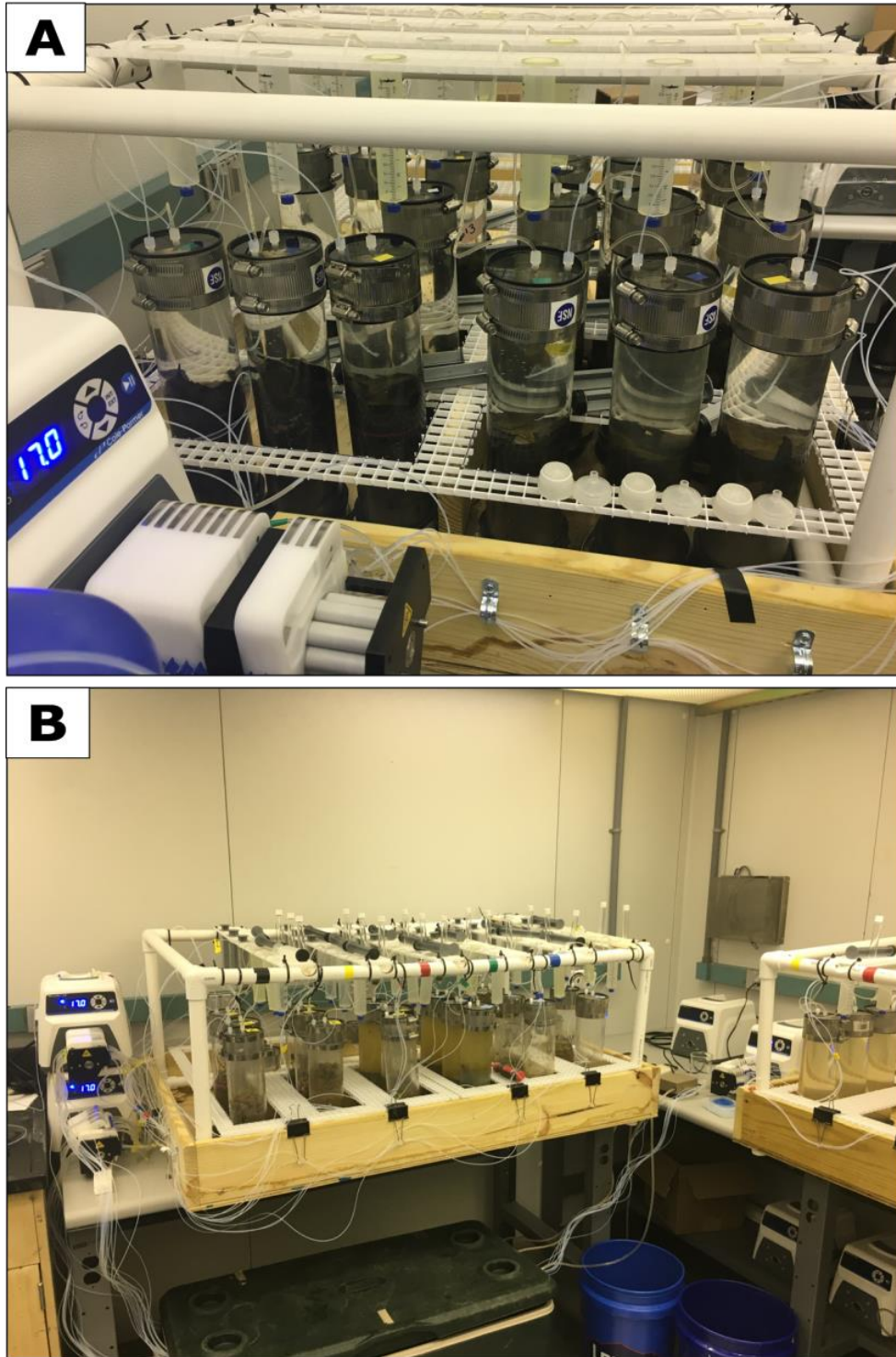


Figure 7.2 Flow-through incubation system with incubating cores viewed from (A) side nearest the peristaltic pumps and (B) front of the of the recirculating system.

Data from long-term United States Geological Survey (USGS) monitoring of the Obion River, Tennessee and Bayou de Chein River, Kentucky, were used to determine a chemical profile of typical floodwater entering a restored wetland within the region. The chemical profile of major and trace ions was then used to create an incubation water solution that simulated water quality conditions of a typical flood (Table 1.2). Since nutrient uptake rates are correlated to ambient nutrient availability, sodium nitrate (NaNO_3^-) and potassium dihydrogen phosphate (KH_2PO_4) were added to the source water to raise N and P concentrations to $10 \text{ mg L}^{-1} \text{ NO}_3^- \text{-N}$ and $1 \text{ mg L}^{-1} \text{ PO}_4^{3-} \text{-P}$ so that neither limited uptake rates. Ensuring that neither N nor P was limiting provided an estimation of maximum nutrient retention potential in the cores and allowed for more direct comparisons among sites and habitats.

Table 1.2 Chemical profile of lab-made water for incubation experiment.

Compounds Added	mg L⁻¹
<u>Major Elements</u>	
KCl	3
KH ₂ PO ₄	4.4
MgSO ₄ *7H ₂ O	27
CaCl ₂	20
NaNO ₃	60
NaHCO ₃	70
<u>Trace Elements</u>	
MnCl ₂	0.5
Fe(NH ₄) ₂ (SO ₄) ₂ *6H ₂ O	3
CoCl ₂ *6H ₂ O	0.1
ZnSO ₄ 7H ₂ O	0.05
CuCl ₂ *2H ₂ O	0.02
NaMoO ₄ *2H ₂ O	0.03
<u>Dissolved Organic Carbon</u>	
C ₆ H ₁₂ O ₆	1

Lab Protocols for Dissolved Nutrient and Gas Sampling and Analyses

Dissolved Nutrients

Nutrient samples were collected from core outflows at 6 (i.e., first water out of the core), 24, and 48 h of incubation. Sampling the initial water exiting the core was necessary to capture any potential nutrient releases during initial soil wetting. All nutrient samples were filtered using a syringe with a 0.45 or 0.7 μm -pore size glass-fiber filter. Dissolved nutrient samples were collected in 20-mL scintillation vials, placed in a cooler with ice during sampling, and frozen until analysis.

Soil Oxygen Demand Measurements

Soil oxygen demand was quantified by measuring O_2 flux within each incubation core, with negative O_2 flux rates indicating oxygen removal by the soil. Triplicate O_2 samples were collected in 12-mL glass exetainer vials at 24 and 48 h. Dissolved O_2 samples could not be collected at 6 h due to excessive air bubble formation within some cores resulting from ebullition from the soils upon submergence. Triplicate samples were collected at each time point at a minimum of 20 min apart. During collection each exetainer was overfill by at least three exetainer volumes (i.e., 36 mL) prior to sample collection to completely evacuate any atmospheric gases within the exetainer. After overfilling, inflow tubes were slowly removed from the exetainers to ensure that the exetainers filled below the meniscus, reducing the risk of atmospheric contact. Once the inflow tubing was completely removed from an exetainer, 180 μL of zinc chloride (ZnCl_2) were injected into the sample to inhibit microbial processes. For samples collected from sites 1, 2, and 4 during the 2021 sampling campaign and all sites sampled during

2022, sodium hydroxide (NaOH) was injected into each exetainer to precipitate carbon dioxide for greenhouse gas determination as part of a companion study (Brown and Duwadi, Dissertations in prep). Sodium hydroxide was always injected before the ZnCl_2 as ZnCl_2 can interfere with NaOH's ability to precipitate dissolved CO_2 . Samples were then quickly capped and checked to make sure no air bubbles were present in the exetainers. All dissolved gas samples were stored submerged in water to prevent atmospheric contamination and refrigerated at 4°C until analysis.

Dissolved Nutrients Analyses

Nitrate and PO_4^{3-} concentrations were measured via colorimetric analysis using a SEAL AQ400 Discrete Analyzer. Nitrate was measured via cadmium coil reduction to NO_2^- followed by a sulfanilamide reaction (EPA Method 353.2). Phosphate (reported as soluble reactive phosphorus (SRP)) was measured using the ascorbic acid method (EPA Method 365.1).

Dissolved O_2 Analysis

Dissolved O_2 concentrations were measured using Membrane-Inlet Mass Spectrometry (MIMS). Each sample was measured for dissolved O_2 and argon (Ar) gases. In anerobic sediments and water, changes in dissolved O_2 concentrations are driven by biological processes such as microbial uptake or physical processes, mainly temperature and barometric pressure. In contrast, changes in Ar concentrations are driven only by physical processes. Biologically-mediated changes in O_2 concentration within an incubation core can be separated from changes from physical processes by comparing changes in the Ar: O_2 ratio (Kana, Darkangelo, Hunt, et

al., 1994). The difference in Ar:O₂ ratios can be used to quantify O₂ flux (as SOD) within each incubation core.

Flux Rate Calculations

Dissolved nutrient and O₂ concentrations were scaled up to an aerial rate (reported as mg m² h⁻¹) using the following equation modified from (Speir et al., 2017) (Equation 1.2).

Equation 1.2:

$$Aerial\ Flux\ (mg\ m^{-2}\ h^{-1}) = \left(\frac{([Core]_{out} - [Core]_{in}) * Core\ flow}{Soil\ Area} \right)$$

where $[Core]_{out}$ and $[Core]_{in}$ are outflow and inflow concentrations (mg L⁻¹) of NO₃⁻, PO₄³⁻, and O₂ from the soil cores. $Core_{flow}$ is the flow rate of a core (L h⁻¹). $Soil\ Area$ is the surface area of an individual core (m²). Positive flux rates indicate a net gain of NO₃⁻, PO₄³⁻, or O₂ in the water column (i.e., nutrient release and O₂ production), and negative fluxes indicate a net loss from the water column (i.e., nutrient retention or O₂ removal) within a core. More negative O₂ flux rates correspond to higher SOD.

Soil Analyses

Soil Processing

Upon return to the lab, any water overlaying the secondary cores was siphoned out, and soils were transferred to individual aluminum sheets. The top 5 cm of soil were then separated using a spackle knife, and rocks and coarse woody debris were removed by hand. These 5-cm

sections were then partitioned into 10-g subsamples for soil pH measurements and 30-g subsamples for moisture content and bulk density determination.

A third subsample was also partitioned from each 5-cm section and used to determine soil total C (TC), total N (TN), and extractible P content. Overall soil masses varied among the cores due to differences in soil type and compaction, and some cores had little soil left after the 10- and 30-mg partitions were removed. Therefore, subsample weights for soil nutrient analysis could not be standardized. While this resulted in differences in subsample masses, the amount of soil analyzed from each subsample was consistent across the cores as very little soil was used for each analysis.

Soil pH

The 10-g subsamples for pH measurements were manually homogenized using a spackle knife prior to analysis. Following homogenization, soil pH was measured using a handheld pH meter in a 1:2 soil-to-water ratio equilibrated for 30 min (Reddy et al., 2013). The 10-g subsamples were first transferred to a beaker and weighed on an analytical balance. Twenty mL of ultra-pure water was then added to the beaker to create a soil slurry. The slurry was stirred for approximately 10 s using a stainless-steel mini whisk every 10 min over a 30 min period. After 30 min of settling, the pH meter was submerged in the slurry and readings were recorded once stabilized, typically after around one min.

Soil Moisture Content and Dry Bulk Density

The 30-g subsamples for soil moisture and dry bulk density measurements were placed in an aluminum tin following partitioning and weighed to the nearest hundredth mg using an analytical balance. Subsamples were then dried at 105° C until all water was evaporated and reweighed. Soil moisture content was measured using the thermogravimetric method (S.R. Evett et al., 2008) and expressed using the following equation (Equation 2.2) as the ratio of water lost to drying to the total soil volume.

Equation 2.2:

$$\text{Soil Moisture Content (g g}^{-1}\text{ of soil)} = \frac{\text{weight of water lost to evaporation (g)}}{\text{dry weight of sample (g)}}$$

Soil bulk density was determined using the ratio of the dry weight of a known amount soil to its volume (Blake & Hartge, 1986). Soil volume was calculated by multiplying the area of the acrylic core (45.58 cm²) by the depth of the soil section (5 cm). The following equation was then used to calculate dry soil bulk density (Equation 3.2):

Equation 3.2:

$$\text{Dry Bulk Density (g cm}^{-3}\text{)} = \frac{\text{mass dry weight (g)}}{\text{soil volume (cm}^3\text{)}}$$

Soil Nutrients

Subsamples for soil nutrient analysis were dried at 60°C for 72 h, homogenized using a soil grinder, and sifted through a 2 mm mesh screen to remove rocks and large roots. Following homogenization, subsamples were transferred into 20-mL plastic scintillation vials and mailed to the Kansas State University Soil Testing Lab for analysis. Soil TN and TC content were analyzed using the catalytic combustion method (Association of Official Analytical Chemist, 2000; Tiessen & Moir, 1993). Extractable soil P was analyzed using Mehlich-3 extraction followed by colorimetric analysis (Mehlich, 1984).

Data Analyses

Nutrient Flux Rate and Soil Data Averaging, Outlier Removal, and Missing Data

To obtain a single value for NO_3^- , PO_4^{3-} , and O_2 fluxes, and soil properties for each habitat, data from all cores within a single habitat at a given site were averaged (Fig. 8.2). Averaging data from all cores collected within a single habitat at a site reduced variability and prevented pseudoreplication as habitats were the experimental units whereas individual cores were measurement units. Nitrate and PO_4^{3-} flux rates were highly variable among cores both within a habitat at a given site and across all sites, leading to the presence of outliers that could have greatly biased mean flux rate estimates for the habitats. Therefore, any individual core flux rates outside the 2.5% and 97.5% quantiles at each sampling time point were removed. Additionally, cores with missing data were omitted before averaging within habitats.

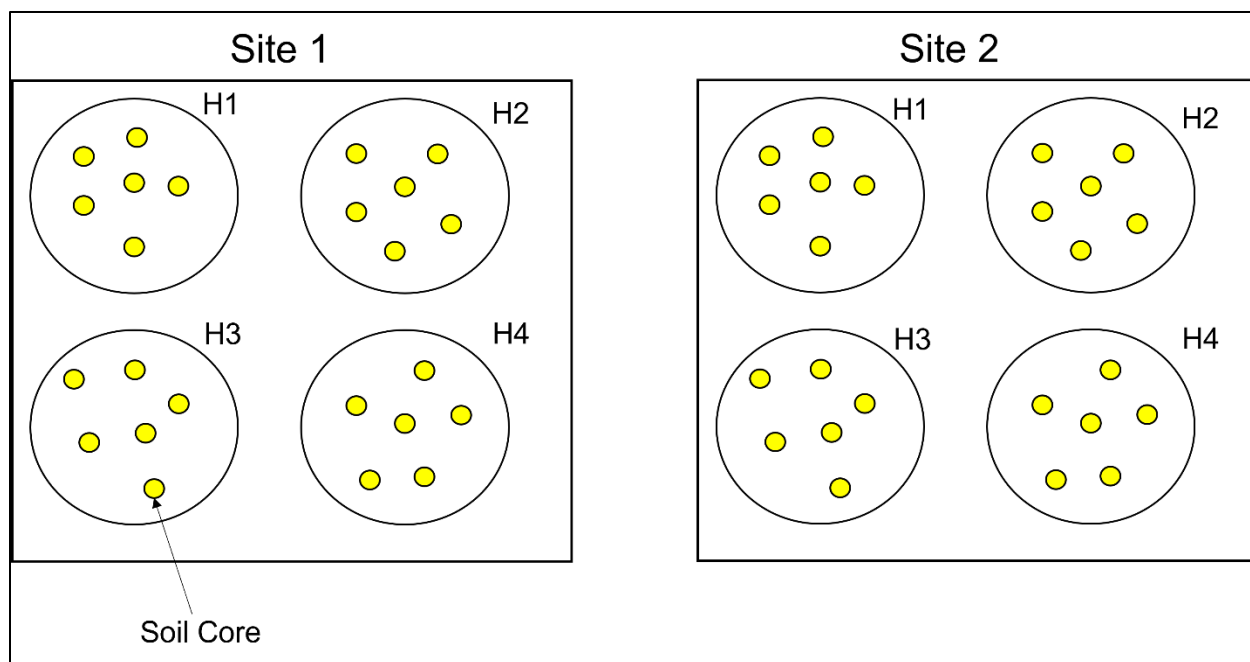


Figure 8.2 Conceptual diagram illustrating core groupings within the habitats. Data collected from multiple core sampling locations (represented by yellow circles) within a habitat (H) at a specific site were averaged, yielding a single value for each replicate.

Statistical Analysis, Model Specifications, Selection Procedures, and Post-hoc Comparisons

ANCOVA's were used to assess potential differences in NO_3^- and PO_4^{3-} flux rates among the habitats at each time point and determine if the covariates measured (e.g., soil parameters and SOD) affected flux rates estimations. All analyses were performed using *R* statistical software (R Core Team, 2022). First, data were analyzed using generalized least squares (GLS) models. Generalized least squares models were selected for their ability to correct for correlated errors within predictor variables by assigning variance-covariance error structures (Zuur et al., 2009). A variance structure was assigned to the “habitat” parameter for each model using the *varIdent* command in the *nlme* package (Pinheiro et al., 2022) to correct for violations of homogeneity.

Model selection was performed using log-likelihood ratio tests. Final models were fit using restricted maximum likelihood (REML) estimations.

An ANOVA with type III sums of squares was applied to the final models for NO_3^- and PO_4^{3-} at each time point to estimate mean flux rates for each habitat and determine if covariates included in the final model affected flux rate estimations. Type III sums of squares were used to correct for imbalances among habitat replicates (natural regeneration $n = 6$, remnant forest $n = 16$, dry shallow water $n = 15$, inundated shallow water $n = 18$, tree planting $n = 18$). The *emmeans* function in the *emmeans* package was used to predict estimated marginal mean flux rates (herein referred to as predicted means) for each habitat (Lenth, 2022). Post-hoc pairwise comparisons were made using Tukey's Honestly Significant Difference (HSD) tests.

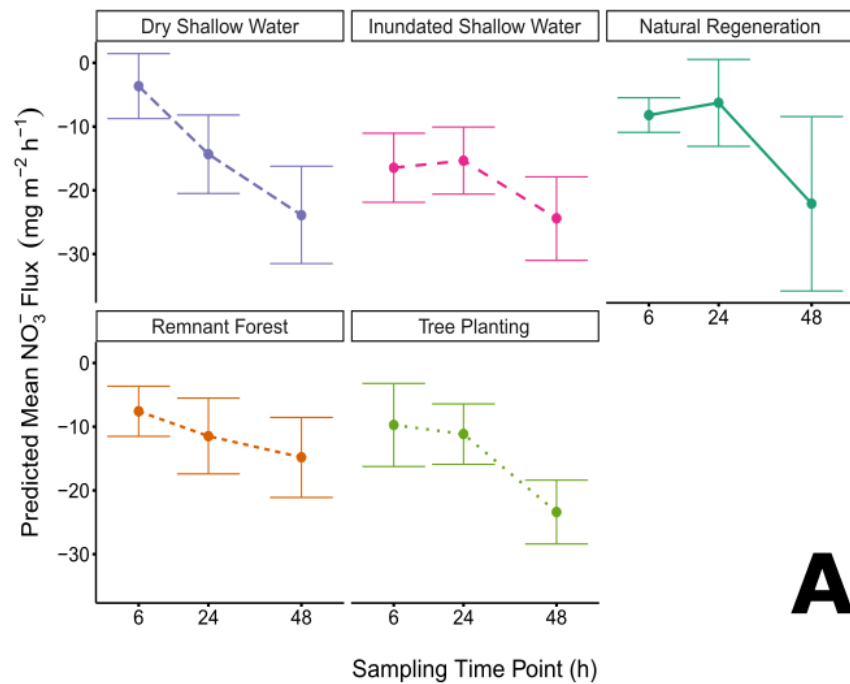
Model Parameters and Interaction Terms Included in the Analyses

Covariates included in each GLS model were soil bulk density, soil TN, TC, and P, soil moisture, soil pH, and interaction terms between habitat and soil moisture and habitat and soil pH. As this study sought to determine differences in nutrient flux rates, habitat was considered a variable of interest rather than a covariate. These interaction terms were selected based on ecological knowledge and data exploration. Prior to analysis, bulk density and soil P were log-transformed to reduce the effect of outliers and correct for patterns in model residuals. For the analysis of PO_4^{3-} flux at 6 h, soil moisture was log transformed to correct for patterns in the residuals. Additionally, soil TC could not be included in the model for NO_3^- flux at 6 h due to degrees of freedom limitations as one site was missing flux data for the 6-h sampling time point. SOD was also included for NO_3^- and PO_4^{3-} flux analyses at 24 and 48 h.

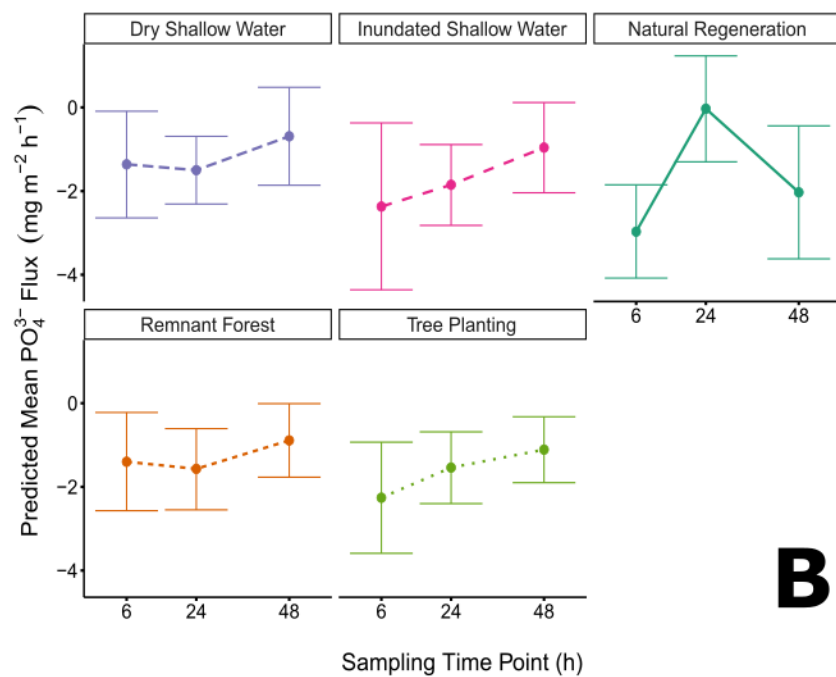
Results

Overall Trends in Nitrate and Phosphate Retention

All habitats retained NO_3^- and PO_4^{3-} at each sampling time point, but flux rates were variable within and among habitats. Nitrate retention increased in all habitats throughout the incubations except in inundated shallow water and natural regeneration habitats between 6 and 24 h (-1.94 and $-1.11 \text{ mg m}^{-2} \text{ h}^{-1}$, respectively) (Fig. 9.2). However, NO_3^- retention was greatest in inundated shallow water habitats across all time points. After 48 h of incubation, all habitats approached a mean NO_3^- retention rate of approximately $23.5 \text{ mg m}^{-2} \text{ h}^{-1}$ excluding remnant forest which lagged the other habitats by approximately $8.2 \text{ mg m}^{-2} \text{ h}^{-1}$. Trends in PO_4^{3-} retention across the incubations were less clear with retention increasing in some habitats as the incubations progressed, while retention rates between sampling time points in other habitats varied. Nitrate retention for all habitats was greatest at 48 h whereas PO_4^{3-} retention was generally greatest at 6 h. Nitrate flux rates were most variable at 48 h, whereas PO_4^{3-} flux rates were highly variable at all time points (Fig. 9.2). When pairwise comparisons were applied to the data, there was a significant difference in NO_3^- retention among the habitats only at 6 hours, with inundated shallow water retaining on average $9.98 \text{ mg m}^{-2} \text{ h}^{-1}$ more NO_3^- than all habitats except tree plantings. There were no differences in PO_4^{3-} retention among the habitats at any sampling time point. Variability in NO_3^- and PO_4^{3-} flux rates within the habitats made it difficult for the models to precisely predict mean flux rates, as indicated by the wide confidence intervals at all sampling time points.



A



B

Figure 9.2 Time series plot of (A) predicted mean NO_3^- and (B) PO_4^{3-} flux rates by habitat and sampling time point

Nitrate Flux Results

Trends in 6 h Nitrate Flux

All habitats retained NO_3^- at 6 h of incubation with inundated shallow water retaining the most NO_3^- ($16.46 \text{ mg m}^{-2} \text{ h}^{-1}$) (Fig 10.2). However, confidence intervals for dry shallow water habitats crossed zero, indicating a potential mean release of NO_3^- . Mean NO_3^- flux rates differed among the habitats (Chi-squared_(4,63) = 11.81, p value = 0.019) after controlling for soil pH, moisture content, and an interaction between soil pH and habitat type. Inundated shallow water habitats retained 101% ($p = 0.046$), 117% ($p = 0.060$), and 351% ($p = 0.008$) more NO_3^- on average than natural regeneration, remnant forest, and dry shallow water habitats, respectively. Inundated shallow water habitats also retained an average of 69% more NO_3^- than tree plantings; however, flux rates were not statistically different. High soil moisture content enhanced NO_3^- retention in all habitats (Table 2.2). The effect of soil pH on NO_3^- retention varied both in strength and direction across habitats (Chi-squared_(4,63) = 9.61, $p = 0.047$) (Fig. 10.1).

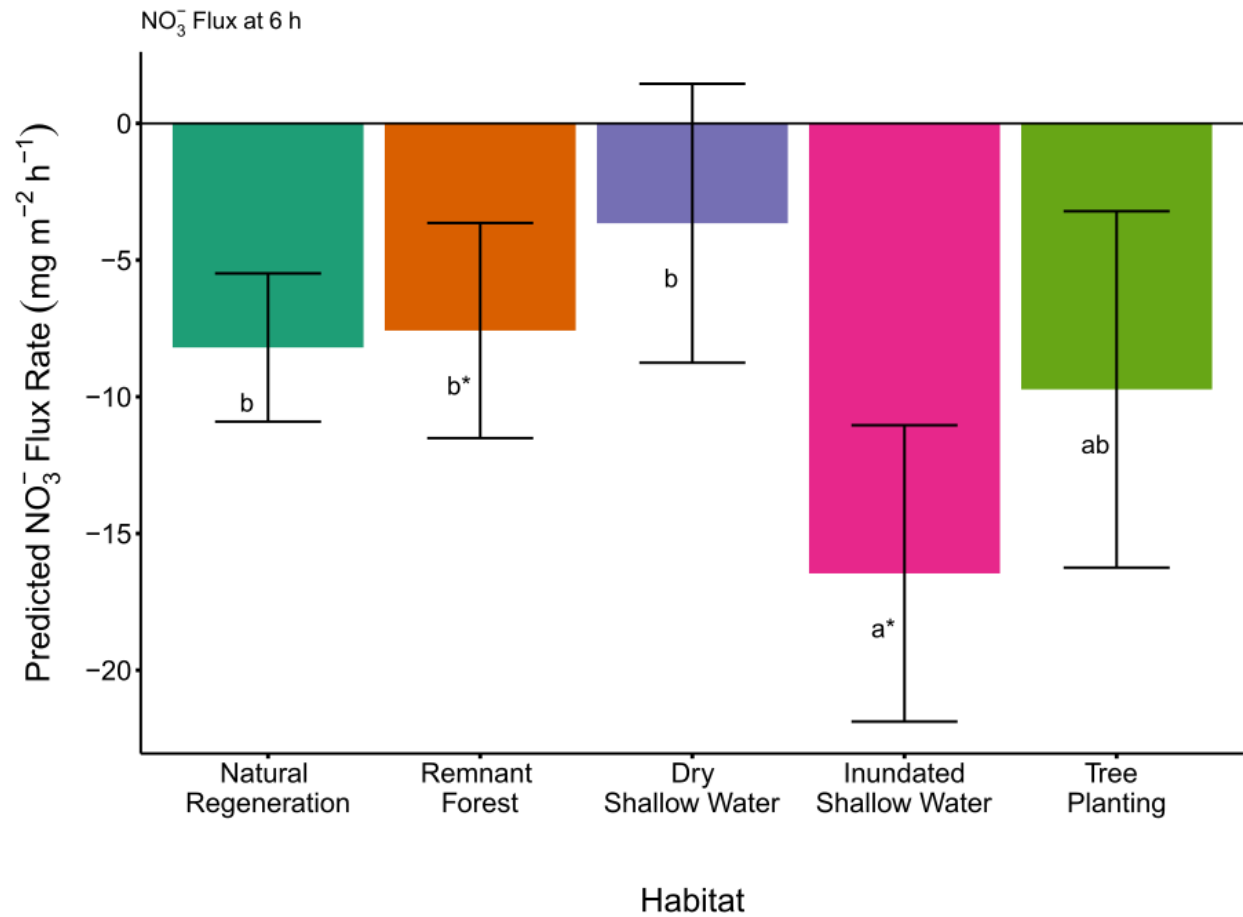


Figure 10.2 Predicted mean NO₃⁻ flux rates by habitat at 6 h. Different letters indicate significant differences ($\alpha = 0.05$); starred letters indicate significant differences at $\alpha = 0.1$. Error bars represent 95% confidence intervals.

Table 2.2 ANCOVA results for 6 h NO₃⁻ flux rates

Source of Variation	DF	Chi-squared Statistic	<i>p</i>
Intercept	1	21.61	<0.001
Habitat	4	11.81	0.019
Soil pH	1	23.82	<0.001
Soil Moisture	1	29.05	<0.001
Habitat:Soil pH	4	9.61	0.048
Habitat:Soil Moisture	4	5.23	0.264

Soil pH and Habitat Interaction.

Increases in soil pH for remnant forest correlated with NO₃⁻ release (positive flux rate). Conversely, increases in soil pH increased NO₃⁻ retention (negative flux rate) in natural regeneration and tree planting habitats. Nitrate retention was greatest in remnant forest habitats at low soil pH (~4), and remnant forests began to release NO₃⁻ when soil pH approached 7 (Fig. 11.2). Nitrate retention in natural regeneration and tree planting habitats was lower compared to the other habitats at low soil pH (~4) but began to retain more NO₃⁻ than the other habitats when soil pH was $\geq \sim 6.5$. The effect of soil pH on NO₃⁻ flux was weaker for inundated and dry shallow water habitats with little change in flux rates observed across the pH gradient.

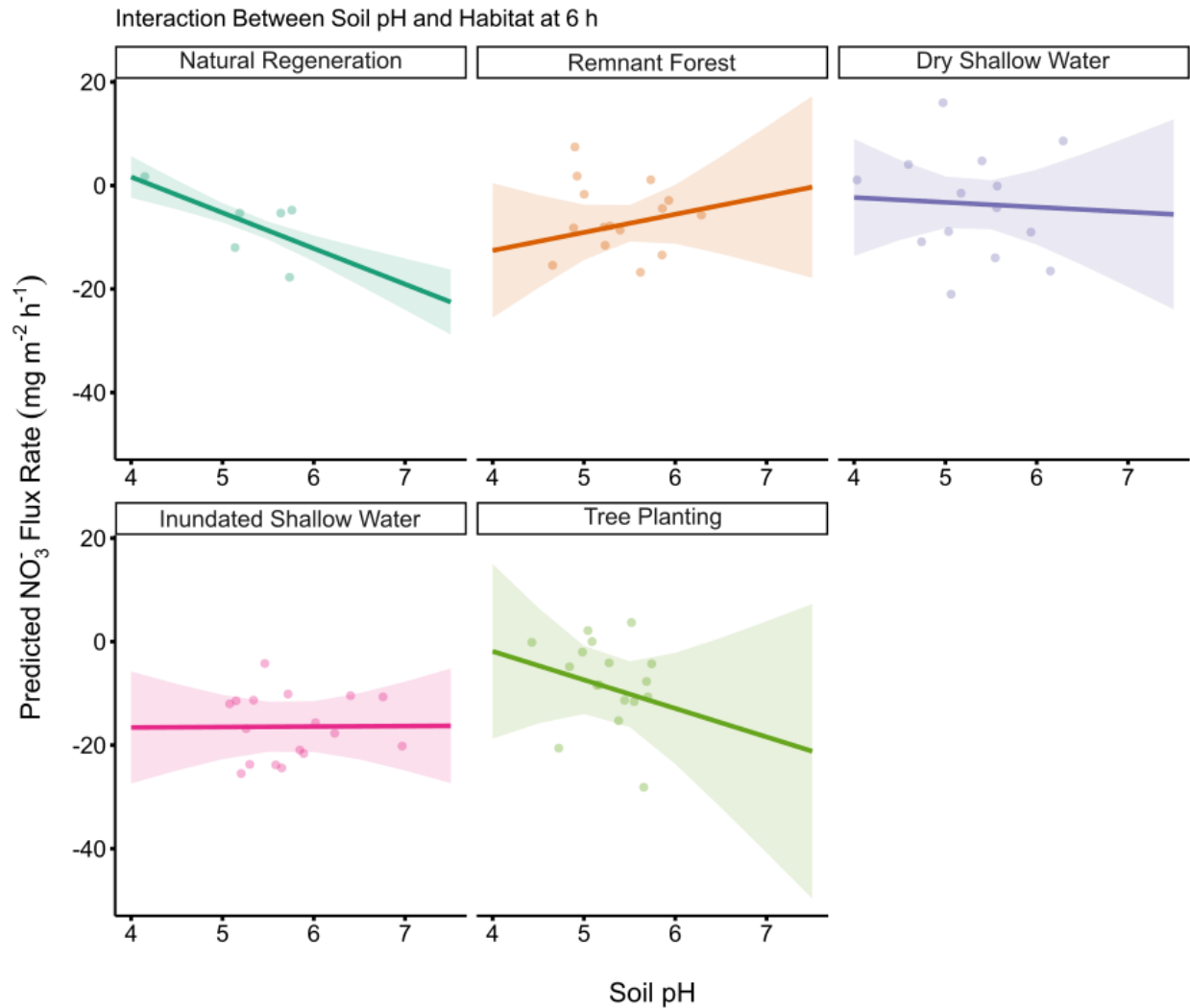


Figure 11.2 Interaction plots of the effect of soil pH on NO_3^- flux at 6 h for each habitat. Bands represent 95% confidence intervals. Points are raw flux rates (points located outside the predicted range are not shown).

Nitrate Flux at 24 h

All treatments retained NO_3^- after 24 h with inundated shallow water habitats retaining the most NO_3^- on average ($15.35 \text{ mg m}^{-2} \text{h}^{-1}$). Mean NO_3^- retention increased between 6 and 24 h

in remnant forest, dry shallow water, and tree planting habitats by 46%, 292%, and 15%, respectively (Fig. 12.2). Natural regeneration and inundated shallow water habitats retained less NO_3^- at 24 h compared to 6 h (24% and 7% decrease, respectively). Confidence intervals for natural regeneration crossed zero, indicating that this habitat may have released NO_3^- at 24 h. However, this likely reflects uncertainty in the model rather than potential mean NO_3^- release as all averaged flux rates for natural regeneration at 24 h were negative (i.e., retaining NO_3^-) (Sup. Table 1.2). Mean NO_3^- flux rates among all habitats excluding natural regeneration became more similar at 24 h compared to 6 h, ranging from -11 to -15 $\text{mg m}^{-2} \text{h}^{-1}$ (tree planting and inundated shallow water habitats, respectively). Nitrate retention in natural regeneration habitats lagged the others by -5 to -9 $\text{mg m}^{-2} \text{h}^{-1}$. Soil moisture, P content, and SOD were included in the final model for NO_3^- flux at 24 h; however, only SOD significantly affected mean NO_3^- retention rate predictions (Table 3.2). Increases in SOD enhanced NO_3^- retention across all habitat types, but there were no differences in mean flux rates among the habitats after controlling for SOD (Chi-squared $_{(4,69)} = 6.40$, $p = 0.171$).

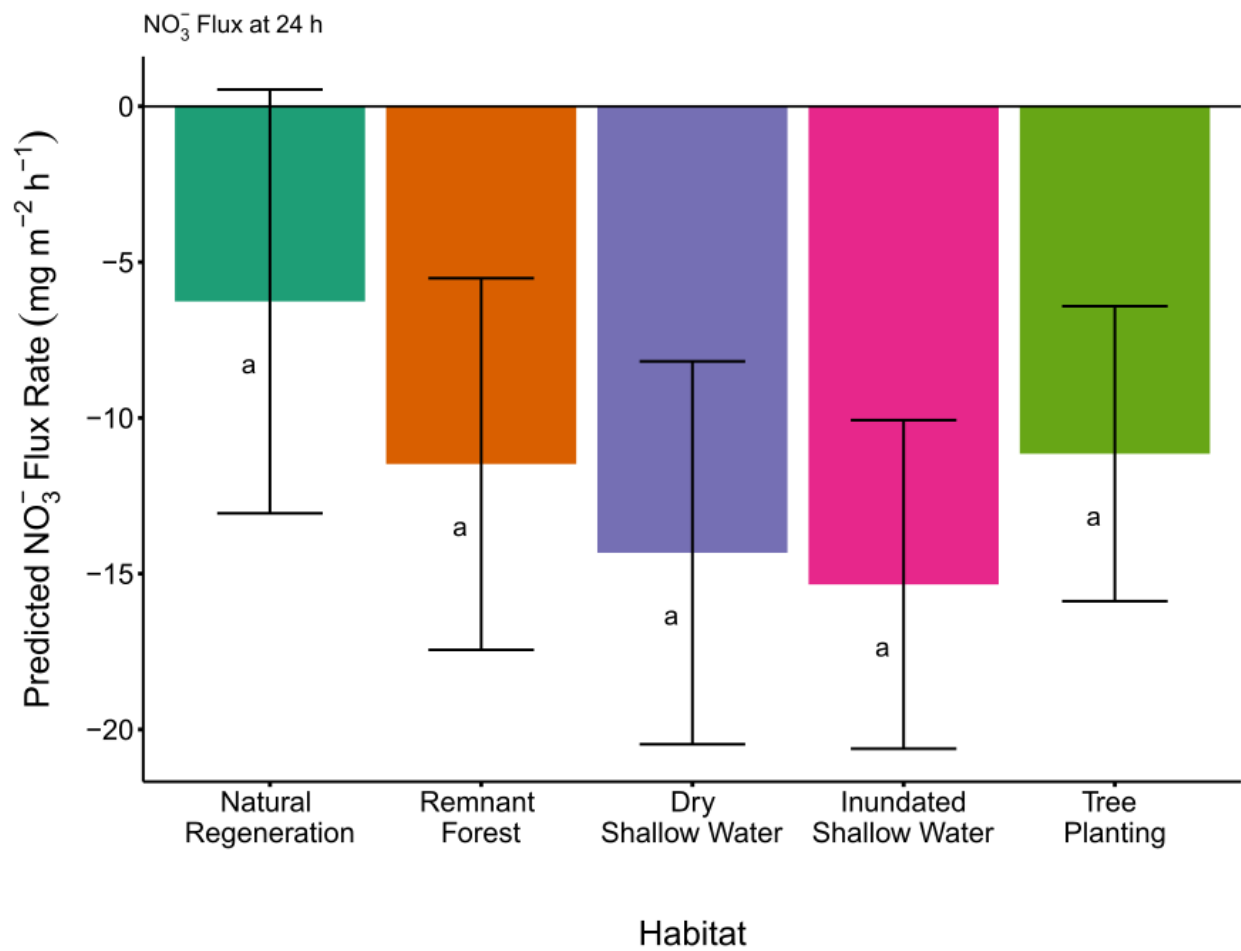


Figure 12.2 Predicted mean NO₃⁻ flux rates by habitat at 24 h. Different letters indicate significant differences ($\alpha = 0.05$). Error bars represent 95% confidence intervals.

Table 3.2 ANCOVA table for 24 h NO₃⁻ flux rates

Source of Variation	DF	Chi-squared Statistic	<i>p</i>
Intercept	1	0.11	0.741
Habitat	4	6.40	0.171
Log(Soil Phosphorus)	1	1.29	0.256
Soil Moisture	1	0.21	0.643
SOD	1	12.35	<0.001

Trends in 48 h Nitrate Flux

All habitats retained NO₃⁻ after 48 h with inundated shallow water habitats retaining the most NO₃⁻ (24.40 mg m⁻² h⁻¹). Between 24 and 48 h, increases in retention rates across habitats ranged from 29% to 253 % (remnant forest and natural regeneration, respectively). All treatments had similar predicted mean NO₃⁻ flux rates ranging from -22 to -24 mg m⁻² h⁻¹ (natural regeneration and inundated shallow water, respectively) excluding remnant forest which lagged the other habitats (predicted mean NO₃⁻ flux rate = -14.8 mg m⁻² h⁻¹) (Fig. 13.2). Mean NO₃⁻ flux rates at 48 h were more variable in natural regeneration habitats than in others with error bars almost twice the size of those for the other habitats. At 48 h, mean NO₃⁻ retention among the habitats was influenced by soil P, TN, and TC (Table 4.2). Increases in soil P and TN content and SOD correlated with an increase in NO₃⁻ retention across all habitats. Conversely, increases in soil TC correlated with a decreased NO₃⁻ retention. There were no differences in predicted mean NO₃⁻ flux rates among the habitats after controlling for soil P, TN, TC, and O₂ flux (SOD).

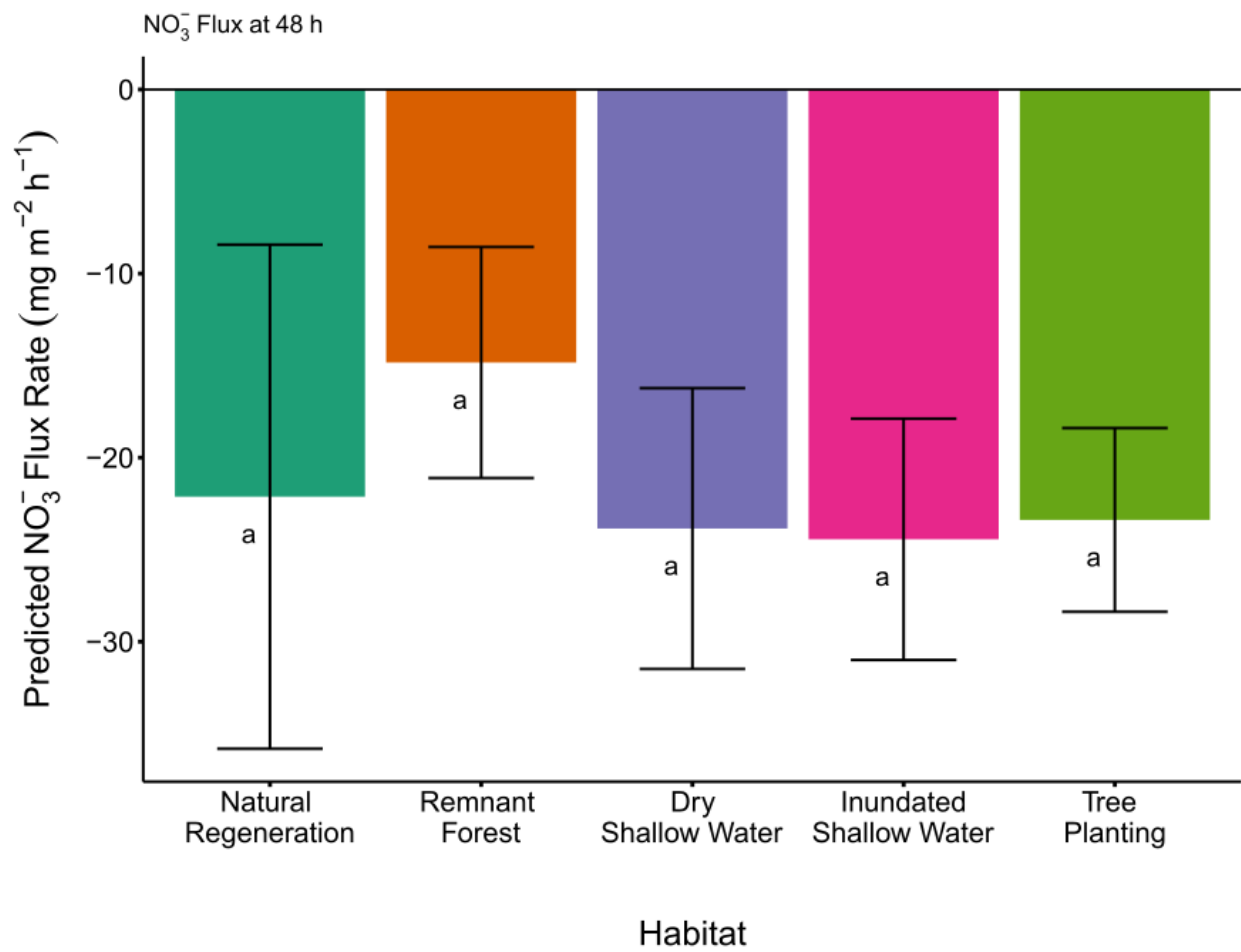


Figure 13.2 Predicted mean NO₃⁻ flux rates by habitat at 48 h. Different letters indicate significant differences ($\alpha = 0.05$). Error bars represent 95% confidence intervals.

Table 4.2 ANCOVA table for 48 h NO₃⁻ flux rates

Source of Variation	DF	Chi-squared Statistic	<i>p</i>
Intercept	1	0.13	0.719
Habitat	4	6.41	0.171
Log(Soil P)	1	4.51	0.034
Soil TN	1	11.11	<0.001
Soil TC	1	10.95	<0.001
SOD	1	8.83	0.002

Phosphate Flux Rates

Trends in 6 h Phosphate Flux

All habitats retained PO₄³⁻ at 6 h of inundation. Natural regeneration habitats retained the most PO₄³⁻ with a predicted mean flux rate of -3.0 mg m⁻² h⁻¹ (Fig. 14.2). Mean PO₄³⁻ flux rates among the habitats were variable, ranging from -1.36 to -2.97 mg m⁻² h⁻¹ (dry shallow water and natural regeneration, respectively). Phosphate retention was much lower in remnant forest and shallow water habitats compared to the others; however, confidence intervals for all habitats were large. At 6 h, PO₄³⁻ retention was influenced by soil moisture and P content. High soil moisture content correlated with an increase in PO₄³⁻ retention; however, the strength of this effect varied across habitats (Table 5.2). There were differences in mean PO₄³⁻ flux rates among habitats type (Chi-squared_(4,68) = 17.91, *p* value = 0.001) after controlling for soil moisture and

the interaction between soil moisture and habitat; however, these differences were not significant when pairwise comparisons were applied to the model.

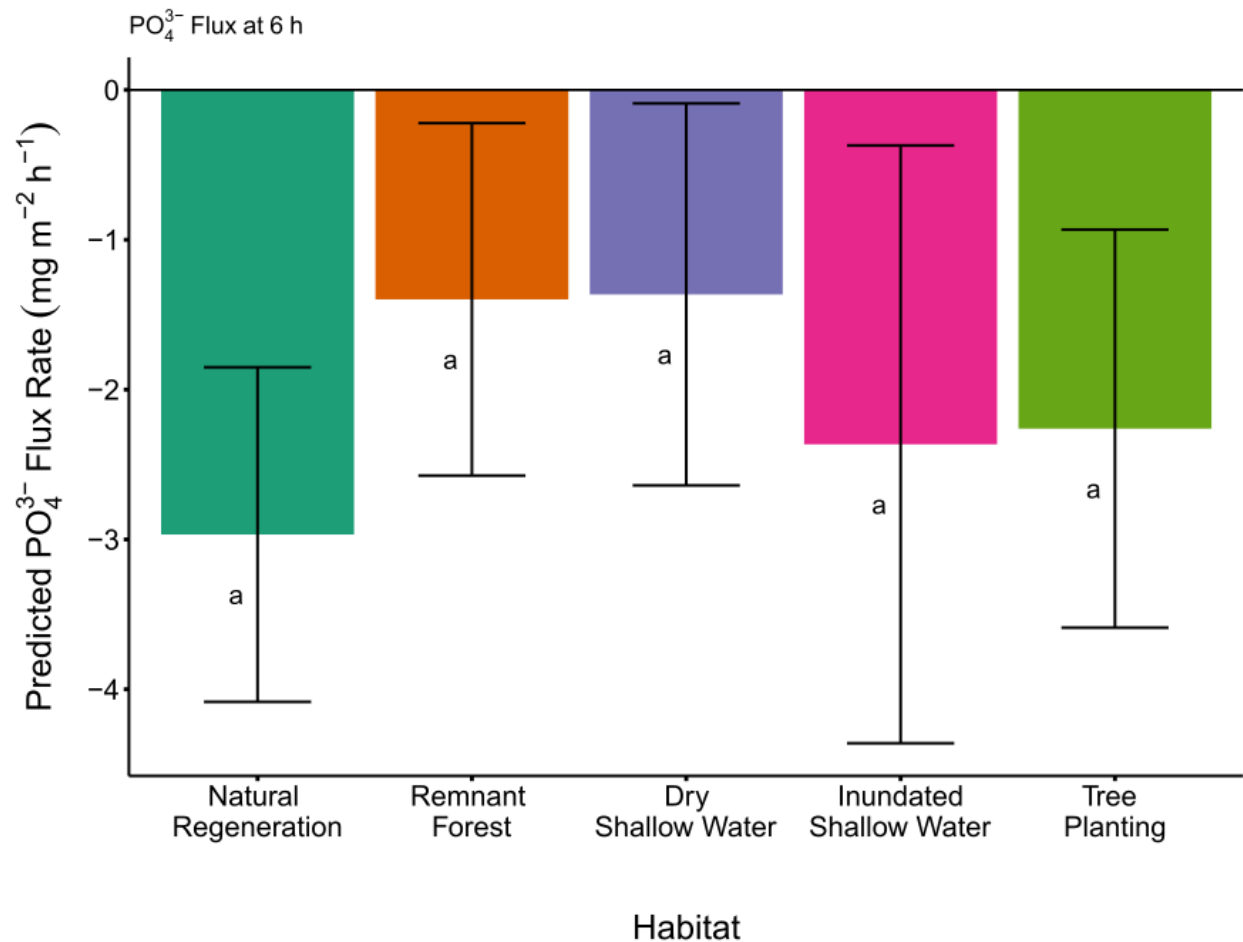


Figure 14.2 Predicted mean PO₄³⁻ flux rates by habitat at 6 h. Different letters indicate significant differences ($\alpha = 0.05$). Error bars represent 95% confidence intervals.

Table 5.2 ANCOVA table for 6 h PO₄³⁻ flux rates

Source of Variation	DF	Chi-squared Statistic	<i>p</i>
Intercept	1	13.95	<0.001
Habitat	4	17.91	0.001
Log(Soil Moisture)	1	66.96	<0.001
Log(Soil P)	1	0.68	0.411
Habitat:Log(Soil Moisture)	4	20.86	<0.001

Soil Moisture and Habitat Interaction.

Increases in soil moisture generally had little effect on mean PO₄³⁻ flux rates among the habitats excluding natural regeneration (Fig. 15.2). Increases in soil moisture increased PO₄³⁻ retention in natural regeneration. The slight correlation between increasing PO₄³⁻ retention and soil moisture observed in the tree planting habitats was likely the result of an outlying soil moisture value. Therefore, the close correlation between soil moisture and PO₄³⁻ retention in natural regeneration habitats may have inflated the significance of this interaction term in the model.

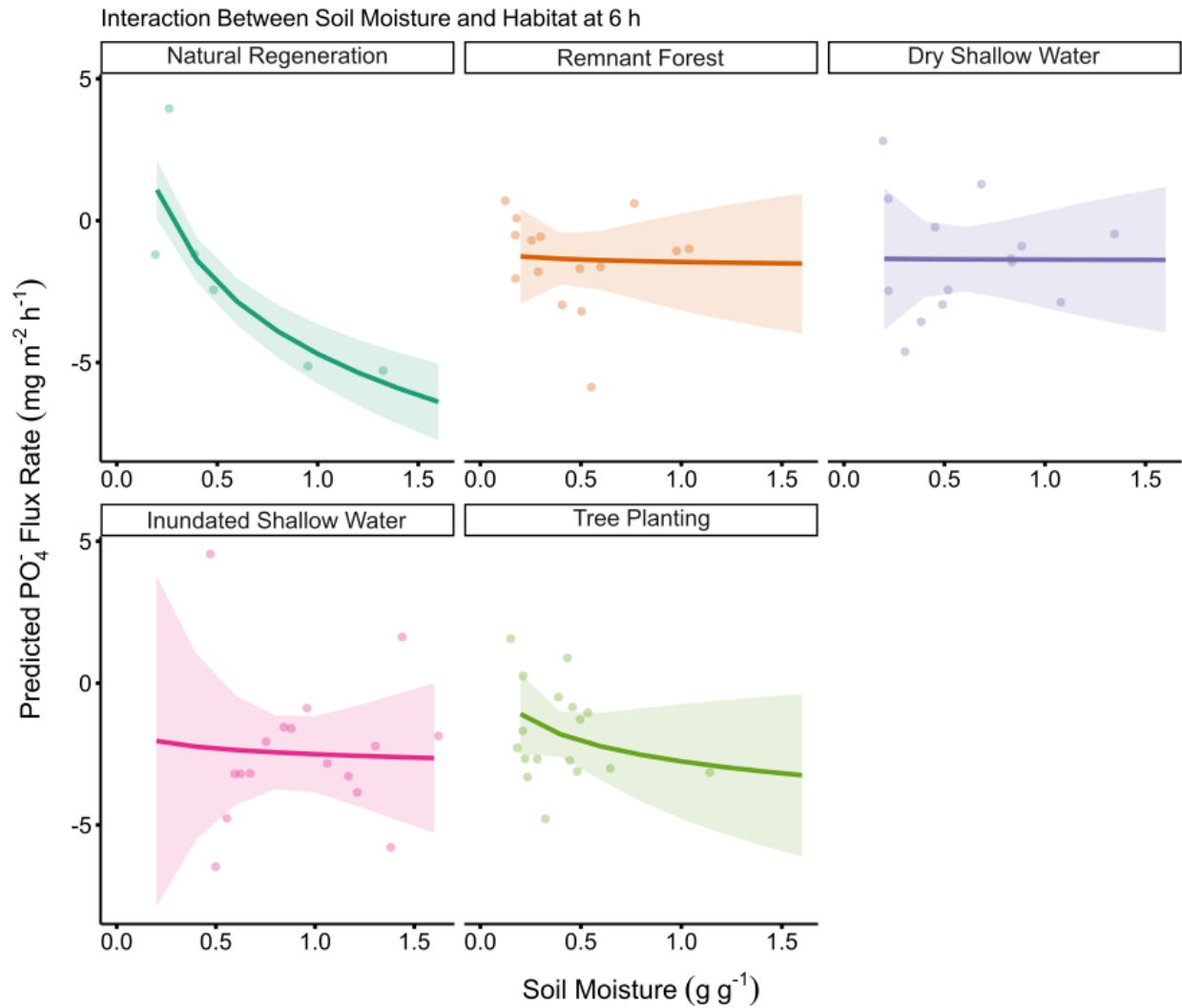


Figure 15.2 Interaction plot showing the effect of soil moisture on PO_4^{3-} flux at 6 h for each habitat. Bands represent 95% confidence intervals. Points are the raw flux rates (points located outside the predicted range are not shown).

Trends in 24 h Phosphate Flux

All habitats retained PO_4^{3-} after 24 h with inundated shallow water habitats retaining the most PO_4^{3-} ($1.9 \text{ mg m}^{-2} \text{h}^{-1}$). Predicted mean flux rates were similar among all habitats except

natural regeneration (Fig. 16.2) and ranged from -0.03 to $-1.9 \text{ mg PO}_4^{3-} \text{ m}^2 \text{ h}^{-1}$ (natural regeneration and inundated shallow water, respectively). Between 6 and 24 h, PO_4^{3-} retention in remnant forest and dry shallow water habitats increased by 12% and 10%, respectively. Conversely, PO_4^{3-} retention decreased in natural regeneration, inundated shallow water, and tree planting habitats by 99%, 22%, and 32 %, respectively. Natural regeneration habitats retained much less PO_4^{3-} compared to other habitats with a predicted mean flux rate of $-0.03 \text{ mg PO}_4^{3-} \text{ m}^{-2} \text{ h}^{-1}$; however, confidence intervals were large. Further, confidence intervals for natural regeneration crossed zero, indicating a potential mean release of PO_4^{3-} at 24 h of incubation.

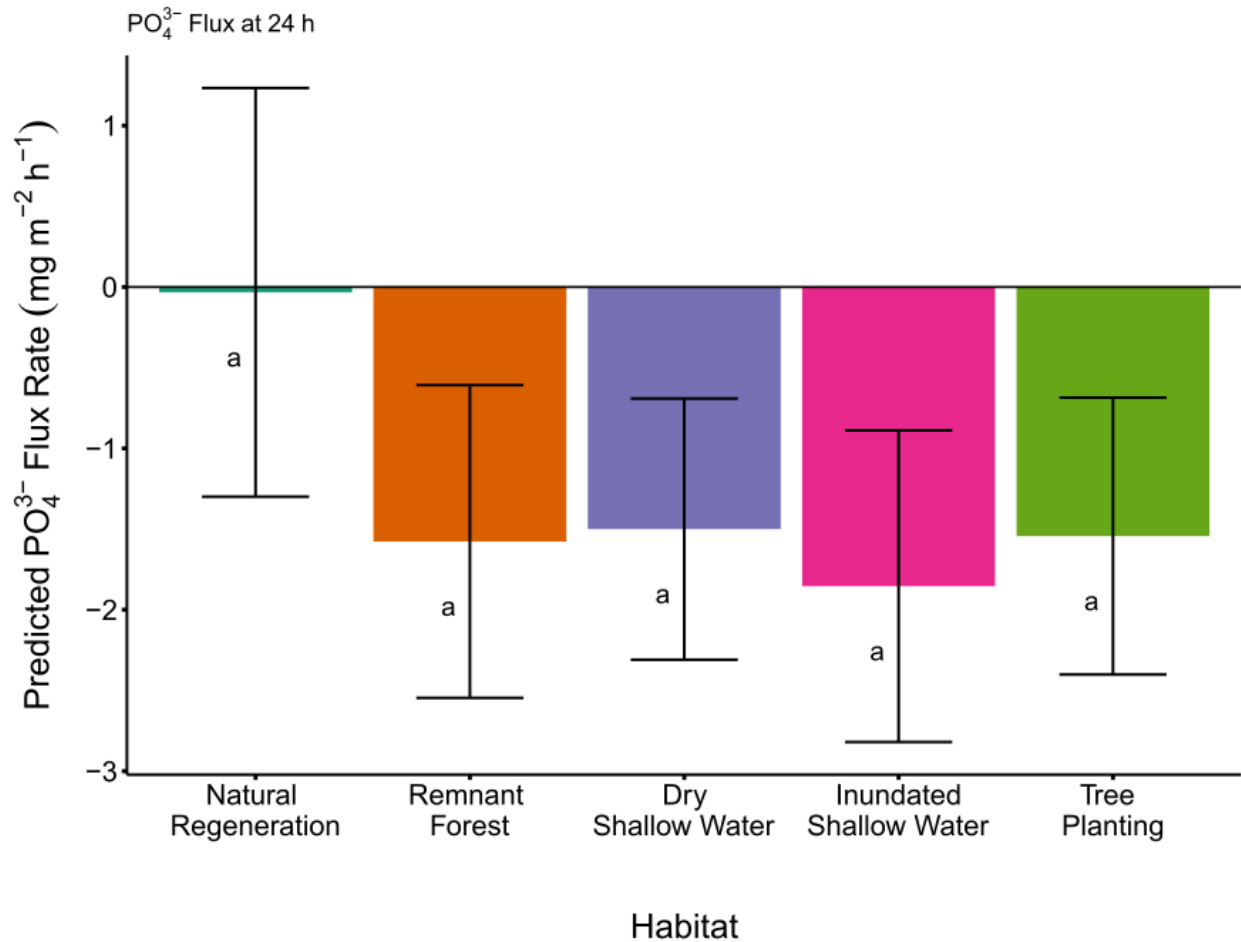


Figure 16.2 Predicted mean PO_4^{3-} flux rates by habitat at 24 h. Different letters indicate significant differences ($\alpha = 0.05$). Error bars represent 95% confidence intervals.

Mean PO_4^{3-} retention rates among the habitats at 24 h were influenced by soil P, soil moisture, and SOD (Table 6.2). High soil moisture and SOD correlated with higher PO_4^{3-} retention; however, the strength of this effect varied across habitats. Conversely, high soil P content reduced PO_4^{3-} retention rates. There were differences in mean PO_4^{3-} flux among the habitats after controlling for soil P, soil moisture, SOD, and an interaction between habitat and

soil moisture (Chi-squared_(4, 68), $p < 0.001$); however, these differences were not significant when post-hoc pairwise comparisons were applied to the model.

Table 6.2 ANCOVA table for 24 h PO₄³⁻ flux rates

Source of Variation	DF	Chi-squared Statistic	<i>p</i>
Intercept	1	26.95	<0.001
Habitat	4	26.94	<0.001
Log(Soil P)	1	4.58	0.032
Soil Moisture	1	34.23	<0.001
SOD	1	20.94	<0.001
Habitat:Soil Moisture	4	18.59	<0.001

Soil Moisture and Habitat Interaction.

Soil moisture content more strongly influence mean PO₄³⁻ flux rate estimates at 24 h than at 6 h but not in all habitats. This effect was most pronounced in natural regeneration habitats which transitioned from a predicted release of PO₄³⁻ at low moisture contents to retaining PO₄³⁻ when soil moisture was $> \sim 0.6 \text{ g g}^{-1}$. Natural regeneration habitats were predicted to retain the most PO₄³⁻ among the habitats when soil moisture content was $> 0.9 \text{ g g}^{-1}$ (Fig. 17.2). While increases in soil moisture were positively correlated with PO₄³⁻ retention in tree planting and dry

shallow water habitats, this correlation was weaker than in natural regeneration. For inundated shallow water, increases in soil moisture correlated with a minor increase in PO_4^{3-} retention. Soil moisture was not correlated with mean PO_4^{3-} retention in remnant forest habitats.

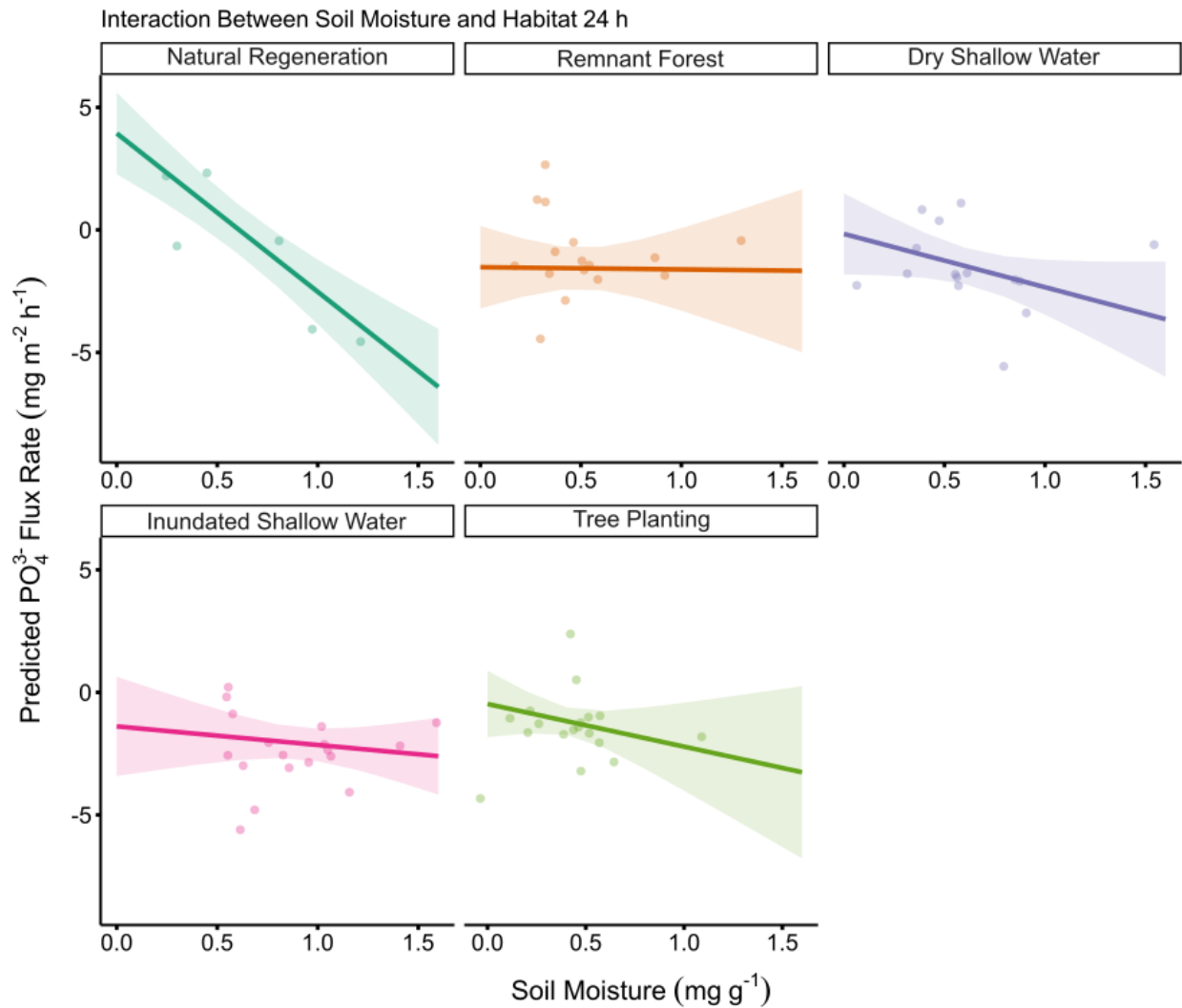


Figure 17.2 Interaction plot showing the effect of soil moisture on PO_4^{3-} flux at 24 h for each habitat. Bands represent 95% confidence intervals. Points are the raw flux rates (points located outside the predicted range are not shown).

Trends in 48 h Phosphate Flux

All habitats retained PO_4^{3-} after 48 h of inundation with natural regeneration retaining the most PO_4^{3-} ($2.0 \text{ mg m}^{-2} \text{ h}^{-1}$) (Fig. 18.2). Mean PO_4^{3-} retention decreased between 24 and 48 h in all habitats excluding natural regeneration which saw a >6000% increase in retention. Among the other habitats, mean PO_4^{3-} retention rates decreased between 30% to 48% (tree planting and inundated shallow water, respectively). At 48 h, mean flux rates among the habitats (excluding natural regeneration) were similar and ranged from -0.7 to $-1.1 \text{ mg m}^{-2} \text{ h}^{-1}$ (dry shallow water and tree planting, respectively). Confidence intervals were large for all habitats with natural regeneration having the most variability. For dry and inundated shallow water habitats, confidence intervals crossed zero, indicating that these habitats potentially released PO_4^{3-} on average. Forty-eight h mean PO_4^{3-} retention rates were only influenced by soil moisture with high soil moisture content correlating with high PO_4^{3-} retention (Table 7.2). There were no differences in predicted mean PO_4^{3-} flux rates among the habitats after controlling for the effect of soil moisture (Chi-squared $_{(4,68)} = 4.22$, $p = 0.378$).

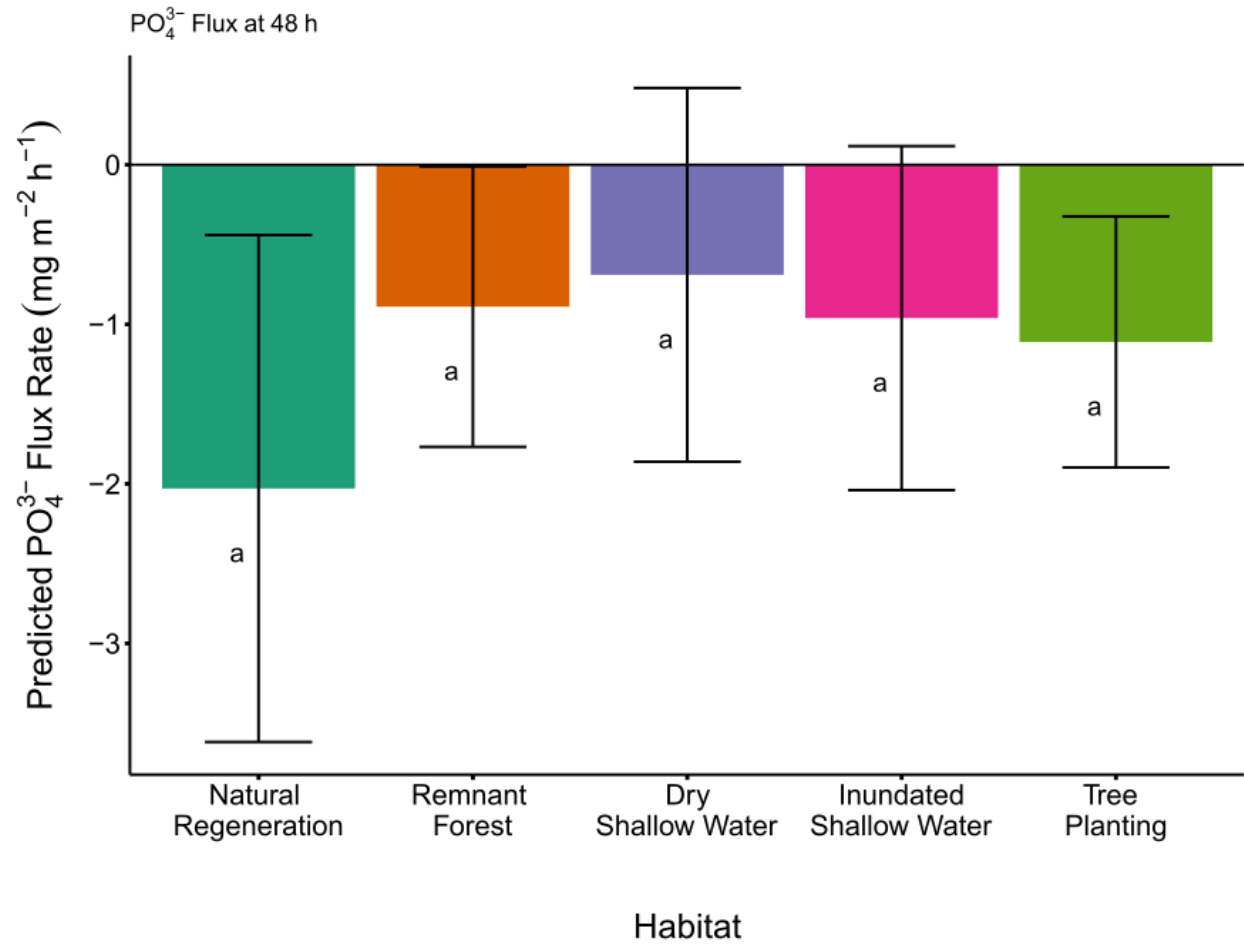


Figure 18.2 Predicted mean PO₄³⁻ flux rates by habitat at 48 h. Different letters indicate significant differences ($\alpha = 0.05$). Error bars represent 95% confidence intervals.

Table 7.2 ANCOVA table for 48 h PO₄³⁻ flux rates

Source of Variation	DF	Chi-squared Statistic	<i>p</i>
Intercept	1	1.18	0.277
Habitat	4	4.22	0.378
Soil Moisture	1	9.84	0.002

Soil Data Summary Statistics

Soil properties were generally variable within and among habitats (Table 8.2). Soil pH was highly variable among individual cores collected within a habitat and across all sites; however, means were similar (mean pH between 5 – 6). Soil nutrients were also variable among the habitats and across nutrient species with soils containing much less P than TN or TC. Soil moisture was the most variable soil property with the greatest disparity in soil moisture content observed in the inundated shallow water habitats (0.28 to 0.5 g g⁻¹ higher mean soil moisture content compared to the other habitats). Mean bulk density was similar among habitats despite differences in soil moisture content.

Table 8.2 Summary statistics for the soil data including mean, standard deviation (SD), and range

Habitat	Soil Moisture (g g⁻¹)			Bulk Density (g cm⁻³)			pH		
	<u>Mean</u>	<u>SD</u>	<u>Range</u>	<u>Mean</u>	<u>SD</u>	<u>Range</u>	<u>Mean</u>	<u>SD</u>	<u>Range</u>
Natural Regeneration	0.60	0.43	0.11 – 1.29	0.85	0.21	0.63 – 1.13	5.32	0.61	4.1 – 5.8
Dry Shallow Water	0.63	0.31	0.24 – 1.44	0.87	0.20	0.53 – 1.21	5.28	0.55	4.0 – 6.2
Inundated Shallow Water	0.91	0.29	0.48 – 1.51	0.84	0.16	0.57 – 1.12	5.73	0.56	5.0 – 7.1
Remnant Forest	0.50	0.27	0.20 – 1.13	0.87	0.15	0.55 – 1.12	5.42	0.41	4.8 – 6.3
Tree Planting	0.41	0.21	0.14 – 1.15	0.96	0.28	0.41 – 1.92	5.27	0.32	4.6 – 5.7

Table 8.2 (continued)

Habitat	Soil TC (mg g⁻¹)			Soil TN (mg g⁻¹)			Soil P (mg g⁻¹)		
	<u>Mean</u>	<u>SD</u>	<u>Range</u>	<u>Mean</u>	<u>SD</u>	<u>Range</u>	<u>Mean</u>	<u>SD</u>	<u>Range</u>
Natural Regeneration	28.44	8.19	17.3 – 38.0	2.51	0.75	1.5 – 3.4	0.06	0.02	0.03 – 0.08
Dry Shallow Water	22.1	8.45	10.3 – 37.8	2.03	0.70	1.0 – 3.2	0.04	0.02	0.02 – 0.10
Inundated Shallow Water	18.35	7.72	7.0 – 37.2	1.76	0.67	0.7 – 3.1	0.04	0.01	0.01 – 0.07
Remnant Forest	31.12	12.46	10.4 – 59.2	2.72	0.98	1.0 – 4.9	0.05	0.02	0.03 – 0.09
Tree Planting	24.56	10.63	15.1 – 63.0	2.07	0.73	1.4 – 4.3	0.05	0.03	0.02 – 0.16

Discussion

Evaluation of Hypotheses

Hypothesis 1: Nitrate and PO_4^{3-} flux rates would differ among habitat types.

My hypothesis was only supported for NO_3^- flux at 6 h as there were no differences in mean NO_3^- flux among any habitats at any other time points. Further, there were no differences in PO_4^{3-} flux among any habitats across all sampling time points. My prediction that SOD would significantly affect NO_3^- and PO_4^{3-} flux across all time points was generally supported as SOD influenced mean flux rates among the habitats at 24 and 48 h for NO_3^- and at 24 h for PO_4^{3-} .

My prediction that inundated shallow water habitats would have the greatest initial NO_3^- retention was supported. Inundated shallow water habitats retained significantly more NO_3^- than all other habitats excluding tree plantings at 6 h. However, my prediction that inundated shallow water habitats would initially retain the least amount of PO_4^{3-} compared to the other habitats was not supported. Inundated shallow water habitats had the second most PO_4^{3-} retention, retaining only 25% $\text{PO}_4^{3-} \text{ m}^{-2} \text{ h}^{-1}$ less than natural regeneration (which had the most PO_4^{3-} retention at 6 h).

Hypothesis 2: Soil characteristics would affect NO_3^- and PO_4^{3-} flux.

My hypothesis that soil structure would influence nutrient flux rates was supported as at least one soil characteristic was identified as having a significant effect on mean NO_3^- and PO_4^{3-} flux rates at every time point. I predicted that soil moisture at the time of core collection would correlate with an increase in NO_3^- retention and a decrease in PO_4^{3-} retention across all sampling time points, and this was moderately supported. High soil moisture content did correlate with

increases in NO_3^- retention; however, this was also true for PO_4^{3-} retention. It appears that initial soil moisture content had a stronger effect on PO_4^{3-} than NO_3^- flux, and that initial soil moisture content affected PO_4^{3-} flux for longer after soils were inundated during incubation. Additionally, the strength of this effect on PO_4^{3-} flux varied among the habitats at 24 and 48 h of incubation due to an interaction between soil moisture and habitat. For NO_3^- , initial soil moisture content appears to strongly influence mean flux rate estimations during initial flooding, but this effect weakens as flood duration increases. By 48 h, initial soil moisture content may no longer affect NO_3^- flux rates.

Soil nutrient content was not as influential on nutrient flux rates as expected. My results supported the prediction that soil nutrient content would affect NO_3^- retention, but only for the 48 h flux rates. At 48 h of flooding, higher soil TN and P correlated with increases in NO_3^- retention as predicted; however, higher soil TC correlated with decreased NO_3^- retention. Soil P was the only soil nutrient that affected mean PO_4^{3-} flux rate estimates for the habitats, and the strength of this effect was variable across sampling time points. Soil P significantly affected mean PO_4^{3-} flux rate estimates at 24 h, but not at 6 h and soil P was not included in the 48-h model. When soil P did influence mean PO_4^{3-} flux rate estimates, my prediction that greater soil P would decrease PO_4^{3-} retention was supported.

I did not predict that soil pH would influence NO_3^- flux. However, soil pH significantly affected mean NO_3^- flux at 6 h of flooding. Increases in soil pH were correlated with increases in NO_3^- retention at 6 h, but soil pH did not influence mean NO_3^- retention at 24 or 48 h. Soil pH did not affect PO_4^{3-} retention at any time point and was not included in any final PO_4^{3-} flux models.

Factors Influencing Nitrate Retention

Soil Moisture

Initial soil moisture content strongly affected mean NO_3^- retention estimates during the first 24 h of flooding, but the strength of this effect decreased at 48 h. The influence of soil moisture on NO_3^- retention may have been due to initial differences in microbial biomass and community structure, as soil moisture can regulate soil microbial abundances and assemblages (Moriarty, 1997; A. L. Peralta et al., 2010, 2014). Moist soils often have low redox potential (Baldwin & Mitchell, 2000a; Paul Keddy, 2000) which supports greater denitrifying microbial abundances and activity compared to drier soils (Klemetsson et al., 1988; Ma et al., 2020; Maag & Vinther, 1996). Therefore, habitats with higher initial soil moisture content, like inundated shallow water, may have contained more anaerobic microbes prior to incubation, resulting in greater initial NO_3^- retention.

Soil Oxygen Demand

The significant effect of SOD on NO_3^- retention at 24 and 48 h suggests that redox potential influenced NO_3^- retention rates. Increases in SOD can reduce soil O_2 content, enhancing denitrification rates (Cornwell et al., 1999; de Klein et al., 2017; Rohe et al., 2020; Seitzinger, 1994). The convergence of NO_3^- retention rates among the habitats at 48 h of flooding may have resulted from O_2 depletion in the cores, leading to more uniform microbial uptake and denitrification and subsequent NO_3^- retention rates. It is unknown if SOD was correlated with NO_3^- retention following initial wetting due to a lack of O_2 flux measurements at 6 h of incubation. However, SOD may be a reliable predictor of the NO_3^- retention potential

given its significant effect on mean NO_3^- retention rates among the habitats at the other time points.

Soil Nutrient Content

Soil Total Nitrogen and Phosphorus.

The influence of soil TN and P on NO_3^- retention was weaker than expected as soil TN and P only affected mean NO_3^- retention at 48 h of incubation. The positive correlations between soil TN and P and NO_3^- retention observed in this study support previous research which found that high soil N and P content enhanced denitrification and increased NO_3^- retention (Kim et al., 2017; Ma et al., 2020; O'Neill et al., 2022; K. Zhang et al., 2012). Conversely, low soil P may reduce NO_3^- retention due to P limitation in microbes (Hartman & Richardson, 2013; Herbert et al., 2020). These results suggest that cores with high soil TN and P content potentially supported greater microbial biomass and activity at 48 h, leading to an increase in NO_3^- retention. While numerous studies have examined how soil N relates to NO_3^- retention, the direct effects of soil P on NO_3^- retention are not well understood, and the significance of soil P at a single time point makes it difficult to generalize this relationship to other wetlands.

Soil Total Carbon.

It is unclear why soil TC was inversely correlated with NO_3^- retention as most major NO_3^- retention processes (denitrification, dissimilatory nitrate reduction (DNRA) (reduction of nitrate to NH_4^+), and biological uptake) are typically C limited (Bernhardt & Likens, 2002;

Groffman et al., 1996; Kelso et al., 1997; S. Lu et al., 2009; Trepel & Palmeri, 2002). The negative correlation between TC and NO_3^- retention observed in the present study may indicate that anammox (reduction of NH_4^+ to N_2) rather than denitrification was driving NO_3^- retention at 48 h. Anammox is favored over denitrification under low redox conditions when soil N:C is high and can be a major pathway for N removal in wetlands (J. Li et al., 2022; Shan et al., 2016). Additionally, anammox may be inhibited in soils with high TC (Shan et al., 2018; Sheng et al., 2018; Z. Wang et al., 2020; Q. Zhang et al., 2018). However, there was limited direct evidence of anammox occurring in the cores, and these results neither support nor contradict the findings of other studies regarding the effects of soil C on NO_3^- retention. Future studies using isotopically labeled N are needed to determine if anammox is a significant N removal pathway within these wetlands and how N cycling processes respond to increases in soil C when N is not limiting.

Soil pH

The effect of soil pH on NO_3^- retention was surprising as the strength and direction of this effect differed among habitats and was only present at 6 h of incubation. Higher soil pH can enhance N removal via denitrification by increasing the availability of labile C and N, supporting the observed effect of pH on NO_3^- retention in the natural regeneration and tree planting habitats (Jha et al., 2020; Saleema et al., 2009; Šimek & Cooper, 2002). However, this relationship was slightly reversed in remnant forest habitats and was absent in the inundated and dry shallow water habitats. It is possible that these conflicting results are due to interactions among soil pH, other soil properties, and associated microbial communities that were not quantified in this study. Prior research has suggested that pH can interact with other soil parameters like moisture and

nutrient content which alters microbial community structure and activity, thereby affecting nutrient cycling rates (Baeseman et al., 2006; Devlin et al., 2000; Firestone et al., 1980).

Therefore, the observed relationship between pH on NO_3^- retention at 6 h of flooding may not be representative of its true effect if there were significant interactions with other soil parameters.

Factors Influencing Phosphate Retention

Soil Moisture

Soil moisture consistently influenced mean PO_4^{3-} retention rates throughout the experiment, and the strength of this relationship varied among habitats until 48 h of incubation. The positive correlation between higher soil moisture and greater PO_4^{3-} retention may be due to increased microbial activity and P sorption as the soil became flooded. Dry soils can reduce microbial activity (Linn & Doran, 1984; Schjønning et al., 2003; Skopp et al., 1990) which potentially explains why the relationship between soil moisture and PO_4^{3-} retention was more pronounced in habitats with drier soils. Drier soils also experience greater soil slaking upon wetting which can enhance P sorption (Bünemann et al., 2013; Chen et al., 2021).

Prior to the 6 h sampling, soil-bound P may have been released as the cores were submerged, and release rates may have differed among the habitats. Soils with low moisture content can release PO_4^{3-} upon initial rewetting, but quickly transition to retaining PO_4^{3-} via rapid uptake by microbes (Baldwin & Mitchell, 2000; Gu et al., 2018; Qiu & McComb, 1995). Retention rates in drier habitats may have lagged those of wetter habitats if P was initially released when soils were submerged as it would take longer for microbial uptake to outpace P

release from the soil. However, all habitats retained PO_4^{3-} at 6 h, and it is uncertain whether there was a net release of PO_4^{3-} upon submergence.

Why soil moisture content disproportionately affected mean PO_4^{3-} retention estimates for natural regeneration habitats is unclear given that the mean soil moisture content was similar among habitats. It is possible that interactions between soil moisture and other unmeasured soil properties created environmental conditions unique to natural regeneration habitats, contributing to this disparity in effect strength. However, further research from a diversity of habitats is needed to fully understand the effect of soil moisture content on PO_4^{3-} retention in floodplain wetlands.

Soil Oxygen Demand

Unexpectedly, SOD positively correlated with PO_4^{3-} retention at 24 h of incubation. As all habitats retained PO_4^{3-} at 24 h, this correlation may be related to microbial uptake. When dissolved P concentrations are high, microbial communities can rapidly increase biomass, resulting in an increase in SOD (Bagheri-Novair et al., 2020; Lieberman et al., 2021a). Therefore, the positive correlation between SOD and PO_4^{3-} retention likely represented increased microbial uptake in response to high amounts of labile P as opposed to SOD driving PO_4^{3-} retention. When O_2 is depleted in the soil, microbial uptake of P can be reduced (J. Ding et al., 2019; Gross et al., 2020) and P may be released (Baldwin & Mitchell, 2000a; J. Ding et al., 2019). This may explain why PO_4^{3-} retention was generally lowest at 48 h as the soil-water interface was likely anoxic.

Additionally, enhanced microbial activity in response to high PO_4^{3-} content may also explain why PO_4^{3-} retention was greatest at 6 h of inundation. Cores were expected to release P upon submergence as mineralized P in the soil became suspended in the water column (J. Ding et al., 2019; Olde Venterink et al., 2002; Xu et al., 2020). The net retention of PO_4^{3-} among the habitats at 6 h suggests that either P release from the soil was minimal or resuspended P was rapidly taken up by microbes when O_2 availability at the soil-water interface was high. A future assessment of SOD during initial soil submergence would improve our understanding of this relationship between SOD and PO_4^{3-} retention as flood durations are often variable, and more research is needed to determine how short-duration floods (≤ 6 h) influence soil redox conditions and nutrient cycling.

Soil Nutrient Content

Soil Phosphorus.

The effect of soil P on mean PO_4^{3-} retention among the habitats at 24 h was consistent with previous research that showed high-P soils retain less PO_4^{3-} than low-P soils (Baldwin & Mitchell, 2000a; Bostic & White, 2007; Dunne et al., 2006). At 24 h of inundation, it is possible that O_2 content at the soil-water interface was sufficiently depleted to cause Fe_2O_3 -bound P to dissociate, resulting in the observed negative correlation between soil P content and PO_4^{3-} retention. Beyond 24 h of flooding, rates of P release from the soil can decrease (Lieberman et al., 2021b; Sheard & Leyshon, 1976). At 48 h of incubation, release of Fe_2O_3 -bound P may have been greatly reduced or ceased, explaining why soil P was not correlated with PO_4^{3-} retention.

Conclusions

Flood duration appears to have a greater effect on wetland nutrient retention capacity compared to habitat type and soil properties, and this effect is relatively uniform across the habitats. Nitrate retention within these wetlands improves with increasing flood duration, but the highest rates of PO_4^{3-} retention occur within the first 24 hours of flooding. Although the optimal flood duration varied between nutrients, there was no tradeoff between NO_3^- and PO_4^{3-} retention. To achieve maximum PO_4^{3-} retention, habitats may only need to hold flood waters for around 6 hours, whereas habitats need to be flooded for at least 48 hours to maximize NO_3^- retention. It is important to note that these incubations used water with artificially high concentrations of NO_3^- and PO_4^{3-} , and additional research is needed to determine if these trends hold under different flood durations and at more natural concentrations of NO_3^- and PO_4^{3-} . Further, additional studies comparing the effects of soil properties on nutrient retention in restored wetlands are needed to better determine how these environmental characteristics influence wetland biogeochemical cycling.

This study highlights the complexities of predicting nutrient retention in restored floodplain wetlands. The influence of environmental factors such as habitat, soil properties, redox state, and flood duration on NO_3^- and PO_4^{3-} retention suggests that accurate predictions of nutrient retention potential cannot be made based solely on habitat type. Therefore, it is necessary to consider the unique environmental characteristics of individual wetlands and their habitats when predicting or evaluating wetland restoration outcomes.

CHAPTER 3: EFFECTS OF INUNDATION FREQUENCY ON NUTRIENT RETENTION AND SOIL CHARACTERISTICS IN RESTORED FLOODPLAIN WETLANDS

Abstract

Understanding the influence of hydrologic patterns on nutrient retention and soil characteristics in floodplain wetlands is critical for effective wetland restoration. However, few studies have evaluated these relationships across the weeks or months prior to sampling. This study correlated inundation frequency (IF), the frequency that an area was covered by water over a defined timeframe, with nitrate (NO_3^-) and phosphate (PO_4^{3-}) retention, and soil properties (i.e., moisture content, bulk density, pH, total carbon (TC) and nitrogen (TN), and phosphorus (P)) measured from soil cores. Inundation frequency was estimated over a 180-d period prior to soil core collection at six restored floodplain wetlands in western Tennessee and Kentucky using the Google Earth Engine PyGEE-SWToolbox. Inundation frequencies at soil core sampling locations were low and variable across all sites, ranging from 0 – 10%. Inundation frequency was positively correlated with NO_3^- retention and soil pH and negatively correlated with soil TN and TC. The strength of these correlations varied among sites for soil pH, TN, and TC. The effect sizes of IF on NO_3^- and pH were large, with a predicted 4% increase in NO_3^- retention and a 0.15 increase in pH values for every 1% increase in IF. These results imply that IF may greatly influence NO_3^- retention potential and several important soil characteristics in restored floodplain wetlands, however, the strength of these relationships may be site specific. Future restorations

should be cognizant how restoration practices will affect hydrologic regimes and develop site-specific restoration plans to improve restoration outcomes.

Introduction

Hydrology is a primary driver of nutrient cycling in wetlands, and flood frequency and duration can greatly influence nutrient retention potential (Baldwin & Mitchell, 2000a; Hansson et al., 2005). Variability in floodplain wetland hydrologic regimes often creates moisture gradients ranging from permanently inundated to frequently dry, in turn influencing nutrient cycling rates and soil characteristics (Paul Keddy, 2000). These cycles continuously alter organic and inorganic nitrogen (N) and phosphorus (P) turnover rates in wetlands, prompting changes in retention and release rates within and among wetlands (Kumaragamage et al., 2019; Morillas et al., 2013).

Wetting and drying cycles greatly influence nutrient retention potential by controlling soil redox conditions and structuring microbial communities (S. P. Faulkner & Patrick Jr., 1992; Olde Venterink et al., 2006; S. Ye et al., 2012). For example, frequent flooding can lower soil redox potential and increase C availability, which enhances denitrification rates. Denitrification generally requires an anoxic environment and may be C limited (Brettar et al., 2002; Seitzinger, 1994). Flooding and drying cycles may also stress soil microbial communities, leading to potentially long-term effects on nutrient cycling (Blackwell et al., 2009; Qiu & McComb, 1995). This chapter explores the linkages between wetland hydrology and both nutrient retention potential and soil characteristics in restored floodplain wetlands to better understand how hydrologic regime influences ecosystem function and structure.

Hydrologic Regimes and Water Residence Time

Water residence time, the amount of time between when water enters and subsequently leaves a defined area, can influence nutrient uptake rates within aquatic ecosystems (Grimm et al., 2003) and is directly related to wetland wetting and drying regimes. All wetland types fall somewhere on a hydrologic continuum that ranges in inundation frequency from seasonally flooded to permanently inundated and from slow to rapid wet-dry cycling (Fig. 1.3). The frequency and duration of these cycles strongly influences water residence times within and among wetlands.

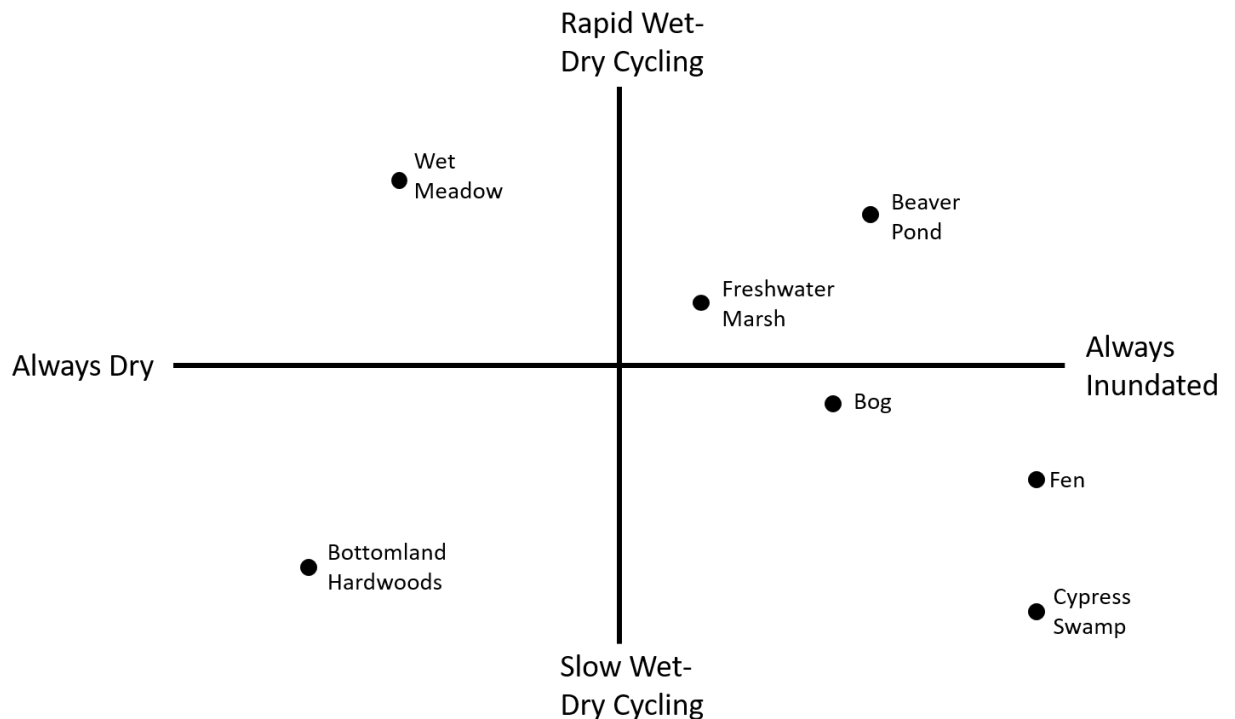


Figure 1.3 A conceptual diagram of wetland types as related to inundation status and wetting-drying frequency (after National Research Council, 1995 and Keddy, 2000).

Effects of Wetting on Nutrient Retention

Phosphorus

Flood frequency and duration influence P dynamics in wetlands. When dry soils are submerged, water column dissolved P may bind to metals like iron (Fe) or aluminum (Al) in the soil (Baldwin & Mitchell, 2000a). However, decreasing soil redox potential due to repeated cycles of wetting and drying can increase P release when soil-bound P dissociates from ferric iron (Fe(III)) as dissolved oxygen (O₂) content declines (Brettar et al., 2002; Schönbrunner et al., 2012; Seitzinger, 1994). Colloidal-bound P may also be released during rewetting and can be a significant source of inorganic P in soil leachate (Gu et al., 2018). Release of organically-bound P also contributes to P export following rewetting as microbes lyse due to osmotic shock following rapid soil submergence (Khan et al., 2019). Microbial P release following soil wetting can constitute as much as 88% of total dissolved P in soil water leachate (Turner et al., 2003). Rewetting the soil can also stimulate microbial metabolism and assimilation of the remineralized P, thereby removing it from the water (Baldwin & Mitchell, 2000a; Noe et al., 2013).

Nitrogen

Soil rewetting influences N cycling by altering soil microbial biomass, community structure and function, and N absorption rates (Grimm et al., 2003; Moriarty, 1997). Upon rewetting, heterotrophic microbial abundance and activity increases, reducing dissolved O₂ content (Moriarty, 1997). During inundation, deeper sediments can become anoxic while shallower sediments can remain oxygenated. Coupled nitrification-denitrification rates may

increase across this redox gradient (Baldwin & Mitchell, 2000a) with nitrate (NO_3^-) produced via nitrification in the upper oxic soil zone which then fuels denitrification in the deeper anoxic zone. Coupled nitrification-denitrification can greatly enhance denitrification rates temporally in aquatic environments (Marchant et al., 2016a; Verhoeven et al., 2018a). Once dissolved oxygen at the soil-water interface is depleted, nitrification is greatly reduced or ceases. Denitrification is then solely fueled by ambient NO_3^- . The frequency of wetting-drying cycles can alter the strength of these effects as rewetting of moist soils has been found to correlate with higher rates of denitrification than the rewetting of dry soils (Olde Venterink et al., 2002).

In deeper anoxic soil layers, dissimilatory nitrate reduction (DNRA) (the reduction of NO_3^- to ammonium (NH_4^+)) can occur in the soil pore water (Baldwin & Mitchell, 2000a). This anoxic environment inhibits nitrification, preventing the NH_4^+ from being converted back to NO_3^- . Reduction of NO_3^- to NH_4^+ can be a significant N sink in riparian wetlands though the contribution of DNRA to overall N retention can be site-specific (Sgouridis et al., 2011). Further, frequent, short-duration flooding can greatly reduce DNRA rates due to DNRA bacteria mortality upon desiccation and competition with denitrifiers.

Abiotic processes also affect N cycling. For example, labile N can be removed from the water column via adsorption to the soil during flooding (Bernot & Dodds, 2005). Further, NH_4^+ may be immobilized via abiotic fixation with clay soils or condensation reactions with activated phenol or quinone rings to form nitrogenous humates (Johnson et al., 2000; Schimel & Firestone, 1989). Under N-enriched conditions, immobilization of N via abiotic processes such as fixation with clay soils or nitrosation, the process of converting organic compounds to nitroso derivatives under acidic conditions, can function as a dominant N immobilization pathway (Yansheng et al.,

2020). Conversely, NH_4^+ may be released from inundated soils due to cation exchange when solute concentrations in the water column are high (Ardón et al., 2013).

Effects of Drying

Phosphorus

When soil dries, P transformations observed during rewetting usually reverse. Soil desiccation can increase microbial mortality, resulting in a release of formerly organically-bound P (Baldwin & Mitchell, 2000a; Schönbrunner et al., 2012). Rapid cycles of wetting and drying can reduce microbial P content within the soil by >50% and may be accompanied by a corresponding increase in dissolved inorganic P (Chen et al., 2021). Additionally, physical processes such as slaking, which occurs when large, dry soil aggregates break down into smaller microaggregates upon being suddenly immersed in water, and P sorption to the soil can also greatly increase inorganic P deposition following drying (Bünemann et al., 2013; Chen et al., 2021).

Nitrogen

Like P, soil desiccation generally causes a release of organically-bound N into the surrounding environment as microbes lyse. Total soil desiccation may kill over 75% of soil microbes (Blackwell et al., 2009; De Groot & Van Wijck, 1993; Qiu & McComb, 1995). Drying also slows denitrification rates due to the loss of an anerobic environment and reduction in denitrifier biomass (Baldwin & Mitchell, 2000a). Aerobic microbes may temporarily increase N

retention following the pulse of N released upon the death of anaerobic microbes (Baldwin & Mitchell, 2000a; Olde Venterink et al., 2002); however, this will cease if soils become completely desiccated. Drying can also create a shifting redox boundary when previously anoxic soils are exposed to air, facilitating coupled nitrification-denitrification (Baldwin & Mitchell, 2000a).

Wetland Hydrology and Soil Properties

Cycles of wetting and drying can also influence soil chemistry and structure. For example, soil pH can vary with flood frequency and may be highest in the most frequently flooded areas in temperate wetlands due to reductions in aerobic microbial respiration rates as soils become anoxic (Paradis & Saint-Laurent, 2017). Bulk density may be greatest in intermittently flooded areas as soils compact in response to increasing moisture content (Bai et al., 2010; Morse et al., 2012). Flooding also affects soil moisture content between floods, as soils may dry more completely when flood frequencies are low (Lovell, 2013); however, few studies have directly assessed the effect of flooding on soil moisture across months or years. Additionally, soil nutrients can be influenced by flood regimes. Regular flooding can increase soil total C (TC) and total N (TN), and soil P content as floodwaters slow organic matter decomposition and deliver nutrient-enriched sediment to the wetland (Bai et al., 2005; Noe et al., 2013; Olde Venterink et al., 2002; J. Wang et al., 2016).

Objectives

Given the difficulty in sampling access to wetlands, maintenance requirements of field equipment, and cost limitations, it is difficult to measure trends in wetland hydrology across

months or years. As such, there is a dearth of research assessing how hydrologic patterns influence wetland nutrient cycling and soil properties. A method increasingly employed to overcome these logistical constraints is the use of remotely sensed data. This study sought to use hydrologic remote sensing data to determine how patterns in wetland inundation frequency (IF) relate to the nutrient flux rates and soil characteristics measured in Chapter Two.

Hypotheses

Hypothesis 1) Wetland inundation frequency correlates with NO_3^- and PO_4^{3-} retention.

Increases in flood frequency and high soil moisture content can lower soil redox potential, facilitating the growth of denitrifying microbes which enhances NO_3^- removal (Marton et al., 2014; A. L. Peralta et al., 2010; Pinay et al., 2007). Therefore, NO_3^- retention at 6 h was predicted to positively correlate with IF. Additionally, drier soils are more oxygenated as there are fewer microbes respiring and soils are in direct contact with the atmosphere (Baldwin & Mitchell, 2000a). This oxygen-rich environment enables labile P to bind with metals in the soil upon rewetting, enhancing PO_4^{3-} retention (Ann et al., 1999; Baldwin & Mitchell, 2000; Noe et al., 2013). Therefore, increases in IF were predicted to be inversely correlated with PO_4^{3-} retention due to lower soil redox potential in response to flooding.

Hypothesis 2) Wetland inundation frequency correlates with soil characteristics.

Select soil characteristics measured in Chapter Two including bulk density, moisture content, TC, TN, and P content, and pH, were predicted to positively correlate with IF. Flooding

can compact soils, leading to increased soil bulk density as IF increases (Bai et al., 2010; Morse et al., 2012). Areas with high IF were also predicted to have greater soil moisture content as regular flooding would presumably prevent soils from drying completely. Additionally, regular flooding can increase soil C, N, and P content by slowing organic matter decomposition rates and delivering nutrient-enriched sediment (Bai et al., 2005; Noe et al., 2013; Olde Venterink et al., 2002; J. Wang et al., 2016). Therefore, soil C, N, and P were predicted to positively correlate with IF. Additionally, soil pH has been positively correlated with soil moisture content under prolonged flooding (Maranguit et al., 2017; McNicol & Silver, 2014; Paradis & Saint-Laurent, 2017). Therefore, soil pH was predicted to positively correlate with IF.

Methods

The PyGEE-SWToolbox

The PyGEE-SWToolbox is an interactive surface water mapping and analysis toolbox within Google Earth Engine (GEE) (Owusu et al., 2022) (URL: <https://github.com/collinsowusu/PyGEE-SWToolbox>). This toolbox was used to estimate the IF of each core location at a given site by automating the traditional mapping and application processes associated with surface water analysis via remote sensing. Sentinel 2 multi-spectral imagery was used to calculate IF for each core location (represented by a single pixel) within a site. Sentinel 2 imagery was chosen over Landsat 2 for its high resolution (10 m² per pixel

compared to 30 m², respectively) as distances between cores were variable with some cores collected <20 m apart.

Site Selection and Timeframe Analyzed

The 22 sites sampled during May through August of 2020, 2021, and 2022 as part of the soil core incubation study described in Chapter Two were analyzed to estimate IF for each core location at each site. Sufficient aerial imagery was only available for six sites. Inundation frequencies for each site were calculated for dates ranging between 30, 90, and 180 d prior to sampling.

For each timeframe, images were considered “useable” when no clouds were covering any of the core sampling locations. The 30-d timeframe only yielded between 2 – 4 images per site. More imagery was available for the 90-d timeframe but the number of images available for each site was still low, ranging from 6 – 10 images per site. Calculating IF for the 180-d timeframe provided a modest increase in the number of useable images, with an average of 13 images available per site. However, image availability varied across sites, ranging from 9 - 21 images per site. Given the limited number of images for each timeframe, the 180-d timeframe was selected to calculate IF as this maximized the chances of detecting relationships between IF and nutrient cycling and soil properties. Additionally, this timeframe included images from the preceding winter and spring when flooding is most frequent.

Image Processing and Inundation Frequency Calculations

Image processing and IF calculations followed protocols outlined in Owusu et al., 2022 and Montgomery et al., 2018. First, a shapefile containing the entire wetland sampled was uploaded to GEE or boundaries were manually drawn. Date ranges for surface water extraction were then selected. The cloud coverage threshold (the percentage of an image covered by clouds) was set to 30% (i.e., 70% of an image must be cloud-free). This threshold reduced the likelihood that an area where soil cores were collected would be covered by clouds. The presence of clouds in images can bias IF estimates as they may be interpreted by GEE as dry land or water, leading to inaccurate data. Cloud cover in each image included in the IF calculations was visually inspected to verify that all soil core sampling locations were not covered by clouds. Any images with clouds covering a sample location that were not filtered out by the 30% coverage threshold were manually removed and IF was recalculated.

Following image processing, surface water data was extracted using the Normalized Water Difference Index (NWDI) (McFeeters, 1996) method with a threshold value set to zero. Pixels with a value greater than the specified NWDI threshold value are considered water whereas values below the threshold are considered non-water pixels. Water frequency was then calculated by applying an “equals frequency” routine, an algorithm for converting pixel frequency output to hydroperiod, to each water mask input raster (i.e., image) (Montgomery et al., 2018). Water mask input rasters are binary, containing only “0” and “1” for land and water, respectively. Binary water masks were then combined (i.e., mosaiced) to create a single, continuous reference raster containing only water values (“1”) which represented the maximum possible extent of water in the study area. This reference raster was then used to calculate water frequency throughout the specified timeframe by comparing the binary water mask rasters for

each image to the reference raster, and counting the number of times a pixel in the same geographic location was identified as water (Montgomery et al., 2018).

Statistical Analysis

Linear Mixed Effects Modelling

Nutrient flux rates at 6, 24, and 48 h of incubation and select soil characteristics (see Hypothesis Two) measured in Chapter Two were individually regressed against IF using linear mixed effects models (see Chapter Two for details on field and lab methods for quantifying nutrient flux and soil properties). The *lme4* package (Bates et al., 2015) in the statistical software *R* was used to fit regressions models (R Core Team, 2022). Plots were created using the *ggeffects* package (Lüdtke, 2018). Final models for the soil parameters and the model for PO_4^{3-} were assigned a random intercept and slope. The final model for NO_3^- was assigned only a random intercept as including a random slope term did not improve model performance. All final models were fit using the restricted maximum likelihood criterion (REML). Effective degrees of freedom and *p* values were calculated in the *lmerTest* package (Kuznetsova et al., 2017) using the Welch-Satterthwaite approximation method (Satterthwaite, 1946).

Outlier Removal and Log Transformations

Nitrate and PO_4^- flux rates beyond the 2.25 and 97.75% quantiles were removed prior to analysis to keep the data used consistent with Chapter Two and prevent extreme values from biasing model results. Nitrate flux, soil moisture, and soil P data were log transformed prior to

analysis to correct for violations of normality and patterns in the residuals. As the NO_3^- flux data contained positive and negative values, these data were raised by a constant of 49 so that the most negative value became a positive number. Nitrate data were then log-transformed and analyzed. Predicted NO_3^- flux rates and CI's were then back-transformed and subtracted by the constant (49) to return the data to its original values for plotting.

Results

Trends in Inundation Frequency

Inundation frequencies of the soil core collection locations were low and variable across all sites, with cores locations being classified as inundated in 0% to 10% of the images analyzed (Table 1.3). Sites were generally most frequently inundated between the December – March preceding when a site was sampled. Mean IF within each site ranged from 1 – 6.4% (Sites 4 and 1, respectively). Inundation frequency was significantly correlated with NO_3^- flux, soil pH, and soil TN and TC (Table 2.3). However, the strength of these correlations for soil pH, TN, and TC varied across sites.

Table 1.3 Inundation frequency (the % that a pixel was classified as water across the images analyzed) ranges, means, and standard deviations (SD) for each site included in the regression analyses.

Site	Range (%)	Mean (%)	SD
1	0 - 10	6.4	4.0
2	0 – 3	1.2	1.3
3	0 – 6	2.6	2.0
4	0 – 4	1.0	1.7
5	0 – 6	3.0	2.3
6	0 – 8	1.5	2.4

Table 2.3 Model summary statistics for each variable that was significantly correlated with inundation frequency. Predicted percent change in NO_3^- flux and soil pH per one percent increase in inundation frequency was included because unstandardized effect sizes cannot be determined using coefficients when a variable has been log transformed.

				% change in response to IF
	<i>p</i>	t. value	Coefficient	(where applicable)
Log (NO_3^-)	0.019	-2.56	-0.04	4% increase
pH	0.030	3.12	0.15	16% increase
Soil TN	0.047	-2.75	-0.22	NA
Soil TC	0.071	-2.39	-2.53	NA

Inundation Frequency and Nitrate Retention

Nitrate retention was only correlated with IF at 6 h of incubation ($p = 0.019$). The effect size of IF on 6 h NO_3^- retention was large with a 4% increase in NO_3^- retention for every 1% increase in IF on average. As NO_3^- data was log-transformed prior to analysis, it was not possible to determine precise rates of increase in NO_3^- retention in $\text{mg m}^{-2} \text{h}^{-1}$. Therefore, the effect size was expressed as a percentage. Accounting for site-specific variations in the relationship between IF and NO_3^- retention improved model performance but had little effect on reducing model variance ($\sigma^2 = 0.02$). Site-dependent regression lines mirrored the regression line of the

overall model (Fig. 2.3). Further, CI's were large for both the overall model and site-specific regression lines (overall model CI's not shown), reflecting the variability in NO_3^- flux rates observed within and across sites.

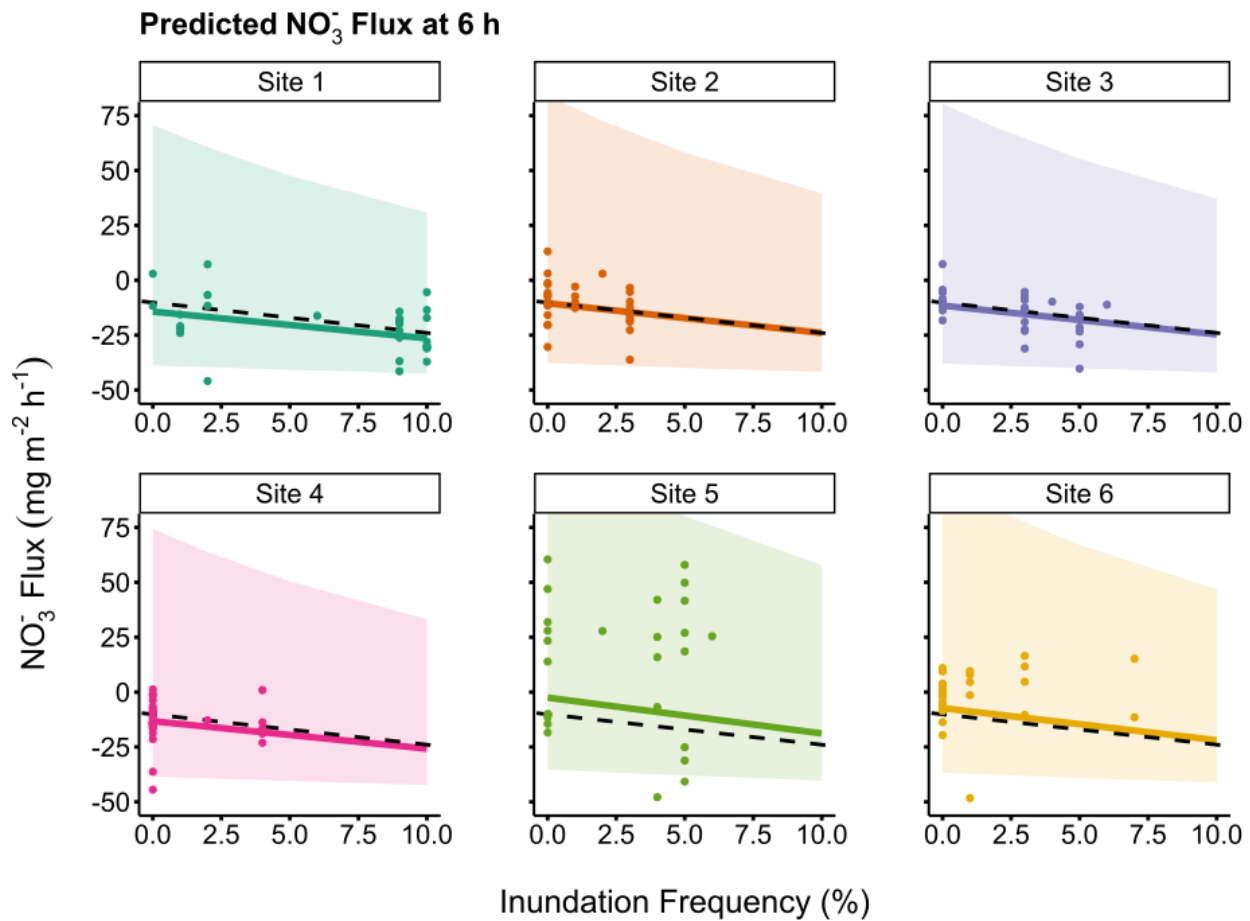


Figure 2.3 Predicted NO_3^- flux rates at 6 h of incubation for each site. The dashed black line represents the overall model regression line. Bands are 95% CI's. Points are observed IF values at each site.

Inundation Frequency and Soil Characteristics

Soil pH was positively correlated with IF whereas TC and TN were negatively correlated with IF. The effect size of IF on soil pH was large with a predicted 16% increase in pH units for every 1% increase in IF ($p = 0.030$). Despite visual differences in predicted pH values among sites, allowing for site-specific intercepts and slopes did little to reduce model variance ($\sigma^2 = 0.28$ and 0.01 for random intercepts and slopes, respectively). This was likely due to overlapping confidence intervals and uneven distributions of IF values among sites, resulting in model uncertainty when predicting pH values (Fig. 3.3). Soil TC and TN were marginally correlated with IF ($p = 0.047$ and 0.071 , respectively) with a 1% increase in IF predicted to decrease TC and TN content by an average of 2.5 and 0.22 mg g^{-1} , respectively. Intercepts and slopes for TC and TN within a single site were similar, implying possible collinearity (Figs. 4.3 & 5.3). Allowing for site-specific slopes and intercepts in the TC model captured a large amount of variance ($\sigma^2 = 81.62$ and 4.05 for random intercepts and slopes, respectively). The relationship between IF and TC (i.e., slope) was weakly influenced by site; however, site strongly influenced predicted mean TC content (i.e., the intercept for each site). The correlation between IF and TN was less affected by site as allowing site-specific intercepts and slopes did not meaningfully reduce model variance ($\sigma^2 = 0.40$ and 0.03 for the random intercept and slope, respectively).

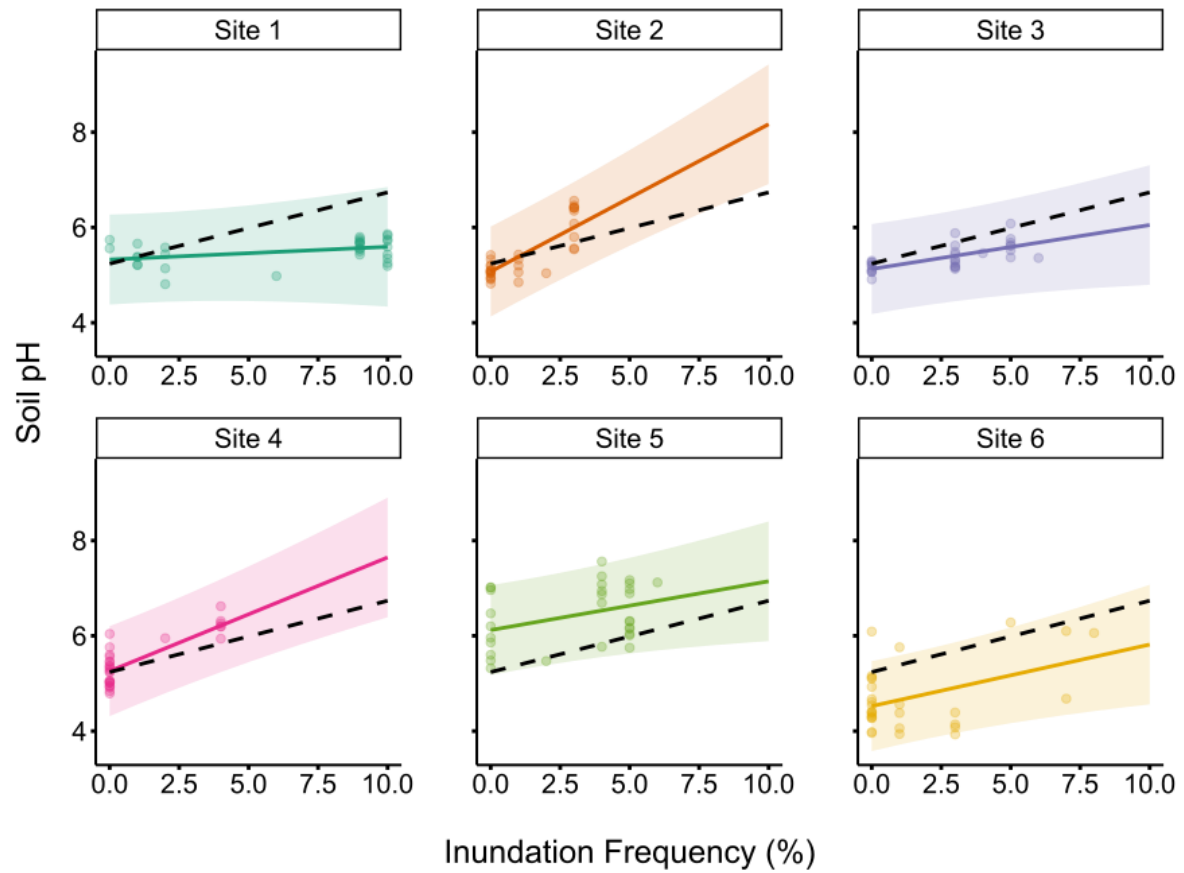


Figure 3.3 Soil pH predictions for each site. The black line represents the overall model regression line. Bands are 95% CI's. Points are observed IF values at each site.

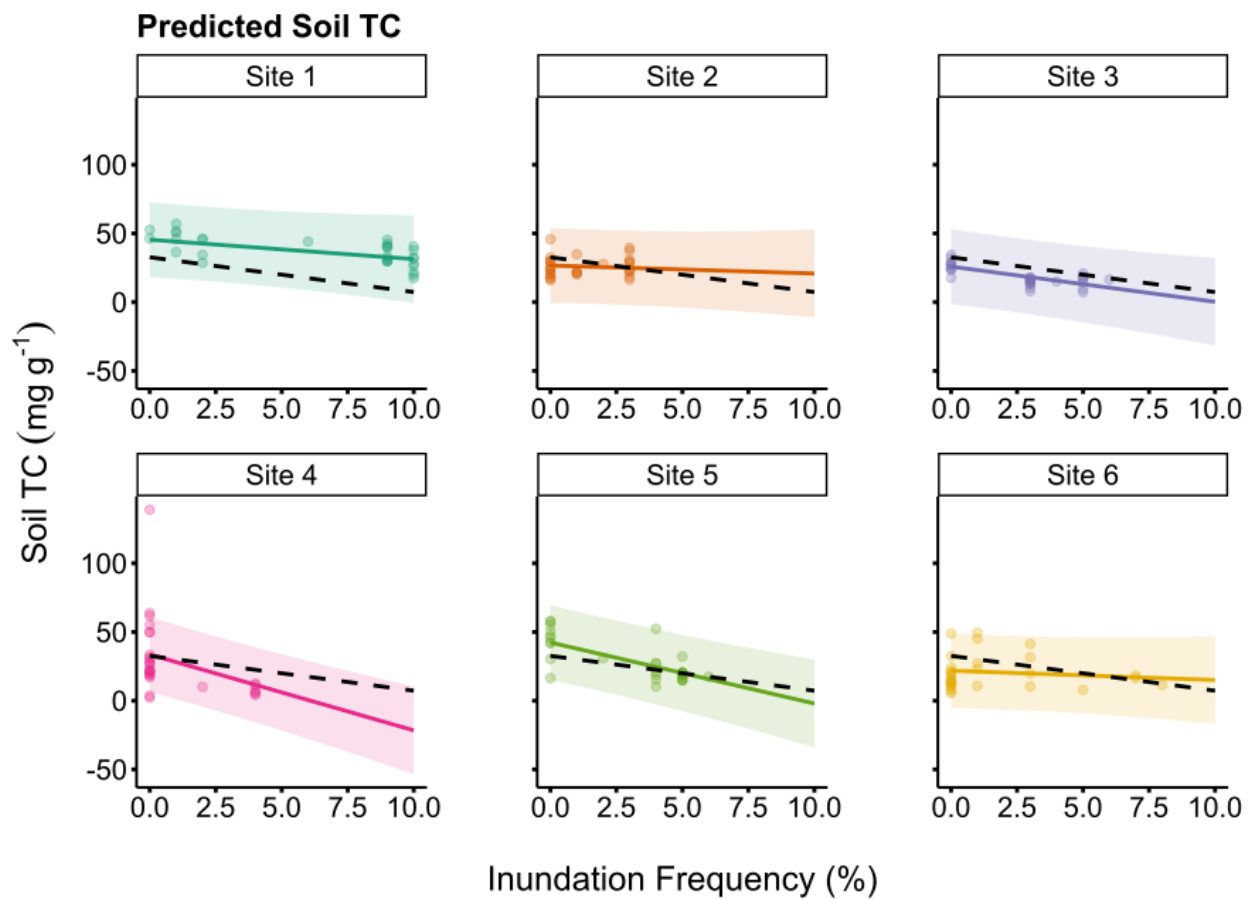


Figure 4.3 Soil TC predictions for each site. The black line represents the overall model regression line. Bands are 95% CI's. Points are observed IF values at each site.

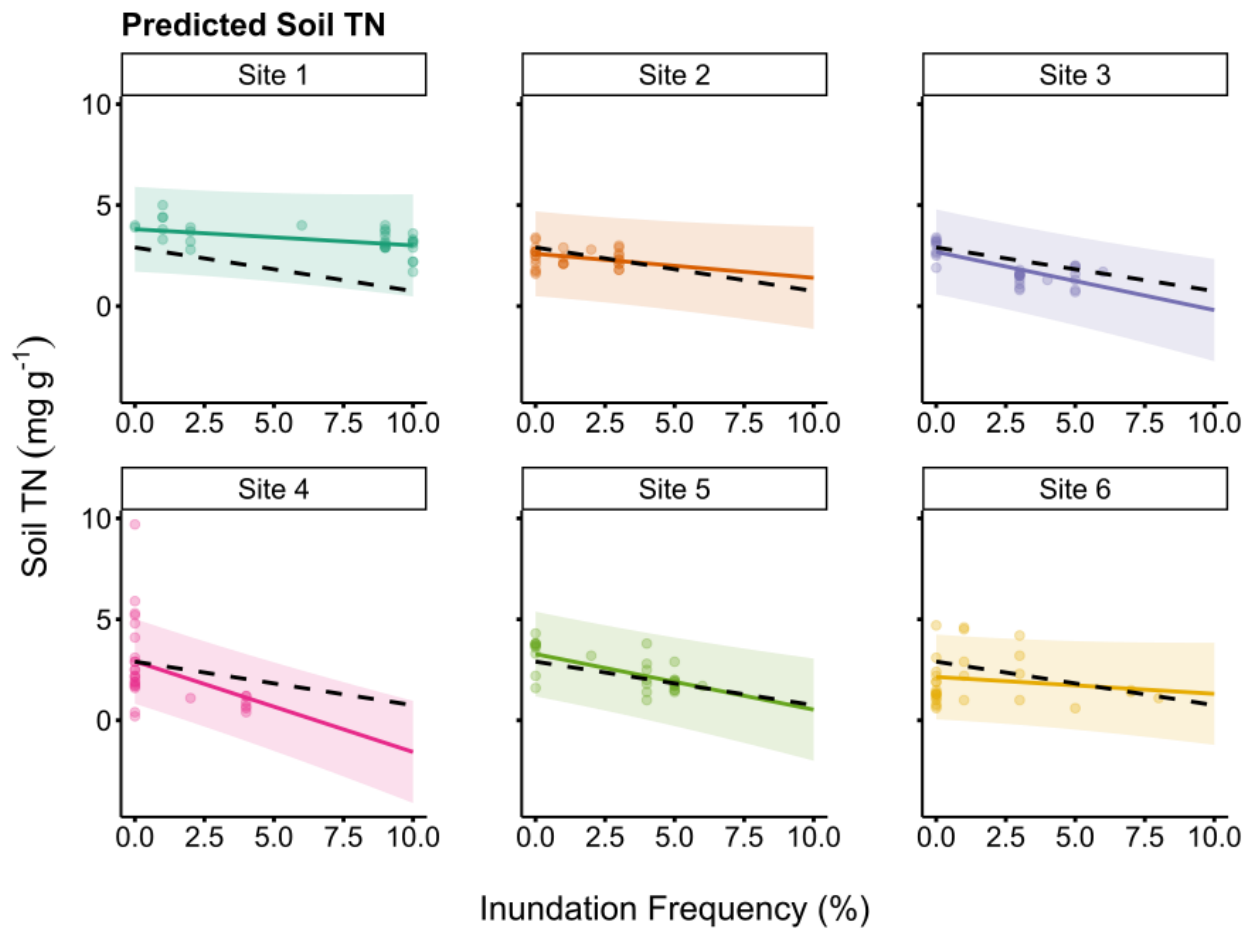


Figure 5.3 Soil TN predictions for each site. The black line represents the overall model regression line. Bands are 95% CI's. Points are observed IF values at each site.

Discussion

Evaluation of Hypotheses

Hypothesis 1: Inundation frequency of a wetland affects NO_3^- and PO_4^{3-} retention.

This hypothesis was moderately supported as there was a significant correlation between NO_3^- flux and IF but not between PO_4^{3-} flux and IF. My prediction that NO_3^- retention would increase as IF increased was supported by these results. My prediction that IF would be negatively correlated with PO_4^{3-} retention was rejected as there was no significant relationship between PO_4^{3-} flux and IF.

Hypothesis 2: Inundation frequency of a wetland affects soil characteristics.

This hypothesis was supported as IF correlated with three (pH, TC, and TN) of the five soil characteristics. However, all my predictions for the relationships between IF and soil pH, TN, and TC were rejected as soil pH increased with IF whereas TN and TC decreased with IF. My predictions that bulk density and moisture content would be positively correlated with IF was also rejected as there was no relationship between these variables and IF.

Inundation Frequency and Nitrate Retention

The positive correlation between NO_3^- retention during initial rewetting and IF supports previous research which found that wetter soils have higher N retention rates than dry soils (Marton et al., 2014; A. L. Peralta et al., 2010; Pinay et al., 2007). The large effect size of IF on NO_3^- retention also indicates that changes in wetland hydrologic regime may strongly affect

NO_3^- retention potential. Moist soils can support higher microbial abundances than dry soils (Blackwell et al., 2009; De Groot & Van Wijck, 1993), and frequent flooding can increase the abundance of N cycling microbes that persist during periods of drying (Baldwin & Mitchell, 2000a; Olde Venterink et al., 2002). These microbial changes likely facilitated rapid N removal from the water upon flooding in the present study.

Flooding also increases anaerobic microbial activity and denitrification rates (Marton et al., 2014; A. L. Peralta et al., 2010; Pinay et al., 2007). For example, increases in flood frequency in freshwater and saltwater marshes have been correlated with a reduction in soil redox potential and enhanced denitrification rates (Hernandez & Mitsch, 2007; Koch et al., 1992; van der Lee et al., 2004; Wigand et al., 2004). Regular flooding also maintains an anoxic environment in deeper soil zones and prevents desiccation, thus keeping the soil primed for rapid N removal during the next flood (Gao et al., 2021; Hernandez & Mitsch, 2007; Song et al., 2014).

In this study, wetland areas that were frequently flooded during the winter and spring prior to soil core collections were often dry at the time of sampling. Despite this, IF was significantly correlated with NO_3^- retention at 6 h even when some areas may not have been flooded in over 30 d prior to sampling. This suggests that patterns in IF can have lasting effects on NO_3^- cycling during initial flooding. While previous studies have shown that NO_3^- retention varies across seasons, flood frequency and magnitude can be a more accurate predictor of year-round NO_3^- retention rates in wastewater treatment and floodplain wetlands (Drake et al., 2018; Hunter & Faulkner, 2001; Song et al., 2012; Spieles & Mitsch, 1999). Therefore, it may be more beneficial to consider the relationship between wetland hydrology and NO_3^- retention across longer timescales rather than hydrologic conditions immediately prior to a flood.

Inundation Frequency and Soil Characteristics

Soil pH

The positive correlation between IF and soil pH was unexpected as some studies have identified a negative relationship between IF/soil moisture content and pH (Bai et al., 2005; Clarke, 1985). Conversely, soils with a pH <6.5 have been found to increase to 7 upon flooding due to the consumption of protons by metal complexes as soil redox is reduced (C. Ding et al., 2019). It is important to note that the relationships between soil pH and IF in this study visually appeared site-specific, though accounting for site-specific variation did not capture much variability in the model. Differences in the relationship between soil pH and IF across sites may provide some insight as to the conflicting conclusions of previous studies as this relationship may be site-specific in other wetlands. In the present study, soil pH values were generally <6.5, potentially supporting the results of Ding et al., (2019). However, more research is needed to determine if the relationship between IF and NO_3^- retention observed in this study applies to other wetlands within the region or abroad.

The chemical profile of sediments delivered to wetlands within the LMRV via flooding may also be influencing this observed relationship between IF and soil pH. The Mississippi River has one of the highest bicarbonate (HCO_3^-) flux rates in the world (Borrok et al., 2018), and potential delivery of HCO_3^- -rich sediments to these wetlands may increase the buffering capacity of regularly flooded soils. However, not all wetlands included in this study are flooded by the Mississippi River, and delivery of high buffering capacity sediment during flooding might be limited to specific sites. Despite its importance to wetland biogeochemical cycling, few studies have directly assessed the relationship between IF and soil pH, making comparisons between the present study and those in the literature challenging.

The finding that soil pH was positively correlated with IF is significant as soil pH influences nutrient cycling rates by altering microbial community structure and function, organic matter decomposition rates, and soil nutrient contents. Soil pH can be strongly correlated with bacterial community structure (Peralta et al., 2013), and high pH can reduce soil bacterial diversity (E. Kang et al., 2021). Reductions in soil redox in response to flooding can reduce aerobic microbial respiration rates, lowering soil pH and reducing organic matter decomposition rates (G. Zhang et al., 2018). Changes in soil pH from flooding can also alter abiotic nutrient cycling processes. For example, P-containing metal complexes in the soil can dissociate upon flooding when pH is high, increasing the potential for P export (Noe et al., 2013). High soil pH can also reduce soil NH_4^+ content as NH_4^+ volatilizes into the atmosphere as ammonia (NH_3^+) (Sgouridis et al., 2011). Increases in pH may also increase organic N mineralization, resulting in greater inorganic N at the soil surface which may be transported downstream during flooding (Bai et al., 2012).

Soil Total Nitrogen and Total Carbon

The observed negative correlation between soil TC and IF may be related to the variations in organic C decomposition rates and alterations to the microbial communities in response to wetland hydrologic regime. Cycles of wetting and drying can rapidly deplete soil organic C as detritus is repeatedly oxidized upon drying (Maynard et al., 2011; Paradis & Saint-Laurent, 2017). Rapid wet-dry cycles in riparian wetlands can also release mineralized C from the soil which is subsequently assimilated by microbes (Baldwin et al., 2015; Valett et al., 2005). Conversely, prolonged flooding is typically associated with higher soil C content due to a

reduction in decomposition rates as oxygen concentrations decrease and stay low, reducing aerobic respiration rates (Bernal & Mitsch, 2008; Segnini et al., 2010).

Like soil TC, the negative correlation between IF and TN could also be related to the effect of hydrology on microbial community structure and functioning. Soil inundation can support N immobilization via microbial uptake or dissimilatory processes like denitrification (Gao et al., 2012; Zak & Grigal, 1991). Denitrification can be a major pathway for soil N loss (Phillips, 2008; van der Salm et al., 2007) and is enhanced by increasing soil moisture content (Marton et al., 2014; A. L. Peralta et al., 2010; Pinay et al., 2007). Additionally, frequent cycles of flooding and drying can support coupled nitrification-denitrification which can rapidly reduce soil N content (Baldwin & Mitchell, 2000a).

The negative correlation between IF and soil TC and TN was unexpected, and contradictions in the literature complicate interpretations. While some studies have reported that frequent inundation increases soil N and C content in wetlands (Bai et al., 2005, 2020; Qi et al., 2021; J. Wang et al., 2016), others have identified an inverse relationship between IF and soil C and N (Argiroff et al., 2017; J. Li et al., 2020). The results from the present study support the results of Argiroff et al., 2017 and Li et al., 2020; however, the significance of the correlations between IF and soil TC and TN are marginal, and additional studies with larger samples sizes are needed to evaluate these trends more precisely.

Conclusions

This study shows that the NO_3^- retention potential at 6 h of flooding and soil characteristics of a restored floodplain wetland may be influenced by IF. The significant correlation between NO_3^- flux at 6 h of incubation and IF supports previous research suggesting that N retention in wetlands is related to hydrology (Drake et al., 2018; Hernandez & Mitsch, 2007; Hunter & Faulkner, 2001; Song et al., 2012). Interestingly, this relationship did not extend to PO_4^{3-} flux. The finding that a 1% increase in IF corresponded to a 4% increase in NO_3^- retention after 6 h of flooding is significant and suggests that hydrologic regime may greatly influence wetland N retention rates during initial flooding. However, the relationship between IF and N retention may cease or be superseded by other factors like interactions among soil properties or changes in microbial community structure and functioning during floods lasting longer than 24 h.

This study also provides novel insights into the relationships between IF and floodplain wetland soil characteristics. Variations in slopes for the soil pH models across sites suggest that there are some site-specific differences in the relationship between pH and IF. Conversely, the relationship between IF and soil TN and TC appears consistent across sites, indicating that these trends may hold across the 16 wetlands sampled in this study that did not have enough imagery available to be included in the analyses. However, additional research is needed to fully understand wetland edaphic responses to IF and extend these relationships to wetlands outside the study area.

While the conclusions presented here are supported by the data, study limitations should be considered when interpreting these results. Only 7-12% of the days within 180-day timeframe

could be included in the IF calculations, and the absence of data on days when imagery was not available could have biased these calculations. Further, nutrient flux and soil data were collected at a single time point at each site, providing only a snapshot of these nutrient cycling processes and soil characteristics. Future studies could reduce the number of wetlands sampled and increase sampling frequency to improve the precision of these analyses and enable more robust evaluations of these relationships to IF over time.

CHAPTER 4: EFFECTS OF VEGETATION TYPE AND HYDROPERIOD ON NITROGEN AND PHOSPHORUS FLUX RATES IN EXPERIMENTAL WETLAND MESOCOSMS

Abstract

Wetland restorations often seek to increase nutrient retention by reestablishing historical vegetation and hydrology. I evaluated the effects of wetland vegetation (herbaceous vegetation (HV), tree saplings (TS), and bare soil (BS)) and hydrologic regime (three-day and three-week hydroperiod) on dissolved nitrate (NO_3^-) and phosphate (PO_4^{3-}) retention, soil oxygen demand (SOD), and nitrogen gas (N_2), methane (CH_4), and nitrous oxide (N_2O) flux rates using wetland mesocosms. Mesocosms were flooded with nutrient-enriched water, and water column NO_3^- and PO_4^{3-} was measured over five days. Mesocosms were then drained, and intact soil cores were collected. Cores were incubated with nutrient-enriched water and sampled for dissolved gases after 12, 24, and 48 h. Vegetation and hydrology interacted to influence NO_3^- and PO_4^{3-} retention, but only beyond 24 h of flooding for PO_4^{3-} . Herbaceous vegetation was most efficient at reducing NO_3^- content in the water regardless of hydroperiod, with >90% reduction in NO_3^- content after three days. All treatments reduced PO_4^{3-} content by >70% after 24 h, beyond which PO_4^{3-} retention differed among the treatments. The three-day hydroperiod and HV treatments had the greatest mean N_2 production and SOD across all sampling time points, but N_2 rates only statistically differed among treatments at 12 h. Nitrous oxide and CH_4 production was minimal in all treatments. These results suggest that wetland vegetation and hydrology can influence nutrient retention and gas production both independently and via their interaction. Further,

differences among treatments weakened as flood duration increased, suggesting that water residence time becomes more influential than vegetation as flood duration increases.

Introduction

Vegetation and hydrology are two primary factors that influence nutrient uptake within riparian floodplain wetlands (Silvan et al., 2004; White et al., 2006). In degraded wetlands, historical flow pathways have often been manipulated to facilitate rapid drainage after floods (Bruland & Richardson, 2005a). These manipulations can disrupt plant community structure and ecosystem functioning and contribute to downstream eutrophication (Olde Venterink et al., 2002). Therefore, the restoration of hydrologic flow regimes is often a major component of wetland restorations. Additionally, wetland restorations employ diverse strategies to improve ecosystem functioning such as reestablishing historical vegetation communities, reconnecting wetlands to the floodplain to reestablish hydric soils that facilitates the growth of various wetland vegetation functional groups. Interactions between restored wetland hydrology and vegetation can affect ecosystem functioning and produce dynamic states of nutrient uptake and release.

Further, these vegetation and hydrology interactions can influence the production of gases involved in various phases of the nitrogen cycle. Nitrogen gas (N_2) production rates are a crucial component of nitrogen (N) cycling in wetlands, which controls the amount of N that is completely removed from aquatic systems (Alldred & Baines, 2016; Hunter & Faulkner, 2001; Reddy et al., 1989). Methane (CH_4) and nitrous oxide (N_2O), two potent greenhouse gases,

emissions can also be affected by these interactions (Maucieri et al., 2017; Whiting & Chanton, 2001). Therefore, understanding how interactions between vegetation and hydrology affects biogeochemical cycling is critical to wetland restoration success. Additionally, it is important to identify any potential tradeoffs that may exist between nutrient retention/removal and greenhouse gas production that could help optimize restoration strategies. This chapter examines how vegetation and hydrology influence nutrient cycling and greenhouse gas production in restored wetlands using experimental mesocosms.

Hydrology-Plant Interactions Influence Nutrient Cycling Rates

Interactions between surface water residence time, plant communities, and soil moisture are known to strongly influence the structure and function of wetland ecosystems. Distribution of plant species and duration of floods are both heavily influenced by these factors. For example, increases in water residence time can result in higher soil moisture levels which can promote tree growth in bottomland hardwood forests (Broadfoot, 1967). In turn, wetland vegetation has also been found to have a significant effect on water residence time by reducing flow velocities, leading to increased heterogeneity in vegetation (Jadhav & Buchberger, 1995; Kjellin et al., 2007). Moreover, soil moisture gradients have been shown to strongly influence the distribution of vegetation functional groups in wetlands (Moor et al., 2017). These interactions influence nutrient cycling in wetlands, resulting in dynamic environments with unique ecosystem functional processes and relationships.

Flow regimes can increase plant species diversity and biomass, leading to higher nutrient retention rates due to vegetation assimilation (Bruland & Richardson, 2005b; Cooper et al., 2017;

Silvan et al., 2004). Hydrologic restoration practices can also alter the water residence time of floodwaters, with longer residence times correlating with higher nutrient retention due to increased microbial and soil uptake (Dettmann, 2001; Johnston, 1991). However, increasing soil moisture can also promote the production of soil CH₄ and N₂O (Bohn et al., 2007; Calabrese et al., 2021), creating potential tradeoffs between nutrient retention and greenhouse gas emissions. In addition, wetland vegetation can significantly influence CH₄ and N₂O emissions, affecting the potential of a wetland to act as a sink or source for these gases (Bezabih Beyene et al., 2022; Sun et al., 2013). Therefore, alterations to wetland hydrology may result in tradeoffs between nutrient retention and greenhouse gas production.

Wetland vegetation species diversity can influence nitrogen (N) and phosphorus (P) retention with rates varying among different functional groups (Taylor et al., 2015; Tyler et al., 2012; White et al., 2006). During restorations, native species that are beneficial to wildlife and representative of the dominant taxa present prior to conversion to cropland are frequently planted (United States Department of Agriculture, 2008). In forested floodplain wetlands, tree plantings are one of the most frequently used revegetation methods when converting cropland back to wetlands under the WRP/WREP program but often fail due to drought-related stress on seedlings or prolonged root saturation (De Steven & Gramling, 2012). Further, few studies have directly assessed how tree plantings influence nutrient cycling in wetlands (Faulkner et al., 2011), and it is uncertain if, or how long it takes to restore historical levels of ecosystem functioning in tree plantings (Mitsch & Wilson, 1996).

In some cases, it may be more efficient to allow habitats to develop through natural succession. Herbaceous vegetation is often the first plant functional group to colonize wetlands. Herbaceous vegetation stored in the seed bank can germinate quickly following the cessation of

crop production, often producing lush herbaceous zone that are resilient to frequent flooding (Bao et al., 2014). Further, herbaceous vegetation often does not have to be planted as long as the seed bank remains intact and may even restore ecosystem function faster than planting trees would. For example, eutrophic wetlands with naturally colonizing vegetation can be more productive and retain a greater amount of nutrients than planted wetlands (Mitsch, Zhang, et al., 2005); however, naturally colonizing wetlands in former croplands may become dominated by quick-growing generalist species, resulting in less plant diversity and a greater potential increase in susceptibility to stress-related mortality. Restored herbaceous wetlands will eventually transition to forest in areas with compatible hydrologic regimes, but this succession can take years to occur. As such, there is a need to evaluate potential differences in nutrient retention between herbaceous vegetation and tree-dominated habitats to better estimate how ecosystem functioning differs between different restoration communities.

Experimental Setting to Test Hydrology-Vegetation Effects on Nutrient Retention

Isolating the effect of a specific factor on the response variable of interest in field studies can be difficult due to confounding variables (Jared Diamond, 1986). Differences in site location and legacy effects from historical agricultural practices may obfuscate correlations among hydrologic regimes, vegetation types, and nutrient retention rates. Additionally, flow path alterations may have created new hydrologic regimes that are incapable of supporting historical plant taxa stored in the seedbank (Miller & Hobbs, 2007). These changes may inhibit the efficiency of ecosystem functioning as repeated attempts at colonization by plant species stored in the seed bank fail to become established, or limitations in dispersal prevent adequate recolonization. Confounding observations in field studies may lead to inaccurate conclusions

about the relationships among vegetation type, hydrology, and nutrient cycling (Galatowitsch & van der Valk, 1996). Given the limitations to field studies, a controlled experimental setting can help isolate causal relationships that may exist among vegetation type, hydrology, and nutrient retention.

As managers can control the types of vegetation planted during restorations and to some extent the duration of flood inundation within restored wetlands, an investigation of the interactions among vegetation type, hydrologic regime, and nutrient uptake is warranted. By controlling for other environmental factors, the effect of specific vegetation types (trees or herbaceous vegetation) associated with different restoration strategies and hydroperiods on N and P retention can be better evaluated and incorporated into future restorations by managers to maximize nutrient retention in restored wetlands.

Objectives

Objectives of this study were **1)** determine if dissolved N and P retention and N_2 , N_2O , and CH_4 production rates differ among bare agricultural soil and two types of restored wetland habitats (herbaceous vegetation and tree plantings); **2)** Evaluate the effect of flood duration on N and P retention and N_2 production rates among vegetation types; and **3)** Determine if tradeoffs exist between N and P removal and the production of two greenhouse gases (N_2O and CH_4).

Hypotheses

Hypothesis 1) Vegetation type affects dissolved NO_3^- , PO_4^{3-} , N_2 , N_2O , and CH_4 flux rates. Herbaceous vegetation was predicted to retain the most dissolved N and P and have the greatest N_2 production, followed by tree planting treatments, and then bare agricultural soil. Aquatic emergent vegetation can provide a more stable supply of carbon (C) and P necessary for maintaining denitrifying microbes near the soil-water interface (Brix, 1997; Reddy et al., 1989; Taylor et al., 2015). Phosphorus uptake was predicted to be highest in vegetated mesocosms as assimilation by plants can be a significant P sink in wetland ecosystems (Gacia et al., 2019; Silvan et al., 2004; Taylor et al., 2015). Bare agricultural treatments were expected to have the lowest dissolved N and P retention, potentially due to the lack of mycorrhizal fungi and assimilation by plants as nutrient uptake pathways and because bare soils were found to have limited retention in a similar study (Taylor et al., 2015).

All treatments were predicted to emit N_2O and CH_4 . Denitrification can be a major source for N_2O emissions (Huang et al., 2013) when the final transformation from N_2O to N_2 is interrupted by the presence of oxygen (O_2) and NO_3^- removal rates can correlate with N_2O emission rates (Freeman et al., 1997). Further, N_2O emissions have been found to be greatly influenced by fluctuations in C:N ratios (M. Li et al., 2017). Consequently, I predicted that N_2 production (presumably as largely a result of denitrification) would be greatest in mesocosms containing herbaceous vegetation and that these mesocosms would emit the most N_2O , as N_2O can be a byproduct of incomplete denitrification. Herbaceous vegetation treatments were also predicted to produce the most CH_4 as previous studies have found that herbaceous vegetation provides a steady supply of labile C in the root zone and the overlying water, enhancing CH_4

production (Lu, Wassmann, Neue, & Huang, 2000; Lu, Wassmann, Neue, Huang, et al., 2000; Sullivan et al., 2013).

Hypothesis 2) Hydroperiod affects nutrient flux rates. I hypothesized that mesocosms with longer inundation periods would retain more N and P. Mesocosms with the longest hydroperiods were predicted to have the greatest soil oxygen demand (SOD) following draining, potentially leading to enhanced denitrification. These soils were presumed to be more primed to convert NO_3^- to N_2 as the soil-water interface was likely at a lower redox state for longer than the soils from the shorter hydroperiod treatment due to prolonged inundation with stagnant water. Further, mesocosms with longer periods of inundation were predicted to have greater N_2 flux rates as rewetting of moist soils has been associated with greater denitrification rates than rewetting of dry soils (Olde Venterink et al., 2002).

Mesocosms with short hydroperiods had more days without water covering the sediment surface, resulting in greater soil desiccation during drying periods. In semi-aquatic ecosystems, total desiccation of soil or sediment can kill as much as three quarters of the total microbes within a recently dried area (Qiu & McComb, 1995). Therefore, mesocosms that had less soil-atmosphere exposure time prior to receiving N and P elevated water were predicted to require less time to build up microbial biomass, resulting in greater N and P retention than in treatments that were dryer at the time of dosing (SOD was used as a coarse proxy for estimating microbial function where more negative O_2 flux rates are indicative of greater microbial activity). Additionally, short-term cycles of wetting and drying have been found to reduce microbially-bound P back into the water column as dissolved P (Chen et al., 2021); therefore, mesocosms with shorter periods of inundation were expected to retain less P than mesocosms with longer inundation periods.

Additionally, mesocosms with the highest CH₄ emissions were predicted to emit the least amount of N₂O and vice versa. Rewetting of moist soils have been found to enhance CH₄ emissions (Mander et al., 2003) whereas rewetting of dryer soils has been associated with increases in N₂O emissions (C. J. Smith et al., 1983). Therefore, N₂O and CH₄ emissions were predicted to be inversely correlated with short-term hydroperiod treatments emitting the most N₂O and treatments with long-term hydroperiods emitting more CH₄.

Methods

Mesocosm Assembly

Thirty-six outdoor mesocosms were assembled at Tennessee Tech University's Shipley Farm following protocol established by (Tyler et al., 2012; Taylor et al., 2015). Each mesocosm consisted of a 379-L plastic tub (122 cm (length) x 61 cm (width) x 61 cm (height)). Tubs were filled with approximately 30 cm of silica sand overlaid with approximately 15 cm of wetland soil. During simulated flooding, a water depth of approximately 10 cm was maintained within the inundated mesocosms. A surface water discharge port consisting of a 1.27-cm bulkhead, barbed hose fitting (1.27-cm hose fitting, 0.64-cm barb) and discharge hose (0.95 x 0.64 cm diameter) was installed near the top of the mesocosms to improve drainage following flooding (Fig. 1.4). Discharge hoses were plugged when not in use. Cookeville, Tennessee, USA municipal water was used to fill four 606-L elevated water storage tanks that served as the water sources for the mesocosms. Sodium thiosulfate was used to dechlorinate water within the storage

tanks. Water was then transferred from the storage tanks to mesocosms through 3.81-cm diameter PVC pipes using a gravity-fed system controlled by ball valves at the outflow of each tub. Mesocosms were placed in four rows of nine, with one tank supplying water to a single row (Figs. 2.4 and 3.4).

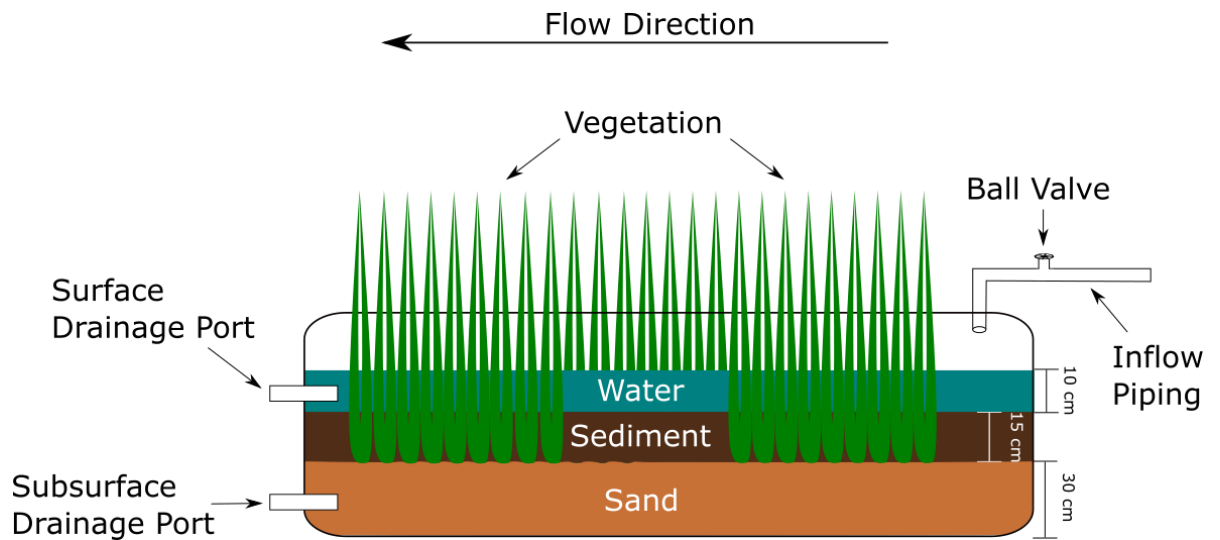


Figure 1.4 Diagram of a mesocosm.

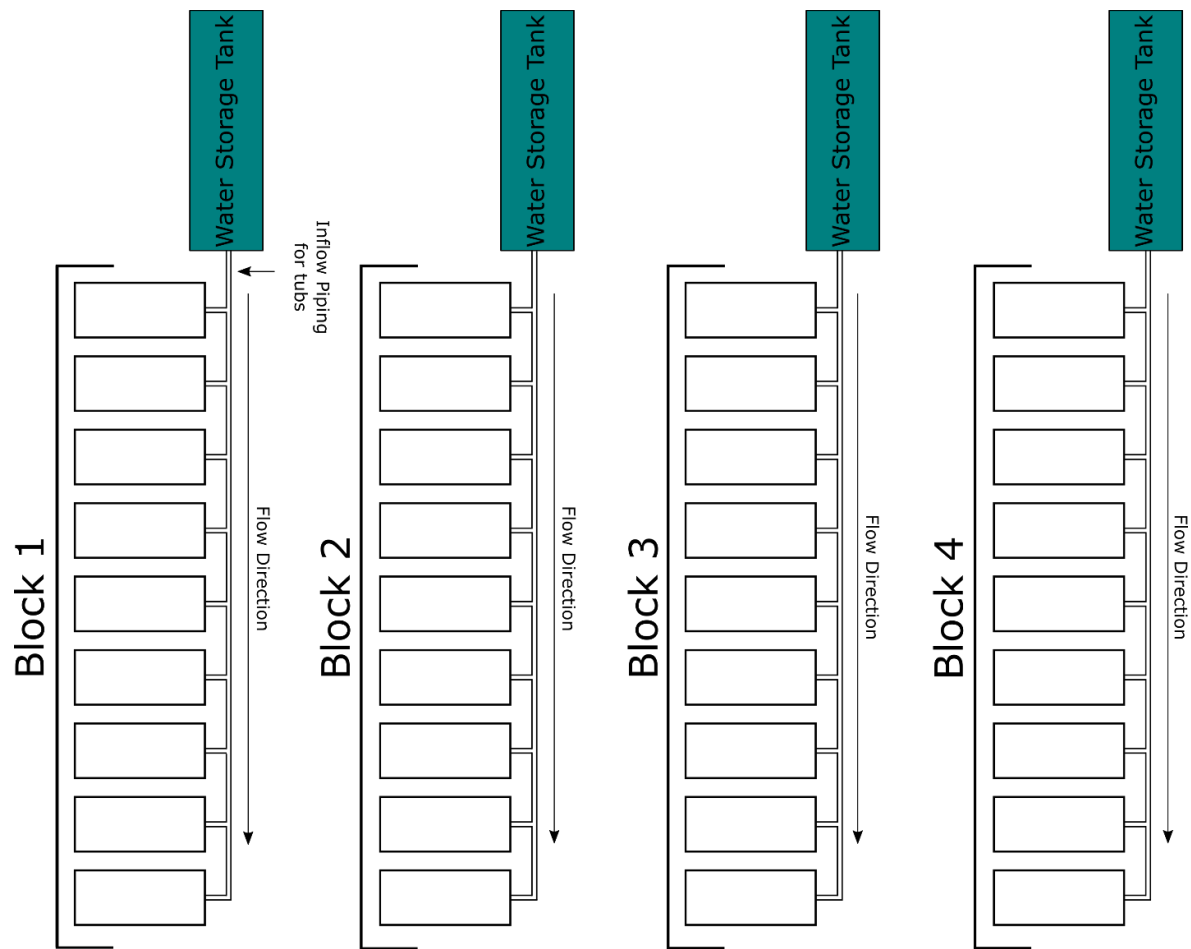


Figure 2.4 Diagram of experimental design and plumbing for the mesocosms.



Figure 3.4 Assembled mesocosms with assigned treatments. Note the nearest tub in the picture (bottom right) was only used to maintain backup trees in case treatment trees died. It was not used in the experiment. No trees died during this study.

Soil Collection and Preparation

Soil for the mesocosms was provided by the West Tennessee River Basin Authority. Topsoil (Falaya Silt Loam, collected < 0.6 m deep) was collected from a stream restoration site in west Tennessee adjacent to the Middle Fork Forked Deer River near Three Way, Tennessee, USA and transported to the mesocosm site. Soil in the mesocosms was overlaid with a small

amount of wetland soil collected from a restored wetland in western Tennessee, USA. The wetland soil was used to seed the mesocosms with microbial taxa representative of those found in restored floodplain wetlands in western Tennessee and Kentucky, USA. Seeding the mesocosms with wetland microbial communities was necessary to establish nutrient uptake pathways representative of those found on the restored wetlands and decreased the incubation time needed for microbial community establishment. Care was taken to ensure that each mesocosm received the approximately same amount of both types of soil during assembly.

Treatment Assignment

One of six treatments were assigned to each mesocosm in a two-factor experiment, with vegetation type and flood duration (referred to as hydroperiod) as factors (Table 1.4). Vegetation treatments had three levels, bare agricultural soil, herbaceous vegetation, and sapling trees (approximately 2 years old, herein referred to as tree planting). The hydrologic factor consisted of two levels, a short hydroperiod and a long hydroperiod. Each treatment consisted of one vegetation level and one hydroperiod level with four replicates per treatment. A two-factor factorial design was used to distribute treatment replicates among the four rows. Treatments were assigned to each mesocosm using a random number generator.

Table 1.4 All possible factor combinations (BS = bare soil, HV = herbaceous vegetation, TP = tree planting; 3-days = 3-day hydroperiod, 3-weeks = 3-week hydroperiod).

Hydrologic Levels	Vegetation Levels		
	Bare Soil	Herbaceous Vegetation	Tree Planting
3-day Hydroperiod	BS – 3-days	HV – 3-days	TP – 3-days
3-week Hydroperiod	BS – 3-weeks	HV – 3-weeks	TP – 3-weeks

Vegetation treatment levels were herbaceous vegetation represented by rice cutgrass (*Leersia oryzoides*), tree plantings (Fig. 4.4) represented by river birch (*Betula nigra*) and bald cypress (*Taxodium distichum*) saplings, and bare soil. Bare soil treatments functioned as the control for the vegetation treatments. Plant species selections were based on the types of vegetation planted by managers during floodplain wetland habitat restorations, common natural vegetation observed on restored wetlands, and by each species' tolerance of prolonged root saturation. Trees were purchased from a local plant nursery. *Leersia oryzoides* was collected from the riparian area of Little Creek in Cookeville Tennessee, USA (Latitude: 36.196383, Longitude: -85.529292). Treatments containing *L. oryzoides* were planted at densities to cover as much exposed soil as possible. Treatments containing *B. nigra* and *T. distichum* were planted with two saplings of each species (four trees per mesocosm) spaced equidistant from each other with saplings of the same species planted on the same side of the mesocosms. Hydrologic

treatments began as soon as the vegetation was established in the mesocosms (approximately one month after planting (June 2022)).

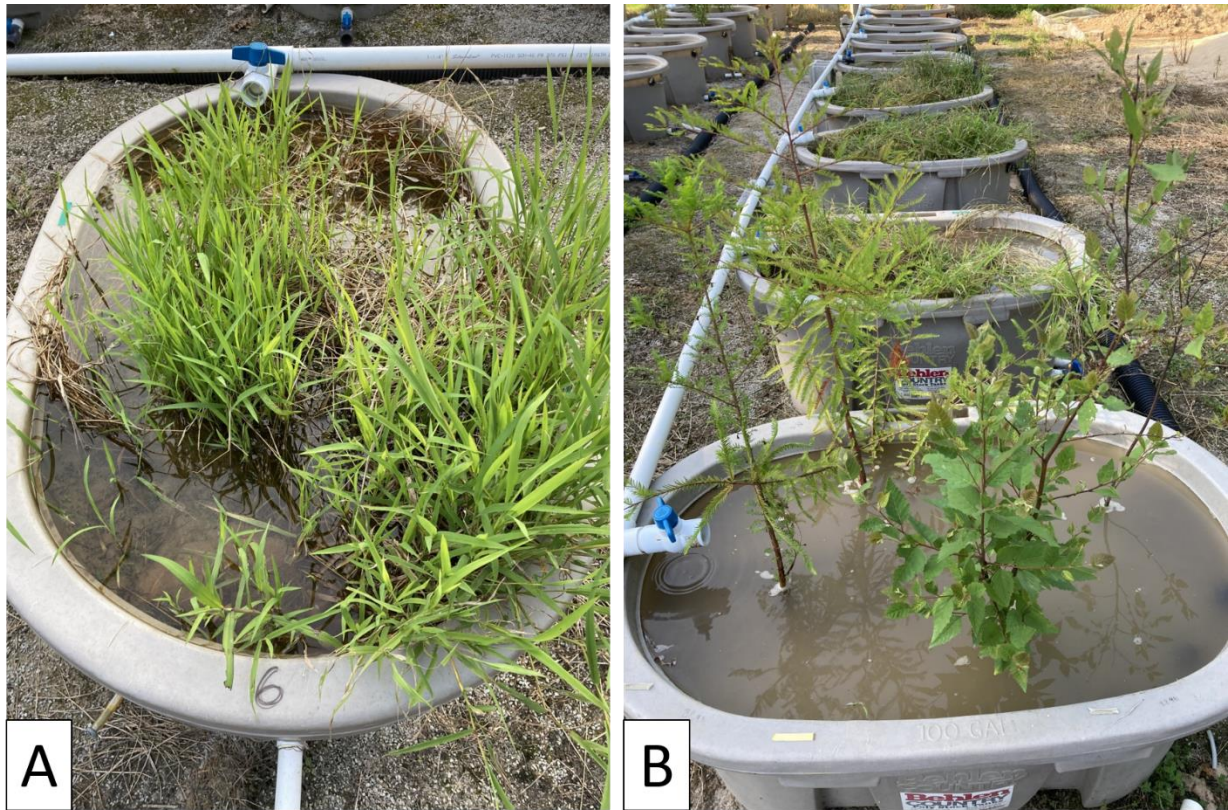


Figure 4.4 Typical herbaceous vegetation (A) and tree planting (B) treatments.

Hydrologic treatment levels included a 3-day (short duration) and 3-week (long duration) hydroperiod. The short duration mesocosms were flooded for three days, drained, and dried for four days, and then flooded again. Long duration mesocosms were flooded for three weeks, drained, and dried for one week, and then flooded again. Nutrient uptake and denitrification rates were measured in each mesocosm following eight weeks of flooding cycles (July and August

2022). Establishing cycles of wetting and drying prior to the experiment allowed soil microbial communities associated with the various frequencies of wetting and drying to propagate.

Nutrient Enrichment and Nutrient Retention Sampling

Mesocosms were flooded with N and P enriched water in early September 2022. The four water storage tanks were filled, dechlorinated, and dosed with sodium nitrate (NaNO_3) and potassium phosphate (KH_2PO_4) to reach target concentrations of $10 \text{ mg L}^{-1} \text{ NO}_3\text{-N}$ and $1 \text{ mg L}^{-1} \text{ PO}_4\text{-P}$ per storage tank. These target concentrations for N and P were selected to ensure nutrient saturation was reached in each mesocosm. Nutrient uptake rates in streams and wetlands increase with increasing water nutrient concentration up to a point where removal ability becomes saturated. Thus, dosing to N and P concentrations that saturate uptake allows the determination of maximum N and P uptake potential to make mesocosm nutrient and dissolved gas flux rates more comparable. Water samples were collected immediately after dosing (day zero) and once per day over the following five days (six days of sampling total).

Water Quality Sampling

Mixing tanks were required to be filled twice to provide enough water to each row to completely fill all mesocosms. Therefore, paired water samples were collected from each tank for the first and second fillings (four samples total per mixing tank) to ensure that starting nutrient concentrations were at target values. Surface water area in the mesocosms was divided in to three roughly equally sized zones, and triplicate filtered water samples were collected from the center of each zone. A 60-mL syringe was used to collect 5 mL of water from each of the

three zones within a mesocosm. This water was then ejected through a syringe filter tip containing a 0.45 μm pore size membrane filter to rinse the syringe, filter, and filter tip with mesocosm water prior to sampling. Ten mL were then be collected from each zone for a total of 30 mL of sample per tub. The syringe was then pulled backwards to create 10 mL of empty head space. Syringes were inverted 10 times to ensure adequate sample mixing within the syringe. One to two mL of sample were pushed through the filter tip to flush the filter again, and approximately 20 mL of water was ejected into a 20-mL scintillation vial. All samples were placed on ice and frozen until analysis. Samples were analyzed for NO_3^- and PO_4^{3-} . This collection process was repeated to collect 40 mL of sample for dissolved organic carbon (DOC). All DOC samples were stored in ashed amber vials and analyzed within 24 h of collection.

Dissolved Nutrients Analysis

Colorimetric analysis on a Seal AQ400 Discrete Analyzer was used to measure NO_3^- , nitrite (NO_2^-), and PO_4^{3-} concentrations in samples. Nitrate and NO_2^- concentrations were measured using the sulfanilamide reaction method (EPA Method 353.2) with a cadmium column reduction. Nitrite was then subtracted from $\text{NO}_3^- + \text{NO}_2^-$ values to yield NO_3^- -N concentrations within each sample. Phosphate was measured as soluble reactive phosphorus (SRP) using the ascorbic acid method (EPA Method 365.1). Dissolved organic carbon was measured using the combustion catalytic oxidation method on a Shimadzu Total Carbon Analyzer (EPA Method 9060A). Samples with concentrations below each instrument's minimum detection limit (MDL) were reported as half of the MDL (Helsel, 1990).

Soil Ash-Free Dry Mass, Algal Biomass, and Post-Dosing Soil Nutrient Sample Collection

All tubs were drained following the last sampling event and allowed to continue draining overnight. Chlorophyll-*a* (chl-*a*), ash-free dry mass (AFDM), and soil total carbon (TC), total nitrogen (TN), and extractible P samples were collected the following morning to estimate surface algal biomass, soil organic matter content, and soil nutrient content. For chl-*a* and AFDM collection, the soil surface area of each tub was partitioned into 25 individual grids (five x five transects, (Fig. 5.4). A random number generator was used to select one of five possible grids on a transect to samples for chl-*a* and AFDM. Once a grid was selected, a 50-mL centrifuge tube (2.7 cm diameter) was pushed into the sediment surface to a depth of 1 cm (1.35 cm² of soil per transect). This process was repeated once along each of the five transects to yield approximately 6.75 cm² of sample per tub. Triplicate soil samples for nutrient analyses were collected using a 2.54 cm diameter hand auger from each of the three zones of a mesocosm where water samples were collected. Ash-free dry mass samples were dried at 60° C for 24 h upon returning to the lab. Chlorophyll-*a* and soil nutrient samples were frozen until analysis.

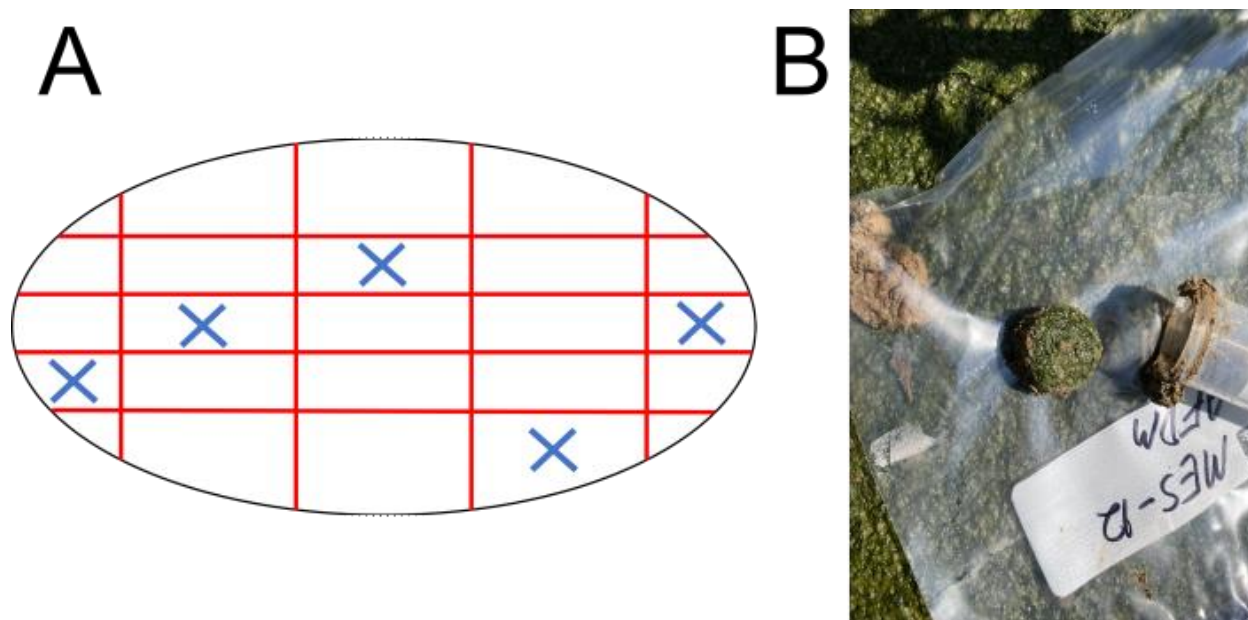


Figure 5.4 Diagram of the sampling grid used for algal biomass and organic matter sampling (A) (blue X's represent hypothetical randomly selected sampling locations. Note: not all grids are the same size due to the oblong shape of the tubs). An example of a soil sample collected for AFDM or chl-*a* determination collected from one grid location within a bare soil – 3-day hydroperiod treatment (B).

Soil Ash-Free Dry Mass, Algal Biomass, and Soil Nutrient Content Analysis

Soil AFDM was analyzed using the combustion method described in Chapter Two. Algal biomass was quantified by estimating the chl-*a* content of each sample. Following collection, chl-*a* samples were frozen for at least 24 h. Chlorophyll-*a* was extracted by submerging each sample in a 95% ethanol (EtOH) solution and heating the samples to 78°C using a water bath. Samples were then stored in total darkness for 24 h to complete the extraction process. Extracted samples were analyzed using the Welschmeyer (non-acidification) method on a Turner Designs

Trilogy fluorometer (Welschmeyer, 1994) and scaled to chl-*a* mg cm⁻² using the calculated surface area of the collection tube (aggregated among the five subsamples). Soil TC, TN, and extractable P were analyzed following methods described in Chapter Two.

Estimation of N₂, O₂, N₂O, and CH₄ Production in Mesocosms

Soil Core Incubation Experiment

Nitrogen gas, O₂, N₂O, and CH₄ flux within each mesocosm was measured by incubating intact soil cores with N- and P-elevated water using a continuous flow-through incubation system (Grantz et al., 2012; Scott et al., 2008; Taylor et al., 2015). Following the draining of the mesocosms and chl-*a* and AFDM sampling, incubation cores were collected using a metal corer and sledgehammer to drive in the cores to a depth of approximately 15 cm (leaving 15 cm of headspace to be filled by incubation water) (see Chapter Two Figs. 3.2 & 4.2). A single core was collected from the center of each mesocosm for the herbaceous vegetation and bare soil treatments. Any leaves for the herbaceous vegetation cores that were taller than the acrylic cores were clipped flush with the core top. Two cores were collected from each tree planting treatment with one core collected in the space between two saplings of the same species. This was done to capture any within-mesocosm variability due to differences in tree species. Cores were capped with a rubber slip cap on the bottom and a plastic PVC cap on the top for transport. Prior to data analysis, a Wilcoxon test was used to compare dissolved gas flux rates between the cores collected from each tree species. There were no significant differences in gas flux rates between cores collected near *B. nigra* and cores collected near *T. distichum*. Therefore, both tree planting cores within a tub were averaged to yield a single flux rate for each tree planting mesocosm.

The top caps of cores were removed upon return to the lab and replaced with an acrylic lid with inflow and outflow tubing attached that was housed in a rubber PVC coupling and secured with pipe straps (see Chapter Two Fig. 5.2). Inflow tubing was extended to just above the soil surface, and outflow tubing was flush with the core top. Cores were incubated in a temperature-controlled chamber in complete darkness to inhibit photosynthesis and O_2 production (see Chapter Two Fig. 5.2).

Air temperatures were maintained at 24 °C throughout the experiment to mimic the typical ambient air temperature of a Mississippi Alluvial Valley floodplain wetland in September. Dechlorinated tap water with elevated NO_3^- -N (10mg L⁻¹) and PO_4^{3-} -P (1 mg L⁻¹) concentrations was pumped through each core. Three lines of inflow tubing not connected to an incubation core were also sampled for dissolved NO_3^- , PO_4^{3-} , and dissolved gases for inflowing nutrient and gas concentrations to calculate flux rates (see Chapter Two Methods for details on sample collection processes). Source water containers were aerated using air stones and pumps when not sampling to prevent oxygen depletion in the source water. Air pumps were turned off during sampling to reduce the risk of introducing bubbles into cores. Masterflex L/S peristaltic pumps were used to pump incubation water through cores at a rate of 2 mL min⁻¹ to achieve an approximately 6 h water residence time. Triplicate gas samples were collected at 12, 24, and 48 h following core filling using 12-mL gas-tight glass exetainers after three exetainer volumes of sample water were purged via overfilling. Overfilling the exetainers removes air bubbles in the sample water and prevents atmospheric contamination. Upon collection, samples were injected first with 180 µL of sodium hydroxide (NaOH) followed by zinc chloride (ZnCl₂) to precipitate dissolved CO₂ that can interfere with CH₄ measurements and to kill microbes within the samples, respectively. Samples were stored completely submerged in tap water at 4 °C until analysis.

Dissolved Gas Analyses

Dissolved gas samples for each core at each time point were analyzed using a Membrane-Inlet Mass Spectrometer (MIMS) with a Secondary Electron Multiplier (SEM) detector to accurately measure trace gases like N_2O and CH_4 . The argon ratio method was used to correct for changes in concentrations due to physical processes such as temperature and atmospheric pressure (Speir et al., 2017). Biologically-mediated changes in dissolved gas concentrations within an incubation core are separated from physically-mediated changes by comparing changes in the ratio of Ar to the gas species being measured (Kana, Darkangelo, Duane Hunt, et al., 1994). The difference in the Ar: O_2 ratio was used to quantify soil oxygen demand (SOD) and used as a proxy to estimate redox potential at the soil-water interface.

During analysis, gas samples were passed through a cold trap to remove unwanted gases. For this cold trap, a slurry of methanol and crushed dry ice was used in place of the traditional cold trap to maintain a temperature of approximately -79°C to freeze any CO_2 in the samples that did not precipitate following injection with NaOH, as CO_2 contamination would interfere with the N_2O measurements (Brown, 2023). Standards for dissolved gas detection were created using deionized water from a constantly stirred standard flask placed inside a water bath held at the core incubation temperature of 24°C . This ensured that dissolved gases in the sample remained at equilibrium with the atmosphere. Standard water was transferred from the standard flask to glass exetainer vials using a peristaltic pump and injected with NaOH and ZnCl_2 following the previously described protocol. Standards were stored on ice during analysis and one standard was analyzed after every six samples to account for signal drift in the MIMS. Gas concentrations in the standard water were incorporated into the gas solubility equations used to convert MIMS

signals to concentrations. Details of how gas concentrations of the standards were calculated can be found in (Brown, 2023). Incorporating standard water gas concentrations improves dissolved gas estimates by accounting for ambient air concentrations in the analysis room and corrects for any changes in atmospheric pressure.

Data Analysis

Nutrient Retention Calculations

Dissolved nutrient retention rates were calculated as $\text{mg m}^{-2} \text{ day}^{-1}$ by first converting nutrient concentrations to whole-mesocosm surface water nutrient mass (the total mass of a nutrient species within a mesocosm water column, corrected for differing water volumes) (Equation 1.4). This was accomplished by multiplying the volume of water in each mesocosm by the nutrient concentration and then dividing by the mesocosm surface area (standardized to 0.74 m^2 for all mesocosms). To calculate per m^2 daily flux rates, final NO_3^- and PO_4^{3-} masses were subtracted by initial nutrient masses (day 0 nutrient masses) and divided by the number of days elapsed until uptake rates became non-linear (modified from Tank et al., 2017) (Equation 2.4). Converting nutrient concentration to nutrient mass improves the precision of estimating total nutrient retention by a mesocosm by correcting for differences in water depth and volume. Using nutrient mass also helps correct scaling nutrient concentrations up to daily m^2 rates without assuming a uniform volume among mesocosms. Volumes among the mesocosms were not equal due to differences in soil compaction and evaporation. Mean percent changes in nutrient flux rates among the treatments across sampling days were also calculated to visualize daily changes in mesocosm flux rates (Equation 3.4).

Equation 1.4:

$$\text{Nutrient Mass (mg m}^2\text{)} = \frac{\text{Volume of Water (L)} * \text{Nutrient Concentration (mg L}^{-1}\text{)}}{\text{Mesocosm Soil Surface Area (m}^2\text{)}}$$

Equation 2.4:

$$\text{Nutrient Flux Rate (mg m}^{-2}\text{ day}^{-1}\text{)} = \frac{\text{Mass}_{\text{Final Day}} - \text{Mass}_{\text{Initial Dosing}}}{\text{Number of Days Until Depletion}}$$

where *Mass* represents whole-water column nutrient mass

Equation 3.4:

$$\text{Percent Change in Mean Daily Flux Rate} = \left(\frac{\text{Mass}_j - \text{Mass}_i}{\text{Mass}_i} \right) * 100$$

where *Mass_j* represents nutrient mass on a day *j*, and *Mass_i* represents nutrient mass of the preceding day.

Gas Flux Rate Calculations

Photosynthetic production by algae and ebullition from the soil within the mesocosms prevented in situ measurements of dissolved gas flux rates as these processes introduce air bubbles into the water. Dissolved gases more readily diffuse into air than water, and the presence of bubbles within the mesocosms would have likely resulted in an underestimation of dissolved gas flux rate estimates. Therefore, the use of soil core incubations to quantify dissolved gas flux rates was necessary. Equations used for calculating dissolved gas concentrations (mg L⁻¹) were derived from (Wiesenburg & Guinasso, 1979) and (Weiss & Price, 1980), respectively (Equations 4.4, 5.4, & 6.4). Dissolved gas concentrations were then scaled to flux rates (mg m⁻²

h⁻¹) using a modified form of the equation outlined in Speir et al., 2017 (Equation 4.4). After calculating gas flux rates for each sample, rates from each group of triplicate samples were averaged to yield one value per gas species per core at each collection time point.

Equation 4.4:

$$Gas_i \text{ conc. } (\mu M) = (Gas_i:Ar_n * Gas_i \text{ solubility}) * \frac{(Gas_i:Ar \text{ solubility})}{Average(Gas_i:Ar \text{ of the standards})}$$

where *Gas_i conc.* is the concentration of a gas in a sample reported as μM . *Gas_i:Ar_n* is the gas:Ar ratio (μM) for the *n*th sample. *Gas_i solubility* and *Gas_i:Ar solubility* are the solubilities of *Gas_i* and the *Gas_i:Ar* ratio (μM) corrected for the temperature and barometric pressure at which the sample was collected, respectively.

Average(Gas_i:Ar of the standards) is the average *Gas_i:Ar* concentration (μM) of the triplicate standards.

Equation 5.4:

$$Elemental \text{ Gas}_i \text{ conc. } (\mu M) = Gas_i \text{ conc. } (\mu M) * \# \text{ of atoms}$$

where *Elemental Gas_i conc.* is the concentration of N, C, or O atoms in a sample for each gas compound for N₂ and N₂O, CH₄, and O₂, respectively. *Gas_i conc.* is the concentration (μM) of a gas in each sampled. *# of atoms* is the number of N, C, or O atoms in each respective gas compound.

Equation 6.4:

$$Gas_i \text{ conc. } (mg \text{ L}^{-1}) = \frac{Elemental \text{ Gas}_i \text{ conc. } (\mu M) * the \text{ molecular mass}}{1000}$$

where $Gas_i \text{ conc.}$ is the concentration in $mg\ L^{-1}$ of each gas as N, C, or O. Elemental Gas_i conc. is the number of N, C, or O atoms in a sample. Molecular mass is the molecular mass of a given compound. Dividing by 1,000 converts the values from $\mu M\ L^{-1}$ to $mg\ L^{-1}$.

Equation 7.4:

$$Aeral\ Flux\ (mg\ m^{-2}\ h^{-1}) = \left(\frac{([Core]_{out} - [Core]_{in}) * Core_{flow}}{Soil\ Area} \right)$$

where $[Core]_{out}$ and $[Core]_{in}$ are outflow and inflow concentrations ($mg\ L^{-1}$) of N_2 , O_2 , N_2O , and CH_4 from the soil cores. $Core_{flow}$ is the flow rate of water through a core ($L\ h^{-1}$). $Soil\ Area$ is the surface area of an individual core (m^2). Positive flux rates for N_2 , O_2 , N_2O , and CH_4 indicate a net gain in the water column (i.e., production), and negative fluxes indicate a net loss (removal) of N_2 , O_2 , N_2O , and CH_4 from the water within a core. Nitrous oxide yield, which represents the proportion of N gas produced as N_2O (reported as a percentage), for each core was also calculated (Equation 8.4). Calculating N_2O yield can be used to evaluate denitrification efficiency as a high N_2O yield can indicate incomplete denitrification (failure of NO_3^- to be converted completely to N_2). Further, examining N_2O yield also helps evaluate potential tradeoffs in nutrient removal and greenhouse gas emissions by comparing how increases in N_2 production affect N_2O production.

Equation 8.4:

$$N_2O \text{ Yield} = \left(\frac{(N_2O \text{ (mg L}^{-1}) + N_2 \text{ (mg L}^{-1}))}{N_2 \text{ (mg L}^{-1})} \right) * 100$$

Statistical Analysis

Model Specifications and Flux Rate Comparisons

ANCOVA's were used to test for differences among treatments for overall NO_3^- , PO_4^{3-} , and DOC flux rates for the dosing experiment and for N_2 production and SOD at each time point for the core incubations. An ANOVA was used to test for differences in chl-*a* content among treatments. Nitrous oxide and CH_4 production rates were too low to be analyzed using parametric methods and were evaluated solely on trends. As such, there were no statistical comparisons among N_2O and CH_4 means among treatments. Models were built using generalized least squares regression with variance structures assigned to vegetation, hydrology, or covariates to correct for unequal variances among factor levels (Zuur et al., 2009). Full model parameters included vegetation, hydrology, soil nutrients, chl-*a*, and AFDM. Only one soil nutrient species was used in each analysis due to significant autocorrelation among soil nutrients. Parameters for all final models were determined using backward selection. Parameter significance during stepwise model selection was evaluated using log-likelihood ratio tests. All final models that included a random structure were fit using restricted maximum likelihood (REML) estimations. The final model for chl-*a* did not include a random structure and was fit using maximum likelihood (ML). All analyses were performed using the statistical software *R* (R Core Team, 2022). Generalized least squares models were run using the *nlme* package (Pinheiro et al., 2022).

ANCOVA's with type III sums of squares were then applied to each final model to determine if there were differences in flux rates among treatments, whether vegetation and hydrology interacted, and which covariates influenced mean flux rate or chl-*a* content estimations. Predicted means and confidence intervals were calculated using the *emmeans* package (Lenth, 2022). Post-hoc pairwise comparisons were made using Tukey's Honestly Significant Difference (HSD) Test.

Nonlinearity in the Phosphate Data

Phosphate content rapidly declined in all treatments after 1 day (24 h) of inundation. This led to an initial steep reduction in PO_4^{3-} content followed by a leveling out and then slow decline between days 2 – 5. As such, there were two distinct linear trends in the PO_4^{3-} data when viewed across the 5-day experiment timeframe. To correct for this violation of the assumption of a linear relationship, the data were split into two groups and modeled separately. One dataset contained PO_4^{3-} flux rates calculated using data up to day 1 while the second dataset contained data from days 2 – 5. A single model including all time points would have underestimated the true retention rate for whichever treatment was most efficient at reducing PO_4^{3-} content. This is because the most efficient treatment would have the lowest PO_4^{3-} content by day 5, resulting in a lower number in the numerator of the flux rate calculations. This would yield a smaller overall retention rate compared to other treatments, potentially leading to the erroneous conclusion that the treatment most efficient at reducing PO_4^{3-} content had the lowest overall retention rate. Breaking these data into two analyses allowed for the determination of which treatment was most efficient at retaining PO_4^{3-} and highlighted how treatment flux rates change across a 5-day flood.

Missing Data

For all analyses, data from mesocosm #4 (bare soil – 3-day hydroperiod) were removed due to missing soil nutrient data and an erroneous value for chl-*a* resulting from incomplete extraction from the soil ($n = 35$ for NO_3^- , PO_4^{3-} , and chl-*a* analyses). Additionally, DOC data collected at day 5 did not include samples from mesocosms 34 – 36 because (1) mesocosm 36 was dry at the time of sampling due to a leak in the tub and (2) a thunderstorm prevented the sampling of mesocosms 34 and 35.

For soil core incubations, no data was collected from mesocosm #33's soil core (herbaceous vegetation – 3-week hydroperiod) during the 12 h sampling event due to a pump issue. The issue was repaired during the 12 h sampling event, and dissolved gas data for mesocosm #33 was included in each subsequent analysis.

Dissolved Gas Data Outlier Removal

To correct for potentially erroneous gas flux rates within a group of triplicate samples, any sample with a flux rate >90% different from the group mean was removed prior to averaging. However, this removal criterion biases heavily against lower values, and N_2O and CH_4 concentrations were very low across all sampling time points. Therefore, no N_2O or CH_4 flux rate data were removed from a set of triplicate samples before averaging.

Soil Nutrient, AFDM, and Algal Data

Changes in pre- and post-dosing soil nutrient concentrations within a given vegetation or hydrologic treatment were evaluated using paired Wilcoxon-Signed Ranked tests. A Kruskal-Wallis test was used to determine if AFDM content differed between the factors and among factor levels. Pairwise comparisons for the AFDM analysis were made using Dunn's test with a Benjamini-Hochberg correction for multiple comparisons. The `ci.median` function in the *misty* package (Yanagida, 2022) was used to estimate medians and confidence intervals using a binomial distribution.

Results

Dissolved Nutrients Starting Concentrations

Mean NO_3^- and PO_4^{3-} concentrations among the mixing tanks were 10.5 and 1.2 mg L^{-1} , respectively. There were marginally significant differences in starting NO_3^- concentration among the mixing tanks ($p = 0.05$); however, post-hoc pairwise comparisons detected no differences (Table 2.4). There were no differences in PO_4^{3-} concentrations among the tanks.

Table 2.4 Mean nutrient concentrations in the mixing tanks.

Mixing Tank ID	NO ₃ ⁻ (mg L ⁻¹)	PO ₄ ³⁻ (mg L ⁻¹)
1a	10.90	1.35
1b	11.80	0.95
2a	9.88	1.15
2b	9.54	1.06
3a	10.30	1.26
3b	9.33	1.26
4a	11.40	1.40
4b	11.20	0.98

Nitrate Retention

All treatments reduced NO₃ in the overlying water by >90% (by mass) after five days of inundation (Fig. 6.4). Herbaceous vegetation was most efficient at reducing NO₃⁻ mass (Table 3.4), with >80% reduction on average by day 3 for both hydrology levels. In the 3-day hydroperiod treatments, herbaceous vegetation had on average 74% greater uptake than bare soils ($p < 0.001$) and 65% greater than tree plantings ($p < 0.001$). The number of days until uptake rates became nonlinear varied across treatments, ranging from 3 to 5 days and generally occurred once NO₃⁻ content was reduced by approximately 85% (Fig. 6.4).

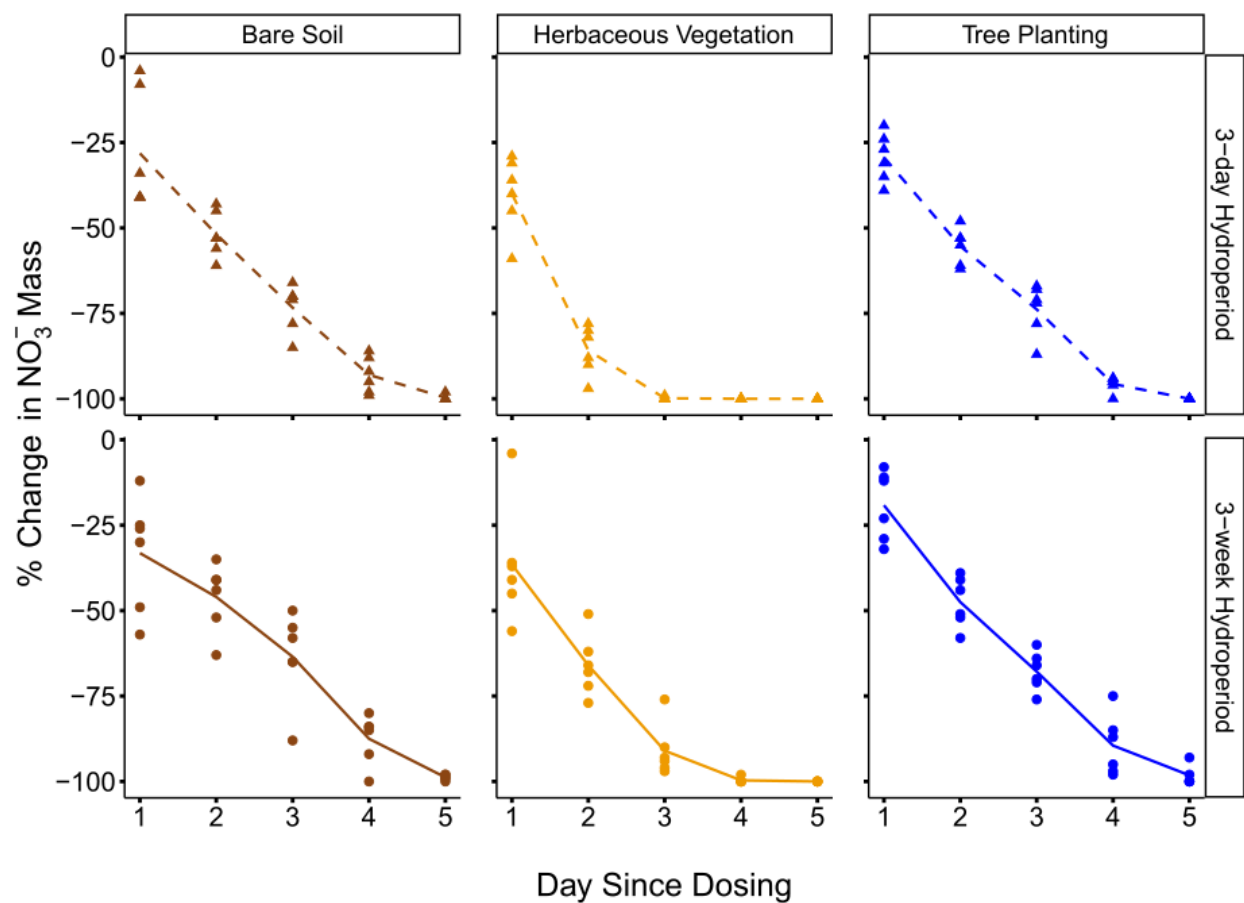


Figure 6.4 Percent change in NO₃⁻ over time. Triangles indicate a 3-day hydroperiod. Circles indicate a 3-week hydroperiod. Lines represent means (3-day hydroperiod = dashed; 3-week hydroperiod = solid).

Table 3.4 Predicted mean NO₃⁻, PO₄³⁻, and DOC flux rates (mg m⁻² day⁻¹) by treatment (no interaction or vegetation type by hydrology level (interaction present). * ± values = standard error

No interaction

Nutrient	<u>Bare Soil</u>	Vegetation		Hydrology	
		<u>Herbaceous</u>	<u>Tree</u>	<u>3-Day</u>	<u>3-Week</u>
		<u>Vegetation</u>	<u>Planting</u>	<u>Hydroperiod</u>	<u>Hydroperiod</u>
PO ₄ ³⁻ - first 24 h	-114 ± 5	-96 ± 4	-109 ± 4	-110 ± 3	-102 ± 5

With Interaction

Vegetation levels grouped by hydrology

Nutrient	3-day Hydroperiod			3-week Hydroperiod		
	<u>Bare Soil</u>	<u>Herbaceous</u>	<u>Tree</u>	<u>Bare Soil</u>	<u>Herbaceous</u>	<u>Tree Planting</u>
		<u>Vegetation</u>	<u>Planting</u>		<u>Vegetation</u>	
NO ₃ ⁻	-251 ± 16*	-437 ± 19	-265 ± 9	-255 ± 16	-343 ± 19	-246 ± 9
PO ₄ ³⁻ - days 2 – 5	-1.70 ± 0.2	-2.50 ± 1	-5.17 ± 1	-0.84 ± 0.2	-5.19 ± 2.52	-1.99 ± 0.64
DOC	99 ± 19	57 ± 10	65 ± 7	166 ± 36	47 ± 11	115 ± 17

Differences in NO_3 uptake rates occurred among vegetation levels (Chi-squared (2, 33), $p < 0.001$), but no differences were observed between hydrology levels (Table 4.4). A significant interaction between vegetation and hydrology was detected (Chi-squared (2, 33), $p = 0.015$) which prevented the assessment of main effects for either factor. However, herbaceous vegetation had the greatest uptake rates regardless of hydrology (Fig. 7.4). When grouped by hydrology, herbaceous vegetation treated with a 3-day hydroperiod had on average 27% more uptake compared to the 3-week hydroperiod ($p = 0.006$) (Fig. 8.4). There were no differences in uptake rates between or within bare soil and tree planting treatments regardless of hydrology. No covariates influenced mean NO_3^- retention rate estimates for the treatments.

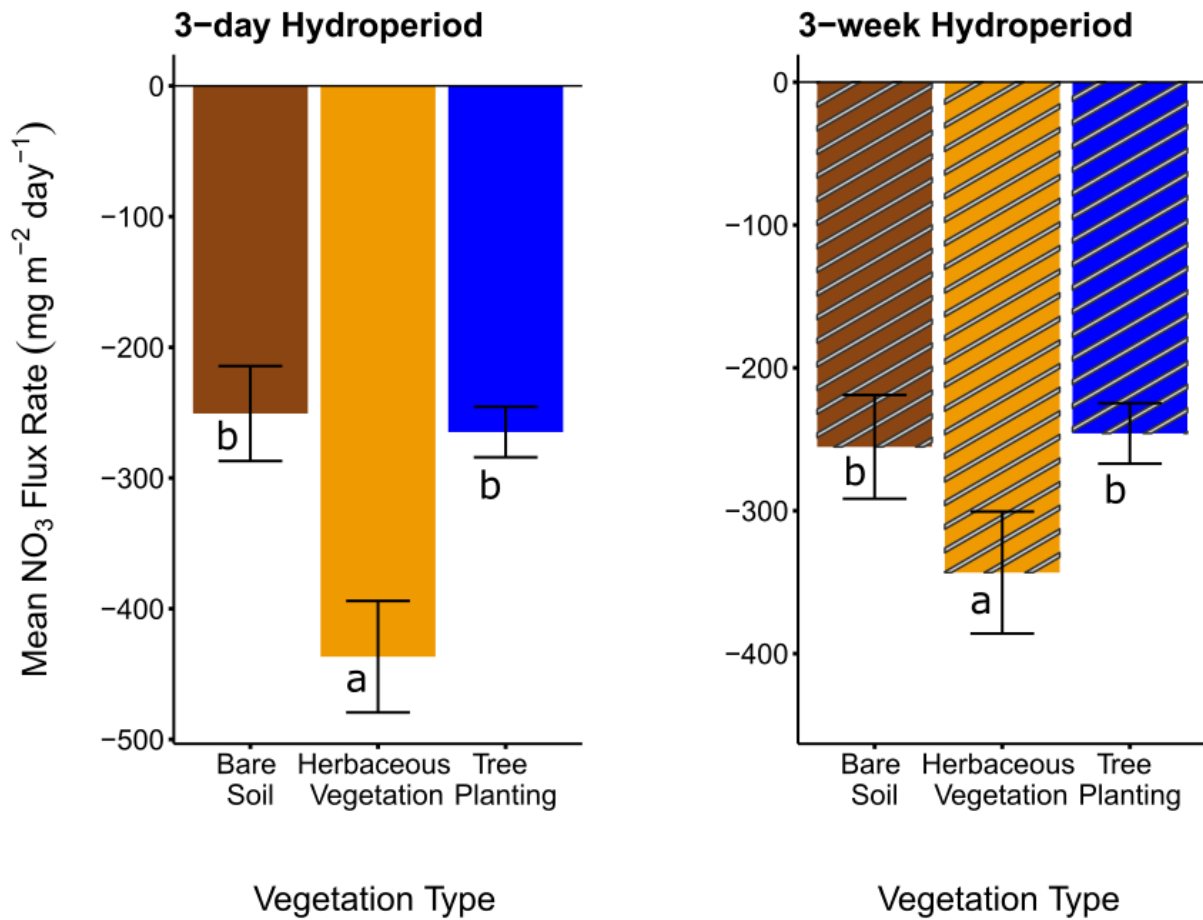


Figure 7.4 Predicted means for NO₃⁻ flux for each vegetation type for the 3-day (solid bars) and 3-week (striped bars) hydroperiods. Different letters indicate significant differences. Error bars represent 95% CI's.

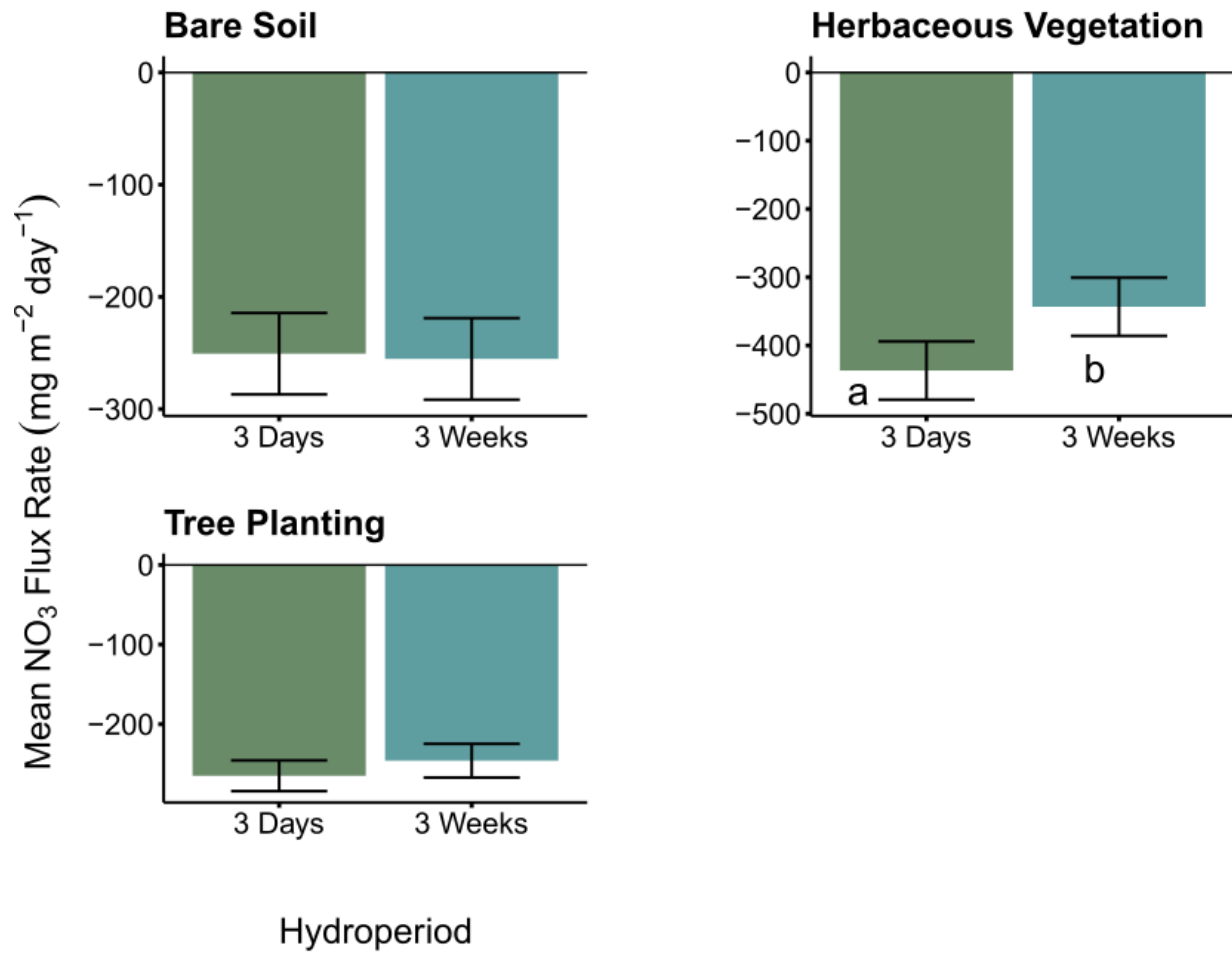


Figure 8.4 Predicted means for NO₃⁻ flux for each hydrology level for bare soil, herbaceous vegetation, and tree planting treatments. Different letters indicate significant differences. There were no differences between hydrology levels for bare soil or tree planting treatments. Error bars represent 95% CI's.

Table 4.4 ANCOVA table for the NO₃⁻ flux rate data.

Source of variation	Chi-squared	<i>p</i>
Vegetation _{2,33}	73.05	< 0.001
Hydrology _{1,35}	0.04	0.83
Vegetation:Hydrology _{2,35}	8.38	0.015

Phosphate Retention

First 24 Hours

All treatments rapidly reduced PO₄³⁻ content in the mesocosms, with an average reduction of >70% PO₄³⁻ (by mass) across all treatments within the first 24 h after dosing (Fig. 9.4). Among the vegetation treatments, bare soil was most efficient at retaining PO₄³⁻, reducing on average >88% of the PO₄³⁻ from the water in the first 24 h. Herbaceous vegetation had the slowest reduction rate, reducing PO₄³⁻ content by an average of 79% after 24 h. Percent reductions in PO₄³⁻ content were similar between hydrology levels, with an average reduction of 85% and 82% in PO₄³⁻ content in the 3-day and 3-week hydroperiod levels, respectively. Additionally, there was no interaction between vegetation and hydrology (Fig. 10.4)

Phosphate retention among treatments was influenced by AFDM content (Chi-squared_(1,33) = 11.67, *p* < 0.001), with a one percent increase in AFDM corresponding to a predicted increase of 35 mg m⁻² day⁻¹ in PO₄³⁻ retention. Significant differences in PO₄³⁻ flux rates were detected among vegetation levels after controlling for AFDM, with bare soil mesocosms having on average 19% more PO₄³⁻ uptake than the herbaceous vegetation mesocosms (*p* = 0.054).

There were no other differences in PO_4^{3-} flux rates among vegetation types or between hydrology levels.

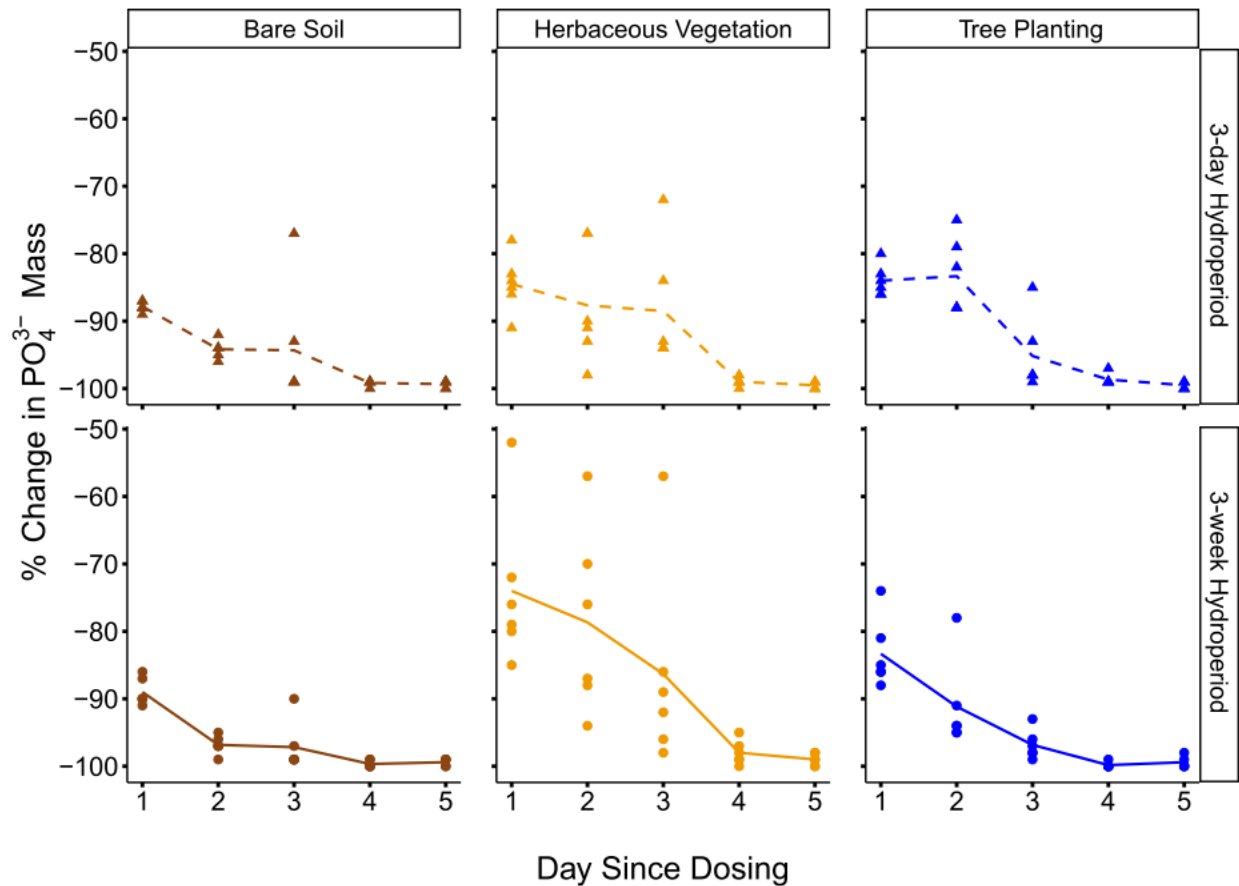


Figure 9.4 Percent change in PO_4^{3-} over time. Triangles indicate a 3-day hydroperiod. Circles indicated a 3-week hydroperiod. Lines represent arithmetic means (3-day hydroperiod = dashed; 3-week hydroperiod = solid).

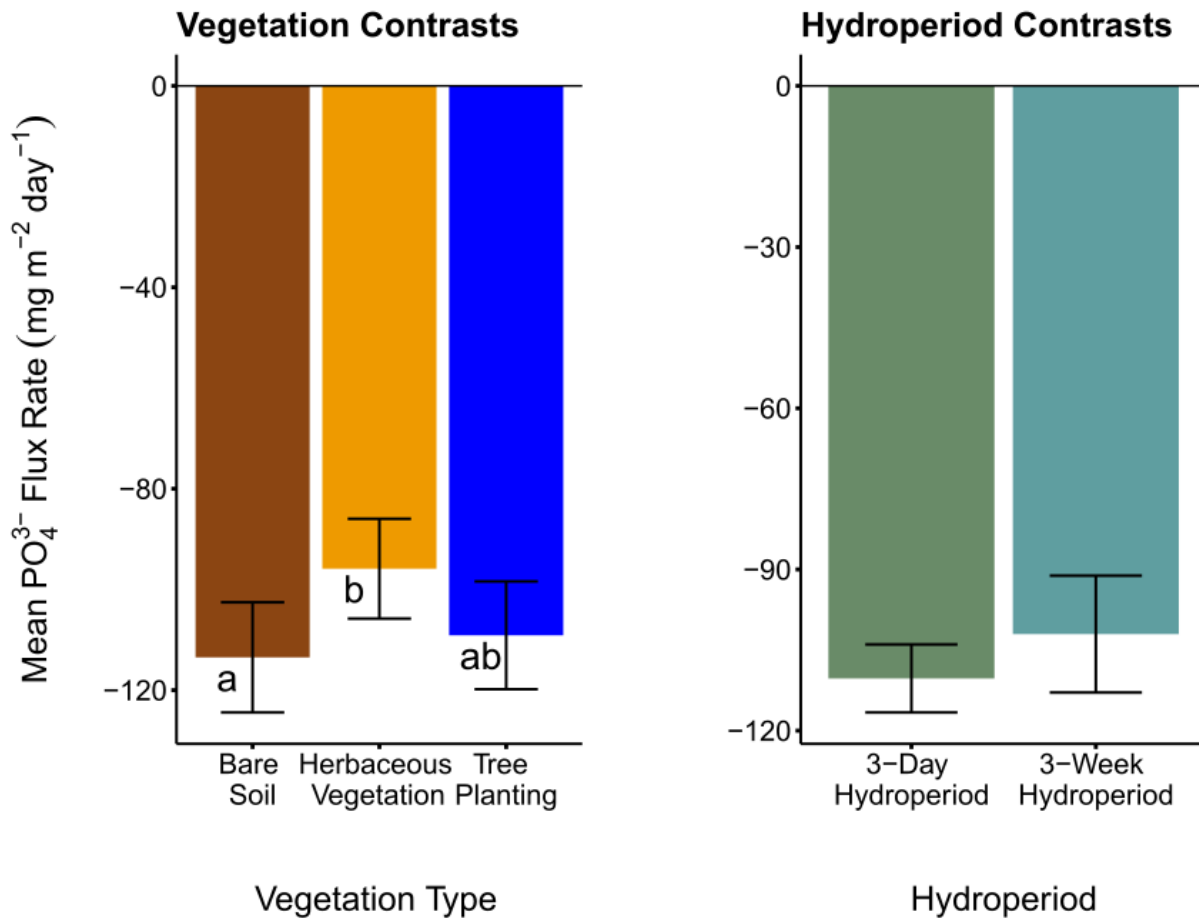


Figure 10.4 Predicted mean flux rates of PO_4^{3-} for the first 24 h of the experiment for mesocosms treated with a 3-day (solid bars) and 3-week (striped bars) hydroperiod. Different letters indicate significant differences. There were no differences between hydrology levels. Error bars represent 95% CI's.

Days 2 - 5

Beyond 24 h, flux rate dynamics shifted, with uptake rates in bare soil treatments lagging the herbaceous vegetation and tree planting treatments. This lag in uptake by bare soil was likely due to bare soil treatments containing less PO_4^{3-} by day 2 compared to the other vegetation

levels, resulting in a slower uptake rate. For days 2 through 5, PO_4^{3-} uptake rates were generally similar within bare soil mesocosms but became variable in the herbaceous vegetation and tree planting treatments. A significant interaction occurred between vegetation and hydrology for the days 2 – 5 dataset (Chi-squared $(2,35)$, $p = 0.042$).

As observed in the 24 h dataset, AFDM content influenced PO_4^{3-} flux rate predictions, with high AFDM associated with higher PO_4^{3-} retention; however, the effect size of AFDM on PO_4^{3-} was weak ($0.02 \text{ mg m}^{-2} \text{ h}^{-1}$ increase in PO_4^{3-} retention per 1% increase in AFDM) (Table 5.4). When grouped by hydrology, tree plantings treated with a 3-day hydroperiod had 200% more uptake on average than bare soils ($p = 0.003$) and 105% more uptake than herbaceous vegetation; however, there were no statistical differences between herbaceous vegetation and tree planting treatments (Fig. 11.4). For the 3-week hydroperiod, herbaceous vegetation had 516% greater PO_4^{3-} uptake on average than bare soil ($p = 0.028$) and 161% greater uptake than tree planting. However, there were no statistical differences in day 2 through 5 uptake rates between herbaceous vegetation and tree planting treatments.

When uptake rates for each hydrologic level were compared across vegetation type for days 2 through 5, bare soil treated with a 3-day hydroperiod had on average 102% ($p = 0.018$) more uptake than the 3-week hydroperiod (Fig. 12.4). Tree plantings with a 3-day hydroperiod had on average 160% ($p = 0.031$) more uptake compared to the 3-week hydroperiod. There were no differences in PO_4^{3-} retention between the two hydrology levels for the herbaceous vegetation treatments for the days 2 through 5 data.

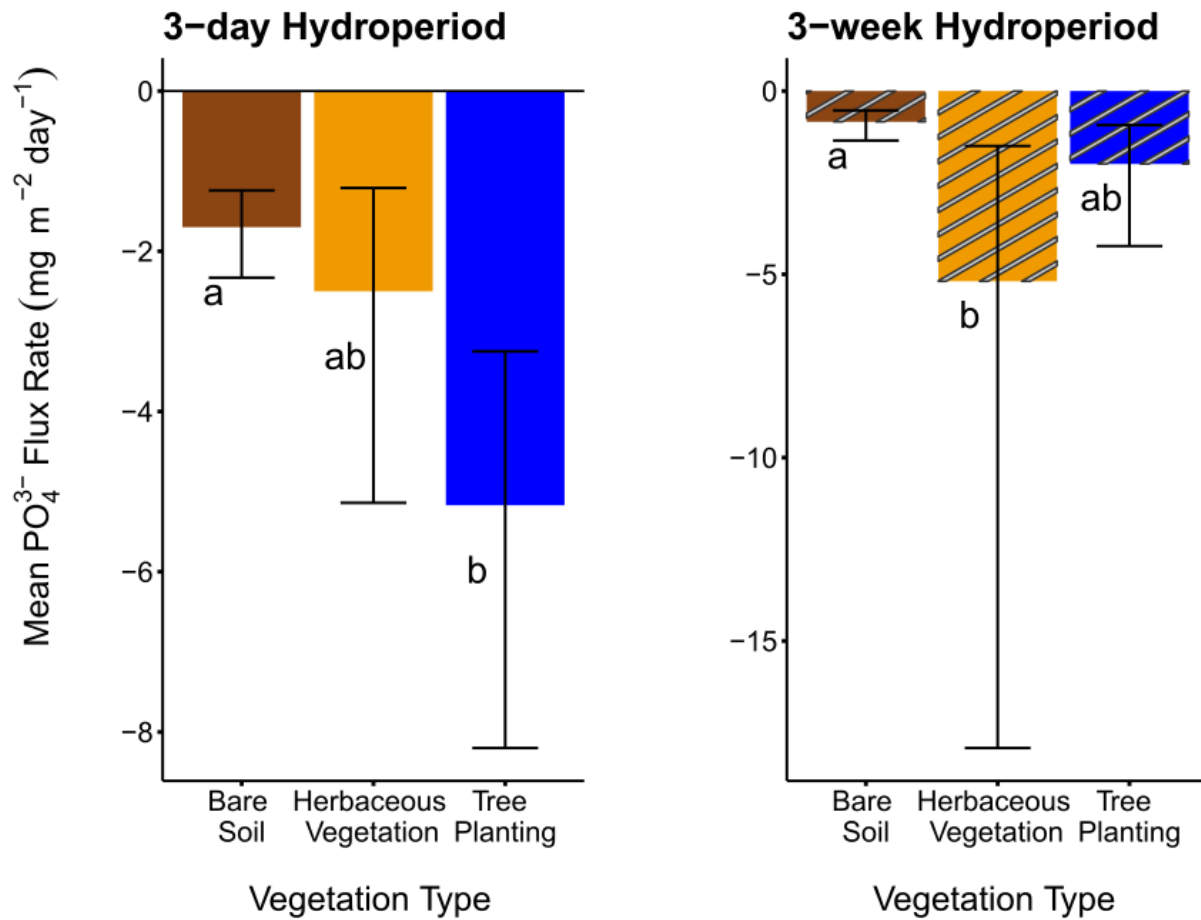


Figure 11.4 Predicted mean flux rates of PO_4^- per day for days 2 through 5 of the experiment for mesocosms treated with a 3-day (solid bars) and 3-week (striped bars) hydroperiod. Log- PO_4^{3-} flux data was back-transformed to its original units for graphing. Different letters indicate significant differences. Error bars represent 95% CI's.



Figure 12.4 Predicted means for PO_4^{3-} flux for each hydrology level for bare soil, herbaceous vegetation, and tree planting treatments. Different letters indicate significant differences. There were no differences between hydrology levels for herbaceous vegetation treatments. Error bars represent 95% CI's.

Table 5.4 ANCOVA table for the PO_4^{3-} flux data.

Source of variation	Chi-squared	<i>p</i>
<u><i>First 24 h</i></u>		
Vegetation _{2,33}	9.16	0.010
Hydrology _{1,33}	0.37	0.543
AFDM _{1,33}	11.67	<0.001
Vegetation:Hydrology _{2,33}	0.60	0.740
<u><i>Days 2 through 5</i></u>		
Vegetation _{2,33}	24.98	<0.001
Hydrology _{1,33}	9.01	0.003
AFDM _{1,33}	0.003	0.957
Vegetation:Hydrology _{2,33}	6.34	0.042

Trends in Dissolved Organic Carbon

After 5 days of inundation, all treatments experienced a net release of DOC, with individual mesocosm flux rates ranging from 8 to 211 $\text{mg m}^{-2} \text{ day}^{-1}$ (herbaceous vegetation – 3-week hydroperiod and bare soil – 3-week hydroperiod, respectively). Bare soil treatments had the greatest amount of DOC release by day 5 regardless of hydrology, while herbaceous vegetation treatments had the lowest release rates for each hydrology level. Mean DOC flux rates

were influenced by chl-*a* content (Chi-squared_(1,32) = 6.42, *p* = 0.011), with increases in chl-*a* content correlating with an increase in DOC content (Table 6.4). Further, the effect size was larger, with a predicted 22% increase in DOC release for every 1 mg m⁻² increase in chl-*a*.

Table 6.4 ANCOVA table for DOC flux data.

Source of variation	Chi-squared	<i>p</i>
Vegetation _{2,32}	4.77	0.092
Hydrology _{1,32}	2.88	0.090
Log(chl- <i>a</i>) _{1,32}	6.42	0.011
Vegetation:Hydrology _{2,32}	6.73	0.035

There was a significant interaction between vegetation and hydrology (Chi-squared_(2,32) = 6.73, *p* = 0.035) which constrained pairwise comparisons to specific vegetation-hydrology combinations (Fig. 13.4). When hydrology levels were compared across vegetation type, bare soil and tree plantings treated with a 3-week hydroperiod had on average 253% and 145% more DOC release compared to those treated with a 3-day hydroperiod (*p* = <0.001 and 0.003, respectively). There were no differences in DOC flux rates among vegetation levels in mesocosms treated with a 3-day hydroperiod. When hydrology was compared by vegetation type, 75% more DOC was release on average in the tree planting mesocosms treated with a 3-week hydroperiod compared to a 3-day hydroperiod (*p* = 0.015). There were no differences in

DOC release rates between hydrology levels for the bare soil and herbaceous vegetation treatments.

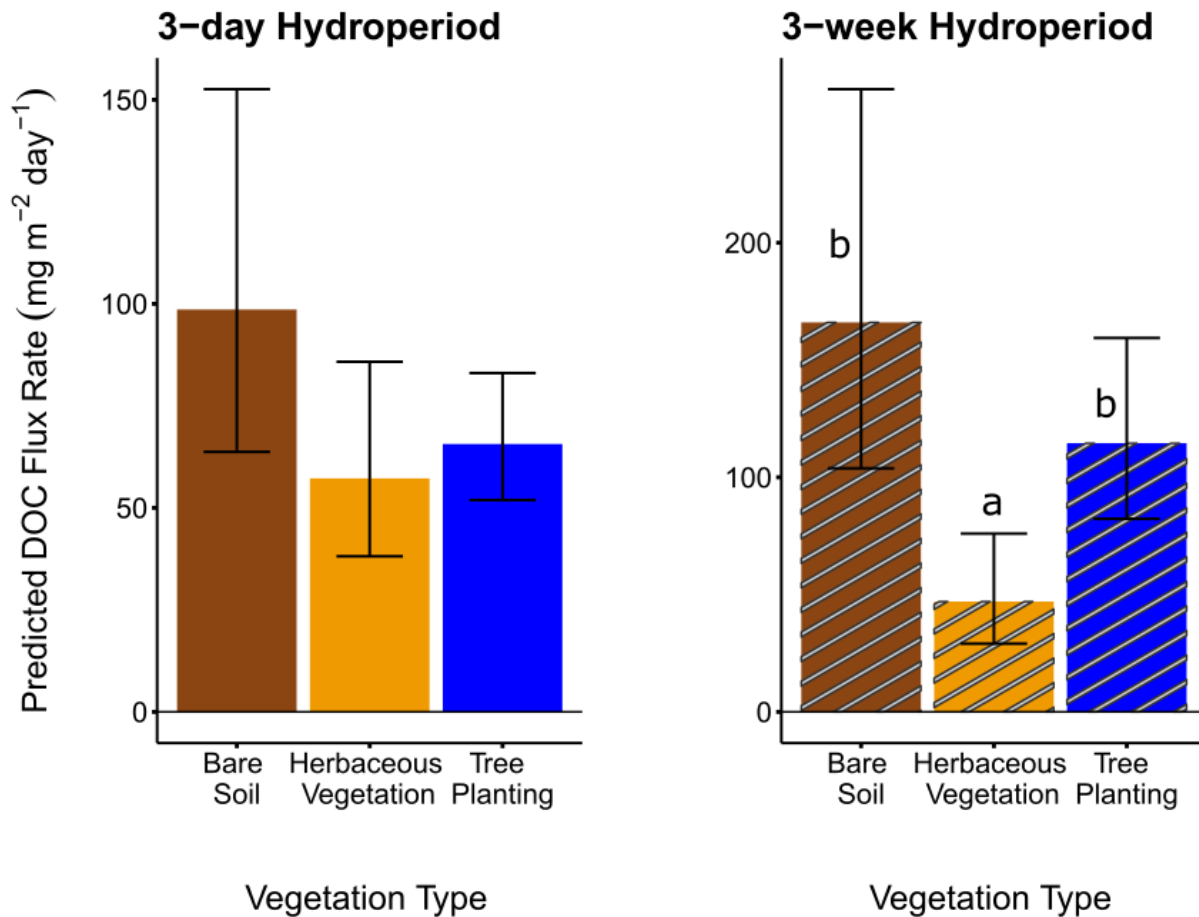


Figure 13.4 Predicted mean DOC flux rates for vegetation levels grouped by hydrology for the 3-day (solid bars) and 3-week hydroperiods (striped bars). Different letters indicate significant differences in mean flux rates. There were no differences among vegetation levels treated with a 3-day hydroperiod. Error bars represent 95% CI's.

Gas Data

Trends in Nitrogen Gas Production

All treatments across all timepoints had net positive N₂ production (i.e., positive flux rates) throughout the experiment, and production rates increased with incubation time (Fig. 14.4, 15.4, 16.4, Table 7.4). Nitrogen gas production within the herbaceous vegetation treatments increased slowly throughout the incubations but started at a much higher production rate compared to bare soil and tree planting treatments (Fig. 14.4). Production rates within the bare soil and tree planting treatments lagged herbaceous vegetation production rates until 48 h at which production rates among all vegetation levels were similar. Between 12 and 48 h of incubation, mean N₂ production increased 64% in the bare soil, 41% in the herbaceous vegetation, and 68% in the tree planting. Mean N₂ gas production rates were greater in the bare soil compared to the tree planting across all timepoints; however, confidence intervals for bare soil and tree planting overlapped.

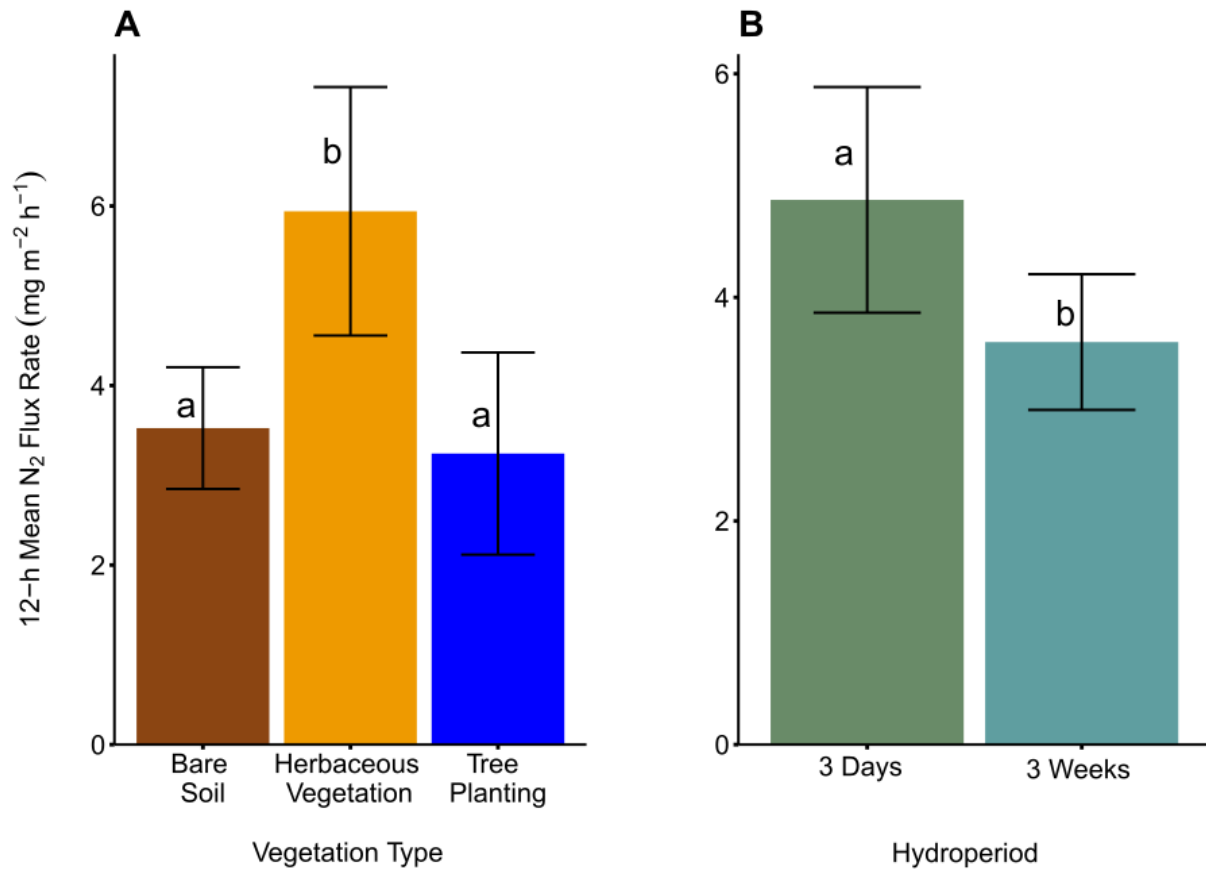


Figure 14.4 12 h N₂ predicted means for each vegetation (A) and hydrologic level (B). Different letters indicate significant differences. Error bars represent 95% CI's.

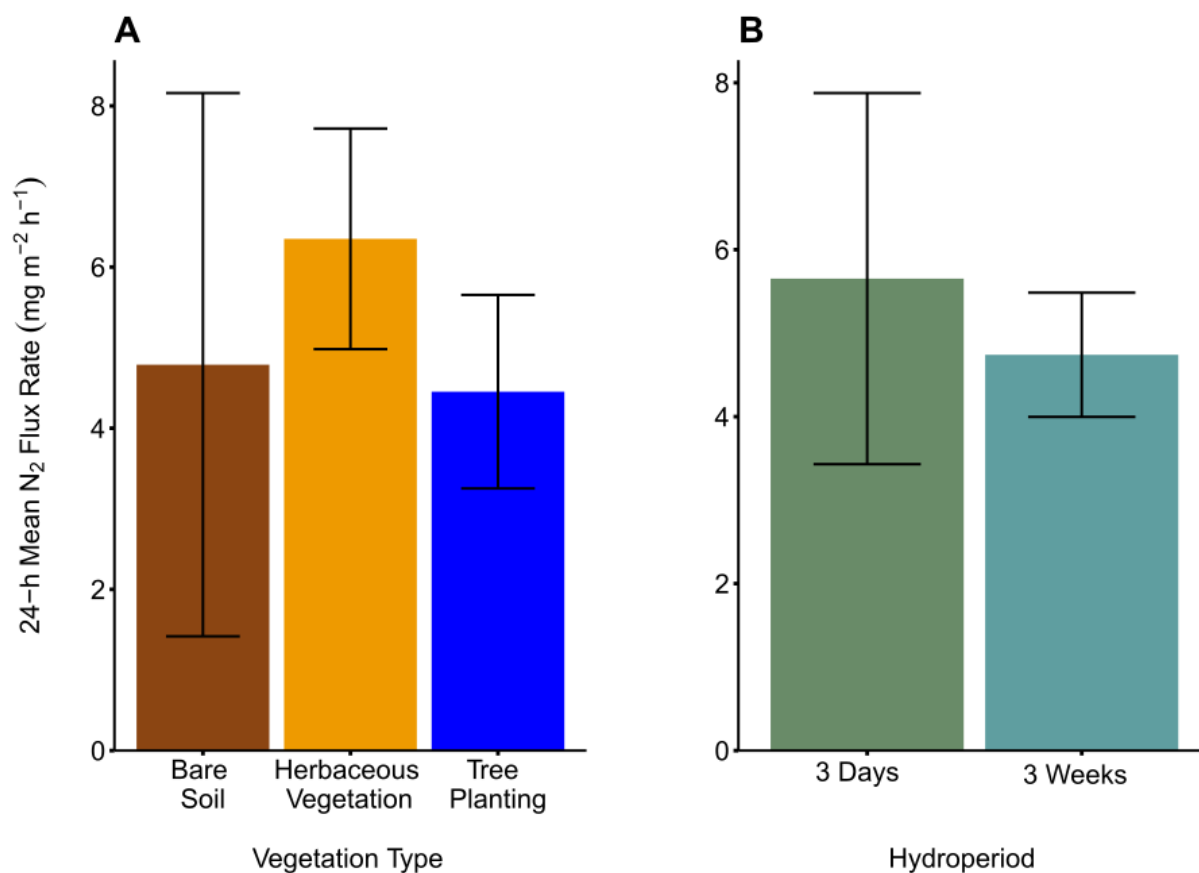


Figure 15.4 24 h N_2 predicted means for each vegetation (**A**) and hydrologic level (**B**). There were no significant differences among the treatments. Error bars represent 95% CI's.

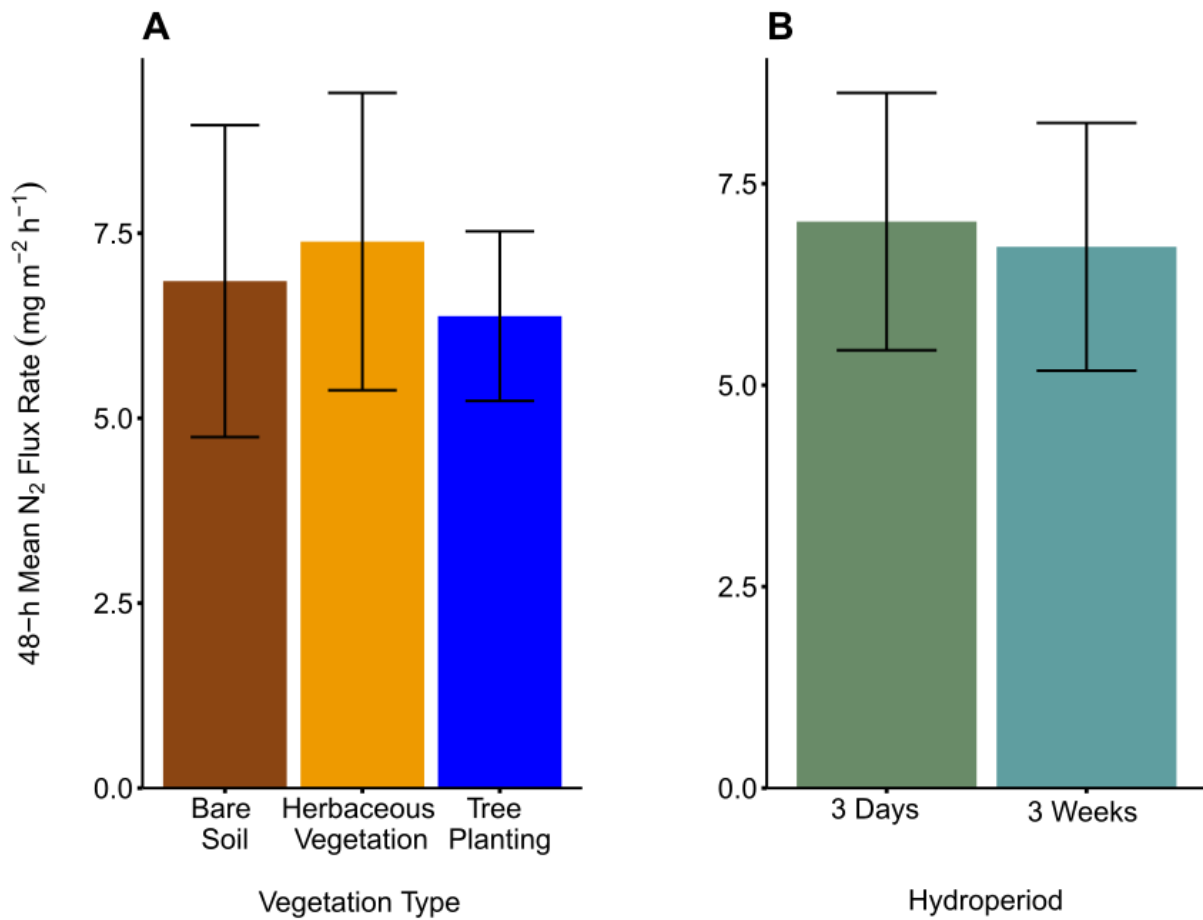


Figure 16.4 48 h N_2 predicted means for each vegetation (**A**) and hydrologic level (**B**). There were no significant differences among the treatments. Error bars represent 95% CI's.

Table 7.4 Predicted means for N₂ flux and SOD (O₂) rates (mg m⁻² h⁻¹) for vegetation and hydrologic levels. *Estimated marginal means ± the standard error (SE).

Gas Data without Significant Interaction							
Gas Species	Incubation Timepoint	Vegetation			Hydroperiod		
		Bare Soil	Herbaceous Vegetation	Tree Planting	3-Days	3-Weeks	
N ₂	12 h	4 ± 0.3*	6 ± 0.6	3 ± 0.5	5 ± 0.5	4 ± 0.3	
N ₂	24 h	4 ± 1.1	6 ± 0.6	4 ± 0.5	6 ± 0.9	5 ± 0.3	
N ₂	48 h	7 ± 0.9	7 ± 0.8	6 ± 0.5	7 ± 0.7	7 ± 0.7	
O ₂	24 h	-29 ± 3.0	-48 ± 3.8	-26 ± 1.8	-36 ± 2.7	-33 ± 2.1	
O ₂	48 h	-53 ± 5.1	-72 ± 5.1	-54 ± 3.5	-63 ± 3.4	-56 ± 4.1	
Gas Data with Significant Interaction							
Vegetation levels grouped by hydrology							
3-day Hydroperiod				3-week Hydroperiod			
		Bare Soil	Herbaceous Vegetation	Tree Planting	Bare Soil	Herbaceous Vegetation	Tree Planting
O ₂	12 h	-26 ± 3.5	-40 ± 7.7	-13 ± 2.9	-13 ± 2.1	-42 ± 5.1	-18 ± 1.8
Hydrology levels grouped by vegetation							
		Bare Soil		Herbaceous Vegetation		Tree Planting	
		<u>3-days</u>	<u>3-weeks</u>	<u>3-days</u>	<u>3-weeks</u>	<u>3-days</u>	<u>3-weeks</u>
O ₂	12 h	-26 ± 3.5	-13 ± 2.1	-40 ± 7.7	-42 ± 5.1	-13 ± 2.9	-18 ± 1.8

Factors Influencing Nitrogen Gas Production

Covariates influencing N₂ production varied across sampling time points. Soil TN was included in the final model for the 12-h N₂ data to stabilize model residuals; however, soil TN did not significantly affect 12-h N₂ production rates. At 24 h, soil TN influenced N₂ production, with a one mg g⁻¹ increase in soil TN predicted to increase N₂ production by 8 mg m⁻² h⁻¹. At 48 h, N₂ production was influenced by chl-*a*, with a one unit increase in chl-*a* predicted to increase N₂ production by 13%.

There were differences in 12-h mean N₂ production rates among the treatments after controlling for soil TN, with herbaceous vegetation treatments producing on average 68% ($p = 0.014$) and 83% ($p = 0.008$) more N₂ than bare soil and tree planting treatments, respectively (Fig. 14.4, Table 8.4). Mesocosms treated with a 3-day hydroperiod had on average 35% more N₂ production at 12 h compared to those treated with a 3-week hydroperiod ($p = 0.027$). There were no differences among the vegetation or hydrology treatments at 24 and 48 h.

Table 8.4 ANCOVA table for N₂ flux rates.

Source of variation	Chi-squared	<i>p</i>
12 h Timepoint		
Vegetation _{2,34}	10.33	0.006
Hydrology _{1,34}	2.64	0.104
Soil TN _{1,34}	2.65	0.104
Vegetation:Hydrology _{2,34}	1.99	0.370
24 h Timepoint		
Vegetation _{2,35}	1.94	0.380
Hydrology _{1,35}	0.064	0.800
Soil TN _{1,35}	10.60	0.001
Vegetation:Hydrology _{2,35}	0.07	0.964
48 h Timepoint		
Vegetation _{2,35}	0.68	0.71
Hydrology _{1,35}	0.14	0.71
Log(chl-a) _{1,35}	0.06	0.88
Vegetation:Hydrology _{2,35}	0.67	0.71

Soil Oxygen Demand

Trends in Soil Oxygen Demand

Soil oxygen demand increased (decreasing negative values indicate removal of dissolved oxygen from the water) among all treatments throughout the core incubations, signifying a greater removal rate of oxygen from the water over time. Herbaceous vegetation had significantly greater SOD (i.e., most negative values) across all time points with bare soil and tree planting treatments having much lower initial SOD that slowly increased throughout the experiment. Tree planting treatments had the greatest increase in SOD between 12 and 24 h of incubation (141% increase) followed by bare soil (69%) and herbaceous vegetation (59%). However, bare soil and tree planting SOD at 12 h lagged herbaceous vegetation treatments by an average of 17 and 22 mg m⁻² h⁻¹, respectively. By 24 h, SOD in bare soil and tree planting treatments were similar, with bare soil having 7% higher SOD at 24 h than tree planting and nearly identical SOD at 48 h (SOD rates of 53 and 54 mg m⁻² h⁻¹, respectively) (Table 9.4). Soil TN was included in the final models for 12- and 48-h SOD to stabilize model residuals. However, soil TN did not have a significant effect on mean SOD predictions for the treatments at either time point.

There was an interaction between vegetation and hydrology at 12 h of incubation (Chi-squared (2, 34) = 11.90, $p = 0.003$), resulting in factor combination-specific pairwise differences in SOD among treatments. In mesocosms treated with a 3-day hydroperiod, bare soil and herbaceous vegetation had on average 102% and 217% greater SOD than tree plantings ($p = 0.032$ & 0.023 , respectively), but bare soil and herbaceous vegetation SOD rates did not differ (Fig. 17.4). Conversely, herbaceous vegetation mesocosms treated with a 3-week hydroperiod had on average 215% and 132% greater SOD than bare soil and tree planting treatments ($p =$

0.003 & 0.007, respectively). When hydrology levels were compared by vegetation type, SOD in bare soil mesocosms was on average 100% greater in the 3-day hydroperiod treatments ($p = 0.013$) (Fig. 18.4) There were no differences between hydrology levels for herbaceous vegetation or tree planting treatments.

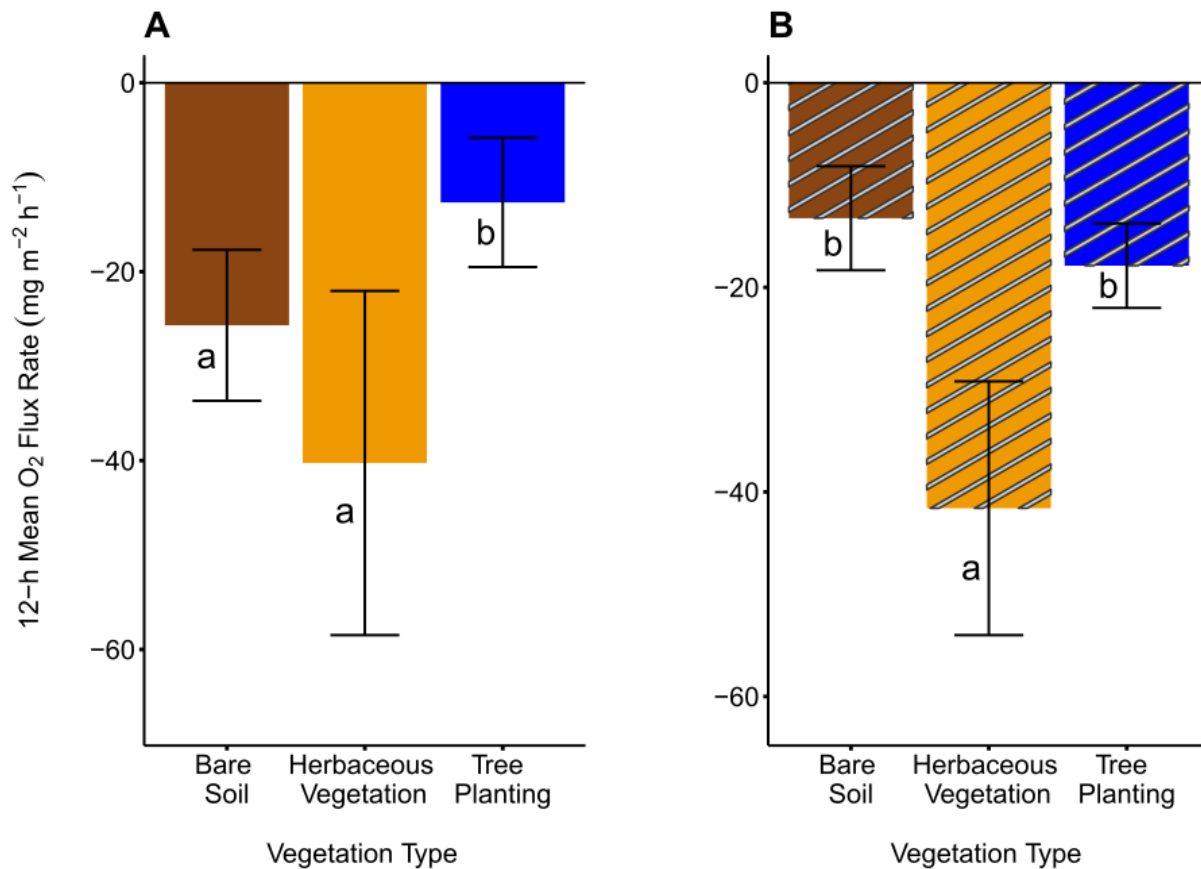


Figure 17.4 12-h predicted mean O₂ flux rates for each vegetation type for mesocosms treated with 3-day (solid bars) (A) and 3-week (striped bars) (B) hydroperiods. Different letters indicate significant differences. Error bars represent 95% CI's.

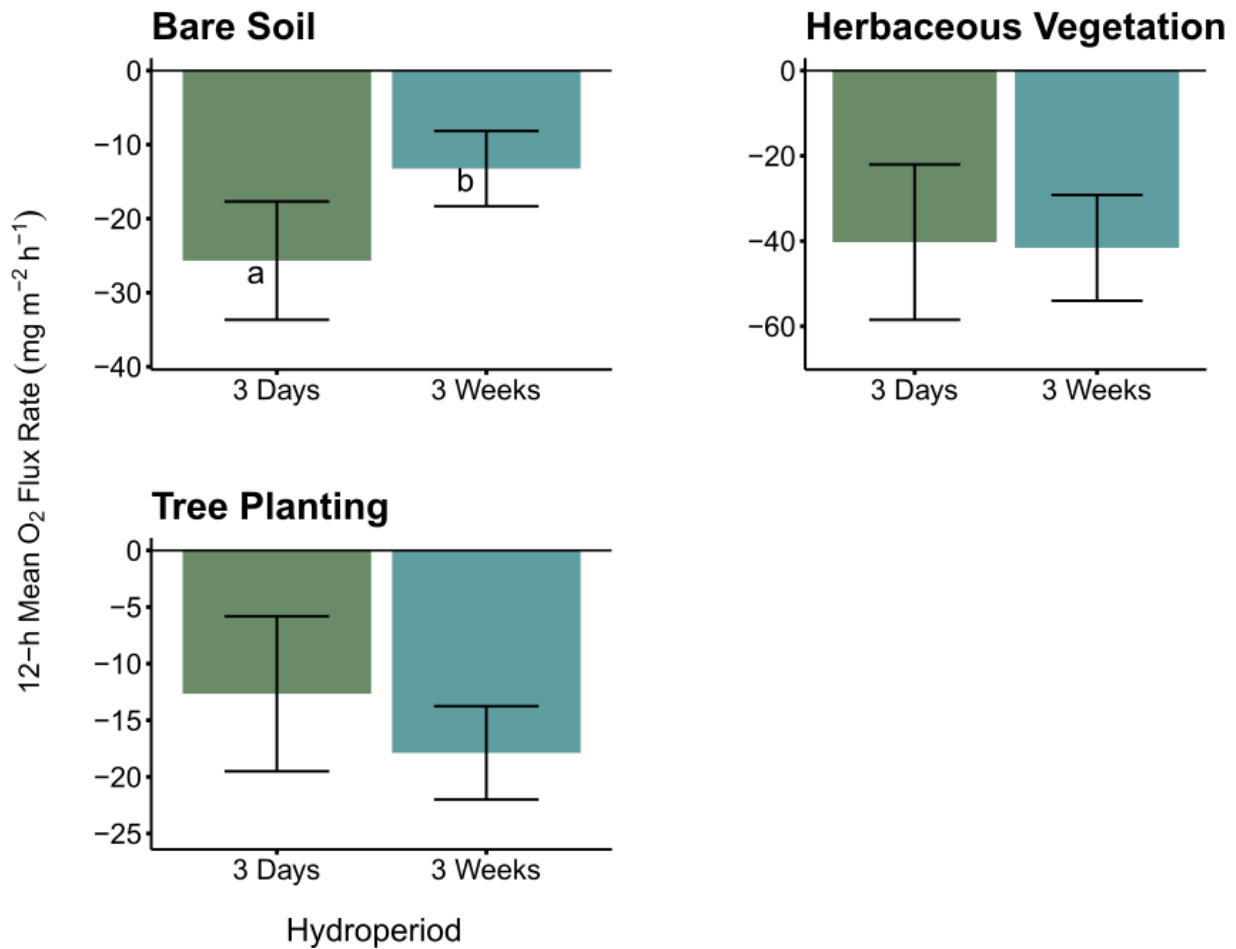


Figure 18.4 12-h predicted mean O₂ flux rates for hydrology levels (green = 3-day hydroperiod, blue = 3-week hydroperiod) grouped bare soil, herbaceous vegetation, and tree planting. Different letters indicate significant differences. There were no differences between hydrology levels for herbaceous vegetation or tree planting treatments. Error bars represent 95% CI's.

Beyond 12 h, there were no significant interactions between vegetation and hydrology. Soil oxygen demand rates differed among vegetation levels at 24 h and 48 h (Table 9.4) but not between hydrology levels. At 24 h, herbaceous vegetation treatments had on average 66% and 92% greater SOD than bare soil and tree planting treatments ($p = 0.003$ & <0.001 , respectively) (Fig. 19.4). These differences among vegetation levels persisted at 48 h, although statistical significances were weaker, with herbaceous vegetation having on average 34% greater SOD compared to bare soil and tree planting treatments (p values = 0.050 and 0.027, respectively) (Fig. 20.4).

Table 9.4 ANCOVA table for SOD flux rates.

Source of variation	Chi-squared	<i>p</i>
12 h Timepoint		
Vegetation _{2,34}	16.70	<0.001
Hydrology _{1,34}	8.92	0.003
Soil TN _{1,34}	0.53	0.47
Vegetation:Hydrology _{2,34}	11.90	0.003
24 h Timepoint		
Vegetation _{2,35}	12.64	0.002
Hydrology _{1,35}	0.36	0.54
Vegetation:Hydrology _{2,35}	0.15	0.92
48 h Timepoint		
Vegetation _{2,35}	6.24	0.044
Hydrology _{1,35}	0.08	0.772
Soil TN _{1,35}	0.22	0.637
Vegetation:Hydrology _{2,35}	2.30	0.317

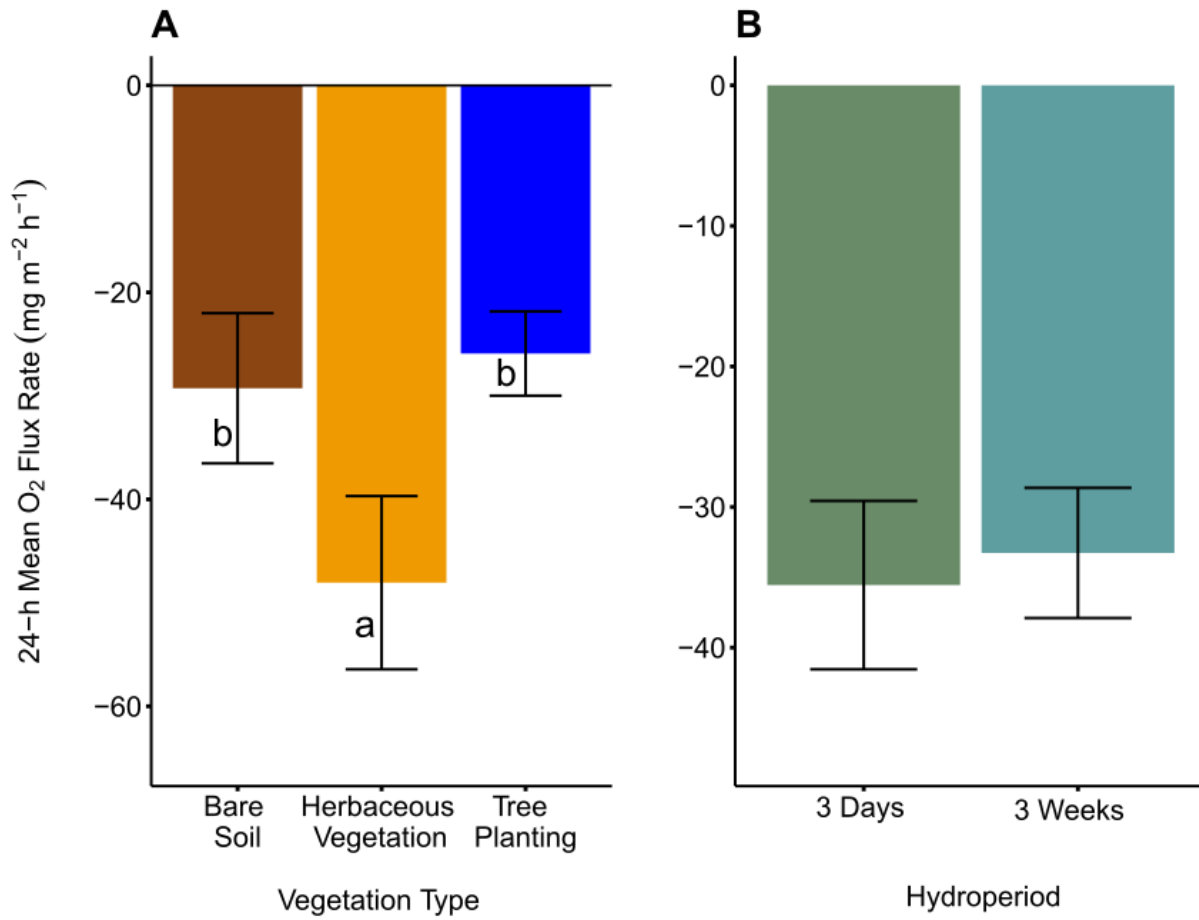


Figure 19.4 24-h predicted mean O₂ flux rates for each vegetation type (A) and hydroperiod (B). Different letters indicate significant differences. There were no differences between hydrology levels. Error bars represent 95% CI's.

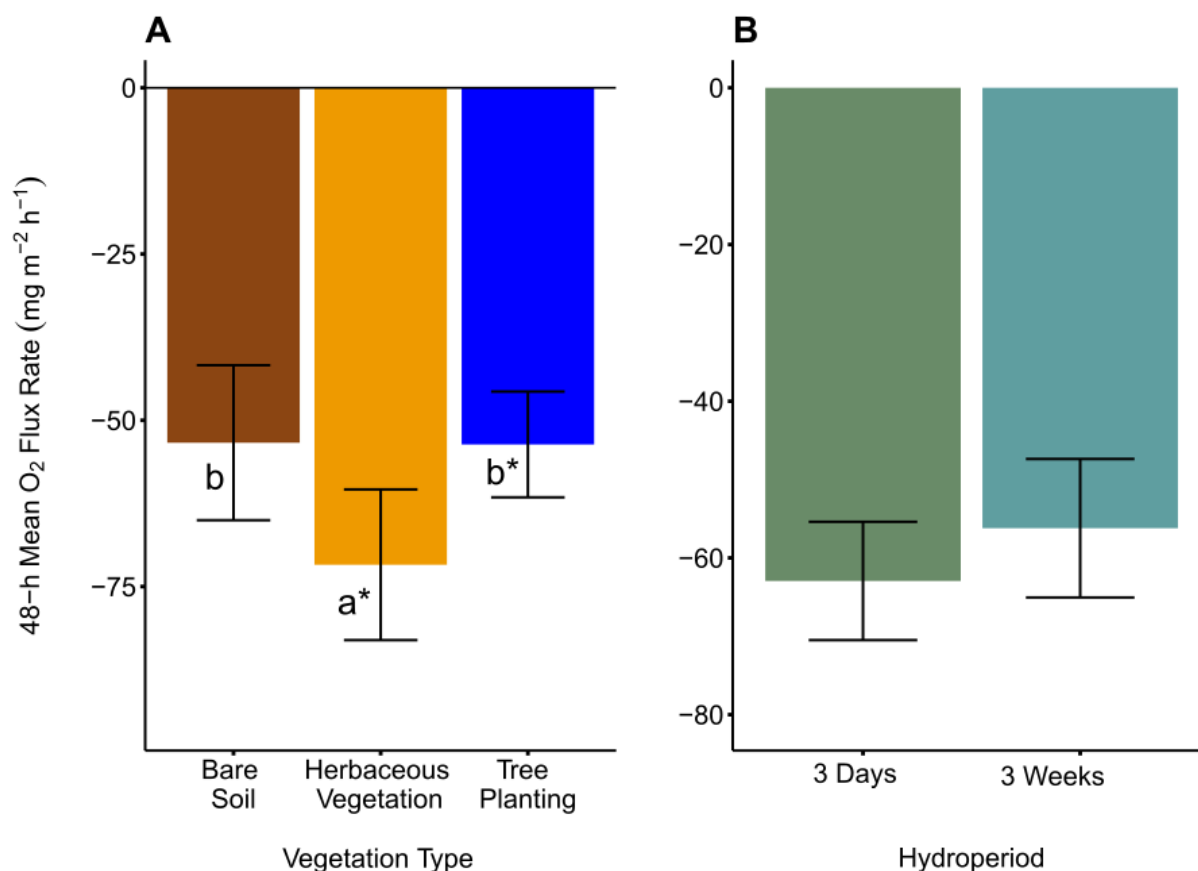


Figure 20.4 48-h predicted mean O₂ flux rates for each vegetation type (A) and hydroperiod (B).

Different letters indicate significant differences at $\alpha = 0.05$. Different letters with stars represent significant differences at the $\alpha = 0.1$ level. There were no differences between hydrology levels.

Error bars represent 95% CI's.

N₂ and SOD Correlations

Nitrogen gas and O₂ flux correlations yielded different relationships among treatments and across timepoints. Increasing SOD was generally correlated with increasing N₂ production, and this trend strengthened as incubation time increased. Correlations between SOD and N₂

production were strongest in the herbaceous vegetation – 3-day hydroperiod treatment across all sampling timepoints ($R^2 \geq 0.69$ for all rounds) (Fig. 21.4). Nitrogen gas and SOD became moderately correlated at 24 h for tree plantings treatments for both the 3-day and 3-week hydroperiod factor levels ($R^2 = 0.55$ and 0.68 , respectively). For bare soil treatments, N_2 and SOD were strongly correlated for the 3-week hydroperiod treatment ($R^2 = 0.91$) and weakly correlated for the 3-day hydroperiod treatment ($R^2 = 0.26$ (Fig. 22.4)). After 48 h, N_2 and SOD were negatively correlated for all treatments except herbaceous vegetation – 3-week hydroperiod; however, this was likely a result of an outlying value (mesocosm # 30) which had was substantially higher ($3.9 \text{ mg m}^{-2} \text{ h}^{-1}$ more N_2 produced) than the treatment mean ($7.13 \text{ mg m}^{-2} \text{ h}^{-1}$) (Fig. 23.4).

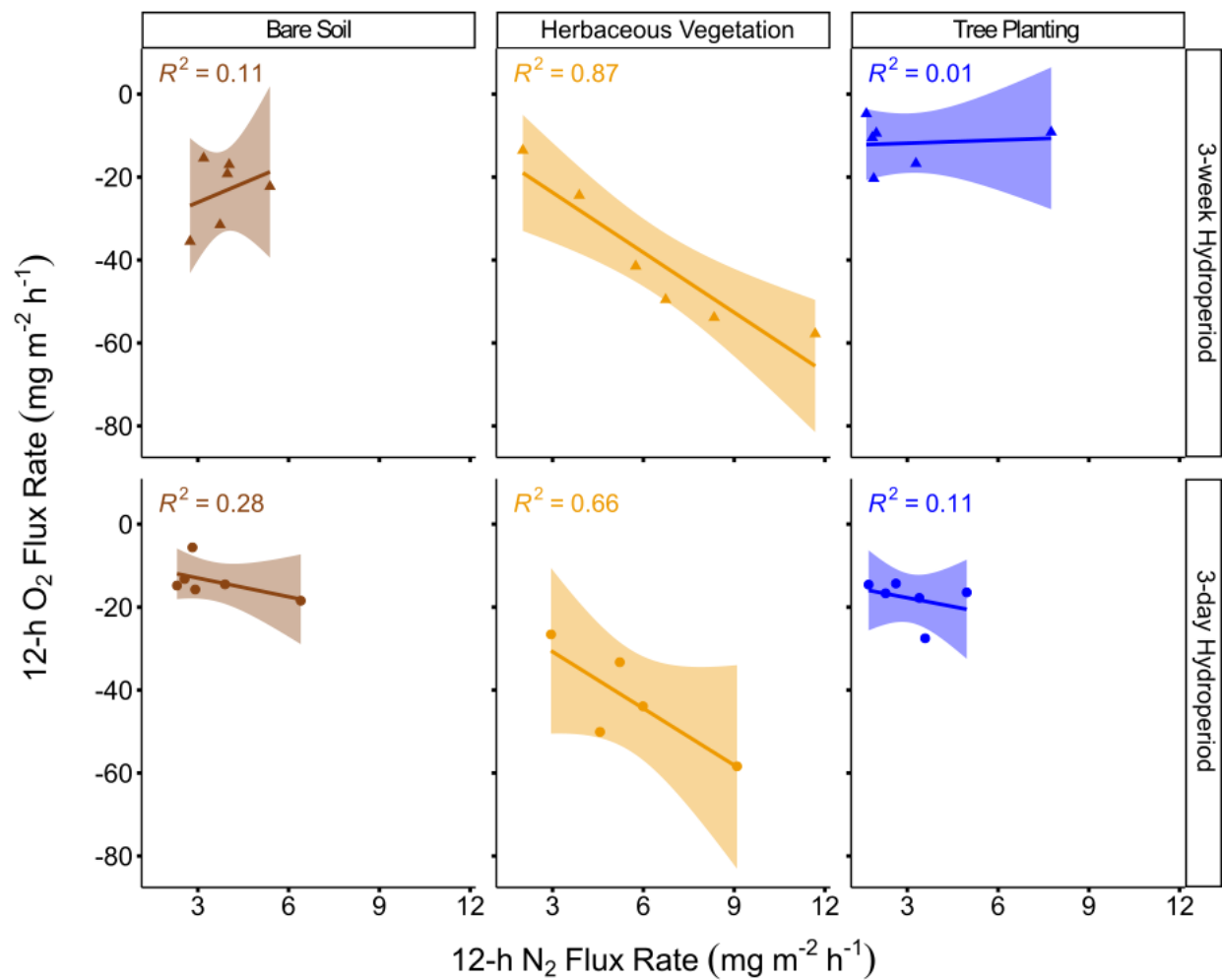


Figure 21.4 O_2 flux regressed against N_2 flux for each factor combination at 12 h of incubation.

Bands are 95% CI's.

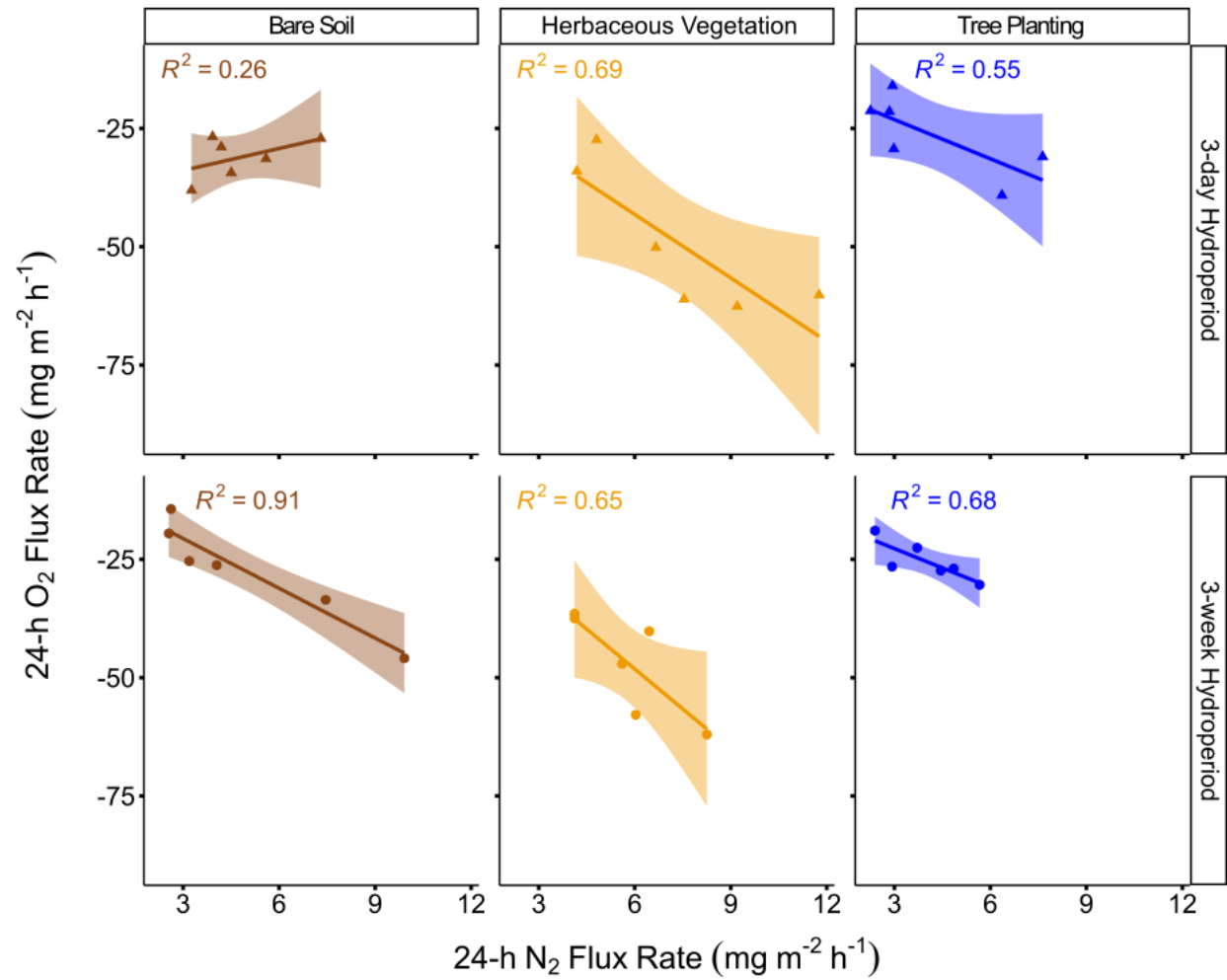


Figure 22.4 O₂ flux regressed against N₂ flux for each factor combination at 24 h of incubation.

Bands are 95% CI's.

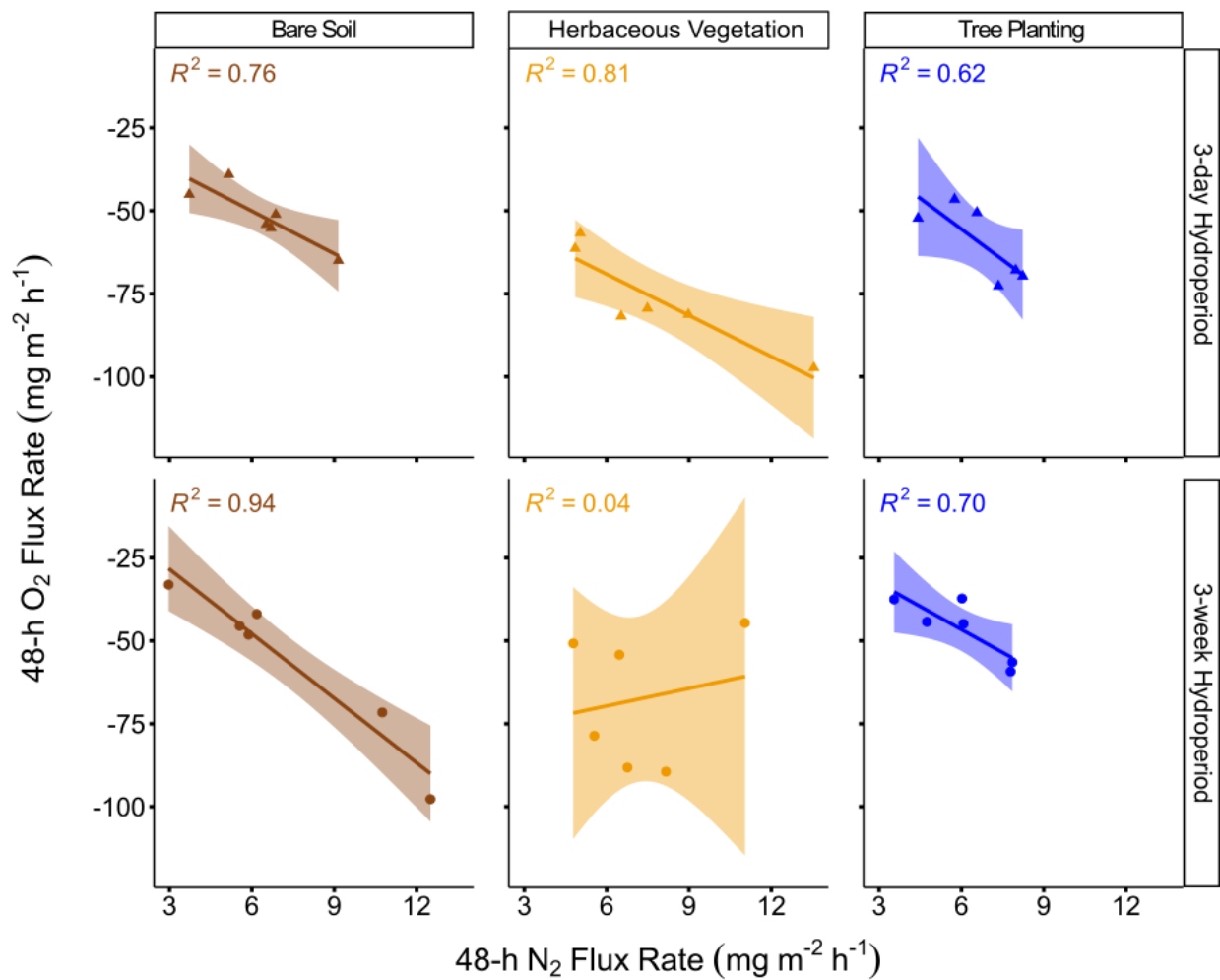


Figure 23.4 O₂ flux regressed against N₂ flux for each factor combination at 48 h of incubation.

Bands are 95% CI's.

Greenhouse Gases

Nitrous Oxide

Minimal N₂O production occurred in all mesocosms, and flux rates decreased among all treatments as the incubations progressed. Flux rates were slightly higher for the 3-day hydroperiod level compared to the 3-week level; however, concentrations among all treatments were so low that any differences were likely not ecologically significant. Nitrous oxide yield was also low with N₂O accounting for <1% of N₂ production among all treatments (Fig. 24.4). Nitrous oxide flux rates were variable among the treatments and arithmetic confidence intervals overlapped for all treatments within each timepoint (Fig. 25.4, 26.4).

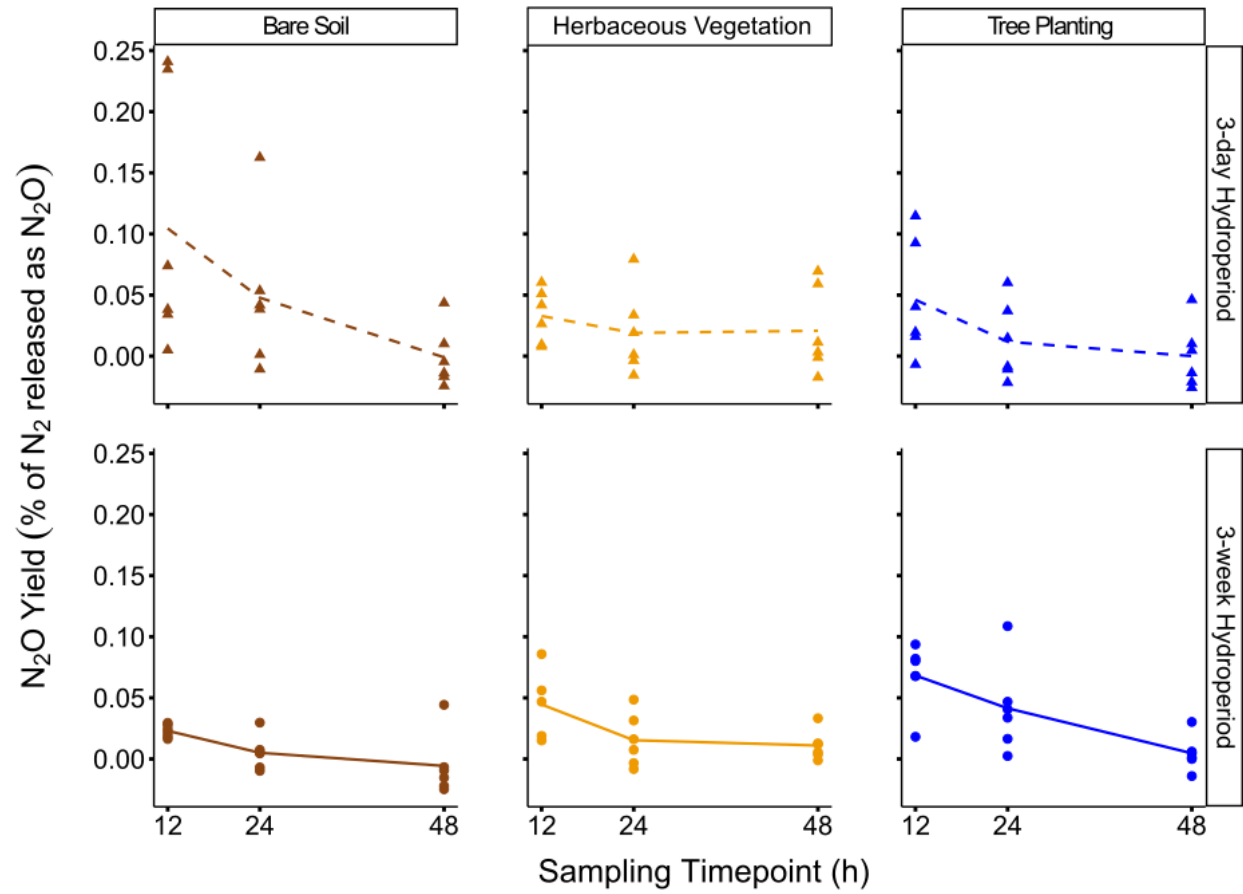


Figure 24.4 N_2O yield for all treatments. Lines represent arithmetic means. Points are observed data.

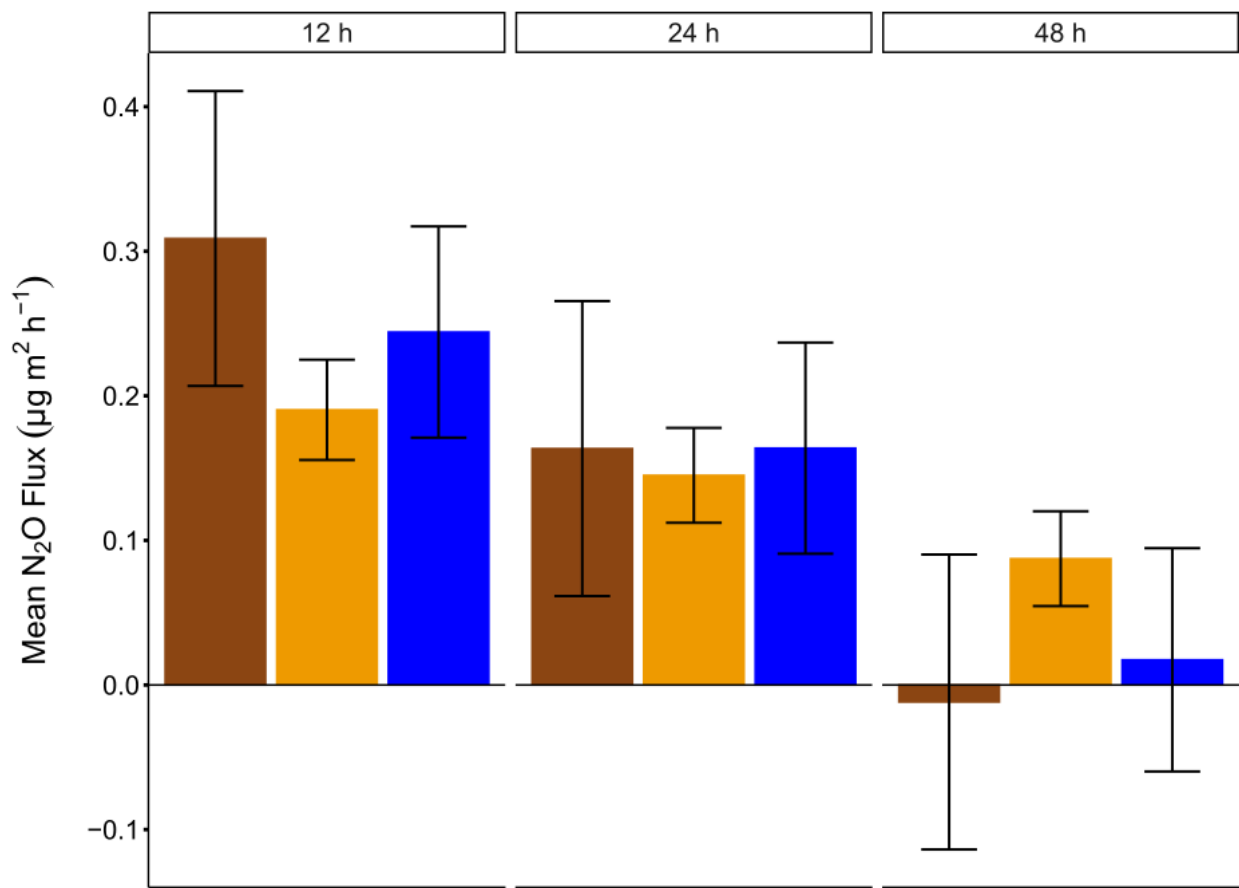


Figure 25.4 Arithmetic mean N₂O flux rates for the bare soil (brown), herbaceous vegetation (yellow), and tree planting (blue) treatments for each sampling time point. Error bars represent 95% CI's.

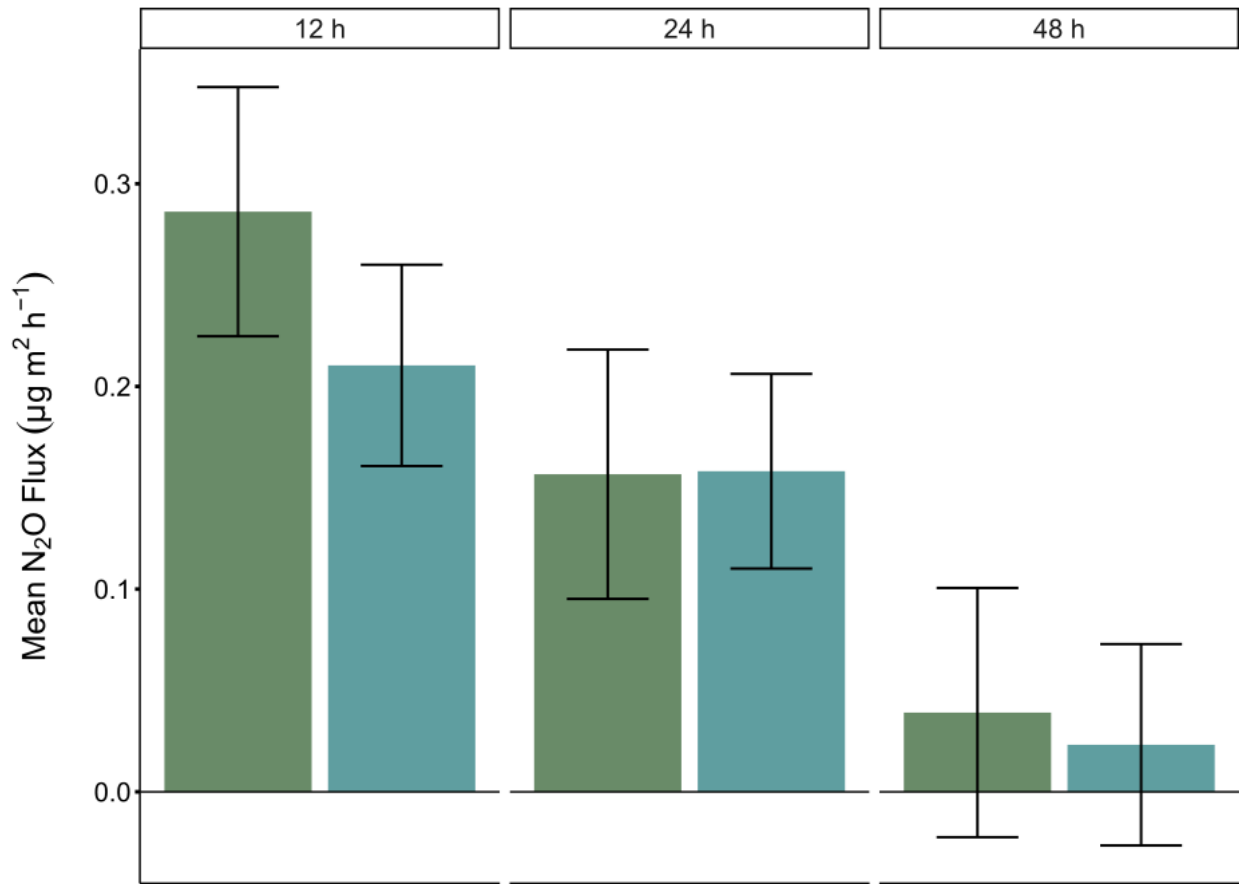


Figure 26.4 Arithmetic mean N₂O flux rates for the 3-day hydroperiod (green) and 3-week hydroperiod (blue) treatments for each sampling time point. Error bars represent 95% CI's.

Methane

Methane production was low across all mesocosms and treatments with all flux rates <4.5 µg m⁻² h⁻¹. Mean flux rates remained near zero for all vegetation treatments except herbaceous vegetation (Fig. 27.4). Methane production increased over time in herbaceous vegetation treatments but was relatively stable in bare soil and tree planting treatments. The 3-day hydroperiod treatments produced more CH₄ than the 3-week hydroperiods across all sampling

time points; however, concentrations were so low that this difference was likely ecologically negligible (Fig. 28.4).

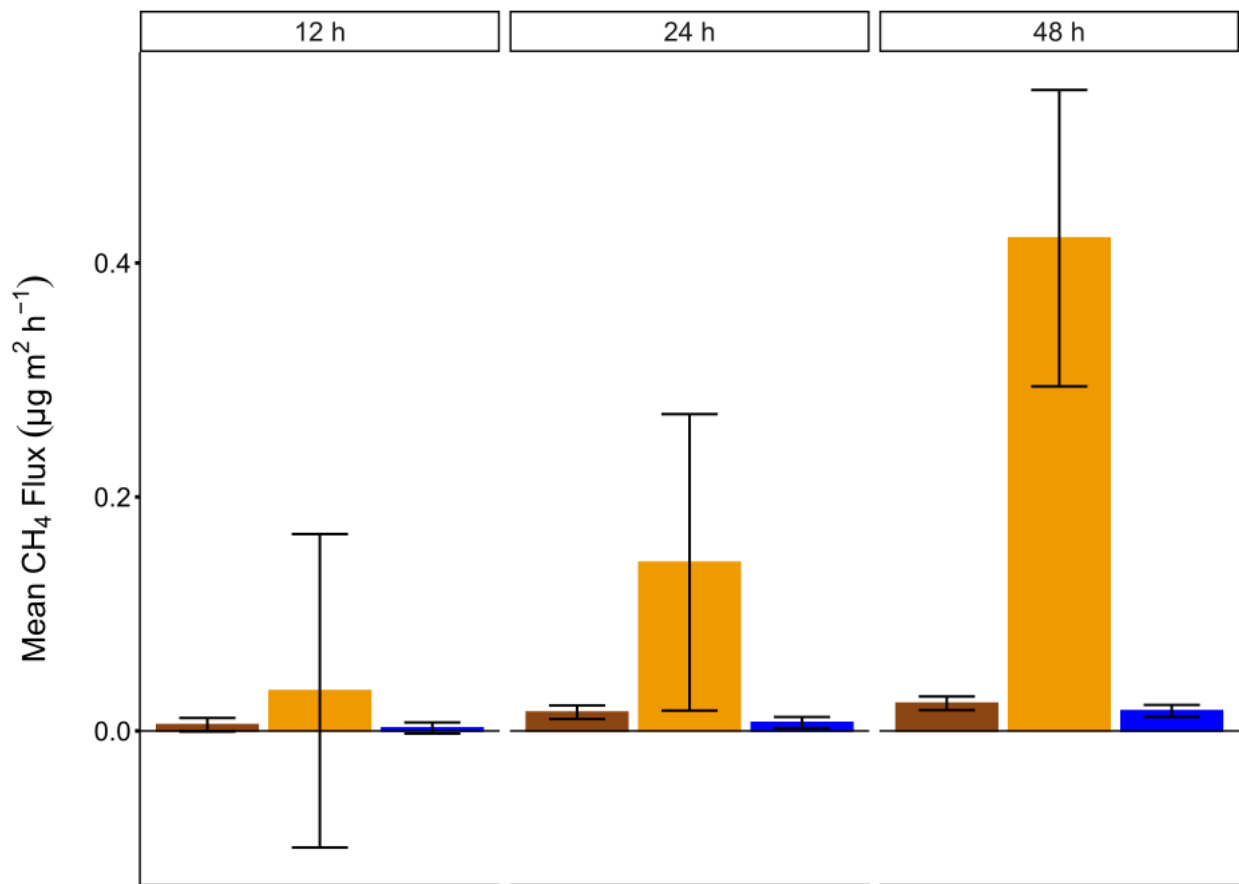


Figure 27.4 Arithmetic mean CH₄ flux rates for the bare soil (brown), herbaceous vegetation (yellow), and tree planting (blue) treatments for each sampling time point. Error bars represent 95% CI's.

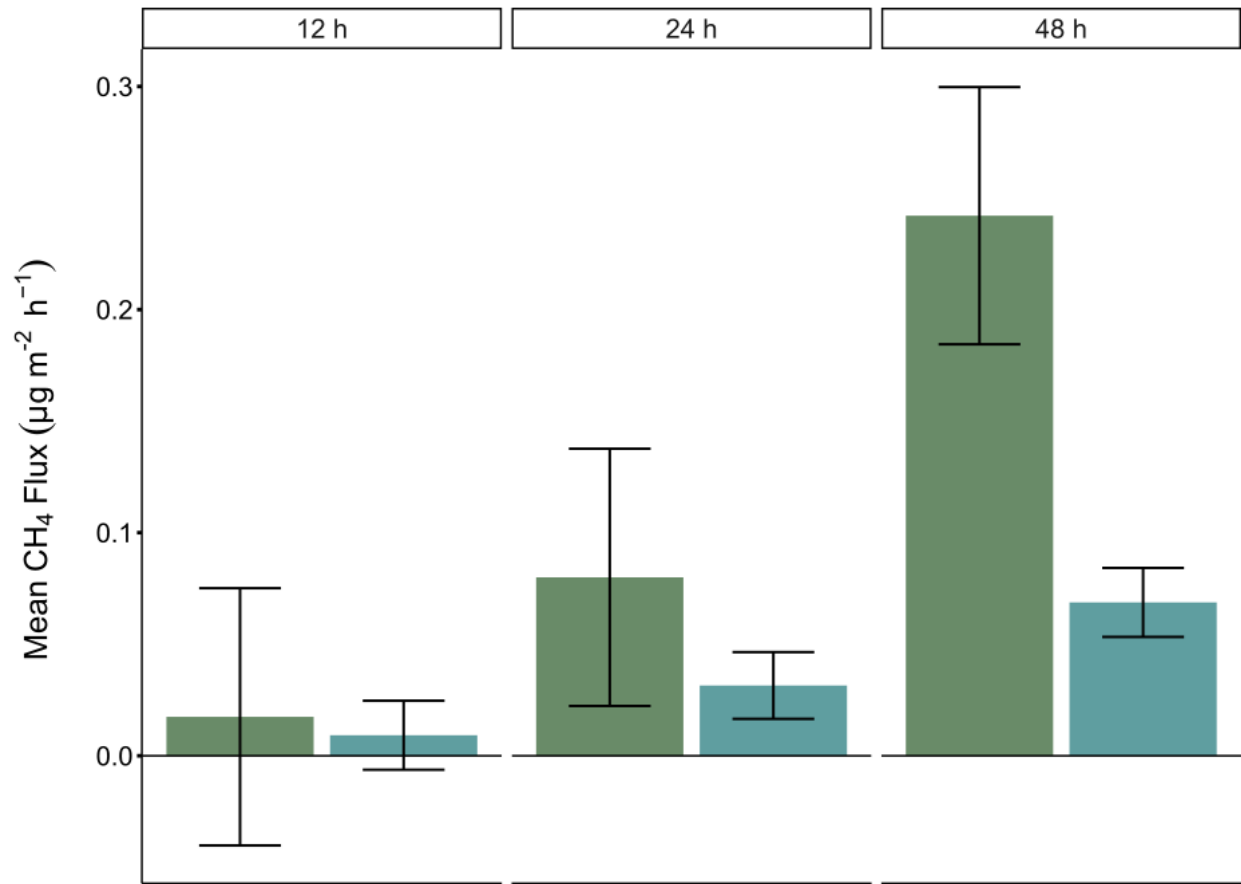


Figure 28.4 Arithmetic mean CH₄ flux rates for the 3-day hydroperiod (green) and 3-week hydroperiod (blue) treatments for each sampling timepoint. Error bars represent 95% CI's.

Soil Nutrients

Soil nutrient content in the pre- and post-dosing samples was low. There were significant differences in pre- and post-dosing soil nutrient contents within treatments. However, these differences likely did not have an ecologically significant effect on nutrient retention as the differences in pre- and post-dosing values were minimal (Table 10.4). The largest difference in soil nutrient content between pre- and post-dosing samples was observed in the herbaceous vegetation treatments in which soil TC increased by 1.45 mg g^{-1} (p value = 0.077). All vegetation treatments experienced statistically significant increases in soil TN following the experiment; however, the largest increase in soil TN among the vegetation levels was only 0.3 mg g^{-1} (tree planting treatment). There was even less change in extractable soil P content with only bare soil treatments having a significant increase in soil P content before and after dosing, and this difference was an increase of only 0.001 mg g^{-1} . When compared between hydrology levels, there were some differences in pre- and post-dosing soil nutrient contents; however, these differences also likely did not have an ecologically significant effect on nutrient retention as the greatest change in soil nutrient content was a 0.4 mg g^{-1} decrease in soil TC (3-week hydroperiod treatment). Ties were present in all statistical tests among vegetation and hydrology levels excluding soil P for herbaceous vegetation, further supporting the conclusion that there were not ecologically significant differences between pre- and post-dosing soil nutrients.

Table 10.4 Wilcoxon Ranked-Sign paired t-test results, differences in pre- and post-dosing soil nutrient content, and the corresponding percent change.

	Soil TC			Soil TN			Soil P		
		Difference	Percent		Difference	Percent	<i>p</i>	Difference	Percent
Vegetation	<u><i>p</i> value</u>	<u>(mg g⁻¹)</u>	<u>Change</u>	<u><i>p</i> value</u>	<u>(mg g⁻¹)</u>	<u>Change</u>	<u>value</u>	<u>(mg g⁻¹)</u>	<u>Change</u>
Bare Soil	0.689	-0.1	-2	0.003	0.3	50	0.076	0	0
Herbaceous Vegetation	0.077	-1.45	-17	0.002	0.2	29	0.733	0	0
Tree Planting	0.09	-0.65	-9	0.002	0.3	50	0.677	-0.01	-50
Hydrology									
3-day Hydroperiod	0.586	-0.45	-6	<0.001	0.3	50	0.107	0	0
3-week Hydroperiod	0.035	-0.4	-6	<0.001	0.3	50	0.009	0.01	100

Chlorophyll-*a* and Ash-free Dry Mass

Chlorophyll-*a* content differed between the hydrology treatments, but not among vegetation levels. The 3-day hydroperiod treatment had on average 336% more chl-*a* than the 3-week hydroperiod treatment. Chlorophyll-*a* was also more variable in the 3-day hydroperiod treatment with values ranging from 2 to 274 mg chl-*a* m⁻² (Fig. 29.4) compared to a range of 2 – 30 mg m⁻² in the 3-week hydroperiod treatment. Surficial AFDM content was low in all mesocosms (median = 30 mg g⁻¹ across all treatments), and there were no differences among the vegetation or hydrologic factor levels (Table 11.4).

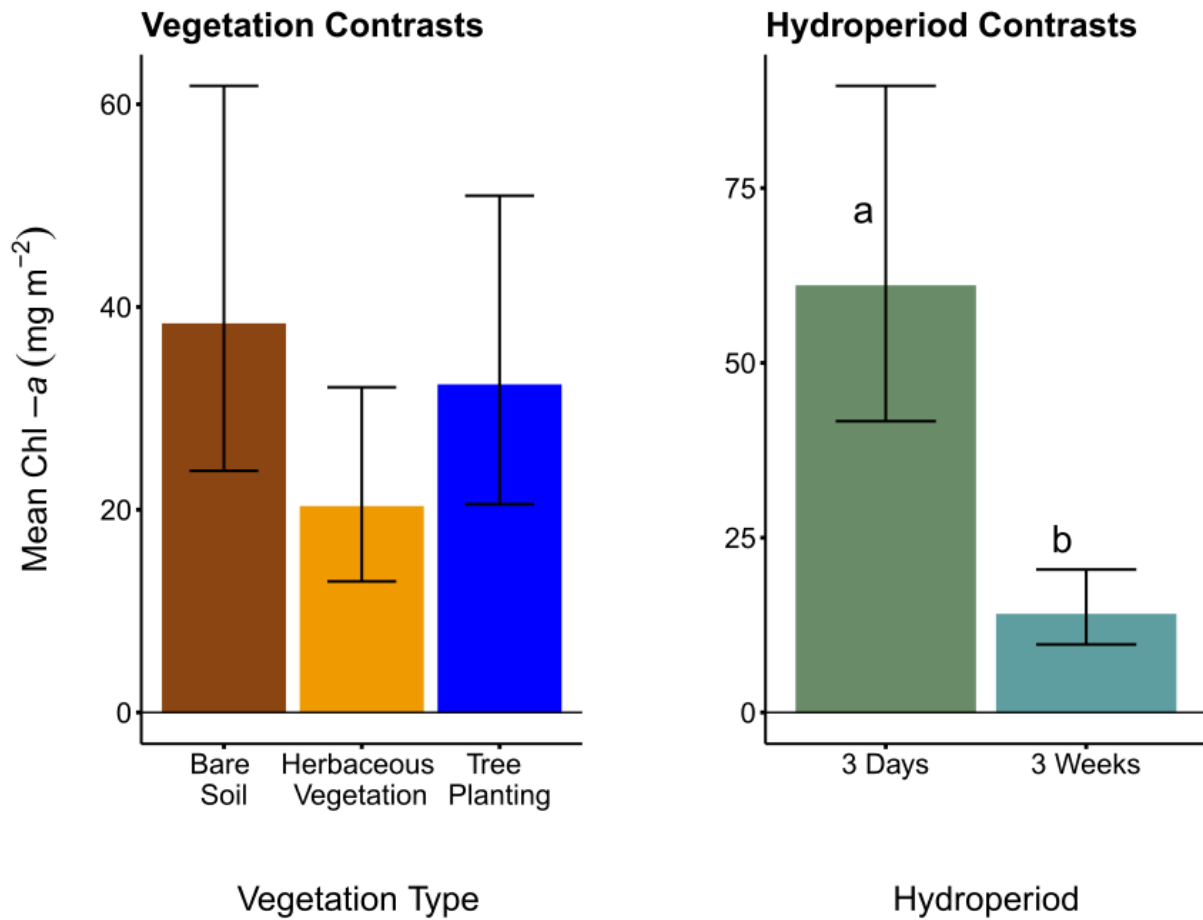


Figure 29.4 Predicted mean chl-*a* content for each vegetation and hydrology level. Different letters indicate significant differences. There were no differences among vegetation levels. Error bars represent 95% confidence intervals.

Table 11.4 ANOVA table for chl-*a* data.

Source of variation	Chi-squared	<i>p</i>
Vegetation _{2,35}	3.16	0.206
Hydrology _{1,35}	13.08	<0.001
Vegetation:Hydrology _{2,35}	0.35	0.838

Discussion

Evaluation of Hypotheses

Hypothesis 1) Vegetation type affects dissolved NO₃⁻, PO₄³⁻, N₂, N₂O, and CH₄ flux rates.

This hypothesis was generally supported as there were differences in nutrient retention among vegetation types, but these differences were dependent on the hydrology level applied. This hypothesis was also partially supported for N₂ and O₂ data; however, I did not predict that these differences would weaken over time. The prediction that herbaceous vegetation would retain the most NO₃⁻ and produce the most N₂ was supported, but this prediction was not supported beyond 12 h of incubation. Further, SOD was greatest in the herbaceous vegetation treatments; although, I did not predict that all treatments would approach a universal mean SOD rate as the incubations progressed.

My hypothesis that N₂O production would be greatest in herbaceous vegetation treatments was not supported as bare soils produced the most N₂O, but only through the first 24 h

of incubation. Results supported my hypothesis that CH_4 production would be greatest in the herbaceous vegetation mesocosms; however, the difference in production rates among the vegetation levels for both N_2O and CH_4 was likely ecologically negligible.

Hypothesis 2) Duration of inundation during wet-dry cycles affects nutrient flux rates.

My hypothesis that nutrient retention would be greatest in the 3-week hydroperiod treatments was partially supported for NO_3^- retention. Due to the interaction between vegetation and hydrology, the direct effect of hydrology on NO_3^- retention could not be assessed. In the herbaceous vegetation and tree planting treatments, NO_3^- retention was greatest in the mesocosms treated with a 3-day hydroperiod. For bare soils, NO_3^- retention was greatest in the mesocosms treated with a 3-week hydroperiod, further highlighting the influence of this interaction between vegetation and hydrology. My prediction that short-term wet-dry cycles would retain less PO_4^{3-} was also partially supported. The analysis of PO_4^{3-} flux rates for the first 24 h following flooding indicated that there was no interaction between vegetation and hydrology and there were no differences in PO_4^{3-} flux rates between the hydrology levels. Conversely, an interaction was present in the analysis of PO_4^{3-} flux rates for days 2 – 5. In this analysis, the treatment most efficient at removing PO_4^{3-} differed between hydrology levels, with tree plantings having the greatest uptake rate for the 3-day hydroperiod treatment and herbaceous vegetation having the greatest uptake in the 3-week hydroperiod treatment.

My hypothesis for N_2 and O_2 was weakly supported as the 3-day hydroperiod treatments produced more N_2 and had higher SOD rates compared to the 3-week hydroperiod treatment. However, I did not predict that these differences would weaken as the incubations progressed.

Additionally, my hypothesis that mesocosms treated with a 3-day hydroperiod would produce more N_2O whereas those treated with a 3-week hydroperiod would produce more CH_4 was supported for N_2O , but not for CH_4 as the 3-day hydroperiod treatments produced more N_2O and CH_4 regardless of time point.

Vegetation-Hydrology Interaction

Nutrient retention within mesocosms was dependent on a combination of vegetation type and hydrologic regime with certain vegetation levels retaining the most nutrients under specific hydrologic conditions. For NO_3^- , herbaceous vegetation had the highest retention rate regardless of hydrology. Conversely, the vegetation type that retained the most PO_4^{3-} differed between hydrology levels. The effect of this interaction on NO_3^- and PO_4^{3-} retention is an important finding both for understanding nutrient dynamics in floodplain wetlands and for wetland management. As seen in this and other studies, interactions between vegetation and hydrology can greatly influence nutrient retention rates by regulating nutrient storage and removal capacities within floodplain wetlands (Baldwin & Mitchell, 2000; S. Faulkner et al., 2011b; Silvan et al., 2004). Further, interactions between soil moisture (as a function of hydrology) and vegetation can influence soil nutrient distribution and composition, leading to shifts in nutrient transformation pathways and rates (Ross et al., 2006). Therefore, attempting to predict NO_3^- and PO_4^{3-} retention rates may lead inaccurate conclusions if only vegetation community composition or hydrologic regime are considered.

Dissolved Nutrients

Nitrate

All treatments were effective at reducing NO_3^- content to near-zero after 5 days of inundation. However, reductions in the herbaceous vegetation mesocosms were much faster than in the other vegetation treatments regardless of hydrology, reaching NO_3^- depletion by day 3. Water residence time had a positive linear relationship with NO_3^- retention among all treatments, but the effect was more pronounced in bare soil and tree planting treatments, as evidenced by their similar daily NO_3^- retention rates. This is consistent with previous studies that found that water residence time was positively correlated with NO_3^- retention in stormwater treatment and riverine wetlands (Carleton et al., 2001; Jansson et al., 1994). Additionally, the NO_3^- removal rates observed in this study were consistent with findings from two previous mesocosm studies which reported that mesocosms planted with *L. oryzoides* also achieved a >90% reduction in NO_3^- content after 3 days of inundation with nutrient-enriched water (Taylor et al., 2015; Tyler et al., 2012). These studies also reported similar removal rates in unvegetated mesocosms with a >60% reduction in NO_3^- content after 2 days of inundation.

The faster reduction of NO_3^- content in the herbaceous vegetation treatments suggests that NO_3^- retention was more influenced by vegetation type and potentially the associated microbial communities than water residence time. Plant and microbial uptake and processes can be a significant pathway of N retention in aquatic systems, particularly under low-flow conditions (Taylor et al., 2015; Vymazal, 2007). Additionally, herbaceous vegetation can provide a steady supply of labile C to microbes via leaf senescence, which can enhance denitrification and N mineralization (Hefting et al., 2005; Korol et al., 2019; Taylor et al., 2015), leading to a reduction in DOC content (Castaldelli et al., 2013; Zarnetske et al., 2011). In this experiment,

DOC flux into the water from sediment/vegetation was lowest in herbaceous vegetation treatments, suggesting microbes were using DOC faster than it was released by plants and/or soil. This likely facilitated the faster reduction of NO_3^- observed in these treatments.

The presence of substantial amounts of algae in the bare soil and tree planting treatments (Sup. Image 1.4) may have also influenced NO_3^- retention. Algae can be a significant NO_3^- retention pathway in aquatic ecosystems (Griffiths et al., 2021); however, chl-*a* content did not appear to affect NO_3^- retention rates in this experiment. Wetlands dominated by emergent vegetation (like *L. oryzoides*) can have higher NO_3^- retention than those dominated by filamentous green algae (Korol et al., 2019), supporting the conclusion that NO_3^- removal from the water was achieved through non-algal mediated pathways. While not a significant predictor of NO_3^- uptake in this study, the effects of algae on NO_3^- retention in wetlands with variable plant communities and hydrologic regimes are poorly understood. Therefore, further research is needed to determine the contribution of algae to NO_3^- retention in wetlands.

Phosphate

Twenty-four Hour Retention Rates.

The rapid reduction of PO_4^{3-} within the first 24 h of inundation was likely due to physical or chemical processes as opposed to biological uptake as abiotic processes are often the dominant P retention pathway upon soil rewetting (Baldwin & Mitchell, 2000a; Craft, 1996; Reddy et al., 1998). However, the significantly lower PO_4^{3-} retention rate in the herbaceous vegetation mesocosms compared to bare soil and tree planting treatments suggests that vegetation type may have also influenced retention rates within the first 24 h of flooding. The

relationship between P retention and vegetation types can vary across vegetation functional groups (Kucey et al., 1989), and *L. oryzoides* may have altered physical and chemical characteristics of the soil that were not measured like pH or bulk density, contributing to the slower uptake rate observed in the herbaceous vegetation treatments.

Another possible reason for the slower mean PO_4^{3-} uptake rate observed in herbaceous vegetation treatments may be related to differences in soil redox conditions. In the soil core incubation experiment, herbaceous vegetation treatments had greater SOD at 6 h compared to bare soil and tree plantings. Herbaceous vegetation treatments may have been primed for rapid increases in SOD due to the availability of organic C from several months of regular leaf senescence which increased microbial biomass and activity, leading to a reduction in O_2 content at the soil-water interface. Starting the core incubations at a lower redox state may have reduced P binding rates with the soil (Ann et al., 1999; Baldwin & Mitchell, 2000; Braskerud et al., 2005), leading to slower PO_4^{3-} retention in herbaceous vegetation treatments.

While there were no ecologically significant differences in soil P content among the treatments after 5 days of flooding, there may have been P bound in the soil that could not be accounted for using the Mehlich III extraction method. High soil pH and iron content can decrease extraction efficiency (J. Kang et al., 2009; Penn et al., 2018), and these variables were not measured in the present study. Therefore, it is possible that a portion of the PO_4^{3-} that was rapidly removed from the water after 24 h of flooding became bound to the soil but could not be accounted for due to limitations of the extraction process.

Retention Rates Across Days 2 – 5.

After 2 days of flooding, PO_4^{3-} retention rates became more variable in the herbaceous vegetation and tree planting treatments. Phosphate removal rates in the bare soil treatments slowed after 24 h of inundation, presumably due to these mesocosms containing less PO_4^{3-} by day 2 than the herbaceous vegetation and tree planting treatments. This resulted in bare soils being predicted to have the lowest PO_4^{3-} retention rates for the day 2 – 5 dataset despite having the greatest PO_4^{3-} retention rate during the first 24 h of flooding. By day 2, vegetation and hydrology began interacting, leading to differences in PO_4^{3-} retention among treatments being contingent on factor combinations. However, only bare soil treatments were significantly different from other vegetation levels regardless of hydrology. Further, retention rates for herbaceous vegetation and tree planting treatments became more similar over time and as the mesocosms approached PO_4^{3-} depletion.

This convergence towards a similar daily retention rate for herbaceous vegetation and tree planting treatments may indicate that water residence time had a stronger effect on PO_4^{3-} retention rates than vegetation or hydrologic regime when considered across 2 – 5 days of flooding. Water residence time has been identified as the main factor controlling PO_4^{3-} in constructed treatment wetlands and likely became the dominant factor regulating PO_4^{3-} retention among treatments as flood duration increased beyond 24 h (Koskiahio et al., 2003; Reinhardt et al., 2005).

Gas Data

Dinitrogen Gas Production and Soil Oxygen Demand

All treatments experienced net N_2 production at each time point in the incubation experiment. I anticipated that the 3-day hydroperiod and herbaceous vegetation treatments would produce the most N_2 , and this occurred across all sampling time points. However, N_2 production in the 3-day hydroperiod and herbaceous vegetation treatments were only statistically greater at 12 h of incubation. Beyond 12 h, N_2 production rates across all treatments converged toward a uniform mean. Vegetation and hydrology did not interact to influence N_2 production rates at any sampling time point.

Greater N_2 production in the 3-day hydroperiod treatment compared to the 3-week treatment supports findings of other studies in which rapid wet-dry cycles can enhance N_2 production, often via coupled nitrification-denitrification processes (Marchant et al., 2016b; Verhoeven et al., 2018b; Xia et al., 2017). The rapid wet-dry cycling of the 3-day hydroperiod treatment potentially supported a mix of aerobic and anerobic microbes that were primed to quickly denitrify available NO_3^- as an oxic-anoxic redox gradient formed in the soil following rewetting (Baldwin & Mitchell, 2000). Coupled nitrification-denitrification likely slowed and ultimately ceased as soil oxygen content was depleted over the course of the incubations, potentially explaining why differences in N_2 production rates between hydrology levels were not significant beyond 12 h.

As with NO_3^- retention, differences in N_2 production between herbaceous vegetation and bare soil and tree planting treatments may have resulted from a lower initial soil redox state in the herbaceous vegetation mesocosms due to high amounts of bioavailable C. Denitrifying

microbes use C as an energy source for cellular respiration, and C can be a limiting nutrient for these species. When C is limited, denitrifying microbes are unable to continue the reduction reactions that convert NO_3^- to N_2 (Dodds & Whiles, 2010). *Leersia oryzoides*'s high biomass turnover rate may have provided sufficient bioavailable C in the form of DOC to prevent C-limitation, thereby enhancing anaerobic microbial biomass accretion and activity. Increased microbial biomass and activity may have reduced soil redox, leading to greater denitrification rates in herbaceous vegetation compared to other treatments (Reddy et al., 1989; Weisner et al., 1994). As incubation time increased, this relationship between soil redox state and denitrification became more apparent as evidenced by the steady increase in SOD across time points. The convergence of N_2 production and SOD rates toward a uniform mean across treatments and lack of differences beyond 12 h further highlights how the effect of water residence time may begin to supersede vegetation type or hydrologic regime as flood duration increases.

Dinitrogen gas and SOD Correlations

The strong correlation between N_2 and SOD at 12 h in herbaceous vegetation treatments provides further evidence that these treatments were at a lower redox state compared to bare soil and tree plantings prior to incubations. This correlation between denitrification and SOD has been identified in previous studies (Baldwin & Mitchell, 2000; Peralta et al., 2010; Taylor et al., 2015) with higher SOD increasing denitrification rates (de Klein et al., 2017; Tomaszek & Czerwieniec, 2003). The decline and rebound of this correlation across sampling time points in herbaceous vegetation treatments is puzzling and appears due to increasing variability at 24 h, but the cause of this increased variability is uncertain. These changes in the relationship between

N₂ production and SOD do not appear related to hydrology as this trend was observed in both 3-day and 3-week hydroperiod treatments.

Greenhouse Gases

Greenhouse gas production across all treatments was much lower than expected, perhaps because of the five-day inundation period prior to the core incubation experiment for N_2O or the relatively short duration that the mesocosms were flooded compared to natural systems for CH_4 . Previous research has found that saturated soils are often CH_4 sources (Bohn et al., 2007; Calabrese et al., 2021) and that N_2O production is typically greatest immediately following inundation (Bronson et al., 1997; Xiong et al., 2007). Areas with high CH_4 production are typically inundated longer than five days and often are permanently or semi-permanently inundated (Bronson et al., 1997), and production rates are greatest in inundated areas with sufficient organic C deposition to fuel methanogenesis (Taylor et al., 2015).

This paradox of mesocosms being inundated too long to produce large quantities of N_2O but not long enough to produce large quantities of CH_4 complicates interpretation of the greenhouse gas data; however, one possible explanation as to why N_2O production was low in the core incubation experiment is that five days of inundation prior to the core experiment resulted in too little O_2 at the sediment-water interface to produce N_2O by the time incubation cores were collected. Nitrous oxide is typically produced as a byproduct of incomplete denitrification in which the presence of oxygen disrupts the final step of converting N_2O to N_2 . Oxygen in the sediment-water interface within the mesocosms may have been depleted over the five days of inundation prior to the experiment. If oxygen at the sediment-water interface was at or near depletion prior to or shortly after beginning the experiment, complete denitrification would likely be favored, reducing the amount of N_2O produced. Nitrous oxide production trended downward as incubation time increased, suggesting that the environment within the cores among all treatments was still being reduced (i.e., hypoxic as opposed to anoxic). This is

supported by coinciding increases in SOD as incubations progressed. Surprisingly, N₂O production was greatest in bare soil as opposed to vegetated mesocosms, perhaps because of root zone oxygen depletion in which root metabolism reduces the soil-water interface environment to an anerobic state (Siam et al., 2019). However, the greater N₂O production rate in bare soil treatments may be a result of the small amount of N₂O produced among treatments as all flux rates fell between 0.2 and -0.02 mg m⁻² h⁻¹ (i.e., likely not ecologically significant). As I was unable to quantify in-situ N₂O flux rates during the nutrient dosing experiment, it is unknown if an ecologically significant amount of N₂O was produced upon initial flooding. However, I suspect that N₂O production was greatest during this five-day period of inundation prior to the core incubation experiment where N₂O flux rates could be measured.

In contrast to N₂O production, CH₄ production may have been limited by not being inundated long enough. Like denitrification, methanogenesis is an anaerobic process that can be interrupted by the presence of O₂ (Dodds & Whiles, 2010). Trends in SOD suggest that conditions in the sediment-water interface were likely hypoxic at the beginning of core incubations (as evidenced by a near-zero CH₄ production for all treatments at 12 h) and able to support very limited methanogenesis. While CH₄ production was low throughout the experiment, mean production in herbaceous vegetation treatments trended higher as incubations progressed and approached 1 mg m⁻² h⁻¹ by 48 h in the herbaceous vegetation – 3-day hydroperiod treatments. No increases in CH₄ flux were observed in bare soil and tree planting treatments across all sampling timepoints. This contrast between herbaceous vegetation and bare soil and tree planting treatments may be related to the root structure of herbaceous vegetation and availability of labile C. The rhizomes of *L. oryzoides* are shallow and bundled and have been associated with depleting O₂ at the sediment-water interface, creating an anerobic environment

within the root zone (Siam et al., 2019). Conversely, bare soil, which was absent of roots, or tree planting treatments, which likely had deeper roots, may not have experienced substantial root-zone O₂ depletion as quickly as herbaceous vegetation treatments. However, quantifying root mass and root zone oxygen depletion was beyond the scope of this study.

The 3-day hydroperiod treatments trended towards higher CH₄ production rates compared to the 3-week hydroperiod treatments, and this may be a source of available carbon for methanogenesis. Mesocosms exposed to 3 weeks of inundation may have experienced periods of hypoxia at the soil-water interface. During these periods, available C may have been depleted via methanogenesis (and denitrification), reducing the amount of C available for methanogenesis during the core incubation experiment. However, CH₄ production rates were not measured during the hydrologic treatment applications prior to the experiment nor during the nutrient dosing experiment. Therefore, this possible explanation as to why CH₄ production rates were highest in the 3-day hydroperiod treatments should be tested in future experiments before definitive conclusions can be drawn.

Methane production in herbaceous vegetation treatments may also have been enhanced by labile C availability and the rate at which it was utilized by microbes. Herbaceous vegetation treatments had the lowest amount of DOC at the end of the dosing experiment (Table 14), as well as lowest DOC release rates, potentially because herbaceous vegetation treatments used available DOC to fuel both denitrification and ultimately CH₄ production once soil oxygen was sufficiently depleted. While neither post-dosing DOC content nor DOC flux rates were included in the analyses due to significant autocorrelation with soil nutrients, DOC use by microbes has been identified as an important regulator for CH₄ production (Lu, Wassmann, Neue, & Huang, 2000a; Sullivan et al., 2013; Taylor et al., 2015). Further, C derived from root zones of other

monocots has been identified as a strong regulator of CH₄ production in inundated soils (Lu, Wassmann, Neue, & Huang, 2000a; Lu, Wassmann, Neue, Huang, et al., 2000b).

Soil Nutrients

Low soil nutrient content in pre- and post-dosing samples suggest that biological assimilatory and/or dissimilatory processes were primarily responsible for aqueous NO₃⁻ and PO₄³⁻ mass reductions. Although there were significant pairwise differences in pre- and post-dosing soil nutrients within some treatments, low concentrations may have overestimated model significance, and these differences are unlikely to be ecologically significant. The significance of soil TN for the N₂ model at 24 h indicated that soil TN needed to be controlled to accurately predict mean N₂ flux rates influenced by vegetation and hydrology. I found no significant differences in N₂ production for either vegetation or hydrology, and soil TN was not correlated with N₂ production at 24 h. Also, soil nutrient content was not a significant parameter in any of the models with significant differences in flux rates among treatments. Therefore, it is unlikely that soil nutrient content had a strong effect on NO₃⁻, PO₄³⁻, N₂, or SOD flux in my experiment. Soil nutrient content in my mesocosms was lower than those typical of wetland ecosystems, and soil nutrient content may not affect flux rates until a soil nutrient content threshold is reached. However, comparative field studies are needed to determine if this lack of a correlation persists in natural wetlands.

Conclusions

All treatments were effective at reducing NO_3^- and PO_4^{3-} content to near-zero after 5 days of inundation in static wetland mesocosms. If this pattern simulates reduction rates in restored wetlands, floodwaters should be held for at least 5 days. Conversely, there may be differences in retention rates among these habitats during floods lasting between 24 – 72 h, especially for N.

Nitrate and PO_4^{3-} retention rates were generally influenced by an interaction between vegetation and hydrology, but this interaction was not always present, and the strength of its effect was dependent on the timeframe considered. While this interaction influenced NO_3^- and PO_4^{3-} retention rates for days 2 – 5 of inundation, treatment level in herbaceous vegetation mesocosms and water residence time in bare soil and tree planting mesocosms appeared to have stronger effects on retention rates.

I also found that potential interactions between vegetation and hydrology did not affect N_2 production. As predicted, herbaceous vegetation and the 3-day hydroperiod treatments resulted in the greatest N_2 production but only during the first 12 h of flooding. Soil redox appeared to influence N_2 production rates as SOD and N_2 production were generally positively correlated across all treatments and sampling time points. This conclusion is further supported by convergence among treatments toward a uniform mean flux rate for N_2 and SOD as incubation time increased. Further, N_2 production was positively correlated with flood duration, further suggesting that increases in flood duration enhance N removal processes like denitrification.

There were no tradeoffs between nutrient retention and greenhouse gas production in this experiment, consistent with results of some previous studies but conflicting with others (Ballantine et al., 2015; Hambäck et al., 2023; Morse & Bernhardt, 2013). Additional field and lab experiments are needed to determine under what conditions these tradeoffs may occur. This

study shows that vegetation, hydrologic regime, interaction between vegetation and hydrology, and water residence time all influence nutrient retention potential, and failure to consider these relationships may hinder achieving optimal nutrient retention capacity in restored floodplain wetlands.

CHAPTER 5: DISSERTATION CONCLUSIONS

Habitat Type, Hydrology, and Soil Properties

This dissertation investigated the dynamic interactions among habitat, hydrology, and soil properties and their collective influence on nutrient retention in restored floodplain wetlands. The primary objectives of these chapters were to contribute to the existing body of knowledge about wetland biogeochemical cycling and provide insights as to which restoration practices optimize nutrient retention. I assessed nutrient retention potential across five restored habitat types, identifying key factors influencing retention rates, examining relationships between flood frequency and nutrient cycling and soil properties, and evaluating effects of different vegetation types and hydrologic regimes on retention rates. The findings from these investigations highlight the significance of vegetation, hydrology, soil properties, and interactions among these factors in influencing nutrient retention in restored floodplain wetlands, and how the strength of these effects and interactions can vary across time and locations.

Chapter Synopses

Chapter Two

Chapter Two evaluated maximum nutrient uptake potentials and compared retention rates among five restored wetland habitat types: inundated shallow water areas, dry shallow water areas, tree plantings, remnant forests, and natural regeneration. All habitats sampled across 22 restored floodplain wetlands in western Tennessee and Kentucky retained nitrate (NO_3^-) and phosphate (PO_4^{3-}) on average throughout a simulated 48-h flood. Soil properties influenced retention rates which varied across flood duration and nutrient species. Further, nutrient retention appeared more affected by flood duration than habitat type when flooding persisted beyond 6 hours.

Chapter Three

Chapter Three examined the relationship between inundation frequency (IF) over 180 days prior to field sampling with nutrient retention and soil properties. Hydrology was positively correlated with NO_3^- retention but only at 6 h of flooding, beyond which IF no longer correlated with NO_3^- retention. Soil total nitrogen (TN) and total carbon (TC) were negatively correlated with IF whereas pH was negatively correlated with IF. There were also site-specific differences in the relationship between IF and soil pH. Minimal to no flooding within 30 days prior to sampling was detected using multispectral photographic imagery. These findings provide evidence that IF may influence ecosystem structure and functioning and suggest that the effects of IF may persist across intermittent dry periods.

Chapter Four

In Chapter Four, an experimental mesocosm study demonstrated how different types of wetland vegetation, hydrologic regimes and their interaction influence nutrient retention and nitrogen gas (N_2), nitrous oxide (N_2O), and methane (CH_4) production rates. Herbaceous vegetation (represented by *Leersia oryzoides* (Rice cutgrass)) reduced dissolved NO_3^- content in mesocosms significantly faster than bare soil or tree planting (represented by *Betula nigra* (River birch) and *Taxodium distichum* (Bald cypress)) treatments regardless of hydrology. Nitrogen gas production also was greater in herbaceous vegetation and 3-day hydroperiod treatments during a simulated 48-h flood but differences among vegetation types and hydrology levels were not observed beyond 6 h of flooding. Nitrous oxide and CH_4 production rates were low across all treatments, suggesting there were no tradeoffs between N removal and N_2O and CH_4 emissions in this experiment. All combinations of vegetation type and hydrology rapidly reduced dissolved PO_4^{3-} content during the first 24 h of flooding. Beyond 2 – 3 days of flooding, effects of vegetation and hydrology weakened, and water residence time became the primary factor regulating nutrient retention in the mesocosms.

Major Factors Influencing Nutrient Retention

Soil Redox Potential

The findings of Chapters Two and Four emphasize the potential importance of soil redox in nutrient retention. In these studies, NO_3^- retention was positively correlated with soil oxygen demand (SOD) across all sampling time points. These findings support previous research which reported that a reduced soil redox environment enhances denitrification and NO_3^- retention rates (Hunting & van der Geest, 2011; Marchant et al., 2016a; Pett-Ridge et al., 2006). While reductions in soil redox potential (represented by increases in SOD) were expected to prompt soil-P release, PO_4^{3-} retention was either unaffected or weakly enhanced by increases in SOD. These positive correlations between microbial abundance and activity and PO_4^{3-} retention suggest that dissolved O_2 content at the soil-water may not have been depleted enough to prompt P dissolution from metal complexes in the soil or any release was negated by microbial uptake. Therefore, during a 1 – 5-day flood, biological uptake may counteract any P release from the soil due to declining O_2 content.

Water Residence time

The results of all three studies support the consensus in the literature that wetland hydrology is a primary regulator of wetland ecosystem structure and function (Baldwin & Mitchell, 2000; Hansson et al., 2005; Paul Keddy, 2000). Increases in inundation time and flood frequency were associated with enhanced NO_3^- retention across all studies in this dissertation. Phosphate retention was generally greatest following initial inundation but slowed as flood

duration increased, although on average, no PO_4^{3-} release was observed in any of these studies. The salient relationship between water residence time and nutrient retention implies that the effects of distinct biogeochemical features of restored wetland habitat types and hydrologic regimes may be superseded by residence time when flooding persists beyond 12 – 24 h.

Management Implications

The results of these studies indicate that hydrology is a key factor influencing wetland nutrient retention, and increasing water residence time during flooding may be an effective strategy for reducing downstream nutrient export. Increasing flood frequency may also enhance N retention without affecting P retention as no correlations between IF and PO_4^{3-} flux were detected in Chapter Three. Therefore, focusing restoration efforts on improving floodplain connectivity and increasing water residence time may be a more economical approach to enhancing nutrient retention than committing substantial capital and labor to revegetation. However, this conclusion needs rigorous field validation before modifying management practices, and other restoration goals like increasing biodiversity must be balanced with maximizing nutrient retention.

While this dissertation expands our knowledge of the complex dynamics of wetland nutrient cycling, additional research is needed to elucidate other facets of wetland biogeochemistry not investigated in these studies. For example, more in situ measurements of nutrient flux rates are needed to determine if these trends hold under natural conditions. Further,

studies conducted in other regions are needed to determine if the relationships identified in this dissertation may be generalized to other areas. Time and effort limitations prevented the inclusion of a seasonal component in this dissertation, constraining study conclusions to the months of May – September. As such, incorporating seasonal variability into future studies would provide a more holistic view of restored floodplain wetland nutrient cycling in this region. Finally, this research may also serve as a foundation for developing mechanistic hypotheses to be tested in future studies.

APPENDIX A: CHAPTER 2 DATA

Site	Habitat	Sampling Time Point (h)	Mean NO ₃ ⁻ Flux (mg m ⁻² h ⁻¹)	Mean PO ₄ ³⁻ Flux (mg m ⁻² h ⁻¹)	Soil Moisture (g g ⁻¹)	Soil Bulk Density (g cm ³)	Soil pH	Soil Total C (mg g ⁻¹)	Soil Total N (mg g ⁻¹)	Extractable Soil P (mg g ⁻¹)
1	Remnant Forest	6	-8.33	-2.80	0.55	0.82	5.0	27.31	2.73	0.050
1	SW - Dry	6	-16.49	-0.67	1.44	0.53	6.1	22.00	2.30	0.038
1	SW - Inundated	6	-15.72	-1.78	1.51	0.58	6.2	27.44	2.34	0.026
1	Tree Planting	6	-8.43	-1.14	0.37	0.93	5.2	23.18	2.20	0.041
2	Natural Regeneration	6	-4.90	3.83	0.11	1.13	5.8	20.23	1.68	0.072
2	Remnant Forest	6	-7.86	1.50	0.30	0.93	5.5	28.72	2.33	0.075
2	SW - Dry	6	-0.19	-2.39	0.28	1.08	5.4	12.67	1.25	0.027
2	SW - Inundated	6	-10.03	-3.98	1.08	0.94	5.8	19.82	1.97	0.035
2	Tree Planting	6	3.87	0.37	0.18	0.94	5.6	24.25	2.13	0.054
3	Remnant Forest	6	NA	NA	0.45	0.90	5.6	33.82	2.88	0.083

Site	Habitat	Sampling Time Point (h)	Mean NO ₃ ⁻ Flux (mg m ⁻² h ⁻¹)	Mean PO ₄ ³⁻ Flux (mg m ⁻² h ⁻¹)	Soil Moisture (g g ⁻¹)	Soil Bulk Density (g cm ³)	Soil pH	Soil Total C (mg g ⁻¹)	Soil Total N (mg g ⁻¹)	Extractable Soil P (mg g ⁻¹)
3	SW - Dry	6	NA	NA	0.65	0.78	5.1	18.02	1.83	0.051
3	SW - Inundated	6	NA	NA	0.78	0.93	5.5	14.98	1.55	0.053
3	Tree Planting	6	NA	NA	0.32	0.78	5.5	27.16	2.18	0.068
4	Remnant Forest	6	-7.99	-5.77	0.56	0.94	5.2	26.78	2.89	0.050
4	SW - Dry	6	-13.87	-3.01	0.56	1.12	5.5	14.98	1.50	0.056
4	SW - Inundated	6	-23.83	-3.26	0.72	0.90	5.6	13.95	1.35	0.038
4	Tree Planting	6	-15.24	-4.90	0.48	1.16	5.4	15.07	1.44	0.055
5	Remnant Forest	6	-16.81	-1.07	1.04	0.55	5.5	50.72	4.27	0.041
5	SW - Dry	6	-21.18	-1.00	0.89	0.78	5.3	34.26	3.10	0.022
5	SW - Inundated	6	-24.46	-2.39	1.23	0.67	5.5	30.09	2.98	0.021

Site	Habitat	Sampling Time Point (h)	Mean NO ₃ ⁻ Flux (mg m ⁻² h ⁻¹)	Mean PO ₄ ³⁻ Flux (mg m ⁻² h ⁻¹)	Soil Moisture (g g ⁻¹)	Soil Bulk Density (g cm ³)	Soil pH	Soil Total C (mg g ⁻¹)	Soil Total N (mg g ⁻¹)	Extractable Soil P (mg g ⁻¹)
5	Tree Planting	6	-28.25	-0.58	0.48	0.71	5.6	36.76	3.33	0.045
6	SW - Dry	6	-1.69	-1.16	0.67	0.94	5.3	23.43	1.94	0.044
6	SW - Inundated	6	-11.29	-1.59	0.97	0.73	5.2	24.08	2.04	0.049
6	Tree Planting	6	-10.80	-1.47	0.55	1.04	5.5	23.54	1.78	0.079
7	Tree Planting	6	-4.79	-3.12	0.38	0.93	4.9	20.15	1.73	0.038
8	Natural Regeneration	6	-12.13	-5.00	0.96	0.67	5.2	37.95	3.30	0.075
8	SW - Inundated	6	-17.82	-3.37	0.48	1.12	6.1	7.04	0.74	0.045
9	Remnant Forest	6	4.82	0.49	0.92	0.65	6.0	46.00	3.54	0.055
9	SW - Dry	6	12.26	0.79	0.41	0.89	6.2	23.43	2.11	0.067
9	SW - Inundated	6	-20.23	-1.05	0.86	0.87	7.1	18.48	1.78	0.056

Site	Habitat	Sampling Time Point (h)	Mean NO ₃ ⁻ Flux (mg m ⁻² h ⁻¹)	Mean PO ₄ ³⁻ Flux (mg m ⁻² h ⁻¹)	Soil Moisture (g g ⁻¹)	Soil Bulk Density (g cm ³)	Soil pH	Soil Total C (mg g ⁻¹)	Soil Total N (mg g ⁻¹)	Extractable Soil P (mg g ⁻¹)
10	Natural Regeneration	6	-5.49	-1.03	0.29	1.11	5.7	17.25	1.53	0.032
10	SW - Inundated	6	-10.46	-2.71	0.90	0.80	6.3	14.71	1.48	0.026
10	Tree Planting	6	-4.04	-3.25	1.15	0.41	5.2	62.99	4.34	0.159
11	Natural Regeneration	6	-5.20	-1.15	0.28	0.84	5.2	25.27	2.34	0.057
11	Remnant Forest	6	1.74	-0.75	0.32	0.86	5.0	24.22	2.17	0.034
11	SW - Dry	6	-10.89	-2.63	0.61	0.88	4.7	23.88	2.33	0.103
11	SW - Inundated	6	-12.01	-6.31	0.66	1.06	5.0	15.05	1.40	0.067
11	Tree Planting	6	-8.47	-3.06	0.41	0.84	5.0	25.59	2.51	0.059
12	Remnant Forest	6	7.26	-1.97	0.31	0.87	5.1	26.00	2.62	0.048
12	SW - Inundated	6	-11.55	-5.67	1.34	0.57	5.3	37.17	3.10	0.035

Site	Habitat	Sampling Time Point (h)	Mean NO ₃ ⁻ Flux (mg m ⁻² h ⁻¹)	Mean PO ₄ ³⁻ Flux (mg m ⁻² h ⁻¹)	Soil Moisture (g g ⁻¹)	Soil Bulk Density (g cm ³)	Soil pH	Soil Total C (mg g ⁻¹)	Soil Total N (mg g ⁻¹)	Extractable Soil P (mg g ⁻¹)
12	Tree Planting	6	2.19	-2.55	0.27	0.95	5.0	22.67	1.77	0.048
13	Remnant Forest	6	-4.48	-1.52	0.35	0.87	5.8	41.18	3.50	0.093
13	SW - Dry	6	-9.18	-4.50	0.40	1.14	5.9	18.50	1.50	0.027
13	SW - Inundated	6	-23.66	-4.59	0.74	0.86	5.2	14.27	1.48	0.019
13	Tree Planting	6	-11.59	-3.16	0.45	1.92	5.5	16.11	1.51	0.035
14	Remnant Forest	6	-8.46	-3.89	0.45	0.94	5.3	26.08	2.45	0.043
14	SW - Inundated	6	-25.66	2.04	1.30	0.59	5.2	23.29	2.53	0.050
14	Tree Planting	6	-11.30	-1.88	0.36	0.95	5.6	22.44	2.06	0.068
15	Remnant Forest	6	-5.55	0.13	0.34	1.12	6.3	13.08	1.16	0.072
15	SW - Dry	6	-4.38	-2.83	0.91	0.62	5.5	37.84	3.06	0.072

Site	Habitat	Sampling Time Point (h)	Mean NO ₃ ⁻ Flux (mg m ⁻² h ⁻¹)	Mean PO ₄ ³⁻ Flux (mg m ⁻² h ⁻¹)	Soil Moisture (g g ⁻¹)	Soil Bulk Density (g cm ³)	Soil pH	Soil Total C (mg g ⁻¹)	Soil Total N (mg g ⁻¹)	Extractable Soil P (mg g ⁻¹)
15	SW - Inundated	6	-10.84	-3.26	1.11	0.78	6.7	23.20	2.30	0.042
15	Tree Planting	6	-4.31	-1.00	0.41	1.00	5.7	26.77	2.35	0.048
16	Natural Regeneration	6	1.74	-2.62	0.65	0.63	4.1	34.09	3.41	0.053
16	SW - Dry	6	4.09	-3.50	0.25	1.02	4.7	10.32	0.98	0.017
16	SW - Inundated	6	-21.76	-3.05	0.59	1.02	6.1	11.06	0.96	0.022
16	Tree Planting	6	-0.13	-2.50	0.40	0.97	4.6	16.31	1.51	0.029
17	Remnant Forest	6	-15.59	-0.64	0.33	0.97	4.8	29.95	2.65	0.029
17	SW - Dry	6	0.94	-0.07	0.65	0.68	4.0	35.08	3.17	0.027
17	Tree Planting	6	-20.48	1.67	0.30	0.98	4.9	21.26	1.98	0.027
18	Remnant Forest	6	-11.67	-1.80	0.20	0.83	5.1	25.40	2.07	0.041

Site	Habitat	Sampling Time Point (h)	Mean NO ₃ ⁻ Flux (mg m ⁻² h ⁻¹)	Mean PO ₄ ³⁻ Flux (mg m ⁻² h ⁻¹)	Soil Moisture (g g ⁻¹)	Soil Bulk Density (g cm ³)	Soil pH	Soil Total C (mg g ⁻¹)	Soil Total N (mg g ⁻¹)	Extractable Soil P (mg g ⁻¹)
18	SW - Dry	6	-8.75	-1.48	0.97	0.71	5.1	18.78	1.73	0.023
18	SW - Inundated	6	-16.79	-1.55	0.80	0.91	5.3	10.89	1.25	0.031
18	Tree Planting	6	-1.89	-2.11	0.14	0.89	5.1	20.60	1.62	0.035
19	Remnant Forest	6	-1.74	-1.66	0.45	0.89	5.2	29.13	2.45	0.032
19	SW - Dry	6	16.18	2.89	0.24	1.21	4.8	10.77	1.17	0.015
19	SW - Inundated	6	-4.37	4.53	0.57	1.02	5.3	9.53	0.77	0.014
19	Tree Planting	6	0.09	1.06	0.37	1.04	5.3	18.28	1.37	0.016
20	Natural Regeneration	6	-17.55	-5.37	1.29	0.71	5.8	35.88	2.80	0.051
20	Tree Planting	6	-7.61	-2.69	0.37	0.90	5.6	18.92	1.54	0.027
21	Remnant Forest	6	0.97	-0.85	0.32	1.11	5.6	10.35	0.95	0.048

Site	Habitat	Sampling Time Point (h)	Mean NO ₃ ⁻ Flux (mg m ⁻² h ⁻¹)	Mean PO ₄ ³⁻ Flux (mg m ⁻² h ⁻¹)	Soil Moisture (g g ⁻¹)	Soil Bulk Density (g cm ³)	Soil pH	Soil Total C (mg g ⁻¹)	Soil Total N (mg g ⁻¹)	Extractable Soil P (mg g ⁻¹)
21	SW - Dry	6	4.82	1.36	0.52	0.73	5.6	27.50	2.55	0.049
21	SW - Inundated	6	-21.01	-1.92	0.78	0.86	5.7	15.27	1.70	0.039
22	Remnant Forest	6	0.97	-0.85	0.32	1.11	5.6	10.35	0.95	0.048
1	Remnant Forest	24	-6.98	-1.83	0.55	0.82	5.0	27.31	2.73	0.050
1	SW - Dry	24	-5.99	-0.48	1.44	0.53	6.1	22.00	2.30	0.038
1	SW - Inundated	24	-13.28	-1.17	1.51	0.58	6.2	27.44	2.34	0.026
1	Tree Planting	24	-9.09	-0.81	0.37	0.93	5.2	23.18	2.20	0.041
2	Natural Regeneration	24	-12.11	2.29	0.11	1.13	5.8	20.23	1.68	0.072
2	Remnant Forest	24	-5.70	-0.64	0.30	0.93	5.5	28.72	2.33	0.075
2	SW - Dry	24	-9.35	-0.69	0.28	1.08	5.4	12.67	1.25	0.027

Site	Habitat	Sampling Time Point (h)	Mean NO ₃ ⁻ Flux (mg m ⁻² h ⁻¹)	Mean PO ₄ ³⁻ Flux (mg m ⁻² h ⁻¹)	Soil Moisture (g g ⁻¹)	Soil Bulk Density (g cm ³)	Soil pH	Soil Total C (mg g ⁻¹)	Soil Total N (mg g ⁻¹)	Extractable Soil P (mg g ⁻¹)
2	SW - Inundated	24	-7.44	-1.38	1.08	0.94	5.8	19.82	1.97	0.035
2	Tree Planting	24	-2.68	-1.04	0.18	0.94	5.6	24.25	2.13	0.054
3	Remnant Forest	24	-15.23	-1.77	0.45	0.90	5.6	33.82	2.88	0.083
3	SW - Dry	24	-25.21	-1.95	0.65	0.78	5.1	18.02	1.83	0.051
3	SW - Inundated	24	-18.62	-2.70	0.78	0.93	5.5	14.98	1.55	0.053
3	Tree Planting	24	-19.80	-1.38	0.32	0.78	5.5	27.16	2.18	0.068
4	Remnant Forest	24	-11.96	-2.80	0.56	0.94	5.2	26.78	2.89	0.050
4	SW - Dry	24	-16.85	-2.47	0.56	1.12	5.5	14.98	1.50	0.056
4	SW - Inundated	24	-17.90	-3.35	0.72	0.90	5.6	13.95	1.35	0.038
4	Tree Planting	24	-14.15	-3.33	0.48	1.16	5.4	15.07	1.44	0.055

Site	Habitat	Sampling Time Point (h)	Mean NO ₃ ⁻ Flux (mg m ⁻² h ⁻¹)	Mean PO ₄ ³⁻ Flux (mg m ⁻² h ⁻¹)	Soil Moisture (g g ⁻¹)	Soil Bulk Density (g cm ³)	Soil pH	Soil Total C (mg g ⁻¹)	Soil Total N (mg g ⁻¹)	Extractable Soil P (mg g ⁻¹)
5	Remnant Forest	24	23.62	-0.94	1.04	0.55	5.5	50.72	4.27	0.041
5	SW - Dry	24	15.07	-2.19	0.89	0.78	5.3	34.26	3.10	0.022
5	SW - Inundated	24	3.50	-2.47	1.23	0.67	5.5	30.09	2.98	0.021
5	Tree Planting	24	10.17	-1.70	0.48	0.71	5.6	36.76	3.33	0.045
6	SW - Dry	24	-15.89	-1.60	0.67	0.94	5.3	23.43	1.94	0.044
6	SW - Inundated	24	-15.85	-2.16	0.97	0.73	5.2	24.08	2.04	0.049
6	Tree Planting	24	-19.66	-1.03	0.55	1.04	5.5	23.54	1.78	0.079
7	Tree Planting	24	-13.00	-2.16	0.38	0.93	4.9	20.15	1.73	0.038
8	Natural Regeneration	24	-17.28	-3.92	0.96	0.67	5.2	37.95	3.30	0.075
8	SW - Inundated	24	-21.60	-2.88	0.48	1.12	6.1	7.04	0.74	0.045

Site	Habitat	Sampling Time Point (h)	Mean NO ₃ ⁻ Flux (mg m ⁻² h ⁻¹)	Mean PO ₄ ³⁻ Flux (mg m ⁻² h ⁻¹)	Soil Moisture (g g ⁻¹)	Soil Bulk Density (g cm ³)	Soil pH	Soil Total C (mg g ⁻¹)	Soil Total N (mg g ⁻¹)	Extractable Soil P (mg g ⁻¹)
9	Remnant Forest	24	-8.63	-1.68	0.92	0.65	6.0	46.00	3.54	0.055
9	SW - Dry	24	-15.13	-1.92	0.41	0.89	6.2	23.43	2.11	0.067
9	SW - Inundated	24	-15.85	-2.02	0.86	0.87	7.1	18.48	1.78	0.056
10	Natural Regeneration	24	-7.03	-0.48	0.29	1.11	5.7	17.25	1.53	0.032
10	SW - Inundated	24	-8.11	-2.70	0.90	0.80	6.3	14.71	1.48	0.026
10	Tree Planting	24	-8.82	-1.94	1.15	0.41	5.2	62.99	4.34	0.159
11	Natural Regeneration	24	-13.41	1.67	0.28	0.84	5.2	25.27	2.34	0.057
11	Remnant Forest	24	-16.53	2.52	0.32	0.86	5.0	24.22	2.17	0.034
11	SW - Dry	24	-20.11	0.50	0.61	0.88	4.7	23.88	2.33	0.103
11	SW - Inundated	24	-18.99	0.24	0.66	1.06	5.0	15.05	1.40	0.067

Site	Habitat	Sampling Time Point (h)	Mean NO ₃ ⁻ Flux (mg m ⁻² h ⁻¹)	Mean PO ₄ ³⁻ Flux (mg m ⁻² h ⁻¹)	Soil Moisture (g g ⁻¹)	Soil Bulk Density (g cm ³)	Soil pH	Soil Total C (mg g ⁻¹)	Soil Total N (mg g ⁻¹)	Extractable Soil P (mg g ⁻¹)
11	Tree Planting	24	-16.66	0.66	0.41	0.84	5.0	25.59	2.51	0.059
12	Remnant Forest	24	4.05	-1.11	0.31	0.87	5.1	26.00	2.62	0.048
12	SW - Inundated	24	-7.20	-2.34	1.34	0.57	5.3	37.17	3.10	0.035
12	Tree Planting	24	-2.30	-1.43	0.27	0.95	5.0	22.67	1.77	0.048
13	Remnant Forest	24	-24.34	-1.42	0.35	0.87	5.8	41.18	3.50	0.093
13	SW - Dry	24	-13.10	-1.77	0.40	1.14	5.9	18.50	1.50	0.027
13	SW - Inundated	24	-34.42	-4.60	0.74	0.86	5.2	14.27	1.48	0.019
13	Tree Planting	24	-29.46	-2.93	0.45	1.92	5.5	16.11	1.51	0.035
14	Remnant Forest	24	-14.98	1.29	0.45	0.94	5.3	26.08	2.45	0.043
14	SW - Inundated	24	-33.00	-3.94	1.30	0.59	5.2	23.29	2.53	0.050

Site	Habitat	Sampling Time Point (h)	Mean NO ₃ ⁻ Flux (mg m ⁻² h ⁻¹)	Mean PO ₄ ³⁻ Flux (mg m ⁻² h ⁻¹)	Soil Moisture (g g ⁻¹)	Soil Bulk Density (g cm ³)	Soil pH	Soil Total C (mg g ⁻¹)	Soil Total N (mg g ⁻¹)	Extractable Soil P (mg g ⁻¹)
14	Tree Planting	24	-19.21	2.25	0.36	0.95	5.6	22.44	2.06	0.068
15	Remnant Forest	24	-7.20	-1.61	0.34	1.12	6.3	13.08	1.16	0.072
15	SW - Dry	24	-19.57	-3.25	0.91	0.62	5.5	37.84	3.06	0.072
15	SW - Inundated	24	-19.77	-2.52	1.11	0.78	6.7	23.20	2.30	0.042
15	Tree Planting	24	-11.51	-1.48	0.41	1.00	5.7	26.77	2.35	0.048
16	Natural Regeneration	24	-5.50	-0.56	0.65	0.63	4.1	34.09	3.41	0.053
16	SW - Dry	24	4.23	0.86	0.25	1.02	4.7	10.32	0.98	0.017
16	SW - Inundated	24	-4.33	-0.78	0.59	1.02	6.1	11.06	0.96	0.022
16	Tree Planting	24	-6.81	-1.35	0.40	0.97	4.6	16.31	1.51	0.029
17	Remnant Forest	24	-5.99	-0.73	0.33	0.97	4.8	29.95	2.65	0.029

Site	Habitat	Sampling Time Point (h)	Mean NO ₃ ⁻ Flux (mg m ⁻² h ⁻¹)	Mean PO ₄ ³⁻ Flux (mg m ⁻² h ⁻¹)	Soil Moisture (g g ⁻¹)	Soil Bulk Density (g cm ³)	Soil pH	Soil Total C (mg g ⁻¹)	Soil Total N (mg g ⁻¹)	Extractable Soil P (mg g ⁻¹)
17	SW - Dry	24	-3.81	-2.02	0.65	0.68	4.0	35.08	3.17	0.027
17	Tree Planting	24	-8.23	-1.60	0.30	0.98	4.9	21.26	1.98	0.027
18	Remnant Forest	24	-23.88	-4.32	0.20	0.83	5.1	25.40	2.07	0.041
18	SW - Dry	24	-43.42	-5.75	0.97	0.71	5.1	18.78	1.73	0.023
18	SW - Inundated	24	-26.79	-5.42	0.80	0.91	5.3	10.89	1.25	0.031
18	Tree Planting	24	-17.50	-4.17	0.14	0.89	5.1	20.60	1.62	0.035
19	Remnant Forest	24	-15.53	-1.37	0.45	0.89	5.2	29.13	2.45	0.032
19	SW - Dry	24	-7.24	-2.18	0.24	1.21	4.8	10.77	1.17	0.015
19	SW - Inundated	24	-9.02	-0.23	0.57	1.02	5.3	9.53	0.77	0.014
19	Tree Planting	24	-18.39	-0.91	0.37	1.04	5.3	18.28	1.37	0.016

Site	Habitat	Sampling Time Point (h)	Mean NO ₃ ⁻ Flux (mg m ⁻² h ⁻¹)	Mean PO ₄ ³⁻ Flux (mg m ⁻² h ⁻¹)	Soil Moisture (g g ⁻¹)	Soil Bulk Density (g cm ³)	Soil pH	Soil Total C (mg g ⁻¹)	Soil Total N (mg g ⁻¹)	Extractable Soil P (mg g ⁻¹)
20	Natural Regeneration	24	-19.86	-4.71	1.29	0.71	5.8	35.88	2.80	0.051
20	Tree Planting	24	-7.07	-1.49	0.37	0.90	5.6	18.92	1.54	0.027
21	Remnant Forest	24	0.47	1.00	0.32	1.11	5.6	10.35	0.95	0.048
21	SW - Dry	24	-14.42	1.14	0.52	0.73	5.6	27.50	2.55	0.049
21	SW - Inundated	24	-2.13	-3.16	0.78	0.86	5.7	15.27	1.70	0.039
22	Remnant Forest	24	-14.57	-0.47	0.32	1.11	5.6	10.35	0.95	0.048
1	Remnant Forest	48	-12.91	-1.93	0.55	0.82	5.0	27.31	2.73	0.050
1	SW - Dry	48	-12.53	-4.59	1.44	0.53	6.1	22.00	2.30	0.038
1	SW - Inundated	48	-11.66	-3.84	1.51	0.58	6.2	27.44	2.34	0.026
1	Tree Planting	48	-10.44	-2.44	0.37	0.93	5.2	23.18	2.20	0.041

Site	Habitat	Sampling Time Point (h)	Mean NO ₃ ⁻ Flux (mg m ⁻² h ⁻¹)	Mean PO ₄ ³⁻ Flux (mg m ⁻² h ⁻¹)	Soil Moisture (g g ⁻¹)	Soil Bulk Density (g cm ³)	Soil pH	Soil Total C (mg g ⁻¹)	Soil Total N (mg g ⁻¹)	Extractable Soil P (mg g ⁻¹)
2	Natural Regeneration	48	-26.75	-1.30	0.11	1.13	5.8	20.23	1.68	0.072
2	Remnant Forest	48	-2.92	-3.21	0.30	0.93	5.5	28.72	2.33	0.075
2	SW - Dry	48	-16.47	-2.90	0.28	1.08	5.4	12.67	1.25	0.027
2	SW - Inundated	48	-15.90	-3.37	1.08	0.94	5.8	19.82	1.97	0.035
2	Tree Planting	48	-23.30	0.73	0.18	0.94	5.6	24.25	2.13	0.054
3	Remnant Forest	48	-17.21	2.71	0.45	0.90	5.6	33.82	2.88	0.083
3	SW - Dry	48	-20.55	2.04	0.65	0.78	5.1	18.02	1.83	0.051
3	SW - Inundated	48	-27.04	2.05	0.78	0.93	5.5	14.98	1.55	0.053
3	Tree Planting	48	-28.71	3.34	0.32	0.78	5.5	27.16	2.18	0.068
4	Remnant Forest	48	-10.61	-1.47	0.56	0.94	5.2	26.78	2.89	0.050

Site	Habitat	Sampling Time Point (h)	Mean NO ₃ ⁻ Flux (mg m ⁻² h ⁻¹)	Mean PO ₄ ³⁻ Flux (mg m ⁻² h ⁻¹)	Soil Moisture (g g ⁻¹)	Soil Bulk Density (g cm ³)	Soil pH	Soil Total C (mg g ⁻¹)	Soil Total N (mg g ⁻¹)	Extractable Soil P (mg g ⁻¹)
4	SW - Dry	48	-16.31	-2.47	0.56	1.12	5.5	14.98	1.50	0.056
4	SW - Inundated	48	-26.73	-3.07	0.72	0.90	5.6	13.95	1.35	0.038
4	Tree Planting	48	-14.03	-2.35	0.48	1.16	5.4	15.07	1.44	0.055
5	Remnant Forest	48	-18.53	-0.77	1.04	0.55	5.5	50.72	4.27	0.041
5	SW - Dry	48	-16.35	0.51	0.89	0.78	5.3	34.26	3.10	0.022
5	SW - Inundated	48	-32.92	-1.04	1.23	0.67	5.5	30.09	2.98	0.021
5	Tree Planting	48	-41.60	-1.02	0.48	0.71	5.6	36.76	3.33	0.045
6	SW - Dry	48	-20.09	-3.27	0.67	0.94	5.3	23.43	1.94	0.044
6	SW - Inundated	48	-16.71	-3.23	0.97	0.73	5.2	24.08	2.04	0.049
6	Tree Planting	48	-16.99	-2.11	0.55	1.04	5.5	23.54	1.78	0.079

Site	Habitat	Sampling Time Point (h)	Mean NO ₃ ⁻ Flux (mg m ⁻² h ⁻¹)	Mean PO ₄ ³⁻ Flux (mg m ⁻² h ⁻¹)	Soil Moisture (g g ⁻¹)	Soil Bulk Density (g cm ³)	Soil pH	Soil Total C (mg g ⁻¹)	Soil Total N (mg g ⁻¹)	Extractable Soil P (mg g ⁻¹)
7	Tree Planting	48	-17.00	-1.62	0.38	0.93	4.9	20.15	1.73	0.038
8	Natural Regeneration	48	-14.39	-3.22	0.96	0.67	5.2	37.95	3.30	0.075
8	SW - Inundated	48	-10.80	-2.41	0.48	1.12	6.1	7.04	0.74	0.045
9	Remnant Forest	48	-5.64	-2.11	0.92	0.65	6.0	46.00	3.54	0.055
9	SW - Dry	48	-1.56	-0.33	0.41	0.89	6.2	23.43	2.11	0.067
9	SW - Inundated	48	-8.66	-1.46	0.86	0.87	7.1	18.48	1.78	0.056
10	Natural Regeneration	48	-15.34	0.33	0.29	1.11	5.7	17.25	1.53	0.032
10	SW - Inundated	48	-16.04	-3.43	0.90	0.80	6.3	14.71	1.48	0.026
10	Tree Planting	48	-25.07	-1.38	1.15	0.41	5.2	62.99	4.34	0.159
11	Natural Regeneration	48	-42.63	-0.48	0.28	0.84	5.2	25.27	2.34	0.057

Site	Habitat	Sampling Time Point (h)	Mean NO ₃ ⁻ Flux (mg m ⁻² h ⁻¹)	Mean PO ₄ ³⁻ Flux (mg m ⁻² h ⁻¹)	Soil Moisture (g g ⁻¹)	Soil Bulk Density (g cm ³)	Soil pH	Soil Total C (mg g ⁻¹)	Soil Total N (mg g ⁻¹)	Extractable Soil P (mg g ⁻¹)
11	Remnant Forest	48	-21.66	-0.46	0.32	0.86	5.0	24.22	2.17	0.034
11	SW - Dry	48	-51.30	3.44	0.61	0.88	4.7	23.88	2.33	0.103
11	SW - Inundated	48	-46.61	2.58	0.66	1.06	5.0	15.05	1.40	0.067
11	Tree Planting	48	-51.12	-0.46	0.41	0.84	5.0	25.59	2.51	0.059
12	Remnant Forest	48	-8.96	-0.85	0.31	0.87	5.1	26.00	2.62	0.048
12	SW - Inundated	48	-12.21	-2.17	1.34	0.57	5.3	37.17	3.10	0.035
12	Tree Planting	48	-10.53	-0.78	0.27	0.95	5.0	22.67	1.77	0.048
13	Remnant Forest	48	-25.66	-0.83	0.35	0.87	5.8	41.18	3.50	0.093
13	SW - Dry	48	-15.16	-0.19	0.40	1.14	5.9	18.50	1.50	0.027
13	SW - Inundated	48	-53.29	-1.15	0.74	0.86	5.2	14.27	1.48	0.019

Site	Habitat	Sampling Time Point (h)	Mean NO ₃ ⁻ Flux (mg m ⁻² h ⁻¹)	Mean PO ₄ ³⁻ Flux (mg m ⁻² h ⁻¹)	Soil Moisture (g g ⁻¹)	Soil Bulk Density (g cm ³)	Soil pH	Soil Total C (mg g ⁻¹)	Soil Total N (mg g ⁻¹)	Extractable Soil P (mg g ⁻¹)
13	Tree Planting	48	-38.09	0.60	0.45	1.92	5.5	16.11	1.51	0.035
14	Remnant Forest	48	-5.08	-1.79	0.45	0.94	5.3	26.08	2.45	0.043
14	SW - Inundated	48	-23.28	-0.91	1.30	0.59	5.2	23.29	2.53	0.050
14	Tree Planting	48	-25.89	-2.42	0.36	0.95	5.6	22.44	2.06	0.068
15	Remnant Forest	48	-13.90	-0.09	0.34	1.12	6.3	13.08	1.16	0.072
15	SW - Dry	48	-23.52	-1.24	0.91	0.62	5.5	37.84	3.06	0.072
15	SW - Inundated	48	-21.14	-1.96	1.11	0.78	6.7	23.20	2.30	0.042
15	Tree Planting	48	-20.83	-0.66	0.41	1.00	5.7	26.77	2.35	0.048
16	Natural Regeneration	48	-50.95	-1.94	0.65	0.63	4.1	34.09	3.41	0.053
16	SW - Dry	48	-35.27	-2.46	0.25	1.02	4.7	10.32	0.98	0.017

Site	Habitat	Sampling Time Point (h)	Mean NO ₃ ⁻ Flux (mg m ⁻² h ⁻¹)	Mean PO ₄ ³⁻ Flux (mg m ⁻² h ⁻¹)	Soil Moisture (g g ⁻¹)	Soil Bulk Density (g cm ³)	Soil pH	Soil Total C (mg g ⁻¹)	Soil Total N (mg g ⁻¹)	Extractable Soil P (mg g ⁻¹)
16	SW - Inundated	48	-35.51	-4.40	0.59	1.02	6.1	11.06	0.96	0.022
16	Tree Planting	48	-24.20	-1.17	0.40	0.97	4.6	16.31	1.51	0.029
17	Remnant Forest	48	-6.23	-0.58	0.33	0.97	4.8	29.95	2.65	0.029
17	SW - Dry	48	-23.37	-0.98	0.65	0.68	4.0	35.08	3.17	0.027
17	Tree Planting	48	-16.13	-0.33	0.30	0.98	4.9	21.26	1.98	0.027
17	wetland	48	-14.96	-1.44	1.14	0.44	4.1	64.97	6.42	0.022
18	Remnant Forest	48	-23.24	-0.79	0.20	0.83	5.1	25.40	2.07	0.041
18	SW - Dry	48	-41.44	-0.06	0.97	0.71	5.1	18.78	1.73	0.023
18	SW - Inundated	48	-23.54	0.19	0.80	0.91	5.3	10.89	1.25	0.031
18	Tree Planting	48	-27.03	-0.35	0.14	0.89	5.1	20.60	1.62	0.035

Site	Habitat	Sampling Time Point (h)	Mean NO ₃ ⁻ Flux (mg m ⁻² h ⁻¹)	Mean PO ₄ ³⁻ Flux (mg m ⁻² h ⁻¹)	Soil Moisture (g g ⁻¹)	Soil Bulk Density (g cm ³)	Soil pH	Soil Total C (mg g ⁻¹)	Soil Total N (mg g ⁻¹)	Extractable Soil P (mg g ⁻¹)
19	Remnant Forest	48	5.61	2.41	0.45	0.89	5.2	29.13	2.45	0.032
19	SW - Dry	48	9.93	0.75	0.24	1.21	4.8	10.77	1.17	0.015
19	SW - Inundated	48	0.82	1.94	0.57	1.02	5.3	9.53	0.77	0.014
19	Tree Planting	48	2.25	1.92	0.37	1.04	5.3	18.28	1.37	0.016
20	Natural Regeneration	48	-24.51	-5.65	1.29	0.71	5.8	35.88	2.80	0.051
20	Tree Planting	48	-13.70	-1.67	0.37	0.90	5.6	18.92	1.54	0.027
21	Remnant Forest	48	-28.87	-0.64	0.32	1.11	5.6	10.35	0.95	0.048
21	SW - Dry	48	-41.77	0.93	0.52	0.73	5.6	27.50	2.55	0.049
22	Remnant Forest	48	-18.57	0.49	0.32	1.11	5.6	10.35	0.95	0.048

APPENDIX B: CHAPTER 3 DATA

Supplemental Table 1.3 Inundation frequency values (%) for all sites from Chapter One that were included in the analyses.

Site	Habitat	Inundation Frequency (%)
1	SW - Inundated	3
1	SW - Inundated	3
1	SW - Dry	3
1	SW - Inundated	3
1	SW - Inundated	3
1	SW - Inundated	3
1	SW - Inundated	3
1	SW - Inundated	3
1	SW - Inundated	3
1	SW - Inundated	3
1	Tree Planting	1
1	Tree Planting	1
1	Tree Planting	0
1	Tree Planting	0
1	Tree Planting	0
1	Tree Planting	1
1	Tree Planting	2

Supplemental Table 1.3 (Continued)

Site	Habitat	Inundation Frequency (%)
1	Tree Planting	1
1	Tree Planting	1
1	Tree Planting	0
1	Remnant Forest	0
1	Remnant Forest	0
1	Remnant Forest	0
1	Remnant Forest	0
1	Remnant Forest	0
1	Remnant Forest	0
1	Remnant Forest	0
1	Remnant Forest	0
1	Remnant Forest	0
1	Remnant Forest	0
4	SW - Inundated	5
4	SW - Dry	5
4	SW - Dry	5
4	SW - Inundated	5
4	SW - Dry	5
4	SW - Inundated	5
4	SW - Inundated	3
4	SW - Inundated	4

Supplemental Table 1.3 (Continued)

Site	Habitat	Inundation Frequency (%)
4	SW - Inundated	5
4	SW - Dry	6
4	Tree Planting	3
4	Tree Planting	3
4	Tree Planting	3
4	Tree Planting	3
4	Tree Planting	3
4	Tree Planting	3
4	Tree Planting	3
4	Tree Planting	3
4	Tree Planting	3
4	Tree Planting	3
4	Remnant Forest	0
4	Remnant Forest	0
4	Remnant Forest	0
4	Remnant Forest	0
4	Remnant Forest	0
4	Remnant Forest	0
4	Remnant Forest	0
4	Remnant Forest	0
4	Remnant Forest	0

Supplemental Table 1.3 (Continued)

Site	Habitat	Inundation Frequency (%)
4	Remnant Forest	0
5	SW - Inundated	10
5	SW - Inundated	10
5	SW - Inundated	10
5	SW - Dry	10
5	SW - Inundated	10
5	SW - Dry	10
5	Tree Planting	9
5	Tree Planting	9
5	Tree Planting	9
5	Tree Planting	9
5	Tree Planting	9
5	Tree Planting	9
5	Remnant Forest	1
5	Remnant Forest	1
5	Remnant Forest	1
5	Tree Planting	10
5	Tree Planting	9
5	Tree Planting	9
5	Tree Planting	9
5	Tree Planting	10

Supplemental Table 1.3 (Continued)

Site	Habitat	Inundation Frequency (%)
5	Tree Planting	9
5	SW - Inundated	2
5	SW - Inundated	1
5	SW - Inundated	1
5	SW - Inundated	2
5	SW - Dry	2
5	SW - Dry	6
5	Remnant Forest	0
5	Remnant Forest	2
5	Remnant Forest	0
5	SW - Dry	10
8	SW - Inundated	4
8	SW - Inundated	4
8	SW - Inundated	4
8	SW - Inundated	0
8	SW - Inundated	0
8	SW - Inundated	4
8	SW - Inundated	4
8	SW - Inundated	4
8	SW - Inundated	4
8	SW - Inundated	2

Supplemental Table 1.3 (Continued)

Site	Habitat	Inundation Frequency (%)
8	Natural	0
8	Regeneration	0
8	Natural	0
8	Regeneration	0
8	Natural	0
8	Regeneration	0
8	Natural	0
8	Regeneration	0
8	Natural	0
8	Regeneration	0
8	Natural	0
8	Regeneration	0
8	Natural	0
8	Regeneration	0
8	Natural	0
8	Regeneration	0

Supplemental Table 1.3 (Continued)

Site	Habitat	Inundation Frequency (%)
8	Natural	0
8	Regeneration	0
8	Natural	0
8	Regeneration	0
8	Natural	0
8	Regeneration	0
8	Natural	0
8	Regeneration	0
8	Natural	0
8	Regeneration	0
8	Natural	0
8	Regeneration	0
8	Natural	0
8	Regeneration	0
9	SW - Inundated	4

Supplemental Table 1.3 (Continued)

Site	Habitat	Inundation Frequency (%)
9	SW - Dry	4
9	SW - Dry	5
9	SW - Dry	5
9	SW - Dry	5
9	SW - Dry	4
9	SW - Inundated	4
9	SW - Inundated	5
9	SW - Inundated	5
9	SW - Inundated	5
9	SW - Inundated	4
9	SW - Inundated	6
9	SW - Inundated	4
9	SW - Dry	5
9	SW - Dry	4
9	SW - Inundated	0
9	SW - Inundated	5
9	SW - Dry	5
9	SW - Dry	5
9	SW - Dry	5
9	Remnant Forest	0
9	Remnant Forest	0

Supplemental Table 1.3 (Continued)

Site	Habitat	Inundation Frequency (%)
9	Remnant Forest	0
9	Remnant Forest	0
9	Remnant Forest	0
9	Remnant Forest	0
9	Remnant Forest	0
9	Remnant Forest	0
9	Remnant Forest	2
9	Remnant Forest	0
18	SW - Inundated	1
18	SW - Dry	0
18	SW - Inundated	0
18	SW - Dry	0
18	SW - Dry	0
18	Tree Planting	0
18	SW - Inundated	7
18	SW - Dry	7
18	SW - Dry	3
18	SW - Inundated	8
18	SW - Inundated	5
18	Tree Planting	0

Supplemental Table 1.3 (Continued)

Site	Habitat	Inundation Frequency (%)
18	Natural	3
18	Regeneration	1
18	Natural	3
18	Regeneration	0
18	Natural	3
18	Regeneration	0
18	Tree Planting	0
18	Natural	0
18	Regeneration	1
18	Natural	1
18	Regeneration	1
18	Natural	0
18	Regeneration	0

Supplemental Table 1.3 (Continued)

Site	Habitat	Inundation Frequency (%)
18	Tree Planting	0
18	Tree Planting	0
18	Tree Planting	0
18	Tree Planting	0
18	Tree Planting	0
18	Tree Planting	0
18	Tree Planting	0

APPENDIX C: CHAPTER 4 PHOTOS AND DATA



Supplemental Photo 1.4 Algal accretion among each vegetation type after four days of inundation during the nutrient dosing experiment.

Supplemental Table 1.4 Flux rates for all dissolved nutrient species (meso. = mesocosm).

Meso. ID	Vegetation	Hydroperiod	Nutrient Flux Rates (mg m ⁻² h ⁻¹)			
			NO ₃ ⁻ up to	PO ₄ ³⁻ up to	PO ₄ ³⁻ Days 2	DOC
			Day 4	24 h	- 5	
1	Tree Planting	3 Days	-205.0	-56.2	-6.7	55.5
2	Tree Planting	3 Days	-186.1	-60.8	-6.4	51.7
3	Bare Soil	3 Days	-230.7	-68.6	-1.5	148.1
4	Bare Soil	3 Days	-244.2	-69.8	-2.2	129.3
5	Bare Soil	3 Days	-227.5	-62.6	-2.0	177.0
6	Herbaceous Vegetation	3 Days	-206.9	-60.8	-3.3	52.9
7	Herbaceous Vegetation	3 Days	-174.8	-46.6	-2.4	45.5
8	Herbaceous Vegetation	3 Days	-189.2	-63.4	-0.5	84.8
9	Tree Planting	3 Days	-223.8	-63.3	-4.2	82.2
10	Herbaceous Vegetation	3 Weeks	-190.5	-54.6	-1.8	45.7
11	Tree Planting	3 Weeks	-194.2	-60.1	-0.8	127.3
12	Tree Planting	3 Weeks	-165.5	-44.7	-2.2	80.7

Supplemental Table 1.4 (Continued)

Meso. ID	Vegetation	Hydroperiod	Nutrient Flux Rates (mg m ⁻² h ⁻¹)			
			NO ₃ ⁻ up to Day 4	PO ₄ ³⁻ up to 24 h	PO ₄ ³⁻ Days 2 - 5	DOC
13	Bare Soil	3 Weeks	-152.9	-52.7	-0.8	143.2
14	Bare Soil	3 Weeks	-150.7	-50.6	-0.6	97.9
15	Tree Planting	3 Weeks	-200.3	-62.2	-2.2	95.7
16	Bare Soil	3 Weeks	-212.3	-70.3	-1.9	103.3
17	Herbaceous Vegetation	3 Weeks	-220.3	-53.3	-3.5	36.6
18	Herbaceous Vegetation	3 Weeks	-228.0	-33.6	-9.5	57.7
19	Herbaceous Vegetation	3 Days	-171.2	-46.7	-6.1	57.8
20	Bare Soil	3 Days	-152.7	-49.7	-2.1	45.4
21	Tree Planting	3 Days	-202.9	-52.8	-3.5	78.3
22	Herbaceous Vegetation	3 Days	-155.3	-40.2	-1.6	42.6
23	Herbaceous Vegetation	3 Days	-150.4	-40.1	-5.6	50.5
24	Tree Planting	3 Days	-177.4	-49.4	-3.5	66.6

Supplemental Table 1.4 (Continued)

Meso. ID	Vegetation	Hydroperiod	Nutrient Flux Rates (mg m ⁻² h ⁻¹)			
			NO ₃ ⁻ up to Day 4	PO ₄ ³⁻ up to 24 h	PO ₄ ³⁻ Days 2 - 5	DOC
25	Tree Planting	3 Days	-224.0	-60.4	-8.9	91.9
26	Bare Soil	3 Days	-183.9	-53.5	-1.7	144.7
27	Bare Soil	3 Days	-207.7	-55.7	-1.3	103.1
28	Herbaceous Vegetation	3 Weeks	-210.3	-49.9	-6.9	35.4
29	Tree Planting	3 Weeks	-170.4	-41.3	-1.2	71.0
31	Bare Soil	3 Weeks	-190.9	-62.3	-0.6	210.6
32	Bare Soil	3 Weeks	-173.0	-52.6	-1.0	104.4
33	Herbaceous Vegetation	3 Weeks	-218.9	-55.4	-14.8	47.1
34	Tree Planting	3 Weeks	-221.9	-58.5	NA	NA
35	Tree Planting	3 Weeks	-168.2	-42.6	-6.1	NA
36	Bare Soil	3 Weeks	-209.5	-53.9	NA	NA

Supplemental Table 2.4 Dissolved gas flux rates for each mesocosm.

Meso. ID	Vegetation	Hydroperiod	Flux Rates (mg m ⁻² h ⁻¹)											
			N ₂ 12 h	N ₂ 24 h	N ₂ 48 h	O ₂ 12 h	O ₂ 24 h	O ₂ 48 h	N ₂ O 12 h	N ₂ O 24 h	N ₂ O 48 h	CH ₄ 12 h	CH ₄ 24 h	CH ₄ 48 h
1	Tree Planting	3 Days	1.9	3.0	7.3	-20.4	-29.3	-72.7	0.459	0.019	-0.070	6.78E-03	8.61E-05	2.61E-02
2	Tree Planting	3 Days	1.6	2.9	5.8	-4.7	-16.0	-46.6	0.055	0.054	-0.099	3.10E-02	2.11E-02	3.37E-02
3	Bare Soil	3 Days	5.4	7.3	9.2	-22.3	-27.1	-65.0	1.210	-0.015	-0.127	2.02E-03	-7.20E-03	-9.44E-04
4	Bare Soil	3 Days	4.0	5.6	6.5	-17.0	-31.4	-54.1	0.023	0.004	-0.074	4.62E-03	1.16E-02	5.00E-02
5	Bare Soil	3 Days	3.2	3.9	5.2	-15.4	-26.8	-39.1	0.161	0.062	-0.081	-1.67E-02	-1.64E-05	-3.00E-03
6	Herbaceous Vegetation	3 Days	5.7	6.7	6.5	-41.5	-50.1	-81.8	0.044	0.062	-0.087	1.06E-02	5.33E-02	1.02E-01
7	Herbaceous Vegetation	3 Days	11.7	11.8	13.6	-57.8	-60.2	-97.3	0.285	0.244	0.027	1.81E-01	6.23E-01	2.03E+00

Supplemental Table 2.4 (Continued)

Meso. ID	Vegetation	Hydroperiod	Flux Rates (mg m ⁻² h ⁻¹)									CH ₄ 12 h	CH ₄ 24 h	CH ₄ 48 h
			N ₂ 12 h	N ₂ 24 h	N ₂ 48 h	O ₂ 12 h	O ₂ 24 h	O ₂ 48 h	N ₂ O 12 h	N ₂ O 24 h	N ₂ O 48 h			
8	Herbaceous Vegetation	3 Days	8.3	9.2	9.0	-53.9	-62.6	-81.3	0.043	-0.028	-0.001	6.76E-02	3.88E-01	1.53E+00
9	Tree Planting	3 Days	2.0	2.8	4.4	-9.4	-21.5	-52.3	0.073	-0.034	-0.124	1.02E-03	-3.06E-03	-2.32E-03
10	Herbaceous Vegetation	3 Weeks	4.6	6.0	6.8	-50.1	-57.9	-88.2	0.283	0.221	0.181	-2.48E-03	2.76E-02	7.60E-02
12	Tree Planting	3 Weeks	5.0	4.9	7.9	-16.5	-27.0	-56.5	0.471	0.229	0.031	7.31E-03	8.45E-03	1.51E-02
13	Bare Soil	3 Weeks	6.4	9.9	12.5	-18.5	-45.9	-97.7	0.096	0.224	0.258	4.16E-02	5.48E-02	7.46E-02
14	Bare Soil	3 Weeks	2.6	2.6	3.0	-13.2	-19.5	-33.1	0.123	0.011	-0.027	2.58E-02	3.88E-02	6.53E-02
15	Tree Planting	3 Weeks	3.6	5.7	7.8	-27.5	-30.4	-59.3	0.319	0.139	0.008	-1.23E-02	-6.75E-03	1.22E-02

Supplemental Table 2.4 (Continued)

Meso. ID	Vegetation	Hydroperiod	Flux Rates (mg m ⁻² h ⁻¹)											
			N ₂ 12 h	N ₂ 24 h	N ₂ 48 h	O ₂ 12 h	O ₂ 24 h	O ₂ 48 h	N ₂ O 12 h	N ₂ O 24 h	N ₂ O 48 h	CH ₄ 12 h	CH ₄ 24 h	CH ₄ 48 h
16	Bare Soil	3 Weeks	2.3	3.2	5.9	-14.8	-25.4	-48.2	0.086	0.084	-0.039	-9.38E-03	-4.78E-04	3.72E-03
17	Herbaceous Vegetation	3 Weeks	9.1	8.3	8.2	-58.4	-62.0	-89.4	0.103	0.037	0.034	-7.66E-03	1.50E-02	5.08E-02
18	Herbaceous Vegetation	3 Weeks	5.2	6.5	6.5	-33.3	-40.2	-54.2	0.442	0.310	0.072	1.35E-01	3.62E-01	4.96E-01
19	Herbaceous Vegetation	3 Days	2.0	4.8	4.9	-13.6	-27.4	-61.4	0.170	0.038	0.306	1.05E-03	-1.18E-03	-2.09E-02
20	Bare Soil	3 Days	2.7	3.3	3.7	-35.5	-38.1	-45.1	0.168	0.255	0.050	6.30E-04	-7.52E-03	1.05E-02
21	Tree Planting	3 Days	3.3	7.6	8.0	-16.7	-31.0	-67.9	0.184	0.138	0.258	1.82E-02	2.81E-02	3.77E-02
22	Herbaceous Vegetation	3 Days	6.7	7.5	7.5	-49.6	-61.1	-79.4	0.140	0.165	0.068	2.44E-02	2.04E-01	4.72E-01

Supplemental Table 2.4 (Continued)

Meso. ID	Vegetation	Hydroperiod	Flux Rates (mg m ⁻² h ⁻¹)											
			N ₂ 12 h	N ₂ 24 h	N ₂ 48 h	O ₂ 12 h	O ₂ 24 h	O ₂ 48 h	N ₂ O 12 h	N ₂ O 24 h	N ₂ O 48 h	CH ₄ 12 h	CH ₄ 24 h	CH ₄ 48 h
23	Herbaceous Vegetation	3 Days	3.9	4.2	5.0	-24.4	-34.0	-56.7	0.291	0.451	0.361	-2.38E-02	4.89E-03	-2.30E-02
24	Tree Planting	3 Days	1.8	6.4	8.2	-10.5	-39.1	-69.7	0.362	0.257	0.061	-7.25E-03	1.01E-02	3.26E-04
25	Tree Planting	3 Days	7.8	2.3	6.6	-9.2	-21.3	-50.5	- 0.039	0.024	0.022	4.42E-03	3.12E-02	5.94E-02
26	Bare Soil	3 Days	4.0	4.2	6.7	-19.2	-28.9	-55.2	0.359	0.246	-0.022	-1.85E-02	-3.26E-04	5.05E-03
27	Bare Soil	3 Days	3.7	4.5	6.9	-31.5	-34.4	-51.1	1.165	0.877	0.235	2.72E-02	8.36E-02	5.11E-02
28	Herbaceous Vegetation	3 Weeks	2.9	4.1	4.8	-26.6	-37.5	-50.8	0.213	0.135	0.023	-5.95E-03	2.44E-02	3.81E-02
29	Tree Planting	3 Weeks	3.4	4.5	6.0	-17.8	-27.4	-37.2	0.081	0.072	-0.063	-4.34E-03	-3.51E-03	-9.76E-03

Supplemental Table 2.4 (Continued)

Meso. ID	Vegetation	Hydroperiod	Flux Rates (mg m ⁻² h ⁻¹)											
			N ₂ 12 h	N ₂ 24 h	N ₂ 48 h	O ₂ 12 h	O ₂ 24 h	O ₂ 48 h	N ₂ O 12 h	N ₂ O 24 h	N ₂ O 48 h	CH ₄ 12 h	CH ₄ 24 h	CH ₄ 48 h
30	Herbaceous Vegetation	3 Weeks	6.0	5.6	11.0	-43.9	-47.1	-44.6	0.080	0.012	0.068	-2.28E-03	4.69E-02	2.84E-01
31	Bare Soil	3 Weeks	2.8	2.6	6.2	-5.6	-14.4	-41.9	0.108	0.026	-0.112	-2.69E-03	6.07E-04	-5.19E-03
32	Bare Soil	3 Weeks	3.9	7.5	10.8	-14.5	-33.6	-71.6	0.073	0.089	-0.085	9.31E-05	3.32E-03	1.01E-02
33	Herbaceous Vegetation	3 Weeks	NA	4.1	5.5	NA	-36.5	-78.6	NA	0.093	-0.003	NA	-1.88E-02	1.95E-02
34	Tree Planting	3 Weeks	1.7	2.9	6.1	-14.6	-26.5	-44.9	0.262	0.557	0.165	-9.33E-03	1.38E-03	-1.23E-04
35	Tree Planting	3 Weeks	2.3	2.4	3.5	-16.7	-18.9	-37.5	0.346	0.255	0.002	2.66E-03	-2.89E-03	1.65E-02
36	Bare Soil	3 Weeks	2.9	4.1	5.6	-15.7	-26.2	-45.5	0.135	0.100	-0.120	8.76E-03	1.46E-02	2.18E-02

Supplemental Table 3.4 Soil nutrient content, chl-*a*, and AFDM data before and after dosing with N and P enriched water.

		Meso.	Pre-dosing Data			Post-dosing Data				
			TC	TN	Extract. P	TC	TN	Extract. P	Chl- <i>a</i>	AFDM
Vegetation	Hydroperiod	I.D.	(mg g ⁻¹)	(mg g ¹)	(mg g ⁻¹)	(mg g ⁻¹)	(mg g ⁻¹)	(mg g ⁻¹)	(mg m ⁻²)	(mg g ⁻¹)
Tree Planting	3-Days	1	5.3	0.5	0.02	5.5	0.9	0.01	124	30
Tree Planting	3-Days	2	5.9	0.5	0.02	5.8	0.9	0.02	16	31
Bare Soil	3-Days	3	6.9	0.6	0.02	7.1	0.9	0.02	129	30
Bare Soil	3-Days	4	7.6	0.6	0.02	NA	NA	NA	NA	NA
Bare Soil	3-Days	5	5.3	0.5	0.01	6.5	0.9	0.01	274	31
Herbaceous Vegetation	3-Days	6	9.3	0.8	0.02	10.2	1.1	0.02	59	35
Herbaceous Vegetation	3-Days	7	10.1	0.8	0.02	6.7	1	0.01	10	32

Supplemental Table 3.4 (Continued)

		Meso.	Pre-dosing Data			Post-dosing Data				
			TC	TN	Extrac. P	TC	TN	Extract. P	Chl- <i>a</i>	AFDM
Vegetation	Hydroperiod	I.D.	(mg g ⁻¹)	(mg g ¹)	(mg g ⁻¹)	(mg g ⁻¹)	(mg g ⁻¹)	(mg g ⁻¹)	(mg m ⁻²)	(mg g ⁻¹)
Herbaceous Vegetation	3-Days	8	7.9	0.6	0.01	7.1	0.9	0.01	51	33
Tree Planting	3-Days	9	5.7	0.5	0.02	6	0.8	0.02	44	30
Herbaceous Vegetation	3-weeks	10	7.2	0.6	0.02	6.5	0.9	0.02	26	29
Tree Planting	3-weeks	11	7.2	0.6	0.01	7.1	1	0.02	20	32
Tree Planting	3-weeks	12	6.7	0.6	0.01	6.5	1	0.01	20	31
Bare Soil	3-weeks	13	6.5	0.5	0.02	8.1	1	0.02	27	33
Bare Soil	3-weeks	14	6.7	0.6	0.01	7.6	0.9	0.01	22	29
Tree Planting	3-weeks	15	8.6	0.7	0.02	8.1	1	0.02	24	32
Bare Soil	3-weeks	16	7.8	0.7	0.01	7.9	1	0.01	23	35

Supplemental Table 3.4 (Continued)

		Meso.	Pre-dosing Data			Post-dosing Data				
			TC	TN	Extrac. P	TC	TN	Extract. P	Chl- <i>a</i>	AFDM
Vegetation	Hydroperiod	I.D.	(mg g⁻¹)	(mg g¹)	(mg g⁻¹)	(mg g⁻¹)	(mg g⁻¹)	(mg g⁻¹)	(mg m⁻²)	(mg g⁻¹)
Herbaceous Vegetation	3-weeks	17	9.8	0.8	0.02	7.7	1.1	0.02	22	30
Herbaceous Vegetation	3-weeks	18	10.2	0.7	0.02	6.8	0.9	0.02	16	31
Herbaceous Vegetation	3-Days	19	8.6	0.7	0.02	7.1	1	0.02	91	28
Bare Soil	3-Days	20	6.3	0.6	0.02	6.4	0.8	0.02	30	27
Tree Planting	3-Days	21	7	0.6	0.02	5.2	0.7	0.01	87	25
Herbaceous Vegetation	3-Days	22	6.6	0.6	0.02	7.9	0.8	0.02	44	25
Herbaceous Vegetation	3-Days	23	9	0.7	0.01	7	1	0.02	32	28
Tree Planting	3-Days	24	7.1	0.6	0.01	6.4	0.8	0.01	129	31

Supplemental Table 3.4 (Continued)

			Pre-dosing Data			Post-dosing Data				
			TC	TN	Extrac. P	TC	TN	Extract. P	Chl- <i>a</i>	AFDM
Vegetation	Hydroperiod	Meso. I.D.	(mg g⁻¹)	(mg g¹)	(mg g⁻¹)	(mg g⁻¹)	(mg g⁻¹)	(mg g⁻¹)	(mg m⁻²)	(mg g⁻¹)
Tree Planting	3-Days	25	7.4	0.7	0.02	7.7	0.9	0.02	78	29
Bare Soil	3-Days	26	5.8	0.6	0.02	5.5	0.8	0.02	46	31
Bare Soil	3-Days	27	5.7	0.5	0.01	6.3	0.8	0.02	115	30
Herbaceous Vegetation	3-weeks	28	8.4	0.7	0.01	8.6	0.9	0.01	13	32
Tree Planting	3-weeks	29	7.9	0.6	0.01	6.7	0.9	0.02	12	26
Herbaceous Vegetation	3-weeks	30	6.8	0.6	0.02	6.3	0.9	0.02	2	30
Bare Soil	3-weeks	31	6	0.5	0.02	5.1	0.9	0.02	8	31
Bare Soil	3-weeks	32	7.5	0.6	0.01	6	1	0.02	6	30

Supplemental Table 3.4 (Continued)

			Pre-dosing Data			Post-dosing Data				
			TC	TN	Extrac. P	TC	TN	Extract. P	Chl- <i>a</i>	AFDM
Vegetation	Hydroperiod	Meso. I.D.	(mg g⁻¹)	(mg g¹)	(mg g⁻¹)	(mg g⁻¹)	(mg g⁻¹)	(mg g⁻¹)	(mg m⁻²)	(mg g⁻¹)
Herbaceous Vegetation	3-weeks	33	5.8	0.5	0.01	6	0.7	0.02	5	24
Tree Planting	3-weeks	34	6	0.6	0.02	5.8	0.8	0.01	7	26
Tree Planting	3-weeks	35	5.8	0.5	0.01	4.5	0.7	0.01	21	26
Bare Soil	3-weeks	36	6.5	0.6	0.01	5.8	0.9	0.01	30	28

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