Agricultural Wetland Restoration: The Role of Sediment Removal, Hydroperiod and Time on Restoration Outcomes

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Dedication

Gale Murray (Southworth) Winikoff
(July 28, 1952 – July 15, 2015)

Mom, I still think about you every day. I cherish the moments when I can feel your presence in the birdsong of the prairie.
I will never forget you.

Abstract

Restoring agricultural wetlands to remediate nutrient runoff, decrease flood risk, and improve wildlife habitat are areas of growing interest. One restoration strategy that may improve species diversity, enhance water retention, and decrease nutrient availability is the removal of accumulated eroded sediment from agricultural wetlands prior to restoration. In this work, we the measured physical and chemical characteristics of soils, characterized plant communities, and examined water column nutrient availability and denitrification potential in 54 restored agricultural wetlands in west central Minnesota. In half of the wetlands hydrologic function was restored by removing and plugging drainage tile and ditches, while hydrology was restored in the remaining basins following sediment removal (Excavation treatment), increasing basin depth by an average 30 cm. Excavation primarily influenced the plant community, by delaying the establishment of two invasive emergent macrophytes, hybrid cattail (*Typha* x *glauca*) and reed canary grass (*Phalaris arundinacea*), but the affect only lasted for 6 years. Contrary to expectations, soil properties, water column dissolved nutrients, and denitrification potential were all primarily influenced by hydroperiod – the number of consecutive days with standing water. Wetlands with longer hydroperiods had less bioavailable P in soils, lower dissolved N and P concentrations, and lower denitrification potential. We also found evidence that vegetation likely plays an important role in dissolved nutrient dynamics over time. Our results suggest that excavation may be an important tool in wetland restoration but its influence was lost as wetlands aged in the absence of invasive species management. Moreover, nitrogen and phosphorus dynamics were almost universally controlled by hydroperiod, with tradeoffs between nitrogen removal and phosphorus remineralization.

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1. Introduction

Twelve thousand years ago Minnesota was covered by a glacier that was no less than 130 meters thick (Brevik 2000). Today, we recognize that glacier as the Des Moines Lobe of the Laurentide Ice Sheet, and it would be the last in a series of glacial advances over the course of the Wisconsin Age, which began 75,000 years ago (Leverett & Sardeson 1932; Kemmis 1991; Jennings & Johnson 2011). As the glacier melted, it deposited crushed bedrock and earth that was carried by the ice sheet as it expanded, contracted, and slid across the landscape (Moran et al. 1980; Clayton & Moran 1982; Evans 2009). The ecosystem that arose from the melted ice was dotted with small depressional wetlands that broke apart the seemingly endless sea of tall grass prairie (Winsor 1987). Today, we call this 777,000 km^2 (77.7 million ha) area the Prairie Pothole Region (PPR), and it stretches from northcentral Iowa and western Minnesota in the United States to central Alberta in Canada (Smith et al. 1964).

Characterizing Prairie Pothole Wetlands

Approximately half of the PPR resides within the geopolitical borders of the United States, wherein 71% of the land area is used for row crop agriculture (Dahl 2014). The size of individual wetlands and the density of basins was historically a function of antecedent moisture and is thus extremely variable in space and time (Niemuth et al. 2010; Vanderhoof et al. 2016). For example, in parts of Saskatchewan, basin densities were as high as 40 basins · km^{-2} in wet years and as low as 1 basin · km^{-2} during periods of drought (Smith et al. 1964). However, on average 16 to 18% of land area in the PPR was wetland prior to European settlement in the mid 1800's (Dahl 2014). Across the PPR approximately 63% of wetlands have been drained for cultivation (Dahl 2014; Gleason et al. 2008). In Minnesota, more than 80% of the state's 2.8 million ha of prairie wetlands have been drained for agriculture, leaving the state with less than 567,000 ha of remaining wetland (Redelfs 1983). By comparison, North and South Dakota historically had a combined 7.6 million ha of wetlands with approximately 40.5% of wetland area being lost, while Iowa lost 99% of the 1.4 million ha it once had (Redelfs 1983; Dahl 2014). Despite huge losses, wetlands continue to be drained, with annual loses of approximately 0.3% of the remaining basins per year (Johnston 2013).

The vast majority of prairie potholes are considered depressional wetlands and are thus largely characterized by their hydroperiod – the number of consecutive days with standing water. The word "depression" is used to describe where water collects on the landscape, in topographic lows or hallows without a stream or river connecting basins to one another. Because depressional wetlands are not connected by surficial flow, they are sometimes called "geographically isolated", however that description is inaccurate (Mushet et al. 2015; Daniel L McLaughlin et al. 2014). Depressional wetlands exchange water and nutrients between themselves and downgradient systems through seasonal migrations of animals and insects (Leibowitz 2003; Cohen et al. 2016; Leibowitz et al. 2018; Lane et al. 2018), groundwater exchange between basins (Daniel L McLaughlin et al. 2014; Evenson et al. 2018; Golden et al. 2016; Rains et al. 2016), and intermittent surficial connections via spill-and-fill mechanisms (Leibowitz et al. 2003, 2016; Vanderhoof et al. 2016). Furthermore, the presence of depressional wetlands on the landscape protects downgradient stream and river networks by processing and removing dissolved nutrients (Marton et al. 2015; Golden et al. 2017).

Since prairie pothole wetlands are not naturally connected by streams, the majority of basins dry out at some point during the growing season, though the duration of this drawdown is extremely variable between basins and years, lasting a few days or weeks up to several months. Temporary wetlands are among the most numerous wetland types of the prairie pothole region, including approximately 50% of all wetted basins (Dahl 2014). These temporary basins have a very short hydroperiod, holding water for two to four weeks following spring snow melt or large precipitation events. By comparison, wetlands with seasonal hydroperiod retain water for a month or longer, drying out sometime in late July or August and begin to refill sometime in the fall. Seasonal wetlands are the second most abundant wetland type in the PPR, constituting nearly 42% of basins (Dahl 2014). Depressional wetlands with a prolonged hydroperiod are often referred to as semipermanent basins, because they have a persistent pool of water throughout the growing season in most years. However, semipermanent wetlands can dry out enough to expose mudflats during periods of extreme or prolonged drought (Cowardin et al. 1979; Stewart & Kantrud 1971).

Although temporary and seasonal wetlands are generally considered important areas of groundwater recharge, all three hydroperiods support stable base flows in stream and river networks while protecting against downgradient flooding (Daniel L McLaughlin et al. 2014; Evenson et al. 2018; Golden et al. 2016; Rains et al. 2016). In addition, depressional wetlands contribute to deep groundwater aquifers that provide potable water (van der Kamp & Hayashi 2009). Modest estimates of infiltration into the deep aquifer indicate approximately 20 $mm \cdot yr^{-1}$ of groundwater recharge within depressional wetlands or 2 $mm \cdot yr^{-1}$ across a typical catchment (Hayashi et al. 1998). Assuming a standard wetland area of 1 ha (2.5 acre), then a typical wetland can contribute 200 m^3 of water per year to the deep groundwater supply. Assuming a typical human consumes 3.7 $L \cdot d^{-1}$ of water (1.4 $m^3 \cdot yr^{-1}$) in food and drink (Sawka et al. 2005), then a 1 ha wetland can support the dietary water needs of approximately 143 people. However, people also use potable water for bathing (49.7 $L \cdot d^{-1}$), cleaning cookware, and washing hands (29.2 $L \cdot d^{-1}$, combined) (Willis et al. 2013). Assuming an additional 78.9 $L \cdot d^{-1}$ (28.8 $m^3 \cdot yr^{-1}$) of per capita potable water use, then a 1 ha depressional wetland can support the groundwater recharge necessary to meet the potable water needs of 6.6 people, representing a substantial groundwater recharge service.

The Song of the Prairie

The PPR is sometimes called the “duck factory”, because the region is responsible for more than 50% of North American waterfowl recruitment in an average year but it comprises just 10% of the waterfowl breeding area (Smith et al. 1964). The most common waterfowl species on the prairie are mallards (*Anas platyrhynchos*), northern pintail (*Anas acuta*), blue-winged teal (*Spatula discors*), green-winged teal (*Anas crecca*), northern shoveler (*Spatula clypeata*), Gadwall (*Mareca strepera*), American wigeon (*Mareca americana*), ring-necked duck (*Aythya collaris*), redhead (*Aythya americana*), canvas-back (*Aythya valisineria*), lesser scaup (*Aythya affinis*), ruddy duck (*Oxyura jamaicensis*), common goldeneye (*Bucephala clangula*), and bufflehead (*Bucephala albeola*) (Smith et al. 1964; Stewart & Kantrud 1974). Trumpeter swans (*Cygnus buccinator*) also breed in prairie potholes, though they are very territorial and guard areas of up to 40 ha (100 acre), so sighting a breeding pair is special and fairly rare (Galatowitsch & van der Valk 1994). While temporary, seasonal, and semipermanent wetlands all provide important habitat for waterfowl, it appears that each type of basin may fulfill specific requirements of several species at different points throughout the year (Kantrud & Stewart 1977; Stewart & Kantrud 1973). Temporary and seasonal wetlands thaw earlier in the spring than semipermanent basins and provide critical food resources including benthic invertebrates to migrating waterfowl (Smith et al. 1964; Kantrud et al. 1989). As deeper basins thaw, differences in plant communities at seasonal and semipermanent basins grow increasingly important. Seeds and tubers of various species of macrophyte become nutritious food resources to waterfowl while other plants provide cover for offspring and adults alike. In late summer and early fall, the presence of standing water on semipermanent basins ensures food resources and emergent macrophytes provide cover for waterfowl as they prepare for another migration (Smith et al. 1964).

Waterfowl are not the only group of birds that utilize prairie wetlands. Some songbirds that breed in and around wetlands include yellow-headed blackbirds (*Xanthocephalus xanthocephalus*), red-winged blackbirds (*Agelaius phoeniceus*), marsh wrens (*Cistothorus palustris*), and the common yellowthroat (*Geothlypis trichas*), which eat aquatic insects such as dragonflies and damselflies. In addition, it is not uncommon to find the bobolink (*Dolichonyx oryzivorus*) in grasslands surrounding prairie wetlands, which is often first recognized because of its distinctive call that is often described as metallic. The more secretive rails including the *Virginia Rail (Rallus limicola*) and Sora (*Porzana carolina*) can be found foraging for variety of wetland plant seeds as well as invertebrates in and around wetlands. These rails are masters of disguise and are more often heard rather than seen. A less elusive and larger member of the rail family that is often spotted in prairie pothole wetlands is the American coot (*Fulica americana*), which is commonly found floating with waterfowl in open pools of semipermanent wetlands.

Some of the largest birds to utilize prairie wetland habitat are the cranes and herons. Sandhill cranes (*Grus canadensis*) are among the most iconic birds on the prairie, but they rely upon small, densely vegetated wetlands for nesting material, cover, and food. Their nests are made of sedges and emergent macrophytes including bulrushes, bur reeds, and cattail. They may build their nests in the wetland itself or in nearby uplands, but the building materials come from the wetland. The cranes also feed in wetlands, consuming a fully omnivorous diet of everything from seeds and tubers to amphibians and reptiles. Among the herons, the least bittern (*Ixobrychus exilis*), American bittern (*Botaurus lentiginosus*), and great egret (*Ardea alba*) are the most numerous in the PPR. The American bittern can be difficult to spot and is likely to be recognized by its distinctive deeply resonant call before it is seen. It builds its nest of cattails, bulrushes, and sedges, forming a platform in densely vegetated shallow water and their preferred foods include some of the most voracious predatory aquatic insect including dragonflies, water beetles, giant water bugs, and water scorpions. Unlike American bitterns, great egrets nest in trees which were historically fairly uncommon in the PPR. These birds will often form fairly large colonies in and around trees surrounded by ponded water, and are often founded stalking aquatic invertebrates and amphibians near the edge of emergent vegetation, where it gives way to an open pool of water.

Some of the less widely known groups of birds in prairie wetlands prefer semipermanent and permanent wetlands, and include grebes and terns. The eared grebe (*Podiceps nigricollis*) prefers deeper patches of emergent vegetation to support their nesting platform, while the pied-billed grebe (*Podilymbus Podiceps*) favors floating nests constructed of cattails, pondweeds, and bulrushes which they build within the emergent macrophyte zone of deeper wetlands. The pied-billed grebe has a particularly varied diet of wetland organisms including dragonfly nymphs, aquatic beetles, snails, leeches, frogs, salamanders, tadpoles and small fish. The black tern (*Childonias niger*) is an exceptionally interesting and uncommon species that nests in prairie wetlands. Although they are often found nesting well away from cover atop muskrat huts, they can build simple nesting platforms within the emergent macrophyte zone of semipermanent wetlands (personal observation). Black terns fly above wetlands searching for prey including amphibians, spiders, dragonflies, damselflies, mayflies, caddisflies, and beetles, which they catch on the wing. However, much of their preferred breeding habitat in the PPR has been eradicated and thus their numbers have been declining for some time.

Amphibian and Floral Diversity

The remarkable diversity of prairie wetland birds is sustained, in large part, by the high productivity of aquatic invertebrates in depressional wetlands and the amphibians that feed on them. Leopard frogs (*Lithobates pipiens*), wood frogs (*Lithobates sylvaticus*), western chorus frogs (*Pseudacris maculata*), gray tree frogs (*Hyla veriscolor*), and Canadian toads (*Anaxyrus hemiophrys*) are regular inhabitants of temporary, seasonal, and semipermanent wetlands alike. Each species has slightly different habitat preferences. The gray tree frog and wood frog are less common in prairie wetlands because, as their names suggest, they like to be near forest. However, wind breaks planted near homesteads and sandbar willow near wetland edges appear to provide some degree of cover for both species (personal observation). Leopard frogs and chorus frogs prefer shallower and more ephemeral types of wetlands or the wet edges of more permanent basins. Unfortunately, the Minnesota Department of Natural Resources has noted that leopard frog populations have been in a state of decline for over 50 years, due to pollution, pesticides, and habitat destruction. Perhaps the most iconic amphibian of the prairie is the tiger salamander (*Ambystoma tigrinum*), which can only occupy fishless prairie pothole wetlands.

The diversity of animals in the prairie pothole region is made possible by the rich plant communities that provide food, shelter, and building materials to everything from invertebrates to sandhill cranes. Wetland drainage, changes in nutrient availability, deposition of eroded sediment, increasing pesticide use, and the introduction of invasive species have shaped the prairie wetlands we see today. Once rare or absent in prairie wetlands, today hybrid cattail (*Typha* x *glauca*) and reed canary grass (*Phalaris arundinaceae*) are almost ubiquitous throughout the region (Galatowitsch & van der Valk 1994). Drainage of temporary wetlands and the incursion of row crop agriculture into the wet meadow of remaining seasonal and semipermanent basins are responsible for huge diversity losses among sedges and forbs in prairie wetlands. Understanding the progression of events that has led to this loss of vegetative diversity provides valuable context for why wetland restoration is such a high priority today and should remain a high priority well into the future.

European Immigration

The American ethos towards wetlands can be traced back to 1763 when George Washington helped to survey the Dismal Swamp of North Carolina and Virginia in the hopes of building a canal for inland transportation (Wooten & Jones 1955). Before the turn of the century, the canal was built and it would take nearly 200 years to begin the restoration of just 107,000 acres of the swamp that once covered over 1 million acres. However, it wasn't until the Swamp Lands Acts of 1849, 1850, and 1860 that the United States government formally endorsed widespread swamp land "reclamation" (Dahl & Allord 1996). The Swamp Lands Acts were designed to quickly expand westward and tame large portions of the great plains by transferring nearly 65 million acres of wetland to 15 states, including Iowa and Minnesota, with the condition that the land be drained for agricultural use (Wooten & Jones 1955). From the perspective of state and federal government, drainage made wasteland into productive agricultural land. For the public, drainage saved lives that would have otherwise been lost to the noxious swamp gases that gave rise to malaria (Winsor 1987). While we now know that malaria is spread through mosquito vectors, it is true that malaria was a serious concern for early settlers in the upper Midwest. For example, in Illinois nearly 30 deaths per 100,000 were linked to malaria between 1870 and 1880. By 1890 widespread wetland drainage decreased that malaria related deaths by two thirds, to 11 deaths per 100,000 (Winsor 1987). Cultural perception of wetlands as wasted space capable of killing loved ones cemented public opinion that wetlands should be villainized. Federal government did nothing to moderate those beliefs, leaving the Swamp Lands Acts as the only formal U.S. policy with regard to the value of wetlands for more than 70 years (Wooten & Jones 1955).

Early wetland drainage was conducted primarily by hand by digging artificial ditches from wet depressions to larger ditches, streams, or rivers. While surface ditches were easier and cheaper to dig, subsurface drainage was preferrable because it required less maintenance and did not remove any land from cultivation. Tile drain quickly gained traction in the Americas following its introduction in 1835 by Scottish farmer John Johnson (Robortella 2015; Smith et al. 1964), though it had been used since the 1700’s in Europe (Yannopoulos et al. 2020). The original tile drain was made of perforated clay shaped into half-cylinders, was buried a few feet beneath the soil surface, and acted as a conduit for water. Over time, the horseshoe shaped tile drain would be replaced by ceramic or cement cylinders and more recently these have been replaced by flexible perforated plastic pipe (Yannopoulos et al. 2020).

The pace of wetland drainage accelerated rapidly in the early 1900’s thanks in part to technological advances and recognition by states across the Midwest that drainage was too expensive to be implemented by individual landowners. In response, states across the American Midwest formalized cost-sharing programs in the second half of the 19th century to aid in drainage efforts (McCorvie & Lant 1993). Although bulky steam powered dredges were in operation in the late 1800’s, it was the advent of steam powered excavators in 1906 that made it easier to dig bigger and deeper drainage ditches and simplified tile drain installation. Rising demand for agricultural commodities and above-average precipitation fueled the expansion of drainage through 1929 (Wooten & Jones 1955; McCorvie & Lant 1993). The dust bowl and great depression decreased the rate of drainage between 1930 and 1939, but demand for agricultural goods rose once more during the war years and the pace of drainage followed shortly thereafter (Wooten & Jones 1955).

Recognizing Lost Ecosystem Services

By 1950, a publicly subsidized network of over 155,000 miles of ditches drained over 103 million acres of the American Midwest (Wooten & Jones 1955) with an additional 39 million acres of drainage bankrolled by individual landowners (McCorvie & Lant 1993), but warning signs had been emerging for decades, signaling lost ecosystem services from the implementation of widespread drainage (Galatowitsch & van der Valk 1994). Across the Mississippi

River Valley, rapid drainage and development in the 1800's resulted in increasingly catastrophic floods throughout the 1900's, sometimes at the cost of hundreds of human lives (Changnon 1998). In Iowa, naturalists and hunters noted the spread of invasive narrowleaf cattail (*Typha angustifolia*), disappearance of native forbs and grasses, and distressingly rapid reductions in waterfowl populations throughout the 1930's (Galatowitsch & van der Valk 1994).

In 1945, multiple reports of methemoglobinemia (blue baby syndrome) in infants fed formula prepared with well water that had abnormally high nitrate concentrations (90 to 140 mg NO_3-N · L^{-1}) raised alarm in the medical community (Comly 1945; Fossen Johnson 2019). Subsequent investigation of well water in Iowa revealed alarmingly high nitrate concentrations in some portions of the state (Comly 1945). Between 1905 and 1955, the concentrations of nitrates in the Iowa and Cedar Rivers had tripled and concentrations in the Des Moines River were 22 mg NO_3-N · L^{-1} (Hershey 1955). It is worth noting that by modern standards these nitrate concentrations are considered unsafe, as they exceed the safe drinking water limit of 10 mg NO_3-N · L^{-1} established by the EPA. While there is some debate about whether the use of inorganic fertilizers was to blame for nitrate pollution in well water, reports of contaminated wells preceded the widespread use of nitrogenous fertilizer, suggesting that land use practices were largely responsible. The most pervasive changes to land use in the first half of the 20th century were the massive wetland drainage campaigns that left Iowa with less than 95% of its original wetlands. More recently, evidence suggests that restoring drained wetlands in the PPR and the Upper Mississippi River Valley could reduce the size and duration of the Gulf of Mexico hypoxic zone (Goolsby 2000; Rabalais et al. 2002; Turner & Rabalais 1994; Turner et al. 2008; Rabalais et al. 2007) by decreasing nitrogen loading in the Mississippi River Basin (Mitsch et al. 2001; Hey 2002).

Recognition that wetlands needed to be restored came early to sportsmen and naturalists, but public opinion has been slow to change and many still see wetlands as impediments to cultivation. Early efforts to restore wetlands in the PPR included the establishment of the Federal Duck Stamp (Pittman-Robertson Act of 1937), which uses money from the sales of waterfowl hunting licenses (duck stamps) to acquire and restore waterfowl habitat. Throughout the 1900’s, a series of flood control acts at least recognized the growing problem of widespread flooding across the Mississippi River Valley (Changnon 1998; Shine & de Klemm 1999), though it is the opinion of many that the federal government invested too heavily and for too long in failing flood control systems. Billions of dollars were spent on levees, dams, and reservoir construction between 1850 and 1950, but floods continued to plague the Midwest (Changnon 1998). Finally, in the 1970’s the adoption of the Water Pollution Control Act (1972) and the Clean Water Act (1977) openly acknowledged the value of healthy aquatic ecosystems and vaguely recognized that wetlands provide important ecosystem services (CWA Section 404), though congress refused to define what constitutes a wetland (Shine & de Klemm 1999).

Paradoxically, despite the preponderance of evidence that wetland drainage had resulted in lost ecosystem services, the U.S. Department of Agriculture continued to subsidize wetland drainage throughout the 1970’s, first through the Agricultural Stabilization and Conservation Service, then through the Soil Conservation Service (McCorvie & Lant 1993). Finally, the Food Security Act of 1985 included the so-called Swampbuster provision, which was targeted at wetland conservation and established the Conservation Reserve Program (CRP) with the goal of soil conservation and habitat restoration (Reynolds et al. 2006). Later, the adoption of the “no net loss” policy of wetland management in the 1990’s secured some protections over wetlands (McCorvie & Lant 1993). Despite substantial advances throughout the second half of the 20th century and growing recognition that wetlands provide essential ecosystem services, a recent Supreme Court decision (Solid Waste Agency of Northern Cook County (SWANCC) v. United States, 2001) suggest that protections provisioned under the Clean Water Act do not extend to depressional wetlands (Dahl 2014; Johnston 2013; van der Valk & Pederson 2003).

Although the implementation of the CRP has restored millions of acres of habitat, including wetlands, with strong indications of recovery in waterfowl productivity (Kantrud 1993; Reynolds et al. 2006) and water quality improvements (Gleason et al. 2011, 2008), there is still a net loss of wetlands every year (Johnston 2013). Moving forward we need to continue to put a strong emphasis on restoration, which is the best solution to habitat loss, flood mitigation (Golden et al. 2016; Leibowitz et al. 2018), and mounting nutrient pollution in groundwater (Rupert 2008) and surface water (McLellan et al. 2015; Hansen et al. 2018; Johnston 1991a; Brunet 2011). In order to get the most out of each restoration it is important that we identify restoration practices that restore as many ecosystem services as possible.

Dissertation Goals

Drained and cultivated depressional wetlands capture the eroded topsoil from the surrounding landscape (hereafter, sediment). After years of cultivation, these depressions may collect anywhere between 15 cm to 2 m of sediment (Shawn Papon, personal communication). The question for land managers is whether sediment removal improves the outcome of wetland restoration or not. The work presented in this dissertation compares two common wetland restoration practices; 1) restoring hydrology and retaining accumulated sediment (Business As Usual, BAU), and 2) restoring hydrology following sediment removal (Excavation, EXC). Because the goals of wetland restoration can be simplified to include restoring wildlife habitat, water storage, water quality improvement, and nutrient removal, we can simplify our assessments to include plant diversity and community composition, soil development, dissolved nutrient analysis, and permanent nitrogen removal (denitrification) potential. Working in partnership with the United States Fish and Wildlife Service Private Lands Office, I followed 54 restored prairie pothole wetlands for four years, between 2016 and 2019.

In **Chapter 2**, I explored how sediment excavation influenced the plant community. The presence of standing water and rapid establishment of wet prairie, sedge, and shallow marsh plants confirmed that restored wetlands performed water retention services. To that end, the presence of obligate wetland plants differentiated wetlands with seasonal and semipermanent hydroperiods. Sediment excavation initially reduced the cover of invasive emergent macrophytes, but over time BAU and EXC plant communities converged (Winikoff et al. 2020).

In **Chapter 3**, I examined whether sediment excavation had a meaningful impact on soil nutrient content and bulk density. Although sediment removal initially increased soil bulk density, the compaction was temporary. Likewise, initial small reductions in soil carbon and nitrogen were short lived. However, all cultivated wetlands had soils that were significantly higher density, depleted of carbon and nitrogen, and with substantially more bioavailable phosphorus when compared with undrained wetland soils. This suggests that sediment removal did very little to change soil properties, but drainage and cultivation changed soils considerably. Furthermore, basins with semipermanent wetland hydroperiod had significantly less soil bioavailable phosphorus, indicating the importance of hydroperiod.

In **Chapter 4**, I assessed how excavation and hydroperiod influence water column dissolved nutrient availability over time. I found that the best predictor of water quality was wetland hydroperiod, with lower dissolved nutrient concentrations in semipermanent compared to seasonal wetlands. In contrast, the excavation effect appeared to have been mediated through the establishment and spread of invasive species within seasonal wetlands.

In **Chapter 5**, I quantified the ability of restored wetlands to permanently remove nitrogen. I examined whether denitrification potential changes as restored wetlands age, quantified differences between wetlands with seasonal and semipermanent hydroperiod, and assessed the effect of sediment excavation. Regardless of sediment presence or absence and wetland age, basins with seasonal hydroperiod had higher denitrification potentials than basins with semipermanent hydroperiod. However, the relative absence of dissolved nitrate in semipermanent wetlands indicates that semipermanent basins are fully capable of processing the nitrogen that they receive.

In **Chapter 6**, I relate my findings to the conceptual framework that has emerged from the application of sediment excavation in wetland restoration and I explore how my results can be integrated into present and future management decisions.

2. Vegetation trajectories of restored agricultural wetlands following sediment removal

Abstract

Recognition of wetland ecosystem services has led to substantial investment in wetland restoration in recent decades. Wetland restorations can be designed to meet numerous goals, among which re-establishing a diverse native wetland plant community is a common aim. In agricultural areas, where previously drained wetland basins can fill with eroded sediment from the surrounding landscape, restoration often includes excavation to expose buried seed banks. The extent to which excavation improves the diversity of wetland plant communities is unclear, particularly in terms of longer-term outcomes. We examined plant species diversity and community composition in 24 restored agricultural wetlands across west-central Minnesota, USA. In all study wetlands, hydrology was restored by removing subsurface drainage and plugging drainage ditches, thus re-establishing groundwater connectivity and hydroperiod ("Business As Usual" treatment). In half of the wetlands, accumulated sediment was removed from the basin and redeposited on the surrounding landscape ("Excavated" treatment). Initially, sediment removal significantly decreased invasive species cover, particularly of *Typha* x *glauca* (hybrid cattail) and *Phalaris arundinacea* (reed canary grass), and increased community diversity and evenness. Over time, the effects of sediment removal diminished, and eventually

disappeared by ca. six years after restoration. While our results demonstrate that sediment removal improves initial restoration outcomes for plant communities, longer-term benefits require sustained management, such as invasive species control or resetting of basins through additional excavation.

Introduction

Since 1780, more than 50% of wetlands have been drained or filled across the contiguous United States (Dahl 1990; Tiner 1984). In Minnesota alone, 50 to 80% of wetlands were drained between 1850 and 1980, constituting a loss of over 5.6 million acres (Dahl 2014). Widespread agricultural drainage has consolidated many smaller wetlands into fewer larger basins (Van Meter & Basu 2015; McCauley et al. 2015). Wetland drainage diminishes existing wetland ecosystem services including providing habitat (Stewart & Kantrud 1974; Cohen et al. 2016), maintaining biodiversity (Thiere et al. 2009), improving water quality (Hey 2002; Johnston et al. 1990; Hansen et al. 2018; Salk et al. 2018), and maintaining hydrologic function (Euliss & Mushet 1996; Neff & Rosenberry 2018; LaBaugh et al. 1998). Seasonally and semipermanently ponded depressional wetlands are often characterized by intermittent surface-water connections and are particularly vulnerable to drainage because of their small size (Tiner 2003a; Cohen et al. 2016). Wetland conservation and restoration remain important areas of investment in the United States despite recent reinterpretations that have weakened legal protections and remediation mandated by federal law (Clean

Water Act 1972) and international treaties (Ramsar Convention Treaty adopted 1973) that recognize the substantial services provided by existing wetlands.

While there is a clear need for and growing commitment to wetland restoration, its scientific underpinnings are still developing. Wetland restoration typically involves reestablishing hydrologic connectivity and function (e.g., water storage) and may entail reshaping and deepening basins to hold more water (Luo et al. 1997; Hayashi & van der Kamp 2000). Hydrologic aspects of wetland restoration are relatively well-studied (Daniel McLaughlin et al. 2014; Mushet et al. 2015; Rains et al. 2016), but effects of sediment excavation are not. In agricultural settings, accumulation of eroded soil in former wetland basins can be extensive and agricultural practices accelerate erosion (Gleason et al. 1998). Accumulated sediment presents a major challenge to restoration since it can influence ecosystem structure and function by shortening hydroperiod, decreasing effective basin size (Tsai et al. 2007) and volume (Luo et al. 1997), increasing nutrient availability (Johnston 1991a; Johnston et al. 1984), and burying seed banks (Jurik et al. 1994; Gleason et al. 2003).

Accumulated sediment can have both direct and indirect effects on wetland plant communities. As little as 0.5 cm of accumulated sediment can decrease seed germination by 4 to 8% of the rates observed in sediment-free controls (Gleason et al. 2003; Jurik et al. 1994). Additional sediment accumulation can further impair recruitment (Moore & Wein 1977; Gleason et al. 2003) until only large seeds, which tend to be more resilient to sedimentation, are able to germinate (Jurik et al. 1994). Extended periods of drawdown due to wetland drainage may compound the effects of sedimentation by depleting an impaired seed bank, and have been shown to decrease plant diversity and density by 60 and 83%, respectively (Wienhold & van der Valk 1989). Furthermore, sediment can influence the relative proportions of native and non-native species found in restored wetlands. Studies investigating the role of sediment deposition on invasion dynamics in mesocosms (Gleason et al. 2003; Kercher & Zedler 2004; Hausman et al. 2007) and natural wetlands (Werner & Zedler 2002) have demonstrated that sediment accumulation favors invasive species and can hamper native species growth and survival. However, relatively few studies have investigated the potential benefits of sediment removal in wetland restoration (but see Klimkowska et al. 2010; Pfeifer-Meister et al. 2012; Beas et al. 2013; Smith et al. 2016). Effects of excavation on invasions could be substantial, since the top 3 to 30 cm of soil can hold high densities of non-native seed, contributing to rapid invasion following hydrologic restoration (Jacquemart et al. 2003; Hausman et al. 2007; Smith et al. 2016). In addition, accumulated agricultural sediments may contain high concentrations of nitrogen and other nutrients that invasive wetland plants are well-adapted to exploit (Zedler & Kercher 2004).

Since accumulated sediment can bury native seed banks and act as a reservoir for invasive species seed (Smith et al. 2016), sediment removal has been employed to expose native species and remove invasive species, despite little empirical evidence that excavation alone will improve restoration outcomes. A central unresolved question is whether excavation can foster native species recruitment and non-native species suppression, both of which are key restoration goals. Snapshot surveys of wetlands at various stages of development have found no discernable effect of time since restoration on community composition (Beas et al. 2013), while longer-term monitoring efforts reveal that plant communities grow more similar over time, following invasive species establishment and spread (Aronson & Galatowitsch 2008). Restored wetlands are particularly vulnerable to invasion because of substantial lags between restoration and establishment of sensitive or rare graminoids and forbs. In systems that are particularly isolated, as in wetlands surrounded by intensively cultivated land, long distance dispersal by wildlife may be the only mechanism available to introduce viable seed (Soons et al. 2008), which could happen unpredictably or infrequently. Attempts to accelerate the rate of species accumulation include seeding and planting, but the effectiveness of these efforts remains unclear (Boers et al. 2007; Adams & Galatowitsch 2008), and community composition of newly restored wetlands is subject to substantial interannual variability (Mitsch et al. 1998).

Sediment removal can be prohibitively expensive, particularly for larger wetland basins. Depressional wetland restorations typically include modest sediment excavation to plug surface drainage ditches. In west-central Minnesota, excavation costs an average of $6.54 USD per cubic meter of sediment (U.S.

Fish and Wildlife Service, personal communication). At $2,000, the cost of excavating the upper six inches (15 cm) of sediment from a half-acre (0.2 ha) wetland basin roughly equals the cost of plugging a drainage ditch. However, excavation triples the overall cost of a two-acre (0.8 ha) wetland restoration.

Given the substantial cost of sediment removal, the need for large-scale wetland restorations for habitat and water quality improvement (Zedler 2003), and a lack of adequate funding for wetland restoration (Stelk et al. 2017), it is imperative to assess the benefits of sediment excavation relative to re-wetting alone. We tested whether incorporating sediment excavation into wetland restoration improved plant-community outcomes and, if so, whether early effects were maintained up to nine years following restoration. Our primary goal was to identify whether excavation altered community composition, either by improving native species recruitment or suppressing non-native and invasive species. We further sought to determine the duration of any excavation effects. We assessed whether excavation was beneficial with regard to 1) increasing native species cover and richness, or 2) decreasing non-native species cover and richness. Finally, we examined how plant communities changed over time following restoration.

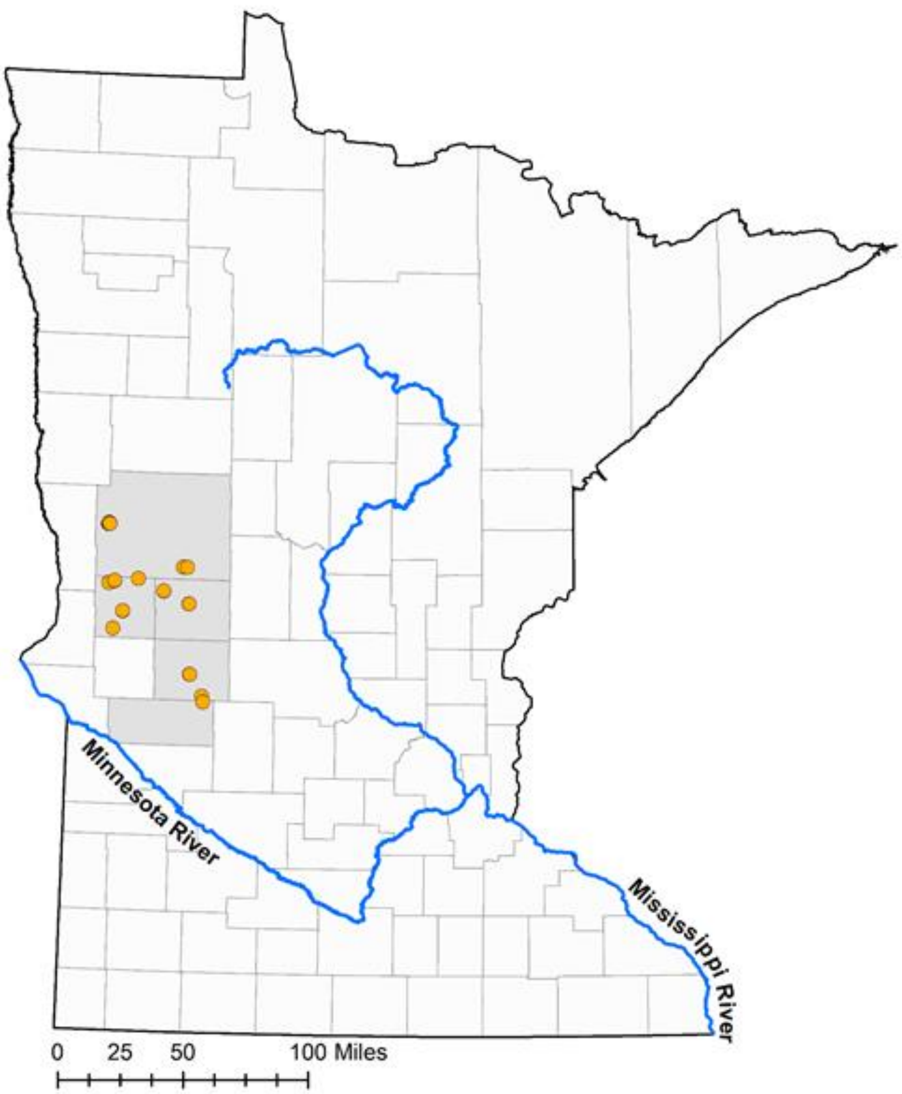

Figure 2. 1. Study area covering five counties in west-central Minnesota. Each point represents clusters of multiple wetlands.

Methods

Site Description

We investigated how excavation and time since restoration (hereafter, wetland age) influenced the plant communities of 24 restored depressional wetlands in the agricultural-dominated landscape of west-central Minnesota (Figure 2.1). Study wetlands were restored between 2009 and 2015 by the United States Fish and Wildlife Service, in partnership with private landowners. All wetlands and surrounding uplands were completely drained by subsurface tile or drainage ditches and were actively cultivated in row-crop agriculture prior to restoration. In most cases, the property owner elected to enroll the surrounding uplands into the United States Department of Agriculture’s Conservation Reserve Program (conservation easements with natural vegetation plantings) at the same time, but not all uplands contributing to the wetland watershed were restored, particularly where wetlands were located near property boundaries. Restored uplands were seeded with a native grass and forb mix while wetlands were neither seeded nor planted. The presence of standing water, historical aerial imagery, and soil characteristics were used to identify the likely former extent of each drained wetland and the depth of accumulated eroded sediment within each basin. Following restoration, private landowners occasionally engaged in management activities such as burning, mowing, and herbicide application within the wetland basins and surrounding uplands. We noted the occurrence of management actions but did not include them in our analyses due to their sporadic nature.

Study wetlands were generally small, ranging from 0.16 to 2.31 ha in area with a mean of 0.64 ha (± 0.49 SD). Watersheds ranged in size from 1.34 to 8.94 ha with a mean watershed to wetland area ratio of 24.52 (median 7.50).

Wetlands were classified as seasonal or semipermanent based on water retention throughout the growing season (discussed in Cowardin and Golet 1995) and the development and persistence of distinct vegetative communities (Stewart & Kantrud 1971), both of which were observed during multiple visits per year during the three years preceding vegetation surveys. We assessed the role of wetland age as the difference between the vegetation survey year and the restoration year. When restoration included the excavation of accumulated sediment from across the entire basin, the wetland was categorized as excavated (EXC). Alternatively, business as usual (BAU) wetlands were restored in the absence of excavation. We chose 12 BAU and EXC wetland pairs, prioritizing pairs with similar age (generally within one year) and hydrology, including 14 basins with seasonal and 10 basins with semipermanent hydroperiods. Whenever possible, pairs were located in close proximity to one another (usually within the same field), but three wetland pairs were located 3.7, 29.7, and 61.5 km apart.

Vegetation Surveys

Following Mulhouse and Galatowitsch (2003), we surveyed the flora in each wetland in mid-summer by meandering around and through all vegetation zones (sedge meadow, emergent zone, and open water). We sampled during mid-summer to have the greatest likelihood of observing both early phenology species in fruit (e.g., spring sedge species) and late-flowering grasses such as

Leersia oryzoides (rice cutgrass). Two to three surveyors worked together to compile a comprehensive species list and estimate percent cover of each species across all zones. Surveyors walked the same path through the wetland, communicating with one another when new species were identified and checking that all surveyors recorded the appropriate species codes. Each surveyor kept independent notes in order to encourage independent estimates of species cover. Upon completion of the meander, surveyors independently estimated species-specific percent cover before comparing estimates with the group. Final cover estimates were agreed upon by all surveyors prior to being recorded. Nomenclature and classification as either native or non-native (hereafter, invasive) followed Chadde (2012) and USDA (2018), and voucher specimens were submitted to the University of Minnesota Herbarium. Putative *Typha angustifolia* (narrowleaf cattail) and *T. latifolia* (broadleaf cattail) are difficult to reliably distinguish and were recorded as their widespread hybrid, *T. x glauca* (hybrid cattail).

Approximately one month following vegetation surveys, we returned to each site to sample plant biomass. We sampled biomass in four quadrats (0.25 m × 0.25 m; 0.0625 m^2) in each wetland. Quadrats were distributed throughout the wetland by visually dividing the basin into four sections and locating one quadrat in each section in an area containing species that were predominant in the basin. We recorded species present in each quadrat, estimated species-specific percent cover, and collected all aboveground biomass. Samples were separated by plant species and air dried before being transported to the lab. All samples were then dried at 60° C in a gravity convection oven for 48 hours prior to being weighed. Quadrat data were compiled across wetlands to develop linear relationships relating cover to biomass ($g \cdot m^{-2}$) for each of the 31 most commonly sampled species. We applied the linear relationships to species-specific cover estimates from our vegetation surveys, thereby estimating the biomass of all 31 species in each wetland basin. Biomass estimates were separately summed across native and invasive species to approximate biomass per unit area in each wetland. These data were used as an indication of native and invasive species biomass within and between wetlands.

Statistical Analyses

To better understand long-term impacts of excavation, we considered the effects of both treatment (BAU vs. EXC) and wetland age (three to nine years) in all statistical models. We performed analysis of covariance (ANCOVA) using generalized linear models (GLMs) with treatment and wetland age as independent variables. We did not include hydrology (e.g., seasonal and semipermanent) in the model because we accounted for effects of hydrology in the study design through our wetland pairs. ANCOVA was performed in R (R Core Team 2020) with Type II sum of squares using the '*car*' package (Fox & Weisberg 2011) and a critical *p*-value of 0.05. When appropriate we performed post-hoc significance tests with Tukey HSD in the '*emmeans*' package. We calculated Shannon’s diversity and Pielou’s evenness indices using the ‘*vegan*’ package (Oksanen et al. 2018) in R.

We calculated invasive and native species richness, abundance (as percent cover), and biomass, for each wetland. Percent cover and biomass were considered separately because we used species-specific allometric equations to estimate biomass based on cover; individual species may have high coverage and low overall biomass (e.g., mosses, duckweeds, and submerged macrophytes), or relatively low coverage and high biomass (e.g., trees and shrubs), but the aggregate biomass across species is likely to differ based on which species are present and dominant. We modeled richness, which constitutes count data, using a GLM with a Poisson distribution. To assess whether two widespread invasive species were driving patterns in overall invasive abundance, we examined how the combined cover of hybrid cattail and *Phalaris arundinacea* (reed canary grass) was influenced by treatment and wetland age. We also considered how treatment and age influenced abundance and biomass of all other non-native species. Since wetland age showed a parabolic relationship with hybrid cattail and reed canary grass cover, we used a quadratic model with a second-order term for wetland age.

To elucidate how invasive species dominance was changing over time, we calculated the ratio of invasive species cover relative to total vegetative cover (hereafter, invasion prevalence ratio). We used the invasion prevalence ratio to assess how excavation and wetland age influenced invasive species dominance over time and across treatments, such that a ratio of 1 would indicate that all vegetative cover is due to invasive species while a ratio of 0 would indicate complete absence of invasive species. To assess how overall community diversity was influenced by treatment and wetland age, we fit separate linear models with Shannon diversity and Pielou evenness as response variables. To partition the influence of the two most common invasive species, we recalculated diversity and evenness with hybrid cattail and reed canary grass excluded. We repeated our statistical analysis on the new metrics and compared our results with diversity and evenness responses calculated from the full dataset.

We employed multivariate methods to test for effects on overall community composition, using cover data as an indicator of abundance. We used non-metric multidimensional scaling (NMDS) ordination to calculate differences between communities at each site (Oksanen et al. 2018) using the ‘vegan’ package in R (metaMDS function). To meet the assumption of equal dispersion, we binned wetland ages into groups (ages 3-4, ages 5-6, ages 7-8, and age 9). Cover data were double relativized (by species and site maxima) and square-root transformed, and Bray-Curtis distance was used to measure dissimilarity; NMDS was implemented using three axes (Oksanen et al. 2018). We used the adonis function in ‘vegan’ to perform permutational multivariate analysis of variance (PERMANOVA) to test for community composition differences between treatments and by wetland age (Anderson 2001). We checked PERMANOVA model assumptions of equal dispersion using the betadisper function in ‘vegan’ followed by a permutation test using the permutest function. We used the similarity percentage (SIMPER)(Clarke 1993) function in vegan to determine individual species' contributions to compositional dissimilarity between groups.

We assessed species-specific responses to treatment and wetland age using each species' covers as a measure of relative abundance, focusing on species recorded in at least 33% of wetlands (n = 8). Percent cover values were binned into 13 cover classes (<1%, 1% - 5%, 5% – 10%, and increasing in 5% intervals up to 60%, the maximum cover observed) to meet model assumptions regarding the mean-variance relationship (Wang et al. 2012). We fit a multivariate GLM model (overall community composition) and univariate GLMs (individual species' responses) to the cover class data using a Poisson distribution and backwards model selection in the '*mvabund'* package in R (Wang et al. 2019).

Results

Native and Invasive Species Response

We identified a total of 206 plant species, with 166 species occurring in BAU sites and 171 species in EXC sites. In BAU sites, there were 135 native and 31 invasive species. In EXC sites, there were 145 native and 26 invasive species. Native species richness was consistently greater (mean 43.8 ± 11.4 SD) than invasive species richness (mean 11.2 ± 2.6 SD). Native and invasive richness were independent of excavation status (p = 0.28 native; p = 0.50

invasive, Appendix 2, Table A2.1), but native richness decreased significantly over time (*p* = 0.036; Figure 2.2a), while invasive richness remained relatively constant as wetlands aged (*p* = 0.21). Most species (*n* = 116) were found in at least three wetlands, 90 species were recorded in only one or two sites. Forty species were detected exclusively at EXC sites and 35 exclusively at BAU sites; however, a single BAU site accounted for 15 of the species unique to BAU sites (Appendix 2, Table A2.2).

Native species cover was not significantly influenced by treatment or wetland age main effects (*p* = 0.87 and *p* = 0.27, respectively), but there was a significant interaction between treatment and wetland age (*p* = 0.05), indicating different trajectories of native species abundance at BAU and EXC sites over time. In BAU wetlands, native species cover remained relatively constant over time; in EXC sites, native species cover decreased proportionally with increasing invasive species cover. Invasive species cover was lower in EXC than BAU sites (Figure 2.2b; *p* = 0.011) and increased significantly with wetland age (*p* = 0.002); there was no significant interaction between treatment and wetland age (*p* = 0.14). By year eight, native and invasive species cover had converged (Figure 2.2b). Combined hybrid cattail and reed canary grass cover was significantly lower in EXC sites (*p* = 0.008) and increased with increasing wetland age (*p* = 0.011). There was no relationship between cover of all other non-native species and treatment or wetland age (*p* = 0.60 and *p* = 0.81, respectively).

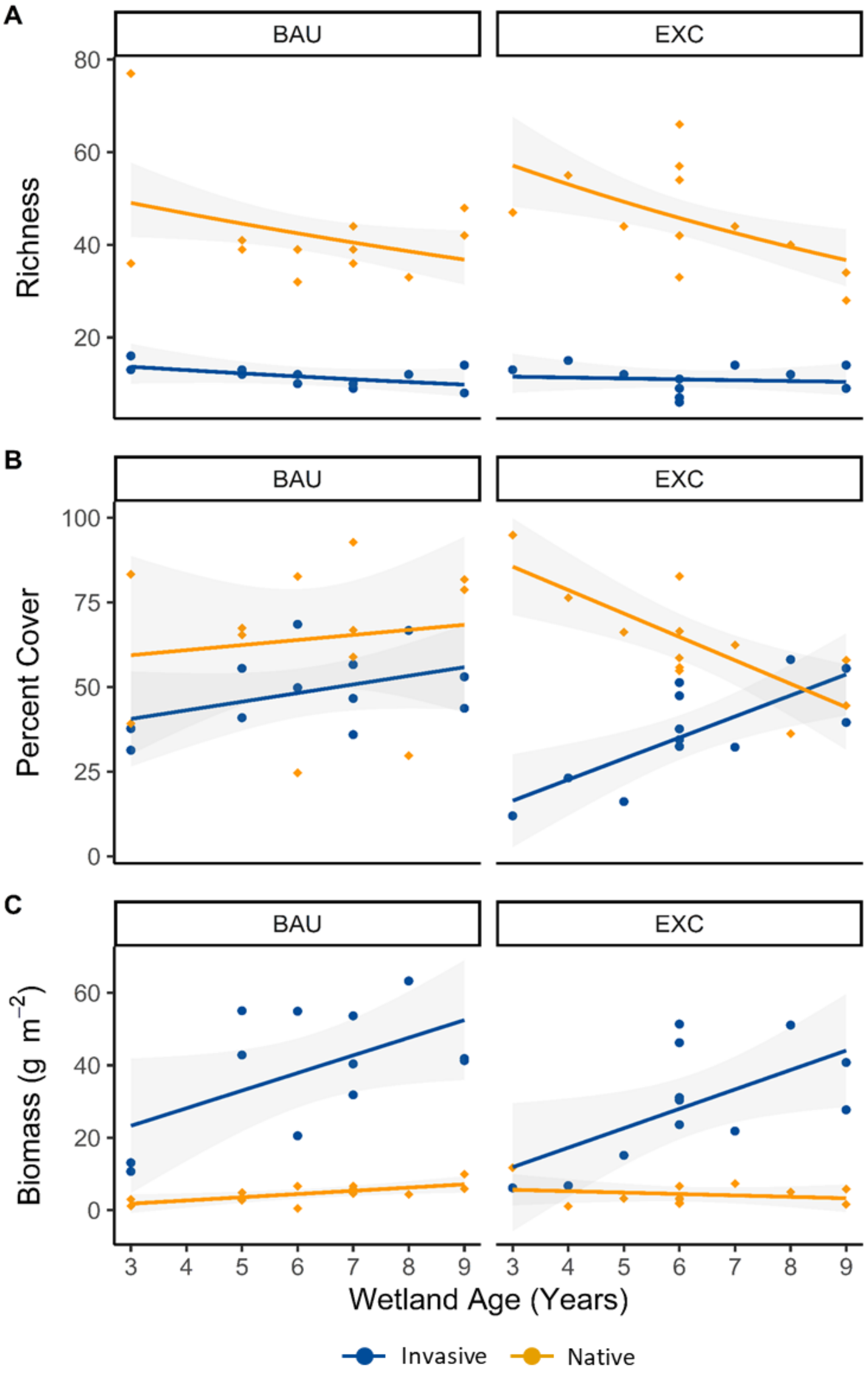

Figure 2. 2. Species richness (A), percent cover (B), and biomass (C) of native and invasive species with 95% confidence intervals for business as usual (BAU; left) and excavated (EXC; right) wetlands.

Despite there being higher native richness, native species biomass was always lower than invasive species biomass (Figure 2.2c). Native biomass was not significantly influenced by treatment (p = 0.77) or wetland age (p = 0.30), but there was a significant interaction between treatment and age (p = 0.044), such that native biomass increased over time in BAU sites and decreased over time in EXC sites (Figure 2.2c). Invasive biomass was not significantly influenced by treatment (p = 0.099), but increased as wetlands aged (p = 0.004); there was not a significant interaction between treatment and age (p = 0.87). The strong, positive relationship between invader biomass and time appears to have been driven by hybrid cattail and reed canary grass, whose combined biomass was not significantly influenced by treatment (p = 0.10), but increased significantly as wetlands aged (p = 0.006, Figure 2.3a). The positive relationship between aggregate biomass of hybrid cattail and reed canary grass with increasing wetland age was similar to the pattern in the cover dataset. As with cover measures, cumulative biomass of all other non-native species did not change with treatment (p = 0.86) or wetland age (p = 0.12).

Excavated and BAU sites had significantly different invasion prevalence ratios as wetlands aged (p = 0.040, Figure 2.3b). Tukey's HSD revealed significantly lower invasive species prevalence at EXC sites compared to BAU sites until six years following restoration (p = 0.013, p = 0.013, p = 0.017, p = 0.068 for years three, four, five, and six, respectively), after which EXC and BAU sites did not have significantly different invasive species prevalence (p = 0.50, p

= 0.74, *p* = 0.37, for years seven, eight, and nine, respectively). This suggests that the benefit of excavation, in terms of reducing overall invasive species prevalence, was lost by year six.

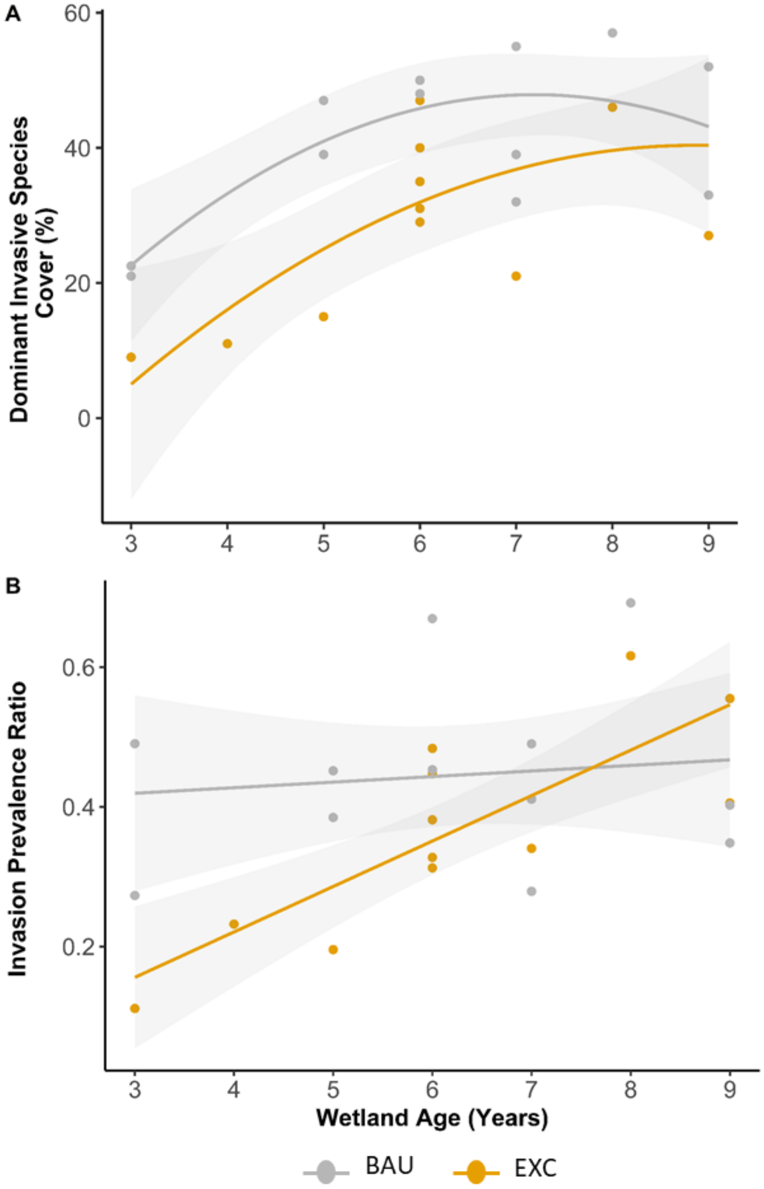

Figure 2. 3. Combined cover of *Typha* x *glauca* (hybrid cattail) and *Phalaris arundinacea* (reed canary grass) over time (A), and relative cover of invasive species to total vegetation cover (B). Business as usual (BAU) and excavated (EXC) sites with linear model overlaid and 90% confidence intervals.

Diversity and evenness were significantly affected by treatment (Figure 2.4; $p = 0.028$ and $p = 0.022$, respectively), such that EXC sites had higher diversity (2.83 ± 0.33 SD) and evenness (0.71 ± 0.063 SD) than BAU sites (2.52 ± 0.33 SD and 0.64 ± 0.07 SD, respectively). Wetland age did not have a significant effect on diversity or evenness ($p = 0.085$ and $p = 0.34$, respectively). The diversity and evenness models without hybrid cattail and reed canary grass revealed different relationships to treatment and wetland age. Without hybrid cattail and reed canary grass, EXC wetlands had marginally higher diversity than BAU sites ($p = 0.064$; BAU 2.80 ± 0.087, EXC 3.01 ± 0.058), and evenness was not significantly influenced by treatment ($p = 0.11$). Wetland age did not significantly influence diversity or evenness ($p = 0.72$ and $p = 0.33$, respectively).

Community Composition

Community composition was marginally influenced by treatment ($p = 0.052$; Figure 2.5). SIMPER analysis revealed that nearly 28% of the difference between BAU and EXC sites was attributable to three species: hybrid cattail, *Lemna minor* (common duckweed), and reed canary grass, all of which were more common in BAU sites than EXC wetlands (Appendix 2, Table A2.3). In contrast, EXC wetlands had more submerged aquatic macrophytes, such as *Utricularia vulgaris* (common bladderwort), *Potamogeton zosteriformis* (flatstem pondweed), and *Stuckenia pectinata* (sago pondweed), as well as more *Salix* *exigua* (sandbar willow); collectively, these species accounted for about 10% of the difference between BAU and EXC sites.

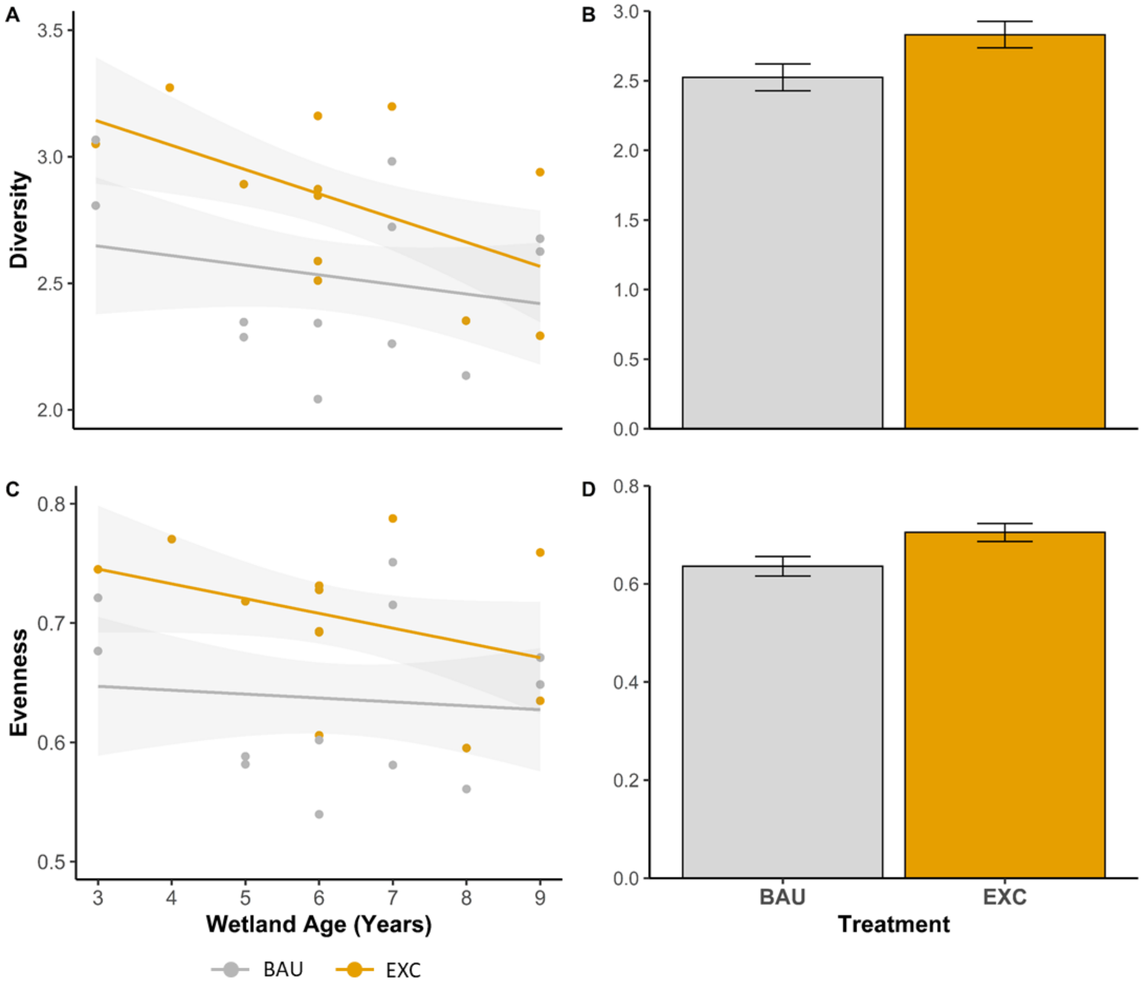

Figure 2. 4. Community diversity (A-B) and evenness (C-D) for business as usual (BAU; grey circles/bars) and excavated (EXC; gold diamonds/bars) wetlands. Grey bands in panels A and C are 95% confidence intervals. Panels B and D show average responses ± standard errors.

Significant shifts in community composition as wetlands aged ($p = 0.001$; Figure 2.5) were mostly attributable to four species. Hybrid cattail accounted for between 9.4 and 14.9% of dissimilarity between wetland ages and was generally more abundant in older wetlands. Reed canary grass accounted for between 3.7 and 9.3% of dissimilarity between wetland age bins and first decreased and then increased in prevalence as wetlands aged. Common duckweed and sphagnum moss (*Sphagnum* spp.) abundances fluctuated across wetland ages and collectively accounted for between 4.5 and 15.7% of dissimilarity between age bins (Appendix 2, Table A2.4). Younger wetlands were more likely to have native perennials such as *Carex stricta* (tussock sedge), *Scirpus cyperinus* (woolgrass), sago pondweed, *Schoenoplectus tabernaemontani* (softstem bulrush), *Alisma triviale* (northern water plantain), and *Scirpus atrovirens* (green bulrush), many of which were also more prevalent in EXC wetlands. Older wetlands were more likely to have higher abundances of sphagnum moss; rhizomatous species including hybrid cattail, reed canary grass, and *Bolboschoenus fluviatilis* (river bulrush); and more cosmopolitan species, including common duckweed and *Ceratophyllum demersum* (coontail), many of which were prevalent in BAU wetlands. Community composition was not significantly affected by seasonal or semipermanent hydroperiod ($p = 0.13$).

Species-specific responses to excavation and wetland age were based on the 72 species observed in at least 33% of wetland basins. Among the subset of commonly encountered species, community composition was marginally influenced by treatment ($p = 0.070$; Figure 2.5) and significantly influenced by wetland age ($p = 0.043$). Univariate analysis revealed three species that were significantly influenced by excavation: common duckweed and *Verbena hastata* (blue vervain) had lower cover in EXC sites (Appendix 2, Table A2.5), while soft-stem bulrush had significantly higher cover in EXC wetlands. Older wetlands had more river bulrush, *Solidago gigantea* (smooth goldenrod), *Symphyotrichum ericoides* (white heath aster), blue vervain, *Elymus repens* (quackgrass), and hybrid cattail. Younger wetlands had more *Spartina pectinata* (prairie cordgrass), soft-stem bulrush, *Panicum virgatum* (switchgrass), and *Echinochloa crus-galli* (barnyard grass). Of the three invasive species most affected by wetland age, quackgrass and hybrid cattail had higher cover in older wetlands, while barnyard grass cover declined over time.

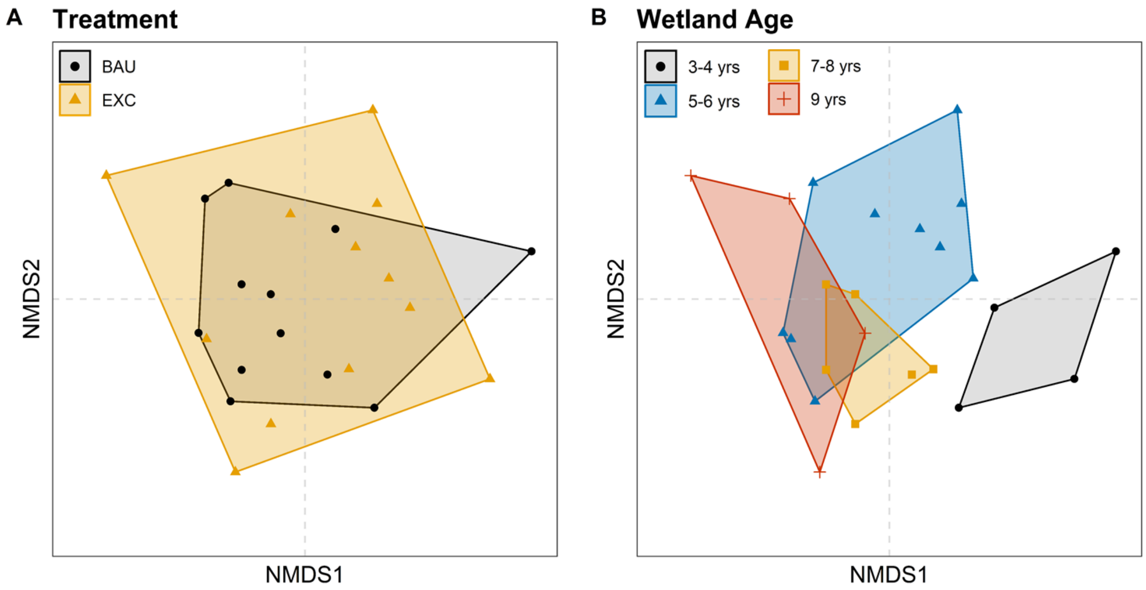

Figure 2. 5**.** Nonmetric multidimensional scaling (NMDS) ordinations of plant community composition for business as usual and excavated treatments (A) and binned wetland ages (B). Treatment hulls show business as usual (black circles) and excavated (gold triangles) sites in ordination space. Wetland age hulls show sites that were 3 to 4 years (●), 5 to 6 years (▲), 7 to 8 years (■), and 9 years old (+).

Discussion

We sought to identify if excavating accumulated sediment in agricultural wetland restorations increases plant diversity and decreases invasive species dominance. We found that excavation restorations initially increased community diversity by decreasing invasive species cover. Decreased invasive species cover was driven by lower abundance of hybrid cattail and reed canary grass in particular. However, these two invasives established and spread quickly, resulting in subsequent declines in native species richness and abundance. Within six years, the proportion of vegetation cover represented by invasive species in BAU and EXC sites had converged, suggesting that the early benefits of excavation were lost. Our results show that excavation imparts plant community benefits, but maintaining these benefits over the longer term is likely to require additional management interventions, such as invasive species control.

Wetland plant communities often converge over time, becoming less diverse (Aronson & Galatowitsch 2008; Lishawa et al. 2010; Mclane et al. 2012), but restorations that include excavating accumulated sediment could improve diversity compared to BAU restorations by promoting native species recruitment or decreasing invasive species abundance. We found that excavation was initially beneficial, with higher community diversity and lower invasive species cover. Our results are in agreement with recent studies in North Dakota and Nebraska confirming that excavation can decrease hybrid cattail density by removing invasive species seed (Smith et al. 2016) and increase species richness (Beas et al. 2013), supporting higher overall diversity (Boers et al. 2007; Weisner & Thiere 2010). However, we did not find significantly higher species richness attributable to excavation. Rather, excavation primarily influenced vegetation by reducing invasive species abundance, specifically that of hybrid cattail and reed canary grass, which was associated with higher diversity through greater evenness.

Our data suggest that rapid accumulation of biomass by hybrid cattail and reed canary grass contributes to their competitive dominance at excavated sites. Hybrid cattail and reed canary grass are among the most effective colonizers following wetland restoration (Wetzel & Van Der Valk 1998; Boers et al. 2007; Galatowitsch et al. 1999). In hybrid cattail, competitive dominance may stem from hybrid vigor (Zapfe & Freeland 2015). Both hybrid cattail and reed canary grass can suppress competitors by reducing light availability (Wetzel & Van Der Valk 1998; Maurer & Zedler 2002; Perry & Galatowitsch 2003), altering temperature (Larkin, Freyman, et al. 2012), or exploiting nutrient availability (Green & Galatowitsch 2001; Woo & Zedler 2002; Lishawa et al. 2014; Atkinson & Cairns 2001). Both species are tall and rhizomatous, traits that enable them to shade out competitors and spread rapidly to access available resources. Hybrid cattail has exceptional nutrient uptake efficiency and the ability to outcompete native species for nitrogen (Larkin, Lishawa, et al. 2012). We also found that aggregate hybrid cattail and reed canary grass cover plateaued at 40 to 60%. At the most densely invaded sites, hybrid cattail biomass and litter appeared to shade out most competitors, notably including other cattails (S. Winikoff, pers. obs.), suggesting that competition for resources may be both inter- and intraspecific. Hybrid cattail and reed canary grass may further benefit from phenological advantages over other species (Maurer & Zedler 2002), capitalizing on available light and nutrients when native species have not yet emerged from dormancy.

In older wetlands, we found that the expansion of hybrid cattail and reed canary grass cover was concomitant with declines in native species abundance and richness. Our results align with conclusions drawn by a 19-year study showing that hybrid cattail and reed canary grass exerted growing influence on community composition as restored wetlands aged (Aronson & Galatowitsch 2008). Other work on wetland plant communities has documented similar patterns of competitive exclusion of native species with rising abundance of these aggressive invasives (Green & Galatowitsch 2001; Lishawa et al. 2010; Larkin, Freyman, et al. 2012). Still, the relationship between species richness and wetland age can be difficult to detect; even in the absence of invasion, species richness accumulates slowly, over decades or even centuries (Verhagen et al. 2001; Weisner & Thiere 2010; Stroh et al. 2012). Rare and uncommon species' establishment are mediated by propagule dispersal mechanisms, likely involving wildlife (Soons et al. 2008), which grow increasingly difficult to predict and protect as natural wetlands become more isolated with increasing human impact (Van Meter & Basu 2015; Vanderhoof et al. 2016; Davidson 2014).

Although we observed higher native species cover and lower invasive species cover, our results did not indicate that excavation significantly altered richness of native or invasive species. Disturbed and eutrophic wetlands often have species richness comparable to reference basins (Beas et al. 2013; Galatowitsch et al. 2000), but with distinct, and less desirable, species composition. Generally, disturbance shifts community composition toward invasive perennials and native annuals and away from native perennials, resulting in no net loss of richness but substantial changes in composition (Galatowitsch et al. 2000; Galatowitsch & van der Valk 1996b). These compositional shifts can have meaningful consequences for ecosystem function and resilience by favoring short-lived annuals and monotypic invasive species to the detriment of other functional groups (Walker 1995, 1992).

We recorded a variety of uncommon native forbs, grasses, and sedges that were only detected in excavated sites, but the effect of excavation on native species was fairly nuanced. Many of the native species that were abundant in excavated wetlands were also common in younger basins, including bladderwort, green bulrush, woolgrass, softstem bulrush, sago pondweed, flatstem pondweed, and water plantain. Likewise, many of the species associated with BAU wetlands were common in older basins, including common duckweed and river bulrush. Together, this suggests that excavation favors native perennial species that emerge in the years immediately following hydrologic restoration, but over time there is substantial accumulation of cosmopolitan native and aggressive invasive species. Our data are in agreement with seed-rain studies, which suggest that prairie wetlands are likely to experience more introductions of invasive cattail and reed canary grass, as well as cosmopolitan native species including river bulrush and blue vervain (Kettenring & Galatowitsch 2011), two species that did well in older wetlands.

Recruiting and establishing bunch-forming sedges and grasses immediately following restoration may help restored wetlands resist invasion (Larkin, Freyman, et al. 2012). Nearly all of the sedge species that we encountered were clump-forming species, including *Carex utriculata* (common beaked sedge), *C. atherodes* (slough sedge), tussock sedge, and *C. cristatella* (crested oval sedge) and *C. vulpinoidea* (fox sedge), which occurred at nearly every wetland. We also observed one clump-forming grass, prairie cordgrass, and two clump-forming bulrushes, green bulrush and river bulrush, forming dense patches in multiple wetlands. These graminoid patches remained intact despite overall encroachment by both hybrid cattail and reed canary grass. At broader scales, vegetative clump size and distribution can influence community dynamics, with communities characterized by many small and relatively few large clumps being more resilient to disturbance than communities with fewer large and midsize clumps (Kéfi et al. 2007). Our wetlands were exposed to years, if not decades, of active cultivation, a major disturbance by any measure, but the persistence of clump-forming species suggests that the seedbank retained the capacity to reassemble a resilient community if sufficiently managed to reduce invasion in the years following restoration.

Whether the goal is maintaining biodiversity, providing wildlife habitat, improving water quality, or providing hydrologic function, there is a pressing need for wetland restoration. Sediment excavation is a promising tool for wetland restorations, resulting in greater diversity, higher native species cover, and lower invasive species cover, but the benefits of excavation only lasted for six years in the present study. Our results reinforce the need for invasive species management following restoration. Targeted management to control the establishment and spread of aggressive invasive species is required to maintain excavation benefits. However, management is expensive, regardless of the actions employed, and we have little information about how restored agricultural wetlands respond to different management activities over extended periods of time. Future studies should focus on identifying and testing the efficacy of novel management practices (e.g., harvesting aboveground biomass; Lishawa et al. 2015) or novel combinations of management practices (e.g., alternating herbicide use and grazing) and monitoring approaches (e.g., unmanned aerial surveys; Lishawa et al. 2017) to control hybrid cattail and reed canary grass, while protecting native perennial species.

3. Sediment excavation as a wetland restoration strategy has short-lived effects on soil nutrients in an agricultural wetland

Abstract

Wetland restoration aims to recover lost ecosystem structure and function, often by attempting to reintroduce historical topography and hydrology to previously drained basins. In highly modified landscapes, accumulation of eroded sediments from the surrounding landscape can decrease basin volume, shorten hydroperiod, and introduce substantial amounts of nutrients, which can alter the recovery of critical components of ecosystem structure and function. We compared how removal of accumulated eroded sediments (“excavation”) or retention of sediments (“business as usual”) during wetland restoration influenced the physical and chemical characteristics of soils in 54 restored agricultural wetlands. Study wetlands included basins with seasonal and semipermanent hydroperiods, and ranged in ages from zero to eight years following restoration. In addition, we compared restored wetlands to seven undrained reference basins. Soils were significantly different in restored and reference wetlands. Restored basins had soils with higher bulk densities, lower organic carbon and total nitrogen, and higher phosphorus content compared to reference basins. Restored wetlands also had lower soil C:P and N:P molar ratios than reference sites. Excavation initially reduced soil organic carbon and total nitrogen content, but excavated wetlands rapidly accumulated soil organic matter following restoration, replacing lost carbon and nitrogen stores. Soil phosphorus dynamics were primarily influenced by wetland hydroperiod, with lower bioavailable phosphorus content and higher N:P and C:P ratios in semipermanently flooded basins. These results indicate that semipermanent basins stored phosphorus more effectively than seasonal wetlands, particularly in organically bound forms. Our results suggest that the effects of sediment excavation on soil C and N pools are short-lived, and effects on P dynamics were likely produced indirectly by modestly increasing wetland hydroperiod, which had a strong influence on P availability. We suggest that, given the choice, restoration planners should prioritize wetlands that will have longer hydroperiods.

Introduction

Globally, greater than 55% of habitable land area is significantly modified by agricultural activity and urbanization (Ellis et al. 2010), altering ecosystem services and threatening biodiversity (Newbold et al. 2015; McGill 2015). Cultivation and urbanization are largely responsible for the loss of between 65 and 70% of natural wetlands in the last century (Davidson 2014). For example, in the upper Mississippi River basin, approximately 80% of the landscape has been modified in some way and an estimated 26 million acres of wetland have been drained (Hey & Philippi 1995). One region of particular interest is the prairie pothole region, an area characterized by an exceptionally high density of drained depressional wetlands, stretching from northwest Iowa, western Minnesota, eastern South Dakota, North Dakota, Manitoba, Saskatchewan, and Alberta. Once known as the “duck factory”, for historically high densities of breeding waterfowl, the prairie pothole region lost over 10 million acres of wetland throughout the 19th and 20th centuries resulting in the widespread consolidation of many smaller water bodies into fewer, larger water bodies that provide fewer ecosystem services (Dahl 2014; Daniel L McLaughlin et al. 2014).

These dramatic losses have come at great cost to ecosystem services, such as surface and groundwater supply and regulation, nutrient cycling, carbon storage, pollution control, erosion control, habitat refugia for migratory species, recreational activities (e.g., hunting, birding, trapping), and biodiversity maintenance (Costanza et al. 1997; Zedler 2003). Recovering the ecosystem services that were once provisioned by natural wetlands is an area of growing interest, since the effects of wetland loss are increasingly realized, but recovering lost services will require substantial wetland restoration over decades yet to come (Gibbs 2000; Mitsch & Day 2006; Moreno-Mateos et al. 2012). Restoring drained depressional wetlands is increasingly recognized as a cost-effective way to restore critical habitat (Gibbs 2000), maintain plant and animal biodiversity (Verones et al. 2013; Jenkins et al. 2003; Houlahan & Findlay 2003), improve water quality (Mitsch & Wang 2000; Johnston 1991b), increase carbon storage (Bernal & Mitsch 2012; Craft et al. 2018), capture and remove nitrogen and phosphorus (Neely & Baker 1989; Reddy et al. 1993; Euliss et al. 2006; Craft

2007), and manage flood risk (Hey & Philippi 1995; Tiner 2003b; McLaughlin et al. 2014; Rains et al. 2016). Thus, identifying restoration strategies and site characteristics to prioritize is urgently important if we are to improve the recovery of ecosystem structure and function in restored wetlands.

The practice of removing accumulated eroded sediment from wetland basins prior to restoring hydrology in depressional wetlands may be a critical tool for recovering lost ecosystem services, particularly those associated with nutrient cycling and sequestration, and water quality improvement. Carbon, nitrogen, and phosphorus storage and water filtration are services that are strongly influenced by the physical and chemical structure of soils. Consequently, soil properties such as high organic matter content, low bulk density, and high iron content can be important indicators of carbon sequestration, nutrient storage, and denitrification, making soil improvements an essential part of high-quality wetland restorations (Meyer et al. 2008; Ballantine & Schneider 2009; Brown et al. 2017; Zurayk et al. 1997; Hogan et al. 2004). Accumulated eroded sediments change soil properties by increasing soil density and introducing nutrients to drained wetlands, but it remains unclear whether removing this accumulated sediment can help recover desirable soil characteristics. In cultivated landscapes, eroded top soil accumulates in drained depressions (Luo et al. 1999; Martin & Hartman 1987), smothering native plants (Werner & Zedler 2002) and seed banks (Gleason et al. 2003; Jurik et al. 1994), introducing invasive species seed (Smith et al. 2016; Winikoff et al. 2020), and depositing nutrient-enriched mineral soil

(Martin & Hartman 1987; Johnston 1991b; Aldous et al. 2005; Kinsman-Costello et al. 2014; Ockenden et al. 2014). Although accumulated sediment excavation and removal have proven a promising means of diminishing invasive species seed banks (Smith et al. 2016; Winikoff et al. 2020), it is not clear whether the practice influences the long-term success of wetland restorations and reduces the availability of nutrients within restored wetland soils.

Some of the ambiguity surrounding the efficacy of sediment removal may exist because physical disturbance, cultivation, and drainage result in similar soil characteristics as those observed in accumulated sediments. Cultivation increases nutrient availability in drained wetlands by breaking apart soil aggregates, mixing and aerating buried soils, and increasing decomposition rates (Murty et al. 2002; Brown et al. 2017; Reicosky 1997; Ucgul et al. 2017). In addition, anthropogenic nitrogen and phosphorus amendments to top soils can have long residence times in the watershed, as these legacy nutrients move through different pools of the biosphere and temporarily bind to soil constituents (Tesoriero et al. 2013; Chen et al. 2018; Sharpley et al. 2013; Lewis et al. 2006). The physical and chemical changes of cultivation are so extreme that it can take decades or centuries for watersheds to recover (Murty et al. 2002; Ballantine & Schneider 2009; Goyette et al. 2018; Van Meter et al. 2016). While restoring water (hydrology) to drained wetlands reintroduces conditions conducive to the recovery of desirable soil properties, it can be difficult to disentangle the direct effects of cultivation and drainage from the indirect effects of cultivation via accumulation of eroded sediments.

Even in the absence of wetland drainage, accumulated eroded sediments can bury the original hydric soils with over a meter of sediment (Oldenborg & Steinman 2019; Luo et al. 1999), which may reduce wetland hydroperiod – the number of consecutive days a basin can hold standing water (Luo et al. 1997; Tsai et al. 2007). Sediments can shorten hydroperiod by increasing surface area and associated evaporative losses (Luo et al. 1997, 1999; Tsai et al. 2007). However, wetland hydroperiod is also a product of groundwater discharge, climate, runoff and - by extension - landscape modification. The role of hydroperiod in the success of restoration is often overlooked, since it is difficult to characterize immediately following restoration and may take many years to develop, but it may be an important predictor of soil development and soil nutrient storage following restoration. Hydroperiod influences the duration of soil saturation, which affects the formation of hydric soils, a defining feature of wetlands. Longer hydroperiods limit dissolved oxygen availability in sediments and constrain organic matter decomposition, which promotes organically bound nutrient accumulation (DeBusk & Reddy 1998; Pant & Reddy 2001), in some cases representing more than half of ecosystem P stores (Chapin et al. 1978). While extended hydroperiods may promote P storage in organic matter, they can also limit mineral-bound inorganic P storage, since iron reducible phosphates are released under prolonged periods of anoxia (Howarth et al. 1995). Wetlands with shorter hydroperiods have more predictable cycles of water depletion. During periods of water draw down, hydric soils are exposed to air, resulting in accelerated decomposition and nutrient mineralization rates. While studies have shown that accumulated eroded sediments reduce hydroperiod (Luo et al. 1997; Tsai et al. 2007), it is unclear whether removing sediments will increase wetland hydroperiod (Snodgrass et al. 2000) or increase the rate of organic C, N, and P accumulation in restored depressional wetland soils.

Restoration success is often assessed using biological indicators because species richness and abundance respond quickly (usually within five years) to hydrologic restoration (Mitsch & Wilson 1996; VanRees-Siewert & Dinsmore 1996; Weiher et al. 1996; Craft et al. 2003; Shoemaker et al. 2017; Stevens et al. 2002). Compared to above-ground biological indicators, soil physical and chemical properties such as bulk density, organic matter, and nutrient content may take longer to recover (Craft et al. 2003; Moreno-Mateos et al. 2012) because desirable soil characteristics are the product of multiple ecosystem processes that operate on extended time scales. For example, in wetlands the formation of soil organic matter depends upon two processes; first, the establishment of a productive emergent macrophyte community (Lishawa et al. 2014), a process which may take between five and fifty years (Lishawa et al. 2013; Winikoff et al. 2020); second, the time it takes decomposers to colonize and decompose standing necromass, which can take over a year in aerobic conditions and nearly four years in anaerobic wetland conditions (DeBusk &

Reddy 1998). As a result, when assessing the success or failure of restoration, observational bias has favored the characterization of biological attributes over short time spans rather than characterization of soil physical and chemical properties over longer time spans, and uncertainty remains regarding how quickly soil properties change following restoration, with some studies indicating initially rapid accumulation in SOM followed by more modest increases (Bush 2008), others indicating initially slow accumulation of SOM followed by rapid increases in pool size (Ballantine & Schneider 2009), and still others suggesting linearly increasing pool size as basins age (Craft et al. 2003; Lishawa et al. 2014). Furthermore, we don't know whether difference in restoration strategy and hydroperiod influence SOM and nutrient pool sizes over time.

Since accumulated eroded sediments can influence a myriad of soil properties and associated ecosystem services, it is imperative that we understand whether removing such sediments alters restoration outcomes. We investigated two wetland restoration strategies, one designed to remove accumulated eroded sediments (excavation, EXC) prior to restoring hydrology, the other designed to restore hydrology by breaking subsurface tile drain and plugging surface drainage ditches, but without removing accumulated sediments (Business As Usual, BAU). Our goal was to evaluate how these two restoration strategies influenced soil characteristics over time (hereafter wetland age) and under different hydroperiods. We assessed the utility of the BAU and EXC wetland restoration strategies by examining soil characteristics across 54 depressional wetlands with variable hydroperiod and time since the restoration of hydrology, quantifying differences in soil bulk density and pools of available carbon, nitrogen, phosphorus, and select metals.

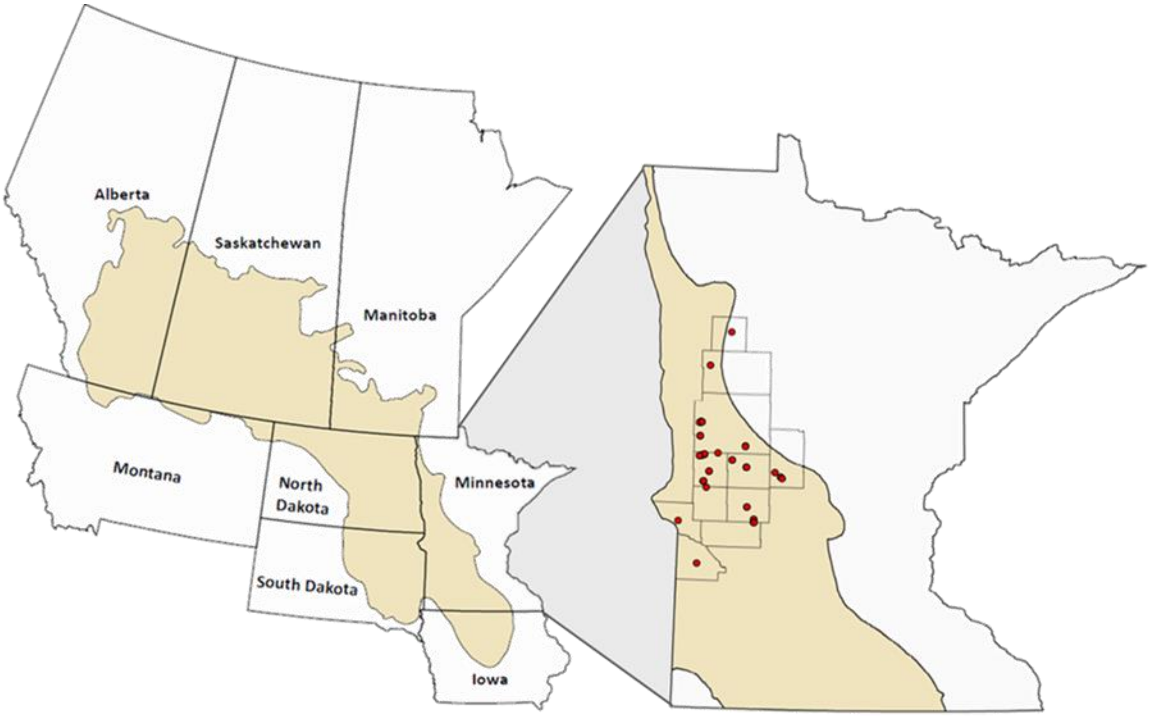

Figure 3. 1. Study sites located in the prairie pothole region of west central Minnesota. Each dot represents one or more wetlands. The broader prairie pothole region stretches across what was historically tallgrass prairie in north-central North America.

Methods

Site Description and Study Design

Study wetlands were located in the prairie pothole region of west central Minnesota (Figure 3.1). Basins were restored between 2009 and 2016 by the United States Fish and Wildlife Service, in partnership with private landowners. The presence of standing water, historical aerial imagery, existing topography, and soil characteristics were used to identify the likely historical extent of wetlands. The combined effects of cultivation and the accumulation of eroded sediments over genetic soils can result in mineral soils with large organic C pools being buried beneath a layer of modified soils (Kolka & Thompson 2006). Therefore, depth of accumulated eroded sediment within each basin was determined by evaluating multiple soil cores and identifying changes in soil properties with depth in the soil profile, including changes in color and texture, changes in soil carbonate content, and presence of shell fragments. Prior to restoration, wetlands and surrounding uplands were drained by subsurface tile or drainage ditches and were actively cultivated in row crop agriculture. We noted additional land-use history information whenever it was made available by landowners (Appendix 1). For example, portions of some watersheds were used to hold livestock including chickens, pigs, and cows prior to cultivation. Property owners often elected to enroll the surrounding uplands into the Conservation Reserve Program at the same time as the restoration, but in some cases portions of the contributing watershed continued to be actively cultivated throughout the study (Table 3.1). The Conservation Reserve Program began in 1985 with the goal of reducing erosional soil loss from marginally productive agricultural lands by establishing perennial native vegetation. In exchange for planting and maintaining native vegetation, landowners are paid a rental fee for the duration of a 10 to 15 year contract by the U.S. Department of Agriculture (Bills 1986; Dunn et al. 1993). Although the contributing watersheds of half of the sites (n = 23) retained some contemporary agriculture, this was often a minor component of overall land use (median 0%, Table 3.1). Proportion cultivation in the contributing watershed was similar between the two restoration strategies (*P* = 0.29, ANCOVA; Appendix 3) and between hydroperiods (*P* = 0.23, ANCOVA). Future work may address the effect of land use on restoration outcomes, but was beyond the scope of this study.

Wetlands were categorized as EXC, when hydrologic restoration followed the removal of accumulated sediment from across the entire basin. Alternatively, when hydrologic restoration occurred in the absence of sediment excavation, basins were categorized as BAU. We surveyed 26 BAU and 28 EXC wetlands (n = 54) between 2016 and 2017. Restored wetlands were generally small, ranging from 0.06 to 2.3 ha in area (mean 0.6 ha, ± 0.4 SD), and were often in small watersheds, between 0.3 to 91.9 ha (mean 11.4 ha ± 21.5 SD) with a mean watershed to wetland area ratio of 30.7 (median 8.0). Wetland age following restoration was defined as the difference between the sampling year and the restoration year. Basins that were wet for the majority of the growing season but dried out annually in July or August were characterized as having seasonal hydroperiod (n = 38), while wetlands with a prolonged hydroperiod generally remained wet throughout the growing season and were characterized as semipermanent basins (n = 16). We incorporated hydroperiod in the study because of inherent differences in biogeochemical cycling that arise from prolonged anoxia in semipermanent wetlands compared to alternating periods of oxygenation and anoxia and freeze-thaw cycles in basins with seasonal hydroperiod.

Wetland hydroperiod characterization was based on water retention throughout the growing season (Cowardin and Golet 1995) and the development and persistence of distinct vegetative communities (Stewart & Kantrud 1971), both of which were observed during multiple visits over the course of the growing season in each sampling year before a hydroperiod was formally assigned. Plant community assemblages are often used to identify hydroperiod because they can reflect water permanence over an extended period of time (Stewart & Kantrud 1971; van der Kamp & Hayashi 2009). While assemblages may be less reliable indicators of hydroperiod immediately following restoration, over time turnover in community composition leads to vegetation showing greater fidelity to hydroperiod (Stroh et al. 2012). Continuous water elevation monitoring is another way to estimate hydroperiod, but we did not have continuous water elevation data from all sites throughout the entire study period. Other methods used to estimate hydroperiod, including watershed to wetland area ratios (Galatowitsch & van der Valk 1996a), are less reliable than vegetative communities and may be influenced by regional differences in climate and local differences in the extent of subsurface drainage both into and out of the watershed.

Prior to beginning the study, we checked that predicted hydroperiod was not associated with excavation depth, among EXC wetlands ($P = 0.24$; ANOVA). Following completion of the study we determined whether sediment removal was significantly related to seasonal or semipermanent hydroperiod by calculating a continuous hydroperiod metric (hereafter permanence). This metric was calculated across the duration of a larger study lasting four years (2016 to 2019) by calculating the mean of the product of maximum and minimum annual recorded depths in each wetland. Depths were measured during repeated visits to gather data for other questions explored in the broader study. Measurements were taken at three evenly spaced locations along a longitudinal transect that spanned from vegetated habitats to the deepest open water habitats that could be reached using chest waders (~1.3 m). This permanence metric generally discriminated between seasonal and semipermanent wetlands ($P < 0.001$; ANOVA), though some seasonal basins had permanence metrics more similar to those of semipermanent basins. Using this metric, we determined that sediment removal (EXC) did not significantly influence water permanence ($P = 0.76$; ANOVA). However, among EXC wetlands the amount of sediment removed was a marginally significant predictor of water permanence ($P = 0.078$; ANOVA).

In autumn of 2018 we identified eight reference wetlands with no known history of drainage. Using Google Earth Pro we identified approximately 30 likely candidate wetlands that were undrained and within our project area. We determined land ownership using publicly available parcel ownership maps and contacted all land owners over the telephone. One private property owner granted us access to two wetlands and answered questions relating to land use history on the property. All other reference basins were located on public lands owned by either the city, county, state, or federal government. Among reference basins located on public lands, the history of land use was pieced together with oral accounts from local residents and U.S. Fish and Wildlife Service employees. We confirmed oral accounts to the best of our ability using digitally archived aerial imagery dating as far back as 1939 (University of Minnesota, Historical Aerial Photographs). Reference basins ranged in size from 0.3 to 1.6 ha (mean 0.9 ± 0.5 SD), which made reference sites, on average, larger than restored basins (mean 0.6 ha, ± 0.4 SD; $P = 0.019$, ANOVA). The contributing watersheds were smaller among reference wetlands (mean 6.6 ha ± 4.8 SD) compared to restored basins (mean 11.4 ha ± 21.5 SD), but the difference was not significant ($P = 0.53$, ANOVA). Cultivated land use in the contributing watershed was much higher in reference basins (median 74.0 %, mean 58.1 % ± 35.3 SD) compared to restored wetlands (median 0%, mean 10.2 % ± 17.6 SD; $P < 0.001$). We compared restoration outcomes with reference basins as an indicator of restoration trajectories relative to the more stable conditions expected at references sites.

Soil Characterization

We collected three intact soil cores from the emergent macrophyte zone in each wetland, taking care to evenly space sampling locations across the basin. Cylindrical cores with 5-cm diameter and 30-cm length were collected using acid-washed plastic terpolymer core liners (AMS Inc. Idaho, USA). We split the plastic soil core liners using mounted cast saws (LacCore National Lacustrine Coring Facility, Minnesota, USA) and divided each core into six evenly spaced sections. We measured bulk density in the top (0 - 5 cm), middle (10 - 15 cm), and bottom (20 - 25 cm) sections of each core before sieving partially dried sections through a 2-cm mesh. Once sieved, all soils were dried at 60° C in a gravity convection oven for at least 48 hours prior to long-term storage.

We quantified soil organic matter and carbonate (CO_3) sequentially with the loss on ignition method (Dean 1974; Heiri et al. 2001), and subsequently estimated organic carbon (C) using a conservative conversion factor of 0.58 since the soils were often heavily modified by years of row-crop agriculture (Pribyl 2010; Abella & Zimmer 2007). We measured total nitrogen (TN) using a Costech ECS 4010 CHNSO Analyzer (Costech Analytical Technologies Inc). Soil pH, bioavailable phosphorus assays, and elemental analysis were completed at the University of Minnesota Soil Testing and Research Analytical Lab (Minnesota, USA). Soil pH was examined prior to phosphorus analyses. Bioavailable phosphorus (P) was extracted from all soil samples using the Bray-I method for acidic samples (Bray & Kurtz 1945) and the Olsen method for basic samples (Olsen et al. 1954). To measure total soil calcium (Ca), iron (Fe), and phosphorus (TP) content, 5 mg of sample from the top 5 cm of each soil core were homogenized prior to nitric acid microwave digestion for elemental analysis with ICP-OES (Fassel & Kniseley 1974; Dahlquist & Knoll 1978). As an indicator of soil P storage capacity, we calculated molar ratios of soil P with regard to Ca and Fe content. We also calculated molar ratios of C, N, and P as an approximation of relative organic N and P storage.

Statistical Analyses

We used mixed effects models to examine whether soils differed between restored and reference conditions throughout the soil profile, controlling for repeated measurements within wetlands by including wetland-specific site identity (Site) as a random effect. We included treatment (restored or reference), and the interaction between treatment and core section (top, middle, or bottom) as fixed effects. Since total P, Ca, and Fe content were only measured in the top layer of the soil profile, we examined differences between restored and reference wetlands involving those elements using one way analysis of variance (ANOVA).

To assess the effects of restoration strategy (BAU or EXC), hydroperiod (Seasonal or Semipermanent), and wetland age (0 to 8 years), on soil characteristics of restored basins, we employed analysis of covariance (ANCOVA) using the mean response of soils across all three replicate cores, resulting in a single, mean observation for each wetland. Our ANCOVA did not include reference wetlands since reference basins did not have a fixed age. The model considered the top 5 cm of the soil profile, which represents the sediments in direct contact with the water column and those actively involved in microbially mediated ecosystem services (e.g., denitrification) and reflects some portion of the recent sediment depositional history. We included terms to account for possible interactive effects of treatment by age and treatment by hydroperiod. We did not have an adequate sample size to account for hydroperiod by age effects in the same model (but see Appendix 3, Table A3.1, Figure A3.1).

Whenever necessary, we truncated outliers and log-transformed response variables to meet model assumptions of homogeneous residual error. Statistical analyses were performed in R (R Core Team 2020) using the base, ‘*lme4*’ and ‘*lmerTest*’ packages (Bates et al. 2020; Kuznetsova et al. 2020) with a critical *P*-value of 0.05. We evaluated significant and marginally significant interactions between factor levels with Tukey HSD post-hoc tests for pairwise comparisons using the ‘*emmeans*’ package in R (Lenth et al. 2020).

Results

Restored Versus Reference

Restored wetlands had significantly higher bulk density and bioavailable phosphorus pools, and lower soil C and N pools, compared to reference wetlands (Figure 3.2). Soil bulk density was higher in restored wetlands (mean 1291.7 $kg \cdot m^{-3}$ ± 165.4 SD) than reference basins (mean 744.7 $kg \cdot m^{-3}$ ± 262.6 SD) across all layers of the soil profile ($P < 0.001$, Table 3.3). In restored wetlands, soils were significantly less compacted in the top 5 cm of the soil profile than in deeper layers ($P < 0.001$), but there was little difference between soil bulk density deeper in the soil profile ($P = 0.12$, Table 3.2). In contrast, bulk density increased steadily with depth in the soil profile at reference basins (*P* < 0.001, Table 3.3).

Despite elevated soil bulk density, restored basins had significantly lower organic C (mean 4.1 $kg \cdot m^{-2}$ ± 1.0 SD) and total N pools (mean 0.35 $kg \cdot m^{-2}$ ± 0.1 SD) compared to reference wetlands (mean 6.0 and 0.48 $kg \cdot m^{-2}$ C and N, respectively) in all layers of the soil profile ($P < 0.01$, Tables 3.2 and 3.3). Organic C pools were significantly higher at the soil surface than at the bottom of the soil profile in both reference and restored basins (Tables 3.2 and 3.3). In restored wetlands, total N pools were also significantly lower at the bottom of the soil profile than in the top ($P < 0.001$) and middle layers ($P = 0.023$), while in reference wetlands, soil N pools did not differ with depth in the soil profile (Table 3.3). Molar ratios of organic C to total N ($C_{organic}:N_{total}$) were lower in restored wetlands (mean 13.7 ± 1.5 SD) than in reference basins (mean 14.8 ± 2.7 SD; $P < 0.01$), but the difference was fairly modest and was driven by the top layer of the soil profile (Table 3.2, Figure 3.2).

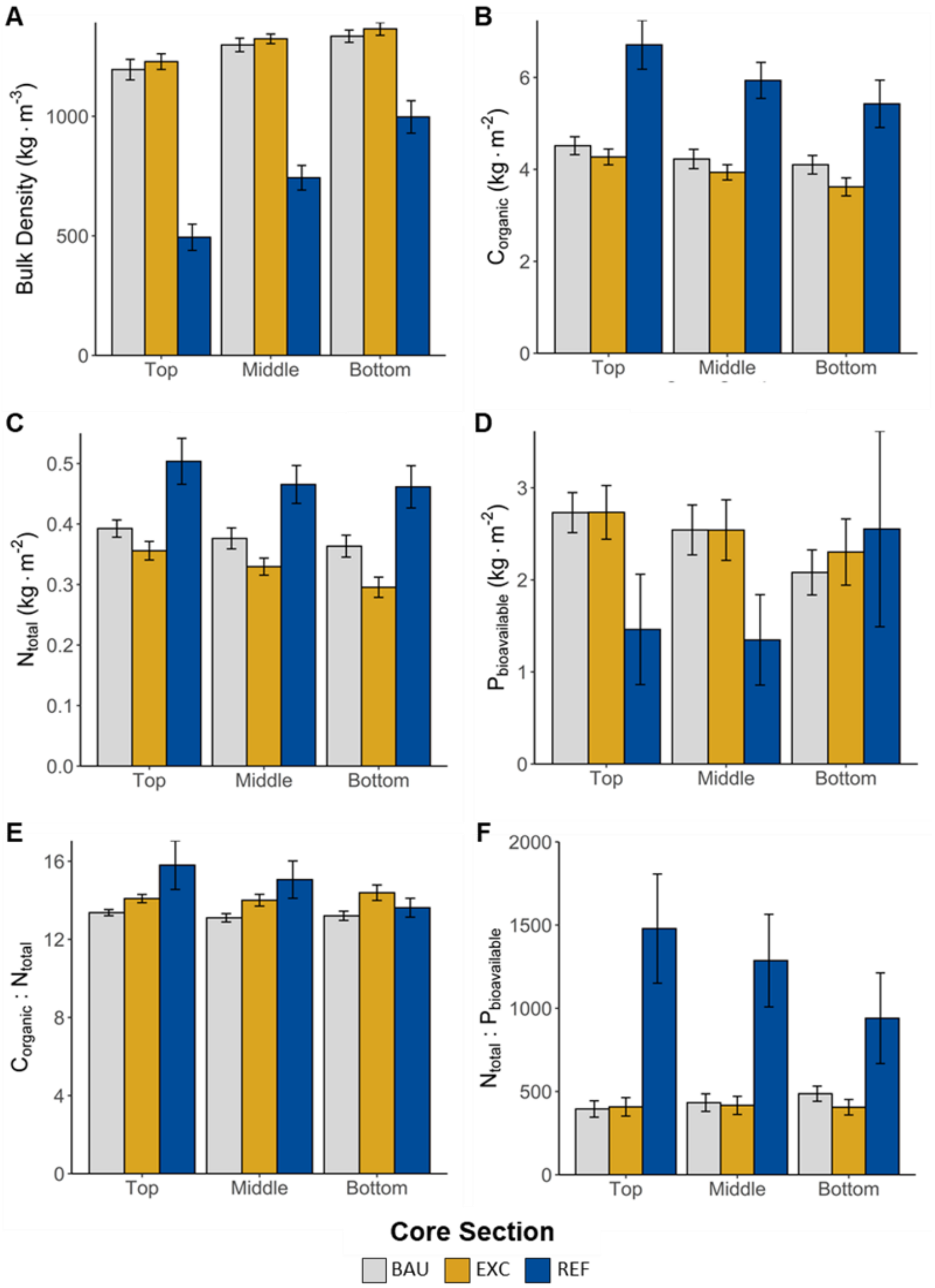

Figure 3. 2. Layer-specific soil bulk density, nutrient pools, and molar ratios in the top (0 – 5 cm), middle (10 – 15 cm), and bottom (20 - 25 cm) layers of the soil profile. Soil bulk density (A), organic carbon (B), total nitrogen (C), and bioavailable phosphorus (D) pool in restored (BAU, Business as Usual; EXC, Excavated) and reference (REF) wetlands. Molar ratios of organic carbon to total nitrogen (E) and total nitrogen to bioavailable phosphorus (F) were substantially lower in restored basins compared to reference. Error bars represent standard error. Statistically significant differences indicated in Table 3.3.

In the top and middle layers of the soil profile, restored wetlands contained approximately two times more bioavailable P than reference basins ($P < 0.01$ and $P = 0.014$, top and middle, respectively; Figure 3.2). Restored basins had significantly smaller bioavailable P pools in the bottom layer of the soil profile compared to the top and middle layers ($P < 0.01$ and $P = 0.034$, respectively); in reference wetlands, bioavailable P pools were significantly larger in the bottom layer of the soil profile than in the top or middle layers ($P = 0.024$ and $P = 0.019$, respectively). The molar ratio of total N to bioavailable P (N_{total}:$P_{bioavailable}$) was approximately three times larger in reference basins compared to restored wetlands ($P < 0.001$; Table 3.2), with significantly higher N_{total}:$P_{bioavailable}$ molar ratios in reference compared to restored wetlands in every layer in the soil profile (Figure 3.2, Table 3.3).

Although restored basins contained substantially larger bioavailable P pools in the top 5 cm of the soil profile than reference wetlands (Table 3.2), total P pools were only marginally larger in restored compared to reference wetlands ($P = 0.057$, Figure 3.3, Table 3.4). The molar ratio of total N to total P (N_{total}:P_{total}) followed a similar pattern to that of N_{total}:$P_{bioavailable}$, with reference basins containing approximately three times higher N_{total}:P_{total} molar ratios compared to restored basins ($P < 0.001$, Table 3.4). Soil Fe pools were substantially larger in restored basins compared to reference wetlands ($P < 0.001$; Table 3.4), which may have contributed to significantly lower total P to Fe (P_{total}:Fe) molar ratios in restored compared to reference basins (*P* < 0.001, Figure 3.3). We did not detect significant differences in soil Ca pools between restored and reference wetlands (*P* = 0.68, Figure 3.3), but restored basins had significantly higher bioavailable P to Ca ($P_{bioavailable}$:Ca) molar ratios compared to reference condition (*P* = 0.024, Table 3.4).

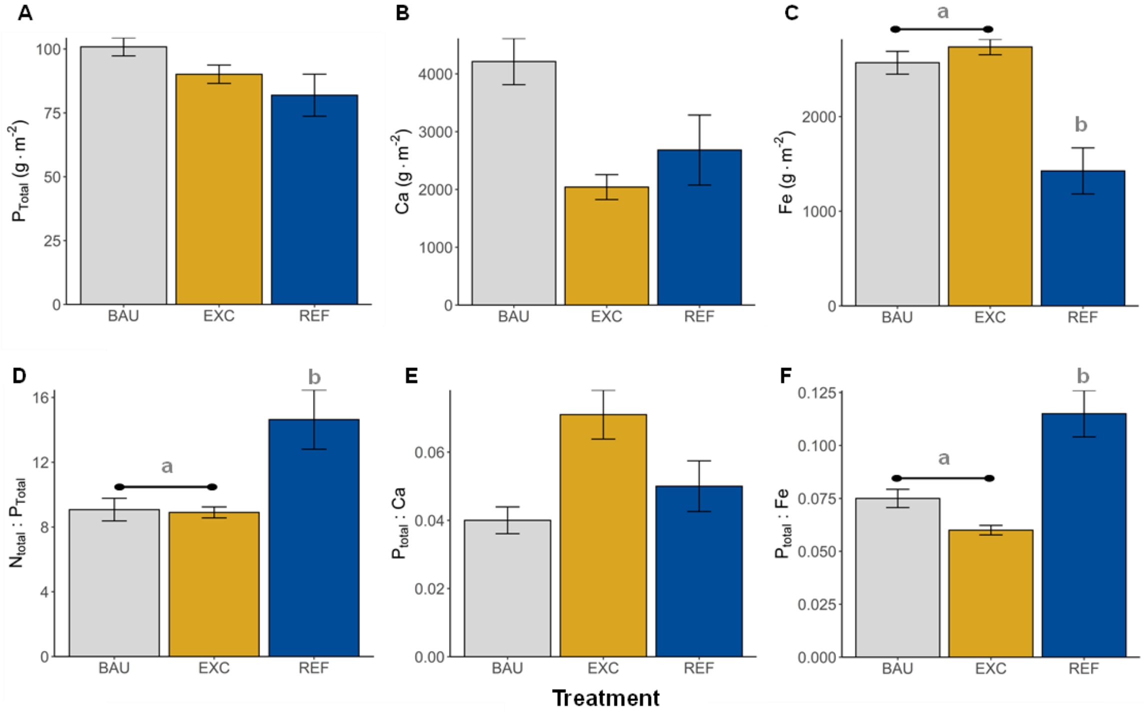

Figure 3. 3. Comparison between restored (BAU, Business as Usual; EXC, Excavated) and reference (REF) total phosphorus and select metal pools in the top layer of the soil profile (0 – 5 cm). Restored wetlands had marginally significantly more total P than restored basins (A; P = 0.057). There were no significant differences in calcium pools (B) or the molar ratio of total phosphorus to calcium (E) in restored and reference wetlands. Iron pools were significantly higher in restored basins (C) and the molar ratio of total phosphorus to iron (F) was lower in restored compared to reference wetlands. Molar nitrogen to total phosphorus ratios were lower in restored compared to reference basins (D).

Restoration Strategies, Hydroperiod, and Time

Among restored wetlands, EXC basins had smaller soil organic C and total N pools compared to BAU basins, but C and N pools grew larger over time at EXC basins (Figure 3.4, Tables 3.5 and 3.6). In EXC basins, soil organic C (mean 4.3 $kg \cdot m^{-2}$) and total N (mean 0.36 $kg \cdot m^{-2}$) pools were smaller than in BAU wetlands (mean 4.5 and 0.39 $kg \cdot m^{-2}$ C and N, respectively; $P = 0.04$ and 0.006, respectively), but the difference was almost entirely driven by EXC basins with semipermanent hydroperiods (Figure 3.4, Tables 3.5 and 3.6). As EXC wetlands aged, they accumulated soil C ($P = 0.01$, Table 3.6) and N ($P = 0.004$), despite a significant decline in bulk density over the same period ($P = 0.04$, Figure 3.4). Similar temporal patterns were not detected in BAU wetlands (Table 3.6, Figure 3.4).

Hydroperiod was a reliable predictor of soil bioavailable P pools (Figure 3.5) and the relative availability of P to other soil elements including N and Fe (Figure 3.6, Tables 3.5 and 3.6). In semipermanent wetlands, bioavailable P pools were approximately half that of seasonal basins ($P < 0.01$, Table 3.5), with hydroperiod representing the only meaningful predictor of bioavailable P (Table 3.6). By comparison, we did not detect meaningful differences in total P and soil Fe pools by restoration strategy, hydroperiod, or wetland age (Figure 3.5, Table 3.6). Soil carbonate pools were smaller in EXC sites compared to BAU basins ($P = 0.041$, Table 3.5), and the trend was driven by excavated basins with seasonal hydroperiod ($P = 0.024$). Total soil Ca followed the same pattern as carbonates (Figure 3.5, Table 3.6).

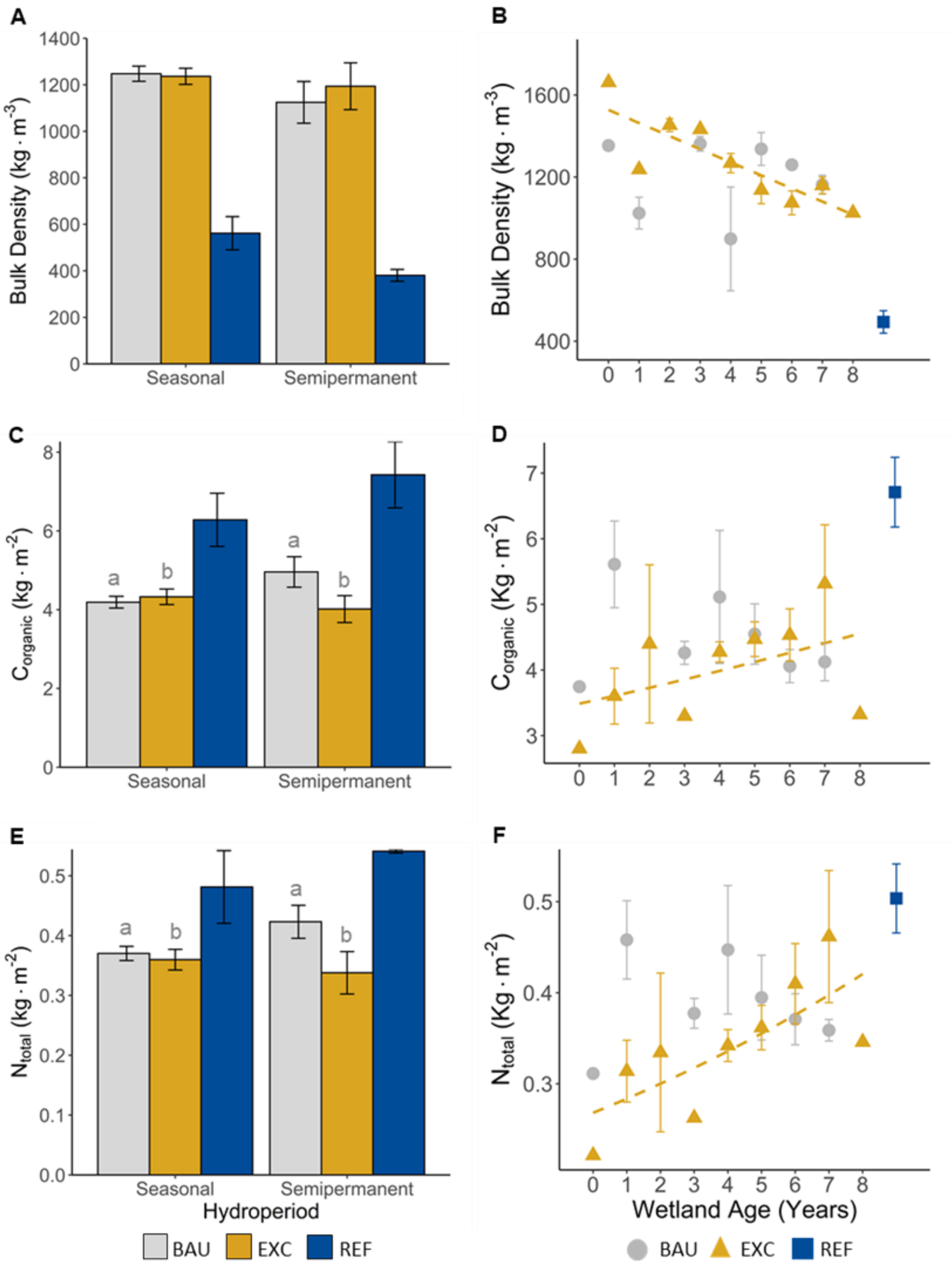

Figure 3. 4. Soil bulk density (A-B), organic carbon (C-D), and total nitrogen pool sizes (E-F) in the top 5 cm of the soils in Business as Usual (BAU) and Excavated (EXC) wetlands. Mean response in basins with seasonal and semipermanent hydroperiod (left) are shown with standard error bars. Letters indicate significant group differences. Significant effects of wetland age since restoration (right) are indicated by color coded trend lines. Error bars represent standard error. Mean response in reference basins (REF) are included for reference only. We did not have a large enough sample size to account for hydroperiod by age effects. Excavated basins had significantly less soil carbon (C) and nitrogen (E) than BAU basins, and both increased over time at EXC basins (D and F).

Molar ratios of total N to bioavailable P (N_{total}:$P_{bioavailable}$) were primarily influenced by hydroperiod, with substantially higher N_{total}:$P_{bioavailable}$ ratios in semipermanent wetlands (mean 627.2 ± 328.2 SD) compared to seasonal basins (mean 306.7 ± 173.8 SD, $P = 0.002$). Total N to total P molar ratios (N_{total}:P_{total}) were also elevated in basins with semipermanent (mean 10.4 ± 4.2 SD) compared to seasonal hydroperiod (mean 8.4 ± 1.6 SD; $P = 0.018$). Furthermore, N_{total}:P_{total} molar ratios increased over time in EXC sites ($P = 0.015$, Table 3.6). The molar ratio of bioavailable P to Fe ($P_{bioavailable}$:Fe) was lower in wetlands with semipermanent compared to seasonal hydroperiods ($P = 0.0065$). In addition, restoration strategy was an important predictor of $P_{bioavailable}$:Fe molar ratios ($P = 0.019$), with modestly lower ratios and substantially less variability in EXC wetlands compared to BAU restorations (Table 3.5). In EXC wetlands the $P_{bioavailable}$:Fe molar ratio increased significantly as wetlands aged ($P = 0.032$; Table 3.6). Similar to bioavailable P, EXC basins had marginally lower total P to Fe molar ratios (P_{total}:Fe) compared to BAU restorations ($P = 0.058$), largely driven by EXC basins with seasonal hydroperiods. Molar ratios of both bioavailable and total P to soil Ca were significantly higher in EXC basins with seasonal hydroperiod compared to all other restoration strategy and hydroperiod combinations (Figure 3.6).

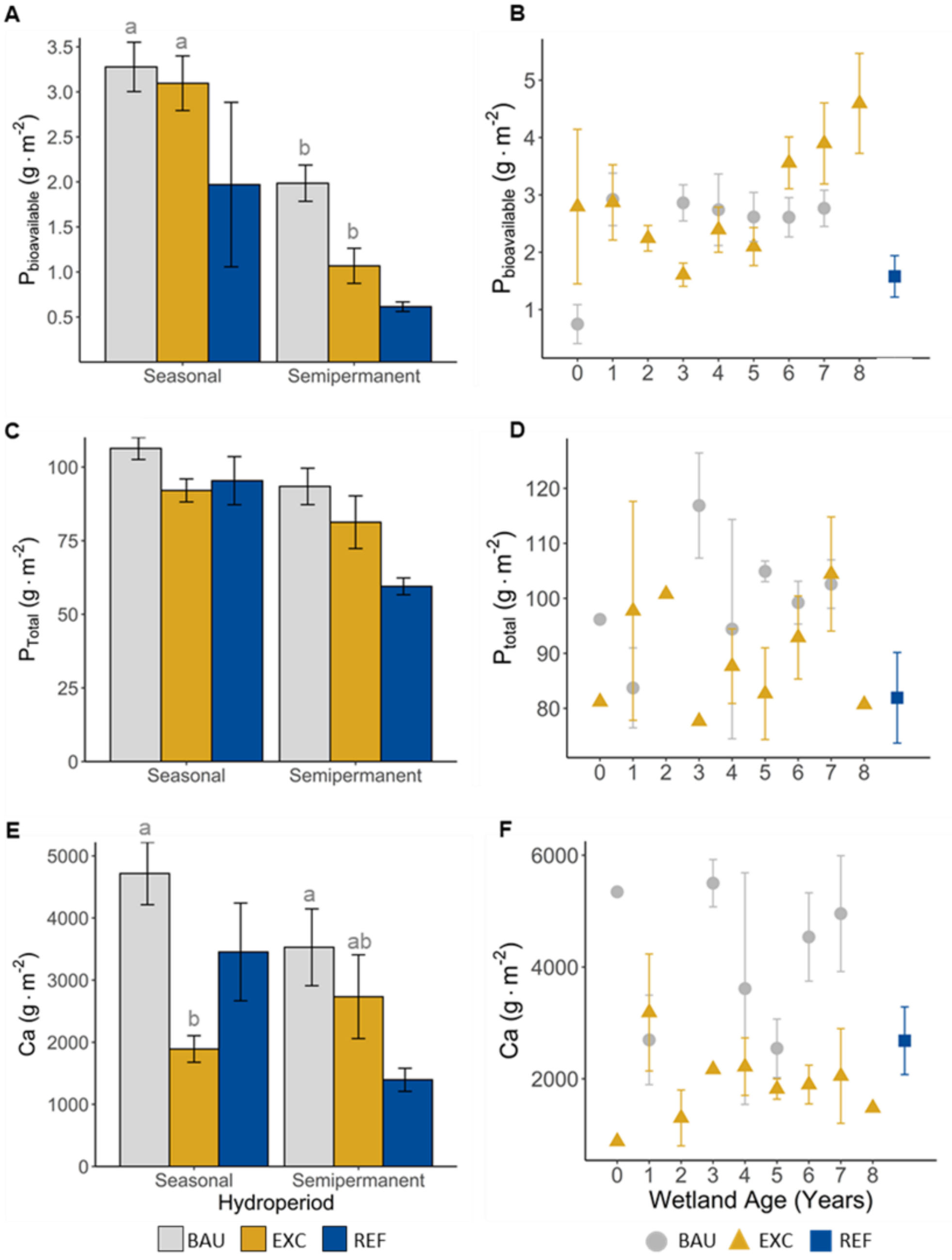

Figure 3. 5. Bioavailable phosphorus (A-B), total phosphorus (C-D), and calcium pool sizes (E-F) in the top layer (0 - 5 cm) of the soil profile in Business as Usual (BAU) and Excavated (EXC) wetlands. Reference basins (REF) are included for reference only. Mean response in basins with seasonal and semipermanent hydroperiod (left) are shown with standard error bars. Letters indicate significant pairwise differences. Significant effects of wetland age since restoration (right) are indicated by color-coded trend lines. Neither bioavailable phosphorus, total phosphorus, nor soil calcium varied with wetland age. We did not have a large enough sample size to account for hydroperiod by age effects.

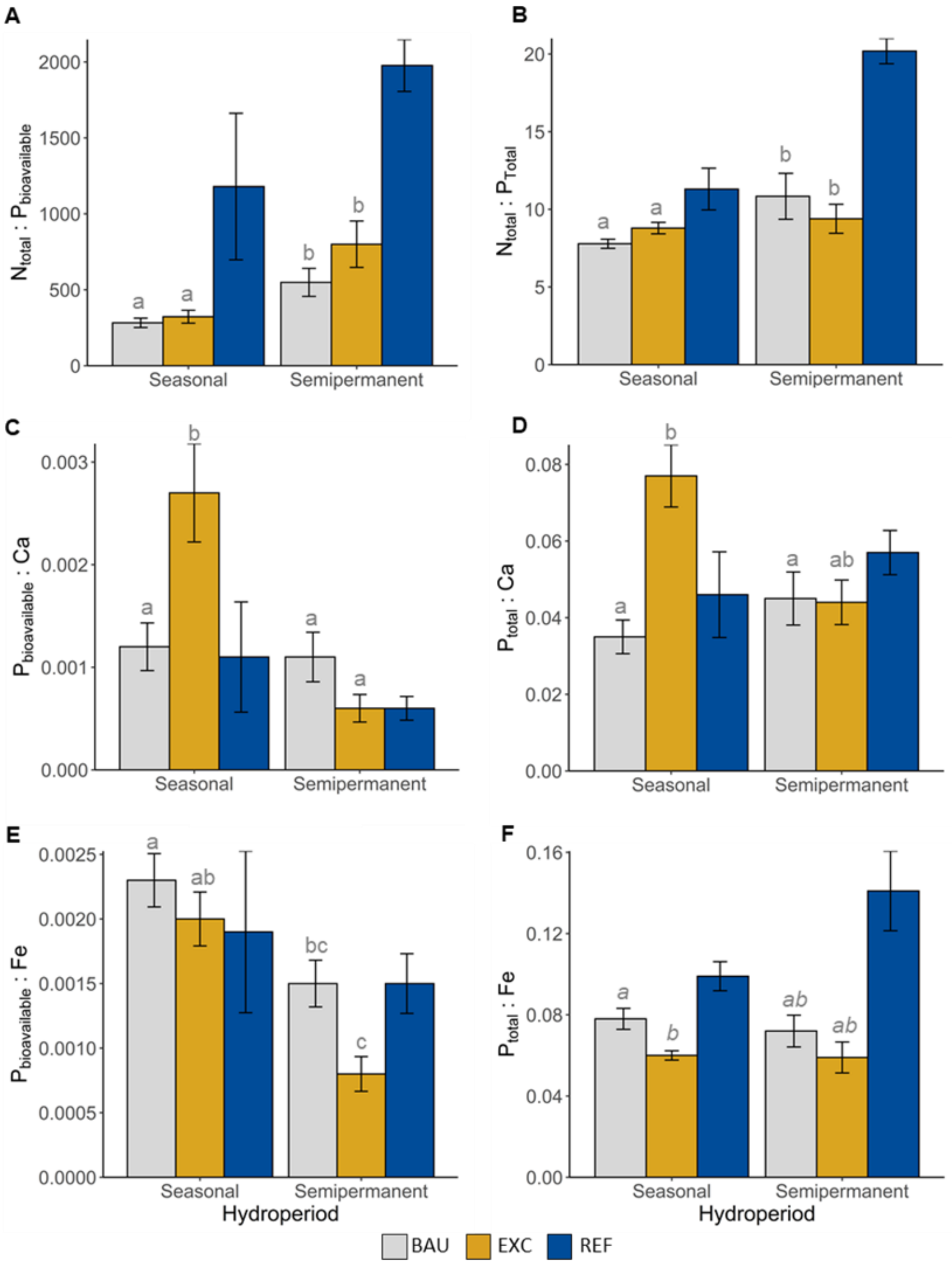

Figure 3. 6. Molar ratios of total nitrogen to bioavailable phosphorus (A) and total phosphorus (B); bioavailable phosphorus to calcium (C) and iron (E); and total phosphorus to calcium (D) and iron (F), in the top layer (0 - 5 cm) of the soil profile. Business as Usual (BAU) and Excavated (EXC) wetlands are grouped by seasonal (left) and semipermanent hydroperiod (right). Reference basins (REF) are included for reference only. Differences between groups are shown as mean response with standard error bars. Letters indicate significant pairwise differences. Total phosphorus to iron molar ratio was marginally significantly higher at BAU basins compared to EXC (P = 0.058).

Discussion

Excavation significantly reduced soil C and N pools, while hydroperiod was primarily responsible for variation in soil P pools. Sediment excavation prior to wetland restoration removed a significant fraction of soil C and N, but pools for both elements rapidly recovered (within eight years) to the business-as-usual condition following restoration of hydrology. Restored wetland soil P dynamics were primarily influenced by hydroperiod of restored basins, with smaller bioavailable P pools and lower N:P molar ratios in semipermanent wetlands. Our results suggest that the effects of sediment excavation on soil C and N pools was short-lived, and any effect of sediment removal on P dynamics was likely indirectly mediated by modest increases in wetland hydroperiod, which was a more reliable predictor of soil P.

Restoration Strategy and Hydroperiod Matter

Removing accumulated eroded sediments during wetland restoration temporarily increased soil bulk density and reduced organic C and total N pools in the top 5 cm of the soil profile, but soil properties in EXC basins recovered to the BAU condition within eight years. Recovery of soil bulk density, organic C, and total N pools were driven almost entirely by excavated basins with semipermanent hydroperiod (n=5), which constituted a small subset of our restored wetland sample size (N=54). Typically, soils are enriched in organic matter nearer the surface where root densities are highest and decomposing litter contribute to the soil organic matter pool, and it is not uncommon for excavation and dredging to uncover soils with lower soil organic matter, organic C, and total N content (Craft et al. 1991; Werkmeister et al. 2018). Over time, bulk density, soil organic matter pools, and decomposition rates can begin to recover, particularly in the top 5-10 cm of the soil profile (Meyer et al. 2008; Streeter & Schilling 2015; Ballantine & Schneider 2009; Atkinson & Cairns 2001; Craft 1996). However, depressional wetland soil characteristics recover at a slow pace, and changes may be difficult to detect in the first 10-15 years following restoration (Meyer et al. 2008; Ballantine & Schneider 2009), which constitutes the age range of most restoration studies, including ours (but see Craft et al 2003; Ballantine and Schneider 2009). Detecting any change over an eight-year period, as we did, is remarkable but more importantly it suggests that the initial short-lived differences between the BAU and EXC basin C and N pools were unlikely to have had long-lasting impacts on ecosystem functioning. Depressional wetlands have highly variable accretion rates, stemming from a large degree of variability in land use history in the surrounding watershed (Craft & Casey 2000), which subsequently alters autochthonous productivity and decomposition rates, the primary drivers of nutrient accumulation in depressional basins (Atkinson & Cairns 2001; Meyer et al. 2008; Ballantine & Schneider 2009; Bernal & Mitsch 2012; Reddy et al. 1993).

Among restored wetlands, pools of bioavailable P, and the relative availability of organic C and total N to P, were primarily influenced by differences in wetland hydroperiod; bioavailable P pools were smaller, and the relative availability of organic C and total N to bioavailable P were higher, in semipermanent wetlands. Previous studies have found that inundation history is a meaningful predictor of soil P release. Soils with a history of continuous or near-continuous inundation released less dissolved P into the water column following brief periods of drawdown (Martin et al. 1997; Pant & Reddy 2001; Aldous et al. 2005). Longer hydroperiods result in the accumulation of decomposing organic matter and associated microbial communities that transform and store P (Hogan et al. 2004; Martin et al. 1997; Pant & Reddy 2001; Aldous et al. 2005). Relatively short drawdown periods, which retain soil moisture and minimize microbial stress, can consolidate organically bound P into more recalcitrant organic molecules (Martin et al. 1997; Pant & Reddy 2001), resulting in simultaneous increases in soil organic matter and P storage (Hogan et al. 2004). In our study, some semipermanent basins did, on occasion, experience brief periods of drawdown with nearly all standing water absent from the basin, but the soils retained substantial moisture. By comparison, seasonally inundated basins annually experienced drawdowns that lasted a week or more with all standing water completely absent from the basin (personal observation). Thus, smaller bioavailable P pools, and elevated $C:P_{bioavailable}$ and $N:P_{bioavailable}$ ratios in semipermanently flooded wetlands (Tables 3.5 and 3.6), suggest elevated soil organic P storage in basins with longer hydroperiods.

The role of excavation in soil P dynamics were more subtle than the effects of hydroperiod. Excavated wetlands had lower $P_{bioavailable}$:Fe molar ratios and, among seasonally inundated basins, higher $P_{bioavailable}$:Ca and P_{total}:Ca molar ratios. Elevated P:Ca ratios among excavated basins may reflect the exposure of unweathered soil parent materials, rich in apatite (Hedley et al. 1995). The relationship between Fe and P is of particular interest, since lower $P_{bioavailable}$:Fe and P_{total}:Fe molar ratios could encourage inorganic P immobilization in EXC basins. Previous studies have found that dredging can reduce internal P loading (Oldenborg & Steinman 2019; Reddy et al. 2007), but P fluxes into and out of wetland soils are mediated by a suite of factors including land use history (Craft & Casey 2000; Craft et al. 2018; Sharpley 1995; Martin & Hartman 1987), water column dissolved P, dissolved oxygen (Fisher & Reddy 2001; Oldenborg & Steinman 2019; Hogan et al. 2004), dissolved nitrate concentration (Surridge et al. 2007; Degasperi et al. 1993), and the availability of cationic electron acceptors (Porter & Sanchez 1992; Diaz et al. 1994; Craft 1996; Hogan et al. 2004). The relative availability of P compared to soil metal constituents can be a valuable indicator of soil P storage capacity (Porter & Sanchez 1992; Surridge et al. 2007; Hogan et al. 2004), because iron (Fe) and aluminum (Al) oxides and hydroxides, and magnesium (Mg) and calcium (Ca) carbonates can coprecipitate phosphate ions, resulting in mineral-bound P retention (Reddy et al. 1999; Cole et al. 1953;

Cooke et al. 1982; Degasperi et al. 1993; Frossard et al. 1995). Moreover, Fe and Al oxides can form fairly stable organic matter complexes with P (Dolfing et al. 1999; Hogan et al. 2004). In our study, EXC basins had lower P:Fe molar ratios compared to BAU basins, suggesting that the soils may have a higher capacity to bind P, particularly bioavailable P.

Natural and Restored Wetlands are Different

Wetland drainage and cultivation significantly reduced soil C and N pools while nearly doubling soil bioavailable P and bulk density in restored basins compared to undrained reference wetlands. Our results add to the substantial body of literature characterizing and quantifying the considerable impacts of wetland drainage and cultivation to soil health (Moreno-Mateos et al. 2012). Both restored and created wetlands have fundamentally different soil characteristics than naturally occurring basins, regardless of restoration strategy employed. Previous work provides ample evidence that created wetlands have substantially higher bulk density and lower soil organic matter than their natural counterparts (Bishel-Machung et al. 1996; Campbell et al. 2002; Ballantine & Schneider 2009), despite substantial background soil variability (Bruland & Richardson 2005). Drainage and cultivation of natural wetlands give rise to similar shifts in soil characteristics. Cultivation influences soil structure by compacting soils (Thomas et al. 1996; Franzluebbers et al. 2000), physically mixing and breaking apart soil aggregates (Jastrow 1996; Amézketa 1999), increasing the rate of erosional deposition (Saini & Grant 1980; Gregorich & Anderson 1985; Bakker et al. 2008), and favoring the accumulation of finer soil particulates with higher inorganic nutrient content (Martin & Hartman 1987; Ockenden et al. 2014; Preston et al. 2013).

Drainage exposes soils to substantially more oxygen, resulting in elevated decomposition rates and nutrient mobilization, eventually leaving soils with depleted soil organic matter and nitrogen pools (Brown et al. 2017; Poeplau et al. 2011; Murty et al. 2002), particularly when compared to reference wetlands (Streeter & Schilling 2015; Meyer et al. 2008; Brown & Norris 2018). The depletion of soil nutrient pools compared with natural wetlands is consistent with lost storage of reactive forms of C and N, which can have substantial repercussions in the atmosphere and biosphere. A meta-analysis by Moreno-Mateos et al. (2012) revealed that 20 years after restoration soil C stores in restored wetlands were still less than half that of natural wetlands. Using modern estimates of global wetland land cover (9,167 x 10^3 km^2) (Lehner & Döll 2004) and a conservative estimate of 64% wetland loss between 1900 and 2000 CE (Davidson 2014), we can reasonably say that approximately 5,156 x 10^3 km^2 (or 515.6 x 10^6 ha) of wetland were drained in the 20th century alone. Assuming inland wetlands hold 0.091 Pg C / 10^6 ha in the top 30 cm of the soil profile (Nahlik & Fennessy 2016), and drained wetland soils contain 31% of C found in natural wetlands (Moreno-Mateos et al. 2012), we calculate that wetland drainage in the 20th century liberated approximately 32.4 Pg C from soil storage.

This means that in the 20th century, drained wetland soils released roughly as much carbon into the atmosphere as global CO_2 emissions in the five years between 1996 and 2000 CE (Olivier et al. 2012). Assuming all of those wetlands were restored today, it would take over 20 years to recover just 8.9 Pg C, but that would offset global CO_2 emissions for the year 2010 CE (Olivier et al. 2012). Current estimates suggest that similar strategies designed to restore and protect coastal wetlands, peatlands, grasslands, and forests could offset 23.8 Pg CO_2 / yr in emissions, but it would only be cost effective to offset 11.3 Pg CO_2 / yr (Griscom et al. 2017). By comparison, our estimates suggest that inland wetland restoration could augment C storage by an additional 0.45 Pg C / yr.

Conclusions

Because drainage and cultivation leave an indelible mark on soil physical and chemical properties, preventing drainage is the best option for maintaining ecosystem services provisioned by wetlands. Still, there is substantial need to restore wetlands that have already been drained and cultivated, whether for water quality improvement (Salk et al. 2018; Kreiling et al. 2013), carbon sequestration (Bernal & Mitsch 2012; Mitsch et al. 2012), flood prevention (Hey & Philippi 1995), or habitat provisioning (Houlahan & Findlay 2003; Lehtinen et al. 1999). Our results suggest sediment excavation modestly reduced soil nutrient pools, and increased inorganic P binding potential by decreasing P:Fe ratios. It may be more important to restore basins that are likely to have longer hydroperiods than to excavate accumulated sediments, thus prioritizing basins that are more likely to effectively trap organically bound P and protect larger bodies of water from P enrichment. To that end, excavation may extend wetland hydroperiod and subsequently improve soil P retention, but it is important not to remove too much sediment, as this could have unintended consequences for wildlife habitat utilization and biodiversity maintenance (Dahl 2014).

Table 3. 1. Land use, land cover in contributing watersheds. Cultivated cover includes row crop agriculture. Developed cover includes roads, homes, and wasteland that is functionally impervious to water infiltration. Impacted cover is the sum of cultivated and developed land use coverages. Grassland cover includes restored tall grass prairie and mixed cool season grass fields periodically harvested as hay. Natural cover is the sum of grassland and forested coverages. Standard deviation is shown parenthetically.

	Restoration Strategy		***Hydroperiod***		***Strategy X Hydroperiod***			
	BAU	***EXC***	***Seasonal***	***Semipermanent***	***BAU X Seasonal***	***BAU X Semipermanent***	***EXC X Seasonal***	***EXC X Semipermanent***
Cultivated (%)	8.29 (19.04)	11.96 (16.22)	8.77 (14.86)	13.59 (22.98)	2.82 (7.02)	15.75 (27.05)	12.65 (17.32)	8.82 (10.48)
Developed (%)	0.37 (0.90)	1.35 (2.25)	0.97 (2.02)	0.66 (1.09)	0.09 (0.34)	0.76 (1.26)	1.55 (2.43)	0.44 (0.60)
Impacted (%)	8.67 (19.50)	13.31 (16.65)	9.74 (15.37)	14.25 (23.54)	2.91 (7.01)	16.52 (27.64)	14.19 (17.70)	9.26 (11.07)
Grassland (%)	62.44 (18.56)	65.71 (21.47)	67.78 (18.77)	55.49 (20.76)	70.28 (10.42)	51.75 (22.17)	66.14 (22.72)	63.72 (16.28)
Forest (%)	7.96 (15.41)	5.35 (8.55)	4.30 (8.67)	12.10 (17.39)	4.27 (8.91)	13.01 (20.83)	4.31 (8.70)	10.09 (6.51)
Natural (%)	70.41 (18.62)	71.05 (17.62)	72.07 (16.38)	67.59 (21.46)	74.55 (11.41)	64.76 (24.97)	70.46 (19.01)	73.81 (9.90)

Table 3. 2. Soil characteristics across in restored and reference basins at all layers in the soil profile; top (0 - 5 cm), middle (10 - 15 cm), and bottom (20 - 25 cm). Standard deviation is shown parenthetically.

	Restored				***Reference***			
	All Core Sections	**Top Section**	**Middle Section**	**Bottom Section**	**All Core Sections**	**Top Section**	**Middle Section**	**Bottom Section**
Bulk Density (kg/m^3)	1291.7 (165.4)	1212.6 (195.6)	1311.6 (125.8)	1350.8 (136.6)	744.7 (262.6)	493.9 (154.6)	743.0 (145.5)	997.2 (191.9)
$CaCO_3$ (kg/m^2)	7.8 (4.2)	7.4 (4.0)	7.9 (4.3)	8.0 (4.4)	5.9 (3.0)	5.1 (3.2)	5.8 (3.0)	6.7 (3.1)
Organic Matter (kg/m^2)	10.6 (1.7)	10.8 (1.6)	10.8 (1.7)	10.3 (1.9)	13.7 (2.3)	14.1 (2.4)	14.1 (1.7)	13.0 (2.9)
Organic Carbon (kg/m^2)	4.1 (1.0)	4.4 (1.0)	4.1 (1.0)	3.9 (1.1)	6.0 (1.4)	6.7 (1.5)	5.9 (1.1)	5.4 (1.5)
Total Nitrogen (kg/m^2)	0.35 (0.09)	0.37 (0.08)	0.35 (0.08)	0.33 (0.10)	0.48 (0.10)	0.50 (0.11)	0.47 (0.09)	0.46 (0.10)
Bioavailable P (g/m^2)	2.5 (1.5)	2.7 (1.3)	2.5 (1.6)	2.2 (1.6)	1.8 (2.1)	1.5 (1.7)	1.3 (1.4)	2.6 (3.0)
$C_{organic}$: N_{total}	13.7 (1.5)	13.7 (1.0)	13.6 (1.4)	13.8 (1.8)	14.8 (2.7)	15.8 (3.5)	15.1 (2.7)	13.6 (1.4)
N_{total} : $P_{bioavailable}$	423.5 (262.3)	401.6 (271.0)	424.4 (277.0)	444.5 (240.8)	1235.1 (826.5)	1478.6 (927.5)	1286.4 (787.3)	940.4 (771.1)
$C_{organic}$: $P_{bioavailable}$	5904.8 (3954.1)	5571.2 (3887.3)	5866.2 (4139.3)	6277.1 (3872.0)	18424.4 (12331.7)	23080.4 (14368.6)	19142.3 (10917.1)	13050.3 (10754.4)

Table 3. 3. Statistical significance of soil characteristics across the soil profile. Restored and reference conditions were compared at each layer of the soil core profile, including top (0 - 5 cm), middle (10 - 15 cm), and bottom (20 - 25 cm). Differences between layers of the soil core profile were compared for reference and restored basins separately to identify whether restoration influences how soil characteristics were influenced by depth in the soil profile.

			Pairwise Interactions								
	Main Effects		***Restored – Reference***			***Restored Only: Between Soil Sections***			***Reference Only: Between Soil Sections***		
	Restored - Reference	**Restored - Reference *X* Core Section**	**Top**	**Middle**	**Bottom**	**Top - Middle**	**Top - Bottom**	**Middle - Bottom**	**Top - Middle**	**Top - Bottom**	**Middle – Bottom**
Bulk Density (kg/m^3)	**< 0.001 ****	**< 0.001 ****	**< 0.001 ****	**< 0.001 ****	**< 0.001 ****	**< 0.001 ****	**< 0.001 ****	0.12	**< 0.001 ****	**< 0.001 ****	**< 0.001 ****
† $CaCO_3$ (kg/m^2)	0.062	**< 0.001 ****	0.43	0.79	1.0	0.44	0.40	1.0	0.26	**< 0.001 ****	0.30
Organic Matter (kg/m^2)	**< 0.001 ****	**0.0086 ****	**< 0.001 ****	**< 0.001 ****	**0.0023 ****	1.0	0.19	0.13	1.0	0.33	0.28
†Organic Carbon (kg/m^2)	**< 0.001 ****	**< 0.001 ****	**< 0.001 ****	**0.0013 ****	**0.0045 ****	**0.048 ***	**< 0.001****	0.14	0.63	**0.039 ***	0.70
† Total Nitrogen (kg/m^2)	**0.0015 ****	**< 0.001 ****	**0.024 ***	**0.028 ***	**0.0024 ****	0.14	**< 0.001****	**0.023 ***	0.91	0.84	1.0
† Bioavailable P (g/m^2)	**< 0.001 ****	**< 0.001 ****	**0.0046 ****	**0.014 ***	0.99	0.51	**< 0.001****	**0.034 ***	1.00	**0.024 ***	**0.019 ***
† $C_{organic} : N_{total}$	**0.0041 ****	**< 0.001 ****	0.056 ·	0.22	1.0	0.79	1.0	0.77	0.75	**< 0.001 ****	**0.036 ***
† $N_{total} : P_{bioavailable}$	**< 0.001 ****	**< 0.001 ****	**< 0.001 ****	**< 0.001 ****	0.33	0.99	0.35	0.70	1.0	**0.0081 ****	**0.026 ***
† $C_{organic} : P_{bioavailable}$	**< 0.001 ****	**< 0.001 ****	**< 0.001 ****	**< 0.001 ****	0.41	1.0	0.33	0.51	0.99	**< 0.001 ****	**0.0032**

† Log transformed

· Marginal Significance

* Significant at $P \leq 0.05$

** Significant at $P \leq 0.01$

Table 3. 4. Top soil section (0-5 cm), comparison of restored and reference soil properties. Statistical results are for analysis of variance.

	Statistical Summary	***Mean (SD)***	
		Restored	**Reference**
Bioavailable P (g/m^2)	**3.0 E-04 ****	2.73 (1.34)	1.46 (1.70)
Total P (g/m^2)	*0.057 ·*	95.29 (19.21)	81.92 (23.30)
Ca (g/m^2)	0.68	3087.35 (1957.21)	2681.64 (1713.27)
Fe (g/m^2)	**1.5 E-08 ****	2655.59 (529.94)	1426.22 (689.10)
	Molar Ratios		
N_{total}: $P_{bioavailable}$	**8.4 E-06 ****	401.64 (270.95)	1478.61 (927.53)
N_{total} : P_{total}	**3.6 E-05 ****	8.98 (2.77)	14.64 (5.18)
$C_{organic}$: $P_{bioavailable}$	**2.71 E-06 ****	5571.2 (3887.3)	23080.4 (14368.6)
$C_{organic}$: P_{total}	**4.04 E-06 ****	123.9 (41.6)	232.6 (97.7)
$P_{bioavailable}$: Ca	**0.024 ***	1.77 E-03 (1.82 E-03)	9.01 E-04 (9.76 E-04)
P_{total} : Ca	0.77	5.58 E-02 (3.40 E-02)	4.98 E-02 (2.08 E-02)
$P_{bioavailable}$: Fe	0.68	1.90 E-03 (9.51 E-04)	1.75 E-03 (1.12 E-03)
P_{total} : Fe	**9.2 E-08 ****	6.72 E-02 (1.91 E-02)	1.15 E-01 (3.07 E-02)

Table 3. 5. Soil characteristics in business as usual (BAU) and excavated (EXC) wetlands with seasonal and semipermanent hydroperiod. Values represent mean response in top (0 - 5 cm) section of soil profile. Standard deviation shown parenthetically.

	Restoration Strategy		***Hydroperiod***		***Strategy X Hydroperiod***			
	BAU	**EXC**	**Seasonal**	**Semipermanent**	**BAU X Seasonal**	**BAU X Semipermanent**	**EXC X Seasonal**	**EXC X Semipermanent**
Bulk Density (kg/m^3)	1195.3 (219.2)	1228.7 (173.4)	1240.6 (149.4)	1146.0 (271.0)	1247.4 (126.2)	1124.3 (297.1)	1236.3 (165.4)	1193.8 (225.1)
Organic Matter (kg/m^2)	11.1 (1.6)	10.4 (1.6)	10.6 (1.3)	11.1 (2.2)	10.6 (0.9)	11.7 (2.2)	10.6 (1.5)	9.8 (1.8)
Organic Carbon (kg/m^2)	4.5 (1.0)	4.3 (0.9)	4.3 (0.8)	4.7 (1.2)	4.2 (0.6)	5.0 (1.3)	4.3 (0.9)	4.0 (0.8)
Total Nitrogen (kg/m^2)	0.39 (0.07)	0.36 (0.08)	0.36 (0.07)	0.40 (0.09)	0.37 (0.05)	0.42 (0.09)	0.36 (0.08)	0.34 (0.08)
Bioavailable P (g/m^2)	2.7 (1.1)	2.7 (1.5)	3.2 (1.3)	1.7 (0.7)	3.3 (1.1)	2.0 (0.7)	3.1 (1.5)	1.1 (0.4)
Total P (g/m^2)	100.9 (18.2)	90.1 (19.0)	97.7 (18.4)	89.6 (20.5)	106.3 (14.6)	93.4 (20.5)	92.0 (18.7)	81.3 (20.0)
CaCO3 (kg/m^2)	9.6 (4.3)	5.4 (2.3)	7.2 (4.2)	7.9 (3.6)	10.7 (4.3)	8.2 (4.1)	5.0 (2.2)	7.4 (2.2)
Ca (g/m^2)	4.21 (2.0)	2.04 (1.1)	3.01 (2.0)	3.28 (1.9)	4.72 (1.9)	3.53 (2.0)	1.89 (1.0)	2.73 (1.5)
Fe (g/m^2)	2.57 (0.6)	2.74 (0.4)	2.70 (0.5)	2.55 (0.6)	2.57 (0.5)	2.56 (0.7)	2.78 (0.4)	2.51 (0.3)
	Molar Ratios							
$C_{organic}$: N_{total}	13.4 (0.8)	14.1 (1.1)	13.8 (1.1)	13.7 (0.8)	13.2 (0.8)	13.6 (0.8)	14.1 (1.2)	14.0 (0.8)
N_{total}: $P_{bioavailable}$	395.1 (251.4)	407.7 (292.5)	306.7 (173.8)	627.2 (328.2)	282.4 (118.7)	548.7 (305.4)	322.5 (203.0)	800.0 (341.5)
N_{total} : P_{total}	9.1 (3.6)	8.9 (1.8)	8.4 (1.6)	10.4 (4.2)	7.8 (1.1)	10.8 (4.9)	8.8 (1.8)	9.4 (2.1)
$C_{organic}$: $P_{bioavailable}$	5.3×10^3 (3.6×10^3)	5.8×10^3 (4.2×10^3)	4.3×10^3 (2.6×10^3)	8.6×10^3 (4.7×10^3)	3.7×10^3 (1.5×10^3)	7.5×10^3 (4.4×10^3)	4.6×10^3 (3.2×10^3)	1.1×10^4 (4.6×10^3)
$C_{organic}$: P_{total}	122.5 (53.7)	125.2 (26.8)	115.6 (25.7)	143.5 (62.4)	103.0 (17.9)	149.1 (73.5)	123.9 (27.0)	131.2 (28.1)
$P_{bioavailable}$: Ca	1.1×10^{-3} (8.6×10^{-4})	2.3×10^{-3} (2.3×10^{-3})	2.1×10^{-3} (2.0×10^{-3})	9.1×10^{-4} (6.9×10^{-4})	1.2×10^{-3} (9.3×10^{-4})	1.1×10^{-3} (7.9×10^{-4})	2.7×10^{-3} (2.3×10^{-3})	5.8×10^{-4} (2.6×10^{-4})
P_{total} : Ca	4.0×10^{-2} (2.0×10^{-2})	7.1×10^{-2} (3.8×10^{-2})	6.0×10^{-2} (3.8×10^{-2})	4.5×10^{-2} (2.0×10^{-2})	3.5×10^{-2} (1.7×10^{-2})	4.5×10^{-2} (2.3×10^{-2})	7.7×10^{-2} (3.9×10^{-2})	4.4×10^{-2} (1.3×10^{-2})
$P_{bioavailable}$: Fe	2.0×10^{-3} (8.1×10^{-4})	1.8×10^{-3} (1.1×10^{-3})	2.2×10^{-3} (9.5×10^{-4})	1.3×10^{-3} (6.0×10^{-4})	2.3×10^{-3} (8.1×10^{-4})	1.5×10^{-3} (5.6×10^{-4})	2.0×10^{-3} (1.0×10^{-3})	7.5×10^{-4} (2.6×10^{-4})
P_{total} : Fe	7.5×10^{-2} (2.2×10^{-2})	6.0×10^{-2} (1.2×10^{-2})	6.7×10^{-2} (1.7×10^{-2})	6.8×10^{-2} (2.3×10^{-2})	7.8×10^{-2} (2.0×10^{-2})	7.2×10^{-2} (2.6×10^{-2})	6.0×10^{-2} (1.1×10^{-2})	5.9×10^{-2} (1.7×10^{-2})

Table 3. 6. Statistical significance of soil properties in restored wetlands. Treatment expresses the divergence of excavated (EXC) basins from business as usual (BAU) wetlands. Hydroperiod indicates whether semipermanently flooded basins differ significantly from seasonally flooded wetlands. Wetland age depicts the effect of time since restoration. Interaction between Treatment and either Hydroperiod or Wetland Age are listed to the right. Directionality of significant trends are shown parenthetically.

	Main Effects			***Interaction Terms***		
	Restoration Strategy	**Hydroperiod**	**Wetland Age**	**Strategy *X* Hydroperiod**	**Strategy *X* Wetland Age**	**Model Fit (R^2)**
Bulk Density (kg/m^3)	0.11	0.12	0.98	0.52	**0.041 * (-)**	0.13
Organic Matter (kg/m^2)	***0.056 ·***	0.18	0.40	0.097	**0.030 (+) ***	0.13
† Organic Carbon (kg/m^2)	**0.040 ***	0.15	0.23	0.15	**0.011 * (+)**	0.14
† Total Nitrogen (kg/m^2)	**0.0055 ****	0.18	0.47	0.17	**0.0038 ** (+)**	0.24
† Bioavailable P (g/m^2)	0.23	**0.0080 ****	0.64	0.13	0.32	0.31
† Total P (g/m^2)	0.37	0.13	0.75	0.96	0.86	0.08
† CaCO3 (kg/m^2)	**0.041 ***	0.15	0.48	**0.024 ***	0.96	0.26
† Ca (kg/m^2)	**0.036 ***	0.13	0.84	***0.052 ·***	0.80	0.29
Fe (kg/m^2)	0.26	0.76	0.65	0.69	0.46	0.00
	Molar Ratios					
$C_{organic}$: N_{total}	0.078	0.63	0.17	0.61	0.50	0.18
† N_{total}: $P_{bioavailable}$	0.91	**0.0020 ****	0.85	0.32	0.87	0.31
† N_{total} : P_{total}	0.15	**0.018 ***	0.40	0.27	**0.015 * (+)**	0.19
$C_{organic}$: $P_{bioavailable}$	0.73	**0.0026 ****	0.99	0.38	0.95	0.29
$C_{organic}$: P_{total}	0.41	**0.024 ***	0.25	0.26	**0.041 * (+)**	0.15
† $P_{bioavailable}$: Ca	0.33	0.54	0.65	**0.015 ***	0.40	0.29
† P_{total} : Ca	**0.032 ***	0.26	0.92	**0.020 ***	0.81	0.31
$P_{bioavailable}$: Fe	**0.019 ***	**0.0065 ****	0.15	0.61	**0.032 * (+)**	0.24
P_{total} : Fe	***0.058 ·***	0.36	0.69	0.62	0.51	0.10

† Log transformed
· Marginal Significance

* Significant at $P \leq 0.05$
** Significant at $P \leq 0.01$

4. Temporal Patterns in Depressional Wetland Water Quality Following Restoration Depend on Hydroperiod Rather Than Restoration Strategy

Abstract

Widespread wetland restoration is increasingly recognized as an effective means of improving water quality, particularly in cultivated landscapes. Agricultural wetland restoration frequently includes excavating accumulated eroded sediments deposited in drained basins from the surrounding landscape. The goal of sediment excavation can include increasing water storage capacity, decreasing invasive species cover, or improving water quality. However, it is unclear whether sediment excavation actually improves water quality and it is even less clear how long any excavation effect might last, particularly as restorations mature. To address this gap in knowledge, we examined dissolved nutrient concentrations in 54 restored agricultural wetlands ranging in age from 1 to 10 years post-restoration in the prairie pothole region of west central Minnesota, USA. In all study wetlands, hydrology was restored by removing subsurface drainage and plugging surface drainage ditches, thus re-establishing hydrology in the basins (“Business As Usual” treatment). In half of the wetlands, accumulated sediment was removed from the basin and redeposited on the surrounding landscape (“Excavated” treatment). Our results show that despite

active removal of accumulated sediment, nitrogen and phosphorus dynamics were almost universally controlled by effects of hydroperiod not restoration strategy, both immediately following restoration and over the ensuing years. The effects of hydroperiod were likely related to changes in redox conditions and appeared to result from both direct mechanisms (fluctuations in water level) and indirect mechanisms (changes in the emergent macrophyte community). Nitrogen and phosphorus responded differently to hydroperiod, concentrating dissolved inorganic phosphorus and organic nitrogen while removing inorganic nitrogen, resulting in widespread N limitation.

Introduction

Freshwater ecosystems continue to suffer from cultural eutrophication – nutrient enrichment through human activity - which contributes to the proliferation of harmful algal blooms (Heisler et al. 2008), hypoxia, and concomitant fish kills (Mallin et al. 2006); changes in aquatic food webs (Hall et al. 1999; Liston et al. 2008; Leech et al. 2018) and dominant plant communities (Woo & Zedler 2002); and increases the risk of detrimental parasite loads in wildlife (Johnson & Chase 2004; Smith & Schindler 2009), all of which have economic and cultural costs (Scholte et al. 2016; Dodds et al. 2009). Eutrophication is the product of both chronic and episodic nutrient enrichment contributing to the degradation of aquatic ecosystems (Heisler et al. 2008). Wetland drainage, cultivation, and the widespread use of inorganic fertilizers are among the most widely recognized drivers of water quality degradation (Rabalais et al. 2002; Mitsch & Day 2006; Hansen et al. 2018). Collectively, these practices decrease water residence time on the landscape and increase nutrient availability which degrades ecosystem services associated with nutrient retention, assimilation, and removal (Costanza et al. 1997). Increasing water residence time on the landscape through wetland restoration may be instrumental to recovering these lost nutrient remediation services.

In North America, one of the areas most impacted by historical wetland drainage is the Prairie Pothole Region, which stretches north and west from northwest Iowa and western Minnesota in the United States to Manitoba, Saskatchewan, and Alberta in Canada (Figure 3.1). This region was once characterized by an abundance of depressional wetlands, averaging 7 basins per km^2 (17.4 per mi^2), with a maximum density of 57 wetlands per km^2 (148 per mi^2), which is more than 1 wetland every 5 acres (Dahl 2014). Throughout the 19th and 20th centuries, 61% of prairie pothole wetlands were drained for cultivation (Dahl 2014), both to increase the amount of arable land and to reduce the inconvenience of farming around basins (Gelso et al. 2008). Most depressional wetlands in this region are relatively small (< 0.5 ha)(Dahl 2014) and thus are highly sensitive to drainage, but these small basins increase water residence time on the landscape (Hey & Philippi 1995; Mitsch et al. 2005; Mitsch & Day 2006), capture nutrients (Salk et al. 2018; Romero et al. 1999; Craft 1996), and improve down-gradient water quality (Mitsch et al. 2005; Brunet 2011). In the prairie pothole region, the presence of depressional wetlands can reduce spring discharge in nearby streams by 70% and nutrient export by 85 to 89 % for nitrogen (N) and phosphorus (P), respectively (Westbrook et al. 2011). Wetlands increase the time it takes for nutrients to move to downstream ecosystems by cycling nutrient through multiple biotic and abiotic pools as evidenced by the form of nutrients entering and leaving basins. Dissolved inorganic nutrients entering wetlands are typically exported in dissolved organic or particulate forms (Romero et al. 1999; Pellerin et al. 2004; Reddy et al. 1999; Davis et al. 1981). To recover the nutrient remediation services provisioned by depressional wetlands, there has been growing interest in wetland restoration and strategies to improve its water-quality benefits.

Depressional wetland restoration often includes removal of accumulated eroded sediments in order to increase basin depth and water storage capacity (Galatowitsch & van der Valk 1994), but there may be additional benefits of sediment removal. The presence of accumulated sediment can influence nutrient cycling, storage, and availability by augmenting soil nutrient availability (Martin & Hartman 1987; Preston et al. 2013; Golterman 2004). Previous studies have shown that restoring water to drained agricultural wetlands can release large quantities of P into the water column, potentially damaging water quality down-gradient (Aldous et al. 2005). While some authors point to relationships between iron-reducible P remineralization and hypoxia as sources for dissolved P (Kinsman-Costello et al. 2014), others suggest that organic matter oxidation in drained soils can result in a fairly large pool of labile P that moves into the water column immediately following re-wetting (Reddy et al. 1999; Aldous et al. 2005). Both mechanisms are likely to occur.

Removing accumulated sediments can indirectly affect dissolved nutrient concentrations through uptake by vegetation. Sediment removal decreases the initial abundance and spread of invasive emergent macrophytes, specifically *Typha* x *glauca* (hybrid cattail) (Smith et al. 2016; Winikoff et al. 2020) and *Phalaris arundinacea* (reed canary grass) (Mahaney et al. 2004), presumably by reducing the invasive species seed bank. However, high levels of nutrients, such as those found in accumulated sediments, can favor aggressive invasive species (Wetzel & Van Der Valk 1998; Woo & Zedler 2002; Daehler 2003), which often have longer growing seasons than native sedges and grasses, allowing invasive species to quickly establish and shade out native competitors (Larkin, Freyman, et al. 2012; Lishawa et al. 2015; Vaccaro et al. 2009; Boers et al. 2007; Wetzel & Van Der Valk 1998). Stands of hybrid cattail may hold more N and P than native species, since cattail can assimilate up to 5-times more N than native competitors (Larkin, Lishawa, et al. 2012). Dense stands of invasive macrophytes can hold substantial quantities of nutrients in above- and below-ground biomass and as microbial biomass on decomposing litter (Garver et al. 1988; Meyers 2013). However, some evidence suggests that hybrid cattail, in particular, creates conditions that promote elevated dissolved inorganic N and P availability, which in turn favors further dominance by hybrid cattail (Angeloni et al. 2006;

Woo & Zedler 2002). The complexity of this system and the interactions therein make it difficult to predict how accumulated sediment removal will influence dissolved nutrient pools in restored wetlands.

Accumulated eroded sediments can shorten wetland hydroperiod – the number of consecutive days with standing water – by decreasing maximum basin volume and increasing surface area and evaporative loss (Luo et al. 1997, 1999; Tsai et al. 2007), with implications for nutrient cycling. Prolonged water residence times in lakes and wetlands promote nutrient assimilation and N removal via denitrification (Zarnetske et al. 2011; Müller et al. 2021). In prairie pothole wetlands, evidence suggests that shorter hydroperiods can promote decomposition and nutrient leaching from plant litter and soil organic matter, resulting in elevated dissolved P and N concentrations, particularly right before complete water loss (LaBaugh et al. 1987; Reddy et al. 1999). But a variety of factors, including dissolved oxygen concentration (redox condition) and availability of dissolved cations, can influence water column nutrient concentrations (Frossard et al. 1995; Reddy et al. 1989), adding possible mechanisms of N and P retention or removal in wetlands with shorter hydroperiods. For example, short periods of drawdown can oxygenate soils, stimulating coupled nitrification-denitrification and subsequent N removal (Reddy et al. 1989). The same conditions can stimulate partial detritus decomposition, which can stabilize organically bound P and increase the likelihood of long-term P burial (Pant & Reddy 2001) or may liberate mineralized P (Reddy et al. 1999).

In addition, wetlands with shorter hydroperiods often have higher dissolved calcium and magnesium carbonate concentrations (LaBaugh et al. 1987) which can coprecipitate with dissolved phosphates, forming one of the many possible arrangements of apatite, a very stable form of mineral P (Reddy et al. 1999; Frossard et al. 1995). The assortment of competing pathways for N and P mineralization, deposition, and removal make it difficult to predict how hydroperiod will affect dissolved nutrient availability.

Dissolved nutrient availability dynamics change over time, reflecting a combination of biogeochemical processes operating at different rates at both the landscape scale and locally within wetlands. Nitrogen and P applied to landscapes decades or even centuries ago can drive water quality degradation in wetlands, lakes, and streams today (McCrackin et al. 2018; Nair et al. 2015; Montgomery et al. 2021; Van Meter et al. 2016; Tesoriero et al. 2013; Murphy et al. 2013). The time lag between nutrient application and water quality degradation is controlled by soil accumulation, mineralization, and groundwater movement, all of which operate at different rates depending on local environmental conditions (Domagalski & Johnson 2011; Jarvie et al. 2013; Sharpley et al. 2013; Van Meter et al. 2016). Within wetlands, the internal dynamics of nutrient retention and removal are closely linked with vegetation, which again, takes time to develop following restoration. Though water quality can respond quickly to environmental changes such as rewetting, patterns arising over time and across space can shed light on how dissolved nutrients in restored wetlands reflect the development of soils and plant communities, which take longer to mature. As such, the explicit consideration of how dissolved nutrients change over time warrants investigation.

Few studies have considered the form and concentration of dissolved nutrients in restored prairie pothole wetlands (but see LaBaugh et al. 1987; Detenbeck et al. 2002; Brunet 2011) much less the effect of different restoration strategies. As a result, it remains unclear whether removing accumulated sediment improves water quality within restored wetlands, and through what mechanisms. We considered two wetland restoration strategies; one was designed to remove accumulated eroded sediments (excavation, EXC) prior to restoring hydrology, the other was designed to restore hydrology alone (Business As Usual, BAU). In both cases, hydrology was restored by breaking subsurface tile drains and plugging surface drainage ditches. Our aim was to examine whether restoration strategy (treatment) and wetland hydroperiod could explain water column dissolved nutrient dynamics over time. We hypothesized that sediment removal would decrease dissolved N and P concentrations by relocating substantial nutrient pools. We also hypothesized that wetlands with a longer hydroperiod would have lower dissolved N and P concentrations in the water column, stemming from higher water residence times and increased likelihood of assimilation, deposition, or - in the case of N - denitrification. To that end, we examined spring dissolved nutrient concentrations over four consecutive years in 54 depressional prairie pothole wetlands with variable restoration strategy, hydroperiod, and time since the restoration of hydrology.

Methods

Site Description and Study Design

Study wetlands were located in the prairie pothole region of west central Minnesota (Figure 3.1). Basins were restored between 2009 and 2016 by the United States Fish and Wildlife Service, in partnership with private landowners. The presence of standing water, historical aerial imagery, existing topography, and soil characteristics were used to identify the likely historical extent of wetlands. Depth of accumulated eroded sediment within each basin was determined by evaluating multiple soil cores and identifying changes in soil properties with depth in the soil profile, including changes in color and texture, changes in soil carbonate content, and presence of shell fragments. Prior to restoration, wetlands and surrounding uplands were drained by subsurface tile or drainage ditches and were actively cultivated in row crop agriculture. We noted additional land-use history information whenever it was made available by landowners (Appendix 1), including the presence of livestock. Property owners often elected to enroll the surrounding uplands into the Conservation Reserve Program at the same time as the restoration, but in some cases portions of the contributing watershed continued to be actively cultivated throughout the study. The Conservation Reserve Program is a federally funded land-retirement program designed to improve soil and water health by restoring native vegetation on retired agricultural land. Land-owners are financially compensated for enrolling land in the program for an extended period of time (10 to 15 years), with the potential for re-enrollment at the end of the contract (Stubbs 2014). Contributing watersheds of half of the sites (n = 23) retained some contemporary agricultural; among those watersheds, cultivation was usually a minor component of overall land use (mean 24% ± 20 S.D.). Only three watersheds contained at least 50% cultivation, animal confinement, or impervious surface cover. Among the most heavily impacted watersheds, only one received runoff directly from row crop agriculture via a drainage ditch. All other watersheds containing substantial contemporary agricultural maintained a minimum grassland buffer of no less than 24 meters between cultivation and the wetted basin.

We surveyed 26 BAU and 28 EXC wetlands (N = 54) between 2016 and 2019. Detailed information about study wetlands and watersheds can be found in Appendix 1. Study wetlands were small, averaging 0.6 ha in area (range 0.06 to 2.3 ha), and were often in small watersheds averaging 11.4 ha (range 0.3 to 91.9 ha) with a mean watershed to wetland area ratio of 30.7 (median 8.0). Wetland hydroperiod was characterized as seasonal (n = 38) or semipermanent (n = 16) based on water retention throughout the growing season (Cowardin and Golet 1995) and the development and persistence of distinct vegetative communities (Stewart & Kantrud 1971), both of which were observed during multiple visits over the course of the growing season in each sampling year before formally assigning a hydroperiod. Prior to beginning the study, we confirmed that semipermanent basins did not have deeper excavations than seasonal wetlands ($p = 0.24$) based on a one-way analysis of variance (ANOVA) test. All preliminary, descriptive statistics were performed using ANOVA in the statistical software R (R Core Team 2020). Wetland age following restoration was defined as the difference between the sampling year and the restoration year.

In autumn of 2018 we identified eight reference wetlands with no known history of drainage, though some had constructed spillways to minimize flooding beyond a specific elevation. We confirmed landowner oral accounts using digitally archived aerial imagery dating as far back as 1939 (University of Minnesota, Historical Aerial Photographs). Reference basins ranged in size from 0.4 to 5.1 ha (mean 1.5 ± 1.5 SD), making reference sites larger than restored basins (mean 0.6 ha, ± 0.4 SD; $p = 0.0001$). The contributing watersheds were smaller for reference wetlands (mean 9.3 ha ± 7.3 SD) compared to restored basins (mean 11.4 ha ± 21.5 SD), but the difference was not statistically significant ($p = 0.78$). Cultivated land use in the contributing watershed was higher in reference basins (n = 6, median 68.5%, mean 47.9% ± 39.0 SD) compared to restored wetlands (n = 23, median 0%, mean 10.2 % ± 17.6 SD; $p < 0.001$). We compared restoration outcomes with reference basins as an indicator of restoration trajectories relative to the more stable conditions expected in references sites. However, we recognize that many reference basins may have remained undrained over the last century because of attributes that made them distinct from wetlands that were drained, such as their greater size or persistent upwelling of groundwater.

Sample Collection and Chemical Analysis

We processed 908 water samples collected between 2016 and 2019. In 2016, we collected surface water samples between June 29 through August 04. From 2017 to 2019, we collected annual surface water samples between May and July, sampling on at least one date per year and per site. Occasionally, seasonal basins were dry on the intended sampling date and samples were not collected. Some wetlands were sampled opportunistically, on more than one date per year. On each sampling date, we collected samples from three points within each wetland, taking care to evenly space samples along a longitudinal transect that intercepted shallow and deep-water habitats within each basin. We filtered water in the field with 25 mm glass fiber filters (0.7 µm pore size, Whatman GF/F) and stored samples frozen in 60 mL HDPE bottles, which were acid washed prior to use. Samples for total dissolved nutrients and dissolved inorganic nutrients were filtered and stored separately.

We measured total dissolved nitrogen (TDN) and dissolved organic carbon (DOC) using combustion-infrared and combustion-chemiluminescence methods on a Shimadzu TOC-L analyzer equipped with a chemiluminescence detector (TNM-L unit, Shimadzu Corporation) (APHA 2005; ASTM 2008). We examined total dissolved phosphorus (TDP) and particulate phosphorus (PP) by persulfate digestion followed by the ascorbic acid method for colorimetric analysis (Murphy & Riley 1962; APHA 1992a). From 2017 to 2018 we measured particulate C and N using a Costech ECS 4010 CHNSO Analyzer (Costech Analytical Technologies Inc). We measured dissolved inorganic nutrients in partnership with the Saint Croix Watershed Research Station and Science Museum of Minnesota on a SmartChem 170 discrete analyzer (AMS Alliance, Florida, USA) with the following methods; ammonium (NH_4^+-N) by the phenol hypochlorite method (APHA 1998); nitrate (NO_3^--N) by the cadmium reduction method (APHA 1992b); and soluble reactive phosphorus (SRP) by the ascorbic acid method (Murphy & Riley 1962). When sample concentrations fell below the method detection limit and above zero we assigned a concentration of one half the method detection limit (Smith 1991).

We calculated dissolved inorganic nitrogen (DIN) as the sum of ammonium and nitrate. The dissolved organic nitrogen (DON) and phosphorus (DOP) fractions were calculated as the difference between the total dissolved fraction and the inorganic fraction. Total nitrogen (TN) and phosphorus (TP) were calculated as the sum of the total dissolved and particulate nutrient pools, while total organic carbon (TOC) was the sum of DOC and particulate carbon. We also calculated the molar ratios of C to N (C:N) and N to P (N:P) for the dissolved inorganic, dissolved organic, total dissolved, particulate, and total nutrient pools.

Statistical Analyses

We examined the effect of restoration treatment (BAU and EXC), age since restoration (one to nine years), and hydroperiod (seasonal and semipermanent) on water column nutrient availability using linear mixed effects models. Our models included wetland-specific site identity and sampling year (e.g., 2016, 2017, 2018, 2019) as random effects to control for repeated measurements at each wetland and inherent interannual variability. We included terms to account for possible interactive effects of treatment by hydroperiod, treatment by age, and hydroperiod by wetland age. We incorporated hydroperiod in the models because of inherent differences in biogeochemical cycling that arise from prolonged anoxia (e.g., semipermanent hydroperiod) compared to alternating periods of oxygenation and anoxia (e.g., seasonal).

Prior to analysis, we identified and truncated outliers to the 99th percentile, using the *OutlierDetection* package in R, because it selects outliers based on consensus across multiple algorithms (Tiwari & Kashikar 2019). We limited outlier detection to dissolved N species because of noise from transient N pulses following storm events, particularly at discrete inlets from agricultural drainage ditches. Whenever appropriate, we log-transformed response variables to meet model assumptions of homogeneous residual error. We included a quadratic term for wetland age when non-linear relationships were visually apparent and significantly improved model fit (ANOVA, critical $P \leq 0.05$). All statistical analyses were performed in R (R Core Team 2020) using the '*lme4*' and '*lmerTest*' packages (Bates et al. 2020; Kuznetsova et al. 2020) with a critical *p*-value of

0.05. We evaluated significant interactions between fixed effects with Tukey HSD post-hoc test, performed using the ‘*emmeans*’ package in R (Lenth et al. 2020).

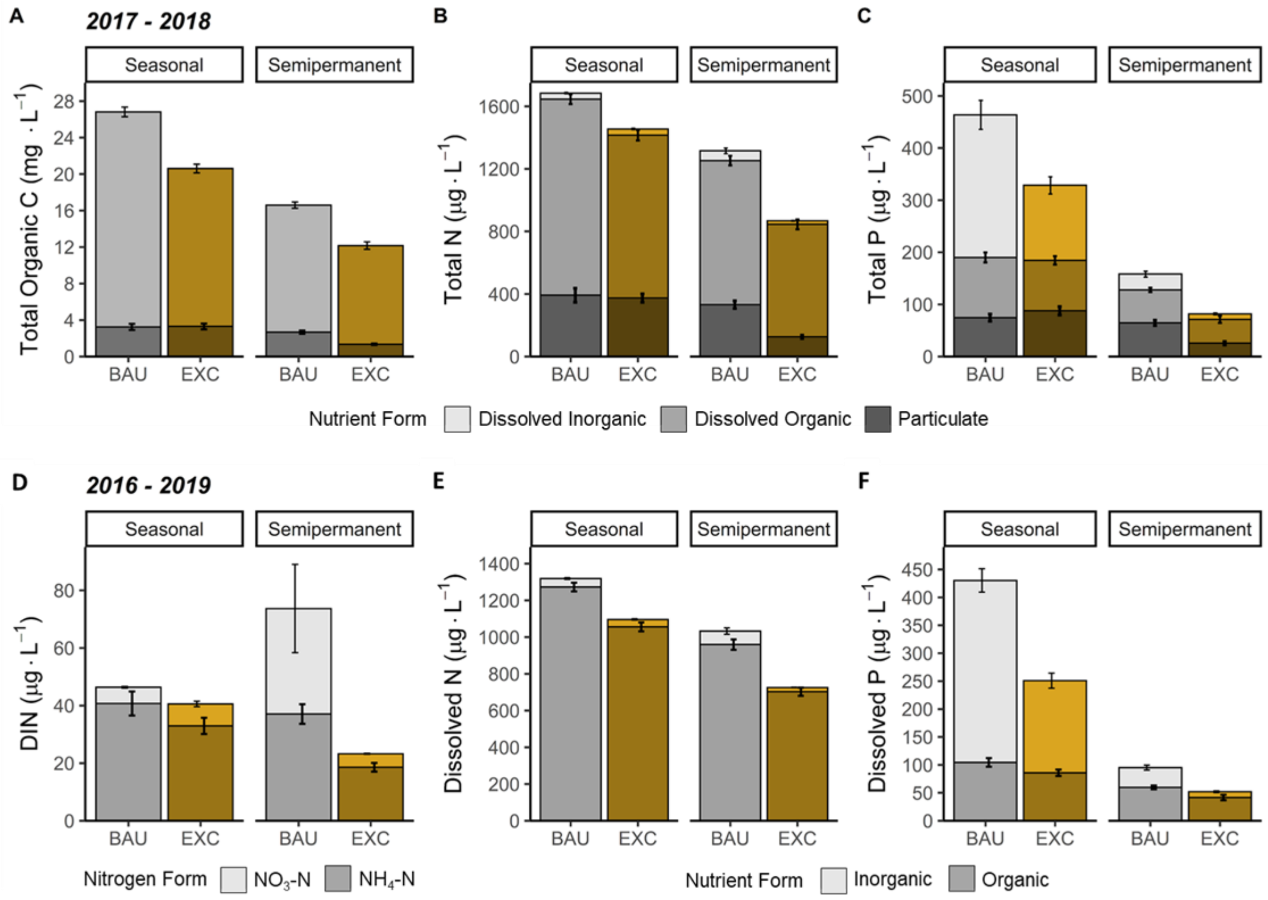

Figure 4. 1. Contribution of particulate and dissolved nutrient forms to water column carbon (A), nitrogen (B), and phosphorus (C), with particulate nutrient fractions shown on the bottom, darkest layer. Carbon only includes organic and particulate fractions. The dissolved nitrogen (E) and phosphorus (F) pools were further subdivided into organic (bottom) and inorganic (top) fractions. Dissolved inorganic nitrogen (D) was further divided into ammonium (bottom) and nitrate (top). Error bars represent the standard error about the mean.

Results

Major Nutrient Pools

Dissolved nutrients dominated the total nutrient pools in the water column, with the particulate fraction representing 22% of total N and 35% of total P, respectively. Particulate C, N, and P concentrations were significantly lower in EXC semipermanent basins compared to all other treatment and hydroperiod combinations (Table 4.1, Figure 4.2), but the contribution of particulates to the total nutrient pool was remarkably consistent across all other treatment by hydroperiod combinations. In EXC basins with semipermanent hydroperiod, particulate N contributed significantly less to total N compared to all other treatment and hydroperiod combinations ($p = 0.001$; Table 4.1). Conversely, particulate P represented a larger portion of total P in semipermanently flooded sites (43%; Figure 4.2) compared to seasonal wetlands (31%) but the relationship was not statistically significant (Table 4.1). As wetlands aged, particulate P contributed substantially less to total P ($p = 0.026$). Since dissolved N and P were the dominant nutrient pools in the water column, our research focused on dissolved rather than particulate pools.

Dissolved Nitrogen

Total dissolved N was primarily in the organic form, with 96.4% of TDN as DON (Figure 4.2). Following restoration, the contribution of DON to TDN decreased in semipermanently flooded basins ($p < 0.001$), but organic N still represented over 90% of the TDN pool (Figure 4.3A). As wetlands aged, TDN and DON concentrations increased (p = 0.034 and 0.013, respectively; Figure 4.4), but as hypothesized this occurred at a slower rate in semipermanently flooded basins compared to basins with seasonal hydroperiod (p = 0.022 and < 0.001 for TDN and DON, respectively). Dissolved organic C concentrations followed similar patterns to DON (Tables 3 and 4; Appendix 4, Figure A4.1).

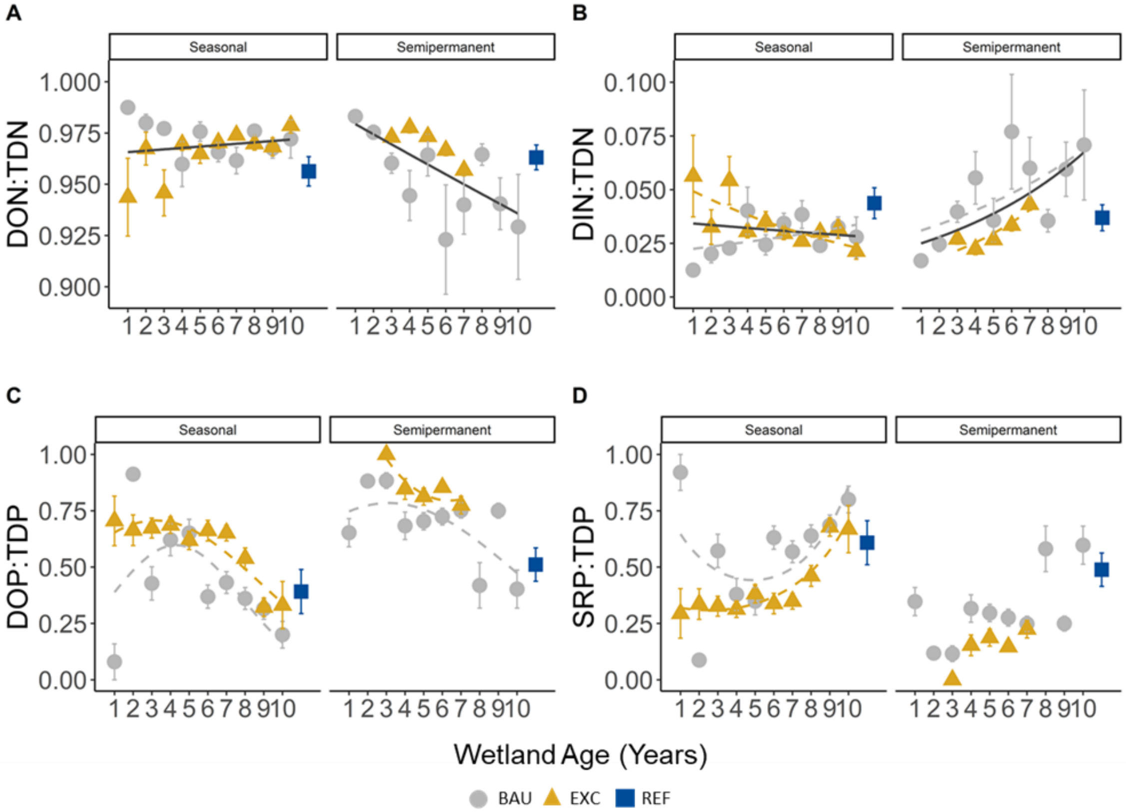

Figure 4. 2. Contribution of dissolved inorganic and organic nutrient fractions to the total dissolved nutrient pool over time in restored (BAU, Business as Usual; EXC, Excavated) and reference (REF, squares) basins. Dissolved nitrogen species shown in panels A (organic) and B (inorganic), and phosphorus species shown in panels C (organic) and D (inorganic). Seasonally inundated basins shown in the left panel and semipermanent basins in the right panel. Each point represents a mean across multiple sites with standard error bars. Trend lines show statistically significant relationships across time in basins with seasonal and semipermanent hydroperiod (solid lines) and in BAU (circles) and EXC (triangles) wetlands (broken lines).

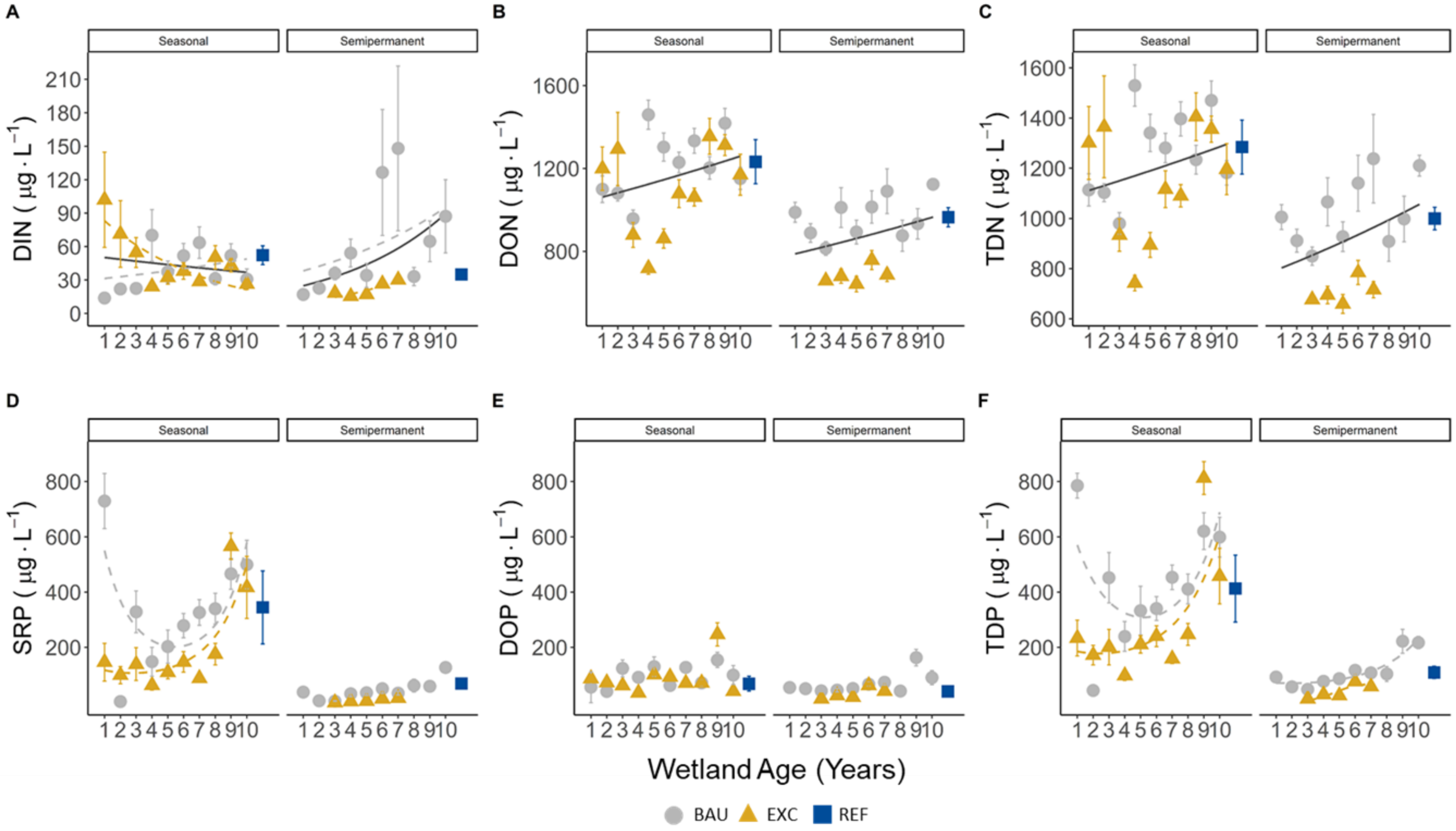

Figure 4. 3. Dissolved nutrient concentrations over time in restored (BAU, Business as Usual; EXC, Excavated) and reference (REF) basins. Seasonally inundated basins shown in the left panel and semipermanent basins in the right panel. Dissolved nitrogen species shown in panels A (inorganic), B (organic), and C (total). Dissolved phosphorus species shown in panels D (inorganic), E (organic), and F (total). Each point represents a mean across multiple sites and years with standard error bars. Trend lines show statistically significant relationships across time in basins with seasonal and semipermanent hydroperiod (solid lines) and in BAU (circles) and EXC (triangles) wetlands (broken lines).

As we predicted, DIN, particularly nitrate, was scarce. We only recorded 6 samples with nitrate concentrations greater than 200 µg/L, and 62 samples with ammonium concentrations greater than or equal to 100 µg/L (N = 908). Temporal trends of DIN concentration were difficult to interpret because the concentrations were so low, but we were able to detect a handful of patterns. Dissolved inorganic N dynamics were largely driven by the interaction between hydroperiod and wetland age ($p < 0.001$), with DIN concentrations decreasing as seasonally flooded basins aged and increasing over time in semipermanently flooded wetlands (Figure 4.4, Table 4.3). The relatively small DIN pool was primarily composed of ammonium, which made up greater than 76% of DIN, while nitrate contributed less than 24% to the DIN pool (Figure 4.2A).

Nitrate concentrations were significantly higher in semipermanent sites compared to seasonal wetlands ($p = 0.039$), but that trend was driven by BAU basins with semipermanent hydroperiod (Figure 4.2A). One site with particularly high nitrate concentrations received water from a drainage ditch servicing an adjacent agricultural field. As one of the older basins included in the study, it likely contributed to age related increases in nitrate concentrations. To assess the influence of nitrate concentrations from the ditch, we repeated DIN and nitrate analyses after removing samples taken near the wetland inlet. Statistically significant relationships between fixed effects and DIN remained significant after completely removing the nitrate outliers. However, previously significant fixed effects became marginally significant after removing these outliers from the nitrate model. Further investigation into nitrate dynamics across the longitudinal transect of this wetland showed patterns consistent with N removal and assimilation as water moves through a wetland. For example, in June of 2018 and 2019 nitrate concentrations ranged from 33,420 to 44,762 µg NO_3-N·L^{-1} at the point where the drainage ditch entered the wetland through a culvert. The culvert was used to move water beneath a road transecting the watershed, and was sampled periodically but was not included in regular sampling efforts. During the same time period, nitrate concentrations within the wetland were significantly lower. At the near-inlet sampling location nitrate concentrations were less than half of concentrations at the drainage ditch, ranging from 0 to 24,266 µg NO_3-N·L^{-1}. In the central pool of the wetland nitrate concentrations fell even further (range 0 to 11 µg NO_3-N·L^{-1}) and near the spillway, where water leaves the wetland in wet years, nitrate concentrations were always below the minimum detection limit of 10 µg NO_3-N·L^{-1} (Appendix 4, Figure A4.2),

Dissolved Phosphorus

In contrast to dissolved N, the dominant form of P varied between wetlands with seasonal and semipermanent hydroperiod. Total dissolved P was primarily comprised of the inorganic form in seasonal wetlands (52% SRP), while DOP was the dominant form of P in semipermanent basins (76% DOP; Figure 4.2C). In BAU wetlands, the contribution of SRP to TDP was initially high and subsequently decreased for the first 4 to 5 years following restoration before increasing between years 6 and 10 (Figure 4.3D, Table 4.3), tracking the trends in overall SRP concentration over the same time frame (Figure 4.4D). In EXC basins the contribution of SRP to TDP was initially low (< 50%) but increased over time to approximately 75% of TDP (Figure 4.3D), following the pattern of SRP in the water column (Figure 4.4D). After initially increasing, the contribution of DOP to the TDP pool decreased over time (Figure 4.3C; Table 4.3). The contribution of SRP and DOP to the TDP pool were driven by temporal patterns in SRP availability ($p < 0.001$; Figure 4.4D), since DOP concentrations did not change over time (p = 0.587; Figure 4.4E).

In agreement with our hypotheses, restoration treatment and hydroperiod were both reliable predictors of dissolved P availability (Table 4.3), but hydroperiod had a larger effect than restoration strategy (Figure 4.4D and 4.4F). Concentrations of TDP and SRP were 3.6 and 8 times higher in seasonal compared to semipermanent wetlands, respectively ($p = 0.002$ and < 0.001 for TDP and SRP, respectively; Figure 4.2). As predicted, sediment removal resulted in significantly lower TDP ($p = 0.001$) and SRP concentrations ($p < 0.001$) in EXC compared to BAU wetlands. As we anticipated, immediately following restoration, seasonally flooded wetlands had fairly high TDP and SRP concentrations, particularly in basins restored with the BAU strategy. As wetlands aged, TDP and SRP concentrations initially decreased and then rebounded to levels observed shortly after restoration, but the initial decline in P concentration only occurred in BAU wetlands (Figure 4.4D and 4.4F). In general, TDP availability increased as wetlands aged ($p < 0.001$), a trend that was driven by SRP dynamics ($p < 0.001$; Figure 4.4D). In EXC basins, TDP and SRP concentrations were initially low and remained low for six to seven years before rapidly increasing, resulting in faster accumulation of dissolved P at EXC compared to BAU wetlands ($p = 0.002$ and < 0.001 for TDP and SRP, respectively; Table 4.3). Temporal patterns in dissolved P availability were primarily driven by seasonally flooded wetlands (Figure 4.4D and 4.4F), which had 3.5 times more TDP than semipermanent basins (Table 4.3).

Molar Ratios

Dissolved nutrient molar ratios changed dramatically over time; but the nature of the temporal change was often moderated by hydroperiod and sometimes by restoration treatment (Figure 4.5, Table 4.3). Dissolved C:N molar ratios were controlled by restoration treatment, hydroperiod, and time, while C:P ratios were primarily influenced by hydroperiod and time (Table 4.3 and 4.4). Molar DOC:DON ratios were significantly lower in EXC sites compared to BAU wetlands ($p = 0.003$, Figure 4.5A). Organic C:N ratios increased over time ($p = 0.033$) but at a faster pace in seasonally flooded basins than in wetlands with semipermanent hydroperiod ($p = 0.020$). Molar DOC:DIN ratios increased over time in seasonal wetlands and decreased over time in semipermanent basins ($p < 0.001$, Figure 4.5B), a pattern that was driven by DIN availability (Figure 4.4A). Molar DOC:DOP ratios were lower at basins with seasonal hydroperiod ($p =$

0.042, Figure 4.5C). Initially following restoration, DOC:DOP ratios increased, but began to fall approximately 5 years after restoration. A similar pattern was observed for DOC:SRP molar ratios, where a sharp decline in DOC:SRP coincided with increasing SRP concentrations (Table 4.3, Figure 4.5D). Organic and inorganic N:P molar ratios also increased following restoration and then decreased around 5 years following restoration (Table 4.3, Figure 4.5E and 4.5F). Inorganic N:P molar ratios were higher in basins where sediment was removed (EXC) compared to BAU restorations (p = 0.015), while organic N:P ratios were higher in semipermanently flooded basins compared to seasonal wetlands (p = 0.016).

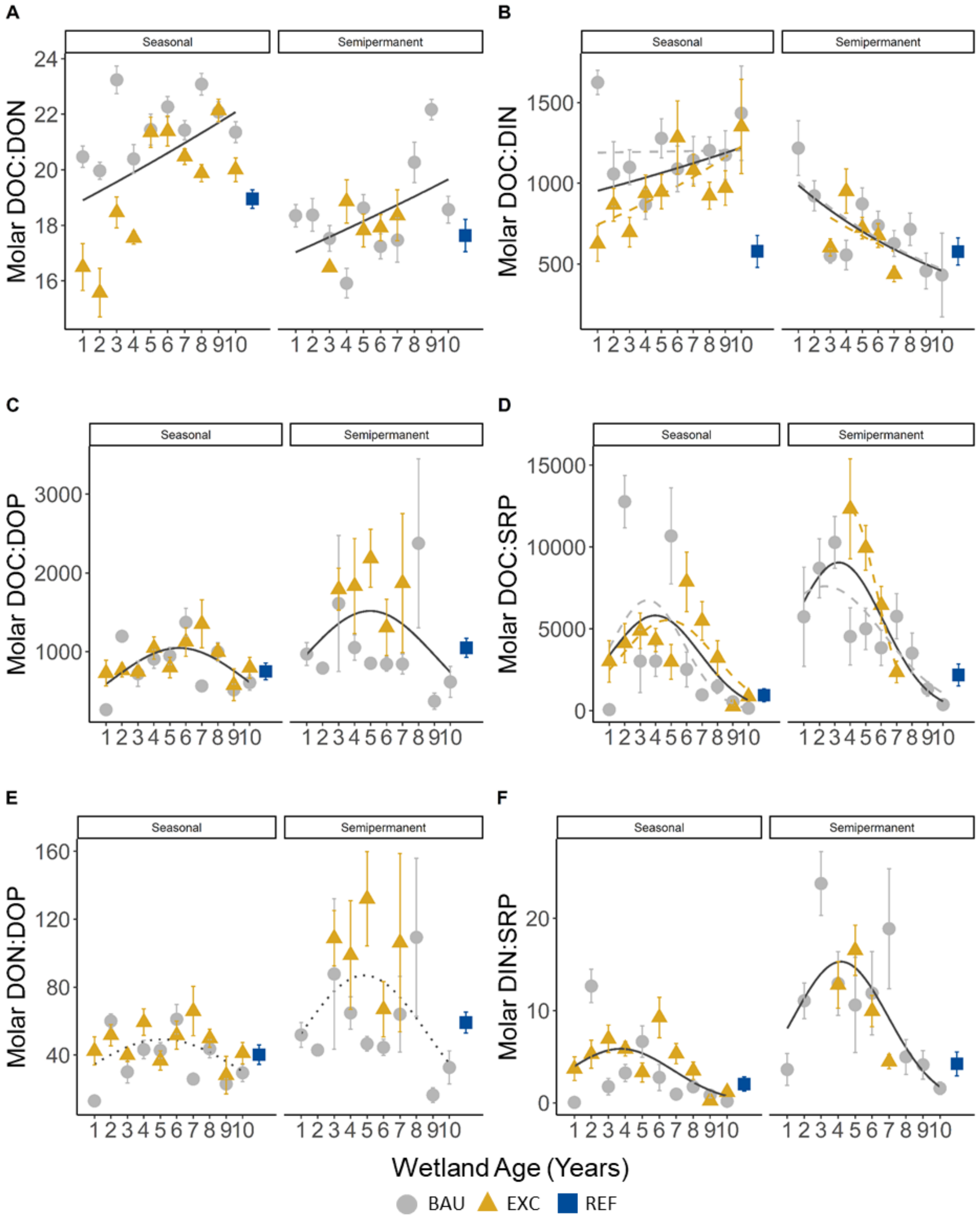

Figure 4. 4. Dissolved nutrient molar ratios across time in restored (Business as Usual, BAU; Excavated, EXC) and reference (REF) wetlands. Seasonal wetlands in the left panel and semipermanent basins in the right panel. Each point represents a mean across multiple sites with standard error bars. Dotted trend lines represent an overall wetland age effect in the absence of hydroperiod or treatment interaction. Solid trend lines show statistically significant relationships across time with hydroperiod interaction, and broken lines indicate time by restoration strategy interactions.

Particulate C:N and N:P molar ratios were near the Redfield ratio (106 C : 16 N : 1 P) representing the approximate stoichiometry of seston (Figure 4.6A and 4.6B; Table 4.2) (Redfield 1958; Hillebrand & Sommer 1999). In contrast, the molar ratios of available nutrients as DOC:TDN (mean 19.1 ± 3.5 SD) and TDN:TDP (mean 33.3 ± 46.0 SD) fell well above Redfield's ratio. The relative availability of more bioavailable DIN:SRP averaged 6.4 (13.7 SD), falling well below Redfield and indicating depleted availability of inorganic N compared to P. Similar to the dissolved nutrient pool, total organic C to total N molar ratios were nearly three-times the Redfield ratio (mean 17.3 ± 3.3 SD). In EXC sites, TOC:TN molar ratios were significantly lower compared to BAU wetlands (p = 0.014), but this trend was driven by the difference between seasonal BAU and EXC basins (mean 19.3 and 17.3 ± 3.0 and 3.2 SD, BAU and EXC, respectively), while in semipermanent wetlands EXC basins had higher TOC:TN values compared to BAU (p = 0.012; mean 15.3 and 16.7 ± 3.0 and 2.6 SD, BAU and EXC, respectively). Over time, TOC:TN ratios increased linearly (p = 0.003). In general, TN:TP ratios were enriched in P (mean 23.1 ± 19.0 SD), slowly increasing until five years following restoration (p = 0.01), at which point values decreased ($p < 0.001$), regardless of restoration strategy or hydroperiod.

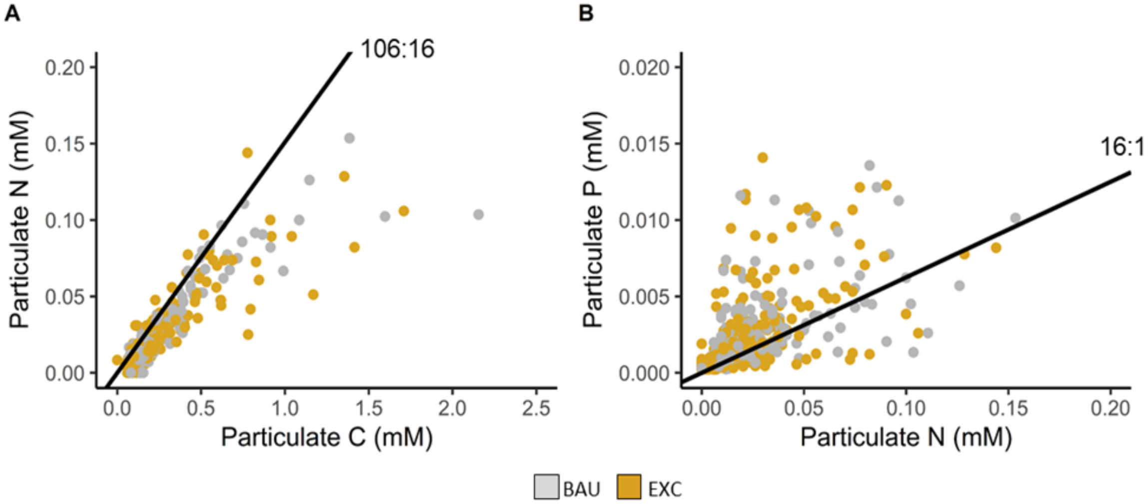

Figure 4. 5. Ratio of particulate molar concentration in business as usual (BAU) and excavated (EXC) basins. Redfield ratios for carbon to nitrogen (106:16) and nitrogen to phosphorus (16:1) are shown as solid black lines. Relative nutrient availability followed similar patterns in reference wetlands (not pictured).

Discussion

We studied 54 restored wetlands over a four-year period to identify how water quality responds to sediment removal and hydroperiod over time. Following restoration, water quality was primarily influenced by hydroperiod. Sediment removal decreased inorganic P concentrations immediately following restoration, but the effect only lasted six years and increases in P over time were driven by dynamics in seasonal wetlands. Over time dissolved nutrient concentrations increased, primarily driven by rising inorganic P and organic N, with relatively larger increases in P compared to N. The relative availability of DOC:DON and DIN:SRP indicate that over time both seasonal and semipermanent wetlands grew increasingly N-limited. Differences in N and P cycling drove stronger N-limited conditions in seasonal compared to semipermanent wetlands. Below, we explore possible mechanisms underlying these patterns and their implications for wetland management.

Dissolved P Dynamics in Seasonal and Semipermanent Wetlands

Concentrations of dissolved P, which dominated water column TP, were strongly influenced by wetland hydroperiod. Although excavation removed substantial amounts of P-enriched sediment, hydroperiod emerged as the most important characteristic controlling available P over time. Concentrations of organic and particulate P were similar in seasonal and semipermanent basins, but SRP concentrations were significantly higher in seasonal wetlands, suggesting that hydroperiod shapes the environmental conditions involved in P cycling within wetlands. Higher dissolved P mobilization in seasonal wetlands could arise from several mechanisms. First, semipermanent wetlands are deeper and have more stable hydrologic conditions than seasonal wetlands due to their connectivity with shallow groundwater. Semipermanent wetlands function as locations for both groundwater discharge and recharge, which makes them less susceptible to regular periods of draw-down. In comparison, seasonal wetlands are usually involved in groundwater recharge and tend to dry out regularly, making them more susceptible to wet-dry cycling, which promotes decomposition of detritus and soil organic matter and results in higher rates of nutrient mineralization. Second, the arrangement of vegetation in semipermanent wetlands, with an open pool colonized by submerged macrophytes, can promote oxygen exchange throughout the water column which can stabilize sediment P and minimize abiotic mobilization. By comparison, the presence of emergent macrophytes throughout seasonal wetlands may prevent gas exchange across the air-water interface by minimizing wind velocity, resulting in low dissolved oxygen, promoting sediment-bound P mobilization.

In prairie pothole wetlands, semipermanent basins rarely experience complete water loss that exposes sediments to air, while water quality in seasonal wetlands is influenced by the annual wet-dry cycles that are characteristic of these basins. Seasonal wetlands are primarily rainwater-fed groundwater recharge wetlands (van der Kamp & Hayashi 2009), have smaller volume (Wetzel 1990; Downing et al. 2006), and have more contact with sediments per unit volume than semipermanent basins. Periods of drawdown expose sediments and stimulate aerobic decomposition and nutrient mineralization from decomposing plant litter (LaBaugh et al. 1987; Reddy et al. 1999). These mineralized nutrients likely move into the water column upon rewetting, resulting in higher dissolved nutrient content in shallow basins compared to their deeper counterparts. In a post hoc analysis, we found a significant negative relationship between water column depth at the point of collection and dissolved P concentration (p = 0.006, Supplementary Methods in Appendix 4, Figure A4.3). However, water column depth alone only explained 1% of variation in this simple model while site identity, included as a random effect to account for repeated measurements over multiple dates, accounted for 66% of variability in dissolved P concentrations (Appendix 4, Table A4.1). This suggests that while wet-dry cycling contributes to mobilization of dissolved P, it is unlikely to be the most important control. We suggest that elevated SRP concentrations in seasonal wetlands were largely controlled by the physical effects of emergent macrophyte stems that promote anoxia and subsequent release of inorganic sediment-bound P.

A defining feature of semipermanent wetlands is the presence of an open pool of water colonized by floating and submerged macrophytes and surrounded by an emergent macrophyte ring (Galatowitsch & van der Valk 1994). By comparison, seasonal basins included in our study were usually colonized by emergent macrophytes throughout the entire basin, specifically by *Typha* x *glauca* (hybrid cattail) and *Phragmites australis* (common reed) (Winikoff et al. 2020). Additionally, *Phalaris arundinacea* (reed canary grass) often expanded well into the emergent macrophyte zone, particularly immediately following restoration, though over time it often retreated (personal observation). Previous studies in prairie pothole wetlands have shown that within emergent macrophyte zones, the water column exists in a nearly permanent state of hypoxia (≤ 3 mg oxygen/L) (Rose & Crumpton 1996). Emergent macrophyte stems and stalks can limit water column dissolved oxygen content by 1) intercepting incident photosynthetically active radiation and decreasing in-situ oxygen delivery through primary production (Morris & Barker 1977; Rose & Crumpton 1996; Larkin, Freyman, et al. 2012), and 2) decreasing wind velocity and shear forces that promote gas exchange across the air-water interface (Liss & Slater 1974). The combination of shading and sheltering within the emergent macrophyte zone can result in persistent hypoxia throughout the growing season (Rose & Crumpton 1996) leading to abiotic P remineralization from sediments (Schlesinger & Bernhardt 2013; Carlton & Wetzel 1987; Patrick & Khalid 1974). In contrast, the submerged aquatic vegetation in semipermanent wetlands can stabilize sediment P by delivering oxygen to the benthos and by physically protecting sediments from resuspension by wind and wave action, while also allowing for air-water gas exchange (Jeppesen et al. 1997; Søndergaard et al. 1992). To test whether differences in dissolved P concentration may be moderated by the physical and chemical effects of the emergent macrophyte community we performed a post hoc analysis of emergent macrophyte cover and dissolved P concentration (Supplementary Methods in Appendix 4). We found a significant positive relationship between SRP and TDP concentrations and cumulative percent cover of three aggressive invasive species common to the region: hybrid cattail, common reed, and reed canary grass ($p < 0.001$; Appendix 4, Figure A4.4). Invasive emergent macrophyte cover and the interaction between cover and hydroperiod explained 50 and 58% of variability in SRP and TDP concentrations, respectively (Appendix 4, Table A4.1). When considered alone, emergent macrophyte cover explained 24 and 23% of variability in SRP and TDP, respectively, providing strong support for the hypothesis that emergent macrophytes alter the physical and chemical environment leading to P mobilization. Taken together, our post hoc analyses provide substantial evidence that the effect of hydroperiod on dissolved P is mediated through wet-dry cycling that promotes mineralization of organic sediment P and the physical effects of the emergent macrophyte community that promote anaerobic conditions and solubility of inorganic sediment-bound P.

The presence of high levels of dissolved P may be indicative of legacy P accumulated from past agricultural activities, but these legacy effects were observed only in environmental settings that promoted P mobilization. Semipermanent wetlands, which tended to be slightly deeper and maintained more open water area over the study period, had low SRP and total P even several years after restoration, irrespective of restoration method. In contrast, shallower wetlands with seasonal hydroperiods showed extremely high concentrations of SRP even when P-rich agricultural sediment had been removed. For example, we found 16 seasonal wetlands with SRP concentrations in excess of values found in 75% of shallow lakes of similar size (Søndergaard et al. 2005). The legacy of past disturbance and fertilization can augment P runoff for decades (Jeppesen et al. 2005; Phillips et al. 2005) or even centuries (McCrackin et al. 2018). Recent evidence suggests that legacy P may contaminate groundwater supplies (Domagalski & Johnson 2011), which could further complicate our understanding of effective mitigation efforts by slowly increasing surface water P far away from the point of disturbance. These spatial and temporal asynchronies make it difficult to identify how legacy P remediation efforts influence contemporary water quality at the landscape scale.

Nitrogen Dynamics in Restored Wetlands

Despite very low inorganic N, DON concentrations were fairly high for shallow lentic systems with small surface areas (Detenbeck et al. 2002; Jeppesen et al. 2005; Søndergaard et al. 2005). Higher TDN in seasonal compared to semipermanent wetlands, and increasing concentrations over time may reflect the assimilation and recycling of N through multiple pools. Limited availability of DIN with concomitant increases in DON are indicative of N removal and recycling (Wetzel 1990; Kovacic et al. 2000; Mitsch & Day 2006; Vymazal & Březinová 2018). Small lentic systems are particularly effective sinks for N (Müller et al. 2021), permanently removing up to 100% of N inflow (Harrison et al. 2009), even in settings with elevated N runoff. Widespread hypoxia in the emergent macrophyte zone - through the mechanisms described above - establishes the appropriate redox conditions for denitrification, while the presence of robust macrophyte communities can further promote N removal via coupled nitrification-denitrification in the rhizosphere (Eriksson & Weisner 1999), which can draw down DIN concentrations.

Apart from denitrification, wetlands and shallow lakes are efficient N traps, removing inorganic N from the water column via assimilation and recycling (Wetzel 1990). In flow-through wetlands with high N loads, macrophytes and associated epiphytes can be responsible for capturing up to 100% of inorganic N flowing into a basin and may hold up to 86% of all N within the wetland (van Donk et al. 1993; Romero et al. 1999). Assimilated N often re-enters the dissolved nutrient pool as DON following plant senescence or as a by-product of decomposing organic matter (Wetzel 1990). Watersheds with abundant wetland cover and high N loads tend to export a larger proportion of TDN as DON (Pellerin et al. 2004; Fasching et al. 2019; McKenna et al. 2020). Organic forms of N can be used by microbes and primary producers (Wiegner & Seitzinger 2004; Johnson & Tank 2009; Mackay et al. 2020; Glibert et al. 2004), with more labile forms of organic N, composed of amino acids and proteins, preferentially consumed when they are consistently available (Fasching et al. 2020). In primarily closed systems with very little surficial connectivity between wetlands, it is reasonable to expect DON concentrations to increase over time, as more bioavailable forms of organic N are mineralized and reassimilated, while less bioavailable forms grow more concentrated.

Biogeochemical Drivers of Shifting Nutrient Stoichiometry

Several threads of evidence, including particulate and dissolved nutrient stoichiometries, indicate that conditions grew increasingly N limited over time, especially in seasonal compared to semipermanent wetlands. Long-term patterns of DIN removal and assimilation with concurrent increases in DON and SRP would suggest N limitation, but these patterns in themselves are insufficient to draw any conclusions. However, suspended particulate stoichiometry can provide critical insight into nutrient limitation within lentic systems and act as the foundation for subsequent deductions (Healey 1975). Assuming particulates represent phytoplankton and bacteria, then particulate C:N and N:P molar ratios can indicate the direction and extent of nutrient limitation (Healey 1975; Guildford & Hecky 2000). Particulate C:N molar ratios greater than 8.3 are considered indicative of dissolved N deficiency (limitation) with extreme N deficiency at ratios greater than or equal to 14.6, while particulate N:P ratios greater than 22 suggest P deficiency (Healey 1975; Guildford & Hecky 2000)(Healey 1975; Klausmeler et al. 2004; Guildford & Hecky 2000; Stutter et al. 2018; Martiny et al. 2014). In this study, particulate C:N and N:P ratios were largely consistent with the Redfield ratio of 106 C: 16 N: 1 P (Redfield 1958) (Figure 4.6A and 4.6B), indicating that suspended particulates were primarily composed of microorganisms (e.g., phytoplankton, bacteria). However, particulate C:N ratios were between 8.3 and 14.6, suggesting moderate N deficiency. Particulate N:P ratios were often below the threshold of 22 (Table 4.2), indicating that P was not a limiting resource and confirming that phytoplankton were likely limited by N availability.

Dissolved nutrient stoichiometry provided additional evidence for N limitation and indicated stronger limitation in seasonal wetlands than in semipermanent basins, with limitation growing stronger as wetlands aged. Using the framework proposed by Stutter and colleagues (2018), wherein dissolved C:N ratios between 11 and 100 indicate net N sequestration by aquatic microbial communities (i.e., limitation), DOC:DON molar ratios in this study were consistently suggestive of N limitation (Table 4.4). As wetlands aged, DOC:DON ratios increased, a pattern that is consistent with the utilization of DON at a faster rate than DOC, and the difference in utilization rates was greater in seasonal compared to semipermanent wetlands, indicating stronger N limitation. Since DON is often considered less labile than DIN, steadily increasing DOC:DON molar ratios also suggest high inorganic N demand, which could reflect either N assimilation or removal. Inorganic N:P molar ratios were often less than the Redfield ratio, and decreased over a 10-year time frame, which is consistent with increasing inorganic N limitation. Taken together, our data are consistent with strong N limitation growing more severe with each passing year.

Conclusions

Healthy wetlands provide essential ecosystem services and are remarkably robust to physical and chemical disturbance, but decades of wetland consolidation (McCauley et al. 2015; Van Meter & Basu 2015), cultivation, and nutrient enrichment (Howarth et al. 2012; Tesoriero et al. 2013; Van Meter et al. 2016; McCrackin et al. 2018) have left the remaining wetlands under incredible strain to maintain historical services. Our study shows that by restoring conditions conducive to microbially mediated N removal and deposition, wetlands can recover from a history of N amendments. Unfortunately, it is not so easy to recover from long-term P enrichment, and restoration practitioners may need to consider either an active management approach or novel restoration strategies to restore high quality seasonal wetland habitat. Active management practices designed to remove or control the remineralization of P warrant investigation with respect to their efficacy, impacts on plant and animal communities, and the cost of widespread implementation. A handful of ideas that continue to resurface include chemically capping sediments using alum treatments (Steinman et al. 2004; Pilgrim et al. 2007), and physically removing P by, 1) harvesting invasive species biomass (Dubbe et al. 1988; Garver et al. 1988; Lishawa et al. 2015, 2017), or 2) grazing livestock in restored basins (Biró et al. 2019, 2020). While wetlands can easily recover some of the ecosystem services that were lost by draining depressional basins, recovering other services may require more creative solutions.

Table 4. 1. Statistical significance of water column particulate and total nutrients across treatment, hydroperiod, and wetland age. Treatment expresses the divergence of excavated (EXC) basins from business as usual (BAU) wetlands. Hydroperiod indicates whether semipermanently flooded basins differ significantly from seasonally flooded wetlands. Wetland age depicts the effect of time since restoration. Directionality of significant trends are shown parenthetically as deviation by EXC treatment from BAU and divergence of semipermanent basins from seasonally inundated wetlands.

	Main Effects				***Interaction Terms***			
	Treatment	**Hydroperiod**	**Age**	**Age^2**	**Treatment *X* Hydroperiod**	**Treatment *X* Age**	**Hydroperiod X Age**	**R^2** (Full Model)
†Particulate C (mg/L)	0.936	0.825	0.615	- - -	0.001 ** (-)	0.672	0.719	0.17
†Particulate N (µg/L)	0.912	0.654	0.410	- - -	0.000 ** (-)	0.870	0.592	0.20
†Particulate P (µg/L)	0.695	0.441	0.189	- - -	0.001 ** (-)	0.859	0.492	0.31
†Total Organic C (mg/L)	0.014 * (-)	0.349	0.045 * (-)	0.047 * (+)	0.806	0.072	0.092	0.78
†Total N (µg/L)	0.232	0.322	0.632	- - -	0.179	0.337	0.974	0.53
†Total P (µg/L)	0.040 * (-)	0.208	0.002 ** (-)	0.000 ** (+)	0.473	0.035 * (+)	0.785	0.78
	Proportion Particulate							
† Particulate N : Total N	0.176	0.111	0.352	- - -	0.001 ** (-)	0.500	0.366	0.17
† Particulate P : Total P	0.257	0.164	0.026 * (+)	< 0.001 ** (-)	0.062	0.902	0.991	0.54
	Molar Ratios							
Particulate C : N	0.809	0.311	0.202	- - -	0.010 ** (+)	0.849	0.399	0.11
Particulate N : P	0.871	0.819	0.957	- - -	0.605	0.815	0.983	0.14

† Log transformed   * Significant at $P \le 0.05$
· Marginal Significance   ** Significant at $P \le 0.01$

Table 4. 2. Mean particulate and total nutrients in business as usual (BAU) and excavated (EXC) wetlands with Seasonal and Semipermanent hydroperiod. Values represent mean response with standard deviation shown parenthetically.

	Restoration Strategy		***Hydroperiod***		***Strategy X Hydroperiod***			
	BAU	**EXC**	**Seasonal**	**Semi-permanent**	**BAU X Seasonal**	**BAU X Semipermanent**	**EXC X Seasonal**	**EXC X Semipermanent**
Particulate C (mg/L)	2.95 (3.13)	2.92 (4.42)	3.28 (4.52)	2.27 (1.80)	3.24 (3.93)	2.66 (1.99)	3.30 (4.84)	1.35 (0.57)
Particulate N (µg/L)	362 (419.7)	325.9 (381.3)	380.5 (453)	271 (255.5)	391.7 (521.2)	331.7 (279)	373.9 (408.8)	126.2 (76.6)
Particulate P (µg/L)	69.6 (70.6)	75.7 (112.2)	82.9 (108)	53 (54.3)	74.7 (80.1)	64.5 (59.2)	87.7 (121.4)	25.6 (23.4)
Total Organic C (mg/L)	21.77 (8.33)	19.21 (9.56)	23.10 (9.58)	15.28 (4.85)	26.83. (7.91)	16.59 (4.84)	20.90 (9.80)	12.16 (3.18)
Total N (µg/L)	1572.9 (1519.2)	1353.2 (758.5)	1549.3 (776.1)	1284 (1728.3)	1684.8 (731.9)	1458.5 (2028.3)	1469.8 (791.7)	867.3 (265.6)
Total P (µg/L)	320.6 (343.2)	286.6 (355.4)	388.9 (397.4)	135.5 (101.6)	479.4 (414.1)	158 (105)	335.7 (378.3)	81.8 (68.3)
	Proportion Particulate							
Particulate N : Total N	0.22 (0.13)	0.22 (0.12)	0.23 (0.13)	0.21 (0.11)	0.21 (0.13)	0.24 (0.12)	0.24 (0.13)	0.16 (0.06)
Particulate P : Total P	0.32 (0.22)	0.37 (0.21)	0.31 (0.21)	0.43 (0.21)	0.22 (0.17)	0.43 (0.21)	0.36 (0.21)	0.42 (0.2)
	Molar Ratios							
Particulate C : N	10.6 (3.5)	11.3 (4.2)	10.8 (3.9)	11.3 (3.9)	10.5 (3.7)	10.6 (3.4)	10.9 (4.1)	13.1 (4.5)
Particulate N : P	14.5 (10.9)	14.2 (12.2)	14.4 (12.9)	14.2 (8.6)	14.4 (12.6)	14.5 (8.9)	14.4 (13.1)	13.5 (7.9)

Table 4. 3. Statistical significance of dissolved nutrient concentrations across with significant P-values in bold font. Treatment expresses the divergence of excavated (EXC) basins from business as usual (BAU) wetlands. Hydroperiod indicates whether semipermanently flooded basins differ significantly from seasonally flooded wetlands. Wetland age depicts the effect of time since restoration. Directionality of significant trends are shown parenthetically as deviation by EXC treatment from BAU and divergence of semipermanent basins from seasonally inundated wetlands.

	Main Effects				***Interaction Terms***			
	Treatment	**Hydroperiod**	**Age**	**Age^2**	**Treatment *X* Hydroperiod**	**Treatment *X* Age**	**Hydroperiod X Age**	**R^2** (Full Model)
†NO3 – N (µg/L)	0.600	**0.039** * (-)	0.338	- - -	0.284	0.550	**0.008** ** (+)	0.13
†NH4 – N (µg/L)	**0.006** ** (-)	**< 0.001** ** (-)	**0.025** * (-)	- - -	0.456	**0.003** ** (+)	**< 0.001** ** (+)	0.39
†DIN (µg/L)	**0.019** * (-)	**< 0.001** ** (-)	**0.029** * (-)	- - -	0.368	**0.010** ** (+)	**< 0.001** ** (+)	0.39
†DON (µg/L)	0.283	0.629	**0.013** * (+)	- - -	0.552	0.983	**< 0.001** ** (-)	0.71
†TDN (µg/L)	0.238	0.852	**0.034** * (+)	- - -	0.488	0.858	**0.022** * (-)	0.68
†SRP (µg/L)	**< 0.001** ** (-)	**< 0.001** ** (-)	**< 0.001** ** (-)	**< 0.001** ** (+)	0.570	**< 0.001** ** (+)	0.136	0.75
†DOP (µg/L)	0.970	0.791	0.587	- - -	0.244	0.846	0.861	0.28
†TDP (µg/L)	**0.001** ** (-)	**0.002** ** (-)	**< 0.001** ** (-)	**< 0.001** ** (+)	0.880	**0.002** ** (+)	0.400	0.76
†DOC (mg/L)	**0.004** ** (-)	0.977	0.196	**0.020** * (+)	0.854	0.246	**< 0.001** ** (-)	0.83
	Proportion Organic and Inorganic							
DON : TDN	0.904	**0.020** * (+)	0.251	- - -	0.119	0.981	**< 0.001** ** (-)	0.14
DIN : TDN	**0.047** * (-)	**< 0.001** ** (-)	**0.001** ** (-)	- - -	0.472	**0.007** ** (+)	**< 0.001** ** (+)	0.38
DOP : TDP	**0.003** ** (+)	**0.003** ** (+)	**0.004** ** (+)	**< 0.001** ** (-)	0.499	**0.040** * (-)	0.286	0.65
SRP : TDP	**0.008** ** (-)	**0.023** * (-)	0.210	**0.015** * (+)	0.847	**0.044** * (+)	0.601	0.54
	Molar Ratios							
DOC : TDN	**0.020** * (-)	0.614	**0.008** ** (+)	- - -	0.069	0.456	**0.001** ** (-)	0.55
† DOC : DON	**0.003** ** (-)	0.273	**0.033** * (+)	- - -	0.066	0.102	**0.020** * (-)	0.53
† DOC : DIN	0.203	**< 0.001** ** (+)	**< 0.001** ** (+)	- - -	0.295	**0.025** * (-)	**< 0.001** ** (-)	0.42
DOC : TDP	0.721	0.633	0.355	**0.031** * (-)	0.113	0.282	0.097	0.44
† DOC : DOP	0.244	**0.042** * (+)	**0.002** ** (+)	**< 0.001** ** (-)	0.396	0.231	**0.040** * (-)	0.34
† DOC : SRP	**0.001** ** (+)	**< 0.001** ** (+)	**< 0.001** ** (+)	**< 0.001** ** (-)	0.624	**0.001** ** (-)	**0.010** ** (-)	0.72
TDN : TDP	**< 0.001** ** (+)	**< 0.001** ** (+)	**< 0.001** ** (+)	**< 0.001** ** (-)	0.658	**0.002** ** (-)	0.108	0.70
† DON : DOP	***0.052*** · (+)	**0.016** * (+)	**0.003** ** (+)	**< 0.001** ** (-)	0.620	0.088	0.076	0.36
† DIN : SRP	**0.015** * (+)	0.278	**< 0.001** ** (+)	**< 0.001** ** (-)	0.265	0.133	**0.012** * (+)	0.71

† Log transformed · Marginal Significance * Significant at $P \leq 0.05$ ** Significant at $P \leq 0.01$

Table 4. 4. Mean dissolved nutrient concentrations in business as usual (BAU) and excavated (EXC) wetlands with seasonal and semipermanent hydroperiod. Values represent mean response with standard deviation shown parenthetically.

	Restoration Strategy		***Hydroperiod***		***Strategy X Hydroperiod***			
	BAU	**EXC**	**Seasonal**	**Semi-permanent**	**BAU X Seasonal**	**BAU X Semipermanent**	**EXC X Seasonal**	**EXC X Semipermanent**
NO3 – N (µg/L)	19.7 (144.6)	7.1 (16.9)	6.9 (14.9)	27.2 (180)	5.7 (4.5)	36.6 (213.7)	7.6 (18.6)	4.7 (1.5)
NH4 – N (µg/L)	39 (56.7)	30.4 (50.4)	35.9 (58.4)	31.6 (41.1)	40.7 (63.5)	37 (47.2)	32.9 (54.9)	18.5 (13.3)
DIN (µg/L)	58.7 (169.3)	37.5 (57)	42.8 (63.5)	58.8 (203.2)	46.3 (65.6)	73.7 (240.4)	40.6 (62.1)	23.2 (13.5)
DON (µg/L)	1130.5 (407.8)	992.5 (454)	1138.7 (442.6)	883.5 (370.1)	1272.5 (359.5)	959.2 (397.4)	1055.2 (468.8)	702.2 (202.5)
TDN (µg/L)	1189.2 (503.6)	1029.9 (490.3)	1181.4 (481.2)	942.3 (511.5)	1318.8 (397.8)	1032.8 (570.2)	1095.7 (508.5)	725.5 (210.5)
SRP (µg/L)	194.2 (280.2)	137.4 (245)	226.7 (296)	28.0 (54.1)	325.9 (319.7)	35.4 (62.4)	164.8 (262.2)	10.5 (13.2)
DOP (µg/L)	83.6 (93.7)	77.9 (100.4)	92.5 (111.1)	54.3 (45.3)	103.4 (116.3)	59.7 (45.4)	85.7 (107.3)	41.5 (42.5)
TDP (µg/L)	255.3 (280)	204 (264.2)	295 (302.1)	82.2 (79.8)	388.4 (313.6)	94.8 (85.6)	236.8 (279.7)	52 (53.5)
DOC (mg/L)	19.36 (6.93)	16.26 (6.89)	19.83 (7.19)	13.16 (3.99)	23.64 (5.87)	14.19 (3.95)	17.46 (6.92)	10.7 (2.85)
	Proportion Organic and Inorganic							
DON : TDN	0.96 (0.06)	0.97 (0.03)	0.97 (0.03)	0.96 (0.07)	0.97 (0.03)	0.95 (0.09)	0.97 (0.03)	0.97 (0.01)
DIN : TDN	0.04 (0.06)	0.03 (0.03)	0.03 (0.03)	0.04 (0.07)	0.03 (0.03)	0.05 (0.09)	0.03 (0.03)	0.03 (0.01)
DOP : TDP	0.56 (0.33)	0.65 (0.3)	0.53 (0.33)	0.76 (0.23)	0.42 (0.32)	0.73 (0.25)	0.61 (0.31)	0.83 (0.14)
SRP : TDP	0.5 (0.48)	0.38 (0.4)	0.52 (0.48)	0.25 (0.25)	0.68 (0.53)	0.28 (0.28)	0.43 (0.42)	0.17 (0.14)
	Molar Ratios							
DOC : TDN	19.5 (3.6)	18.8 (3.3)	20 (3.3)	17.3 (3.2)	21.3 (2.6)	17.2 (3.4)	19.1 (3.4)	17.5 (2.7)
DOC : DON	20.2 (3.4)	19.4 (3.3)	20.6 (3.2)	18 (3)	22 (2.4)	18 (3.1)	19.7 (3.3)	18 (2.8)
DOC : DIN	963 (684.5)	933.4 (821.9)	1055.4 (841)	709.4 (447.7)	1160.2 (764.9)	725.2 (475.7)	990 (879.8)	671.5 (372)
DOC : TDP	508.4 (522.3)	734.4 (1007)	508 (596)	883.9 (1124.4)	372.7 (404.7)	672.2 (597)	592.5 (675.8)	1391.1 (1761)
DOC : DOP	951.8 (1505.8)	1123.8 (1628.8)	943.5 (1226)	1242.7 (2094.9)	867.5 (729.1)	1038.8 (2014)	985.9 (1429.3)	1716 (2212.7)
DOC : SRP	3931.6 (7164.9)	4684.9 (7841.3)	3578.4 (7472.9)	6047.2 (7343.9)	2644.9 (6673)	5599.3 (7449.9)	4202.6 (7911.1)	7300 (6942.2)
TDN : TDP	27.4 (29.2)	39.5 (57.5)	25.5 (28.8)	51.6 (68.1)	17.3 (18.2)	39.5 (34.8)	30.7 (32.7)	80.4 (108.4)
DON : DOP	48.9 (82.7)	59.1 (85.5)	46.4 (59.4)	70.1 (118.3)	39.1 (33.6)	58.9 (112.1)	50.4 (69.4)	96.2 (128.4)
DIN : SRP	6.9 (17.1)	5.9 (9.1)	3.9 (7.6)	12.4 (21.2)	2.3 (5.4)	12.9 (24)	4.9 (8.6)	10.9 (10.1)

5. Denitrification Potential Depends on Hydroperiod and Restoration Strategy in Restored Depressional Wetlands

Abstract

Widespread wetland restoration is increasingly recognized as an effective nitrate mitigation strategy in cultivated landscapes. Agricultural wetland restoration often includes excavating accumulated sediments deposited in drained basins from the surrounding landscape. The goals of sediment excavation can be to improve water quality, increase water storage capacity, and decrease invasive species cover. However, it is unclear whether sediment excavation influences a key nutrient removal pathway, denitrification. To address this gap in knowledge, we examined ambient and potential denitrification rates and nitrification rates in restored agricultural wetlands in the prairie pothole region of west central Minnesota, USA. In all study wetlands, hydrology was restored by removing subsurface drainage and plugging surface drainage ditches, thus re-establishing hydrology in the basins (“Business As Usual” treatment). In half of the wetlands, accumulated sediment was also removed from the basin and redeposited on the surrounding landscape (“Excavated” treatment). In addition to testing the effects of excavation on denitrification, we accounted for differences between wetlands with seasonal and semipermanent hydroperiod. Denitrification potential was influenced by wetland restoration strategy, where EXC basins had lower rates of removal compared to BAU wetlands, which may have been driven by differences in vegetation that promote a wider soil redox gradient in the rhizosphere. The hydroperiod of restored wetlands was consistently a good predictor of denitrification potential, with approximately 50% higher nitrogen removal rates in seasonal compared to semipermanent wetlands. The effect of hydroperiod was likely driven by regular shifts in redox conditions, which promote nutrient mineralization and nitrification. Denitrification was limited by the availability of nitrate across all sites and dates. Differences between ambient denitrification and nitrification rates were consistent with strong competition for available nitrate. Our results show that these systems are well equipped to process much larger quantities of nitrate than they receive from internal nitrate delivery via nitrification.

Introduction

Humans have changed the structure and function of ecosystems globally by removing native vegetation in favor of row crop agriculture (Dahl 2014), draining and consolidating wetlands (Dahl 2014; Van Meter & Basu 2015; McCauley et al. 2015; McCauley & Jenkins 2005), and doubling nitrogen (N) availability through widespread overapplication of inorganic fertilizers (Vitousek et al. 1997; Smil 1999; Robertson & Vitousek 2009; McIsaac et al. 2001). These landscape level changes have resulted in massive increases in the dissolved N load moving through rivers, lakes, and streams, as well as widespread eutrophication in both freshwater and marine systems (Dodds et al. 2009; Robert J. Diaz & Rosenberg 2008; Seitzinger et al. 2000; Goolsby 2000; Turner & Rabalais 1991, 1994; Rabalais et al. 2002). The deleterious effects of this cultural eutrophication continue to grow more apparent with each passing year, resulting in compromised human and animal health (Pilotto et al. 1997; De Roos et al. 2003; Ward et al. 2018; Schullehner et al. 2018), threats to fisheries health and sustainability through harmful algal blooms, hypoxia and changing food webs (R.J. Diaz & Rosenberg 2008; Rabalais et al. 2007; Jenny et al. 2016; Vadeboncoeur et al. 2003); lost recreational and cultural value; and declines in local and regional biodiversity (Dodds et al. 2009). Despite efforts to raise awareness and address inefficiencies in N application (Robertson & Vitousek 2009; Dinnes et al. 2002), approximately 80% of farmers do not follow the recommended fertilization rate and timing suggested by University researchers (Stuart et al. 2014). Even so, the N load reductions required to mitigate human impacts can only be met if N management and best-practices are combined with N removal strategies including headwater wetland restorations (McLellan et al. 2015).

In North America, the midcontinental interior plains are home to the prairie pothole region, which is characterized by an abundance of depressional wetlands that have been drained for cultivation. Prairie pothole wetlands are often drained because they are small, fairly shallow, and lack persistent perennial connectivity to larger water bodies including lakes and rivers (Tiner 2003a; Cohen et al.

2016). Studies in the prairie pothole region have demonstrated that higher wetland cover significantly reduces stream and riverine nitrate loads (Hansen et al. 2018; Brunet 2011), and in the greater Mississippi River Basin agricultural wetland restoration could remove 50% of nitrate discharged from the Mississippi River into the Gulf of Mexico (Goolsby 2000; Goolsby & Battaglin 2000; Cheng et al. 2020). Meta-analyses integrating data from around the globe have found that depressional basins are biogeochemical hotspots (Fisher & Acreman 2004; Marton et al. 2015; McKenna et al. 2020) and their presence on the landscape contributes to cleaner water in streams and rivers (Hansen et al. 2018; Brunet 2011; Fisher & Acreman 2004).

Despite evidence for landscape scale benefits of wetlands, the relationship between wetland cover and dissolved N concentrations varies widely in individual lakes and streams. Estimates of N removal efficiency in individual wetlands vary from less than 1% to greater than 99% (Jordan et al. 2011), of which up to 100% can be attributable to permanent N removal via denitrification (Seitzinger 1988). However, much of the work on denitrification has focused on streams, rivers, reservoirs, lakes, and flow-through wetlands that have discrete inlets and outlets (Cheng et al. 2020; Mitsch et al. 2005; Mitsch & Day 2006; Hey & Philippi 1995). As a result, small depressional wetlands, with diffuse inlets and irregular surficial water export, have been underrepresented in the N removal literature. In the absence of well constrained estimates of depressional wetland denitrification rates in, it is difficult to account for the contribution of these basins to landscape scale N cycling, especially since their primary nexus of connectivity is through groundwater and intermittent surface water connections (Leibowitz 2003; Fisher & Acreman 2004; Evenson et al. 2018). Characterizing denitrification in small depressional wetlands is particularly important because they constitute the majority of restorable basins (Van Meter & Basu 2015). To accurately quantify how large-scale restoration contributes to N load reduction, we need to better characterize the role of depressional wetlands in permanent N removal. In particular, we need a better understanding of which restoration strategies and locations to prioritize in order to optimize N removal.

Characterizing N removal is complicated by the many metabolic pathways involved in N cycling, including assimilation, mineralization, nitrification, dissimilatory nitrate reduction to ammonium, sulfur-driven nitrate reduction, iron-driven nitrate reduction, anoxic ammonia oxidation, and respiratory denitrification (Burgin & Hamilton 2007; Schlesinger & Bernhardt 2013). However, the most commonly characterized N removal pathway is respiratory denitrification (hereafter denitrification), which is controlled by a suite of environmental factors including temperature, pH, dissolved and soil organic carbon, nitrate and nitrite availability, and redox conditions (Knowles 1982). Since environmental characteristics are often highly variable both within and between small lentic systems (Bennion & Smith 2000; Søndergaard et al. 2005; Whigham & Jordan 2003), identifying restoration strategies or site characteristics with predictable effects on both ambient and potential denitrification rates - measured in the presence of ample carbon and nitrate - are of considerable interest.

Three factors may be particularly important controls on denitrification in restored agricultural wetlands; the presence of accumulated eroded sediments, wetland hydroperiod, and time since restoration. Drained and cultivated wetlands accumulate eroded sediment from the surrounding landscape (Luo et al. 1999; Gleason et al. 1998). Accumulated sediment, contains substantial nutrient, chokes out native plants, alters wetland food webs, and decreases wetland hydroperiod – the number of consecutive days with standing water (Gleason et al. 1998). As a result, sediment excavation and removal is often employed in wetland restoration to increase water storage capacity and restore hydroperiod (Luo et al. 1997); decrease invasive species cover (Smith et al. 2016; Winikoff et al. 2020); and reduce inorganic nutrient availability (Chapter 4). Elevated inorganic nutrient availability can promote denitrification (Mulholland et al. 2008; Ballantine et al. 2014), whether from sediment deposition or from elevated decomposition rates resulting from shorter hydroperiod (Chapter 4)(Euliss et al. 2004; Reddy et al. 1999). However, differences in the plant community could decrease denitrification, particularly when changes in community composition reduce the area of the aerobic-anerobic interface, which is important for coupled nitrification-denitrification (Reddy et al. 1989; Risgaard-Petersen & Jensen 1997; Risgaard-Petersen et al. 1994). For example, tussock-forming sedges, which have diverse microtopography that increases redox gradients (Werner & Zedler

2002), and submerged macrophytes, which oxygenate the soil surface (Mørck Ottosen et al. 1999), are choked out by sediment deposition. Thus, it is unclear whether a restoration strategy that influence so many aspects of ecosystem structure can have a predictable influence on an important ecosystem function, such as denitrification, and how that relationship changes over time.

In this work, we surveyed denitrification potential (DNP) in 37 restored agricultural prairie pothole wetlands ranging in age from 3 to 10 years after restoration. We tested whether DNP differed between basins restored using one of two commonly adopted restoration strategies; reflooding and dredging prior to reflooding. In addition, we sought to identify whether hydroperiod and wetland age since restoration influenced DNP.

Methods

Site Description and Study Design

Study wetlands were located in the prairie pothole region of west central Minnesota (Figure 5.1). All 37 wetlands were restored between 2009 and 2016 (Appendix 1) by the United States Fish and Wildlife Service (U.S. FWS), in partnership with private landowners. Wetlands and surrounding uplands were drained by subsurface tile drains or drainage ditches and were cultivated in row crop agriculture prior to restoration. Fish and Wildlife Service biologists identified the likely historical extent of wetlands using historical aerial imagery, existing topography, and soil characteristics. Changes in soil properties with depth in the soil profile, including changes in color and texture, changes in soil carbonate content, and presence of shell fragments were used to assess the depth of accumulated eroded sediment within each basin.

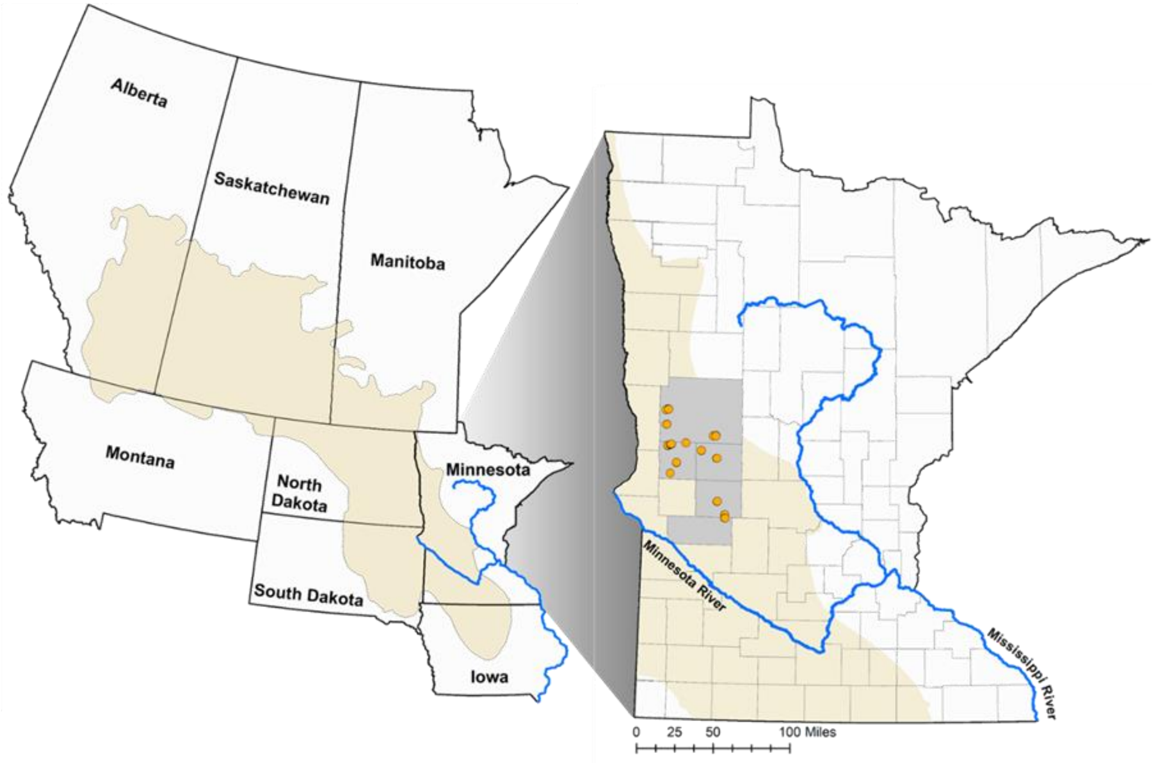

Figure 5. 1. Study sites located in the prairie pothole region of west central Minnesota. Each dot represents one or more wetland. The broader prairie pothole region stretches across what was traditionally tallgrass prairie in north-central North America.

Property owners often elected to enroll the surrounding uplands into the Conservation Reserve Program at the same time as the restoration, but in 18 wetlands, portions of the contributing watershed continued to be actively cultivated throughout the study. Among watersheds with contemporary agriculture, row crop cultivation was usually a minor component of overall land use (mean 22.9% ± 19.5 SD) with two watersheds containing greater than 50% cultivation. Among the two most heavily farmed watersheds, only one received runoff directly from row crop agriculture via a drainage ditch. All other watersheds containing contemporary agricultural maintained a minimum grassland buffer of 24-meters between cultivation and the wetted basin.

Wetlands were categorized as excavated (EXC), when hydrologic restoration followed the removal of accumulated sediment from across the entire basin. Alternatively, when hydrologic restoration occurred in the absence of sediment excavation, basins were categorized as business as usual (BAU) wetlands. We measured denitrification and nitrification rates in 18 BAU and 19 EXC wetlands (N = 37) between 2017 and 2018. We sampled 19 wetlands in both 2017 and 2018, while the remaining 18 basins were sampled once; among the basins sampled in both years, 11 were BAU, 8 were EXC; 12 had seasonal hydroperiod, and 7 were semipermanent. Detailed information about study wetlands and watersheds can be found in Appendix 1. Study wetlands were small, ranging from 0.1 to 2.3 ha (mean 0.6 ha, ± 0.5 SD), and were often in small watersheds between 1.0 to 91.9 ha (mean 14.3 ha ± 25.0 SD) with a mean watershed to wetland area ratio of 35.5 (median 8.0). Wetland hydroperiod - the number of consecutive days with standing water - was characterized as seasonal (n = 23) or semipermanent (n = 14) based on water retention throughout the growing season (Cowardin and Golet 1995) and the development and persistence of distinct vegetative communities (Stewart & Kantrud 1971). Prior to beginning the study, we confirmed that among EXC basins, semipermanent wetlands did not have deeper excavations than seasonal basins (Chapter 4). Wetland age following restoration was defined as the difference between the sampling year and the restoration year.

In 2017 we measured denitrification rates and potentials approximately monthly at a subset of basins including 7 BAU and 5 EXC (8 seasonal and 4 semipermanent) wetlands (N = 12). These basins ranged in size from 0.2 to 2.3 ha (mean 0.6 ± 0.6 SD), meaning intensively sampled sites were a similar size to the sites surveyed only in the spring. Contributing watersheds were smaller among the intensively sampled basins (mean 5.0 ha ± 3.7 SD) compared to the survey wetlands (mean 14.3 ha ± 25.0 SD). Among the intensively sampled wetlands, four watersheds contained contemporary cultivation, with half of the wetlands containing less than 2% cultivation and half with greater than or equal to 40% cultivation cover. Results for three basins were lost during the July sampling series due to file corruption and data entry errors. Unfortunately, there was no way to recover the lost data for that month.

Sample Collection

To characterize denitrification potential over the course of the growing season, we collected samples from a subset of 12 wetlands in the first two weeks of each month from June through October of 2017. To characterize spring denitrification potential, we collected samples from survey sites between May and June in 2017 and 2018. Water and sediment were collected from each study basin. On one occasion we used water from an adjacent wetland since there was insufficient standing water in our target basin. Water was collected from the center of each basin in acid-washed 1-L HDPE bottles following triplicate rinsing with site water. Sediments were collected from the top 5 cm of the soil profile (Inwood et al. 2007) using a cylindrical coring device and stored in airtight plastic bags with headspace removed prior to closure. We collected sediments from four evenly spaced locations within the emergent macrophyte zone of each wetland that were homogenized to form a composite sediment sample. Water and sediments were stored in the dark at approximately 4 degrees Celsius, for up to 48 hours prior to running assays.

Laboratory Analysis

In the laboratory, a subset of each water sample was filtered through glass fiber filters (0.7 µm pore size, Whatman GF/F) for chemical analysis. Samples were stored frozen in acid-washed 60-mL HDPE bottles until analysis for concentrations of nitrate as nitrogen (NO_3-N), ammonium as nitrogen (NH_4^+-N), total dissolved nitrogen (TDN), dissolved organic carbon (DOC), and soluble reactive phosphorus (SRP). Total dissolved nitrogen and DOC were analyzed at the University of Minnesota. Water samples for TDN and DOC were acidified with 50 µL of 2 M HCl prior to analysis with combustion-infrared and combustion-chemiluminescence methods on a Shimadzu TOC-L analyzer equipped with a chemiluminescence detector (TNM-L unit, Shimadzu Corporation) (APHA 2005; ASTM 2008). Water samples for dissolved inorganic nutrients were analyzed in partnership with the Saint Croix Watershed Research Station and Science Museum of Minnesota on a SmartChem 170 discrete analyzer (AMS Alliance, Florida, USA) with the following methods: NH_4^+-N by the phenol hypochlorite method (APHA 1998; Solorzano 1969); NO_3-N by the cadmium reduction method (APHA 1992); and SRP by the ascorbic acid method (Murphy & Riley 1962). When sample concentrations fell below the method detection limit and above zero we assigned a concentration value of one half the method detection limit (Smith 1991).

Homogenized composite sediment samples were analyzed for bulk density, soil organic matter, and total carbon (C) and nitrogen (N) content. Twenty milliliters of sediment were transferred to a pre-weighed aluminum dish, weighed, and then dried for at least 48 hours at 60 degrees Celsius prior to reweighing. Sediments were then pulverized to a fine powder and a subsample was removed for total C and N analysis using a Costech ECS 4010 CHNSO Elemental Analyzer (Costech Analytical Technologies Inc). Soil organic matter (OM) was assessed using the loss on ignition method (Heiri et al. 2001).

Denitrification Assay

We measured both ambient (unamended control, DeN) and potential (nutrient amended, DNP) denitrification rates (Groffman et al. 1999) to identify whether C or N availability limited NO_3-N removal and to assess the potential of basins to remove available NO_3-N. We performed denitrification assays in the laboratory using the chloramphenicol-amended acetylene block technique (Brock 1961; Smith & Tiedje 1979; Groffman et al. 1999; Robertson et al. 1999) in sediment slurries. Acetylene (CAS No. 74-86-2) inhibits the transformation of nitrous oxide (N_2O) to dinitrogen gas (N_2), resulting in the accumulation of N_2O as an indicator of denitrification. We added chloramphenicol (CAS No. 56-75-7) at a rate of 10 mg/L to prevent de novo enzyme synthesis and bacterial proliferation (Smith & Tiedje 1979).

Within 48 hours of sample collection, DeN and DNP assays were run in parallel by incubating 40 ± 3 g wet sediment with 40 mL unfiltered site water in 125 mL glass incubation bottles (Wheaton®) equipped with a grey butyl septa screw cap (DWK Life Sciences #240563). Prior to capping, all incubation bottles were amended with 160 µL of 0.77 M chloramphenicol solution. We ran three replicates of each treatment including control, carbon amendment (160 µL of 2 M glucose solution), nitrate amendment (160 µL of 1.8 M potassium nitrate solution), and amendments of both glucose and nitrate. After homogenizing the slurry solution, we flushed each bottle with helium for 5 minutes to remove oxygen from the incubation bottles, added 10 mL acetylene gas, homogenized the slurry with the headspace by shaking vigorously, and waited 20 minutes before taking an initial headspace sample. Slurries were incubated at room temperature on a roller table in the dark for between 2 and 2.5 hours with exact times documented at initial and final headspace sampling times. Headspace samples (10 mL) were injected into helium flushed 10 mL glass headspace vials (Agilent No. 5182-0838) sealed with grey butyl headspace stopper septa (Agilent No. 5183-4476). Gas samples were analyzed on a gas chromatograph fitted with an electron capture detector and thermal conductivity detector (Spokas et al. 2005). All conversions between N_2O partial pressures in vials and incubation bottles were based on equations presented by Groffman and colleagues (1999) and Robertson and colleagues (1999), using a Bunsen correction coefficient of 0.554. We expressed all denitrification as areal rates of N removal.

Nitrification Assay

We measured ambient nitrification rates to assess the balance between the rate of internal nitrate delivery and DNP using the nitrapyrin inhibition method (Hall 1984) and following the procedure detailed by Strauss and Lamberti (2000). Nitrapyrin (CAS No. 1929-82-4) inhibits NH_4^+-N oxidation (Bedard & Knowles 1989). Nitrapyrin inhibition has been widely used to measure nitrification (Strauss & Lamberti 2000; Strauss et al. 2002, 2004; Arango & Tank 2008; Levi et al. 2012; Roy & Knowles 1995; Powell & Prosser 1985). Since nitrapyrin is minimally soluble in water, it must be added in solution, with dimethyl-sulfoxide (DMSO; CAS No. 67-68-5) as a solvent (Powell & Prosser 1985). Control flasks were also amended with DMSO to control for solvent effects with all assays run in duplicate. Ambient nitrification was calculated as the difference in NH_4^+-N concentrations in nitrapyrin-inhibited and control flasks and was reported as an areal rate. Nitrification rates measured using this technique may over-estimate true rates since the method ensures optimal redox conditions by mixing the slurry continuously on a shaker table. However, we did not measure nitrification potential, which requires NH_4^+-N amendments to alleviate potential demand (Arango & Tank 2008). The difference between nitrification and DNP was calculated using the mean response of DNP across all N-amended replicates.

Statistical Analyses

We assessed whether C, N, or both C and N limited DNP for each site and sampling date using two-way analysis of variance (ANOVA) (Tank & Dodds 2003). We considered a significant positive effect of C or N amendment relative to controls to indicate limitation by that nutrient. In contrast, when the nutrient amendment resulted in a significant reduction in DNP, the nutrient was considered inhibitory. When one nutrient was limiting, one was not, and there was a significant negative interaction, we considered this limitation by one nutrient and inhibition by the other.

To test whether restoration treatment, hydroperiod, and month influenced DNP, we constructed a linear mixed effects model with site as a random effect, followed by Tukey HSD post-hoc tests to identify statistical differences between group means when appropriate. We did not include interaction terms. We used a similar approach to test the effect of restoration treatment, hydroperiod, and wetland age among the spring denitrification survey sites, eliminating month as an explanatory variable. We examined the effect of restoration treatment and hydroperiod on soil and water column environmental parameters using two-way analysis of variance without interaction terms. Separately, we performed backward and forward stepwise model selection with Akaike's information criterion (AIC) to identify which combination of environmental and test metrics best predicted spring DNP (Akaike 1974). Our full model included restoration treatment, hydroperiod, wetland age, soil organic matter, soil total C, soil total N, molar ratio of soil C:N, DOC, TDN, NH_4^+-N, NO_3-N, SRP, and mean depth of water column at sampling locations (see methods from chapter 3). Since the same conditions that promote denitrification also promote P mobilization, we examined the relationship between water column NO_3-N and SRP concentrations prior to model selection and found a mild positive relationship that was not statistically significant ($p = 0.76$; linear regression). Following model selection, we identified the portion of variability in the full dataset that was attributable to the selected variables by fitting the model with site as a random effect to account for repeated measurements at 19 wetlands that were sampled in both 2017 and 2018. To test the effects of restoration treatment, hydroperiod, and wetland age on ambient nitrification rates and the difference between DNP and ambient nitrification, we formed a simple linear model with a single, mean observation for each wetland. Whenever appropriate, we log-transformed response variables to meet model assumptions of homogeneous residual error. All statistical analyses were performed in R (R Core Team 2020) using the '*lme4*' and '*lmerTest*' packages (Bates et al. 2020; Kuznetsova et al. 2020) with a critical *p*-value of 0.05. Model selection was performed using the '*MASS*' and '*cAIC4*' packages (Saefken et al. 2019; Ripley et al. 2021).

Results

Environmental Characteristics

Water column dissolved nutrient concentrations varied considerably between sites and dates; in general, dissolved NO_3-N concentrations were very low (mean 11 µg/L ± 31.9 SD), while other dissolved nutrients, including NH_4^+-N, SRP, DOC, and TDN had much higher availability (Table 5.1). Ammonium concentrations were nearly 6 times greater than those of NO_3-N (mean 63.3 µg/L ± 144.7 SD) but there was considerable variability between sites and dates. Dissolved organic C and TDN concentrations were significantly lower in EXC and semipermanent basins compared to their BAU ($p = 0.003$ and 0.031, DOC and TDN, respectively) and seasonal wetland counterparts ($p < 0.001$ and $p = 0.005$, DOC and TDN, respectively; Table 5.1). Semipermanent wetlands were nearly 35 cm deeper than seasonal basins ($p < 0.001$) and had significantly lower SRP concentrations ($p = 0.002$). Soil organic matter, total carbon, total nitrogen, and moisture were similar between treatments and hydroperiods, but bulk density was significantly higher in EXC compared to BAU basins ($p = 0.036$; Table 5.1).

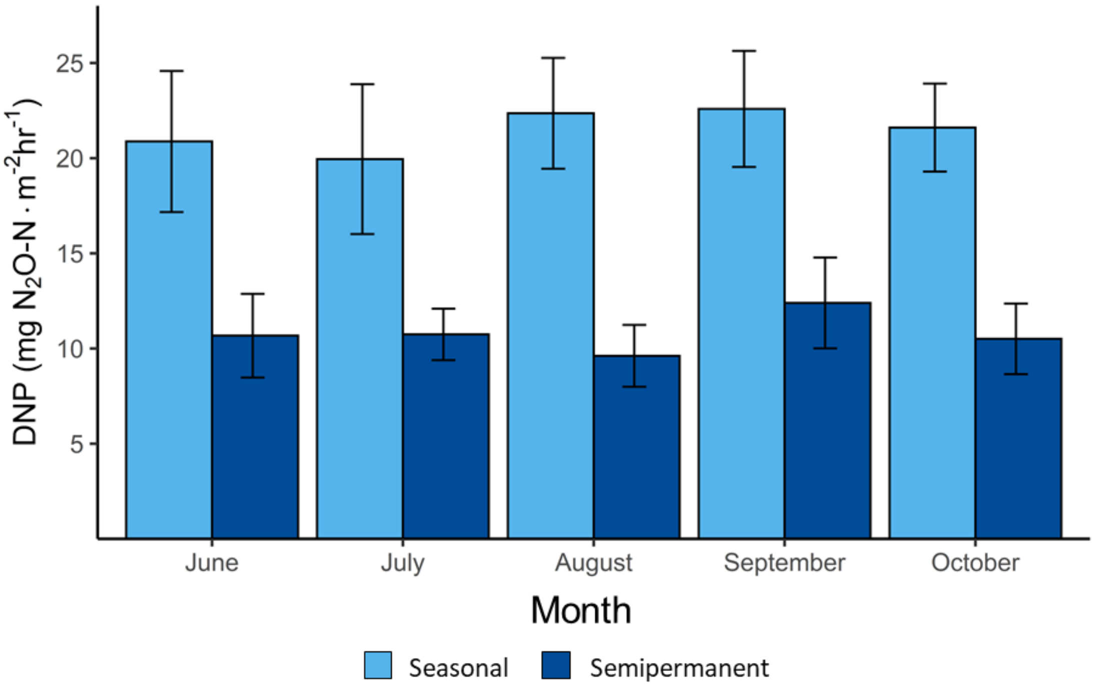

Figure 5. 2. Denitrification potential in seasonal and semipermanent wetlands from June through October 2017. Bars represent mean response with standard error bars. Denitrification potential in seasonal basins were statistically significantly higher than in semipermanent basins across all months..

Monthly Denitrification

Throughout the growing season, DNP was overwhelmingly limited by NO_3-N availability across all sites and dates (Table 5.2). The proportion of sites showing signs of secondary C-limitation increased steadily throughout the growing season from only 25% of sites in June to 67% of sites in October. Curiously, a handful of sites also showed mild C-inhibition, particularly early in the growing season when the smallest proportion of sites were limited by C availability (Table 5.2). Across all sites and months, denitrification was considerably higher with N amendments compared to controls, regardless of the presence of added C (Table 5.4). Since addition of both C and N and N alone resulted in similarly elevated DNP, we included all N-amended replicates in estimates of DNP for subsequent statistical tests.

Hydroperiod was the strongest predictor of DNP, but month had a meaningful influence on ambient DeN rates (Table 5.3). Semipermanently flooded basins had significantly lower DNP than seasonal wetlands ($p = 0.002$; Figure 5.2; Table 5.4), but there was no meaningful difference between DNP at EXC and BAU wetlands ($p = 0.164$; Table 5.3). Ambient DeN was not consistently influenced by restoration treatment or hydroperiod ($p = 0.779$ and 0.788, respectively; Table 5.3), but DeN was higher in July and October compared to other months (Table 5.3). Ambient DeN rates were low (mean 0.19 mg N_2O-N/m^{2}hr^1 ± 0.32 SD) and DNP was nearly 100-times greater than ambient rates (mean 17.8 mg N_2O-N/ m^{2}hr^1 ± 11.0 SD).

Spring Denitrification Survey

Ambient dissolved NO_3-N was nearly absent (Table 5.1) resulting in primary NO_3-N limitation of spring DNP and secondary limitation by C-availability in approximately half of the sites surveyed (Table 5.2). Ambient DeN was low (mean 0.08 mg N_2O-N/m^{2}hr^1 ± 0.11 SD) and was not significantly influenced by sediment excavation ($p = 0.71$, Table 5.5), hydroperiod ($p = 0.66$), or wetland age ($p = 0.32$). In contrast, N-amended DNP rates were more than 200-times greater than DeN rates (mean 18.4 mg N_2O-N/m^{2}hr^1 ± 12.1 SD), and DNP was significantly influenced by both restoration treatment ($p = 0.022$) and hydroperiod ($p = 0.001$; Table 5.5), but not wetland age ($p = 0.79$). In EXC basins, DNP was approximately 20% lower than in BAU wetlands, while in semipermanent wetlands DNP was approximately 50% lower than in seasonal basins (Table 5.6, Figure 5.3).

The model selection process revealed three variables that explained 32% of variability in DNP, including restoration treatment, NO_3-N concentration, and mean water column depth. Water column NO_3-N was positively correlated with DNP and with SRP which suggests a possible relationship between the conditions that result in P mineralization and NO_3-N availability. Conversely, mean water column depth and DNP were negatively correlated (Figure 5.4).

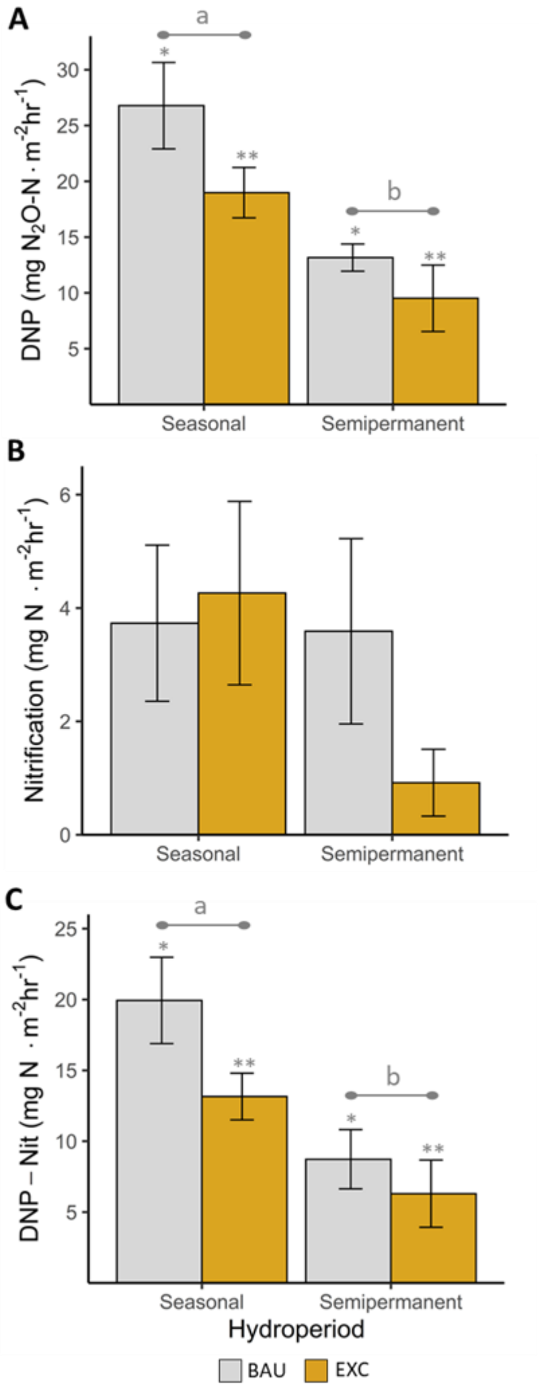

Figure 5. 3. Denitrification potential (A) and nitrification (B) rates in business as usual (BAU) and excavated (EXC) sites across hydroperiods. Bars represent mean response with standard error brackets. The difference between denitrification potential and nitrification rates (C) were significantly lower in semipermanent basins (letters) and in basins restored with sediment excavation (*).

Nitrate Removal Verses Production

Although ambient nitrification (mean 3.5 mg N·m^{-2}hr^{-1} ± 4.9 SD) was 50-times larger than DeN (mean 0.08 mg N·m^{-2}hr^{-1} ± 0.11 SD), nitrification was not sufficient to meet potential demand by denitrifiers (mean 18.4 mg N·m^{-2}hr^{-1} ± 12.1 SD). Nitrification was not significantly influenced by restoration strategy, hydroperiod, or wetland age (Table 5.5). The difference between DNP and nitrification favored removal across all treatment and hydroperiod combinations (Figure 5.3), and the difference was larger in BAU ($p = 0.026$) and seasonally inundated basins ($p = 0.001$) than in EXC and semipermanent wetlands, respectively (Tables 5.5 and 5.6). The difference between DNP and nitrification was 20% larger in BAU (mean 14.3 mg N·m^{-2}hr^{-1} ± 9.5 SD) than in EXC wetlands (mean 11.3 mg N·m^{-2}hr^{-1} ± 6.6 SD); a trend that was driven by basins with seasonal hydroperiod (Figure 5.3C).

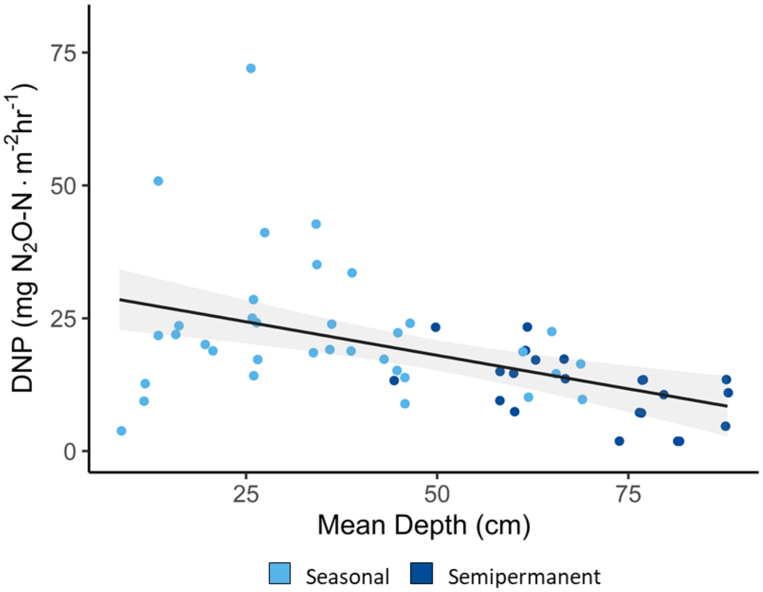

Figure 5. 4. Denitrification potential in response to mean water column depth. Trend lines represent overall effect and 95% confidence interval across both seasonal and semipermanent hydroperiods.

Discussion

Denitrification potential responded quickly to restoration, rapidly reaching rates similar to natural depressional wetlands and exceeding rates in many restored wetland (Bruland et al. 2006; Ballantine et al. 2017; Alldred & Baines 2016). Data compiled by a recent meta-analysis showed that measurements of denitrification in systems with longer hydroperiod resulted in lower rates of N removal compared to measurements from basins dominated by emergent macrophytes (Alldred & Baines 2016), which aligns well with our findings (Figure 5.5). Denitrification was primarily influenced by hydroperiod, with higher nitrogen removal rates in seasonal compared to semipermanent wetlands, regardless of when DNP was measured during the growing season. Denitrification was also influenced by sediment excavation, with lower N removal in EXC basins than in BAU wetlands. Denitrification potential (DNP) always exceeded internal nitrate delivery via nitrification, resulting in persistent primary N-limitation of denitrification and fairly low background DeN. Despite high variability, DNP responded quickly to added nitrate, suggesting a large capacity to remove excess nitrate under a wide range of environmental conditions. We explore factors contributing to variability and maintenance of high rates of N removal despite a wide range of environmental conditions in restored wetlands.

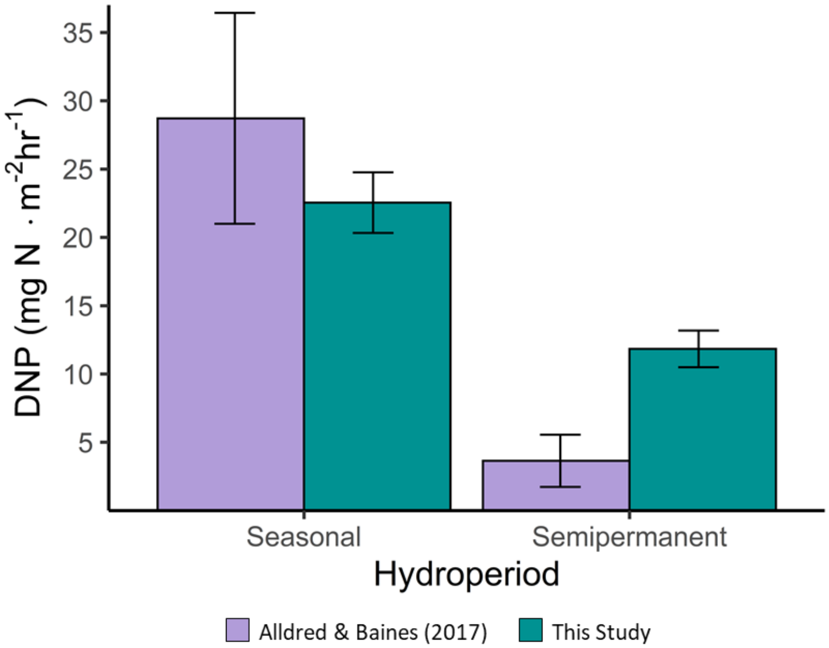

Figure 5. 5. Denitrification potential by hydroperiod in our study compared to values reported for freshwater wetlands dominated by emergent (seasonal) and submerged (semipermanent) macrophytes reported in a meta-analysis by Alldred and Baines (2017). Error bars represent standard error about the mean.

Hydroperiod Was the Strongest Predictor of Denitrification

Hydroperiod was the strongest and most consistent predictor of DNP in both the spring survey and the intensively sampled monthly assessments of N removal, with elevated rates in seasonal basins compared to their semipermanent counterparts. In our study, the three most conspicuous differences between seasonal and semipermanent wetlands were, 1) the persistence of standing water throughout the growing season, 2) water column depth, and 3) presence or absence of a pool with submerged macrophytes, all of which are reasonable proxies for the variability of redox conditions in space or time. Other authors have shown that variability in redox conditions supports high denitrification potentials either by maintaining a community of nitrifiers in close proximity to denitrifiers (Svensson & Leonardson 1996; Eriksson & Weisner 1999; Kreiling et al. 2011) or by alternating between conditions that are favorable for nitrification and denitrification over time (Groffman et al. 2009; Seitzinger et al. 2006). Shallow lentic systems like depressional wetlands have a large degree of spatial and temporal variability in redox conditions (Rose & Crumpton 1996; Eriksson & Weisner 1999; Svensson & Leonardson 1996; Reddy et al. 1989; Minett et al. 2013; Risgaard-Petersen & Jensen 1997). Compared to larger lakes and reservoirs, small lentic systems have a higher proportion of edge habitat per unit volume. These edge habitats have strong moisture and redox gradients that exercise a powerful control over subsequent N removal (Orr et al. 2007; Burgin & Groffman 2012; Burgin et al. 2010) and the spatial position of these gradients changes within and between growing seasons as water levels rise and fall (Orr et al. 2007; Burgin et al. 2010). In our study, large fluctuations in water column depth may have been a primary driver of elevated DNP in seasonal compared to semipermanent wetlands.

Compared with deeper water bodies, shallow lentic systems are more susceptible to freeze-thaw and wet-dry cycling throughout the water column and underlying soils; cycling that alters redox conditions and liberates considerable N and P nutrient into the water column and pore water (Chapter 3), which can promote denitrification (Finlay et al. 2013; Orr et al. 2007; Weller et al. 2011). Deep freezing releases nutrient from lysed cells during spring thaw and physically forces separation between soil aggregates as the freezing water expands (Al-Omari et al. 2015; Xie et al. 2015). Increasing the availability and potential mobility of dissolved NO_3-N in pore water and surface water increases redox potential (Conrad et al. 2019) and stimulates denitrification (Firestone et al. 1980). Likewise, drought-induced water column drawdown increases redox potential considerably by aerating soils. Increased oxygen availability promotes aerobic decomposition and nutrient mineralization while cell stress and death further augment nutrient availability upon rewetting and re-establishment of anaerobic conditions (Burgin & Groffman 2012; Birch 1958). These pulses of nitrate caused by periodic shifts in redox conditions stimulate denitrification which responds rapidly to dissolved nutrient availability (Groffman & Tiedje 1988). In our study, semipermanent wetlands were on average 34.7 cm deeper than seasonal wetlands and model selection favored water column depth as a predictor of DNP, with lower DNP in deeper water, likely because water column depth was a good proxy for temporal variability in redox conditions and subsequent N removal.

Restoration Strategy Influenced Denitrification

Lower rates of permanent N removal in EXC compared to BAU wetlands were likely driven by changes in ecosystem structure following sediment removal. Previous work in these wetlands has demonstrated that sediment excavation alters the physical and chemical structure of wetland soils (Chapter 3), decreases water column nutrient availability (Chapter 4), and decreases the density of invasive macrophytes (Chapter 2), all of which can contribute to DNP. In this study, we found significantly elevated soil bulk density in EXC wetlands which may limit the mobility of dissolved nutrients across the soil water interface (Perrone & Madramootoo 1994), and we found lower concentrations of DOC and TDN in EXC compared to BAU wetlands, both of which are important substrates for biogeochemical cycling (Wiegner & Seitzinger 2004; Markager et al. 2011; Mackay et al. 2020; Johnson et al. 2009; Johnson & Tank 2009; Glibert et al. 2021).

Although we were not able to directly evaluate the role of vegetation on DNP, work in other systems suggests that lower macrophyte abundance in EXC wetlands could have contributed to lower DNP. In a recent meta-analysis, the presence of well-developed stands of vegetation were sufficient in themselves to increase denitrification rates by over 50% above the unvegetated baseline (Alldred & Baines 2016). It is generally accepted that invasive macrophytes have higher above ground biomass than native competitors (Ehrenfeld 2003, 2010), increase primary productivity, augment the pace of nutrient cycling (Angeloni et al. 2006), and increase the size of available nutrient pools (Ehrenfeld 2010; Bachand & Horne 1999), which may promote denitrification. However, emergent macrophytes can also promote coupled nitrification-denitrification through delivery of oxygen to their roots and adjacent rhizosphere (Eriksson & Weisner 1999; Kreiling et al. 2011), and wetland plants deliver more oxygen into the rhizosphere when they have higher aboveground biomass, regardless of species identity (Wiebner et al. 2002). Thus, in wetlands with high invasive species cover and biomass we should expect to see higher rates of DNP not only because of increases in nutrient cycling and availability but also because invasive species tend to have higher above ground biomass resulting in larger gradients of soil redox potential and higher rates of coupled nitrification-denitrification. Previous work in our wetlands showed that sediment removal decreased invasive emergent macrophyte cover for six years following hydrologic restoration (Chapter 2), which may have contributed to differences in N removal.

Balancing Nitrate Supply and Demand

Denitrification potential always exceeded nitrification rates, resulting in widespread limitation of DNP by availability of NO_3-N. However, ambient rates of N removal (DeN) were considerably lower than nitrification rates. Although a handful of ecosystems are limited by labile C, it is typical for DeN to be limited by NO_3-N (Groffman et al. 2009). Many depressional wetlands receive agricultural runoff during spring thaw and following large precipitation events (Hayashi et al. 2016) but external NO_3-N delivery is limited because basins lack a persistent surficial connection to other water bodies. As a result, the availability of NO_3-N is largely mediated by aerobic organic matter mineralization and nitrification, which may be separated in space or time (Eriksson & Weisner 1999; Risgaard-Petersen & Jensen 1997; Groffman & Tiedje 1988) from the denitrifying microbial community, which requires anaerobic conditions. Because of this spatial and temporal separation, ambient rates of DeN can be controlled by both the internal production of and competition for NO_3-N. In our study, contrasting relationships between nitrification, DNP, and DeN are likely driven by a combination of priming effects resulting from seasonal pulses of dissolved NO_3-N following freeze-thaw and dry-wet cycles (McClain et al. 2003; Groffman et al. 2009; Hansen et al. 2016) and competition for NO_3-N.

Alternative pathways of N cycling, including assimilation, reduction, and removal were likely temporary nutrient sinks in our wetlands. Assimilatory uptake is likely one of the most important alternative N sinks in our wetlands. Depressional wetlands are highly productive and densely vegetated, which provides surfaces for epiphyte colonization, an important nutrient sink (Wetzel 1990; Castaldelli et al. 2015). Alternative dissimilatory metabolic pathways competing for NO_3-N (besides DeN) include anaerobic ammonia oxidation (anammox) and fermentative dissimilatory nitrate reduction to ammonia (DNRA) (Burgin & Hamilton 2007). All three of these metabolic pathways share a similar requirement for anoxia, but conditions that are favorable for anammox include high concentrations of both NH_4^+-N and NO_3-N in combination with low labile carbon availability (Jetten et al. 1999; Burgin & Hamilton 2007).

In our wetlands, fairly low concentrations of dissolved inorganic N were commonplace and high DOC was nearly ubiquitous (Table 5.4, Chapter 3), making it unlikely that anammox contributed meaningfully to inorganic N cycling. Alternatively, fermentative DNRA is favorable under strong reducing conditions with limited NO_3-N availability and high concentrations of labile C (Burgin & Hamilton 2007). While we did not measure the lability of C, our wetlands had high DOC concentrations, low NO_3-N concentrations (Chapter 4), and we found patterns of nutrient availability that were consistent with reducing conditions. For example, our wetlands had high concentrations of dissolved inorganic P and elevated concentrations of NH_4^+-N compared to NO_3-N, which suggests anaerobic conditions. Furthermore, some of our wetlands smelled strongly of hydrogen sulfide and we found evidence of purple sulfur bacteria (genus *Chromatiaceae*; personal observation, Figure 5.6), a genus of photoautotrophic bacteria that favor anaerobic conditions. Together, this suggests that conditions were favorable for fermentative DNRA, which could contribute to some portion of N-cycling in restored prairie pothole wetlands and is a topic that warrants further investigation.

Figure 5. 6. Benthic biofilms consisting of green and purple microbes were found in wetlands that also had a strong hydrogen sulfide odor.

Conclusions

Our work indicates that the potential for permanent N removal in restored agricultural prairie pothole wetlands was largely controlled by spatial and temporal variability in redox conditions mediated through hydroperiod and the effect of restoration treatment on emergent macrophyte density. Even though seasonal basins have higher potential for denitrification per unit area, we should consider the importance of water residence time when comparing the effectiveness of seasonal and semipermanent basins for permanent N removal. Water bodies with longer water residence times are thought improve the conversion of NO_3-N to N_2 rather than to N_2O, a strong greenhouse gas (Mosier et al. 1998). When N removal and remediation is a goal of wetland restoration, we should consider how water permanence and vegetative community influence the variability of redox potentials in space and time. It is important that we address how to optimize redox potential and remove dissolved nitrogen from water, while protecting high quality habitat for a diverse community of native flora and fauna.

Table 5. 1. Water quality and soil characteristics across denitrification study sites. Mean values with standard error shown parenthetically. Significant differences between restoration treatment and hydroperiod group means by a two-way analysis of variance are indicated by bold font (critical p = 0.05).

	Treatment		***Hydroperiod***	
	BAU	**EXC**	**Seasonal**	**Semipermanent**
Water Column				
DOC (mg/L)	**17.6 (5.8)**	**14.5 (6.4)**	**18.5 (6.5)**	**12.3 (3.4)**
TDN (mg/L)	**1.05 (0.34)**	**0.89 (0.40)**	**1.07 (0.40)**	**0.83 (0.30)**
NH_4^+-N (ug/L)	45.2 (54.1)	83.6 (207.5)	50.4 (59.6)	84.1 (227.7)
NO_3^--N (ug/L)	6.2 (4.5)	15.2 (46.1)	13.7 (40.5)	5.4 (4.0)
SRP (ug/L)	212.1 (304.8)	147.9 (231.4)	**263.1 (317.0)**	**51.2 (77.6)**
Mean Depth (cm)	49.5 (20.8)	47.5 (26.0)	**35.1 (17.7)**	**69.8 (12.5)**
Soil				
Bulk Density (g/cm^3)	**0.89 (0.13)**	**0.98 (0.13)**	0.95 (0.10)	0.91 (0.18)
Soil Moisture (%)	75.0 (33.1)	63.5 (14.1)	64.8 (10.7)	77.1 (39.6)
Soil Organic Matter (%)	10.7 (4.6)	9.1 (2.4)	9.5 (2.0)	10.6 (5.5)
Total Carbon (%)	5.0 (3.1)	3.7 (0.8)	4.0 (1.0)	5.0 (3.6)
Total Nitrogen (%)	0.35 (0.27)	0.26 (0.06)	0.28 (0.06)	0.35 (0.32)

Table 5. 2. Denitrification potential limitation. Percent of sites with primary N limitation, secondary C limitation, and C inhibition of denitrification across the growing season in 2017 and in the spring of 2017 and 2018.

	Sites	***1° N Limitation***	***2° C Limitation***	***2° C Inhibition***
June	12	100 %	25 %	42 %
July	9	100 %	44 %	0 %
August	12	100 %	50 %	17 %
September	12	100 %	50 %	17 %
October	12	100 %	67 %	0 %
Spring 2017 - 2018				
Spring 2017	28	100 %	50 %	0 %
Spring 2018	29	100 %	45 %	0 %
Treatment: BAU	30	100 %	50 %	0 %
Treatment: EXC	27	100 %	44 %	0 %
Hydroperiod: Seasonal	35	100 %	60 %	0 %
Hydroperiod: Semipermanent	22	100 %	27 %	0 %

Table 5. 3. Statistical significance of denitrification (mg N · $m^{-2}hr^{-1}$) across months, restoration treatments, and hydroperiod. Treatment groups include business as usual (BAU) and excavated (EXC) wetlands; hydroperiod includes seasonal and semipermanent wetlands. Significant P-values shown in bold with direction of effect shown parenthetically.

			Month			
Amendment	**Treatment (EXC)**	**Hydroperiod (Semipermanent)**	**July**	**August**	**September**	**October**
Control	0.779	0.788	**< 0.001 ** (+)**	0.216	0.589	**0.018 * (+)**
N	0.181	**0.004 ** (-)**	0.095	0.123	0.591	0.175
C+N	**0.036 * (-)**	**0.001 ** (-)**	0.957	0.711	0.624	0.811
C+N, N	0.164	**0.002 ** (-)**	0.288	0.189	0.108	0.166

† Log transformed
· Marginal Significance
* Significant at $P \leq 0.05$
** Significant at $P \leq 0.01$

Table 5. 4. Monthly denitrification (mg N · $m^{-2}hr^{-1}$) in business as usual (BAU) and excavated (EXC) wetlands with seasonal and semipermanent hydroperiod. Values represent mean response with standard deviation shown parenthetically.

	Treatment		*Hydroperiod*		*Month*				
Amendment	**BAU**	**EXC**	**Seasonal**	**Semipermanent**	**June**	**July**	**August**	**September**	**October**
Control	0.19 (0.27)	0.18 (0.4)	0.19 (0.34)	0.19 (0.3)	0.08 (0.12)	0.55 (0.72)	0.17 (0.18)	0.11 (0.12)	0.27 (0.3)
C	0.03 (0.05)	0.01 (0.02)	0.01 (0.01)	0.04 (0.07)	0.01 (0.02)	0.03 (0.03)	0.02 (0.02)	0.01 (0.01)	0.04 (0.1)
N	16.6 (10.7)	18.6 (7.3)	20.7 (9.9)	11.1 (3.7)	19.8 (12.5)	14 (6.8)	16.1 (7.7)	17.9 (8)	16.2 (7)
C+N	18.9 (13.2)	20 (10.5)	23.5 (12.7)	11.3 (4.8)	18.9 (15.5)	17.7 (9.6)	20.1 (10.9)	20.5 (10.2)	19.6 (9.1)
C+N, N	17.2 (12.1)	18.7 (9.4)	21.4 (11.6)	10.8 (4.7)	17.6 (14.5)	15.9 (8.1)	18.1 (9.2)	19.2 (8.9)	17.9 (7.8)

Table 5. 5. Statistical significance of spring denitrification and nitrification across restoration treatment (business as usual, BAU; excavated, EXC), hydroperiod (seasonal, semipermanent) and Wetland Age. Statistically significant P-values are shown in bold with symbols indicating degree of significance.

Amendment	**Response**	**Treatment (EXC)**	**Hydroperiod (Semipermanent)**	**Age**
Control	**DeN (mg N/m^2·hr)**	0.711	0.657	0.319
N	**DNP (mg N/m^2·hr)**	**0.034 * (-)**	**0.002 ** (-)**	0.691
C+N	**DNP (mg N/m^2·hr)**	**0.019 * (-)**	**0.001 ** (-)**	0.864
C+N, N	**DNP (mg N/m^2·hr)**	**0.022 * (-)**	**0.001 ** (-)**	0.790
- - -	**Nitrification (mg N/m^2·hr)**	0.342	0.245	0.513
- - -	**DNP – Nitrification (mg N/m^2·hr)**	**0.026 * (-)**	**0.001 * (-)**	0.420

† Log transformed * Significant at $P \leq 0.05$
· Marginal Significance ** Significant at $P \leq 0.01$

Table 5. 6. Mean spring denitrification and nitrification rates in business as usual (BAU) and excavated (EXC) wetlands with seasonal and semipermanent hydroperiod. Values represent mean response with standard deviation shown parenthetically.

		Restoration Treatment		***Hydroperiod***	
Amendment	**Response**	**BAU**	**EXC**	**Seasonal**	**Semipermanent**
Control	**DeN (mg N/m^2·hr)**	0.09 (0.12)	0.08 (0.11)	0.08 (0.12)	0.08 (0.1)
C	**DNP (mg N/m^2·hr)**	0.03 (0.07)	0.01 (0.03)	0.01 (0.03)	0.04 (0.08)
N	**DNP (mg N/m^2·hr)**	17.7 (11.5)	15.1 (9.4)	19.8 (11.6)	11.4 (5.9)
C+N	**DNP (mg N/m^2·hr)**	22.9 (15.5)	17.7 (11.2)	25.3 (15)	12.8 (6.7)
C+N, N	**DNP (mg N/m^2·hr)**	20.4 (13.5)	16.2 (10.3)	22.5 (13.1)	11.8 (6.3)
- - -	**Nitrification (mg N/m^2·hr)**	3.7 (4.4)	3.4 (5.4)	4.1 (5.3)	2.6 (4.1)
- - -	**DNP – Nitrification (mg N/m^2·hr)**	14.3 (9.5)	11.3 (6.6)	15.8 (8)	7.9 (5.9)

6. Synthesis and Management Recommendations

Background

Land use changes have resulted in a net loss of 53% of natural wetlands in the contiguous United States, with one third of those losses occurring in the corn belt states of Illinois, Indiana, Iowa, Michigan, Minnesota, Ohio, and Wisconsin (Dahl 1990). In the Prairie Pothole Region 63% of the original 7 million ha of wetland have been lost to agricultural drainage (Dahl 2014). Every year, more small basins are drained and consolidated into fewer, larger wetlands (Oslund et al. 2010; Johnston 2013; Wright & Wimberly 2013; Van Meter & Basu 2015; Vanderhoof et al. 2016), largely because they are not afforded the same protections as other waters (van der Valk & Pederson 2003). The cost of wetland drainage has been larger and more frequent flood events (Hey & Philippi 1995; Changnon 1998; Pattison-Williams et al. 2018), less water in streams and rivers during periods of drought (Daniel L McLaughlin et al. 2014; Evenson et al. 2018; Golden et al. 2016; Rains et al. 2016), nitrogen (N) and phosphorus (P) pollution in surface and groundwater (Johnston et al. 1990; DeSimone et al. 2009; Cross & Jacobson 2013; Jacobson et al. 2017; Hansen et al. 2018; Lewandowski et al. 2008; Keeler & Polasky 2014), and biodiversity loss (Gibbs 2000; Lehtinen et al. 1999). Wetland restoration is the best way to recover these lost ecosystem services and may be the only way to meet the N management goals in the Mississippi River Valley (McLellan et al. 2015; Cheng et al. 2020). Therefore, it is essential that we identify which restoration strategies optimize desired ecosystem services.

Wetland restoration includes reestablishing hydrologic regimes to support wetland ecosystems. In agricultural wetlands this often involves plugging drainage ditches and breaking subsurface tile drain. In an agricultural setting, restoration can also involve removing accumulated eroded sediment collected in the drained basin. Sediment excavation is often used to increase the depth of a basin and ensure an open pool, but this practice can have unintended consequences for wildlife. Deep excavations in small basins can result in very little area for foraging and may increase the risk of predation by concentrating waterfowl to an even smaller area within the basin (Galatowitsch & van der Valk 1994).

Additional rationale for sediment excavation has included, rebuilding historical topography, exposing buried seed banks, and nutrient mitigation. Restoring basin topography should recreate historical soil moisture gradients that favor distinct plant communities (Seabloom & van der Valk 2003), thus increasing the utility of habitat for wildlife. The topography approach prioritizes restoration of physical attributes with the expectation that biological communities and biogeochemical function will follow. Evidence suggests that this approach works to some extent, but sedge meadow communities developed more slowly than other communities and restored basins are usually less diverse than in natural wetlands (Seabloom & van der Valk 2003; Aronson & Galatowitsch 2008). In contrast, the buried seed hypothesis suggests that removing accumulated sediment exposes a diverse native seed bank. This is predicated on early research showing that sediment deposition chokes out native plants and prevents the germination of native seed (Jurik et al. 1994; Gleason et al. 2003). However, simply removing sediment may not be sufficient to improve native species abundance following restoration; viability of native species seed is highly variable and decreases significantly over time (Erlandson 1987; Galinato & Van Der Valk 1986; van der Valk & Davis 1978, 1979). Furthermore, some evidence suggest that redox gradients generated by the microtopography of native sedge growth forms may be essential for native species recruitment (Werner & Zedler 2002).

More recently, the sediment nutrient hypothesis has emerged as an alternative benefit of sediment excavation. This hypothesis emerged from recognition that the erosion and deposition of nutrient rich topsoil may be a significant source of nutrient upon rewetting of restored basins. In some respects, this idea emerged from the same data that led to the Food Security Act of 1985, which established the conservation reserve program in part for soil conservation. Growing recognition that nutrient rich topsoil was washing away from agricultural fields led some researchers to investigate differences in rates of sediment deposition and sediment nutrient content between prairie and agricultural wetlands (Martin & Hartman 1987; Johnston 1991b; Johnston et al. 1984). When researchers found that changes in dissolved nutrient availability could shift wetland plant communities into alternate stable states dominated by aggressive invasive species (Wetzel & Van Der Valk 1998; Woo & Zedler 2002; Green & Galatowitsch 2002), it became clear that eroded sediment may contribute to nutrient availability and thus shifts in vegetation. To date, research has done more to characterize the negative impacts of sediment deposition than to identify whether sediment removal achieves hypothesized results and desirable outcomes.

Key Findings

The studies described in this dissertation were designed to assess how sediment excavation influences a variety of metrics used to describe the success of wetland restoration including, soil properties, plant communities, water quality, and N removal potential. While we found some indications that excavation can be a beneficial practice, its utility is limited. Somewhat unexpectedly, hydroperiod was almost universally the best predictor of soil and water column nutrient availability (Chapters 3 and 4), and of denitrification potential (Chapter 5). Underscoring the complexity of these systems, temporal shifts in dissolved nutrients were synchronized with the establishment of and spread of emergent vegetation.

Vegetation – Our results showed that sediment excavation can impart short-term benefits on the emergent macrophyte community by increasing the time it takes for two key aggressive invasive species to establish. However, the benefits of excavation were lost within 6 years of restoring water to the basin. Our results were consistent with a reduction in the size of the invasive species seed bank at excavated wetlands (Smith et al. 2016), but we did not find evidence that excavation exposed a more diverse or specious native plant community. This suggests that when sediment excavation is employed with the goal of improving species diversity, an invasive species management plan should be in place for subsequent years to take advantage of the depleted invasive seed bank and prevent the establishment of these aggressive invasive species while the native plant community establishes.

Soils – In our study of restored cultivated wetlands, excavation had very little effect on soil nutrient content, though wetlands with longer, semipermanent, hydroperiod had significantly less bioavailable P in the top 10 cm of the soil profile. A criterion for enrollment in our study was past cultivation within the wetland basin. Cultivation mixes and homogenizes soils (Elliott 1986; Cambardella & Elliott 1993), through use of disc plows, chisel plows, or moldboard plows. These plows regularly mix soil 15 to 30 cm beneath the soil surface (Hume 1940, 1943; Alamouti & Navabzadeh 2007). Since it is not unusual for more than 30 cm of eroded sediment to accumulate within drained depressional basins (personal observation), sediment and underlying soils are often mixed together, making it difficult to accurately distinguish where mixing ends. The layer of homogenized soil and sediment is often referred to as the plow-layer or plow-horizon when describing soils because it has distinct properties that distinguish it from soil layers that develop in undisturbed systems (Allmaras et al. 1967). It can be challenging to remove only this plowed layer during restoration without disturbing underlying soils. As a result, unless restorations are certain to remove only the plow layer and do so completely, then it is unlikely that soils in the emergent macrophyte zone will have substantially different chemistry in basins with and without accumulated sediment. However, excavation could be particularly useful in larger, deeper restorations that are more likely to stride the line between seasonal and semipermanent hydroperiod. In these cases, excavation may increase the hydroperiod of the basin which could reduce the availability of soil bioavailable P.

Water Quality and Nitrogen Removal – In our research, hydroperiod was the strongest predictor of water quality and denitrification potential, but we found modest reductions in dissolved inorganic nutrient content in excavated wetlands compared to wetlands that retained sediment. These results indicate that any effect of accumulated sediment on dissolved nutrients operated through the inorganic nutrient pool and was small compared to the effect of hydroperiod. We found clear and consistent trends of lower dissolved N and P concentrations in semipermanent basins, but these basins also possessed a lower ability to respond to large pulses of nitrate. However, the difference in dissolved N between seasonal and semipermanent wetlands was trivial compared to the differences in dissolved P content. Seasonal wetlands had inorganic P concentrations that were comparable to hyper-eutrophic shallow lakes, but they also had twice the N removal capacity.

Differences in nutrient availability and processing point toward the existence of tradeoffs between N and P remediation in seasonal and semipermanent wetlands. Specifically, basins with shorter hydroperiod are well equipped for N removal but have elevated P content while basins with longer hydroperiod are less equipped to process large pulses of N but are better at P storage. However, nitrate concentrations were almost always near the detection limit (regardless of hydroperiod) and evidence from the wetland receiving large pulses of nitrate from an adjacent agricultural field (Site FF.080, Figure A4.2) suggests that semipermanent wetlands were capable of removing and assimilating large external nitrate loads. Since all of the wetlands in our study were capable of high rates of N removal via denitrification, there are likely more water quality benefits in prioritizing P remediation by restoring semipermanent wetlands.

Synthesis

Restored prairie pothole wetlands constitute a complicated network of wetlands connected through subsurface water exchange. The complexity of these systems arises in part from the intense and indelible history of disturbance from cultivation, but also from their position on the landscape. Depressional wetlands reside partway between terrestrial and aquatic ecosystems, adopting patterns of structural and functional development from both land and water. The blend of terrestrial and aquatic traits makes it difficult to predict how wetlands will respond to management and restoration strategies in a general sense. However, we found that prairie pothole wetlands respond in some predictable ways to sediment excavation during wetland restoration.

The effect of Excavation was less pronounced and shorter-lived than we anticipated at the beginning of our research. We were interested to find that sediment excavation operated by decreasing invasive species abundance rather than increasing native species recruitment. However, the effect of excavation on plant community assemblages and dissolved nutrient dynamics were lost when invasive species established and spread across wetlands. This suggests that invasive species management should be a priority in order to maintain any benefits of excavation.

Contrary to our hypotheses at the beginning of this project, hydroperiod was the most important driver of nutrient availability and processing. In semipermanent wetlands, lower soil bioavailable P, less water column dissolved N and P, and sluggish denitrification potential compared to seasonal wetlands were likely driven by differences in redox potential (dissolved oxygen), which may have been mediated by the emergent plant community. This resulted in substantial tradeoffs between seasonal and semipermanent wetlands (Figure 6.1). For example, the ability to remove N was twice as high in seasonal than in semipermanent wetlands, but dissolved P was more than four-times larger in seasonal basins. Furthermore, the soil bioavailable P pool was nearly two times larger in seasonal than in semipermanent wetlands. However, soil total P was the same in seasonal and semipermanent basins, suggesting that the differences in hydroperiod that shape plant community assemblages are also instrumental to liberating legacy P in soils and stimulating N removal.

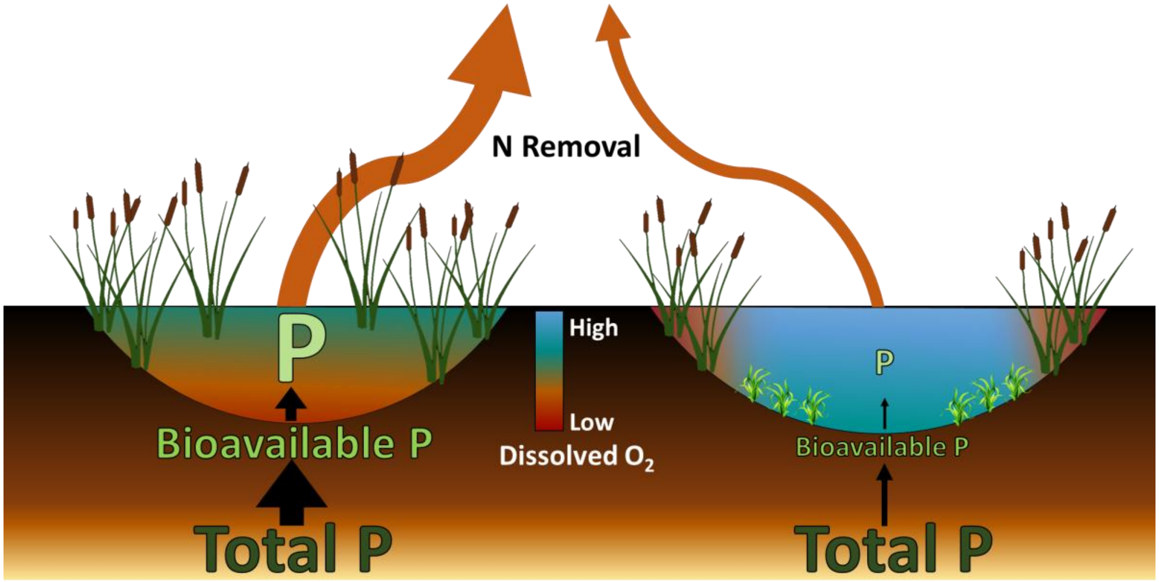

Figure 6. 1. Conceptual diagram of N and P tradeoffs in seasonal and semipermanent wetlands.

I hypothesize that temporal differences in hydrology and spatial differences in vegetation result in distinct patterns of oxygen availability in seasonal and semipermanent wetlands that influence sediment P mobilization and N removal. This hypothesis is visually represented in Figure 6.1. Tradeoffs were likely driven by differences in spatiotemporal patterns of oxygen availability.

Seasonal wetlands likely had lower dissolved oxygen availability when standing water was present but higher variability in oxygen throughout the growing season. Semipermanent wetlands likely had more spatial variability in dissolved oxygen availability, with higher overall oxygen content.

Previous work suggests that dense stands of invasive emergent macrophytes can block air movement and prevent gas exchange across the air-water interface resulting in lower dissolved oxygen availability (Rose & Crumpton 1996), which favors denitrification and dissolution of mineral-bound P (Figure 6.1). In our study, restored seasonal wetlands were dominated by dense stands of invasive hybrid cattail, while semipermanent wetlands often retained an area of deeper water colonized by submerged vegetation and featuring an open canopy above the water surface. The open canopy allows for air-water gas exchange and increases availability of light at the water surface (Rose & Crumpton 1996; Wetzel & Van Der Valk 1998). Furthermore, submerged macrophytes can oxygenate the rhizosphere directly in semipermanent basins (Risgaard-Petersen et al. 1994; Steinberg & Coonrod 1994; Wiebner et al. 2002; Laskov et al. 2006), preventing the dissolution of mineral-bound P (Figure 6.1) and promoting coupled nitrification-denitrification. *The combination of in-situ oxygen production and air-water gas exchange in semipermanent wetlands likely causes elevated dissolved oxygen concentrations within the open pool that gradually transitions to anoxia within the emergent macrophyte ring, resulting in a spatial redox gradient*.

In contrast, seasonal wetlands have less spatial variability and more temporal variability in redox conditions. Dense stands of emergent macrophytes throughout seasonal wetlands limit air movement and reduce light availability, which prevents air-water gas exchange and restricts in-situ oxygen production (Figure 6.1). However, Annual water drawdown in seasonal basins can accelerate organic matter decomposition and increase microbial stress which moves P from bulk soils to the bioavailable P pool (Figure 6.1). *Thus, seasonal wetlands are likely more strongly influenced by intense temporal fluctuations in redox conditions throughout the growing season.*

Despite these critical differences in spatiotemporal oxygen availability, both seasonal and semipermanent wetlands were well equipped to respond to large pulses of N (Chapter 5, Figure A4.2). This suggests that we should prioritize P management when deciding whether to employ sediment excavation in wetland restoration. It may be best to spend available funds to excavate semipermanent basins, where benefits to water quality were more dramatic. Subsequent invasive species management would likely maintain these benefits indefinitely. Regardless, all wetlands perform critical ecosystem services and any restoration is better than no restoration.

Applications to Management

Based on our results, it may be wise to consider prioritizing accumulated sediment excavation in semipermanent rather than seasonal wetlands.

Semipermanent wetlands have better water quality and delaying the spread of invasive emergent macrophytes may be easier to maintain when invasives must compete with submerged macrophytes. Unlike semipermanent wetlands, seasonal basins have optimal germination conditions for hybrid cattail and reed canary grass throughout the entire basin. By comparison, semipermanent basins maintain some area that is too deep to be colonized by cattail (Waters & Shay 1990). In semipermanent basins, reducing invasive emergent macrophyte cover can buy time for native submerged macrophytes to colonize further into the transitional zone between emergent and submerged vegetation, thus increasing competition for light and setting back invasive species advancement.

Another consideration is inertia and the perceived value of different habitats. Unfortunately, wetland consolidation will continue until depressional wetlands are afforded equal protections under the law as navigable waters (van der Valk & Pederson 2003). It is relatively easy and affordable to install plastic tile drain and an entire field can be tiled in just a few days (personal observation). From the perspective of the modern farmer, every acre is taxable and every acre could yield some degree of profit, thus drainage makes sense for many (Leitch 1989). Moreover, the public has a tendency to perceive wetlands as wasteland, but view lakes and ponds more favorably (Dobbie 2013). People place a high value on being able to see water from their work, homes, while commuting, and while recreating (Mahan 1996), and semipermanent wetlands maintain an open pool year-round making them more aesthetically pleasing. Lastly, many of the wetland restorations in the PPR are funded by the conservation reserve program and landowners retain the right to cultivate the land again upon completion of the 10 to 15-year contract. It is likely that semipermanent basins with an open pool will be perceived somewhat more favorably by landowners, whereas seasonal wetlands are easy to drain and have lower aesthetic value (Doss & Taff 1996; Reynolds & Regalado 2002).

Invasive Species Management: Promising Approaches

The most promising approach for restoring wetlands and generating stable ecosystem structure and functional attributes is to consider management practices that draw down soil and water column nutrient availability. Resource competition theory tell us that decreasing ambient nutrient availability forces organisms to occupy smaller niche spaces which promotes biodiversity and succession (Tilman 1994; Cardinale et al. 2012; Tilman 1985, 1990, 1982). In wetlands, a number of studies have demonstrated that two invasive species, reed canary grass and hybrid cattail, can be released from competitive forces when N and P are abundant (Green & Galatowitsch 2002; Wetzel & Van Der Valk 1998; Woo & Zedler 2002). Once released from nutrient competition, invasive species can shade out competitors and alter patterns of nutrient availability (Tuchman et al. 2009; Angeloni et al. 2006; Larkin, Lishawa, et al. 2012; Larkin, Freyman, et al. 2012). Furthermore, traditional herbicide-based invasive species control likely exacerbates the problem by increasing dissolved nutrient availability even further (Lawrence et al. 2016). Likewise, burning fails to remove P from the basin, which can push systems into alternate stable states even in the absence of N amendments (Schindler 1974; Schindler et al. 2008). However, invasive species harvest has the potential to remove substantial nutrient from restored wetlands (both N and P), promote light availability, and improve the quality of waterfowl and songbird habitat (Svedarsky et al. 2019; Lishawa et al. 2015; Grosshans et al. 2011).

Vegetation management may be the most effective tool to optimize P removal, increase plant diversity, and improve wildlife habitat in restored wetlands. Plant harvest should focus on the most aggressive invasive species that have the largest ecosystem impact. For example, hybrid cattail (*Typha X glauca*) management has the potential to remove substantial nutrients (Emery & Perry 1996), oxygenate the water column (Rose & Crumpton 1996; Liss & Slater 1974), and open up the canopy to promote competition by native species while increasing usability by waterfowl (Grosshans et al. 2011). Hybrid cattail biomass removal in late summer (August to September) coincides with peak biomass and tissue nutrient content (Dubbe et al. 1988; Garver et al. 1988; Emery & Perry 1996); ease of access due to low standing water (LaBaugh et al. 1998; Niemuth et al. 2010); and low probability of disturbing sensitive wildlife that breeds and broods in and around wetlands (e.g., waterfowl and amphibians) (Kantrud & Stewart 1977; Niemuth et al. 2014). Although frozen ground makes winter the best time to harvest when considering ease of access and minimizing damage to sensitive species, it also coincides with the period of lowest N and P content in plant tissues (Garver et al. 1988; Dubbe et al. 1988). Harvesting in late summer, prior to nutrient translocation, provides the greatest opportunity to remove nutrient and decrease invasive species biomass (Grosshans et al. 2011).

Annual cattail harvest over multiple years could generate a positive feedback loop whereby continuous nutrient removal promotes competition and diversification, which could decrease nutrient availability and increase competition even further. Assuming only the above-ground portion of plants are harvested, annual P removal could range from 3.14 to greater than 12.32 kg P/ha (Dubbe et al. 1988; Emery & Perry 1996), which would represent approximately 2.5 to 9.7 times the dissolved inorganic P stored in the water column of seasonal wetlands described in this dissertation (estimated 1.27 kg P/ha). Other authors have estimated cattail stands contain 5 to 15 kg P/ha in harvestable biomass (Svedarsky et al. 2019). Thus, harvest over multiple years could draw down not only surface water dissolved P, but also sediment and pore water P availability (Roy 2017).

While cattail harvest presents meaningful potential for nutrient removal, there are practical concerns including how to harvest plants quickly and with minimal environmental impact, and where to dispose of harvested biomass. In a perfect world we would already have the necessary machinery for harvesting plants on loosely consolidated sediments and a market ready to receive and utilize cattail biomass. The largest initial logistical challenge is designing equipment and machinery that can harvest plants in 30 to 60 cm of standing water and muck. Other authors have addressed the topic of machinery and equipment in some detail (Svedarsky et al. 2019), but the choice of equipment ultimately depends on inundation and moisture content of the harvested material. European companies have developed reed harvesters with specialized tracks that minimize damage to poorly consolidated soils.

The second challenge is how to dispose of cattail biomass with minimal or no net cost. To that end, recent changes in the energy and reuse economies have been of some aid. Pelletizing dried cattail and common reed for heating systems is a tractable solution for disposing of harvested biomass and cattail pellets can produce similar energy yields as traditional wood pellets (Grosshans et al. 2011; Svedarsky et al. 2019). Cattail biomass can also be processed with sewage sludge to create a high quality compost with minimal odor in as little as fourteen weeks (Manios et al. 2003). But perhaps the most exciting use of cattail biomass is as silage for anaerobic bioenergy production, specifically biohydrogen and methane (Nkemka et al. 2015).

Harvesting cattail biomass following wetland restoration could remove substantial nutrient from restored wetlands, improve waterfowl habitat, and create conditions that are suitable for native vegetation. Invasive species harvest could be paired with sediment excavation to take advantage of initial reductions in invasive species cover following re-wetting and encourage the formation of self-sustaining native populations. Sediment excavation deepens wetland basins, which may contribute to modestly extended water permanence and improve water quality. In semipermanent wetlands, sediment excavation paired with cattail harvest has the potential to improve water quality, wildlife habitat, and community diversity.

Literature Cited

Abella SR, Zimmer BW (2007) Estimating Organic Carbon from Loss-On-Ignition in Northern Arizona Forest Soils. Soil Science Society of America Journal 71:545–550

Adams CR, Galatowitsch SM (2008) The transition from invasive species control to native species promotion and its dependence on seed density thresholds. Applied Vegetation Science 11:131–138

Akaike H (1974) A New Look at the Statistical Model Identification. IEEE Transactions on Automatic Control 19:716–723

Al-Omari A, Beck K, Brunetaud X, Török Á, Al-Mukhtar M (2015) Critical degree of saturation: A control factor of freeze-thaw damage of porous limestones at Castle of Chambord, France. Engineering Geology 185:71–80

Alamouti MY, Navabzadeh M (2007) Investigation of plowing depth effect on some soil physical properties. Pakistan Journal of Biological Sciences 10:4510–4514

Aldous A, McCormick P, Ferguson C, Graham S, Craft C (2005) Hydrologic regime controls soil phosphorus fluxes in restoration and undisturbed wetlands. Restoration Ecology 13:341–347

Alldred M, Baines SB (2016) Effects of wetland plants on denitrification rates: a meta-analysis. Ecological Applications 26:676–685

Allmaras RR, Burwell RE, Holt RF (1967) Plow-Layer Porosity and Surface Roughness from Tillage as Affected by Initial Porosity and Soil Moisture at Tillage Time. Soil Science Society of America Journal 31:550–556

Amézketa E (1999) Soil aggregate stability: A review. Journal of Sustainable Agriculture 14:83–151

Anderson MJ (2001) A new method for non-parametric multivariate analysis of variance. Austral Ecology 26:32–46

Angeloni NL, Jankowski KJ, Tuchman NC, Kelly JJ (2006) Effects of an invasive cattail species (Typha x glauca) on sediment nitrogen and microbial community composition in a freshwater wetland. FEMS Microbiology Letters 263:86–92

APHA (1992a) 4500-P Phosphorus. In: Standard Methods for Examination of Water and Wastewater. Greensberg, AE, Clesceri, LS, Eaton, AD, & Franson, MAH, editors. American Public Health Association, Washington, DC pp. 108–117.

APHA (1998) 4500 - NH3 Nitrogen (Ammonia). In: Standard Methods for Examination of Water and Wastewater. Stieg, S, Fisher, BR, Mathre, OB, & Wright, TM, editors. American Public Health Association, Washington, DC pp. 108–117.

APHA (1992b) 4500 - NO3 Nitrogen (Nitrate). In: Standard Methods for Examination of Water and Wastewater. Greensberg, AE, Clesceri, LS, Eaton, AD, & Franson, MAH, editors. American Public Health Association, Washington, DC pp. 87–94.

APHA (2005) 5310 Total Organic Carbon (TOC). In: Standard Methods for the Examination of Water and Wastewater. Huffman, EWD et al., editors. American Public Health Association, Washington, DC pp. 19–26.

Aronson MFJ, Galatowitsch SM (2008) Long-term vegetation development of restored prairie pothole wetlands. Wetlands 28:883–895

ASTM (2008) Standard Test Method for Total Chemically Bound Nitrogen in Water by Pyrolysis and. 3

Atkinson RB, Cairns JJ (2001) Plant Decomposition and Litter Accumulation in Depressional Wetlands: Functional Performance of Two Wetland Age Classes That Were Created Via Excavation. Wetlands 21:354–362

Bachand PAM, Horne AJ (1999) Denitrification in constructed free-water surface wetlands: II. Effects of vegetation and temperature. Ecological Engineering 14:17–32

Bakker MM, Govers G, van Doorn A, Quetier F, Chouvardas D, Rounsevell M (2008) The response of soil erosion and sediment export to land-use change in four areas of Europe: The importance of landscape pattern. Geomorphology 98:213–226

Ballantine K, Schneider R (2009) Fifty-five years of soil development in restored freshwater depressional wetlands. Ecological Applications 19:1467–1480

Ballantine KA, Anderson TR, Pierce EA, Groffman PM (2017) Restoration of denitrification in agricultural wetlands. Ecological Engineering 106:570–577

Ballantine KA, Groffman PM, Lehmann J, Schneider RL (2014) Stimulating Nitrate Removal Processes of Restored Wetlands. Environmental Science & Technology 48:7365–7373

Bates D, Maechler M, Bolker B, et al. (2020) Package “lme4”: Linear Mixed-Effects Models using “Eigen” and S4. R package version 3.2.0 120

Beas BJ, Smith LM, LaGrange TG, Stutheit R (2013) Effects of sediment removal on vegetation communities in Rainwater Basin playa wetlands. Journal of Environmental Management 128:371–379

Bennion H, Smith MA (2000) Variability in the water chemistry of shallow ponds in southeast England, with special reference to the seasonality of nutrients and implications for modelling trophic status. Hydrobiologia 436:145–158

Bernal B, Mitsch WJ (2012) Comparing carbon sequestration in temperate freshwater wetland communities. Global Change Biology 18:1636–1647

Bills NL (1986) The Acreage Conservation Reserve: Title XII of the Food Security Act of 1985. Ithaca, New York

Birch HF (1958) The effect of soil drying on humus decomposition and nitrogen availability. Plant and Soil 10:9–31

Biró M, Molnár Z, Öllerer K, et al. (2020) Conservation and herding co-benefit from traditional extensive wetland grazing. Agriculture, Ecosystems and Environment 300:106983

Biró M, Molnár Z, Babai D, et al. (2019) Reviewing historical traditional knowledge for innovative conservation management: A re-evaluation of wetland grazing. Science of the Total Environment 666:1114–1125

Bishel-Machung L, Brooks RP, Yates SS, Hoover KL (1996) Soil Properties of Reference Wetlands and Wetland Creation Projects in Pennsylvania. Wetlands 16:532–541

Boers AM, Veltman RLD, Zedler JB (2007) Typha × glauca dominance and extended hydroperiod constrain restoration of wetland diversity. Ecological Engineering 29:232–244

Bray RH, Kurtz LT (1945) Determination of total, organic, and available forms of phosphorus in soils. Soil Science 59:39–45

Brevik EC (2000) Limits to Ice Thickness in Iowa During the Late Wisconsinan. Journal of the Iowa Academy of Science 107:46–50

Brown J, Norris MD (2018) Detecting soil and plant community changes in restored wetlands using a chronosequence approach. Wetlands Ecology and Management 26:299–314

Brown R, Zhang Z, Comeau LP, Bedard-Haughn A (2017) Effects of drainage duration on mineral wetland soils in a Prairie Pothole agroecosystem. Soil and Tillage Research 168:187–197

Bruland GL, Richardson CJ (2005) Spatial Variability of Soil Properties in Created, Restored, and Paired Natural Wetlands. Soil Science Society of America Journal 69:273–284

Bruland GL, Richardson CJ, Whalen SC (2006) Spatial variability of denitrification potential and related soil properties in created, restored, and paired natural wetlands. Wetlands 26:1042–1056

Brunet NN (2011) Prairie Pothole Drainage and Water Quality. University of Saskatchewan

Burgin AJ, Groffman PM (2012) Soil O2 controls denitrification rates and N2O yield in a riparian wetland. Journal of Geophysical Research 117:1G01010

Burgin AJ, Groffman PM, Lewis DN (2010) Factors Regulating Denitrification in a Riparian Wetland. Soil Science Society of America Journal 74:1826

Burgin AJ, Hamilton SK (2007) Have we overemphasized the role of denitrification in aquatic ecosystems? A review of nitrate removal pathways. Frontiers in Ecology and the Environment 5:89–96

Bush JK (2008) Soil Nitrogen and Carbon after Twenty Years of Riparian Forest

Development. Soil Science Society of America Journal 72:815–822

Cambardella CA, Elliott ET (1993) Carbon and Nitrogen Distribution in Aggregates from Cultivated and Native Grassland Soils. Soil Science Society of America Journal 57:1071–1076

Campbell DA, Cole CA, Brooks RP (2002) A comparison of created and natural wetlands in Pennsylvania, USA. Wetlands Ecology and Management 10:41–49

Cardinale BJ, Duffy JE, Gonzalez A, et al. (2012) Biodiversity loss and its impact on humanity. Nature 486:59–67

Carlton RG, Wetzel RG (1987) Distributions and fates of oxygen in periphyton communities. Canadian Journal of Botany 65:1031–1037

Castaldelli G, Soana E, Racchetti E, Vincenzi F, Fano EA, Bartoli M (2015) Vegetated canals mitigate nitrogen surplus in agricultural watersheds. Agriculture, Ecosystems and Environment 253–262

Chadde SW (2012) A Great Lakes Wetland Flora: A Complete Guide to the Wetland and Aquatic Plants of the Midwest. 4th ed. CreateSpace Independent Publishing Platform, Lexington, KY

Changnon SA (1998) The historical struggle with floods on the mississippi river basin: Impacts of recent floods and lessons for future flood management and policy. Water International 23:263–271

Chapin FS, Barsdate RJ, Barèl D (1978) Phosphorus Cycling in Alaskan Coastal Tundra: A Hypothesis for the Regulation of Nutrient Cycling. Oikos 31:189–199

Chen D, Shen H, Hu M, Wang J, Zhang Y, Dahlgren RA (2018) Legacy Nutrient Dynamics at the Watershed Scale: Principles, Modeling, and Implications. 1st ed. Elsevier Inc.

Cheng FY, Van Meter KJ, Byrnes DK, Basu NB (2020) Maximizing US nitrate removal through wetland protection and restoration. Nature 588

Clarke KR (1993) Non-parametric multivariate analyses of changes in community structure. Austral Ecology 18:117–143

Clayton L, Moran SR (1982) Chronology of Late Wisconsinan Glaciation in Middle North America. Quaternary Science Reviews 1:55–82

Cohen MJ, Creed IF, Alexander L, et al. (2016) Do geographically isolated wetlands influence landscape functions? Proceedings of the National Academy of Sciences of the United States of America 1–9

Cole C V., Olsen SR, Scott CO (1953) The Nature of Phosphate Sorption by Calcium Carbonate. Soil Science Society of America Journal 17:352

Comly HH (1945) Cyanosis in infants caused by nitrates in well water. Journal of the American Medical Association 129:112–116

Conrad S, Löfgren S, Bauer S, Ingri J (2019) Seasonal Variations of Redox State in Hemiboreal Soils Indicated by Changes of δ56Fe, Sulfate, and Nitrate in Headwater Streams. ACS Earth and Space Chemistry 3:2816–2823

Cooke GD, Heath RT, Kennedy RH, McComos MR (1982) Change in Lake Trophic State and Internal Phosphorus Release After Aluminum Sulfate Application. JAWRA Journal of the American Water Resources Association 18:699–705

Costanza R, D'Arge R, De Groot R, et al. (1997) The value of the world's ecosystem services and natural capital. Nature 387:253–260

Cowardin LM, Carter V, Golet FC, LaRoe ET (1979) Classification of wetlands and deepwater habitats of the United States.

Cowardin LM, Golet FC (1995) US Fish and Wildlife Sevice 1979 wetland classification: A review. Vegetatio 118:139–152

Craft C (2007) Freshwater input structures soil properties, vertical accretion, and nutrient accumulation of Georgia and U.S. tidal marshes. Limnology and Oceanography 52:1220–1230

Craft C, Megonigal P, Broome S, Stevenson J, Freese R, Cornell J, Zheng L, Sacco J (2003) The pace of ecosystem development of constructed Spartina alterniflora marshes. Ecological Applications 13:1417–1432

Craft C, Vymazal J, Kröpfelová L (2018) Carbon sequestration and nutrient accumulation in floodplain and depressional wetlands. Ecological Engineering 114:137–145

Craft CB (1996) Dynamics of nitrogen and phosphorus retention during wetland ecosystem succession. Wetlands Ecology and Management 4:177–187

Craft CB, Casey WP (2000) Sediment and nutrient accumulation in floodplain and depressional freshwater wetlands of Georgia, USA. Wetlands 20:323–332

Craft CB, Seneca ED, Broome SW (1991) Porewater chemistry of natural and created marsh soils. Journal of Experimental Marine Biology and Ecology 152:187–200

Cross TK, Jacobson PC (2013) Landscape factors influencing lake phosphorus concentrations across Minnesota. Lake and Reservoir Management 29:1–12

Daehler CC (2003) Performance comparisons of co-occurring native and alien invasive plants: implications for conservation and restoration. Annual Review of Ecology, Evolution, and Systematics 34:183–211

Dahl TE (2014) Status and Trends of Prairie Wetlands in the United States 1994 to 2009. U.S. Department of the Interior; Fish and Wildlife Service, Ecological Services, Washington D.C.

Dahl TE (1990) Wetlands losses in the United States 1780's to 1980's. Washington D.C.

Dahl TE, Allord GJ (1996) The hisotry of wetlands in the conterminous United States. In: National water summary on wetland resources. Fretwell JD, Williams JS, Redman

PJ, C, editor. U.S. Geological Survey Water-Supply Paper 2425, Washington, D.C. pp. 19–26.

Dahlquist RL, Knoll JW (1978) Inductively Coupled Plasma-Atomic Emission Spectrometry: Analysis of Biological Materials and Soils for Major, Trace, and Ultra-Trace Elements. Applied Spectroscopy 32:1–30

Davidson NC (2014) How much wetland has the world lost? Long-term and recent trends in global wetland area. Marine and Freshwater Research 65:934–941

Davis C, Baker J, van der Valk A, Beer C (1981) Prairie pothole marshes as traps for nitrogen and phosphorus in agricultural runoff. Selected Proceedings of the Midwest Conference on Wetland Values and Management 153–163

Dean WE (1974) Determination of Carbonate and Organic Matter in Calcareous Sediments and Sedimentary Rocks by Loss on Ignition: Comparison with Other Methods. Journal of Sedimentary Petrology 44:242–248

DeBusk WF, Reddy KR (1998) Turnover of Detrital Organic Carbon in a Nutrient-Impacted Everglades Marsh. Soil Science Society of America Journal 62:1460–1468

Degasperi CL, Spyridakis DE, Welch EB (1993) Alum and nitrate as controls of short-term anaerobic sediment phosphorus release: An in vitro comparison. Lake and Reservoir Management 8:49–59

DeSimone LA, Hamilton PA, Gilliom RJ (2009) Quality of water from domestic wells in principal aquifers of the United States, 1991–2004: Overview of major findings. U.S. Department of the Interior; U.S. Geological Survey Circular 1332, Reston, Virginia

Detenbeck NE, Elonen CM, Taylor DL, Cotter AM, Puglisi FA, Sanville WD (2002) Effects of agricultural activities and best management practices on water quality of seasonal prairie pothole wetlands. Wetlands Ecology and Management 10:335–354

Diaz OA, Reddy KR, Moore PA (1994) Solubility of inorganic phosphorus in stream water as influenced by pH and calcium concentration. Water Research 28:1755–1763

Diaz Robert J., Rosenberg R (2008) Spreading dead zones and consequences for marine ecosystems. Science 321:926–929

Diaz R.J., Rosenberg R (2008) Spreading dead zones and consequences for marine ecosystems. Science 321:926–929

Dinnes DL, Karlen DL, Jaynes DB, Kaspar TC, Hatfield JL, Colvin TS, Cambardella CA (2002) Nitrogen management strategies to reduce nitrate leaching in tile-drained midwestern soils. Agronomy Journal 94:153–171

Dobbie MF (2013) Public aesthetic preferences to inform sustainable wetland management in Victoria, Australia. Landscape and Urban Planning 120:178–189

Dodds WK, Bouska WW, Eitzmann JL, Pilger TJ, Pitts KL, Riley AJ, Schloesser JT, Thornbrugh DJ (2009) Eutrophication of U.S. freshwaters: Analysis of potential economic damages. Environmental Science and Technology 43:12–19

Dolfing J, Chardon WJ, Japenga J (1999) Association between colloidal iron, aluminum, phosphorus, and humic acids. Soil Science 164:171–179

Domagalski JL, Johnson HM (2011) Subsurface transport of orthophosphate in five agricultural watersheds, USA. Journal of Hydrology 409:157–171

van Donk E, Gulati RD, Iedema A, Meulemans JT (1993) Macrophyte-related shifts in the nitrogen and phosphorus contents of the different trophic levels in a biomanipulated shallow lake. Hydrobiologia 251:19–26

Doss CR, Taff SJ (1996) The Influence of Wetland Type and Wetland Proximity on Residential Property Values. Journal of Agricultural and Resource Economics 21:120–129

Downing JA, Prairie YT, Cole JJ, et al. (2006) The global abundance and size distribution of lakes, ponds, and impoundments. Limnology and Oceanography 51:2388–2397

Dubbe DR, Garver EG, Pratt DC (1988) Production of cattail (Typha spp.) biomass in Minnesota, USA. Biomass 17:79–104

Dunn CP, Stearns F, Guntenspergen GR, Sharpe DM (1993) Ecological benefits of the Conservation Reserve Program. Conservation Biology 7:132–139

Ehrenfeld JG (2010) Ecosystem consequences of biological invasions. Annual Review of Ecology, Evolution, and Systematics 41:59–80

Ehrenfeld JG (2003) Effects of Exotic Plant Invasions on Soil Nutrient Cycling Processes. Ecosystems 6:503–523

Elliott ET (1986) Aggregate Structure and Carbon, Nitrogen, and Phosphorus in Native and Cultivated Soils. Soil Science Society of America Journal 50:627–633

Ellis EC, Goldewijk KK, Siebert S, Lightman D, Ramankutty N (2010) Anthropogenic transformation of the biomes, 1700 to 2000. Global Ecology and Biogeography 19:589–606

Emery SL, Perry JA (1996) Decomposition rates and phosphorus concentrations of purple loosestrife (Lythrum salicaria) and cattail (Typha spp.) in 14 MN wetlands. Hydrobiologia 323:129–138

Eriksson PG, Weisner SEB (1999) An experimental study on effects of submersed macrophytes on nitrification and denitrification in ammonium-rich aquatic systems. Limnology and Oceanography 44:1993–1999

Erlandson CS (1987) The potential role of seed banks in the restoration of drained prairie wetlands. Iowa State University

Euliss NH, Gleason RA, Olness A, McDougal RL, Murkin HR, Robarts RD, Bourbonniere

RA, Warner BG (2006) North American Prairie Wetlands are Important Nonforested Land-Based Carbon Storage Sites. Science of the Total Environment 361:179–188

Euliss NH, Mushet DM (1996) Water-level fluctuation in wetlands as a function of landscape condition in the prairie pothole region. Wetlands 16:587–593

Euliss NHJ, LaBaugh JW, Fredrickson LH, Mushet DM, Laubhan MK, Swanson GA, Winter TC, Rosenberry DO, Nelson RD (2004) The Wetland Continuum: A Conceptual Framework for Interpreting Biological Studies. Wetlands 24:448–458

Evans DJA (2009) Controlled moraines: origins, characteristics and palaeoglaciological implications. Quaternary Science Reviews 28:183–208

Evenson GR, Golden HE, Lane CR, McLaughlin DL, D’Amico E (2018) Depressional wetlands affect watershed hydrological, biogeochemical, and ecological functions. Ecological Applications 28:953–966

Fasching C, Akotoye C, Bižić M, et al. (2020) Linking stream microbial community functional genes to dissolved organic matter and inorganic nutrients. Limnology and Oceanography 65:S71–S87

Fasching C, Wilson HF, D’Amario SC, Xenopoulos MA (2019) Natural Land Cover in Agricultural Catchments Alters Flood Effects on DOM Composition and Decreases Nutrient Levels in Streams. Ecosystems 22:1530–1545

Fassel VA, Kniseley RN (1974) Inductively Coupled Plasma Optical Emission Spectroscopy. Analytical Chemistry 46:1110A-1120A

Finlay JC, Small GE, Sterner RW (2013) Human influences on nitrogen removal in lakes. Science 342:247–250

Firestone MK, Firestone RB, Tiedje JM (1980) Nitrous Oxide from Soil Denitrification: Factors Controlling its Biological Production. Science 208:749–751

Fisher J, Acreman MC (2004) Wetland nutrient removal: A review of the evidence. Hydrology and Earth System Sciences 8:673–685

Fisher MM, Reddy KR (2001) Phosphorus Flux from Wetland Soils Affected by Long-Term Nutrient Loading. Journal of Environment Quality 30:261–271

Fossen Johnson S (2019) Methemoglobinemia: Infants at risk. Current Problems in Pediatric and Adolescent Health Care 49:57–67

Fox J, Weisberg S (2011) An R Companion to Applied Regression. 2nd ed. Sage Publications Inc., Thousand Oaks, CA

Franzluebbers AJ, Stuedemann JA, Schomberg HH, Wilkinson SR (2000) Soil organic C and N pools under long-term pasture management in the Southern Piedmont USA. Soil Biology and Biochemistry 32:469–478

Frossard E, Brossard M, Hedley MJ, Metherell A (1995) Reactions Controlling the Cycling of P in Soils. In: Phosphorus in the Global Environment: Transfers, Cycles, and Management. Tiessen, H, editor. John Wiley & Sons, Ltd, West Sussex, England pp. 107–138.

Galatowitsch SM, Anderson NO, Ascher PD (1999) Invasiveness in wetland plants in temperate North America. Wetlands 19:733–755

Galatowitsch SM, van der Valk AG (1996a) Characteristics of recently restored wetlands in the prairie pothole region. Wetlands 16:75–83

Galatowitsch SM, van der Valk AG (1994) Restoring Prairie Wetlands: An Ecological Approach. Iowa State University Press, Ames, IA

Galatowitsch SM, van der Valk AG (1996b) Vegetation and environmental conditions in recently restored wetlands in the Prairie Pothole Region of the USA. Vegetatio 126:89–99

Galatowitsch SM, Whited DC, Lehtinen R, Husveth J, Schik K (2000) The vegetation of wet meadows in relation to their land-use. Environmental Monitoring and Assessment 60:121–144

Galinato MI, Van Der Valk AG (1986) Seed germination traits of annuals and emergents recruited during drawdowns in the Delta Marsh, Manitoba, Canada. Aquatic Botany 26:89–102

Garver EG, Dubbe DR, Pratt DC (1988) Seasonal patterns in accumulation and partitioning of biomass and macronutrients in Typha spp. Aquatic Botany 32:115–127

Gelso BR, Fox JA, Peterson JM (2008) Farmers' Perceived Costs of Wetlands: Effects of Wetland Size, Hydration, and Dispersion. American Journal of Agricultural Economics 90:172–185

Gibbs JP (2000) Wetland loss and biodiversity conservation. Conservation Biology 14:314–317

Gleason R, Euliss N, Hubbard D (2003) Effects of sediment load on emergence of aquatic invertebrates and plants from wetland soil egg and seed banks. Wetlands 23:26–34

Gleason RA, Euliss NH, Tangen BA, Laubhan MK, Browne BA (2011) USDA conservation program and practice effects on wetland ecosystem services in the Prairie Pothole Region. Ecological Applications 21:S65–S81

Gleason RA, Jr NHE, Euliss NH (1998) Sedimentation of prairie wetlands. Great Plains Research 8:97–112

Gleason RA, Laubhan MK, Tangen BA, Kermes KE (2008) Ecosystem services derived from wetland conservation practices in the United States Prairie Pothole Region with an emphasis on the U.S. Department of Agriculture Conservation Reserve and Wetlands Reserve Programs.

Glibert PM, Heil CA, Hollander D, Revilla M, Hoare A, Alexander J, Murasko S (2004)

Evidence for dissolved organic nitrogen and phosphorus uptake during a cyanobacterial bloom in Florida Bay. Marine Ecology Progress Series 280:73–83

Glibert PM, Heil CA, Madden CJ, Kelly SP (2021) Dissolved organic nutrients at the interface of fresh and marine waters: flow regime changes, biogeochemical cascades and picocyanobacterial blooms—the example of Florida Bay, USA. Biogeochemistry 4

Golden HE, Creed IF, Ali G, et al. (2017) Integrating geographically isolated wetlands into land management decisions. Frontiers in Ecology and the Environment 15:319–327

Golden HE, Sander HA, Lane CR, Zhao C, Price K, D'Amico E, Christensen JR (2016) Relative effects of geographically isolated wetlands on streamflow: A watershed-scale analysis. Ecohydrology 9:21–38

Golterman HL (2004) The Chemistry of Phosphate and Nitrogen Compounds in Sediments. Klumer Academic Publishers, Dordrecht

Goolsby DA (2000) Mississippi basin nitrogen flux believed to cause Gulf hypoxia. Eos 81:321–332

Goolsby DA, Battaglin WA (2000) Nitrogen in the Mississippi Basin-estimating sources and predicting flux to the Gulf of Mexico. USGS Fact Sheet 135–00

Goyette JO, Bennett EM, Maranger R (2018) Low buffering capacity and slow recovery of anthropogenic phosphorus pollution in watersheds. Nature Geoscience 11:921–925

Green EK, Galatowitsch SM (2001) Differences in wetland plant community establishment with additions of nitrate-N and invasive species (Phalaris arundinacea and Typha ×glauca). Can. J. Bot. 79:170–178

Green EK, Galatowitsch SM (2002) Effects of Phalaris arundinacea and nitrate-N addition on the establishment of wetland plant communities. Journal of Applied Ecology 39:134–144

Gregorich E, Anderson D (1985) Effects of cultivation and erosion on soils of four toposequences in the canadian prairies. Geoderma 36:343–354

Griscom BW, Adams J, Ellis PW, et al. (2017) Natural climate solutions. Proceedings of the National Academy of Sciences of the United States of America 114:11645–11650

Groffman PM, Butterbach-Bahl K, Fulweiler RW, Gold AJ, Morse JL, Stander EK, Tague C, Tonitto C, Vidon P (2009) Challenges to incorporating spatially and temporally explicit phenomena (hotspots and hot moments) in denitrification models. Biogeochemistry 93:49–77

Groffman PM, Tiedje JM (1988) Denitrification Hysteresis During Wetting and Drying Cycles in Soil. Soil Science Society of America Journal 52:1626

Grosshans RE, Venema HD, Cicek N, Goldsborough G (2011) Cattail Farming for Water Quality: Harvesting Cattails for Nutrient Removal and Phosphorous Recovery in the Watershed. Nutrient Recovery and Management 2011 1382–1407

Guildford SJ, Hecky RE (2000) Total nitrogen, total phosphorus, and nutrient limitation in lakes and oceans: Is there a common relationship? Limnology and Oceanography 45:1213–1223

Hall RI, Leavitt PR, Quinlan R, Dixit AS, Smol JP (1999) Effects of agriculture, urbanization, and climate on water quality in the northern Great Plains. Limnology & Oceanography 44:739–756

Hansen AT, Dolph CL, Finlay JC (2016) Do wetlands enhance downstream denitrification in agricultural landscapes? Ecosphere 7

Hansen AT, Dolph CL, Foufoula-Georgiou E, Finlay JC (2018) Contribution of wetlands to nitrate removal at the watershed scale. Nature Geoscience 11:127–132

Harrison JA, Maranger RJ, Alexander RB, Giblin AE, Jacinthe PA, Mayorga E, Seitzinger SP, Sobota DJ, Wollheim WM (2009) The regional and global significance of nitrogen removal in lakes and reservoirs. Biogeochemistry 93:143–157

Hausman CE, Fraser LH, Kershner MW, de Szalay FA (2007) Plant community establishment in a restored wetland: Effects of soil removal. Applied Vegetation Science 10:383–390

Hayashi M, van der Kamp G (2000) Simple equations to represent the volume-area-depth relations of shallow wetlands in small topographic depressions. Journal of Hydrology 237:74–85

Hayashi M, van der Kamp G, Rosenberry DO (2016) Hydrology of Prairie Wetlands: Understanding the Integrated Surface-Water and Groundwater Processes. Wetlands 36:237–254

Hayashi M, van der Kamp G, Rudolph DL (1998) Water and solute transport between a prairie wetland and adjacent uplands, 1. Water balance. Journal of Hydrology 207:42–55

Healey FP (1975) Physiological indicators of nutrient deficiency in algae. Fisheries and Marine Services Tech Rep 5:30

Hedley MJ, Mortvedt JJ, Bolan NS, Syers JK (1995) Phosphorus Fertility Management in Agroecosystems. In: Phosphorus in the Global Environment: Transfers, Cycles, and Management. Tiessen, H, editor. John Wiley & Sons, Ltd, West Sussex, England pp. 59–92.

Heiri O, Lotter AF, Lemcke G (2001) Loss on ignition as a method for estimating organic and carbonate content in sediments: Reproducibility and comparability of results. Journal of Paleolimnology 25:101–110

Heisler J, Glibert PM, Burkholder JM, et al. (2008) Eutrophication and harmful algal blooms: A scientific consensus. Harmful Algae 8:3–13

Hershey HG (1955) Quality of surface waters of Iowa, 1886-1954. Iowa City, Iowa

Hey DL (2002) Nitrōgen farming: Harvesting a different crop. Restoration Ecology 10:1–10

Hey DL, Philippi NS (1995) Flood reduction through wetland restoration: The Upper Mississippi River basin as a case history. Restoration Ecology 3:4–17

Hillebrand H, Sommer U (1999) The nutrient stoichiometry of benthic microalgal growth: Redfield proportions are optimal. Limnology and Oceanography 44:440–446

Hogan DM, Jordan TE, Walbridge MR (2004) Phosphorus retention and soil organic carbon in restored and natural freshwater wetlands. Wetlands 24:573–585

Houlahan JE, Findlay CS (2003) The effects of adjacent land use on wetland amphibian species richness and community composition. Canadian Journal of Fisheries and Aquatic Sciences 60:1078–1094

Howarth R, Swaney D, Billen G, Garnier J, Hong B, Humborg C, Johnes P, Mörth C, Marino R (2012) Nitrogen fluxes from the landscape are controlled by net anthropogenic nitrogen inputs and by climate. Frontiers in Ecology and the Environment 10:37–43

Howarth RW, Jensen HS, Marino R, Postma H (1995) Transport To and Processing Of P In Near-Shore and Oceanic Waters. In: Phosphorus in the Global Environment: Transfers, Cycles, and Management. Tiessen, H, editor. John Wiley & Sons, Ltd, West Sussex, England pp. 323–346.

Hume AN (1943) Crop Yields as related to Depth of Plowing. Bulletins Paper 369

Hume AN (1940) Depth of Plowing and Crop Yields. Bulletins Paper 344

Jacobson PC, Hansen GJA, Bethke BJ, Cross TK (2017) Disentangling the effects of a century of eutrophication and climate warming on freshwater lake fish assemblages. PLoS ONE 12:1–17

Jacquemart A-L, Champluvier D, De Sloover J (2003) A Test of Mowing and Soil-Removal Restoration Techniques in Wet Heaths of the High Arenne, Belgium. Wetlands 23:376–385

Jarvie HP, Sharpley AN, Withers PJA, Scott JT, Haggard BE, Neal C (2013) Phosphorus Mitigation to Control River Eutrophication: Murky Waters, Inconvenient Truths, and “Postnormal” Science. Journal of Environmental Quality 42:295–304

Jastrow JD (1996) Soil aggregate formation and the accrual of particulate and mineral-associated organic matter. Soil Biology and Biochemistry 28:665–676

Jenkins DG, Grissom S, Miller K (2003) Consequences of prairie wetland drainage for crustacean biodiversity and metapopulations. Conservation Biology 17:158–167

Jennings CE, Johnson MD (2011) The quaternary of minnesota. 1st ed. Elsevier Inc.

Jenny JP, Francus P, Normandeau A, Lapointe F, Perga ME, Ojala A, Schimmelmann A, Zolitschka B (2016) Global spread of hypoxia in freshwater ecosystems during the last three centuries is caused by rising local human pressure. Global Change Biology 22:1481–1489

Jeppesen E, Søndergaard M, Jensen JP, et al. (2005) Lake responses to reduced nutrient loading - An analysis of contemporary long-term data from 35 case studies. Freshwater Biology 50:1747–1771

Jeppesen E, Jensen JP, Søndergaard M, Lauridsen T, Pedersen LJ, Jensen L (1997) Top-down control in freshwater lakes: The role of nutrient state, submerged macrophytes and water depth. Hydrobiologia 342–343:151–164

Jetten MSM, Strous M, Van de Pas-Schoonen KT, et al. (1999) The anaerobic oxidation of ammonium. FEMS Microbiology Reviews 22:421–437

Johnson LT, Tank JL (2009) Diurnal variations in dissolved organic matter and ammonium uptake in six open-canopy streams. Journal of the North American Benthological Society 28:694–708

Johnson LT, Tank JL, Arango CP (2009) The effect of land use on dissolved organic carbon and nitrogen uptake in streams. Freshwater Biology 54:2335–2350

Johnson PTJ, Chase JM (2004) Parasites in the food web: Linking amphibian malformations and aquatic eutrophication. Ecology Letters 7:521–526

Johnston CA (1991a) Sediment and nutrient retention by freshwater wetlands: effects on surface water quality. Critical Reviews in Environmental Science and Technology 21:491–565

Johnston CA (1991b) Sediment and nutrient retention by freshwater wetlands: Effects on surface water quality. Critical Reviews in Environmental Control 21:491–565

Johnston CA (2013) Wetland losses due to row crop expansion in the dakota prairie pothole region. Wetlands 33:175–182

Johnston CA, Bubenzer GD, Lee GB, Madison FW, McHenry JR (1984) Nutrient trapping by sediment deposition in a seasonally flooded lakeside wetland. Journal of environmental quality 13:283–290

Johnston CA, Detenbeck NE, Niemi GJ (1990) The Cumulative Effect of Wetlands on Stream Water Quality and Quantity. A Landscape Approach. Biogeochemistry 10:105–141

Jordan SJ, Stoffer J, Nestlerode JA (2011) Wetlands as Sinks for Reactive Nitrogen at Continental and Global Scales: A Meta-Analysis. Ecosystems 14:144–155

Jurik TW, Wang SC, van der Valk AG (1994) Effects of sediment load on seedling emergence from wetland seed banks. Wetlands 14:159–165

van der Kamp G, Hayashi M (2009) Groundwater-wetland ecosystem interaction in the semiarid glaciated plains of North America. Hydrogeology Journal 17:203–214

Kantrud HA (1993) Duck nest success on Conservation Reserve Program land in the prairie pothole region. Journal of Soil & Water Conservation 48:238–242

Kantrud HA, Krapu GL, Swanson GA (1989) Prairie Basin Wetlands of the Dakotas: A Community Profile. U.S. Fish and Wildlife Service Biological Report 85:116 pp

Kantrud HA, Stewart RE (1977) Use of Natural Basin Wetlands by Breeding Waterfowl in North Dakota. Journal of Wildlife Management 41:243–253

Keeler BL, Polasky S (2014) Land-use change and costs to rural households: A case study in groundwater nitrate contamination. Environmental Research Letters 9

Kéfi S, Rietkerk M, Alados CL, Pueyo Y, Papanastasis VP, ElAich A, De Ruiter PC (2007) Spatial vegetation patterns and imminent desertification in Mediterranean arid ecosystems. Nature 449:213–217

Kemmis TJ (1991) Glacial landforms, sedimentology, and depositional environments of the Des Moines Lobe, northern Iowa. The University of Iowa

Kercher SM, Zedler JB (2004) Multiple disturbances accelerate invasion of reed canary grass (Phalaris arundinacea L.) in a mesocosm study. Oecologia 138:455–464

Kettenring KM, Galatowitsch SM (2011) Seed Rain of Restored and Natural Prairie Wetlands. Wetlands 31:283–294

Kinsman-Costello LE, O’Brien J, Hamilton SK (2014) Re-flooding a Historically Drained Wetland Leads to Rapid Sediment Phosphorus Release. Ecosystems 17:641–656

Klausmeler CA, Litchman E, Daufreshna T, Levin SA (2004) Optimal nitrogen-to-phosphorus stoichiometry of phytoplankton. Nature 429:171–174

Klimkowska A, Kotowski W, Van Diggelen R, Grootjans AP, Dzierża P, Brzezińska K (2010) Vegetation Re-development After Fen Meadow Restoration by Topsoil Removal and Hay Transfer. Restoration Ecology 18:924–933

Knowles R (1982) Denitrification. Microbiological Reviews 46:43–70

Kolka RK, Thompson JA (2006) Wetland geomorphology, soils, and formative processes. In: Ecology of Freshwater and Estuarine Wetlands. Batzer, DP & Sharitz, RR, editors. University of California Press, Berkeley, CA pp. 7–42.

Kovacic DA, David MB, Gentry LE, Starks KM, Cooke RA (2000) Effectiveness of Constructed Wetlands in Reducing Nitrogen and Phosphorus Export from Agricultural Tile Drainage. Journal of Environmental Quality 29:1262–1274

Kreiling RM, Schubauer-Berigan JP, Richardson WB, Bartsch LA, Hughes PE, Cavanaugh JC, Strauss EA (2013) Wetland management reduces sediment and nutrient loading to the upper Mississippi river. Journal of environmental quality 42:573–583

Kreiling RM, Richardson WB, Cavanaugh JC, Bartsch LA (2011) Summer nitrate uptake and denitrification in an upper Mississippi River backwater lake: The role of rooted aquatic vegetation. Biogeochemistry 104:309–324

Kuznetsova A, Brockhoff PB, Christensen RHB, Jensen SP (2020) Package “lmerTest”: Tests in Linear Mixed Effects Models. R package version 3.2.5 30

LaBaugh JW, Winter TC, Adomaitis VA, Swanson GA (1987) Hydrology and chemistry of selected prairie wetlands in the Cottonwood Lake area, Stutsman County, North Dakota, 1979-82. US Geological Survey Professional Paper 1431

LaBaugh JW, Winter TC, Rosenberry DO (1998) Hydrologic functions of prairie wetlands. Great Plains Research 8:17–37

Lane CR, Leibowitz SG, Autrey BC, LeDuc SD, Alexander LC (2018) Hydrological, Physical, and Chemical Functions and Connectivity of Non-Floodplain Wetlands to Downstream Waters: A Review. Journal of the American Water Resources Association 54:346–371

Larkin DJ, Freyman MJ, Lishawa SC, Geddes P, Tuchman NC (2012) Mechanisms of dominance by the invasive hybrid cattail Typha × glauca. Biological Invasions 14:65–77

Larkin DJ, Lishawa SC, Tuchman NC (2012) Appropriation of nitrogen by the invasive cattail Typha × glauca. Aquatic Botany 100:62–66

Laskov C, Horn O, Hupfer M (2006) Environmental factors regulating the radial oxygen loss from roots of Myriophyllum spicatum and Potamogeton crispus. Aquatic Botany 84:333–340

Lawrence BA, Lishawa SC, Rodriguez Y, Tuchman NC (2016) Herbicide management of invasive cattail (Typha × glauca) increases porewater nutrient concentrations. Wetlands Ecology and Management 24:457–467

Leech DM, Pollard AI, Labou SG, Hampton SE (2018) Fewer blue lakes and more murky lakes across the continental U.S.: Implications for planktonic food webs. Limnology and Oceanography 63:2661–2680

Lehner B, Döll P (2004) Development and validation of a global database of lakes, reservoirs and wetlands. Journal of Hydrology 296:1–22

Lehtinen RM, Galatowitsch SM, Tester JR (1999) Consequences of habitat loss and fragmentation for wetland amphibian assemblages. Wetlands 19:1–12

Leibowitz SG, Wigington PJ, Schofield KA, Alexander LC, Vanderhoof MK, Golden HE (2018) Connectivity of Streams and Wetlands to Downstream Waters: An Integrated Systems Framework. Journal of the American Water Resources Association 54:298–322

Leibowitz SG (2003) Isolated wetlands and their functions: an ecological perspective. Wetlands 23:517–531

Leibowitz SG, Mushet DM, Newton WE (2016) Intermittent Surface Water Connectivity: Fill and Spill Vs. Fill and Merge Dynamics. Wetlands 36:S323–S342

Leibowitz SG, Vining KC, Leibowits SG, Vining KC (2003) Temporal connectivity in a prairie pothole complex. Wetlands 23:13–25

Leitch JA (1989) Politicoeconomic Overview of Prairie Potholes. In: Northern Prairie Wetlands. Van der Valk, AG, editor. Iowa State University Press, Ames, IA pp. 2–15.

Lenth R, Singmann H, Love J, Buerkner P, Herve M (2020) Package “emmeans”: Estimated Marginal Means, aka Least-Squares Means. R package version 3.2.0 73

Leverett F, Sardeson FW (1932) Quaternary Geology of Minnesota and Parts of Adjacent States. USGS Professional Paper 161:149

Lewandowski AM, Montgomery BR, Rosen CJ, Moncrief JF (2008) Groundwater nitrate contamination costs: A survey of private well owners. Journal of Soil and Water Conservation 63:153–161

Lewis DB, Kaye JP, Gries C, Kinzig AP, Redman CL (2006) Agrarian legacy in soil nutrient pools of urbanizing arid lands. Global Change Biology 12:703–709

Lishawa SC, Jankowski KJ, Geddes P, Larkin DJ, Monks AM, Tuchman NC (2014) Denitrification in a Laurentian Great Lakes coastal wetland invaded by hybrid cattail (Typha × glauca). Aquatic Sciences 483–495

Lishawa SC, Carson BD, Brandt JS, Tallant JM, Reo NJ, Albert DA, Monks AM, Lautenbach JM, Clark E (2017) Mechanical harvesting effectively controls young typha spp. Invasion and unmanned aerial vehicle data enhances post-treatment monitoring. Frontiers in Plant Science 8:1–14

Lishawa SC, Treering DJ, Vail LM, Mckenna O, Grimm EC, Tuchman NC (2013) Reconstructing plant invasions using historical aerial imagery and pollen core analysis: Typha in the Laurentian Great Lakes. Diversity and Distributions 19:14–28

Lishawa SC, Albert DA, Tuchman NC (2010) Water level decline promotes Typha X glauca establishment and vegetation change in Great Lakes coastal wetlands. Wetlands 30:1085–1096

Lishawa SC, Lawrence BA, Albert DA, Tuchman NC (2015) Biomass harvest of invasive Typha promotes plant diversity in a Great Lakes coastal wetland. Restoration Ecology 23:228–237

Liss PS, Slater PG (1974) Flux of gases across the Air-Sea interface. Nature 247:181–184

Liston SE, Newman S, Trexler JC (2008) Macroinvertebrate community response to eutrophication in an oligotrophic wetland: An in situ mesocosm experiment. Wetlands 28:686–694

Luo H-R, Smith LM, Allen BL, Haukos DA (1997) Effects of sedimentation on playa wetland volume. Ecological Applications 7:247–252

Luo HR, Smith LM, Haukos DA, Allen BL (1999) Sources of recently deposited sediments in playa wetlands. Wetlands 19:176–181

Mackay EB, Feuchtmayr H, De Ville MM, et al. (2020) Dissolved organic nutrient uptake by riverine phytoplankton varies along a gradient of nutrient enrichment. Science of the Total Environment 722:137837

Mahan BL (1996) Valuing urban wetlands: A property price approach. Oregon State University

Mahaney WM, Wardrop DH, Brooks RP (2004) Impacts of sedimentation and nitrogen enrichment on wetland plant community development. Plant Ecology 175:227–243

Mallin MA, Johnson VL, Ensign SH, MacPherson TA (2006) Factors contributing to hypoxia in rivers, lakes, and streams. Limnology and Oceanography 51:690–701

Manios T, Laux D, Manios V, Stentiford E (2003) Cattail plant biomass as a bulking agent in sewage sludge composting; effect of the compost on plant growth. Compost Science and Utilization 11:210–219

Markager S, Stedmon CA, Søndergaard M (2011) Seasonal dynamics and conservative mixing of dissolved organic matter in the temperate eutrophic estuary Horsens Fjord. Estuarine, Coastal and Shelf Science 92:376–388

Martin DB, Hartman WA (1987) The Effect of Cultivation on Sediment Composition and Deposition in Prairie Pothole Wetlands. Water, Air, and Soil Pollution 34:45–53

Martin HW, Ivanoff DB, Graetz DA, Reddy KR (1997) Water Table Effects on Histosol Drainage Water Carbon, Nitrogen, and Phosphorus. Journal of Environmental Quality 26:1062–1071

Martiny AC, Vrugt JA, Lomas MW (2014) Concentrations and ratios of particulate organic carbon, nitrogen, and phosphorus in the global ocean. Scientific Data 1:1–7

Marton JM, Creed IF, Lewis DB, Lane CR, Basu NB, Cohen MJ, Craft CB (2015) Geographically isolated wetlands are important biogeochemical reactors on the landscape. BioScience 65:408–418

Maurer DA, Zedler JB (2002) Differential invasion of a wetland grass explained by tests of nutrients and light availability on establishment and clonal growth. Oecologia 131:279–288

McCauley LA, Anteau MJ, Van Der Burg MP, Wiltermuth MT (2015) Land use and wetland drainage affect water levels and dynamics of remaining wetlands. Ecosphere 6:1–22

McCauley LA, Jenkins DG (2005) GIS-based estimates of former and current depressional wetlands in an agricultural landscape. Ecological Applications 15:1199–1208

McClain ME, Boyer EW, Dent CL, et al. (2003) Biogeochemical Hot Spots and Hot Moments at the Interface of Terrestrial and Aquatic Ecosystems. Ecosystems 6:301–312

McCorvie MR, Lant CL (1993) Drainage district formation and the loss of midwestern wetlands, 1850-1930. Agricultural History 67:13–39

McCrackin ML, Muller-Karulis B, Gustafsson BG, Howarth RW, Humborg C, Svanbäck A, Swaney DP (2018) A Century of Legacy Phosphorus Dynamics in a Large Drainage Basin. Global Biogeochemical Cycles 32:1107–1122

McGill B (2015) Land Use Matters. Nature 520:38–39

McIsaac GF, David MB, Gertner GZ, Goolsby DA (2001) Nitrate flux in the Mississippi River. Nature Communications 414:166–167

McKenna OP, Osorio JM, Behrman KD, Doro L, Mushet DM (2020) Development of a novel framework for modeling field-scale conservation effects of depressional wetlands in agricultural landscapes. Journal of Soil and Water Conservation 75:695–703

Mclane CR, Battaglia LL, Gibson DJ, Groninger JW (2012) Succession of exotic and native species assemblages within restored floodplain forests: A test of the parallel dynamics hypothesis. Restoration Ecology 20:202–210

McLaughlin Daniel, Kaplan DA, Cohen MJ (2014) A significant nexus: Geographically isolated wetlands influence landscape hydrology. Water Resour. Res. 50:7153–7166

McLaughlin Daniel L, Kaplan DA, Cohen MJ (2014) A significant nexus: Geographically isolated wetlands influence landscape hydrology. Water Resources Research 50:7153–7166

McLellan E, Robertson D, Schilling K, Tomer M, Kostel J, Smith D, King K (2015) Reducing nitrogen export from the corn belt to the gulf of mexico: Agricultural strategies for remediating hypoxia. Journal of the American Water Resources Association 51:263–289

Van Meter KJ, Basu NB (2015) Signatures of human impact: size distributions and spatial organization of wetlands in the Prairie Pothole landscape. Ecological Applications 25:451–465

Van Meter KJ, Basu NB, Veenstra JJ, Burras CL (2016) The nitrogen legacy: Emerging evidence of nitrogen accumulation in anthropogenic landscapes. Environmental Research Letters 11:35014

Meyer CK, Baer SG, Whiles MR (2008) Ecosystem recovery across a chronosequence of restored wetlands in the Platte River Valley. Ecosystems 11:193–208

Meyers LM (2013) Wetland Assessment and Nutrient Dynamics in North Dakota. North Dakota State University

Minett DA, Cook PLM, Kessler AJ, Cavagnaro TR (2013) Root effects on the spatial and temporal dynamics of oxygen in sand-based laboratory-scale constructed biofilters. Ecological Engineering 58:414–422

Mitsch WJ, Wu X, Nairn RW, Weihe PE, Wang N, Deal R, Boucher CE (1998) Creating and restoring wetlands: a whole-ecosystem experiment in self-design. BioScience 48:1019–1030

Mitsch WJ, Zhang L, Stefanik KC, Nahlik AM, Anderson CJ, Bernal B, Hernandez M, Song K (2012) Creating wetlands: Primary succession, water quality changes and self-design over 15 years. BioScience 62:237–250

Mitsch WJ, Day JW, Gilliam JW, Groffman PM, Hey DL, Randall GW, Wang N (2001) Reducing Nitrogen Loading to the Gulf of Mexico from the Mississippi River Basin: Strategies to Counter a Persistent Ecological Problem. BioScience 51:373–388

Mitsch WJ, Day JW (2006) Restoration of wetlands in the Mississippi-Ohio-Missouri (MOM) River Basin: Experience and needed research. Ecological Engineering 26:55–69

Mitsch WJ, Day JW, Zhang L, Lane RR (2005) Nitrate-nitrogen retention in wetlands in the Mississippi River Basin. Ecological Engineering 24:267–278

Mitsch WJ, Wang N (2000) Large-scale coastal wetland restoration on the Laurentian Great Lakes: Determining the potential for water quality improvement. Ecological Engineering 15:267–282

Mitsch WJ, Wilson RF (1996) Improving the Success of Wetland Creation and Restoration with Know-How, Time, and Self-Design. Ecological Applications 6:77–83

Montgomery JA, Eames JM, Klimas C (2021) A 16-Year Investigation of Legacy Phosphorus Discharge From Prairie Wolf Slough: A Wetland Restored On A Former Farmed Field. Restoration Ecology 29

Moore JM, Wein RW (1977) Viable seed populations by soil depth and potential site recolonization after disturbance. Canadian Journal of Botany 55:2408–2412

Moran SR, Clayton L, Hooke RL, Fenton MM, Andriashek LD (1980) Glacier-Bed Landforms of The Prairie Region of North America. Journal of Glaciology 25:457–476

Mørck Ottosen LD, Risgaard-Petersen N, Nielsen LP (1999) Direct and indirect measurements of nitrification and denitrification in the rhizosphere of aquatic macrophytes. Aquatic Microbial Ecology 19:81–91

Moreno-Mateos D, Power ME, Comin FA, Yockteng R (2012) Structural and Functional Loss in Restored Wetland Ecosystems. PLoS biology 10:e1001247

Morris PF, Barker WG (1977) Oxygen transport rates through mats of Lemna minor and Wolffia sp. and oxygen tension within and below the mat. Canadian Journal of Botany 55:1926–1932

Mosier A, Kroeze C, Nevison C, Oenema O, Seitzinger S, van Cleemput O (1998) Closing the global N2O budget: Nitrous oxide emissions through the agricultural nitrogen cycle. Nutrient Cycling in Agroecosystems 52:225–248

Mulholland PJ, Helton AM, Poole GC, et al. (2008) Stream denitrification across biomes and its response to anthropogenic nitrate loading. Nature Letters 452:202–205

Mulhouse JM, Galatowitsch SM (2003) Revegetation of prairie pothole wetlands in the mid-continental US: twelve years post-reflooding. Plant Ecology 169:143–159

Müller B, Thoma R, Baumann KBL, Callbeck CM, Schubert CJ (2021) Nitrogen removal processes in lakes of different trophic states from on-site measurements and historic data. Aquatic Sciences 83:https://doi.org/10.1007/s00027-021-00795-7

Murphy J, Riley JP (1962) A modified single solution method for the determination of phosphate in natural waters. Analytica Chimica Acta 27:31–36

Murphy JC, Hirsch RM, Sprague LA (2013) Nitrate in the Mississippi River and its tributaries, 1980 – 2010: an update. U.S. Geological Survey 31 p.

Murty D, Kirschbaum MUF, Mcmurtrie RE, Mcgilvray H (2002) Does conversion of forest to agricultural land change soil carbon and nitrogen? A review of the literature. Global Change Biology 8:105–123

Mushet DM, Calhoun AJK, Alexander LC, et al. (2015) Geographically Isolated Wetlands: Rethinking a Misnomer. Wetlands 35:423–431

Nahlik AM, Fennessy MS (2016) Carbon storage in US wetlands. Nature Communications 7:1–9

Nair VD, Clark MW, Reddy KR (2015) Evaluation of Legacy Phosphorus Storage and Release from Wetland Soils. Journal of Environmental Quality 44:1956–1964

Neely RK, Baker JL (1989) Nitrogen and Phosphorus Dynamics and the Fate of Agricultural Runoff. In: Northern Prairie Wetlands. Van der Valk, AG, editor. Iowa State University Press, Ames, IA pp. 92–131.

Neff BP, Rosenberry DO (2018) Groundwater Connectivity of Upland-Embedded Wetlands in the Prairie Pothole Region. Wetlands 38:51–63

Newbold T, Hudson LN, Hill SLL, et al. (2015) Global effects of land use on local terrestrial biodiversity. Nature 520:45–50

Niemuth ND, Fleming KK, Reynolds RE (2014) Waterfowl conservation in the US prairie pothole region: Confronting the complexities of climate change. PLoS ONE 9

Niemuth ND, Wangler B, Reynolds RE (2010) Spatial and temporal variation in wet area of wetlands in the Prairie Pothole Region of North Dakota and South Dakota. Wetlands 30:1053–1064

Nkemka VN, Gilroyed B, Yanke J, Gruninger R, Vedres D, McAllister T, Hao X (2015) Bioaugmentation with an anaerobic fungus in a two-stage process for biohydrogen and biogas production using corn silage and cattail. Bioresource Technology 185:79–88

Ockenden MC, Deasy C, Quinton JN, Surridge B, Stoate C (2014) Keeping agricultural soil out of rivers: Evidence of sediment and nutrient accumulation within field wetlands in the UK. Journal of Environmental Management 135:54–62

Oksanen J, Blanchet FG, Friendly M, et al. (2018) vegan: Community Ecology Package. R package version 2.5-4

Oldenborg KA, Steinman AD (2019) Impact of sediment dredging on sediment phosphorus flux in a restored riparian wetland. Science of the Total Environment 650:1969–1979

Olivier JGJ, Janssens-Maenhout G, Peters JAHW (2012) Trends in global CO2 emissions. The Hague

Olsen SR, Cole C V., Watanabe FS, Dean LA (1954) Estimation of Available Phosphorus in Soils by Extraction with Sodium Bicarbonate. United States Department of Agriculture Circular No. 939 1–19

Orr CH, Stanley EH, Wilson KA, Finlay JC (2007) Effects of restoration and reflooding on soil denitrification in a leveed midwestern floodplain. Ecological Applications 17:2365–2376

Oslund FT, Johnson RR, Hertel DR (2010) Assessing wetland changes in the prairie pothole region of Minnesota from 1980 to 2007. Journal of Fish and Wildlife Management 1:131–135

Pant HK, Reddy KR (2001) Hydrologic Influence on Stability of Organic Phosphorus in Wetland Detritus. Journal of Environmental Quality 30:668–674

Patrick WH, Khalid RA (1974) Phosphate Release and Sorption by Soils and Sediments: Effect of Aerobic and Anaerobic Conditions. Science 186:53–55

Pattison-Williams JK, Pomeroy JW, Badiou P, Gabor S (2018) Wetlands, Flood Control and Ecosystem Services in the Smith Creek Drainage Basin: A Case Study in Saskatchewan, Canada. Ecological Economics 147:36–47

Pellerin BA, Wollheim WM, Hopkinson CS, McDowell WH, Williams MR, Vörösmarty CJ, Daley ML (2004) Role of wetlands and developed land use on dissolved organic nitrogen concentrations and DON/TDN in northeastern U.S. rivers and streams. Limnology and Oceanography 49:910–918

Perrone J, Madramootoo CA (1994) Characterizing bulk density and hydraulic conductivity changes in a potato cropped field. Soil Technology 7:261–268

Perry LG, Galatowitsch SM (2003) A test of two annual cover crops for controlling Phalaris arundinacea invasion in restored sedge meadow wetlands. Restoration Ecology 11:297–307

Pfeifer-Meister L, Johnson BR, Roy BA, Carreño S, Stewart JL, Bridgham SD (2012) Restoring wetland prairies: tradeoffs among native plant cover, community composition, and ecosystem functioning. Ecosphere 3

Phillips G, Kelly A, Pitt J-A, Sanderson R, Taylor E (2005) The recovery of a very shallow eutrophic lake, 20 years after the control of effluent derived phosphorus. Freshwater Biology 50:1628–1638

Pilgrim KM, Huser BJ, Brezonik PL (2007) A method for comparative evaluation of whole-lake and inflow alum treatment. Water Research 41:1215–1224

Pilotto LS, Douglas RM, Burch MD, et al. (1997) Health effects of exposure to cyanobacteria (blue-green algae) during recreational water-related activities. Australian and New Zealand Journal of Public Health 21:562–566

Poeplau C, Don A, Vesterdal L, Leifeld J, Van Wesemael B, Schumacher J, Gensior A (2011) Temporal dynamics of soil organic carbon after land-use change in the temperate zone - carbon response functions as a model approach. Global Change Biology 17:2415–2427

Porter PS, Sanchez CA (1992) The effect of soil properties on phosphorus sorption by Everglades Histosols. Soil Science 154:387–398

Preston TM, Sojda RS, Gleason RA (2013) Sediment accretion rates and sediment composition in prairie pothole wetlands under varying land use practices, Montana, United States. Journal of Soil and Water Conservation 68:199–211

Pribyl DW (2010) A critical review of the conventional SOC to SOM conversion factor. Geoderma 156:75–83

R Core Team (2020) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria

Rabalais NN, Turner RE, Gupta BK Sen, Platon E, Parsons ML (2007) Sediments tell the history of eutrophication and hypoxia in the northern Gulf of Mexico. Ecological Applications 17:129–143

Rabalais NN, Turner RE, Wiseman WJ (2002) Gulf of Mexico hypoxia, a.k.a. “The dead zone.” Annual Review of Ecology and Systematics 33:235–263

Rains MC, Leibowitz SG, Cohen MJ, et al. (2016) Geographically isolated wetlands are part of the hydrological landscape. Hydrological Processes 30:153–160

Reddy KR, Fisher MM, Wang Y, et al. (2007) Potential Effects of Sediment Dredging on Internal Phosphorus Loading in a Shallow , Subtropical Lake. Lake and Reservoir Management 23:27–38

Reddy KR, Delaune RD, Debusk WF, Koch MS (1993) Long-term nutrient accumulation rates in the Everglades. Soil Science Society of America Journal 57:1147–1155

Reddy KR, Kadlec RH, Flaig E, Gale PM (1999) Phosphorus retention in streams and wetlands: A review. Critical Reviews in Environmental Science and Technology 29:83–146

Reddy KR, Patrick Jr WH, Lindau CW, Patrick WH, Lindau CW (1989) Nitrification-denitrification at the plant root-sediment interface in wetlands. Limnology and Oceanography 34:1004–1013

Redelfs AE (1983) Wetlands Values and Losses in the United States. Oklahoma State University

Redfield AC (1958) The biological control of chemical factors in the environment. American Scientist 46:205–221

Reicosky DC (1997) Tillage-induced CO2 emission from soil. Nutrient Cycling in Agroecosystems 49:273–285

Reynolds JE, Regalado A (2002) Reynolds and Regalado_2002_The effects of wetlands and other factors on rural land values.pdf. The Appraisal Journal 72:182–190

Reynolds RE, Shaffer TL, Loesch CR, Cox RR (2006) The Farm Bill and Duck Production in the Prairie Pothole Region: Increasing the Benefits. Wildlife Society Bulletin 34:963–974

Ripley B, Venables B, Bates DM, Hornik K, Gebhardt A, Firth D (2021) Support Functions and Datasets for Venables and Ripley’s MASS. 170

Risgaard-Petersen N, Jensen K (1997) Nitrification and denitrification in the rhizosphere of the aquatic macrophyte Lobelia dortmanna L. Limnology & Oceanography 42:529–537

Risgaard-Petersen N, Rysgaard S, Nielsen LP, Revsbech NP (1994) Diurnal Variation of Denitrification and Nitrification in Sediments Colonized by Benthic Microphytes. Limnology and Oceanography 39:573–579

Robertson GP, Vitousek PM (2009) Nitrogen in agriculture: Balancing the cost of an essential resource. Annual Review of Environment and Resources 34:97–125

Robortella J (2015) Finger Lakes Farmer’s Invention Changed the World. Democrat & Chronicle, May 20

Romero JA, Comín FA, García C (1999) Restored wetlands as filters to remove nitrogen. Chemosphere 39:323–332

De Roos AJ, Ward MH, Lynch CF, Cantor KP (2003) Nitrate in public water supplies and the risk of colon and rectum cancers. Epidemiology 14:640–649

Rose C, Crumpton WG (1996) Effects of emergent macrophytes on dissolved oxygen dynamics in a prairie pothole wetland. Wetlands 16:495–502

Roy ED (2017) Phosphorus recovery and recycling with ecological engineering: A review. Ecological Engineering 98:213–227

Rupert MG (2008) Decadal-scale changes of nitrate in ground water of the United States, 1988-2004. Journal of environmental quality 37:240–248

Saefken B, Ruegamer D, Baumann P, Kruse R-M, Greven S, Kneib T (2019) Conditional Akaike Information Criterion for “lme4” and “nlme” Version. 20

Saini G, Grant W (1980) Long-Term Effects of Intensive Cultivation on Soil Quality in the Potato-Growing Areas of New Brunswick (Canada) and Maine (USA). Can. J. Soil

Sci. 60:421–428

Salk KR, Steinman AD, Ostrom NE (2018) Wetland restoration and hydrologic reconnection result in enhanced watershed nitrogen retention and removal. Wetlands 38:349–359

Sawka MN, Cheuvront SN, Carter III R (2005) Human Water Needs. Nutrition Reviews 63:S30–S39

Schindler D (1974) Eutrophication and Recovery in Experimental Lakes: Implications for Lake Management. Science 184:897–899

Schindler DW, Hecky RE, Findlay DL, Stainton MP, Parker BR, Paterson MJ, Beaty KG, Lyng M, Kasian SEM (2008) Eutrophication of lakes cannot be controlled by reducing nitrogen input: Results of a 37-year whole-ecosystem experiment. PNAS 105:11254–11258

Schlesinger WH, Bernhardt ES (2013) The Global Cycles of Nitrogen and Phosphorus. In: Biogeochemistry: An Analysis of Global Change. pp. 445–468.

Scholte SSK, Todorova M, van Teeffelen AJA, Verburg PH (2016) Public Support for Wetland Restoration: What is the Link With Ecosystem Service Values? Wetlands 36:467–481

Schullehner J, Hansen B, Thygesen M, Pedersen CB, Sigsgaard T (2018) Nitrate in drinking water and colorectal cancer risk: A nationwide population-based cohort study. International Journal of Cancer 143:73–79

Seabloom EW, van der Valk AG (2003) The development of vegetative zonation patterns in restored prairie pothole wetlands. Journal of Applied Ecology 40:92–100

Seitzinger S, Harrison JA, Böhlke JK, Bouwman AF, Lowrance R, Peterson B, Tobias C, Van Drecht G (2006) Denitrification Across Landscapes and Waterscapes: A Synthesis. Ecological Applications 16:2064–2090

Seitzinger SP (1988) Denitrification in freshwater and coastal marine ecosystems: Ecological and geochemical significance. Limnology and Oceanography 33:702–724

Seitzinger SP, Kroeze C, Styles R V. (2000) Global distribution of N2O emissions from aquatic systems: Natural emissions and anthropogenic effects. Chemosphere - Global Change Science 2:267–279

Sharpley A, Jarvie HP, Buda A, May L, Spears B, Kleinman P (2013) Phosphorus legacy: Overcoming the effects of past management practices to mitigate future water quality impairment. Journal of Environmental Quality 42:1308–1326

Sharpley AN (1995) Dependence of runoff phosphorus on extractable soil phosphorus. Journal of Environmental Quality 24:920–926

Shine C, de Klemm C (1999) Wetlands, Water and the Law: Using law to advance wetland conservation and wise use. Bonn, Germany

Shoemaker CM, Ervin GN, DiOrio EW (2017) Interplay of water quality and vegetation in restored wetland plant assemblages from an agricultural landscape. Ecological Engineering 108:255–262

Smil V (1999) Nitrogen in crop production: An account of global flows. Global Biogeochemical Cycles 13:647–662

Smith AG, Stoudt JH, Gollop JB (1964) Prairie Potholes and Marshes. In: Waterfowl Tomorrow. Linduska, JP, Nelson, AL, & Hines, B, editors. United States Department of the Interior pp. 39–50.

Smith C, DeKeyser ES, Dixon C, Kobiela B, Little A (2016) Effects of Sediment Removal on Prairie Pothole Wetland Plant Communities in North Dakota. Natural Areas Journal 36:48–58

Smith RL (1991) Chemical Concentration Data Near the Detection Limit (EPA/903/8-91/001). 1–4

Smith VH, Schindler DW (2009) Eutrophication science: where do we go from here? Trends in Ecology and Evolution 24:201–207

Snodgrass JW, Komoroski MJ, Bryan AL, Burger J (2000) Relationships among isolated wetland size, hydroperiod, and amphibian species richness: Implications for wetland regulations. Conservation Biology 14:414–419

Søndergaard M, Jeppesen E, Jensen JP (2005) Pond or lake: Does it make any difference? Archiv fur Hydrobiologie 162:143–165

Søndergaard M, Kristensen P, Jeppesen E (1992) Phosphorus release from resuspended sediment in the shallow and wind-exposed Lake Arresø, Denmark. Hydrobiologia 228:91–99

Soons MB, van der Vlugt C, van Lith B, Heil GW, Klaassen M (2008) Small seed size increases the potential for dispersal of wetland plants by ducks. Journal of Ecology 96:619–627

Steinberg SL, Coonrod HS (1994) Oxidation of the Root Zone by Aquatic Plants Growing in Gravel-Nutrient Solution Culture. Journal of Environmental Quality 23:907–913

Steinman A, Rediske R, Reddy KR (2004) The reduction of internal phosphorus loading using alum in Spring Lake, Michigan. Journal of Environmental Quality 33:2040–2048

Stelk M, Christie J, Weber R, et al. (2017) Wetland Restoration: Contemporary Issues and Lessons Learned. Windham, Maine

Stevens CE, Diamond AW, Gabor TS (2002) Anuran Call Surveys On Small Wetlands In Prince Edward Island, Canada Restored By Dredging Of Sediments. Wetlands 22:90–99

Stewart RE, Kantrud HA (1974) Breeding Waterfowl Populations in the Prairie Pothole Region of North Dakota. USGS Northern Prairie Wildlife Research Center 76:70–79

Stewart RE, Kantrud HA (1971) Classification of Natural Ponds and Lakes in the Glaciated Prairie Region. U.S. Department of the Interior, U.S. Fish and Wildlife Service, Washington, D.C.

Stewart RE, Kantrud HA (1973) Ecological Distribution of Breeding Waterfowl Populations in North Dakota. The Journal of Wildlife Management 37:39–50

Streeter MT, Schilling KE (2015) A comparison of soil properties observed in farmed, restored and natural closed depressions on the Des Moines Lobe of Iowa. Catena 129:39–45

Stroh PA, Hughes FMR, Sparks TH, Mountford JO (2012) The influence of time on the soil seed bank and vegetation across a landscape-scale wetland restoration project. Restoration Ecology 20:103–112

Stuart D, Schewe RL, Mcdermott M (2014) Reducing nitrogen fertilizer application as a climate change mitigation strategy: Understanding farmer decision-making and potential barriers to change in the US. Land Use Policy 36:210–218

Stubbs M (2014) Conservation reserve program (CRP): Status and issues (CRS Report No. R42783).

Stutter MI, Graeber D, Evans CD, Wade AJ, Withers PJA (2018) Balancing macronutrient stoichiometry to alleviate eutrophication. Science of the Total Environment 634:439–447

Surridge BWJ, Heathwaite AL, Baird AJ (2007) The Release of Phosphorus to Porewater and Surface Water from River Riparian Sediments. Journal of Environmental Quality 36:1534–1544

Svedarsky D, Grosshans R, Venema H, Ellis-Felege S, Bruggman J, Ostlund A, Lewis J (2019) Integrated Management of Invasive Cattails as Biofuel and as a Wetland Management Strategy in the Northern Great Plains of the United States and Canada. Mires and Peat 25:1–14

Svensson JM, Leonardson L (1996) Effects of bioturbation by tube-dwelling chironomid larvae on oxygen uptake and denitrification in eutrophic lake sediments. Freshwater Biology 35:289–300

Tank JL, Dodds WK (2003) Nutrient limitation of epilithic and epixylic biofilms in ten North American streams. Freshwater Biology 48:1031–1049

Tesoriero AJ, Duff JH, Saad DA, Spahr NE, Wolock DM (2013) Vulnerability of streams to legacy nitrate sources. Environmental science & technology 47:3623–3629

Thiere G, Milenkovski S, Lindgren P-E, Sahlén G, Berglund O, Weisner SEB (2009) Wetland creation in agricultural landscapes: Biodiversity benefits on local and regional scales. Biological Conservation 142:964–973

Thomas GW, Haszler GR, Blevins RL (1996) The effects of organic matter and tillage on maximum compactability of soils using the proctor test. Soil Science 161:502–508

Tilman D (1994) Competition and Biodiversity in Spatially Structured Habitats. Ecology 75:2–16

Tilman D (1982) Competition for Two Resources. In: Resource Competition and Community Structure. Princeton University Press, Princeton, New Jersey pp. 61–97.

Tilman D (1990) Constraints and Tradeoffs: Toward a Predictive Theory of Competition and Succession. Oikos 58:3–15

Tilman D (1985) The Resource-Ratio Hypothesis of Plant Succession. The American Naturalist 125:827–852

Tiner RW (2003a) Estimated extent of geographically isolated wetlands in selected areas of the United States. Wetlands 23:636–652

Tiner RW (2003b) Geographically isolated wetlands of the United States. Wetlands 23:494–516

Tiner RW (1984) Wetlands of the United States: Current Status and Recent Trends. US Fish and Wildlife Service, National Wetlands Inventory 1–76

Tiwari V, Kashikar A (2019) Package “OutlierDetection.” 13

Tsai J-S, Venne LS, McMurry ST, Smith LM (2007) Influences of land use and wetland characteristics on water loss rates and hydroperiods of playas in the Southern High Plains, USA. Wetlands 27:683–692

Tuchman NC, Larkin DJ, Geddes P, Wildova R, Jankowski K, Goldberg DE (2009) Patterns of environmental change associated withTypha xglauca invasion in a Great Lakes coastal wetland. Wetlands 29:964–975

Turner RE, Rabalais NN (1991) Changes in Mississippi River Water Quality This Century. BioScience 41:140–147

Turner RE, Rabalais NN (1994) Coastal eutrophication near the Mississippi river delta. Nature 368:619–621

Turner RE, Rabalais NN, Justic D (2008) Gulf of Mexico hypoxia: Alternate states and a legacy. Environmental Science and Technology 42:2323–2327

Ucgul M, Saunders C, Fielke JM (2017) Discrete element modelling of tillage forces and soil movement of a one-third scale mouldboard plough. Biosystems Engineering 155:44–54

USDA NRCS (2018) The PLANTS Database. National Plant Data Team, Greensboro, NC 27401-4901 USA

Vaccaro LE, Bedford BL, Johnston CA (2009) Litter accumulation promotes dominance of invasive species of cattails (Typha spp.) in Lake Ontario wetlands. Wetlands 29:1036–1048

Vadeboncoeur Y, Jeppesen E, Vander Zanden MJ, Schierup HH, Christoffersen K, Lodge DM (2003) From Greenland to green lakes: Cultural eutrophication and the loss of benthic pathways in lakes. Limnology and Oceanography 48:1408–1418

van der Valk AG, Davis CB (1979) A reconstruction of the recent vegetational history of a prairie marsh, Eagle Lake, Iowa, from its seed bank. Aquatic Botany 6:29–51

van der Valk AG, Davis CB (1978) The role of seed banks in the vegetation dynamics of prairie glacial marshes. Ecology 59:322–335

van der Valk AG, Pederson RL (2003) The SWANCC decision and its implications for prairie potholes. Wetlands 23:590–596

Vanderhoof MK, Alexander LC, Todd MJ (2016) Temporal and spatial patterns of wetland extent influence variability of surface water connectivity in the Prairie Pothole Region, United States. Landscape Ecology 31:805–824

VanRees-Siewert K, Dinsmore JJ (1996) Influence of Wetland Age on Bird Use of Restored Wetlands in Iowa. Wetlands 16:577–582

Verhagen R, Klooker J, Bakker JP, Diggelen R Van (2001) Restoration success of low-production plant communities on former agricultural soils after top-soil removal. Applied Vegetation Science 4:75–82

Verones F, Saner D, Pfister S, Baisero D, Rondinini C, Hellweg S (2013) Effects of consumptive water use on biodiversity in wetlands of international importance. Environmental Science and Technology 47:12248–12257

Vitousek PM, Aber JD, Howarth RW, Likens GE, Matson PA, Schindler DW, Schlesinger WH, Tilman DG (1997) Human alteration of the global nitrogen cycle: Sources and consequences. Ecological Applications 7:737–750

Vymazal J, Březinová TD (2018) Removal of nutrients, organics and suspended solids in vegetated agricultural drainage ditch. Ecological Engineering 118:97–103

Walker B (1995) Conserving Biological Diversity through Ecosystem Resilience. Conservation Biology 9:747–752

Walker BH (1992) Biodiversity and ecological redundancy. Conservation Biology 6:18–23

Wang Y, Naumann U, Eddelbuettel D, Wilshire J, Warton D (2019) mvabund: Statistical Methods for Analysing Multivariate Abundance Data. R package version 4.0.1

Wang Y, Naumann U, Wright ST, Warton DI (2012) mvabund - an R package for model-based analysis of multivariate abundance data. Methods in Ecology and Evolution 3:471–474

Ward MH, Jones RR, Brender JD, de Kok TM, Weyer PJ, Nolan BT, Villanueva CM, van Breda SG (2018) Drinking water nitrate and human health: An updated review. International Journal of Environmental Research and Public Health 15:1–31

Waters I, Shay JM (1990) A field study of the morphometric response of Typha glauca shoots to a water depth gradient . Canadian Journal of Botany 68:2339–2343

Weiher E, Wisheu IC, Keddy PA, Moore DRJ (1996) Establishment, persistence, and management implications of experimental wetland plant communities. Wetlands 16:208–218

Weisner SEB, Thiere G (2010) Effects of vegetation state on biodiversity and nitrogen retention in created wetlands: a test of the biodiversity-ecosystem functioning hypothesis. Freshwater Biology 55:387–396

Weller DE, Baker ME, Jordan TE (2011) Effects of riparian buffers on nitrate concentrations in watershed discharges: new models and management implications. Ecological applications 21:1679–1695

Werkmeister C, Jacob DL, Cihacek L, Otte ML (2018) Multi-Element Composition of Prairie Pothole Wetland Soils along Depth Profiles Reflects Past Disturbance to a Depth of at Least one Meter. Wetlands 38:1245–1258

Werner KJ, Zedler JB (2002) How sedge meadow soils, microtopography, and vegetation respond to sedimentation. Wetlands 22:451–466

Westbrook CJ, Brunet N, Phillips I, Davies J-M (2011) Wetland Drainage Effects on Prairie Water Quality: Final Report. Saskatoon

Wetzel PR, Van Der Valk AG (1998) Effects of nutrient and soil moisture on competition between Carex stricta, Phalaris arundinacea, and Typha latifolia. Plant Ecology 138:179–190

Wetzel RG (1990) Land-water interfaces: Metabolic and limnological regulators. Verh. Internat. Verein. Limnol. 24:6–24

Whigham DF, Jordan TE (2003) Isolated wetlands and water quality. Wetlands 23:541–549

Wiebner A, Kuschk P, Stottmeister U (2002) Oxygen release by roots of Typha latifolia and Juncus effusus in laboratory hydroponic systems. Acta Biotechnologica 22:209–216

Wiegner TN, Seitzinger SP (2004) Seasonal bioavailability of dissolved organic carbon and nitrogen from pristine and polluted freshwater wetlands. Limnology and Oceanography 49:1703–1712

Wienhold CE, van der Valk AG (1989) The impact of duration of drainage on the seed banks of northern prairie wetlands. Canadian Journal of Botany 67:1878–1884

Willis RM, Stewart RA, Giurco DP, Talebpour MR, Mousavinejad A (2013) End use water consumption in households: Impact of socio-demographic factors and efficient devices. Journal of Cleaner Production 60:107–115

Winikoff SG, Larkin DJ, Meier SL, Finlay JC (2020) Vegetation trajectories of restored agricultural wetlands following sediment removal. Restoration Ecology 1–11

Winsor RA (1987) Environmental imagery of the wet prairie of east central Illinois, 1820-1920. Journal of Historical Geography 13:375–397

Woo I, Zedler JB (2002) Can nutrients alone shift a sedge meadow towards dominance by the invasive Typha × glauca? Wetlands 22:509–521

Wooten HH, Jones LA (1955) Drainage of Fields: The History of Our Drainage Enterprises. In: The Yearbook of Agriculture - Water. 84th Congress, 1st Session, House Document No. 32, Washington D.C. pp. 478–491.

Wright CK, Wimberly MC (2013) Recent land use change in the Western Corn Belt threatens grasslands and wetlands. Proceedings of the National Academy of Sciences of the United States of America 110:4134–4139

Xie S, Qu J, Lai Y, Zhou Z, Xu X (2015) Effects of Freeze–thaw Cycles on Soil Mechanical and Physical Properties in the Qinghai–Tibet Plateau. Journal of Mountain Science 12:DOI: 10.1007/s1162 9-014-3384-7

Yannopoulos SI, Grismer ME, Bali KM, Angelakis AN (2020) Evolution of the materials and methods used for subsurface drainage of agricultural lands from antiquity to the present. Water (Switzerland) 12

Zapfe L, Freeland JR (2015) Heterosis in invasive F1 cattail hybrids (Typha × glauca). Aquatic Botany 125:44–47

Zarnetske JP, Haggerty R, Wondzell SM, Baker MA (2011) Dynamics of nitrate production and removal as a function of residence time in the hyporheic zone. Journal of Geophysical Research: Biogeosciences 116:doi:10.1029/2010JG001356

Zedler JB (2003) Wetlands at your service: Reducing impacts of agriculture at the watershed scale. Frontiers in Ecology and the Environment 1:65–72

Zedler JB, Kercher S (2004) Causes and consequences of invasive plants in wetlands: Opportunities, opportunists, and outcomes. Critical Reviews in Plant Sciences 23:431–452

Zurayk R, Nimah M, Geha Y, Rizk C (1997) Phosphorus retention in the soil matrix of constructed wetlands. Communications in Soil Science and Plant Analysis 28:521–535

Appendix 1

Table A1. 1. Wetland and watershed summary information.

	Wetland Characteristics						Watershed Characteristics					
Site ID	**Treatment**	**Hydroperiod**	**Restoration Year**	**Sediment Removed (in)**	**Area: Perimeter Ratio**	**Area (ha)**	**Area (ha)**	**Watershed: Wetland Ratio**	**Slope**	**Cultivation (% Cover)**	**Grassland (% Cover)**	**Upgradient Wetland (T/F)**
DL.001	EXC	Seasonal	2009	42	16.6	0.4	7.8	18.8	3.4	0.0	77.4	TRUE
DL.019	EXC	Seasonal	2011	48	6.9	0.1	0.3	4.5	1.9	0.0	77.0	FALSE
FF.001 [a]	BAU	Seasonal	2009	0	22.5	0.8	3.4	4.5	4.6	13.4	56.4	TRUE
FF.002 [a]	BAU	Seasonal	2009	0	19.4	0.5	2.9	5.4	3.9	0.0	63.8	FALSE
FF.003 [a]	BAU	Seasonal	2009	0	19.0	0.5	1.7	3.4	3.5	0.0	70.5	FALSE
FF.004 [a]	EXC	Seasonal	2009	12	14.3	0.3	1.5	5.5	4.1	30.8	50.7	FALSE
FF.007 [a]	BAU	Semipermanent	2009	0	22.4	0.7	2.9	3.9	3.9	0.0	74.4	FALSE
FF.008	EXC	Seasonal	2009	12	8.8	0.1	1.8	15.7	2.7	0.0	93.6	FALSE
FF.032 [*, a, b]	BAU	Seasonal	2010	0	15.5	1.0	7.6	8.0	2.9	1.4	53.4	TRUE
FF.033 [*, a, b]	BAU	Seasonal	2010	0	11.0	0.2	1.7	10.0	3.1	0.0	69.0	FALSE
FF.034 [*, a, b]	EXC	Seasonal	2010	6	10.8	0.2	8.3	46.4	3.6	1.8	43.6	TRUE
FF.038	BAU	Seasonal	2010	0	15.8	0.5	2.1	4.5	2.3	0.0	77.7	FALSE
FF.039	BAU	Seasonal	2010	0	19.3	0.5	1.5	3.1	1.8	0.0	61.7	FALSE
FF.042 [a, b]	EXC	Seasonal	2011	10	16.6	0.4	4.6	11.1	4.7	0.0	83.4	TRUE
FF.043 [a, b]	EXC	Seasonal	2011	6	11.0	0.2	2.8	17.1	4.6	0.0	87.7	TRUE
FF.045 [a, b]	BAU	Seasonal	2011	0	13.1	0.3	2.5	9.9	4.9	0.0	84.4	TRUE
FF.046	BAU	Semipermanent	2011	0	22.7	0.9	3.2	3.5	5.4	0.0	70.7	FALSE
FF.047 [a, b]	BAU	Semipermanent	2011	0	18.8	0.5	2.3	4.6	4.7	0.0	78.3	FALSE
FF.048 [a]	EXC	Seasonal	2011	6	9.8	0.1	1.0	6.9	3.5	0.0	85.6	FALSE
FF.049 [a]	BAU	Semipermanent	2011	0	28.6	1.4	78.8	55.9	3.7	74.3	7.8	TRUE
FF.051 [a]	EXC	Seasonal	2011	12	10.1	0.1	3.2	21.7	3.0	0.0	95.3	FALSE
FF.056 [a]	BAU	Seasonal	2012	0	15.3	0.4	2.1	5.9	3.3	0.0	74.3	FALSE
FF.057 [a]	EXC	Seasonal	2012	12	12.4	0.2	58.7	279.1	5.6	12.5	23.5	TRUE
FF.058 [a]	EXC	Seasonal	2012	6	9.7	0.1	60.2	479.8	5.6	12.2	25.1	TRUE
FF.059 [a]	EXC	Semipermanent	2012	18	19.9	0.6	2.2	3.9	6.4	0.0	64.6	FALSE
FF.062 [*, a]	BAU	Semipermanent	2012	0	18.7	0.8	9.1	10.8	14.7	0.0	37.5	TRUE

	Wetland Characteristics						***Watershed Characteristics***					
Site ID	**Treatment**	**Hydroperiod**	**Restoration Year**	**Sediment Removed (in)**	**Area: Perimeter Ratio**	**Area (ha)**	**Area (ha)**	**Watershed: Wetland Ratio**	**Slope**	**Cultivation (% Cover)**	**Grassland (% Cover)**	**Upgradient Wetland (T/F)**
FF.064 [a]	EXC	Semipermanent	2012	36	20.6	0.6	13.3	21.0	4.8	0.0	88.5	TRUE
FF.072 [a]	BAU	Semipermanent	2013	0	22.4	1.2	5.7	4.9	7.2	5.0	65.0	FALSE
FF.073 [a]	EXC	Semipermanent	2013	18	18.6	0.5	7.6	15.7	7.6	3.8	67.4	TRUE
FF.074 [a]	BAU	Seasonal	2013	0	26.5	1.4	10.0	7.2	2.1	0.7	75.9	TRUE
FF.075	BAU	Seasonal	2013	0	20.1	1.0	3.9	4.0	2.2	1.8	73.3	FALSE
FF.076	BAU	Seasonal	2013	0	24.4	1.0	8.1	7.9	1.6	0.0	77.2	TRUE
FF.077	BAU	Seasonal	2013	0	17.2	0.8	3.4	4.2	1.6	0.0	76.1	FALSE
FF.080 [a, b]	BAU	Semipermanent	2012	0	37.2	2.3	15.1	6.6	6.0	53.4	28.8	FALSE
FF.081 [a, b]	EXC	Seasonal	2012	10	16.4	0.5	4.7	9.1	4.9	39.9	43.5	FALSE
FF.083 [a]	EXC	Seasonal	2014	12	10.7	0.2	1.9	11.7	6.3	43.6	47.7	FALSE
FF.084 [a]	EXC	Seasonal	2014	12	11.1	0.2	1.5	7.1	10.7	27.0	58.8	FALSE
FF.085 [a, b]	EXC	Seasonal	2015	8	14.6	0.4	1.8	4.9	6.5	0.0	79.5	FALSE
FF.086 [a, b]	BAU	Semipermanent	2015	0	16.9	0.5	3.7	7.8	8.1	0.0	50.7	TRUE
FF.087 [a, b]	BAU	Semipermanent	2015	0	15.8	0.6	4.6	7.4	5.1	0.0	69.2	TRUE
MO.004 [a]	EXC	Seasonal	2009	8	15.0	0.4	2.8	6.8	4.6	27.8	53.9	FALSE
MO.005 [a]	BAU	Seasonal	2009	0	20.3	0.8	4.5	5.9	5.0	25.0	53.9	FALSE
MO.006 [a]	EXC	Semipermanent	2012	12	26.6	1.1	89.0	80.5	7.5	20.5	48.8	TRUE
MO.007 [a]	EXC	Semipermanent	2012	12	24.3	1.0	91.9	91.6	7.5	19.9	49.3	TRUE
MO.009	EXC	Seasonal	2010	18	13.9	0.3	4.5	16.5	2.6	42.2	48.7	TRUE
MO.010	BAU	Seasonal	2015	9	25.7	1.1	7.9	7.4	2.9	0.0	86.5	FALSE
MO.018 [a]	EXC	Seasonal	2015	12	10.0	0.2	3.2	15.3	8.9	0.0	91.5	FALSE
MO.019	BAU	Semipermanent	2016	0	9.2	0.2	22.4	122.8	9.4	40.6	48.3	TRUE
MO.020 [a]	BAU	Semipermanent	2015	0	18.4	0.6	8.9	14.2	11.6	0.0	38.5	FALSE
MO.021	EXC	Seasonal	2015	6	16.8	0.5	2.9	5.3	2.3	0.0	81.1	FALSE
SC.004	EXC	Seasonal	2012	12	10.0	0.2	5.2	33.5	2.8	0.0	87.5	TRUE
SC.005	EXC	Seasonal	2012	12	7.1	0.1	4.2	47.1	2.6	0.0	88.3	TRUE
SC.006	EXC	Seasonal	2012	8	15.5	0.4	5.0	13.8	2.8	47.0	39.9	FALSE
SC.012	EXC	Seasonal	2016	8	8.7	0.1	4.9	34.4	5.0	6.0	57.6	TRUE
AG.001	REF	Seasonal			14.9	0.3	1.9	5.7	2.2	82.4	0.0	FALSE
AG.003	REF	Seasonal			20.6	0.6	8.7	13.4	4.2	76.1	0.0	TRUE

	Wetland Characteristics						*Watershed Characteristics*					
Site ID	**Treatment**	**Hydroperiod**	**Restoration Year**	**Sediment Removed (in)**	**Area: Perimeter Ratio**	**Area (ha)**	**Area (ha)**	**Watershed: Wetland Ratio**	**Slope**	**Cultivation (% Cover)**	**Grassland (% Cover)**	**Upgradient Wetland (T/F)**
AG.004	REF	Semipermanent			27.4	1.0	3.8	3.7	4.0	73.1	0.0	FALSE
AG.005	REF	Seasonal			25.0	1.2	17.4	15.0	7.0	90.2	0.0	FALSE
AG.006	REF	Seasonal			26.3	1.0	5.0	5.2	5.1	74.8	0.0	FALSE
AG.007	REF	Seasonal			16.2	0.4	5.5	13.3	6.1	63.8	25.7	FALSE
AG.008	REF	Semipermanent			31.2	1.4	5.7	4.1	4.3	4.7	71.0	FALSE
LC.001	REF	Semipermanent			34.8	1.6	4.6	2.8	7.4	0.0	55.1	FALSE
LC.002	REF	Semipermanent			44.1	5.1	23.6	4.6	6.4	0.0	50.4	FALSE

* Past land use included animal confinement or pasture.

[a] Denitrification Potential Assays (Chapter 4)

[b] Seasonal Denitrification Potential Assays (Chapter 4)

Appendix 2

Table A2. 1. Statistical significance from ANCOVA for plant community summary metrics. Treatment describes the difference between excavated (EXC) and business as usual (BAU) wetlands. Wetland age describes the effect of time since restoration.

	Treatment	***Wetland Age***	***Treatment * Wetland Age***	***Quadratic Term***
Richness				
Invasive	0.50	0.21	0.57	---
Native	0.28	0.036 *	0.44	---
Percent Cover				
Invasive	0.011 *	0.0020 **	0.14	---
Native	0.87	0.27	0.050 *	---
Cattail, Reed Canary Grass	0.0080 **	0.011 *	0.26	0.031 *
Other Invasives	0.60	0.81	0.15	---
Biomass				
Invasive	0.099	0.0036 **	0.87	---
Native	0.77	0.30	0.044 *	---
Cattail, Reed Canary Grass	0.10	0.0055 **	0.88	---
Other Invasives	0.86	0.12	0.99	---
Diversity				
Overall	0.028 *	0.085	0.42	---
Without Cattail and Reed Canary Grass	0.064 ·	0.72	0.54	
Evenness				
Overall	0.022 *	0.34	0.56	---
Without Cattail and Reed Canary Grass	0.11	0.33	0.82	
Invasion Prevalence Ratio				
Invasive Species Cover : Total Vegetation Cover	0.12	0.017 *	0.040 *	---

****** Significant *P*-values ≤ 0.01

***** Significant *P*-values ≤ 0.05

· Marginally significant *P*-values

Table A2. 2. Uncommon species detected exclusively at BAU or EXC sites. Species listed occurred at more than one and less than eight wetlands. Wetland indicator status is based on classifications by the Minnesota Pollution Control Agency, Floristic Quality Index (2014).

Scientific Name	***Common Name***	***Invasion Status***	***Life Cycle***	***Wetland Indicator Status***	***No. Wetlands***
BAU Sites					
Carex utriculata	Beaked Sedge	Native	Perennial	OBL	2
Linaria vulgaris	Butter and Eggs	Invasive	Perennial	---	2
Lotus corniculatus	Bird’s foot trefoil	Invasive	Perennial	FAC-	2
Helianthus tuberosus	Jerusalem artichoke	Native	Perennial	FAC	3
EXC Sites					
Carex atherodes	Slough Sedge	Native	Perennial	OBL	2
Chenopodium album	Lamb's quarters	Invasive	Annual	FAC-	2
Conyza canadensis	Canadian horseweed	Native	Annual, Biennial	FAC-	2
Erigeron strigosus	Prairie fleabane	Native	Annual, Biennial	FAC-	2
Leersia oryzoides	Rice cutgrass	Native	Perennial	OBL	2
Persicaria lapathifolia	Nodding smartweed	Native	Annual	FACW+	2
Ranunculus recurvatus	Hooked Buttercup	Native	Perennial	FACW	2
Rorippa palustris	Bog yellow-cress	Native	Annual, Biennial	OBL	2
Salix eriocephala	Diamond willow	Native	Perennial	FACW	2
Viola canadensis	Canadian white violet	Native	Perennial	FACU	2
Pycnanthemum virginianum	Virginia mountain mint	Native	Perennial	FACW+	3
Sparganium eurycarpum	Giant bur-reed	Native	Perennial	OBL	4

Table A2. 3. Summary of SIMPER results for species contribution to overall difference between treatments (BAU and EXC). Treatments where the species was most dominant is listed. Wetland indicator status is based on classifications by the Minnesota Pollution Control Agency, Floristic Quality Index (2014).

Restoration Treatment	***Scientific Name***	***Common Name***	***Invasion Status***	***Life Cycle***	***Indicator Status***	***Contribution (%)***
BAU	*Typha x glauca*	Hybrid Cattail	Invasive	Perennial	OBL	12.81
BAU	*Lemna minor*	Common Duckweed	Native	Perennial	OBL	8.39
BAU	*Phalaris arundinacea*	Reed Canary Grass	Invasive	Perennial	FACW+	6.79
EXC	*Utricularia vulgaris*	Common Bladderwort	Native	Perennial	OBL	4.28
BAU	*Sphagnum spp.*	Sphagnum Moss Species	Native	Perennial	---	3.61
BAU	*Bolboschoenus fluviatilis*	River Bulrush	Native	Perennial	OBL	2.80
BAU	*Ceratophyllum demersum*	Coontail, Hornwort	Native	Perennial	OBL	1.97
EXC	*Salix exigua*	Sandbar Willow	Native	Perennial	OBL	1.89
BAU	*Carex stricta*	Tussock Sedge	Native	Perennial	OBL	1.83
EXC	*Stuckenia pectinata*	Sago Pondweed	Native	Perennial	OBL	1.81
EXC	*Potamogeton zosteriformis*	Flatstem Pondweed	Native	Perennial	OBL	1.79
EXC	*Salix amygdaloides*	Peach-leaf Willow	Native	Perennial	FACW+	1.77
EXC	*Scirpus atrovirens*	Green Bulrush	Native	Perennial	OBL	1.70
EXC	*Alisma triviale*	Northern Water Plantain	Native	Perennial	OBL	1.60
BAU	*Melilotus alba, M. officinalis*	Sweet Clover	Invasive	Annual, Biennial	FACU	1.48
EXC	*Scirpus cyperinus*	Woolgrass	Native	Perennial	OBL	1.45
EXC	*Schoenoplectus tabernaemontani*	Softstem Bulrush	Native	Perennial	OBL	1.42
EXC	*Equisetum arvense*	Field Horsetail	Native	Perennial	FAC	1.41
EXC	*Solidago gigantea*	Smooth Goldenrod	Native	Perennial	FACW	1.33
EXC	*Eleocharis spp.*	Spikerush	Native	Annual, Perennial	FACW	1.23
EXC	*Juncus tenuis*	Path Rush	Native	Perennial	FAC	1.12
EXC	*Leersia oryzoides*	Rice cutgrass	Native	Perennial	OBL	1.09
BAU	*Spartina pectinata*	Prairie Cordgrass	Native	Perennial	FACW+	1.08
BAU	*Persicaria amphibia*	Water Smartweed	Native	Perennial	OBL	1.04
BAU	*Echinochloa crus-galli*	Barnyard Grass	Invasive	Annual	FACW	1.03
BAU	*Glyceria grandis*	American Manna Grass	Native	Perennial	OBL	1.03
BAU	*Poa pratensis*	Kentucky Bluegrass	Invasive	Perennial	FAC-	0.95
EXC	*Persicaria maculosa*	Lady's Thumb	Invasive	Annual, Perennial	FACW	0.93
BAU	*Symphyotrichum puniceum*	Redstem Aster	Native	Perennial	OBL	0.88

Table A2. 4. Summary of SIMPER results for species specific contribution to overall difference between wetland age groups. Wetland ages where individual species were most dominant are listed. Wetland indicator status is based on classifications by the Minnesota Pollution Control Agency, Floristic Quality Index (2014).

Dominant Age Group	***Scientific Name***	***Common Name***	***Invasion Status***	***Life Cycle***	***Wetland Indicator Status***	***Contribution (%)***
9 Years vs. 3-4 Years						
9 Years	*Typha x glauca*	Hybrid Cattail	Invasive	Perennial	OBL	13.48
9 Years	*Lemna minor*	Common Duckweed	Native	Perennial	OBL	8.44
9 Years	*Phalaris arundinacea*	Reed Canary Grass	Invasive	Perennial	FACW+	5.68
9 Years	*Bolboschoenus fluviatilis*	River Bulrush	Native	Perennial	OBL	5.47
3-4 Years	*Carex stricta*	Tussock Sedge	Native	Perennial	OBL	4.37
3-4 Years	*Scirpus cyperinus*	Woolgrass	Native	Perennial	OBL	3.29
3-4 Years	*Stuckenia pectinata*	Sago Pondweed	Native	Perennial	OBL	3.01
3-4 Years	*Schoenoplectus tabernaemontani*	Softstem Bulrush	Native	Perennial	OBL	2.64
3-4 Years	*Alisma triviale*	Northern Water Plantain	Native	Perennial	OBL	2.31
9 Years	*Salix exigua*	Sandbar Willow	Native	Perennial	OBL	2.28
3-4 Years	*Echinochloa crus-galli*	Barnyard Grass	Invasive	Annual	FACW	2.23
3-4 Years	*Leersia oryzoides*	Rice cutgrass	Native	Perennial	OBL	2.23
9 Years	*Salix lucida*	Shining Willow	Native	Perennial	FACW+	2.06
3-4 Years	*Utricularia vulgaris*	Common Bladderwort	Native	Perennial	OBL	2.02
9 Years vs. 5-6 Years						
9 Years	*Lemna minor*	Common Duckweed	Native	Perennial	OBL	11.57
5-6 Years	*Typha x glauca*	Hybrid Cattail	Invasive	Perennial	OBL	9.41
9 Years	*Phalaris arundinacea*	Reed Canary Grass	Invasive	Perennial	FACW+	9.28
9 Years	*Bolboschoenus fluviatilis*	River Bulrush	Native	Perennial	OBL	6.01
5-6 Years	*Utricularia vulgaris*	Common Bladderwort	Native	Perennial	OBL	5.31
9 Years	*Salix exigua*	Sandbar Willow	Native	Perennial	OBL	2.90
9 Years	*Salix lucida*	Shining Willow	Native	Perennial	FACW+	2.56
5-6 Years	*Sphagnum spp.*	Sphagnum Mosses	Native	Perennial	---	2.17
5-6 Years	*Salix amygdaloides*	Peach-leaf Willow	Native	Perennial	FACW+	2.16
9 Years	*Solidago gigantea*	Smooth Goldenrod	Native	Perennial	FACW	2.11
5-6 Years	*Potamogeton zosteriformis*	Flatstem Pondweed	Native	Perennial	OBL	2.06
5-6 Years	*Scirpus atrovirens*	Green Bulrush	Native	Perennial	OBL	2.00
5-6 Years	*Melilotus alba, M. officinalis*	Sweet Clover	Invasive	Annual, Biennial	FACU	1.68
9 Years	*Equisetum arvense*	Field Horsetail	Native	Perennial	FAC	1.63
9 Years vs. 7-8 Years						
9 Years	*Lemna minor*	Common Duckweed	Native	Perennial	OBL	10.33
7-8 Years	*Typha x glauca*	Hybrid Cattail	Invasive	Perennial	OBL	9.92
9 Years	*Phalaris arundinacea*	Reed Canary Grass	Invasive	Perennial	FACW+	7.33
7-8 Years	*Sphagnum spp.*	Sphagnum Mosses	Native	Perennial	---	5.38
9 Years	*Bolboschoenus fluviatilis*	River Bulrush	Native	Perennial	OBL	5.30
9 Years	*Salix exigua*	Sandbar Willow	Native	Perennial	OBL	2.91
9 Years	*Salix lucida*	Shining Willow	Native	Perennial	FACW+	2.55
9 Years	*Salix amygdaloides*	Peach-leaf Willow	Native	Perennial	FACW+	2.16
9 Years	*Solidago gigantea*	Smooth Goldenrod	Native	Perennial	FACW	2.11
7-8 Years	*Ceratophyllum demersum*	Coontail, Hornwort	Native	Perennial	OBL	1.85
7-8 Years	*Glyceria grandis*	American Manna Grass	Native	Perennial	OBL	1.77
7-8 Years	*Poa pratensis*	Kentucky Bluegrass	Invasive	Perennial	FAC-	1.75
7-8 Years	*Spartina pectinata*	Prairie Cordgrass	Native	Perennial	FACW+	1.72
7-8 Years	*Alisma triviale*	Northern Water Plantain	Native	Perennial	OBL	1.52

Dominant Age Group	***Scientific Name***	***Common Name***	***Invasion Status***	***Life Cycle***	***Wetland Indicator Status***	***Contribution (%)***
			7-8 Years vs. 3-4 Years			
7-8 Years	*Typha x glauca*	Hybrid Cattail	Invasive	Perennial	OBL	19.46
3-4 Years	*Carex stricta*	Tussock Sedge	Native	Perennial	OBL	4.58
7-8 Years	*Sphagnum spp.*	Sphagnum Moss Species	Native	Perennial	---	4.53
3-4 Years	*Phalaris arundinacea*	Reed Canary Grass	Invasive	Perennial	FACW+	3.69
3-4 Years	*Scirpus cyperinus*	Woolgrass	Native	Perennial	OBL	3.22
3-4 Years	*Stuckenia pectinata*	Sago Pondweed	Native	Perennial	OBL	3.15
7-8 Years	*Lemna minor*	Common Duckweed	Native	Perennial	OBL	2.96
3-4 Years	*Schoenoplectus tabernaemontani*	Softstem Bulrush	Native	Perennial	OBL	2.57
3-4 Years	*Leersia oryzoides*	Rice cutgrass	Native	Perennial	OBL	2.34
3-4 Years	*Echinochloa crus-galli*	Barnyard Grass	Invasive	Annual	FACW	2.33
3-4 Years	*Utricularia vulgaris*	Common Bladderwort	Native	Perennial	OBL	2.3
3-4 Years	*Alisma triviale*	Northern Water Plantain	Native	Perennial	OBL	2.13
3-4 Years	*Eleocharis spp.*	Spikerush	Native	Annual, Perennial	FACW	2.05
7-8 Years	*Ceratophyllum demersum*	Coontail, Hornwort	Native	Perennial	OBL	2
			7-8 Years vs. 5-6 Years			
7-8 Years	*Typha x glauca*	Hybrid Cattail	Invasive	Perennial	OBL	12.45
5-6 Years	*Lemna minor*	Common Duckweed	Native	Perennial	OBL	6.63
5-6 Years	*Phalaris arundinacea*	Reed Canary Grass	Invasive	Perennial	FACW+	5.91
7-8 Years	*Sphagnum spp.*	Sphagnum Moss Species	Native	Perennial	---	5.81
5-6 Years	*Utricularia vulgaris*	Common Bladderwort	Native	Perennial	OBL	5.48
7-8 Years	*Ceratophyllum demersum*	Coontail, Hornwort	Native	Perennial	OBL	2.57
5-6 Years	*Scirpus atrovirens*	Green Bulrush	Native	Perennial	OBL	2.21
5-6 Years	*Salix amygdaloides*	Peach-leaf Willow	Native	Perennial	FACW+	2.22
5-6 Years	*Potamogeton zosteriformis*	Flatstem Pondweed	Native	Perennial	OBL	2.13
7-8 Years	*Bolboschoenus fluviatilis*	River Bulrush	Native	Perennial	OBL	1.95
5-6 Years	*Melilotus alba, M. officinalis*	Sweet Clover	Invasive	Annual, Biennial	FACU	1.91
7-8 Years	*Glyceria grandis*	American Manna Grass	Native	Perennial	OBL	1.85
7-8 Years	*Poa pratensis*	Kentucky Bluegrass	Invasive	Perennial	FAC-	1.83
7-8 Years	*Spartina pectinata*	Prairie Cordgrass	Native	Perennial	FACW+	1.76
			5-6 Years vs. 3-4 Years			
5-6 Years	*Typha x glauca*	Hybrid Cattail	Invasive	Perennial	OBL	14.91
3-4 Years	*Phalaris arundinacea*	Reed Canary Grass	Invasive	Perennial	FACW+	6.36
5-6 Years	*Utricularia vulgaris*	Common Bladderwort	Native	Perennial	OBL	4.8
5-6 Years	*Lemna minor*	Common Duckweed	Native	Perennial	OBL	4.68
3-4 Years	*Carex stricta*	Tussock Sedge	Native	Perennial	OBL	4.66
3-4 Years	*Scirpus cyperinus*	Woolgrass	Native	Perennial	OBL	3.34
3-4 Years	*Stuckenia pectinata*	Sago Pondweed	Native	Perennial	OBL	3.22
3-4 Years	*Schoenoplectus tabernaemontani*	Softstem Bulrush	Native	Perennial	OBL	2.78
3-4 Years	*Leersia oryzoides*	Rice cutgrass	Native	Perennial	OBL	2.49
3-4 Years	*Alisma triviale*	Northern Water Plantain	Native	Perennial	OBL	2.36
3-4 Years	*Echinochloa crus-galli*	Barnyard Grass	Invasive	Annual	FACW	2.32
3-4 Years	*Eleocharis spp.*	Spikerush	Native	Annual, Perennial	FACW	2.18
5-6 Years	*Sphagnum spp.*	Sphagnum Moss Species	Native	Perennial	---	1.89
5-6 Years	*Potamogeton zosteriformis*	Flatstem Pondweed	Native	Perennial	OBL	1.86

Table A2. 5. Individual species influenced by treatment (BAU and EXC) and wetland age. Univariate coefficient estimates and P-values are listed for species with significant and marginally significant results. Treatment coefficients represent deviation from the mean (BAU) by the treatment (EXC). Wetland indicator status is based on classifications by the Minnesota Pollution Control Agency, Floristic Quality Index (2014).

Scientific Name	***Common Name***	***Invasion Status***	***Life Cycle***	***Wetland Indicator Status***	***Coefficients***		***P-values***	
					Treatment	**Age**	**Treatment**	**Age**
Bolboschoenus fluviatilis	River Bulrush	Native	Perennial	OBL	- 0.20	0.10	0.23	0.046 *
Echinochloa crus-galli	Barnyard Grass	Invasive	Annual	FACW	- 0.043	- 0.061	0.74	0.027 *
Elymus repens	Quackgrass	Invasive	Perennial	FACU	- 0.11	0.11	0.47	0.011 *
Lemna minor	Common Duckweed	Native	Perennial	OBL	- 0.88	0.080	0.006 **	0.29
Panicum virgatum	Switchgrass	Native	Perennial	FAC+	- 0.28	- 0.097	0.054 ·	0.012 *
Schoenoplectus tabernaemontani	Softstem Bulrush	Native	Perennial	OBL	0.44	- 0.16	0.050 *	0.014 *
Solidago gigantea	Smooth Goldenrod	Native	Perennial	FACW	- 0.045	0.079	0.77	0.020 *
Spartina pectinata	Prairie Cordgrass	Native	Perennial	FACW+	- 0.093	- 0.073	0.55	0.057 ·
Symphyotrichum ericoides	White Heath Aster	Native	Perennial	FAC-	0.0014	0.068	0.94	0.030 *
Typha x glauca	Hybrid Cattail	Invasive	Perennial	OBL	- 0.23	0.12	0.18	0.018 *
Verbena hastata	Blue Vervain	Native	Biennial, Perennial	FACW	- 0.30	0.067	0.029 *	0.061 ·

****** Significant *P*-values < 0.01

***** Significant *P*-values < 0.05

· Marginally significant *P*-values

Appendix 3

Supplementary Methods: Identifying Land Cover in Study Watersheds

To better understand whether landscape may have influenced restoration strategy or basin hydroperiod, we estimated land use and land cover in the contributing watersheds of each basin. We delineated watersheds in ArcGIS using the NRCS Engineering Toolbox, which was suited to low-gradient systems with abundant subsurface drainage. Accurate watershed delineation required both high resolution (3 m) LiDAR elevation data and detailed culvert maps showing connectivity between ditches, stream networks, and flow paths. Elevation data was accessed through the Minnesota Geospatial Data Commons. Whenever possible we used a detailed culvert data layer provided by the Bois de Sioux Watershed District. When detailed maps of subsurface connectivity were not available, we mapped known culverts using coordinate data collected in the field.

We extracted watershed-level land cover data from the National Land Cover Database data layer (NLCD 2016) and manually edited coverages to match aerial imagery. For ease of interpretation, we combined all NLCD cover classes identified in some way as Developed into a single “Developed” group. We called the sum of Developed and Cultivated land cover “Impacted”. Since the Pasture/Hay cover class has perennial vegetative cover and the Grassland/Herbaceous cover class was often misclassified as Pasture/Hay, we considered both cover types to be “Grassland”. Finally, we grouped Deciduous, Evergreen, and Mixed Forest cover classes into a single “Forest” metric, and we called the sum of Grassland and Forest land cover, “Natural”. Differences in land cover between basins with different restoration strategies, hydroperiods, and ages were assessed using analysis of covariance, performed in R (R Core Team 2020).

Soil Hydroperiod-by-Wetland Age Interaction

Table A3. 1. Analysis of covariance statistical results for Hydroperiod by Wetland Age interactions. Significant P-values in bold font. Hydroperiod indicates whether semipermanently flooded basins differ significantly from seasonally flooded wetlands. Wetland age depicts the effect of time since restoration. Interactions between Hydroperiod and Wetland Age are listed to the right.

	Main Effects		***Interaction Term***	
	Hydroperiod	**Wetland Age**	**Hydroperiod *X* Wetland Age**	**Model Fit (R^2)**
Bulk Density (kg/m^3)	**0.039 ***	**0.02 ***	0.19	0.10
Organic Matter (kg/m^2)	**0.024 ***	0.092	**0.049 ***	0.05
† Organic Carbon (kg/m^2)	0.10	0.25	0.25	0.01
† Total Nitrogen (kg/m^2)	***0.060 ·***	**0.037 ***	0.19	0.06
† Bioavailable P (g/m^2)	0.21	0.58	0.44	0.24
† Total P (g/m^2)	0.17	0.94	0.39	0.00
† CaCO3 (kg/m^2)	0.50	0.20	0.78	0.00
† Ca (kg/m^2)	0.51	0.52	0.72	0.00
Fe (kg/m^2)	0.90	0.94	0.62	0.00
	Molar Ratios			
$C_{organic}$: N_{total}	0.53	**0.013 ***	0.71	0.08
† N_{total}: $P_{bioavailable}$	**0.037 ***	0.74	0.81	0.31
† N_{total} : P_{total}	**0.0059 ****	0.069	0.063	0.12
$C_{organic}$: $P_{bioavailable}$	***0.060 ·***	0.94	0.77	0.28
$C_{organic}$: P_{total}	**0.020 ***	0.35	0.12	0.07
† $P_{bioavailable}$: Ca	0.19	0.84	0.86	0.12
† P_{total} : Ca	0.18	0.42	0.44	0.00
$P_{bioavailable}$: Fe	0.25	0.62	0.61	0.16
P_{total} : Fe	0.36	0.77	0.26	0.00

† Log transformed

· Marginal Significance

* Significant at $P \leq 0.05$

** Significant at $P \leq 0.01$

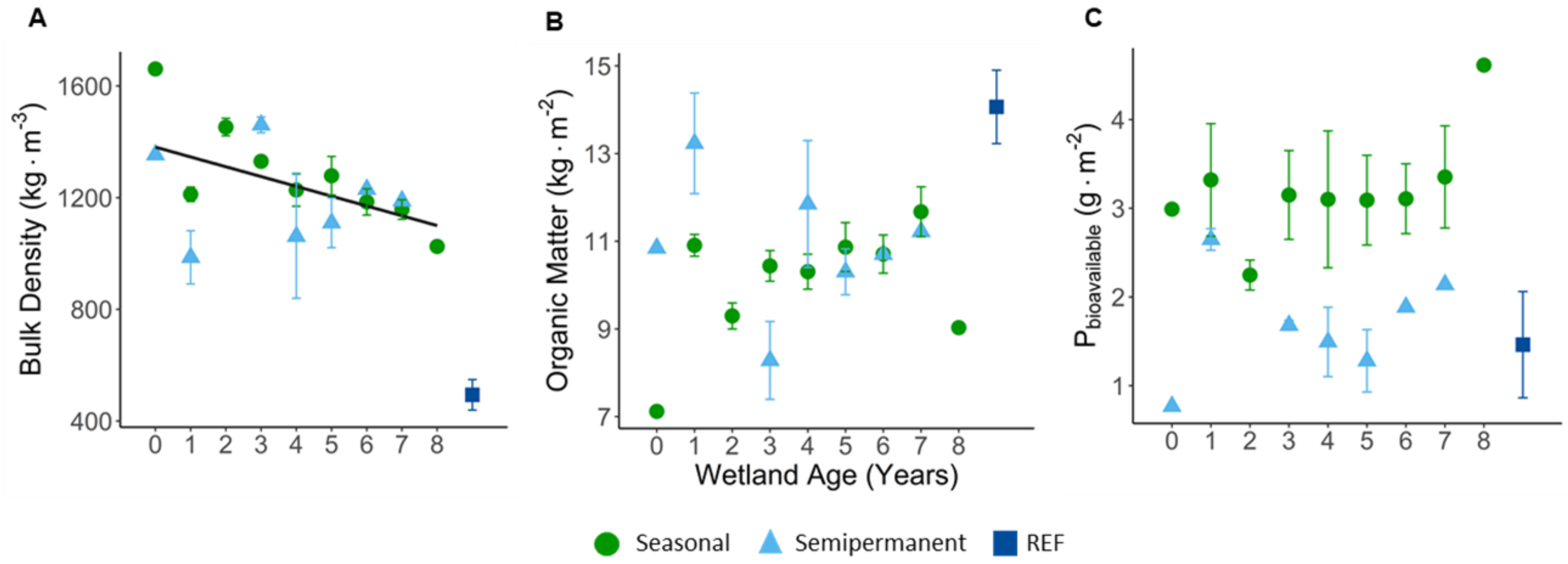

Figure A3. 1**.** Bulk density (A), organic matter (B), and bioavailable phosphorus (C) over time in the top layer (0 - 5 cm) of the soil profile in seasonally flooded (circles) and semipermanently (triangles) flooded wetlands, with reference basins (squares) to the far right. Significant effects of wetland age since restoration are shown with trend lines.

Appendix 4

Supplementary Methods: Post Hoc Analyses

To assess whether water column depth influenced TDP and SRP concentrations, we formed a mixed effects model with water column depth as a fixed effect and site as a random effect. We included mean dissolved nutrient response from all dates that we visited the wetlands in the final dataset. We did not include hydroperiod as a fixed effect because hydroperiod and water column depth and hydroperiod are strongly correlated with one another.

To examine the effect of invasive emergent macrophyte cover on TDP and SRP concentrations, we developed a mixed effects model with site as a random effect. The summed cover of *Typha* x *glauca* (hybrid cattail), *Phragmites australis* (common reed), and *Phalaris arundinacea* (reed canary grass) during the summer of 2018 accounted for the primary fixed effect (Winikoff et al. 2020). However, we were also interested in the interaction between hydroperiod and emergent macrophyte cover on dissolved P concentrations since hydroperiod could moderate the influence of vegetative cover. Our dataset only included observations from the 2018 growing season since vegetative cover can show remarkable variability from year to year (Winikoff et al. 2020). All analyses were performed in R statistical software (R Core Team 2020) with the `lme4` package (Bates et al. 2020).

Literature Cited

Bates D, Maechler M, Bolker B, et al (2020) Package “lme4”: Linear Mixed-Effects Models using “Eigen” and S4. R package version 3.2.0 120.

R Core Team (2020) R: A language and environment for statistical computing. In: R Foundation for Statistical Computing, Vienna, Austria. https://www.r-project.org/.

Winikoff SG, Larkin DJ, Meier SL, Finlay JC (2020) Vegetation trajectories of restored agricultural wetlands following sediment removal. Restoration Ecology 1–11. doi: 10.1111/rec.13128

Table A4. 1. Statistical results of TDP and SRP in response to wetland depth, emergent invasive macrophyte cover, and the interaction between vegetation and hydroperiod.

	Fixed Effects				
	Depth (cm)	**Vegetation**	**Vegetation *X* Hydroperiod**	**R^2** (Fixed Effects)	**R^2** (Full Model)
†SRP (µg/L)	**0.038 *** (-)	- - -	- - -	0.003	0.66
†TDP (µg/L)	**0.009 **** (-)	- - -	- - -	0.01	0.67
†SRP (µg/L)	- - -	**< 0.001 **** (+)	**< 0.001 **** (-)	0.50	0.76
†TDP (µg/L)	- - -	**< 0.001 **** (+)	**< 0.001 **** (-)	0.58	0.89
†SRP (µg/L)	- - -	**0.012 *** (+)	- - -	0.24	0.90
†TDP (µg/L)	- - -	**0.016 *** (+)	- - -	0.23	0.93

† Log transformed   * Significant at $P \leq 0.05$
· Marginal Significance   ** Significant at $P \leq 0.01$

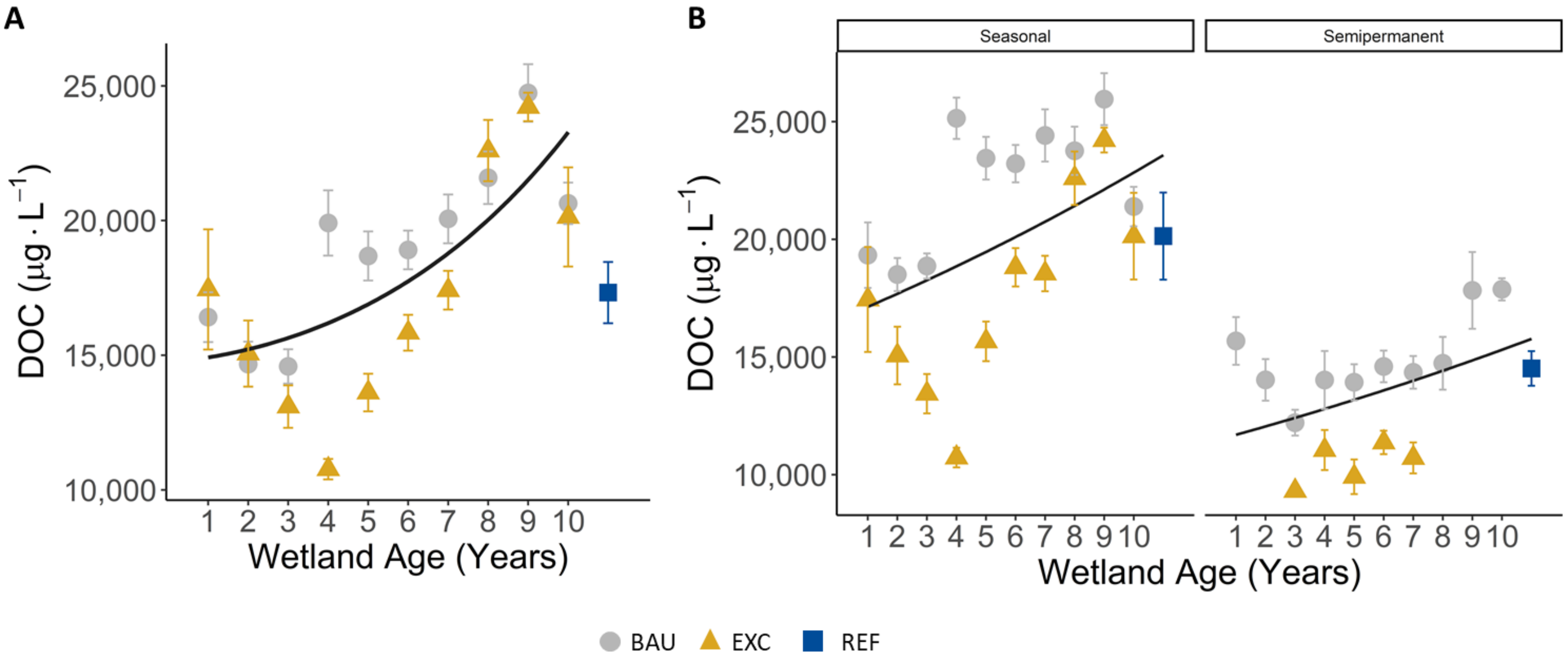

Figure A4. 1**.** Dissolved organic carbon over time in restored (BAU, Business as Usual; EXC, Excavated) and reference (REF) basins. Overall temporal trends (A) and trends in seasonal and semipermanent wetlands (B) across wetlands aged one to ten years post-restoration. Trend lines show statistically significant relationships across time. As wetlands aged DOC concentrations increased slowly at first and then more rapidly (A). The increase in DOC concentration occurred at a slower rate in semipermanent compared to seasonal wetlands (B).

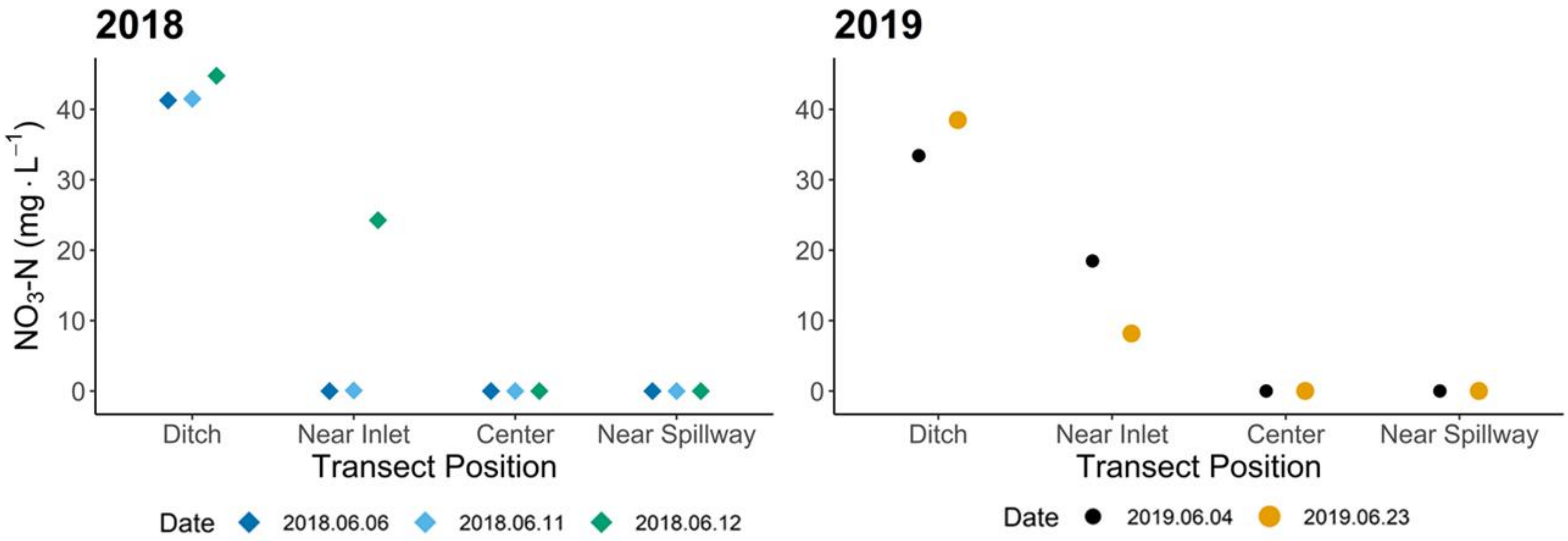

Figure A4. 2**.** Longitudinal transects of June nitrate concentration in a wetland receiving water from a drainage ditch servicing an adjacent agricultural field. The site identified as FF.080 consistently had water with nitrate concentrations three to four times the legal limit entering the wetland from the drainage ditch (Ditch) which passed under a road via a culvert. Nitrate concentrations at our sampling points within the emergent and submerged macrophyte zones of the wetland (Near Inlet, Center, Near Spillway) followed a longitudinal transect and showed significant N removal as water moved through the basin. All transects were assumed to be at steady state but sampling on June 11 and 12, 2018 followed a rainfall event.

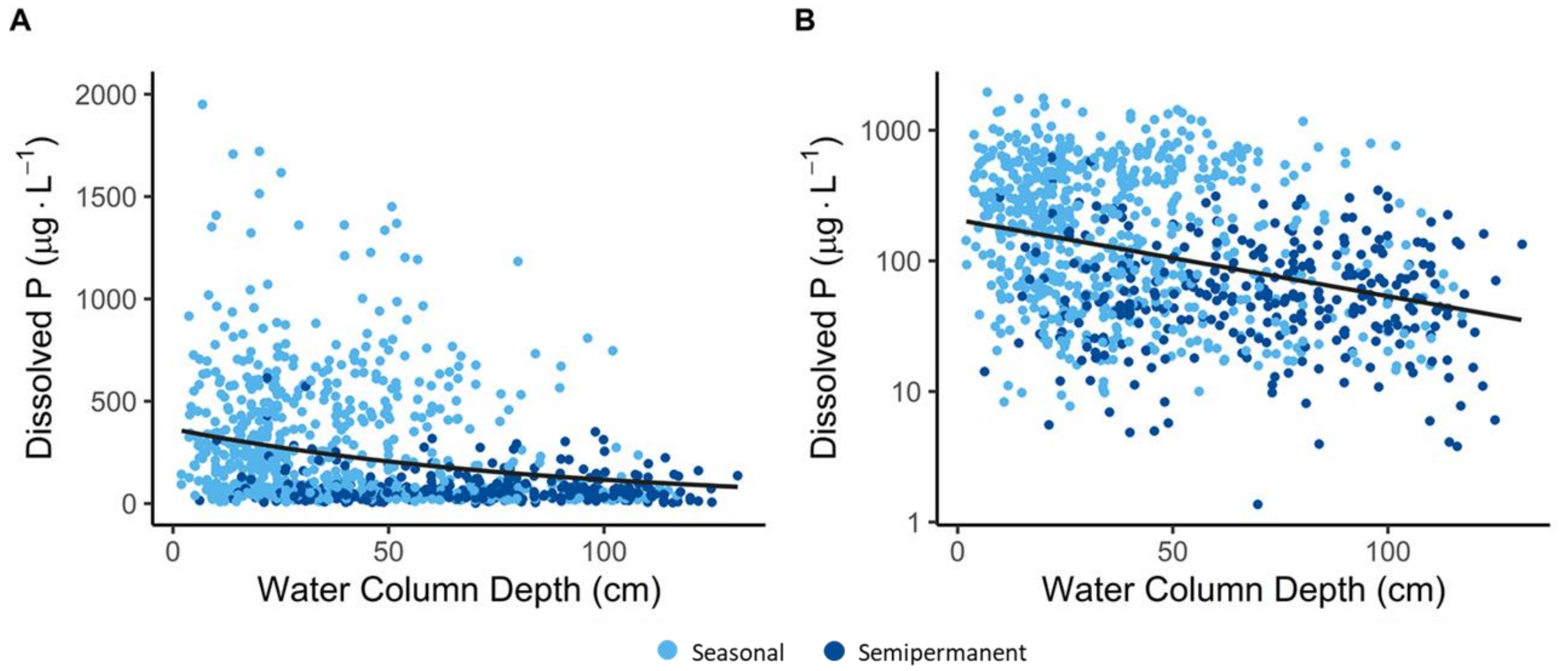

Figure A4. 3**.** Dissolved P in response to water column depth in seasonal and semipermanent wetlands in the normal scale with best fit line log-transformed (A) and the log-normal scale with untransformed line of best fit (B). There was a significant negative relationship between water column depth and dissolved P (log transformed to meet model assumptions).

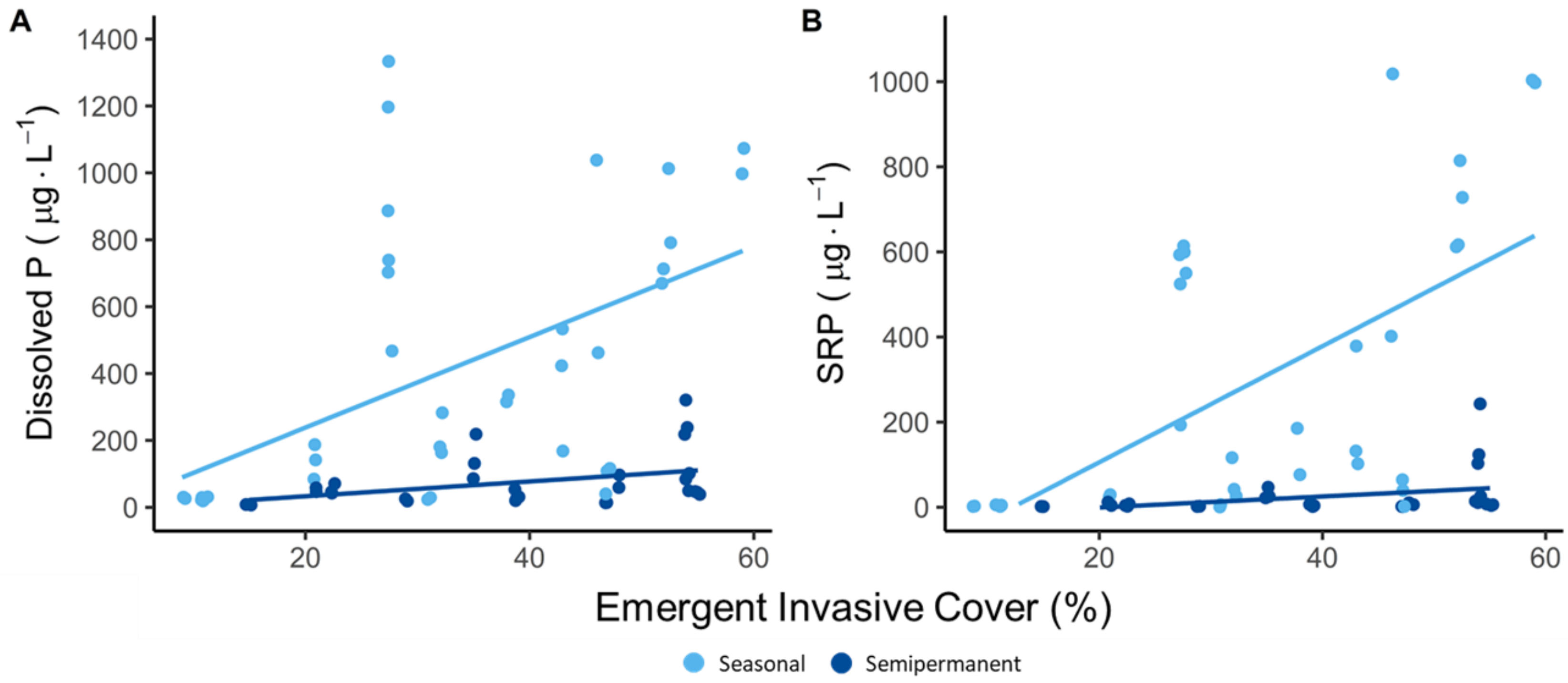

Figure A4. 4. Dissolved P (A) and SRP (B) in response to emergent invasive macrophyte cover in seasonal and semipermanent wetlands. Solid lines indicate a statistically significant relationship between P and cover by hydroperiod. There was a strong positive relationship between water column P concentrations and macrophyte cover in wetlands with seasonal hydroperiod, and there was a weak positive relationship in semipermanent basins.