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Effects of grazer exclusion on carbon cycling in created freshwater wetlands

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RIT

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By:

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List of Tables and Figures

Abstract

Wetland ecosystems play a significant role in the global carbon cycle, and yet are increasingly threatened by human development, climate change, and shifts in populations of large grazers. The loss of intact wetland systems heightens the need for effective wetland creation and restoration. However, wetland ecosystems are highly complex, complicating efforts to replace the functionality and delivery of ecosystem services associated with natural wetlands. Increasing waterfowl populations pose a threat to the development and persistence of created wetlands, largely through intensive grazing that can shift vegetation community structure or altogether limit desired plant establishment. This study capitalizes on a long-term herbivore exclusion experiment to evaluate how herbivore management impacts carbon storage in two created wetlands in Western New York State, USA. Changes in plant communities, above- and belowground biomass, soil carbon, and decomposition rates were evaluated in plots with and without the influence of grazers. Grazing reduced vegetation cover by approximately 34% in the height of the growing season, and led to similar reductions in aboveground biomass in a permanently flooded wetland, but had minor impacts in a seasonally flooded wetland. In the permanently flooded wetland, where we also measured fluxes of carbon dioxide and methane, this shift in vegetation resulted in reduced carbon uptake through primary productivity and a 27% reduction in soil carbon. During the summer, carbon fixation in grazer exclusion plots was 49% higher than in control plots, but methane emissions was also 62% higher. Our results suggest that grazers play an important role in vegetation dynamics in created wetlands and as a result shift carbon storage and greenhouse gas production.

Introduction

Freshwater wetlands are among the most ecologically and economically valuable ecosystems in the world due to their ability to provide ecosystem services such as habitat for migratory waterfowl (Zedler and Kercher, 2005), nutrient cycling (Aerts et al., 1999; DeAngelis et al., 2010), and carbon storage (Costanza et al., 1997; Chmura et al., 2003; Kayranli et al., 2010). Carbon storage is a vital service provided by wetlands, with an estimated 830 Tg yr^{-1} sequestered globally (DeDeyn et al., 2008; Kayranli et al., 2010). Urban and agricultural development is threatening wetlands, resulting in the need for creation and restoration of wetlands. However, created wetlands tend to have lower species diversity and unstable hydrological regimes (e.g. Confer and Niering, 1992; Shafer and Steever, 2000; Campbell et al., 2002), resulting in a lack of functionality relative to their natural counterparts.

Wetland ecosystems are driven by complex interactions between biotic and abiotic factors—including hydrology, nutrient cycling, competition, and grazing—which influence ecosystem structure and function. Recreating these functions are a key challenge to restoration efforts (e.g. Campbell et al., 2002; Fennessy et al., 2008). Notably lost is the potential for carbon storage and sequestration, where created and restored wetlands lack the vegetation communities and soil properties to efficiently cycle carbon (Kayranli et al., 2009). Further, intensive grazing on newly planted vegetation communities can exacerbate vegetation and carbon cycling differences between created and natural wetlands.

Intensive herbivory in wetlands can cause a top-down cascade that leads to environmental degradation. Wetlands have long been thought to be primarily controlled by bottom-up factors, with hydrology and nutrient availability determining community composition and ecosystem

processes. More recently, studies have suggested that top-down factors may also play an important role in wetlands, with herbivory influencing vegetation communities which in turn alters nutrient cycling (Silliman and Zieman, 2001; Silliman and Bertness, 2002). Hydrology plays a key role in this top-down dynamic, with stable hydrologic regimes attracting herbivorous waterfowl, in particular Canada geese (*Branta canadensis*) and ducks (*Anas spp.*), to wetlands for nesting and feeding (Murkin et al., 1997; Lor and Malecki, 2006). Created wetlands, which often have deep standing water and young palatable vegetation, offer desirable habitat for migratory waterfowl (Isola et al., 2000), which consume vegetation and then excrete nutrients elsewhere during migration (Tamisier and Boudouresque, 1994). Waterfowl populations have been increasing in population since the 1950s, primarily due to them inhabiting suburban areas with limited predators (Ankney, 1996). This increase in population can cause created wetlands to be particularly vulnerable to intensive grazing from waterfowl.

Emergent vegetation is a key driver of carbon cycling in freshwater wetlands. Their photosynthetic activity, coupled with anoxic conditions, makes wetlands substantial carbon sinks (DeDeyn et al., 2008; Kayranli et al., 2010; Mitsch et al., 2013). Vegetation fixes inorganic C from the atmosphere through photosynthesis, stores organic carbon in its above and belowground biomass, and transfers the carbon to the sediments through decomposition and root exudation. Soil carbon is often stored for long periods of time due to anaerobic soil conditions (Collins and Kuehl, 2001; Mitsch and Gosselink, 2007).

Wetlands also act as a major greenhouse gas source due to methane (CH_4) production. CH_4 is produced by methanotrophic microorganisms, and is released from the soils through ebullition, bubbling, and plant mediated transport, in which emergent plants act as a conduit for CH_4 (Bartlett and Harriss, 1993; Armstrong et al., 1996; Kayranli, 2010). In wetlands dominated

by emergent macrophytes, nearly 90% of emitted methane can be transported by plants (Bergström et al., 2007), therefore a reduction in plant biomass due to grazing may significantly reduce methane emissions. Clipping studies in wetlands support this central role of vegetation and have shown large reductions in CH_4 emissions when vascular plants were removed, likely due to reduced methanogenesis and plant transport (Waddington et al., 1996; Noyce et al., 2014). However, herbivore exclusion studies have shown substantially higher CH_4 emissions in grazed plots (Dingemans et al., 2011; Winton and Richardson, 2017), which have been attributed to lower belowground biomass leading to less oxygen transport to the sediments, resulting in lower rates of CH_4 oxidation (Winton and Richardson, 2017). In contrast, Dingemans et al. (2011) found no differences in CH_4 production or oxidation rates between caged and uncaged plots and therefore concluded that the higher CH_4 emissions in grazed plots were due to more efficient plan mediated transport in grazer damaged plants.

Different plant species also store and cycle carbon differently due to their functional traits, specifically their rates of carbon uptake through photosynthesis. Variation in their tissue chemistry, notably their CN ratios, also leads to variations in the rate at which they decompose and deposit nutrients into the soils, where higher nitrogen content leads to faster decomposition rates (Lubchenco, 1983; DeDeyn et al., 2008). Due to these variations among species, higher biodiversity within a system has the potential to yield higher and more consistent carbon storage (DeDeyn, et al., 2008; Lange et al., 2015). It is therefore important to consider the role of vegetation diversity in wetlands and its influence on carbon cycling.

Intensive grazing by waterfowl can greatly reduce plant cover in wetlands and thereby diminish carbon cycling. Preferential grazing of desirable species means that heavy grazing can also strongly alter plant community composition (Ström et al., 2005; Dingemans et al., 2011;

Lodge, 2017; Winton and Curtis, 2017). This reduction and shift in composition of vegetation can result in a lower rates of gross primary productivity (GPP) which then lessens the organic carbon brought into and stored in the sediments (Bagchi and Richie, 2010). Lodge (2017) found that in created wetlands, where vegetation communities are relatively young and not fully established, intensive grazing can inhibit the development of desired plant communities. Often waterfowl target younger, more palatable plants, leading to a shift in vegetation dominance when the wetlands are young and particularly vulnerable to grazing pressures (Lubchenco, 1983; Evers et al., 1998; Kennedy et al., 2018). With increasing waterfowl populations, heavy grazing can outpace the growth and development of stable vegetation communities (Lodge, 2017), leading to wetlands with diminished carbon storage potential.

This study builds upon the findings of Lodge (2017), who found that heavy grazing in a created wetland reduced plant growth by 27% and reduced peak growing season plant diversity by 41%, suggesting the possibility of shifts in vegetation community composition from long-term grazer management. This study continues the long-term grazer exclusion experiment and focuses on quantifying shifts in carbon storage associated with intensive herbivory. The overarching objective of this study was to better understand the impacts of grazers on carbon cycling, with the intent to help managers develop management practices that promote carbon sequestration in created wetlands. An increased understanding of herbivory and its influences on created wetland carbon cycling and storage can help inform the construction, management, and monitoring of these ecosystems to create more functional wetlands that properly cycle carbon. The objectives of this experiment were to quantify the effects grazers have on carbon cycling in created freshwater wetlands through changes in biomass, gas fluxes, and soil carbon. We tested three hypotheses to evaluate the role of grazers in created wetlands. First, we hypothesized that

grazers would reduce total plant cover and biomass, which will reduce the amount of carbon being pulled into the system through primary productivity. Second, that the reduction in plant biomass from grazing would reduce methane emissions. Third, that the decrease in plant biomass would lead to decreased carbon input and storage in sediments.

Methods

Site Description

This experiment took place between May and October of 2017 and 2018, using experimental plots established in 2014 by Lodge (2017). Plots were located High Acres Nature Area (HANA), a series of natural and created wetlands in Western New York, USA (43° 5' N, 77° 23' W) owned and managed by Waste Management of New York, LLC. The study site was composed of two created wetlands, Area 1 North and Area 3 (Figure 1). Area 1 North (A1N) (Figure 1), approximately 1.87 ha of shallow emergent marsh, that previously used as a gravel depository, but was abandoned in the 1960s, left to fallow, and converted to an emergent wetland in 2009 (Stantec, 2009). Prior to its use as a gravel depository, the site was used for agricultural purposes. The wetland is fed by the adjacent remnant quarry pond, and contains a culvert in the south end which controls water flow to the pond directly south of A1N, allowing the control of water level and consistent standing water year-round since 2014 (Lodge, 2017). Soils in A1N have relatively low organic matter (OM), nitrate, ammonium, and total phosphorus (TP) (Lodge, 2017). The vegetation in A1N is dominated by broad and narrow leaf arrowhead (*Sagittaria spp.*), pickerelweed (*Pontedaria cordata*), and white pond lily (*Nymphaea odorata*).

Area 3 (A3), approximately 1.63 ha, was a cattle pasture prior to its conversion to a wooded wetland and wet meadow in 2012. It is fed primarily through precipitation and runoff

from adjacent ponds. The site is divided into three distinct sections, denoted as A3A (south), A3P (middle), and A3C (north) (Figure 1). A3A is inhabited by wet meadow plants and has little to no standing water throughout the growing season (May - September), whereas A3P and A3C maintain standing water during early summer (Lodge, 2017). In 2016, the region suffered a summer-long drought. During this time, A1N lost very little water due to being primarily groundwater-fed and controlled by an outlet, while A3 experienced more severe drought (Lodge, 2017). The hydrology in A3 is primarily dependent on rain, so the site had very little standing water throughout the summer. The vegetation communities of A3A and A3P are dominated by a variety of wet meadow plants, including goldenrod (*Asteraceae solidago*), cattail (*Typha* spp.), and rice cutgrass (*Leersia oryzoides*). A3C is dominated primarily by cattail and rice cutgrass.

In June of 2014, sixteen pairs of plots were established at each site, with each set consisting of a 1 m^2 hardware mesh caged plot, an uncaged plot marked with poles. As described by Lodge (2017), plots were arranged in blocks of 4 pairs randomly across A1N and in distinct regions in A3 for a total of 64 plots. A three-sided cage-control plot was included in every block of four pairs (Figure 1). The three-sided caged plots acted as a cage control to ensure the response variables are unaffected by the cages themselves. These were included in the original design, however they showed no effects and we therefore omitted them from this study.

Grazing Presence

We quantified waterfowl populations through observations in both sites upon every visit to the wetlands. Species, abundance, date, and time of day was recorded by researchers and trained volunteers. We quantified grazing density by number of individuals per hectare from 2017 to 2018 and compiled grazer density by season (winter, spring, summer, and fall). Other

herbivores, including deer, muskrats, and beavers, were present in both sites but were not directly observed.

Hydrologic Conditions

We assed water depths by averaging three points in each plot every six weeks in the growing season since 2014; this data has been compiled since 2014. The region suffered a drought in the summer before this experiment took place. During this time, A1N lost very little water due to being primarily groundwater-fed, while A3 experienced more severe drought. Normal precipitation returned to the region the following year.

Soil Characteristics and Elemental Compositions

We extracted soil cores from each plot in October 2018 for nutrient analysis with a syringe corer (2.5 cm diameter x 10 cm depth) and analyzed them for bulk density and soil elemental composition. Carbon and nitrogen percentages were analyzed on a Perkin Elmer 2400 CHNS-O Elemental Analyzer and molar C:N was calculated. We measured bulk density from the surface of the soils to a depth of 10 cm and converted to g m^{-2} to estimate the areal total soil carbon.

Vegetation Cover

We conducted vegetation surveys every six weeks between June and August 2017 and May and August 2018. Surveys included estimation of total plant cover within the plot as well as stem counts for each species and total grazer damage within the plot (Bakker, 1985; Koh et al., 2009). Percent cover was estimated by at least two observers per plots. With every vegetation survey, we quantified damage by estimating the amount of total leaf damage done to the

vegetation by large grazers, relative to the abundance of each species (Brinson et al., 1981; Winton and Richardson, 2016).

Aboveground Biomass

We estimated aboveground biomass throughout growing season in 2018 by collecting plants from field locations nearby, but outside, of plots, and drying them in the lab and then using allometric equations to estimate biomass within plots. We picked individual plants from the bottom of the stem and immediately measured stem heights, leaf heights, and leaf widths. We dried the plants at 60°C and weighed them for biomass to create regression curves based on allometric relationships for dominant species at the peak of the growing season. Regression curves for each species are listed in Table A.4. We identified dominant species using the vegetation surveys, with the ten most abundant species selected for each site, which in combination contributed at least 80% of total cover. During vegetation surveys, we selected five individuals for each species and measured their characteristics, which were then used to estimate the total biomass from the regression curves. We multiplied the average biomass calculations of each species by the number of stems per species to estimate the total aboveground biomass in each plot (Brinson et al., 1981;Wang et al., 2013; Chen, 2016). We analyzed carbon and nitrogen composition of the ten most abundant species from samples collected in August for ise in the decomposition study, using a Perkin Elmer 2400 CHNS-O Elemental Analyzer and then used these values to estimate the total aboveground carbon.

Belowground Biomass

We extracted soil cores (6 cm diameter x 20 cm depth) from each plot in October 2018, with one core per plot to minimize damage. The cores were washed through a 1 mm mesh sieve,

dried at 60°C and weighed (Evers et al., 1998; Wang et al., 2013; Chen, 2016). We analyzed carbon and nitrogen composition of belowground biomass as above to estimate total carbon in belowground biomass.

Decomposition

We selected dominant plant species for each site, which were selected by the species that in combination contributed at least 60% of the total cover in each wetland, air dried these species in the laboratory, and sorted them into litterbags (Brinson et al., 1981). We collected plants from the field in August, towards the end of the growing season. We selected four species for A1N (*Typha latifolia, Sagittaria filiformis*, *Pontedaria cordata*, and *Nymphaea ordata*) and three for A3 (*Asteraceae solidago*, *Leersia oryzoides*, and *T. latifolia*). We placed the bags in the plots in September 2018 and collected after 30, 61, 181, and 211 days. Once collected, we thoroughly cleaned each bag of any soil and invertebrates, dried it in an oven, and weighed the contents. We calculated decomposition rates (k-values) of each species and treatment by the difference of the original organic matter and the organic matter at each time point, divided by the original to create an exponential regression curve depicting decomposition over time (Deghi et al., 1980; Moorhead et al., 1999).

Gas Fluxes

We measured carbon gas fluxes using the static chamber method (Ryan, 1991; Long and Hallgren, 1993; Caroll and Crill, 1997; Hunt, 2003) in A1N only. We took measurements during the peak growing season (June-July) and at the beginning of plant senescence (August-September) in both 2017 and 2018. We measured fluxes in the eight pairs of caged and uncaged plots in A1N most affected by intensive grazing, as determined by Lodge (2017), which allowed

us to determine the maximum impact of grazers on gas fluxes. The chamber we used was 1 m^2 in dimension and ranged from 1 to 1.7 m in height, depending on the individual plot. The chamber fit over the tops of the plots with a clear plastic sheet curtain that rolled over the sides and secured at the sediment surface to prevent any lateral exchange of water and air. We measured CO_2 gas exchange with the atmosphere in both the light and the dark using a LI-COR 820 connected to a pump that recirculated air within the chamber. The clear plastic sheet we used for the light treatment allowed approximately 67% of photosynthetically active radiation to pass through. For dark measurements, we covered the chamber with an opaque tarp. We continuously monitored temperature throughout the sampling periods both inside and outside the chamber, and used a cooling system to maintain internal temperatures within 5°C of external temperature (Caroll and Crill, 1997).

We measured CO_2 exchange using the first stable 5 minutes of the light and dark measurement periods to calculate the ecosystem-atmosphere CO_2 flux. We calculated gross primary productivity (GPP) by subtracting the dark measurement (ecosystem respiration, ER) from the light measurement (net ecosystem exchange, NEE) for each plot to estimate photosynthesis. Because submerged plants may directly take up dissolved inorganic carbon (DIC) released from heterotrophs in the sediments and water column - not reflected in our measured changes of CO_2 in the chamber headspace - we have likely underestimated ER and GPP.

We collected samples for CH_4 analysis every 15 minutes during both dark and light chamber periods, for a total of four samples per chamber closure. Samples were analyzed for CH_4 concentration using a Shimadzu Model 2014 gas chromatograph fitted with a flame ionization detector (FID) and a methanizer.

In 2018, we measured the light response of CO_2 flux by sequentially covering the chamber with shade cloths that reduced light availability by 18% and 38%. We constructed separate light response curves for the summer and fall to estimate the total CO_2 uptake throughout the growing season (Ögren and Evans, 1993) and the Pmax, which indicates the maximum photosynthesis occurring in the ecosystem per light availability. Equations for the light response curves were

$$y=a+b^{cx}$$

Where a is the asymptote of the curve, b is scale, c is the grow rate, and x is the light availability in μmol.

Statistical Analyses

We performed all statistical analyses using the JMP Pro 14 statistical software. We evaluated each dataset for homogeneity of variance and normality prior to statistical analysis. Heterogeneity among blocks within each site was analyzed by including block as a random factor in analyses. To compare factors between sites, we used the uncaged controls.

For data that met the requirements of normality, including vegetation cover, above and belowground biomass, soil nutrients, GPP, ER, NEE, and decomposition rates, we used a full-factorial two- way ANOVA to compare the intra-site differences between these variables and treatment and month when applicable. We used a Turkey's post-hoc test to determine the differences among the means.

When comparing the means of non-normal data, including gazer populations, grazer damage, and methane emissions, we used a one-way Kruskal-Wallis test to determine the effect of treatment, followed by a Mann Whitney U test to compare means.

Results

Grazing Pressure

Waterfowl were consistently abundant in A1N throughout the course of the study with Canada goose (*Branta canadensis*), mallard ducks (*Anas platyrhynchos*), and common gallinules (*Gallinula galeata*). Peak populations were seen in summer 2017, with decreasing populations thereon. The majority of 2018 experienced lower waterfowl populations than 2017, however fall 2018 had populations similar to those of 2017 (Figure 2). Grazers were not observed in A3 from 2016 to 2018.

Hydrologic Conditions

A1N had consistent depths ranging from 1 to 50 cm, and remaining above 7 cm throughout the time of the study (Figure 3a). Depths during the growing season were consistently deeper in A1N (2017: 24. 4 ± 7.8 cm, 2018: 27.5 ± 8.7 cm; mean ± SE) than in A3 (2017: 1.5 ± 2.8 cm, 2018: 2.6 ± 5.4 cm). A3 had standing water in 2014 and 2015, but was only flooded seasonally in subsequent years, and was completely dry by August in both 2017 and 2018 (Figure 3b).

Soil Carbon and Nitrogen

Soil carbon was significantly higher in the caged plots in A1N ($p=0.004$), (A1N, caged: 6.42 ± 0.23 %, uncaged: 5.06 ± 0.25 %; mean ± SE). While A3 had no significant difference between soil carbon in the plots, caged plots had 27% greater carbon composition than uncaged plots (Figure 4).

CN ratios were significantly higher in A1N than in A3 (p=0.001), with no grazing effect at either site (Figure 4). Both sites displayed a significant block effect for CN ratios (Table A.1).

Vegetation

There was a significant interaction between grazing effect and month in the vegetation cover of A1N in 2018 (Table A.2), where cover increased throughout the growing season and was higher in ungrazed treatments in all months except August 2018 (Figure A.1). A3 showed similar patterns of seasonal growth, but had no significant difference between treatments in individual months, excepting July 2017, where uncaged plots had higher vegetation cover (p=0.0007). Plant species composition shifted over the growing season at both sites and treatments. In both years, species richness in A1N increased throughout the growing season, and was higher during the height of the growing season in caged plots than uncaged plots by approximately 15% in both years (Table 1). Uncaged plots in A1N were dominated by graminoids and herbaceous plants, with a dominance of *Sagittaria* spp. throughout the entirety of the study period. *N. odorata* was also prominent in uncaged plots in 2018. Caged plots had a dominance of *Sagittaria* spp. and to a lower extent *L. oryzoides*. Dominance in A3 varied throughout the year between *P. pensylvanicum*, *L. oryzoides*, *P. arundinacea*, and *S. canadensis,*, and had a variety of graminoid and herbaceous species, and one shrub species (Table A.3). Grazers in A1N showed a preference for *S. filiformis*, *P. cordata*, *S. latifolia*, and *N. odorata*, relative to species abundance, and while there was no significant difference between preferences for species, *S. filiformis* tended to be selected for most often (*S filiformis*: 31.62 ± 4.79; *S. latifolia*: 12.55 ± 4.58; *P. cordata*: 22.5 ± 5.95; *N. odorata*: 17.30 ± 6.31 relative % damage; mean ± SE) (Figure 5). No other vegetation species had damage at either site.

Aboveground biomass in both sites was dependent on month and treatment (Table 2). Plant biomass in A1N was consistently lower in uncaged plots (Figure 6a). During the height of the growing season (July) caged plots in A1N had 58% more aboveground biomass than the uncaged plots. The aboveground biomass in A3 was not significantly impacted by grazers, but tended to have higher biomass in caged plots (Figure 6b). Aboveground biomass was highest in August in A3, where caged plots had 45% more plant biomass than uncaged plots.

Belowground plant biomass in the top 10 cm was 50% higher in A1N than in A3, although there was no significant difference between sites (Table 1; Figure 7). Belowground biomass in A1N tended to be higher in caged plots (Caged: 555.51 ± 127.20; Uncaged: 338.46 ± 421.39 g m^{-2}; mean ± SE), however there was no significant effect of grazing at either site.

Gas Fluxes

Carbon dioxide fluxes varied across seasons (summer and fall) and were strongly influenced by grazing. Across grazer treatments there was significantly higher NEE in the summer compared to the fall both years (2017: $p<0.001$; 2018: $p=0.041$). There was also a strong interaction between season and treatment in 2017 for NEE, with significantly higher primary productivity rates in the summer caged plots (Summer caged: 0.69 ± 0.04; Summer uncaged: 0.30 ± 0.09; Fall caged 0.20 ± 0.09; Fall uncaged: 0.17 ± 0.06 g C assimilated m^{-2} hr^{-1}; mean ± SE) (Figure 8a; Table 2). ER was significantly higher in caged plots in both 2017 and 2018 (2017: $p<0.001$; 2018: $p=0.017$) and was significantly higher in the summer compared to the fall in 2018 ($p=0.024$), but showed no interaction between treatment and season in either year. GPP was significantly higher in the summer of both years (2017: $p<0.001$; 2018: $p=0.026$), and there was a strong interaction between season and treatment for both years, with significantly higher

primary productivity in caged plots during the summer. In summer 2017, which showed the strongest grazer effect, cage plots fixed 55% more carbon than uncaged plots (Figure 8a).

Photosynthetic light response curves showed a higher uptake of carbon in caged plots in the summer (Figure A.2) with a Pmax of 0.68 g m^{-2} hr^{-1} and an initial uptake of 0.07 g m^{-2} hr^{-1} per µmol m^{-2} s^{-1} and had a Pmax of 0.45 g m^{-2} hr^{-1} and an initial slope of 0.02 g m^{-2} hr^{-1} per µmol m^{-2} s^{-1} in uncaged plots. Fall response curves showed much lower rated of carbon uptake with Pmax values in uncaged plots that were 41% lower than those in uncaged summer plots. There was no caged and uncaged plots in the fall; caged plots had a Pmax of 0.28 g m^{-2} hr^{-1} and uncaged had 0.31 g m^{-2} hr^{-1}, and both had an initial slope of 0.04 g m^{-2} hr^{-1} per µmol m^{-2} s^{-1}.

Methane emissions in the light were significantly higher in the summer than in the fall (Summer, uncaged: 4.56 ± 1.15 mg m^{-2} hr^{-1}; Fall, uncaged: 0.77 ± 0.12 mg m^{-2} hr^{-1}; mean ± SE) (Figure 9a). In the summer, CH_4 fluxes under ambient light were 62% higher in caged plots than uncaged plots. There was no significant seasonal or treatment patterns in methane emissions in the dark (Figure 9b). The difference between light and dark emissions within a plot did not show any consistent trends across season or treatment (Table 3).

Decomposition Rates

Decomposition rates in A1N varied between species, with *N. odorata* having significantly faster rates than the other species tested at the site (p=0.001) (Figure 10). *N. odorata* was the only species to have a significantly lower k-value in caged plots than in uncaged plots (p=0.046), and also had lower C:N than other species (*A. solidago*: 26.10 ± 0.06; *L. oryzoides*: 30.81 ± 2.82; *N odorata*: 17.01 ± 0.20; *P. cordata*: 31.93 ± 0.55; *S. latifolia*: 21.34 ± 0.55; *T. latifolia*: 21.11 ± 0.69; C:N ± SE). Differences in these ratios were largely driven by species differences in nitrogen compositions. In A3, there was a significant difference in decomposition

rates across species (p=0.002), with *T. latifolia* decomposing at a rate approximately 34% slower than *A. solidago* and *L. oryzoides* in uncaged plots (Figure 10; Table 4).

Discussion

Freshwater wetlands are important contributors to the global carbon budget due to their ability to store large amounts of carbon lover long periods of time. Created wetlands tend to lack the functionality and stability of natural wetlands with high variation between individual wetlands, and may fail to properly cycle carbon when intensive grazing is prevalent (Hirota et al., 2005). Herbivorous waterfowl were seen in A1N throughout the course of this study, and Lodge (2017) observed a similar abundance of waterfowl grazers in A1N from 2014 - 2016. Lodge (2017) also reported small populations of grazers in A3, when the site had standing water throughout most of the year, whereas we observed no grazers in A3 from 2017-2018 as the site became drier. Our two created wetlands showed differences in their response to grazing, where A1N showed strong top-down dynamics, in which vegetation, gas fluxes, and soil properties were significantly influenced by grazing treatments. The vegetation species observed in A1N were typical emergent and submerged wetland plants. A3, in contrast, dominated by wet meadow plants, and showed no significant shifts in plant biomass or cover with grazers, suggesting a lack of strong top-down dynamics. Soil at this site had a higher nutrient content, suggesting that bottom-up processes may dominate.

In A1N, where grazing and seasonality were important drivers of vegetation dynamics, we observed differences in plant species throughout the growing season in caged versus uncaged plots. Caged plots were more diverse, with higher plant cover and aboveground biomass throughout the growing season, suggesting that the grazers were limiting the more competitive

species. This is consistent with the findings of Lodge (2017), who found that species richness was 1.3 times higher in caged treatments. Aboveground biomass was also significantly lower in grazed plots in A1N, especially in the peak growing season between June and August. This is consistent with Bakker (1985) and more recently Dingemans et al. (2011), who reported seasonal patterns of vegetation cover and a significant decrease in stem count in the presence of grazers in freshwater wetlands. Likewise, Mulder and Ruess (1998) reported a significant decrease in aboveground biomass in their grazed treatments in salt marshes. Shifts in the vegetation dominance were seen in both caged and uncaged plots throughout the season (Table A.3), especially in A1N, where caged plots tended to have higher coverage of *P. cordata* and *S. filiformis*. This is consistent with the grazing preferences of waterfowl at the site (Figure 5) in that they often sought out these species for consumption. This was similar to the findings of Bagchi and Richi (2010) in grasslands, who reported shifts in vegetation dominance consistent with grazer preferences, with a lower abundance of selectively grazed plants and higher diversity in ungrazed plots. In our uncaged plots, these species were often damaged by grazing and observed in lower frequencies, whereas plants in the caged plots were able to grow to maturity and eventually became less palatable to grazers (Goranson et al., 2004). Vegetation cover remained significantly greater in caged plots in spring of 2018 in A1N, suggesting that the effects of grazer exclusion carry over year to year, and allow more plant growth in the absence of grazing. In created wetlands, which typically have younger plant communities, this may suggest the importance of limiting grazing so as to encourage the growth and establishment of stable and diverse plant communities. It typically takes 15-20 years for vegetation communities to fully develop in created wetlands due to the disturbed soils and sediments (Mitsch and Wilson, 1996).

While belowground biomass was not significantly influenced by grazing pressures, there was a clear trend of higher belowground biomass in caged plots in A1N. Lodge (2017) also observed higher belowground biomass in these caged plots, however our overall belowground biomass was higher than theirs, suggesting an increase in the biomass as the wetland matures. We acknowledge that belowground biomass was measured only to 20 cm below the surface of the soil, and therefore may underestimate total belowground biomass. Our results are consistent with that of Myers et al. (1995), who recommend managing grazer intensities to encourage the establishment of restored wetland habitat.

The pattern we observed in soil carbon was consistent with grazing studies conducted in a range of ecosystems (e.g. North American, prairie: Frank et al., 1995; Mongolian steppes: Cui et al., 2005; Himalayan grasslands: Bagchi and Richie, 2010), in which percent soil carbon is significantly reduced by heavy grazing practices. Our values, measured to 10 cm depth, may be an underestimate and preclude evaluation of shifts occurring in deeper layers.

Decomposition rates varied by site and species, where *N. odorata* and *T. latifolia* showed significantly faster decomposition rates in caged plots, the latter of which only having an effect in A3. *T. latifolia* decomposted more quickly in A3 than in A1N, likely because of the permanent flooding in A1N. The decomposition rates we observed were consistent with their CN ratios, where species with a lower CN ratio (*N odorata*: 17.01 ± 0.20; *S. latifolia*: 21.34 ± 0.55; C:N ± SE) decomposed quicker (Figure 10). The differences in CN ratios were largely driven by the differences in nitrogen composition, which suggests that species with higher nitrogen composition will be removed more quickly and contribute less to soil carbon storage. *N. odorata* was influenced by grazing, as it was one of the preferred species in grazers' diet selectivity (Figure 5), and so a reduction of cover due to grazing may have lead to a reduction in soil C in

the uncaged plots, which had lower percent C and higher CN. This suggests that the increase in soil carbon may be driven more by the magnitude of biomass in the ungrazed plots rather than the shift in species composition.

Carbon inputs to these wetlands primarily come from emergent macrophyte primary production, and net storage is dependent on decomposition. These systems are an important carbon sink, with important implications for climate change (Bridgham et al., 2006). In this study we observed a significant influence of grazers on carbon fluxes, with caged plots sequestering an average of 53 % more CO_2 through NEE than uncaged plots during the height of the growing season. Our average NEE fluxes (0.5 - 20 g CO_2 m^{-2} day^{-1}) were substantially higher than the range of other freshwater emergent wetlands (0.5 - 3.0 g CO_2 m^{-2} day^{-1}) (Mader et al., 2008; Mitsch et al., 2013; Mitsch et al., 2014; Pugh et al., 2017), however our values are representative only of the growing season, where other studies took into account the entire year. The grazer influence decreases in the fall. There was no significant difference between carbon uptake and leaf area (Figure A.3), suggesting the differences in carbon uptake was dependent on season and treatment more so than leaf area. Our light response curves suggest higher photosynthetic efficiency in the summer, and in caged plots, with more rapid response and higher Pmax (Figure A.2). Carbon sequestration was two times greater in summer (June and July) than fall (August and September) in both grazed and ungrazed treatments. Over the course of the entire growing season, more carbon was sequestered in the ungrazed treatments, but rates were only difference in June and July. Similar results were seen in Hirota et al. (2005), which reported significantly lower carbon uptake in grazed plots attributed to the substantial reduction in aboveground biomass.

While wetlands are an important CO_2 sink, they are also a major source of methane (Bartlett and Harriss, 1993; Kayranli, 2010). In this study, methane emissions were higher in caged plots under ambient light (Figure 9a), suggesting that plant-mediated processes, such as transport and root exudates, are key to methane production and emission in these systems. The range of methane emissions we observed (10 - 600 mg CH_4 m^{-2} day^{-1}) was similar to those reported for natural wetlands (e.g. 100-700 mg CH_4 m^{-2} day^{-1}, Bridgham et al., 2006; Saarnio et al., 2009; Dingemans et al., 2011). Seasonal variation at our sites was similar to those of Pugh et al. (2018), who saw higher fluxes in summer than in fall. However, the positive impact of grazer exclusion on methane emissions that we observed differs from others who report a significant increase in CH_4 emission with intensive grazing, (e.g. Allen-Diaz et al., 2004; Hirota et al., 2005; Dingemans et al., 2011; Scott and Curtis, 2017; Figure 9). This suggests that our methane emissions were strongly influenced by plant biomass (Segers, 1998; Bodelier et al., 2006; Bergström et al., 2007), at least during the growing season.

Overall we found that both carbon pools and carbon fluxes were significantly impacted by intensive grazing during the growing season (Figure 11). Carbon fluxes were substantially higher in the absence of grazers, with higher intake of atmospheric carbon into the wetland. Ungrazed wetlands pulled in approximately 9.36 g C m^{-2} day^{-1} more than the grazed system through GPP. Carbon pools, aboveground biomass and soil carbon, estimated by the carbon composition, were significantly lower in treatments subjected to intensive grazing. These results indicate that intensive grazing can significantly limit the carbon storage potential of created wetlands and underscores the importance of managing waterfowl populations in newly created wetlands where vegetation communities are not fully established. By limiting waterfowl numbers, and by extension grazing intensities, created wetlands will more rapidly develop stable,

diverse vegetation communities that are less susceptible to grazers (Lubchenco, 1983; Evers et al., 1998; Kennedy et al., 2018) and maximize potential for carbon sequestration.

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Tables and Figures

Figure 1. *Two created wetlands where the study took place. Area 1 North (left) was created in 2009 and is divided into four blocks with nine plots in each. Area 3 (right) was created in 2012 and contains sixteen plots in total. White circles indicate pairs of caged and uncaged plots.*

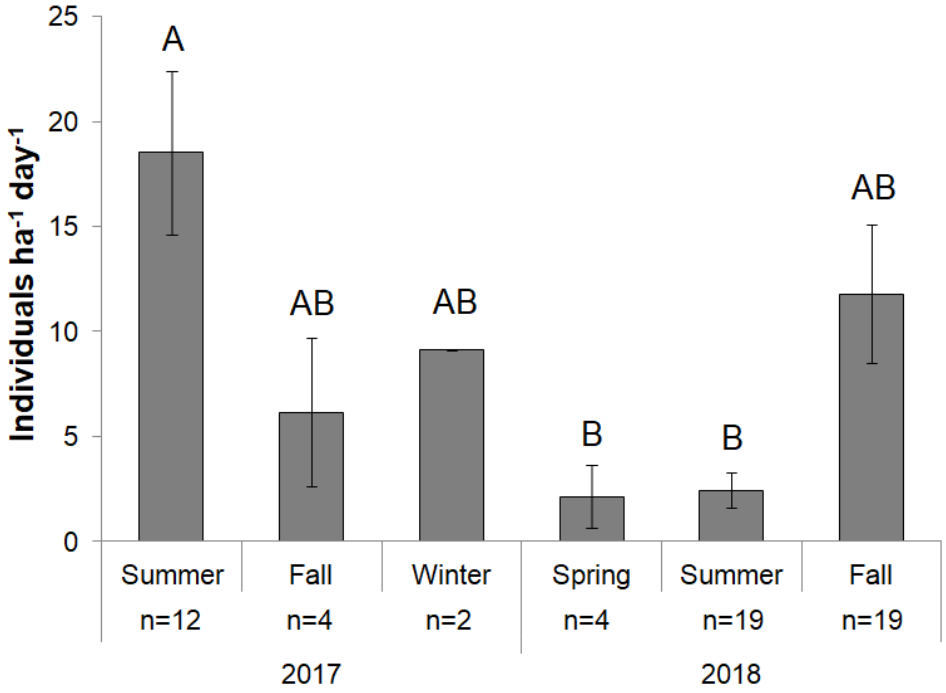

Figure 2. *Waterfowl observations in A1N June 2017 and November 2018 (Spring: March-May, Summer: June-August, Fall: September-November, Winter: December-February).*

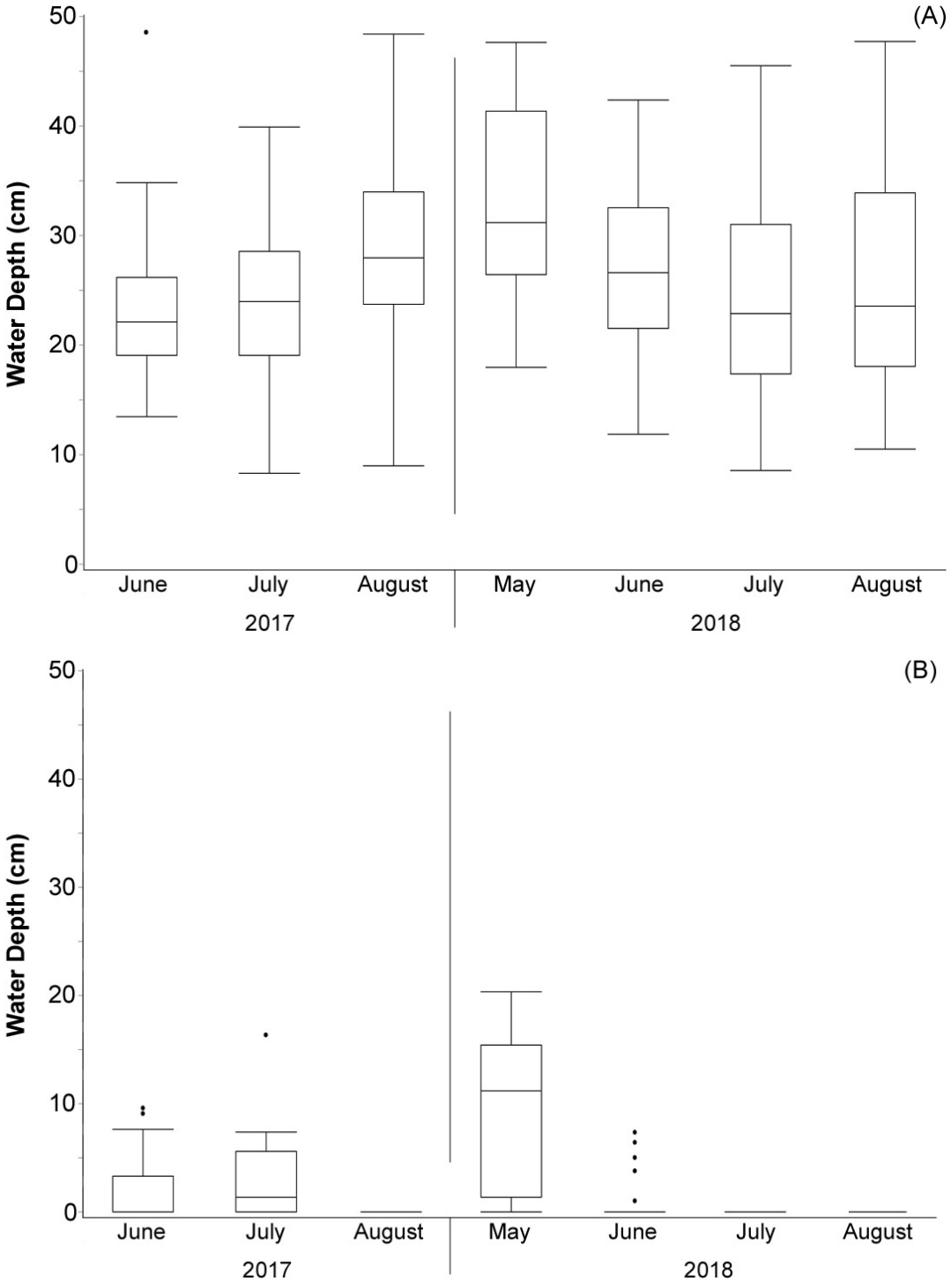

Figure 3. *Average water depth for A1N (A) and A3 (B) throughout the growing season (May-August) of 2017 to 2018.*

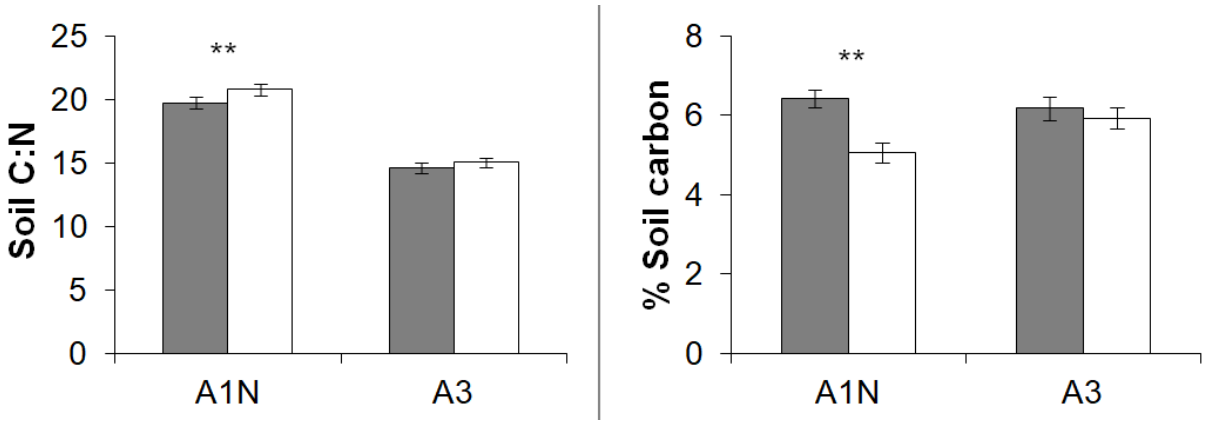

Figure 4. *Percent soil carbon and molar soil C:N in A1N and A3 in caged and uncaged plots. Stars above bars indicate differences between treatments. Two stars indicate p < 0.01.*

Table 1. *Results of one- and two-way ANOVA on the effects and interactions of month (Mo), and treatment (Tr) for vegetation cover, aboveground biomass, and belowground biomass in A1N and A3. Significant interactions are bolded, interactions <0.001 are starred.*

Factor	Month		Treatment		Mo x Tr	
	F	*p*	F	*p*	F	*p*
A1N						
Species Richness 2017	$F_{2,93} = 5.00$	**0.042**	$F_{2,93} = 11.47$	**0.003**	$F_{2,93} = 2.08$	0.13
Species Richness 2018	$F_{3,166} = 14.76$	**<0.001***	$F_{3,166} = 27.67$	**<0.001***	$F_{3,166} = 1.28$	0.29
Aboveground Biomass	$F_{3,60} = 25.85$	**<0.001***	$F_{1,126} = 13.37$	**<0.001***	$F_{3,108} = 5.37$	**0.002**
Belowground Biomass			$F_{1,30} = 1.73$	0.2		
A3						
Species Richness 2017	$F_{2,93} = 0.95$	0.39	$F_{2,93} = 0.18$	0.68	$F_{2,93} = 1.44$	0.24
Species Richness 2018	$F_{3,166} = 2.41$	0.07	$F_{3,166} = 0.01$	0.93	$F_{3,166} = 1.40$	0.25
Aboveground Biomass	$F_{3,60} = 9.34$	**<0.001***	$F_{1,126} = 2.37$	0.13	$F_{3,108} = 4.79$	0.13
Belowground Biomass			$F_{1,30} = 0.02$	0.97		

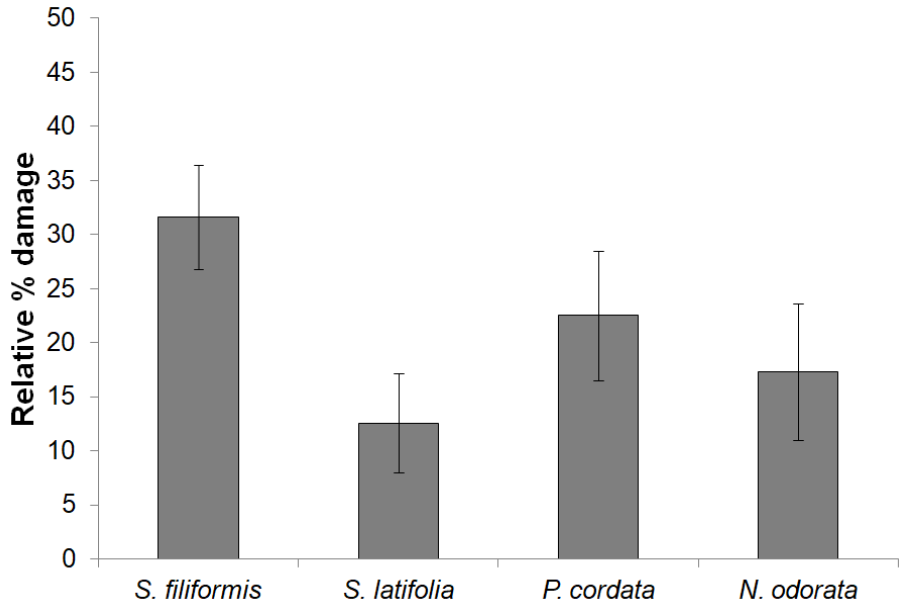

Figure 5. *Grazer damage for each species normalized to vegetation species abundance. There was no significant difference between selection for any species.*

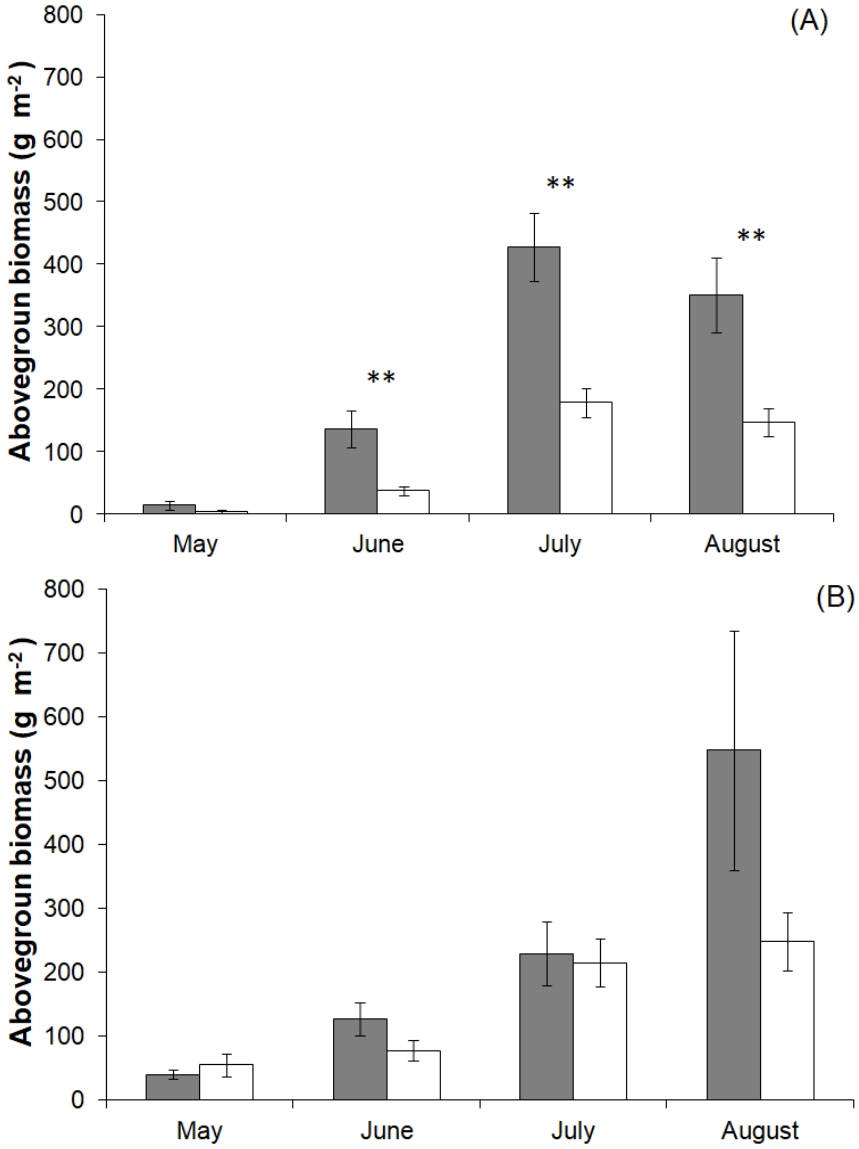

Figure 6. *Aboveground biomass during the 2018 growing period in Area 1 North (A) and Area 3 (B) with caged (grey) and uncaged (white) treatments. Two stars indicate a significant difference between treatments of $p < 0.01$, one star indicates $p < 0.05$.*

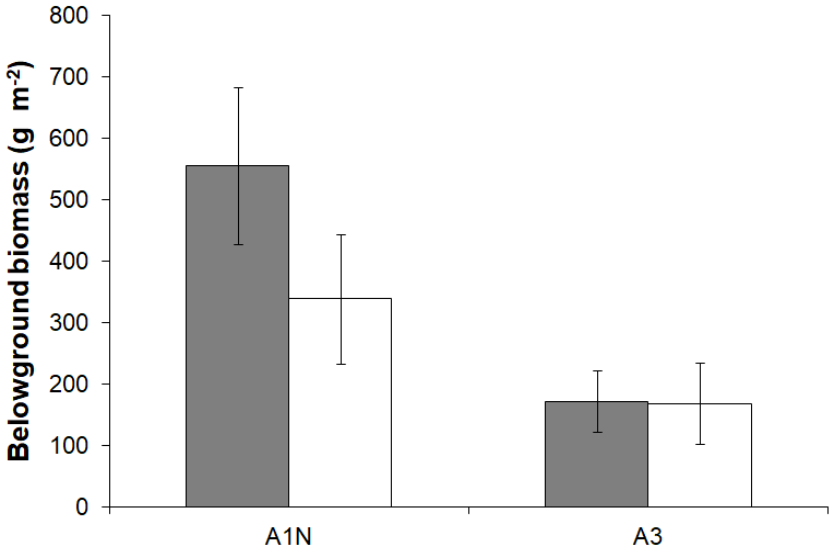

Figure 7. *Belowground biomass during the 2018 growing period in A1N and A3 for caged (grey) and uncaged (white) treatments. No significant difference was found between treatments or sites.*

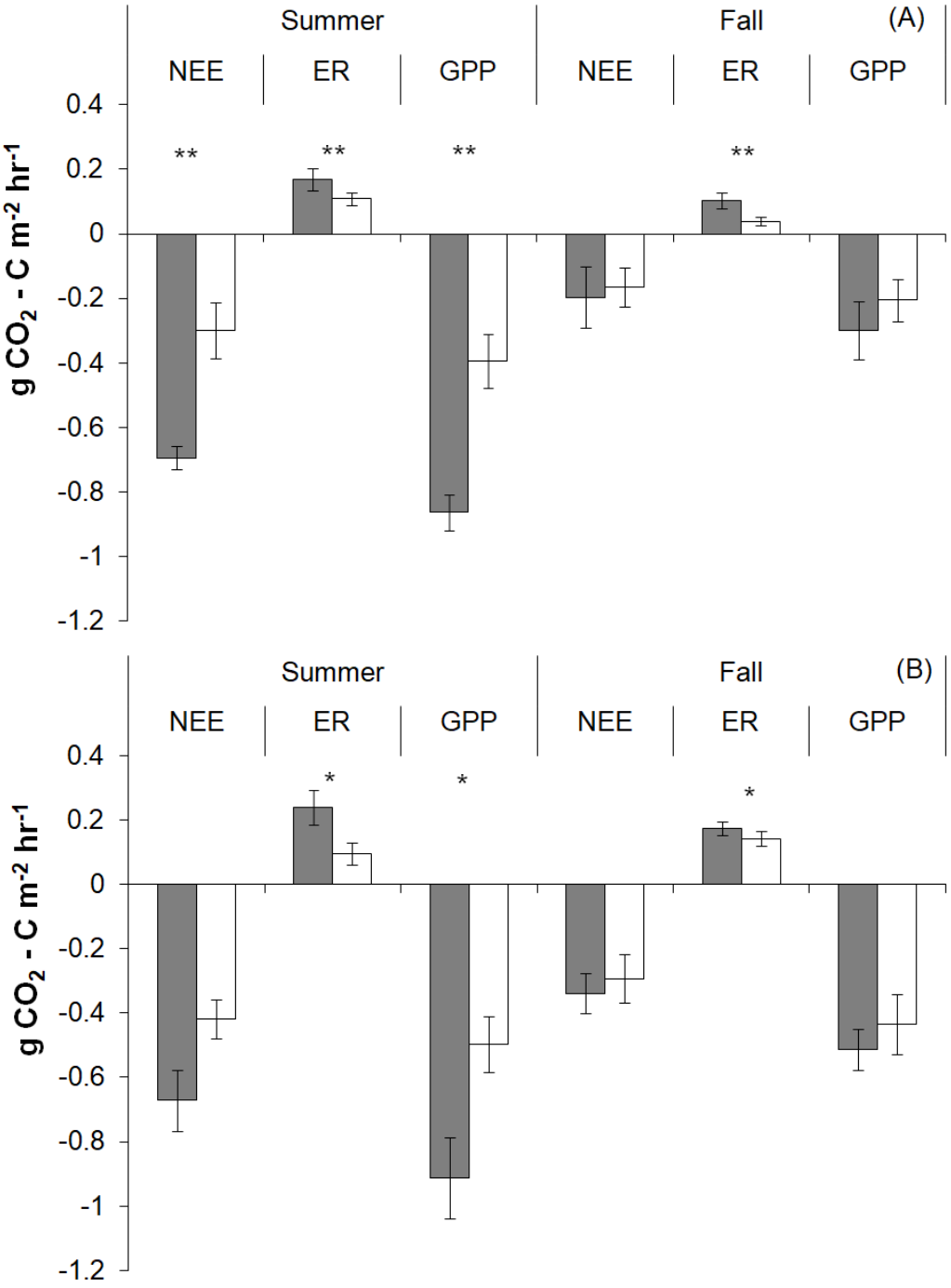

Figure 8. *Net ecosystem exchange (NEE), ecosystem respiration (ER) and gross primary production (GPP) in A1N in 2017 (A) and 2018 (B) for caged (grey) and uncaged (white) treatments. Summer measurements were taken in June-July, fall measurements were taken in August-September. Two stars indicate $p < 0.01$ between caged and uncaged plots, one star indicates $p < 0.05$.*

Table 2. *Results of two-way ANOVA evaluating the effect of season (summer and fall), and treatment (caged and uncaged) on NEE, GPP, and ER in A1N in 2017 and 2018. Significant p-values are bolded.*

2017 Factor		NEE	ER	GPP
Season	F	$F_{1,29} = 16.39$	$F_{1,30} = 6.05$	$F_{1,30} = 25.23$
	p	**<0.001***	**0.021**	**<0.001***
Treatment	F	$F_{1,29} = 7.01$	$F_{1,30} = 7.85$	$F_{1,30} = 14.17$
	p	**0.013**	**<0.001***	**<0.001***
Ssn x Tr	F	$F_{1,29} = 7.37$	$F_{1,30} = 0.06$	$F_{1,30} = 6.27$
	p	**0.011**	0.82	**0.018**
2018 Factor		NEE	ER	GPP
Season	F	$F_{1,30} = 9.63$	$F_{1,30} = 0.05$	$F_{1,30} = 5.56$
	p	**0.004**	0.83	**0.026**
Treatment	F	$F_{1,30} = 2.58$	$F_{1,30} = 6.41$	$F_{1,30} = 4.87$
	p	0.12	**0.017**	**0.036**
Ssn x Tr	F	$F_{1,30} = 3.21$	$F_{1,30} = 4.12$	$F_{1,30} = 4.69$
	p	0.08	0.052	**0.039**

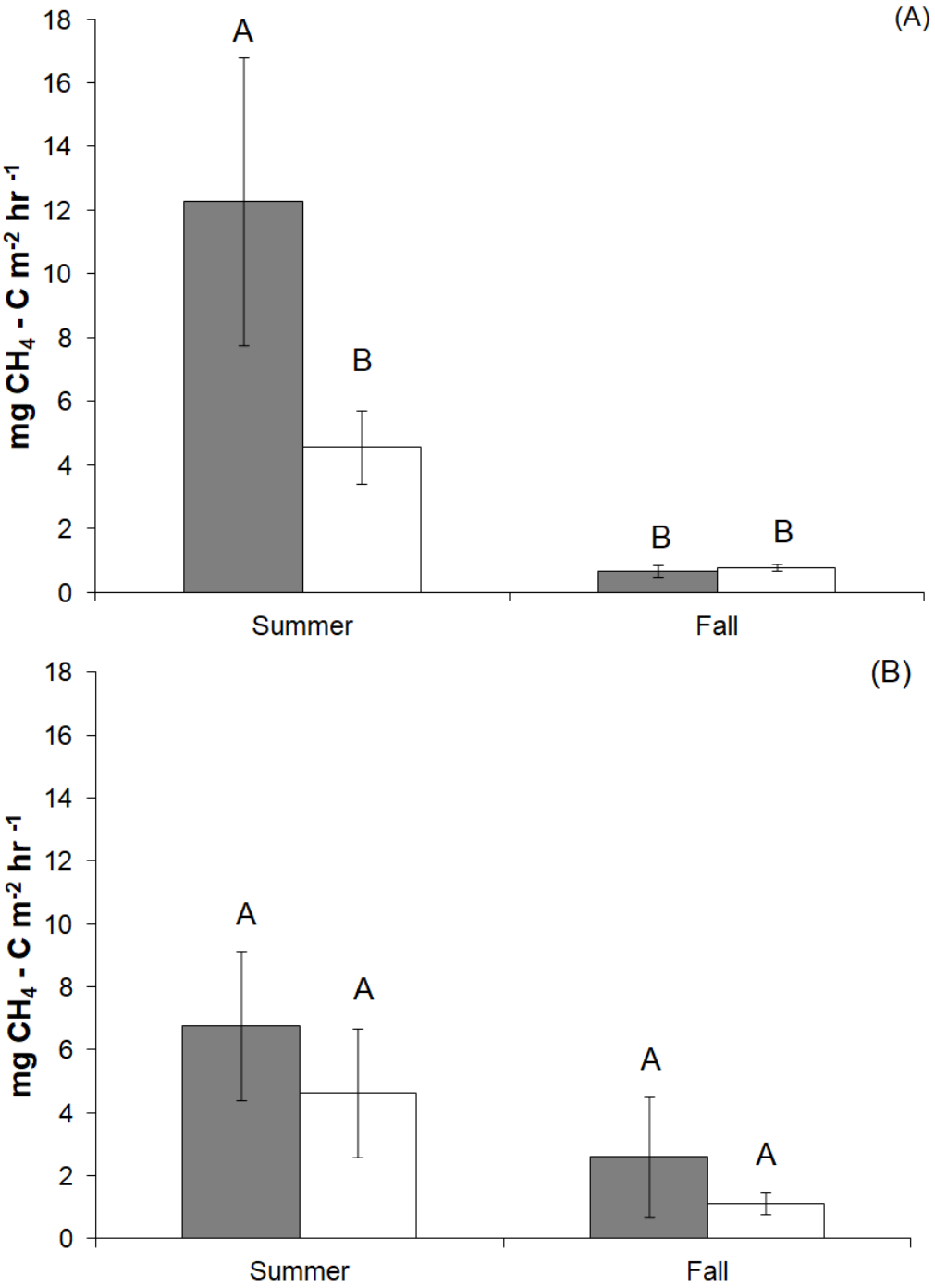

Figure 9. *Methane emissions throughout the growing season in caged (grey) and uncaged (white) plots in the light (A) and in the dark (B).*

Table 3. *Results of two-way ANOVA comparing the effects of grazing and season on methane emissions in the light and dark treatments. Significant interactions are bolded, interactions <0.001 are starred.*

Factor	Season		Grazing Treatment		Ssn x Tr	
	F	*p*	F	*p*	F	*p*
Light	$F_{1,30}$=21.65	**<0.001***	$F_{1,30}$=5.26	**0.033**	$F_{1,30}$=5.59	**0.029**
Dark	$F_{1,6}$=2.82	0.14	$F_{1,16}$=0.84	0.37	$F_{1,16}$=0.02	0.89

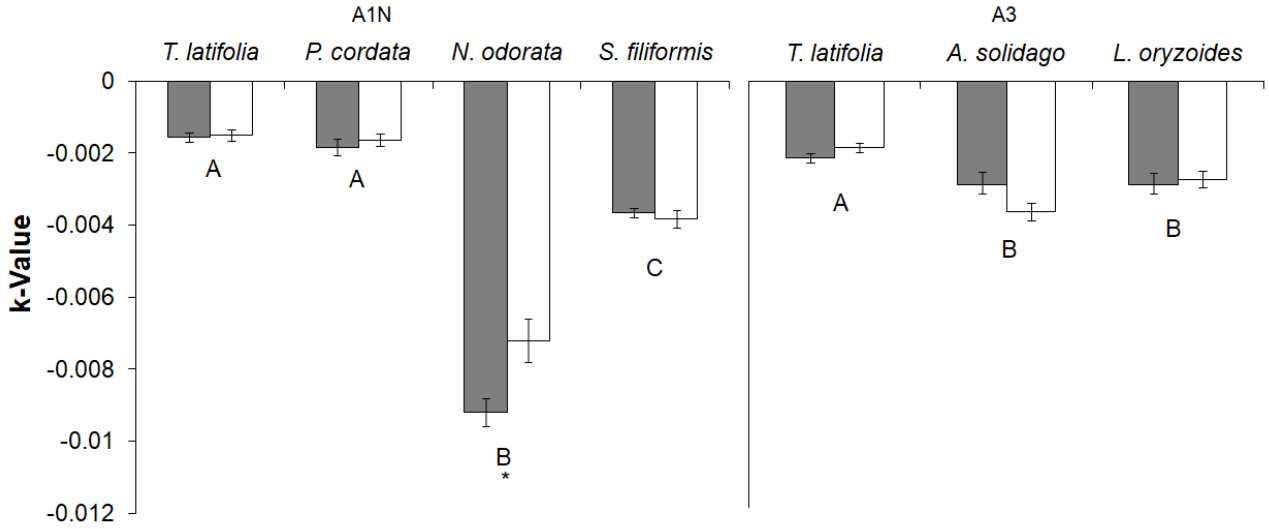

Figure 10. *Decomposition rates in A1N and A3 in caged (grey) and uncaged (white) plots. Letters below bars indicate statistical differences between species in sites, stars indicate statistical differences between grazing treatments. One star indicates p < 0.05.*

Table 4. *Results of two-way ANOVA comparing decomposition rates in A1N and A3 between species and grazing treatment. Significant interactions are bolded, interactions <0.001 are starred.*

Factor	Species		Treatment		Spp x Tr	
	F	*p*	F	*p*	F	*p*
A1N	$F_{1,46}$=214.74	**<0.001***	$F_{1,46}$=6.12	**0.018**	$F_{1,46}$=5.49	0.06
A3	$F_{1,33}$=8.18	**0.002**	$F_{1,33}$=0.02	0.90	$F_{1,33}$=1.75	0.19

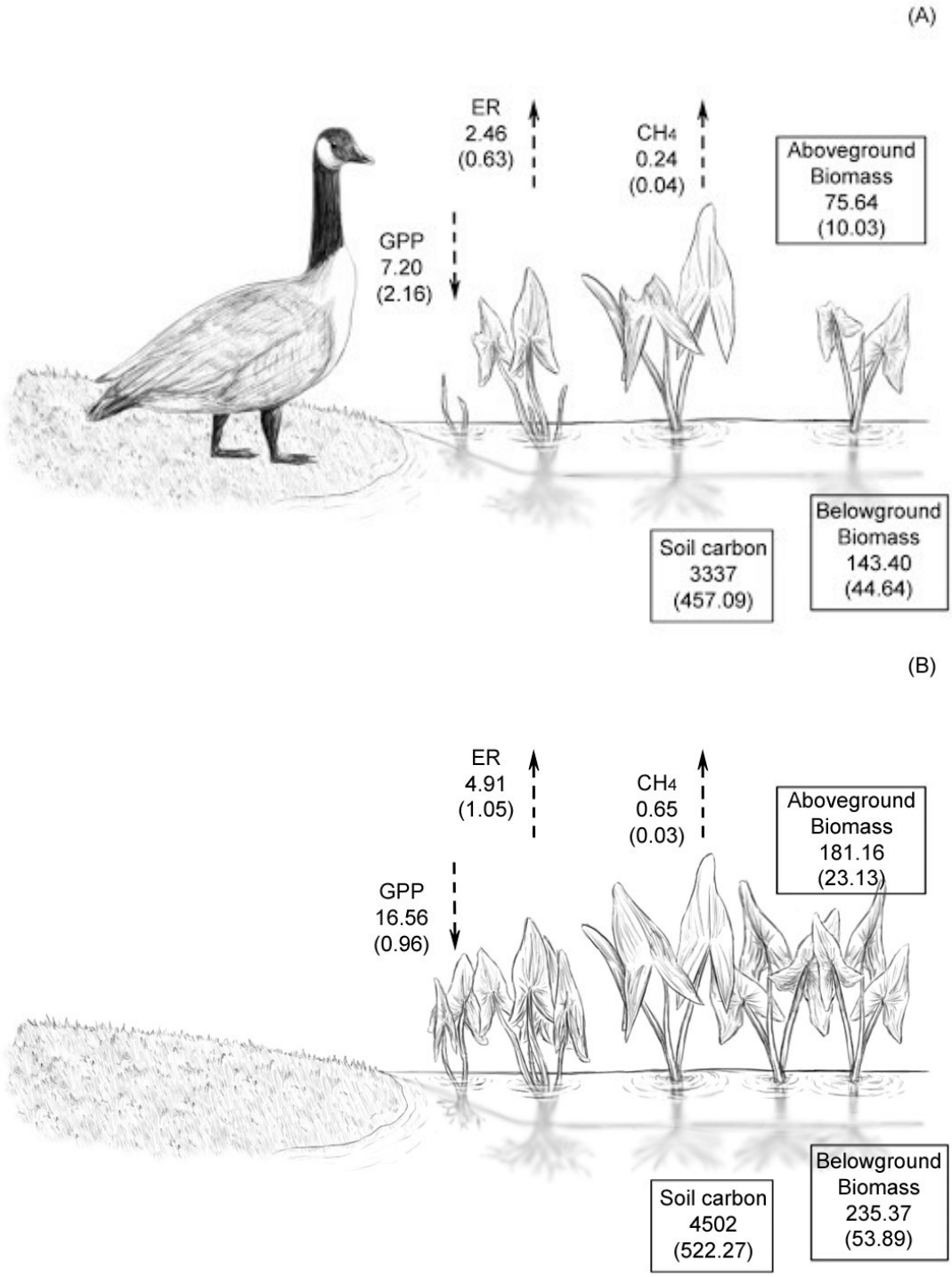

Figure 11. *Schematic of ecosystems with (A) and without (B) grazing. Average values of each variable are listed with standard error in parentheses, with values taken from a caged and uncaged plots in a grazed wetland (A1N) during the peak of the growing season. Carbon pools are denoted by boxes, with units of g m^{-2}, carbon fluxes are denoted by dashed arrows, with units of g m^{-2} day^{-1}.*

Appendix

Table A.1: *Results of ANOVAs examining random block effects test on A1N and A3 parameters. Significant p-values are bolded.*

Factor	Block Effect	
	F	*p*
A1N		
Total plant cover	$F_{3,108}$=2.18	0.09
Aboveground biomass	$F_{3,60}$=1.68	0.18
Belowground biomass	$F_{3,12}$=0.67	0.59
GPP	$F_{1,30}$=0.95	0.39
NEP	$F_{1,29}$=1.02	0.37
ER	$F_{1,29}$=1.86	0.18
Methane (light)	$F_{1,10}$=0.07	0.79
Methane (dark)	$F_{1,10}$=0.40	0.55
Soil C	$F_{3,12}$=2.75	0.09
Soil C:N	$F_{3,26}$=4.63	**0.01**
A3	F	*p*
Total plant cover	$F_{2,109}$=0.12	0.88
Aboveground biomass	$F_{2,61}$=9.07	**<0.01**
Belowground biomass	$F_{2,13}$=0.92	0.42
Soil C	$F_{2,13}$=0.91	0.43
Soil C:N	$F_{2,29}$=14.16	**<0.01**

Table A.2: *Results of two-way ANOVA on the effects and interactions of month (Mo), and treatment (Tr) for vegetation cover A1N and A3 in 2017 and 2018. Significant interactions are bolded, interactions <0.001 are starred.*

Factor	Month		Treatment		Mo x Tr	
	F	*p*	F	*p*	F	*p*
A1N						
Vegetation Cover 2017	$F_{2,93} = 21.06$	**<0.001***	$F_{2,93} = 15.80$	**<0.001***	$F_{2,93} = 0.25$	0.78
Vegetation Cover 2018	$F_{3,166} = 70.34$	**<0.001***	$F_{3,166} = 42.67$	**<0.001***	$F_{3,166} = 2.69$	**0.048**
A3						
Vegetation Cover 2017	$F_{2,93} = 7.87$	**<0.001***	$F_{2,93} = 3.36$	**0.039**	$F_{2,93} = 4.66$	0.051
Vegetation Cover 2018	$F_{3,166} = 16.88$	**<0.001***	$F_{3,166} = 1.53$	**0.015**	$F_{3,166} = 2.05$	0.48

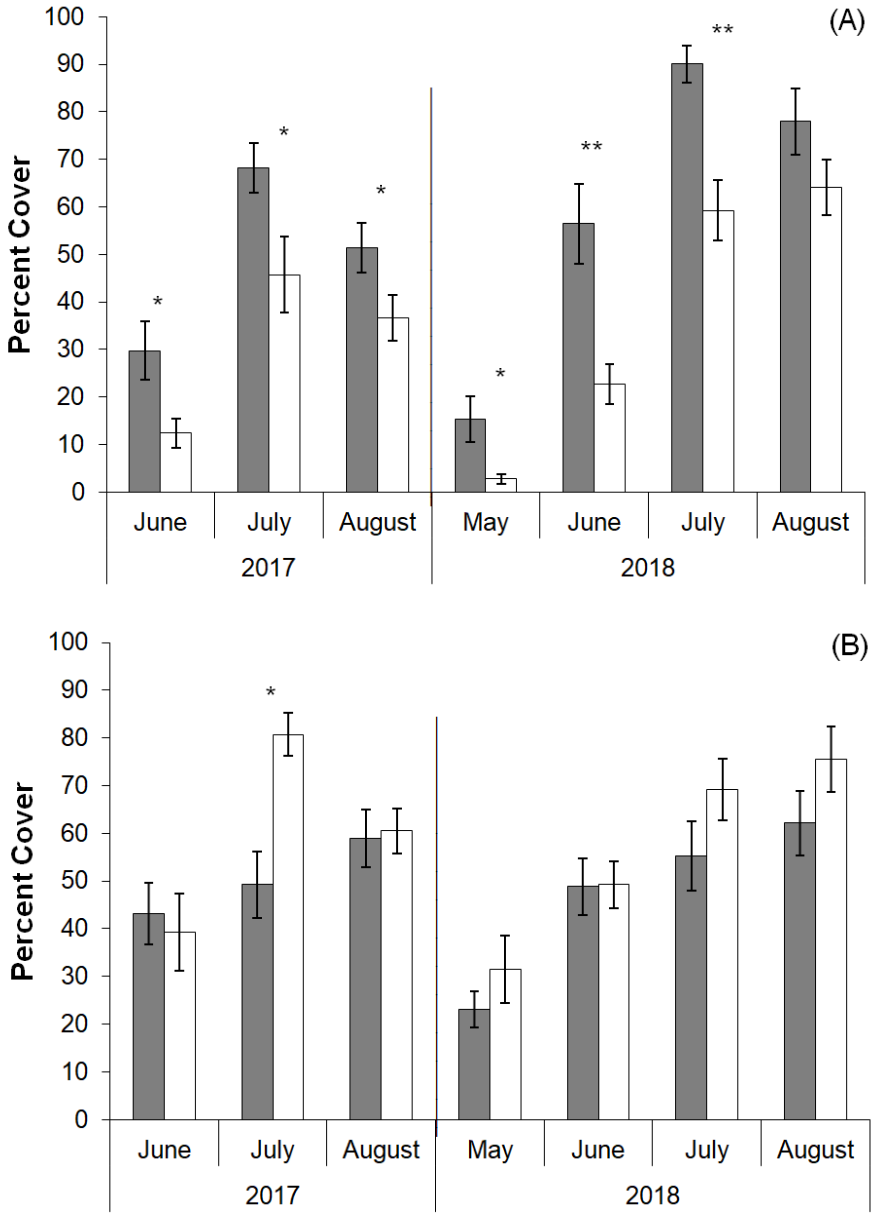

Figure A.1: *Vegetation cover in A1N (A) and A3 (B) during the 2017 and 2018 growing seasons in caged (grey) and uncaged (white) plots. Two stars indicate p < 0.01, one star indicates p < 0.05 between caged and uncaged treatments. In 2017 A1N vegetation cover was significantly highest in July caged and uncaged and August caged. 2018 A1N cover was highest in caged plots in July and August. 2017 A3 cover was highest in July and August, caged and uncaged, and June uncaged. 2018 A3 cover was highest in July uncaged, and August caged and uncaged.*

Table A.3: *Species compositions in A1N and A3 in caged and uncaged plots. '+' indicated species that were present, '-' indicates species that were absent. Stars indicate species that were present but had < 5% cover.*

A1N Caged		2017			2018			
Species	Classification	June	July	August	May	June	July	August
Echinochloa colona	Graminoid	+	+	-	-	-	-	-
Leersia oryzoides	Graminoid	-	+	+	+	+	+	+
Schoenoplectus tabernaemontani	Graminoid	-	-	-	-	+	+	+
Alisma plantago-aquatica	Herbaceous	+	+	+	+	+	+	+
Lythrum salicaria	Herbaceous	-	+*	+	+*	+*	+*	+*
Nymphaea odorata	Herbaceous	+	+	-	+	+	+	+
Pontederia cordata	Herbaceous	-	+	+	+	+	+	+
Potamogeton crispus	Herbaceous	+	+	+	-	+	+	+
Sagittaria filiformis	Herbaceous	+	+	+	+	+	+	-
Sagittaria latifolia	Herbaceous	+	+	+	-	-	+	+
Typha latifolia	Herbaceous	+	-	+	+	+	+	+

A1N Uncaged		2017			2018			
Species	Classification	June	July	August	May	June	July	August
Echinochloa colona	Graminoid	-	-	-	-	-	-	-
Leersia oryzoides	Graminoid	-	+	+	-	-	+	-
Schoenoplectus tabernaemontani	Graminoid	-	-	-	-	-	-	-
Alisma plantago-aquatica	Herbaceous	-	+*	-	+*	-	+*	+
Lythrum salicaria	Herbaceous	-	-	-	-	-	-	-
Nymphaea odorata	Herbaceous	+*	+	+	+	+	+	+
Pontederia cordata	Herbaceous	-	+	+	+	+	+	+
Potamogeton crispus	Herbaceous	+	+	+	-	+	+	+
Sagittaria filiformis	Herbaceous	+	+	+	+	+	+	+
Sagittaria latifolia	Herbaceous	+*	+	+	-	-	+	+
Typha latifolia	Herbaceous	+	-	-	-	-	-	-

A3 Caged		2017			2018			
Species	Classification	June	July	August	May	June	July	August
Andropogon gerardii	Graminoid	+	+	+*	-	+	-	-
Cynodon dactylon	Graminoid	-	-	+*	+*	+	-	-
Cyperus esculentus	Graminoid	+	+	+	-	+*	-	-
Echinochloa colona	Graminoid	+*	+*	-	-	-	+	+
Eleocharis obtusa	Graminoid	+*	-	-	-	-	-	-
Juncus inflexus	Graminoid	-	+	+	-	+	+	+
Leersia oryzoides	Graminoid	+*	+*	-	+*	-	-	-
Phalaris arundinacea	Graminoid	+	+	+	+	+	+	+
Schoenoplectus tabernaemontani	Graminoid	+	-	-	+	+	-	-
Alisma plantago-aquatica	Herbaceous	-	-	-	-	-	-	-
Asteraceae solidago	Herbaceous	-	+	-	+	+	+	+
Atropa belladonna	Herbaceous	-	-	+*	+*	+*	+	+
Cirsium vulgare	Herbaceous	-	-	-	+*	+	+	+
Daucus carota	Herbaceous	-	-	-	-	-	-	-
Dipsacus sylvestris	Herbaceous	-	-	-	-	-	-	-
Epilobium hirsutum	Herbaceous	+*	+	+	+*	-	+	+
Erechtites hieraciifolius	Herbaceous	+*	-	+*	-	-	-	-
Eupatorium maculatum	Herbaceous	+	+	+	-	+	+*	+*
Eupatorium perfoliatum	Herbaceous	-	-	-	-	-	-	-
Leucanthemum vulgare	Herbaceous	+*	+	+	-	-	+	+
Lythrum salicaria	Herbaceous	-	+	+	+*	+	+	+
Persicaria maculosa	Herbaceous	-	-	-	-	-	-	-
Persicaria pennsylvanica	Herbaceous	-	-	-	+*	+*	+*	+*
Persicaria punctata	Herbaceous	+	+	+	-	-	+	+
Polygonum pensylvanicum	Herbaceous	+	+	+	+	+	+	+
Potamogeton crispus	Herbaceous	-	-	-	-	-	+	+
Sagittaria filiformis	Herbaceous	+	+	+*	-	+	-	-
Sagittaria latifolia	Herbaceous	-	+	-	-	-	+	+
Taraxacum officinale	Herbaceous	+*	+	+*	+*	+	+	+
Typha angustifolia	Herbaceous	+*	+	+	+*	+	+	+
Typha latifolia	Herbaceous	+*	-	+*	+	-	+*	+*
Xanthium strumarium	Herbaceous	-	-	-	-	-	-	-
Eastwoodia elegans	Shrub	+	+	+*	+	-	+	+

A3 Uncaged		2017			2018			
Species	Classification	June	July	August	May	June	July	August
Andropogon gerardii	Graminoid	+	-	-	-	-	-	-
Cynodon dactylon	Graminoid	+	+	-	-	-	+	+
Cyperus esculentus	Graminoid	+*	+	+	-	+*	+	-
Echinochloa colona	Graminoid	-	+	+	+	+	+	-
Eleocharis obtusa	Graminoid	+	+	+	-	+	+	+
Juncus inflexus	Graminoid	-	+	+*	+*	-	-	-
Leersia oryzoides	Graminoid	+*	+	+	+	+	+	+
Phalaris arundinacea	Graminoid	+	+	+	+	+	+	+*
Schoenoplectus tabernaemontani	Graminoid	+	-	-	+	+	+	+*
Alisma plantago-aquatica	Herbaceous	+	+	+	+	+	+	+
Asteraceae solidago	Herbaceous	-	+	+	+	+*	+	+*
Atropa belladonna	Herbaceous	-	+	+	+	+	+	+
Cirsium vulgare	Herbaceous	-	-	-	-	+	+	+
Daucus carota	Herbaceous	+	+	+	-	+*	+*	+
Dipsacus sylvestris	Herbaceous	+	-	-	-	-	-	-
Epilobium hirsutum	Herbaceous	+	-	-	+	-	-	+
Erechtites hieraciifolius	Herbaceous	-	-	-	-	-	+	+
Eupatorium maculatum	Herbaceous	-	-	+*	-	+*	+	+
Eupatorium perfoliatum	Herbaceous	-	-	-	+*	+*	+	+
Leucanthemum vulgare	Herbaceous	-	+*	-	-	-	-	+
Lythrum salicaria	Herbaceous	-	+	+	+*	+	+	+
Persicaria maculosa	Herbaceous	-	-	-	+*	-	+	-
Persicaria pennsylvanica	Herbaceous	+	+	-	+	+	+	-
Persicaria punctata	Herbaceous	+	+*	-	-	-	+	-
Polygonum pensylvanicum	Herbaceous	+	+	+	-	+	+	+
Potamogeton crispus	Herbaceous	+	-	-	-	-	-	-
Sagittaria filiformis	Herbaceous	+	+	+*	-	+*	-	-
Sagittaria latifolia	Herbaceous	-	+	-	-	-	+*	-
Taraxacum officinale	Herbaceous	+	-	+*	-	+	-	-
Typha angustifolia	Herbaceous	+*	+	+*	+	+	+	+
Typha latifolia	Herbaceous	+	+	+	+	-	+	+
Xanthium strumarium	Herbaceous	-	+*	-	-	-	+	+
Eastwoodia elegans	Shrub	+*	+	+	-	-	+	+

Table A.4. *Regression curves used to estimate aboveground biomass.*

Species	Common Name	Site	Measured characteristics	Equation	R^2
A. plantago-aquatica	Water Plantain	A1N, A3	Stem height	$y = 0.0083x^{1.4622}$	0.9866
A. solidago	Goldenrod	A3	Stem height	$y = 0.0008x^{2.1044}$	0.8565
Cyperus spp.	Sedge	A1N, A3	Stem height	$y = 0.0003x^{1.7334}$	0.9397
D. carota	Queen Anne's Lace	A3	Stem height	$y = 9E\text{-}06x^{2.9424}$	0.8559
J. inflexus	Hard Rush	A3	Stem height	$y = 5E\text{-}05x^{2.1626}$	0.8933
L. oryzoides	Rice Cut Grass	A1N	Stem height	$y = 3E\text{-}05x^{2.3}$	0.8141
L. salicaria	Purple Loosestrife	A1N, A3	Height of tallest branch	$y = 0.0003x^{2.3441}$	0.9402
N. odorata	Pond Lily	A1N	Diameter of leaf	$y = 0.0015x^{2.4125}$	0.9534
P. arundinacea	Reed Canary Grass	A3	Stem height	$y = 3E\text{-}05x^{2.5}$	0.8243
P. cordata	Pickerel Weed	A1N	Stem height	$y = 0.0002x^{1.9867}$	0.8741
P. crispus	Pondweed	A1N	Length of leaf	$y = 4E\text{-}05x^{3.3901}$	0.7086
Polygonum spp.	Smartweed	A3	Height of tallest branch	$y = 0.0005x^{2.2375}$	0.9286
S. filiformis	Narrowleaf Arrowhead	A1N	Area of leaf	$y = 0.0089x^{1.1331}$	0.9688
S. latifolia	Broadleaf Arrowhead	A1N	Area of leaf	$y = 0.0084x^{1.1062}$	0.9498
T. angustifolia	Narrowleaf Cattail	A3	Stem height	$y = 6E\text{-}07x^{3.2183}$	0.8078
T. latifolia	Broadleaf Cattail	A1N, A3	Stem height	$y = 2E\text{-}05x^{2.7462}$	0.8664

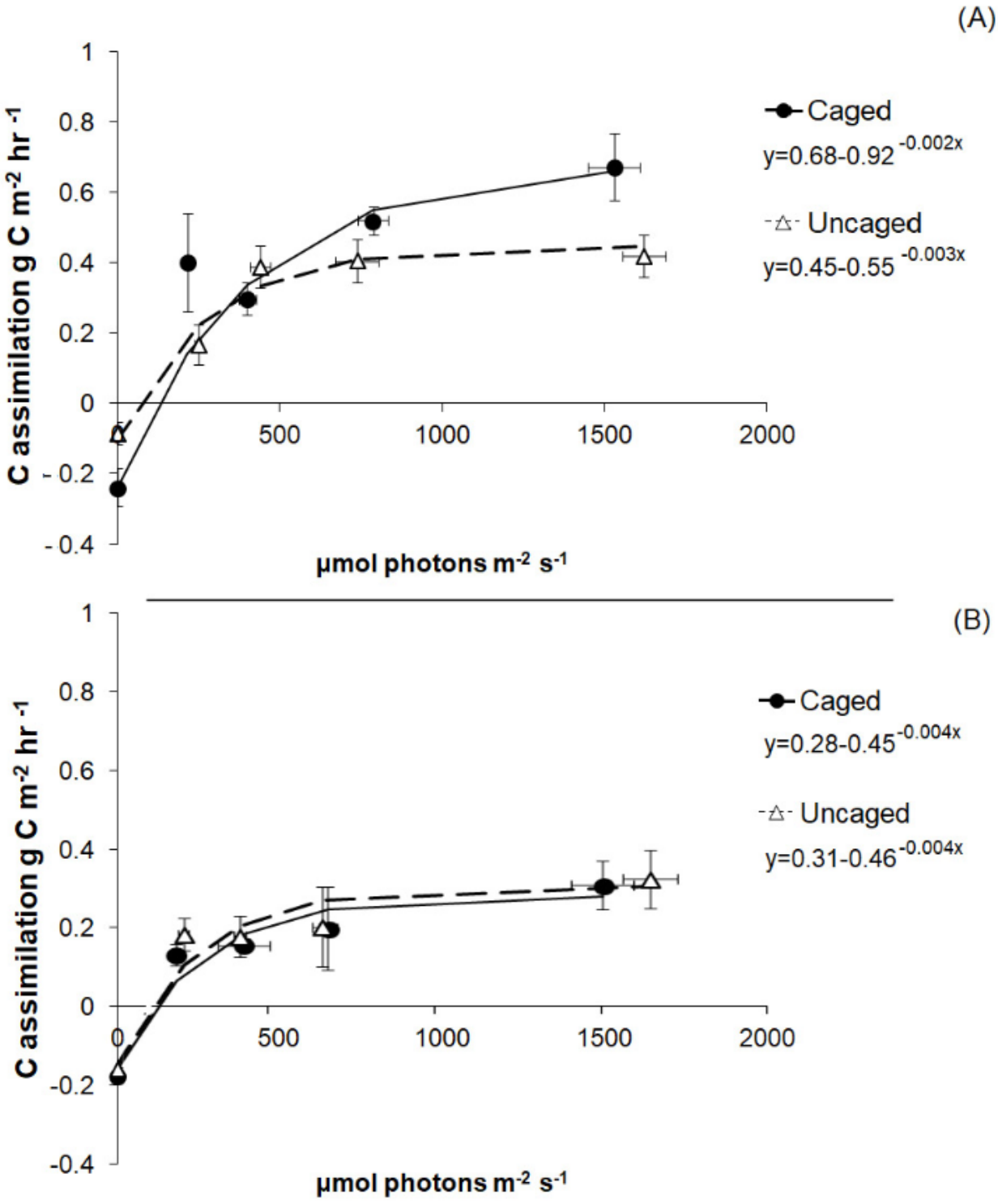

Figure A.2. *Photosynthetic light response curves for net ecosystem production (NEE) in summer, June 1 - August 14 (A) and fall, August 15 - September 30 (B). Equations for each line are listed in the legend.*

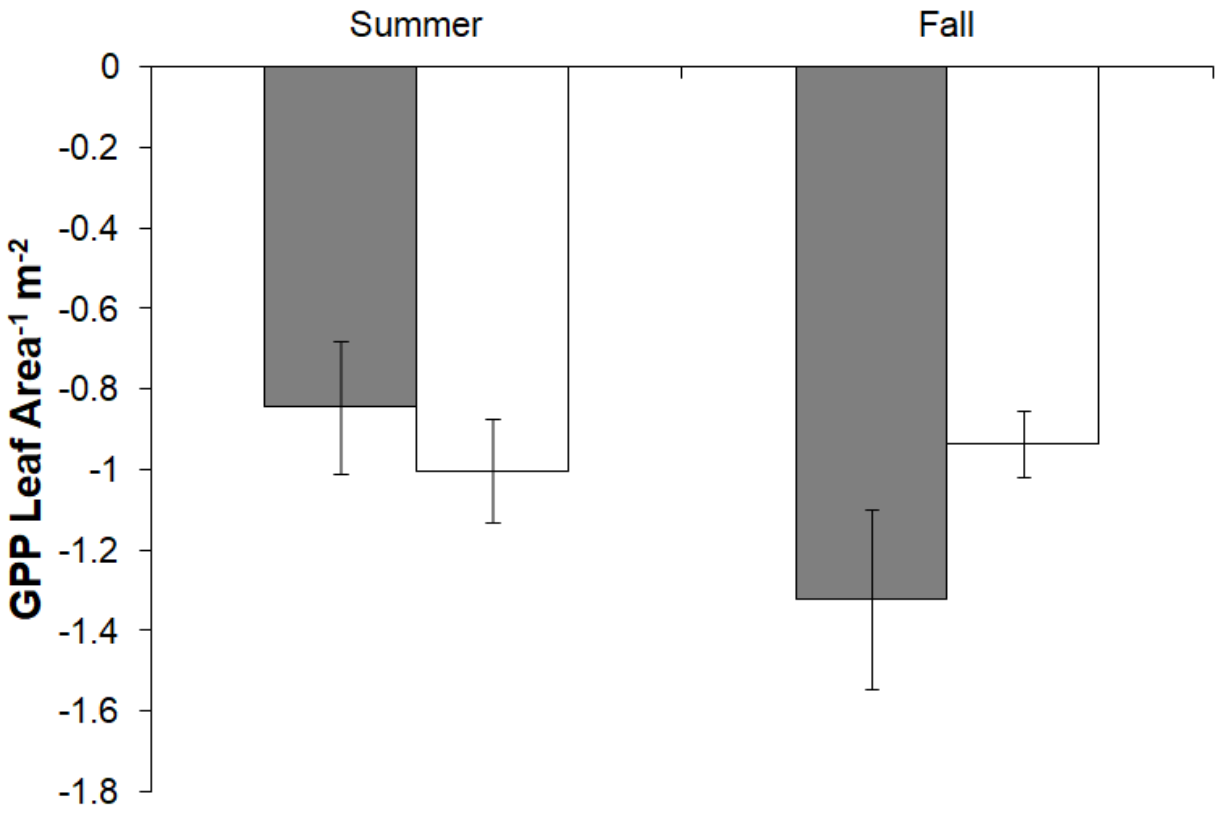

Figure A.3. *GPP (g C m^{-2} hr^{-1}) per leaf area (m^2) for summer and fall of 2018.*