Title:
Examination of nitrate cycling and retention mechanisms in a semi-arid floodplain

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Abstract:

There is a paucity of process-level information regarding nutrient dynamics in floodplain ecosystems, particularly in arid and semi-arid environments. Similarly, few studies directly address the significance of spatiotemporal heterogeneity on floodplain biogeochemical processes. This study used isotopic nitrate (NO_3-^{15}N) enrichment to identify major N-cycling pathways in a semi-arid floodplain. Mesocosms were placed in a floodplain and received one of three nutrient amendments: ambient (control - CTR), $^{15}NO_3$-N at 5 mg L^{-1} (^{15}N) or $^{15}NO_3$-N at 5 and PO_4-P at 1mg L^{-1} (^{15}N+P). We examined spatial heterogeneity by using soils from two extensive floodplain habitats: forests and grasslands; while temporal effects were addressed by performing experiments during seasons with distinct temperature regimes (April and July). The mean water temperature was significantly higher in July than April (29.2 ± 0.2 and 17.5 ± 0.1°C), as were nitrate loss rates ($K_{NO3\text{-}N}$) (23.1 ± 0.9 and 16.6 ± 1.2 µg L^{-1} hr^{-1}) and initial Chl-*a* concentrations (226.8 ± 4.3 and 5.0 ± 0.1 µg L^{-1}). The increase in Chl-*a* concentrations during the experiments was similar for both sampling dates. The phytoplankton community was dominated by chlorophytes and diatoms in April, and euglenophytes and N-fixing cyanobacteria in July. Isotopic mass balance and Chl-*a* data suggest resource competition between phototrophic and heterotrophic organisms at warmer temperatures. However, temporal differences in N-cycling could not be solely attributed to temperature. Mass balance and soil nutrient analysis suggest that cooler temperatures coupled with preceding moist soil conditions enabled the soil biota to play a larger role in sequestering water column nutrients. The possible increase in labile organic matter coupled with warmer temperatures in July appeared to enhanced microbial catabolism resulting in higher potential denitrification and an eventual loss of N from the water column.

Introduction:

Flood pulsing is the primary physical process altering floodplain biogeochemical processes, biological production and ecological state (Junk et al., 1989; Tockner et al., 2000, Scholz et al., 2002). Following a flood pulse, and at the onset of river-floodplain hydrologic disconnection, floodplain processes are biologically driven; primary production, resource competition and in situ nutrient cycling increase while nutrient spiraling decreases (Hein et al., 1999; Vegas-Vilarrubia and Herrera, 1993; Tockner, 2000). However, as hydrologic residence time increases, nutrient limitations increase and water column primary productivity decreases (Ertl, 1995; Hein et al., 1999; Castillo, 2000). Thus, the nutrient cycling mechanisms within a floodplain are constantly changing.

In addition, floodplains are spatially heterogeneous; a characteristic that appreciably impacts nutrient cycling dynamics and results in patchiness of floodplain biogeochemical processes (Ward and Stanford, 1995; Schilling and Lockaby, 2005). Flood pulsing causes floodplain areas to transition from terrestrial to aquatic habitats. Once hydrologic disconnection and dry out ensue, these flooded areas may rapidly shift back to terrestrial habitats or remain inundated, significantly altering the existing nutrient pools and associated fluxes.

Flood timing plays an equally important role in controlling floodplain nutrient pools and fluxes (Malard et al., 2000; Robertson et al., 2001). Ahearn et al. (2004) describe stream runoff hydrologic seasons which are characterized by distinct physiochemical properties. Flood pulse physiochemical characteristics, such as nutrient concentrations and water temperature can enhance or reset floodplain biogeochemical cycles during hydrologic disconnection (Gallo et al., in review). Current literature demonstrates that the constant shift from aquatic to terrestrial habitats is important in maintaining floodplain function (Ward and Stanford, 1995; Scholz et al.,

2002; Arthington et al., 2005; Walls et al., 2005), yet the biogeochemical mechanisms though which floodplain function is preserved, particularly in arid systems, are weakly understood.

Many floodplain studies have focused on nutrient cycling and spiraling within the aquatic ecosystem and have overlooked the impact of soils on nutrient fluxes during hydrologically static conditions. While there is an extensive body of literature examining water column nutrient cycling and resource competition within lakes, streams, permanently flooded wetlands and temporary agricultural wetlands such as rice paddies, few studies such as those performed by Heffernan and Sponseller (2004), Van Der Lee et al. (2004), Valett et al. (2005), and Sheibley et al. (in review) address the role of soils in arid and semi-arid floodplain systems.

A majority of permanently flooded wetlands are sinks of particulate and dissolved nitrogen and phosphorous; while riparian buffer strips tend to be sinks for total nitrogen, total phosphorous and dissolved inorganic nitrogen, and sources of soluble reactive phosphorous (Fisher and Acreman, 2004). The results from the large body of literature regarding N-cycling in permanent wetlands is to a degree inapplicable to arid floodplain systems due to the pulsing nature of floodplains as actively flooded wetlands. In addition, riparian buffer strips tend to lack the spatial heterogeneity and hydraulic retention that make floodplains ecologically significant.

The increase in public awareness and scientific interest in the restoration and adaptive managements of river-floodplain systems make information regarding nutrient cycling of particular importance in establishing successful management strategies and achievable restoration goals. The primary objective of this research was to use ^{15}N enrichment field mesocosm experiments and natural $\delta^{13}C$ analysis to identify the major fluxes of dissolved inorganic nitrogen (DIN), specifically in the form of nitrate (NO_3-N) following inundation in a semi-arid floodplain. Due to the low ambient NH_4 concentrations at the experimental floodplain

(Gallo et al., in review), we have focused our study on NO_3-N dynamics. A simplified conceptual model of the nitrogen cycle in a floodplain during anoxic soil conditions is illustrated in Figure 1.

Our study site, a floodplain located in the California Central Valley has been documented to have water column NO_3-N concentrations as high as 6.5 mg L^{-1} during hydrologically static conditions (Gallo, unpublished data) and high concentrations of NO_3 inputs from the river onto the floodplain (>1mg L^{-1}) (Ahearn et al., 2004). Although data demonstrate that the floodplain has the ability to process high concentrations of dissolved nitrate (Gallo et al., in review; Sheibley et al., in review), the mechanisms through which NO_3-N is cycled remained largely unidentified.

Methods:

Study Site –

The experiments were performed at the Cosumnes River Preserve floodplain, 34 km south of Sacramento in the Central Valley of California. The field site is at an elevation of 1.5 m to 4 m above sea level and has a Mediterranean climate with average rainfall of 46cm yr^{-1}, most of which occurs during the winter and spring months. Because there are no major water diversions or impoundments along the Cosumnes River, the floodplain responds to the natural winter and spring watershed hydrology (Whitener and Kennedy, 1999).

The experimental mesocosms were placed in a floodplain pond which in most years remains inundated until late summer. Natural restoration processes at the site have resulted in high floodplain spatial (habitat) heterogeneity, which includes ponds, herbaceous grasslands and early and mid successional forests (add reference here?). Soil cores from a floodplain forest and grassland were chosen for our experiment based on previous monitoring at the study site, which

documented dramatic post-flooding water quality changes between a flooded grassland and forest (Gallo, unpublished data). In addition, these two habitats cover extensive floodplain surface area, therefore we chose to use grassland and forest soils in order to assess spatial heterogeneity effects on NO_3-N cycling and aquatic geochemistry.

Experimental design:

Soil cores 15 cm in depth from the grassland (herein grass) and forest were placed in 5.1 cm diameter x 100 cm height clear polycarbonate tubes. Each tube received 1 of 3 water column nutrient amendments: control (CTR), $^{15}NO_3$-N addition at 5 mg L^{-1} (^{15}N) and $^{15}NO_3$-N addition at 5 mg L^{-1} + PO_4-P addition at 1 mg L^{-1} (^{15}N+P). Phosphorous was added at 1 mg L^{-1} in order to eliminate phosphorous limitation within one set of replicates. Nitrogen was added as 98% ^{15}N-KNO_3 and phosphorous was added as $NaH_2PO_4 . H_2O$. In order to assess the temporal aspect of nutrient cycling, the experiments were conducted in spring (April) and summer (July) of 2003, months with distinctly different temperature regimes. There were 3 replicates of each soil type x nutrient treatment combination for a total of 18 columns per date. All the nutrient addition solutions were prepared in the field utilizing floodplain pond water. The pond water was filtered through 150μm mesh to exclude macro-zooplankton and minimize herbivory effects. Each tube was capped and sealed at the bottom (the soil end) in order to prevent water losses or additions due to changes in the piezometric head of the pond; and was capped at the top (the water surface end) to prevent material from falling into the tube during the duration of the experiment. We drilled holes on the sides of the tubes to allow for air circulation.

The mesocosms were placed in the floodplain pond at a water depth of 85 cm during April and 75 cm during July. We use a completely randomized design and used SAS V8 (The SAS Institute) to randomize the placement of the tubes in the field. We placed a HOBO water

temperature logger (Onset Corp., model H20-001) adjacent to our mesocosms in order to monitor diel temperature changes. The logger recorded data ever 30 minutes for the duration of the experiment.

Every 24 – 72 hours we took in vivo chlorophyll a (Chl-*a*) readings using a hand held field fluorometer (Turner Designs Aquafluor). Simultaneously we collected and field filtered (0.2µm syringe filters - Pall Acrodisk) water samples for nitrate nitrogen (NO_3-N) and orthophosphate (PO_4-P) analysis. The experiments continued until NO_3-N concentrations of the ^{15}N and ^{15}N + P treatments approached ambient levels (approximately 0.02 – 0.05 mg L^{-1}).

Water and Soil Analysis:

At the completion of the field study, the mesocosms were removed from the pond and the remaining water poured into bottles; the soil cores remaining in the tubes were tightly sealed and kept intact. During this process we lost one April*forest*control replicate. The water and soil were kept cool and dark until laboratory processing.

We analyzed our water samples for total suspended solids (TSS), volatile suspended solids (VSS), NO_3-N, PO_4-P and initial and final chlorophyll-a ($_{init}$Chl-*a*, $_{final}$Chl-*a*). We determined TSS by filtering water through a 0.45 µm pre-weighed 25 mm glass fiber filter (Whatman), weighing the filter after drying it at 60 ºC for 24 – 48 hours, and taking the difference between the two weights. VSS was determined by combusting the TSS samples in a muffle furnace at 500°C for 2 hours. We used the conductimetric analyzer method described by Carlson (1986) and Yu et al. (1994) to determine NO_3-N, and a spectrophotometer (Perking Elmel Lambda 38) with the method described by Clescseri et al. (1998) to determine PO_4-P in the water samples. Laboratory chlorophyll-a (Chl-a) measurements were made using the pigment extraction fluorometric method described by Clescseri et al. (1998).

KCl extraction was used to determine the amount of exchangeable or available nitrogen (N_{soil_ex}) from the top 3 cm of the soil cores (Stark and Hart, 1996). We analyzed the extract using the conductimetric analyzer method. In addition, we measured redox potential (Eh) of the soil cores when they were removed from the plastic tubes using a platinum electrode and Zobell's solution.

We qualitatively analyzed the algal community present in the mesocosms, and identified the most common taxa to the lowest possible taxonomic level using the keys provided by Entwisle et al. (1997).

Nitrate loss rates:

Some mesocosms reached ambient NO_3-N levels before the end of the experiment, while some did not completely reach ambient levels. Therefore, using JMP IN 5.1 (The SAS Institute) and based on goodness of fit (r^2 and p-values) we applied either a linear or quadratic regression model to our daily NO_3-N concentrations in order to calculate the time in days (t) that it took each mesocosm to reach ambient concentrations as follows:

$$t = m * 0.05 + I$$

$$t = (a * 0.05)^2 + (b * 0.05) + c$$

Where m is the slope of the line in L.days mg^{-1}, I is the y-intercept in days, 0.05 is the ambient NO_3-N concentration in mg $L^{-1}$and a, b and c are regression constants in $days^{1/2}$ L mg^{-1}, days L mg^{-1} and days, respectively. Because most of the data fit a quadratic model, we were unable to apply a simple linear regression in order to determine the NO_3-N loss rate (as the slope of the regression). Therefore, the NO_3-N loss rate (k_{NO_3-N}) for each ^{15}N and ^{15}N +P mesocosm was calculated as follows:

$$k_{NO3-N} = \frac{[i] * 1000}{t * 24}$$

Where k is in μg $L^{-1}hr^{-1}$, i is the initial NO_3-N concentration in mg L^{-1} and t is the time in days to reach ambient NO_3-N concentrations. Quadratic models present changing rates, therefore the nitrate loss rates reported are averaged over t.

Isotope analysis:

We collected particulate matter on pre-combusted and weighed 0.45μm glass fiber filters (Whatman) in order to determine the ^{15}N ($^{15}_{TSS}N$), total nitrogen ($_{TSS}TN$), $\delta^{13}C$ ($\delta^{13}_{TSS}C$), and total carbon ($_{TSS}TC$) pools of suspended solids, which included algae, large bacterioplankton and microzooplankton (<150 μm). Filters were dried at 60°C until they reached constant weight and the filters were packed into tin capsules for combustion and introduction into the mass spectrometer as described by Dalsgaard et al. (2000) and Harris (UC Davis stable isotope facility), and were analyzed with a Europe Integra Mass spectrometer.

The upper 3 cm of soil was prepared for determination of the ^{15}N soil pool ($^{15}_{soil}N$), which included ^{15}N assimilated by soil flora and fauna, as well as exchangeable or available inorganic ^{15}N. Soil samples were air dried, ground, and weighed into tin capsules for ^{15}N-total nitrogen ($_{soil}TN$), $\delta^{13}C$ ($^{13}_{soil}C$) and soil carbon ($_{soil}C$) analysis as described by Boutton and Yamasaki (1996) and Harris (UC Davis stable isotope facility).

Mass balance:

Mass in mg of ^{15}N for each of the nitrogen pools was calculated as follows:

Initial and final NO_3-^{15}N in water column ($^{15}_{NO3-N\ \text{initial}}N$; $^{15}_{NO3-N\ \text{final}}N$):

$$^{15}_{NO3-N\ \text{initial}}N = (NO_3\text{-}N_{initial} - NO_3{-}N^{CTR}_{initial})* WV_{initial} *0.98$$

$$^{15}_{NO3-N\ \text{final}}N = (NO_3\text{-}N_{final} - NO_3{-}N^{CTR}_{final})* WV_{final} *0.98$$

Where NO_3-$N_{initial}$ and NO_3-N_{final} are NO_3-N concentrations in mg L^{-1}, $WV_{initial}$ and WV_{final} are the initial and final water volumes in each experimental tube in L, $NO_3-N_{initial}^{CTR}$ and $NO_3-N_{final}^{CTR}$ are the mean ambient NO_3-N concentrations (from the CTR treatments) and 0.98 denotes the percent concentration of ^{15}N in the KNO_3 added.

The NO_3-^{15}N removed from the water column for analytical purposes during the experiment ($_{removed}^{15}N$) was calculated as:

$$_{removed}^{15}N = (WV_{initial} - WV_{final}) * \overline{NO_3\text{-}^{15}N} * 0.98$$

Where $\overline{NO_3\text{-}^{15}N}$ is the average water column NO_3-N concentration in mg L^{-1} in each tube over the duration of the experiment.

Isotopic nitrogen as suspended solids (algae + microzooplankton) in the water column at the end of the experiment ($_{TSS}^{15}N$) was calculated as:

$$_{TSS}^{15}N = TSS * WV_{final} * {}^{15}N_{TSS}$$

Where TSS are total suspended solids in the water column of each tube in mg L^{-1}, and $^{15}N_{TSS}$ is the mass of ^{15}N in mg per mg of suspended solids from isotopic analysis.

Exchangeable or available ^{15}N and ^{15}N incorporated into soil biomass ($_{soil}^{15}N$) was calculated as:

$$_{soil}^{15}N = WT_{soil} * {}^{15}N_{soil}$$

Where WT_{soil} is the dry weight of the top 3 cm of our soil cores in g and $^{15}N_{soil}$ is the mass of ^{15}N in mg per g of dry soil.

The ^{15}N mass balance equation for each of the ^{15}N and ^{15}N+P treatments is:

$$_{NO3-N\ \text{initial}}^{15}N = {}_{NO3-N\ \text{final}}^{15}N + {}_{removed}^{15}N + {}_{TSS}^{15}N + {}_{soil}^{15}N + {}_{unacc}^{15}N$$

where the ^{15}N unaccounted for in our analysis was assumed to be due primarily to denitrification and (${}_{vol+den}{}^{15}N$) was calculated as follows:

$$ {}_{unacc}{}^{15}N = {}_{NO3\text{-}N\text{initial}}{}^{15}N - ({}_{NO3-N\ final}{}^{15}N + {}_{TSS}{}^{15}N + {}_{soil}{}^{15}N + {}_{removed}{}^{15}N) $$

Statistical Analysis:

We performed repeated-measures analysis on our daily fluorescence and PO_4-P data using SAS V8 (The SAS Institute). We performed ANCOVA analysis using ${}_{init}$Chl-*a* as the covariate to determine if there were significant differences in ${}_{final}$Chl-*a* levels between treatments, and Welch ANOVA tests to determine if there were significant differences in ${}_{init}$Chl-*a*, ${}_{final}$Chl-*a* and PO_4-P within treatments. ANCOVA analysis, as described by Steel et al., (1997) and J. Dubcovsky (personal communication) were performed using JMP IN 5.1 (The SAS Institute) on *t*, $k_{NO3\text{-}N}$, N_{soil_ex}, ${}_{removed}{}^{15}N$, ${}_{TSS}{}^{15}N$, ${}_{soil}{}^{15}N$, ${}_{unacc}{}^{15}N$ and TSS using ${}_{NO3-N\ initial}{}^{15}N$ as the covariate. We transformed the ${}_{NO3-N\ final}{}^{15}N$ and ${}_{unacc}{}^{15}N$ data prior to ANCOVA analysis in order to meet normality of residuals. We performed ANOVA analysis in soil and TSS carbon to nitrogen ratios (${}_{soil}$C:N, ${}_{TSS}$C:N), $\delta\,{}_{soil}{}^{13}C$, $\delta\,{}_{TSS}{}^{13}C$ and ${}_{soil}$TN. We used the Tukey-Kramer test to compare means and Cochran's C to test for homogeneity of variances in all of our data.

Results:

Unless otherwise noted, all significant differences mention henceforth are at $p \leq 0.05$.

Water and Soil Analysis:

Mean water temperatures in April were significantly lower than July temperatures (17.5 ± 0.1°C and 29.2 ± 0.2°C, respectively). Water temperatures ranged from 12.8°C to 23.6°C in April and from 24.2 to 36.9 in July, with a significantly larger diel temperature variations in July than April (8.7 ± 0.6°C and 4.1 ± 0.2°C, respectively). There was significantly

more $_{NO3-N\ \mathrm{initial}}{}^{15}\mathrm{N}$ in the April experiment than in the July experiment (6.41 ± 0.05 mg and 5.99 ± 0.03 mg, respectively). The experiments had significantly different average durations of 13.6 ± 1.0 days in April, and 8.0 ± 0.3 days in July (Table 1). The water column had significantly less TSS in April than July (28.8 ± 9.3 mg L^{-1} and 68.9 ± 15.6 mg L^{-1}, respectively) and there were no significant differences across nutrient treatments or habitats within dates. The %VSS (mass loss on ignition) ranged between 73 and 92% of TSS with no significant differences observed between treatments. The redox potential of the soil replicates at the end of the experiments was in the +100 to +250 mV range, well within anoxic soil conditions.

There were no significant differences in $_{init}$Chl-*a* between soil type x nutrient treatment within each experimental date (Table 2), but there was significantly more $_{init}$Chl-*a* in July than April (226.8 ± 4.3 ppb and 5.0 ± 0.1 ppb, respectively). In-vivo fluorescence peaked at days 10 and 13 in April, and on the last day in July (Figure 3). In April the CTR treatments had significantly less $_{final}$Chl-*a* than the ^{15}N and the ^{15}N+P treatments, and did not have a significant increase of Chl-*a* over the duration of the experiment ($p<0.05$). Interestingly, while there were no significant differences in $_{final}$Chl-*a* between treatments in July, the ^{15}N+P treatment did not exhibit a significant increase in Chl-*a* over the duration of the experiment (Figure 4).

The algal taxa observed in April were markedly different from the taxa observed in July. The April phytoplankton community was dominated by the Chlorophytes *Scenedesmus* spp., *Ankistrodesmus* spp. and *Botryococcus* spp.; and the Diatoms *Navicula* spp. and *Synedra* spp. In contrast, the July community was dominated by Euglenophytes, the Chlorophyte *Chlamydemonas* spp. and N-fixing cyanobacteria, including *Microcystis* spp., *Anabaena* spp. *and Nodularia* spp.

Initial (day 0) PO_4-P concentrations were significantly higher in July than April (1.27 ± 0.22 mg L^{-1}, 0.41 ± 0.12 mg L^{-1}, respectively), with the ^{15}N+P having significantly higher PO_4-P concentrations than the CTR and ^{15}N treatments within each date (Table 2). There was a significant decrease of PO_4-P in the CTR and ^{15}N treatments during the first 24 hours of the experiment in July, and no significant changes in April (Figure 5). In addition, there were no significant PO_4-P differences between the CTR and ^{15}N treatments within dates or between soils.

There were no significant differences in $_{soil}N$ between nutrient treatments or dates, however, there were significant differences in $_{soil}N$ across date*habitat treatments with the highest concentrations in the April*forest treatments and the lowest in April*grass (Table 3). The forest soils had significantly higher soil available N (N_{soil_ex}) in July than in April (89.5 ± 4.3 μg g^{-1}, 37.9 ± 2.4 μg g^{-1}, respectively) and the forest soil had higher available N than grassland soil (68.9 ± 8.2 μg $g^{-1}$and 58.6 ± 5.7 μg g^{-1}, respectively). The July*forest treatments had the highest levels of N_{soil_ex}, while the April*forest treatments had the lowest (Table 3).

Nitrate loss rates:

April $k_{NO3\text{-}N}$ were significantly slower than July rates (16.6 ± 1.2 ug L^{-1} hr^{-1}, 23.1 ± 0.9 ug L^{-1} hr^{-1}, respectively). The ^{15}N treatments had significantly slower $k_{NO3\text{-}N}$ than the ^{15}N+P treatments (17.4 ± 1.6 μg L^{-1} hr^{-1}, 22.2 ± 0.7 μg L^{-1} hr^{-1}, respectively). Overall, the July*grass treatments had the fastest $k_{NO3\text{-}N}$, while the April*^{15}N treatments had the slowest (Table 1). There were no significant changes in NO_3-N concentrations of the CTR treatments across dates (Figure 6).

Isotope analysis and mass balance:

The April $\delta_{TSS}^{13}C$ was significantly lower than in July (-27.0 ± 3.6‰, -24.1 ± 1.1‰; respectively). In addition, the CTR treatments were more depleted than the ^{15}N+P treatments

(Table 2). The $_{TSS}$C:N ratio was significantly higher in April than July (9.4 ± 0.3, 7.2 ± 0.1, respectively), with the April*Grass treatments having the highest ratios July*Grass having the lowest (Table 2). The April $^{15}_{TSS}N$ pool was significantly smaller than the July $^{15}_{TSS}N$ (0.38 ± 0.03 mg, 0.97 ± 0.05 mg, respectively) and the Grass treatments had significantly less $^{15}_{TSS}N$ than the Forest treatments (0.61 ± 0.09 mg, 0.73 ± 0.10 mg, respectively). The CTR treatments had a significantly smaller $^{15}_{TSS}N$ mass than the ^{15}N and ^{15}N+P treatments (0.01 ± <0.1 mg). Overall, the July*^{15}N treatments had the highest $^{15}_{TSS}N$, while the April*^{15}N treatments had the lowest (Table 5).

The July $\delta^{13}_{soil}C$ was significantly higher than the April $\delta^{13}_{soil}C$ (-24.6 ± 0.3‰ and -25.7 ± 0.2‰, respectively). The July*CTR treatments were the most enriched (-23.8 ± 0.5‰) while the April*^{15}N+P were the most depleted (-25.6 ± 0.5‰). Interestingly, there was no significant difference in $\delta^{13}_{soil}C$ between the grass and forest soils (Table 2). $_{soil}$C:N was significantly higher in the grassland than the forest (12.9 ± 0.1 and12.3 ± 0.1 respectively). There were no significant differences in $\delta^{13}_{soil}C$ across dates or nutrient treatments (Table 2); however, we did observe significant differences in $_{soil}$C. There was significantly more $_{soil}$C in July than in April (42.8 ± 1.9 μg C mg^{-1} soil and 36.5 ± 3.0 μg C mg^{-1} soil) and more $_{soil}$C in the forest than in the grassland treatments. Although not numerically significantly, within habitats, the CTR treatments had the highest levels of soil C, while the ^{15}N+P treatments had the lowest (Table 4). The soils cores had significantly more $^{15}_{soil}N$ in April than July (1.12 ± 0.10 mg, 0.20 ± 0.05 mg,). The April*Forest*^{15}N+P and April*Grass*^{15}N treatments were the largest $^{15}_{soil}N$ pool while the July*Grass treatments were the smallest (Table 5)

There was significantly more $_{NO3-N\ final}{}^{15}N$ (i.e., the amount of ^{15}N remaining in the water column at the end of the experiment) in the ^{15}N than in the ^{15}N+P treatments (0.12 ± 0.03 mg, 0.01 ± <0.01 mg, respectively). The April*Forest*^{15}N treatment had the highest $_{NO3-N\ final}{}^{15}N$ while the April*Grassland*^{15}N+P had the lowest (Table 5). The $_{removed}{}^{15}N$ mass (i.e., the amount of ^{15}N removed during sampling for chemical analyses) was significantly larger in April than July (0.76 ± 0.02 mg, 0.41 ± 0.01, respectively). The $_{unacc}{}^{15}N$ pool was significantly smaller in April than July (4.02 mg ± 0.13, 4.25 mg ± 0.10, respectively). The ^{15}N treatments had significantly less $_{unacc}{}^{15}N$ than the ^{15}N+P treatments (3.90 mg ± 0.11, 4.38 ± 0.10, respectively) and the forest treatments had significantly less $_{unacc}{}^{15}N$ than the grassland treatments (4.00 ± 0.08, 4.28 ± 0.15, respectively).

The smallest ^{15}N pool was the $_{NO3-N\ final}{}^{15}N$, which accounted for 0 to 3.1 ± 1.1% of the ^{15}N (Figure 6-a). The $_{removed}{}^{15}N$ was the third largest pool and accounted for 12.0 ± 0.3% of the ^{15}N in April while it only accounted for 7.1 ± 0.2% in July (Figure 6-b). Interestingly, the $_{soil}{}^{15}N$ pool was the second largest in April (17.6 ± 1.6%) and fourth largest in July (3.4 ± 0.8%, Figure 6-c); while the $_{TSS}{}^{15}N$ pool was the fourth largest in April (5.9 ± 0.5%) and the second largest in July (16.5 ± 0.9, Figure 6-d). The largest pool across dates, habitats and treatments was the $_{unacc}{}^{15}N$, accounting for 63.0 ± 1.9% ^{15}N in April and 72.4 ± 1.6% in July (Figure 6-e).

Discussion:

We observed a strong temporal pattern to ^{15}N incorporation into the $_{soil}{}^{15}N$ and $_{TSS}{}^{15}N$ pools. There was more ^{15}N incorporated into the $_{TSS}{}^{15}N$ in July than April, while ^{15}N incorporation into $_{soil}{}^{15}N$ was greater in April than July. The largest ^{15}N pool in our study was the unaccounted

($_{unacc}^{15}N$) and assumed to be denitrified pool. Our data suggest a coupling of soil and water column processes on N-cycling, which are by affected by spatial (soil properties) and temporal heterogeneity.

Primary producers, Chl-a and the $_{TSS}^{15}N$ pool

A summary of the Chl-*a* and $_{TSS}^{15}N$ results show that the planktonic community was N limited in April and C limited in July, and there were no significant differences in $_{final}$Chl-*a* between date*habitat*nutrient amendment in the ^{15}N and ^{15}N+P treatments after adjusting for differences in $_{init}$Chl-*a*. Interestingly, within date*habitat*nutrient amendment, the July*^{15}N+P treatments did not show an increase in Chl-*a* over the duration of the experiment. In addition, there was a larger incorporation of ^{15}N into the July $_{TSS}^{15}N$ pool and TSS were more ^{13}C enriched in July than April.

The July $_{TSS}$C:N was slightly below the ideal molar C:N of 7.7 ± 0.4 (Geider and La Roche, 2002), while the April $_{TSS}$C:N was above; suggesting slight C limitations in July and N limitations in April. The $_{TSS}$C:N observed are linked to the dominant photosynthetic algae present in the water column. The phytoplankton community during July was dominated by N-fixing cyanobacteria, which can significantly contribute to the dissolved inorganic nitrogen pool and can be carbon and phosphorous limited. In contrast, the April phytoplankton community was dominated by green algae and diatoms, taxa which are limited by ambient concentrations of dissolved inorganic nutrients.

Once adjusted for $_{init}$Chl-*a*, we did not observe differences in $_{final}$Chl-*a* between date*habitat*nutrient ammendment, suggesting that the thermal aspect of flood timing may not have a significant impact on photosynthetic productivity. While our findings are not consistent with studies indicating that flood pulse temperature has a significant effect on floodplain primary

productivity (Robertson et al., 2001), we suggest that temporal differences in flood pulse water quality and resource competition may have a larger impact on the phytoplankton community than water temperature alone.

Higher $_{init}$Chl-*a*; and therefore higher primary productivity in July compared to April, led us to hypothesize that the phytoplankton community would play a larger role in nitrogen cycling during the summer than during the spring. While supported by the mass balance data, the Chl-*a* data does not entirely support our hypothesis. Within date*habitat*nutrient amendments, there was an expected increase of Chl-*a* in the April ^{15}N and ^{15}N+P treatments, however, there was no Chl-*a* response to ^{15}N+P amendments in July. Since we observed an increase of Chl-*a* in the July CTR and ^{15}N treatments, we suggest that the addition of phosphorous in the ^{15}N+P treatment may have facilitated nutrient competition between heterotrophic bacterioplankton and phytoplankton, leading to an increase in non-photosynthetic biomass.

The nutritional needs of the April phytoplankton community (green algae and diatoms) would suggest a greater incorporation of ^{15}N into the $_{TSS}^{15}$N pool than during July (N- fixing cyanobateria). However, we observed significantly more ^{15}N incorporated into the $_{TSS}^{15}$N pool during July. Although phytoplankton nutritional needs may have been lower in July, we propose that collectively, the larger number of photosynthetic and heterotrophic organisms present in the water column led to larger ^{15}N incorporation into the $_{TSS}^{15}$N pool. The incorporation of ^{15}N into the $_{TSS}^{15}$N pool was likely due to ^{15}N uptake by heterotrophic bacterioplankton, and to trophic transfers from heterotrophic and photosynthetic plankton to microzooplankton (protozoa) via grazing. Competition between photosynthetic and heterotrophic plankton has been documented in mesocosm experiments (Joint et al, 2002; Klug, 2005) and tropical, neo-tropical and temperate floodplain systems (Hein et al., 1999; Castillo, 2000; Castillo et al., 2003; Rejas et al., 2005).

Further more, Joint et al. (2002) demonstrate that bacterioplankton have the ability to inhibit algal growth through nutrient competition, Aspetsberger et al. (2002) document that high contributions of phytoplankton biomass to water column particulate OM can support high bacterial productivity and Doi et al. (2003) suggest that the role of phototrophic organisms on nutrient cycling increases with increasing biomass. Therefore, we suggest that water column biomass may have a greater impact than life history on nutrient cycling pathways.

Finally, in regards to carbon resources, the July TSS were more enriched in $_{TSS}^{13}C$, suggesting a greater utilization of terrestrially derived carbon (Hamilton and Lewis, 1992; Vizinni et al., 2005) and a decrease in selectivity of carbon resources by planktonic organisms due to increasing carbon limitations (Doi et al., 2003; Lehmann et al., 2004). We suggest carbon subsidies from the soils and litter layer to the water column following re-wetting of severely desiccated soils in July consistent with observations made by Baldwin and Mitchell (2000). Subsidies of terrestrially derived nutrients to the aquatic ecosystem have been observed in numerous freshwater wetland studies and are of particular importance to floodplain systems (Robertson et al., 1999; Tockner et al., 1999; O'Connell et al., 2000; Hein el at. 2003). Release of labile SOM into the water column would enhance bacterioplankton metabolism, competition and subsequent ^{15}N uptake, elucidating on the results of our study.

Soils and the $_{TSS}^{15}$N ***pool-***

A summary of the soil analysis and $_{TSS}^{15}$N pool data demonstrate a larger soil organic matter (SOM) pool in forest, decreased SOM in nutrient amended treatments, enriched $_{soil}^{13}$C in July and a larger $_{soil}^{15}$N pool in April.

The higher $_{soil}$C and $_{soil}$N concentrations, particularly during July, indicate a larger SOM pool in the forests than in the grassland. It is well documented that SOM pools in the uppermost

centimeters of the soil profile tend to be larger in forested systems than in grasslands (Jobbagy and Jackson, 2000). The differences stem mainly from SOM sources and their vertical distribution. The accumulation of a litter layer in forest soils leads to the concentration of SOM in the uppermost centimeters of the soil profile. In contrast, reduced litter accumulation coupled with evenness of the vertical distribution of plant roots in grasslands lead to reduced SOM pools in the topmost centimeters of the soils.

The $_{soil}$C:N suggest that there were no $_{soil}$C limitations during our experiments; however, we did observe reduced $_{soil}$C in the nutrient amendments mesocosms, with the ^{15}N+P treatments having the lowest concentrations. Utilization of soil C during oxic and anoxic respiration in wetland soils has been well documented (D'Angelo and Reddy, 1999; Morris and Bradley, 1999). We suggest that nitrogen and phosphorous alleviated soil nutrient limitations and stimulated microbial respiration, thus leading to the lower $_{soil}$C concentrations observed.

The relative $_{soil}^{13}C$ enrichment in July suggests an increase in microbial respiration and biomass during the warmer summer months. Microbial catabolic processes (respiration) preferentially discriminate against heavy carbon isotopes; resulting in ^{13}C depleted effluxed $CO_{2(g)}$ and ^{13}C enriched microbial biomass (Santruckova et al., 2002; Biasi et al., 2005). However, the smaller incorporation of ^{15}N into the July $_{soil}^{15}N$ pool is not consistent with an increase in soil microbial biomass and subsequent $_{soil}^{13}C$ enrichment. We suggest that re-wetting of desiccated soils and subsequent release of highly labile SOM available for the surviving soil biota produced the enriched $\delta\,_{soil}^{13}C$ observed in July.

Soils within our study site tend to remain moist through the spring and can be severely desiccated by the summer, leading to larger soil microbial mortality during the warmer months. It is well documented that rewetting or flooding of soils can release large quantities of nutrients

and labile SOM, mostly from the desiccated microbial community (Baldwin and Mitchell, 2000; Scholz et al., 2002). Additionally, studies suggests that OM recycling, as well as utilization of labile organic compounds for microbial metabolism may lead to higher $\delta^{13}C$ values in soil microbes (Boschker and Middelburg, 2002; Santruckova et al., 2002; Biasi et al., 2005).

Release of nutrients following rewetting is supported by the higher concentrations of N_{soil_ex} observed in July. The smaller mass of ^{15}N incorporated into the July $^{15}_{soil}N$ pool suggests that during the summer, the ^{15}N in the soils was utilized as an electron acceptor during catabolic soil processes, rather than cell building material in anabolic processes. This is supported by the N_{soil_ex} data, which show that .while there were higher concentrations of N_{soil_ex} in July to meet nutritional needs of the soil biota, the incorporation of ^{15}N into soil biomass was larger in April. The constant soil moisture due to repeated inundation during the spring resulted in larger soil microbial biomass and anabolic nutrient demands; which is reflected in the larger mass of ^{15}N fixed into the soils during April.

In summary, our soils data suggest that differences in SOM quality can be attributed to temporal effects such as the drying and re-wetting of soils which dictates their degree of desiccation; whereas differences in SOM quantity can be attributed to the characteristics of the terrestrial vegetation present at each site and the degree of microbial activity within the soil.

Temperature, the $^{15}_{unacc}N$ pool and mass balance-

Water temperatures and $K_{NO3\text{-}N}$ were significantly higher in July, while the $^{15}_{unacc}N$ was larger during July in the forest soils and across ^{15}N+P treatments.

Wetland nutrient cycling rates are highly dependent on temperature (Mulholland et al., 1997; Baldwin and Mitchell, 2000 Kadlec and Reddy, 2001). As water temperatures increase, metabolic processes of soil and water column organisms increase, leading to a more rapid

depletion of dissolved nutrients from the water column and soils. Sheibley et al. (in review), documented an increase of $k_{NO3\text{-}N}$ with an increase in ambient temperatures. Thus, temperature, and its direct impact on biogeochemical processes in our experimental units to some extent account for the shorter duration and faster $k_{NO3\text{-}N}$ observed in July. However, the soils data suggest that temperature is not the sole driver of NO_3 cycling rates. Nutrient concentrations, hydrologic residence time, redox soil conditions and processes mediated by primary producers also impact nutrient pools (Kadlec and Reddy, 2001; Fisher and Acreman, 2004). As the Chl-*a* and ${}^{15}_{TSS}\mathrm{N}$ data demonstrate, water column resource competition can alter ^{15}N pools and fluxes, and could contribute to the faster July $k_{NO3\text{-}N}$.

With respect to $k_{NO3\text{-}N}$ differences between treatments across dates, we can conclude that alleviation of nutrient limitations in the water column and soils through additions of phosphorous during April lead to faster rates in the ^{15}N+P than in the ^{15}N treatments. In addition, we suggest that the spatial differences in $k_{NO3\text{-}N}$ observed in July may be due to differences in the soil microbial community; which is illustrated by the lower ${}_{soil}\mathrm{C}$ and larger ${}^{15}_{unacc}\mathrm{N}$ pool.

The largest ^{15}N pool in our study was the unaccounted ^{15}N pool (${}^{15}_{unacc}\mathrm{N}$). We feel confident in assuming that nitrate reducing conditions within our soils rapidly developed, and that the unaccounted ^{15}N mass in our budget was indeed denitrified via microbial respiration. The soil redox potentials at the end of the experiments were well within nitrate reducing conditions (Mitsch and Gosselink, 2000). In addition, there is evidence documenting the rapid development of anoxic conditions within floodplain soils following inundation, which are accompanied by dramatic increases in soil respiration (Ford et al., 2002; Valett et al., 2005). By converting our $k_{NO3\text{-}N}$ to denitrification rates (in ug cm^{-3} hr^{-1}) as outlined by Sheibley et al. (in review), we were able to compare our calculated denitrification rates to the measured

denitrification potentials in their study. The rates calculated in this study (120 to 420 ng N cm^{-3} hr^{-1} after accounting for ^{15}N incorporation into all other pools) fall well within the range of denitrification potentials (2 to 768 ng N cm^{-3} hr^{-1}) measured by Sheibley et al. (in review). Although our denitrification rates are quite high compared to those reported in natural floodplain systems (Spink, et al., 1998), our calculated nitrate loss rates (143 to 503 mg N m^{-2} day^{-1}) fall well within the range of reported denitrification and nitrate loss rates due to microbial metabolism in constructed wetlands. Poe at al. (2003) reported denitrification rates of 470 mg N m^{-2} day^{-1}; while Bachand and Horne (2000b) reported rates averaging 554 mg N m^{-2} day^{-1} and they observed rates as high as 1100 mg N m^{-2} day^{-1}. Reilly et al.(2000) reported average loss rates of 552 mg N m^{-2} day^{-1} and in their review of nitrate loss rates, Bachard and Horne (2000b) reported rates ranging from 2 to 4000 mg N m^{-2} day^{-1}.

The $^{15}_{unacc}N$ pool was larger in July, when the mean daily temperatures and primary productivity (as measured by $_{init}$Chl-*a*) were higher. Ford et al. (2002) observed near anoxic water at the soil-water interface of their floodplain site in the late afternoon, during the highest rates of water column primary productivity. They also reported that high daytime water column productivity resulted in high nighttime respiration rates that lead to near anoxic conditions in surface waters. Based on the results of their study, the sensitivity of microbial processes to temperature reported by Kadlec and Reddy (2001) and on our TSS, $_{init}$Chl-*a*, $_{soil}C$ and $^{15}_{soil}N$ data we suggest that the high photosynthetic and respiration rates, coupled with the warmer temperatures documented in July resulted in high denitrification rates and a large flux of ^{15}N into the atmosphere. In addition, we suggest that phosphorous additions enhanced denitrification rates by alleviating nutrient limitations of heterotrophic organisms, resulting in the larger $^{15}_{unacc}N$ pool observed in the ^{15}N+P treatments.

The mass balance approach of this study demonstrates that during hydrologically static conditions, habitat heterogeneity, through differences in resource availability and biological features has the potential to significantly alter floodplain biogeochemical processes and N-cycling. Our documented impact of thermal heterogeneity on N-cycling, suggest that soils will play a larger role in N retention within the floodplain during cooler temperatures. Finally, we suggest that at warmer temperatures, the water column will play a larger role in N retention while catabolic metabolism in the soils will result in large N fluxes out of the floodplain system.

In natural systems, inter-annual variations in the mechanisms through which spatial heterogeneity and flood timing (as physicochemical and thermal heterogeneity) influence nutrient cycling exist, and we expect future floodplain studies to expand upon nutrient cycling mechanisms across a wide spatiotemporal range.

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Tables:

Table 1. Mean (± SE) duration and nitrate loss rates ($k_{NO3\text{-}N}$) of the ^{15}N amended treatments during both experimental dates. Means with equal superscripts within a column are not significantly different ($p>0.05$).

Date	Habitat	Nutrient Treatment	Duration (days)	$k_{NO3\text{-}N}$ (ug l^{-1} hr^{-1})
April	Forest	^{15}N	16.6 ± 0.7^{a}	12.6 ± 0.5^{c}
		^{15}N+P	10.4 ± 0.0^{b}	$20.6 \pm <0.1^{b}$
	Grass	^{15}N	16.8 ± 1.1^{a}	12.7 ± 0.8^{c}
		^{15}N+P	10.7 ± 0.3^{b}	20.3 ± 0.6^{ab}
July	Forest	^{15}N	8.8 ± 0.4^{b}	20.4 ± 1.1^{a}
		^{15}N+P	9.1 ± 0.1^{b}	20.3 ± 0.2^{a}
	Grass	^{15}N	7.8 ± 0.5^{b}	23.3 ± 1.5^{a}
		^{15}N+P	7.3 ± 0.2^{b}	25.2 ± 0.6^{a}

Table 2. Mean (± SE) initial orthophosphate (PO_4^3-P_{init}) and Chlorophyll-*a* ($_{init}$Chl-*a*), final Chlorophyll-*a* ($_{final}$Chl-*a*), Δ PBD in water column suspended solids and soils ($\delta_{TSS}^{13}C$ and $\delta_{soil}^{13}C$) and C:N ratio in suspended solids and soils ($_{TSS}$C:N and $_{soil}$C:N) in all treatments. Means with equal subscripts within a column are not significantly different (p>0.05)

Date	Habitat	Nutrient Treatment	PO_4^3-P_{init} (mg L^{-1})	Chl-a_{init} (ppb)	Chl-a_{final} (ppb)*	$\delta_{TSS}^{13}C$ (‰)	$_{TSS}$C:N	$\delta_{soil}^{13}C$ (‰)	$_{soil}$C:N
April	Forest	CTR	$0.07 \pm <0.01^{e}$	5.5 ± 0.1^{a}	8.5 ± 1.2^{b}	-32.5 ± 0.9^{c}	9.5 ± 0.1^{abc}	-25.3 ± 0.3^{ab}	12.1 ± 0.2^{a}
		^{15}N	$0.07 \pm <0.01^{e}$	4.7 ± 0.3^{a}	40.9 ± 5.4^{a}	-27.1 ± 0.9^{b}	7.9 ± 0.3^{bcd}	-25.0 ± 0.8^{ab}	12.3 ± 0.3^{a}
		^{15}N+P	1.09 ± 0.06^{b}	4.9 ± 0.5^{a}	47.4 ± 4.9^{a}	-24.5 ± 0.2^{ab}	10.1 ± 0.3^{a}	-25.7 ± 0.6^{ab}	$12.0 \pm <0.1^{a}$
	Grass	CTR	$0.08 \pm <0.01^{e}$	5.2 ± 0.2^{a}	8.4 ± 1.2^{b}	-31.4 ± 0.7^{c}	10.1 ± 0.8^{a}	-25.5 ± 0.5^{ab}	12.7 ± 0.3^{a}
		^{15}N	$0.08 \pm <0.01^{e}$	4.9 ± 0.1^{a}	39.3 ± 2.2^{a}	-25.5 ± 0.5^{ab}	9.3 ± 0.7^{abc}	-26.3 ± 0.3^{b}	13.2 ± 0.7^{a}
		^{15}N+P	1.07 ± 0.03^{bc}	5.0 ± 0.4^{a}	41.0 ± 4.6^{a}	-23.0 ± 0.3^{a}	9.5 ± 0.2^{ab}	-26.2 ± 0.1^{ab}	12.9 ± 0.3^{a}
July	Forest	CTR	0.66 ± 0.03^{cd}	227.6 ± 4.0^{b}	255.6 ± 6.8^{ab}	-24.3 ± 0.5^{ab}	7.2 ± 0.1^{d}	-23.3 ± 1.0^{a}	12.8 ± 0.7^{a}
		^{15}N	0.73 ± 0.20^{bcd}	222.9 ± 8.7^{b}	338.1 ± 13.3^{ab}	-24.2 ± 0.4^{ab}	7.5 ± 0.2^{cd}	-25.7 ± 0.5^{ab}	12.4 ± 0.2^{a}
		^{15}N+P	2.49 ± 0.14^{a}	236.7 ± 9.3^{b}	319.0 ± 28.6^{ab}	-23.1 ± 0.3^{a}	7.3 ± 0.2^{d}	-24.9 ± 0.2^{ab}	12.5 ± 0.1^{a}
	Grass	CTR	0.68 ± 0.05^{bcd}	207.4 ± 8.6^{b}	336.2 ± 26.5^{ab}	-25.1 ± 0.7^{ab}	6.3 ± 0.1^{d}	-24.2 ± 0.4^{ab}	13.0 ± 0.3^{a}
		^{15}N	0.53 ± 0.01^{d}	239.8 ± 16.7^{b}	338.8 ± 23.4^{ab}	-24.7 ± 0.6^{ab}	7.4 ± 0.4^{cd}	-24.7 ± 0.8^{ab}	12.5 ± 0.2^{a}
		^{15}N+P	2.55 ± 0.11^{a}	226.1 ± 9.2^{b}	296.7 ± 32.5^{ab}	-23.4 ± 0.9^{a}	7.5 ± 0.2^{cd}	-24.8 ± 0.5^{ab}	13.3 ± 0.3^{a}

* For comparisons of Chl-a_{final} across dates we used Chl-a_{init} as the covariate.

Table 3. Mean (± SE) soil nitrogen (Soil N) and available or exchangeable nitrogen (N_{soil_ex}) of date*habitat treatments. Nutrient amendments are pooled. Means with equal superscripts within a column are not significantly different ($p>0.05$).

Date	Habitat	Soil N (mg g^{-1} soil)	N_{soil_ex} (mg g^{-1} soil)
April	Forest	3.9 ± 0.2^{a}	0.37 ± 0.05^{c}
	Grass	2.1 ± 0.2^{c}	0.39 ± 0.02^{c}
July	Forest	3.7 ± 0.2^{ab}	1.01 ± 0.03^{a}
	Grass	3.0 ± 0.2^{b}	0.79 ± 0.06^{b}

Table 4. Mean (± SE) soil carbon (Soil C) of treatments during both experimental dates. Means with equal superscripts are not significantly different ($p>0.05$).

Nutrient Treatment	Habitat	Soil C (mg g^{-1} soil)
CTR	Forest	49.4 ± 2.9^{a}
^{15}N		46.0 ± 4.1^{ab}
^{15}N+P		45.6 ± 1.7^{ab}
CTR	Grass	34.6 ± 4.0^{bc}
^{15}N		33.2 ± 3.6^{bc}
^{15}N+P		31.3 ± 4.5^{c}

Table 5. Mean (± SE) masses of ^{15}N pools in nutrient amended treatments. Means with equal superscripts within a column are not significantly different.

Date	Habitat	Nutrient Treatment	$^{15}N_{NO3-N\ initial}$ (mg) *	$^{15}N_{NO3-N\ final}$ (mg) **	$^{15}N_{removed}$ (mg) +	$^{15}N_{TSS}$ (mg) ++	$^{15}N_{soil}$ (mg) X	$^{15}N_{unacc}$ (mg)^
April	Forest	^{15}N	6.32 ± 0.04^{a}	0.20 ± 0.07^{a}	$0.86 \pm (0.02)^{a}$	$0.38 \pm (0.03)^{c}$	0.96 ± 0.07^{bc}	$3.93 \pm (0.05)^{cd}$
		^{15}N+P	6.45 ± 0.11^{a}	0.0^{a}	$0.72 \pm (0.01)^{b}$	$0.49 \pm (0.05)^{bc}$	1.30 ± 0.12^{ab}	$3.94 \pm (0.05)^{cd}$
	Grass	^{15}N	6.22 ± 0.07^{a}	0.17 ± 0.08^{a}	$0.78 \pm (0.02)^{ab}$	$0.27 \pm (0.07)^{c}$	1.50 ± 0.17^{a}	$3.54 \pm (0.20)^{d}$
		^{15}N+P	6.48 ± 0.14^{a}	$0.01 \pm <0.01^{a}$	$0.71 \pm (0.02)^{b}$	$0.36 \pm (0.03)^{bc}$	0.72 ± 0.01^{cd}	$4.67 \pm (0.14)^{ab}$
July	Forest	^{15}N	5.78 ± 0.06^{b}	0.06 ± 0.04^{a}	$0.44 \pm (0.03)^{c}$	$1.15 \pm (0.14)^{a}$	0.28 ± 0.10^{cd}	$3.85 \pm (0.24)^{bcd}$
		^{15}N+P	5.94 ± 0.06^{b}	$0.01 \pm <0.01^{a}$	$0.44 \pm (0.01)^{c}$	$0.90 \pm (0.07)^{ab}$	0.32 ± 0.07^{d}	$4.27 \pm (0.11)^{abc}$
	Grass	^{15}N	5.82 ± 0.06^{b}	0.06 ± 0.03^{a}	$0.39 \pm (0.03)^{c}$	$0.97 \pm (0.06)^{ab}$	0.13 ± 0.09^{d}	$4.26 \pm (0.11)^{abc}$
		^{15}N+P	5.96 ± 0.06^{b}	0.02 ± 0.01^{a}	$0.39 \pm (0.02)^{c}$	$0.85 \pm (0.03)^{ab}$	0.07 ± 0.04^{d}	$4.63 \pm (0.05)^{a}$

* Initial (day 0) ^{15}N added to water column as NO_3-^{15}N ($^{15}N_{NO3-N\ initial}$).

** ^{15}N remaining in the water column as NO_3-^{15}N at the end of the experiment ($^{15}N_{NO3-N\ final}$).

\+ ^{15}N removed from the water column over the duration of the experiment for fluorescence and nutrient analysis ($^{15}N_{removed}$).

++ ^{15}N incorporated into total suspended solids - planktonic biomass + microzooplankton ($^{15}N_{TSS}$).

X ^{15}N incorporated into soils as biomass and exchangeable N ($^{15}N_{soil}$).

^ ^{15}N mass unaccounted for in our study and assumed to be denitrified ($^{15}N_{unacc}$).

Figures Legends:

Figure 1. Simplified conceptual model of water column nitrate nitrogen (NO_3-N) pools and fluxes in a floodplain following inundation during reduced soil conditions.

Figure 2. Conceptual model of the mass balance approach to our experimental design. ${}^{15}_{NO3-N\ \mathrm{initial}}\mathrm{N}$ denotes initial (day 0) ^{15}N pool in the water column as NO_3-^{15}N; ${}^{15}_{NO3-N\ \mathrm{final}}\mathrm{N}$ is the remaining ^{15}N pool in the water column as NO_3-^{15}N at the end of the experiment; ${}^{15}_{removed}\mathrm{N}$ is the ^{15}N removed from the water column over the duration of the experiment for fluorescence and nutrient analysis; ${}^{15}_{TSS}\mathrm{N}$ is the ^{15}N mass incorporated into total suspended solids (planktonic biomass + microzooplankton); ${}^{15}_{soil}\mathrm{N}$ is the ^{15}N incorporated into soil pool as biomass and exchangeable N and ${}^{15}_{unacc}\mathrm{N}$ is the unaccounted ^{15}N mass assumed to be denitrified.

Figure 3. Mean (± SE) field Chl-*a* in-vivo readings in control (CTR), ^{15}N and ^{15}N+P amended mesocosms with (a) Forest soils during April, (b) Forest soils during July, (c) Grassland soils during April and (d) Grassland soils during July.

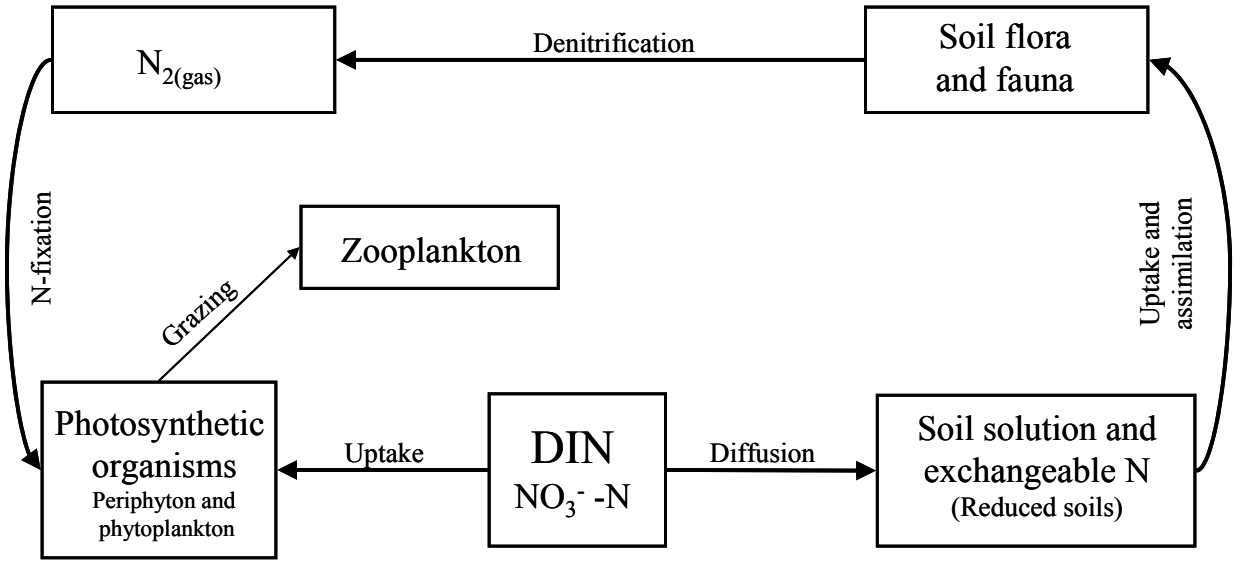
Figure 4. Mean (± SE) initial (day 0) and final extracted Chl-*a* in control (CTR), ^{15}N and ^{15}N+P amended mesocosms with Forest (F) and Grassland (G) soil cores during (a) April and (b) July. A (*) denotes treatments with significant ($p<0.05$) increase in extractable Chl- *a* over the duration of the experiment are marked with a *.

Figure 5. Mean (± SE) Orthophosphate (PO_4^{3-}) concentrations over the duration of the experiments in April and July mesocosms with (a) Forest soils and (b) Grassland soils. Since there were no significant differences in PO_4^{3-} concentrations between the control and ^{15}N only amended treatments, for graphical purposes, the control and ^{15}N data have been pooled into a single data series (CTR + ^{15}N).

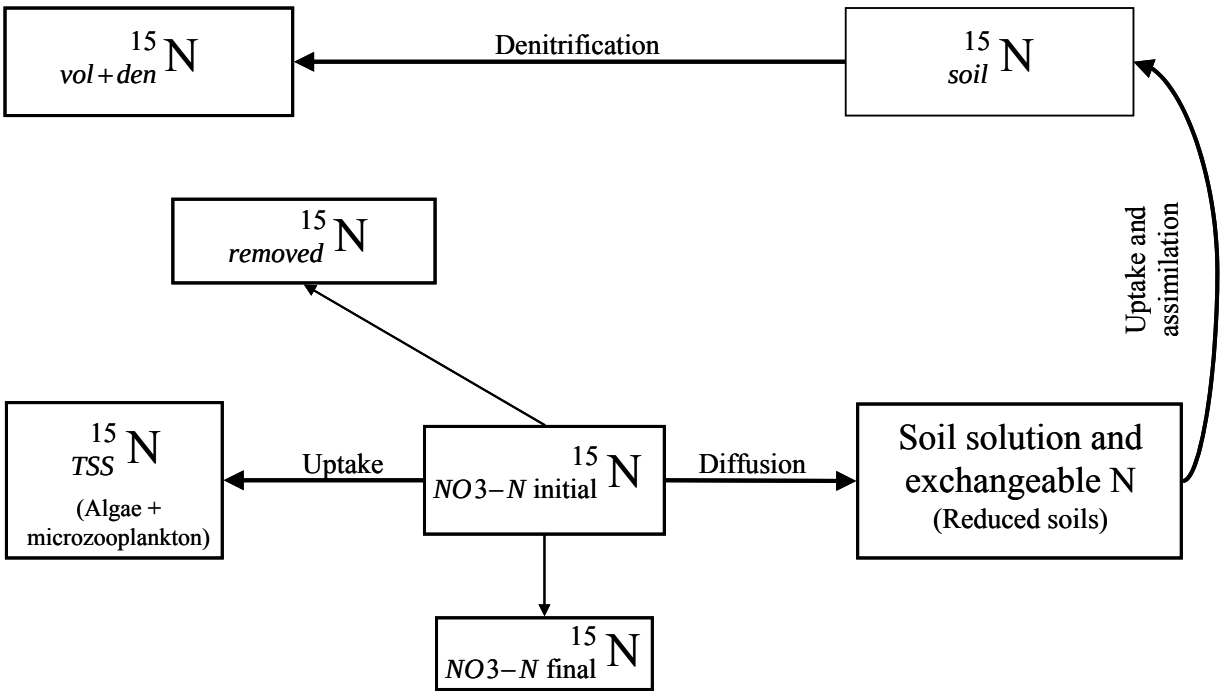
Figure 6. Mean (± SE) nitrate (NO_3^-) concentrations over the duration of the experiments in control (CTR), ^{15}N and ^{15}N+P amended mesocosms during April and July with (a) Forest soils and (b) Grassland. NO_3 concentrations in the control (CTR) treatments remained near detection limits.

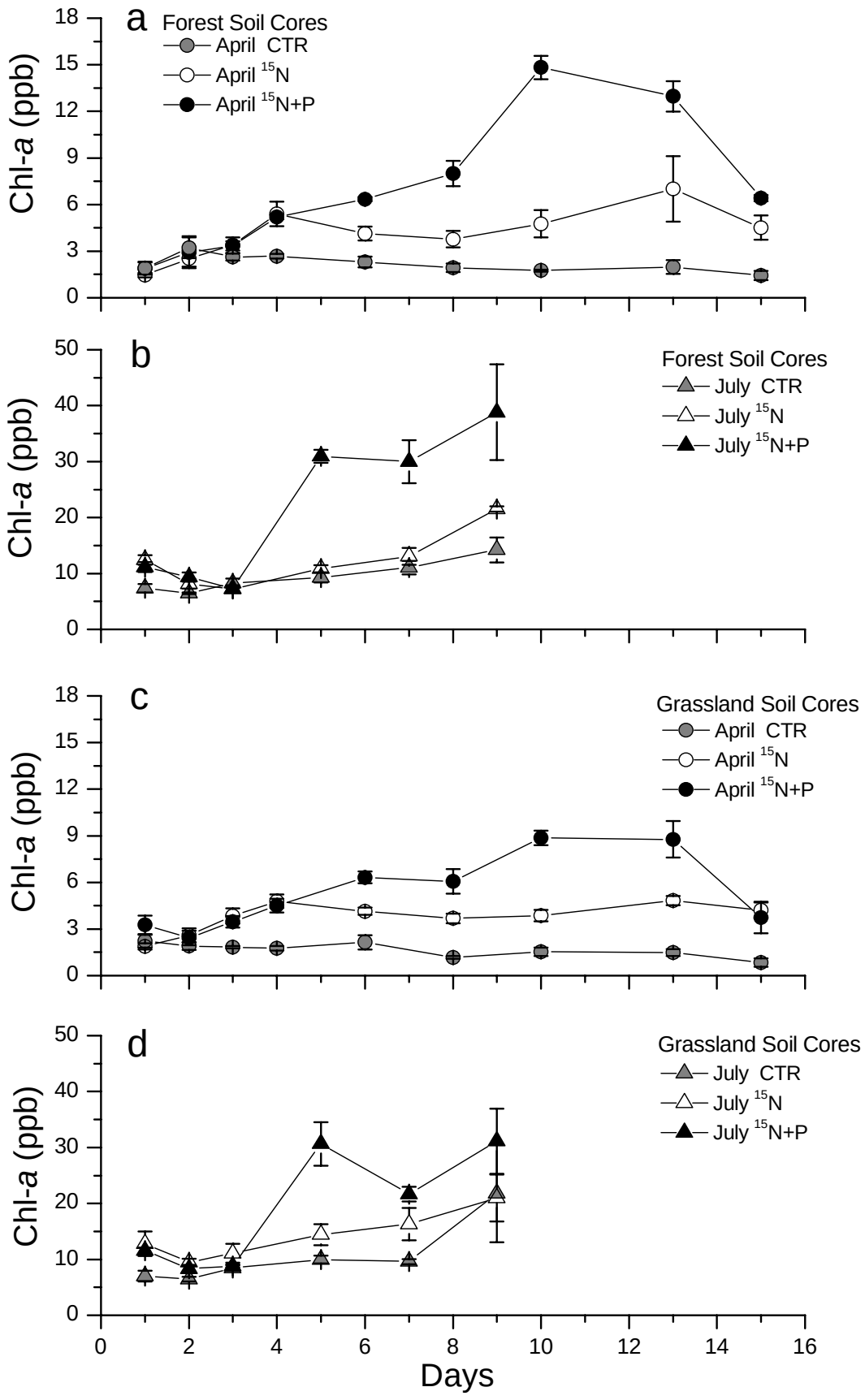
Figure 7. Mean (± SE) final ^{15}N mass balance in percentages of initial (day 0) ^{15}N mass added to water column as NO_3-^{15}N (% NO_3-^{15}N)of (a) ^{15}N remaining in the water column as NO_3-^{15}N at the end of the experiment (${}^{15}_{NO3-N\,\mathrm{final}}\mathrm{N}$), (b) ^{15}N removed from the water column over the duration of the experiment for fluorescence and nutrient analysis (${}^{15}_{removed}\mathrm{N}$), (c) ^{15}N incorporated into total suspended solids - planktonic biomass + microzooplankton (${}^{15}_{TSS}\mathrm{N}$), (d) ^{15}N incorporated into soils as biomass and exchangeable N (${}^{15}_{soil}\mathrm{N}$) and (e) ^{15}N mass unaccounted for in our study and assumed to be denitrified (${}^{15}_{unacc}\mathrm{N}$). Bars with equal subscripts were not significantly different ($p \geq 0.05$).

1

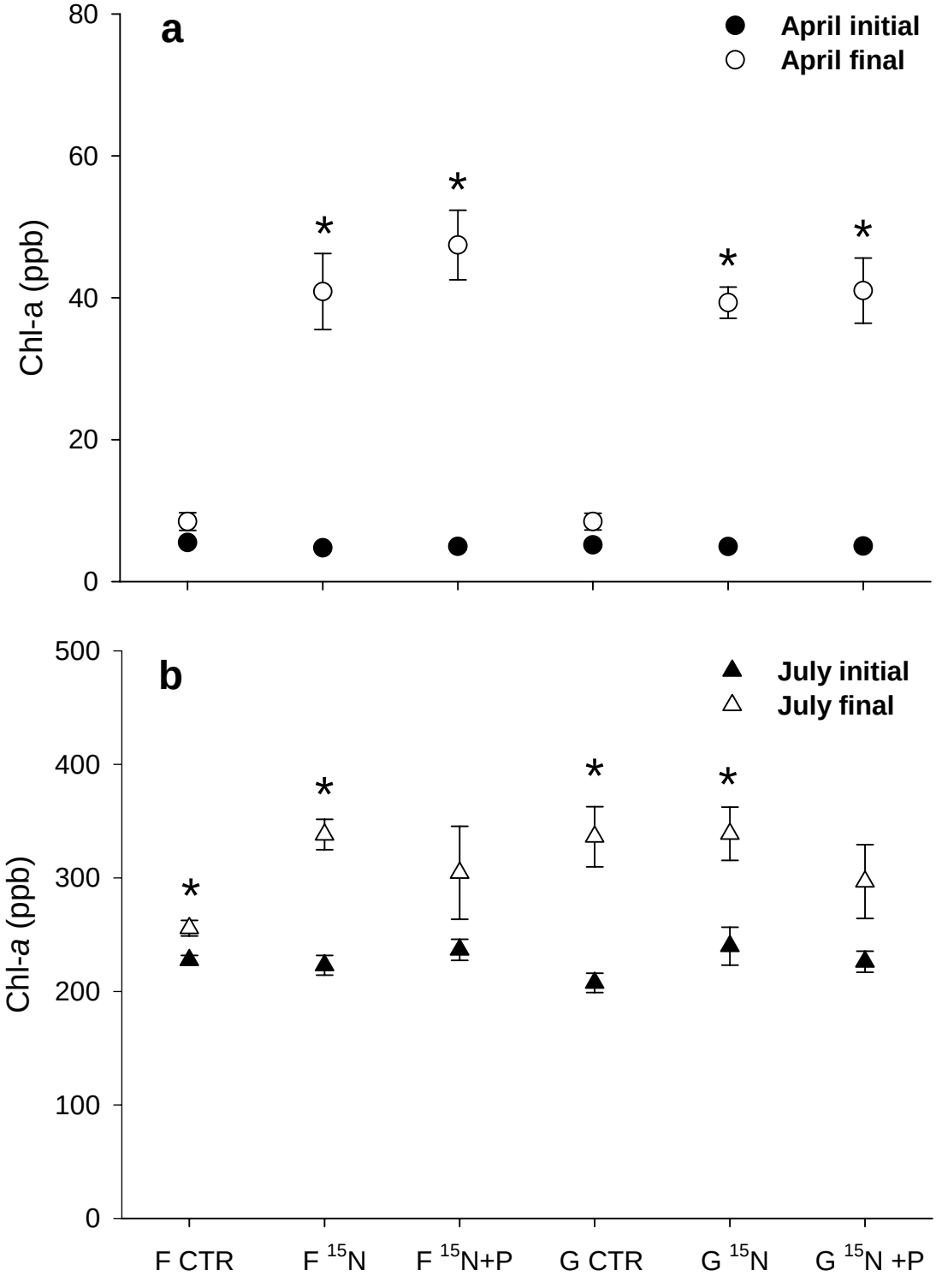

$N_{2(gas)}$
Denitrification
Soil flora and fauna
N-fixation
Zooplankton
Grazing
Uptake and assimilation
Photosynthetic organisms
Periphyton and phytoplankton
Uptake
DIN
NO_3^- -N
Diffusion
Soil solution and exchangeable N
(Reduced soils)

2

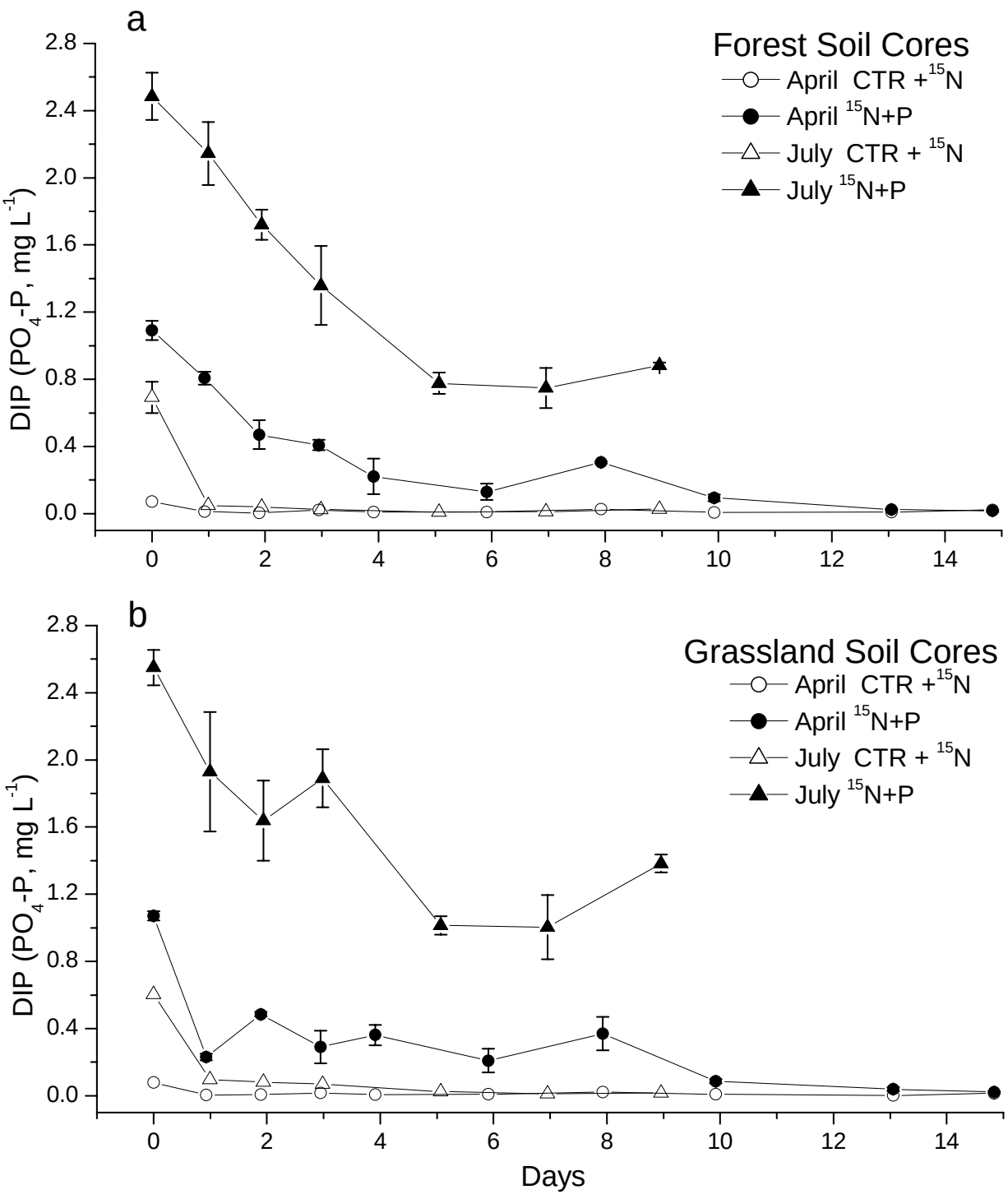

15 N vol + den
Denitrification
15 N soil
15 N removed
Uptake and assimilation
15 N TSS
(Algae + microzooplankton)
Uptake
15 N NO3−N initial
Diffusion
Soil solution and exchangeable N
(Reduced soils)
15 N NO3−N final


a
Forest Soil Cores
April CTR
April 15N
April 15N+P
Chl-a (ppb)
b
Forest Soil Cores
July CTR
July 15N
July 15N+P
Chl-a (ppb)
c
Grassland Soil Cores
April CTR
April 15N
April 15N+P
Chl-a (ppb)
d
Grassland Soil Cores
July CTR
July 15N
July 15N+P
Chl-a (ppb)
Days

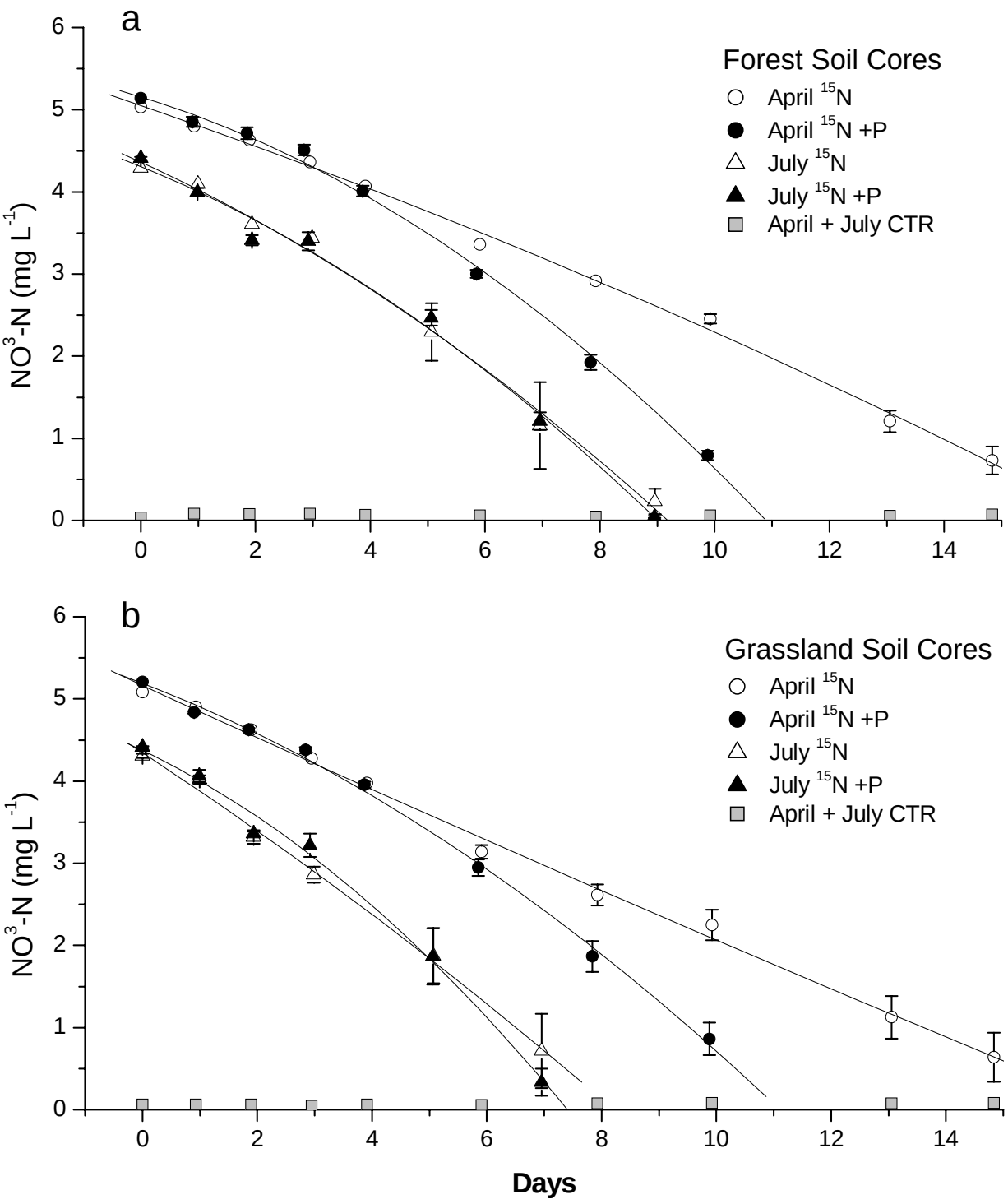
1


a
April initial
April final
Chl-a (ppb)
80
60
40
20
0
b
July initial
July final
Chl-a (ppb)
500
400
300
200
100
0
F CTR
F 15N
F 15N+P
G CTR
G 15N
G 15N +P

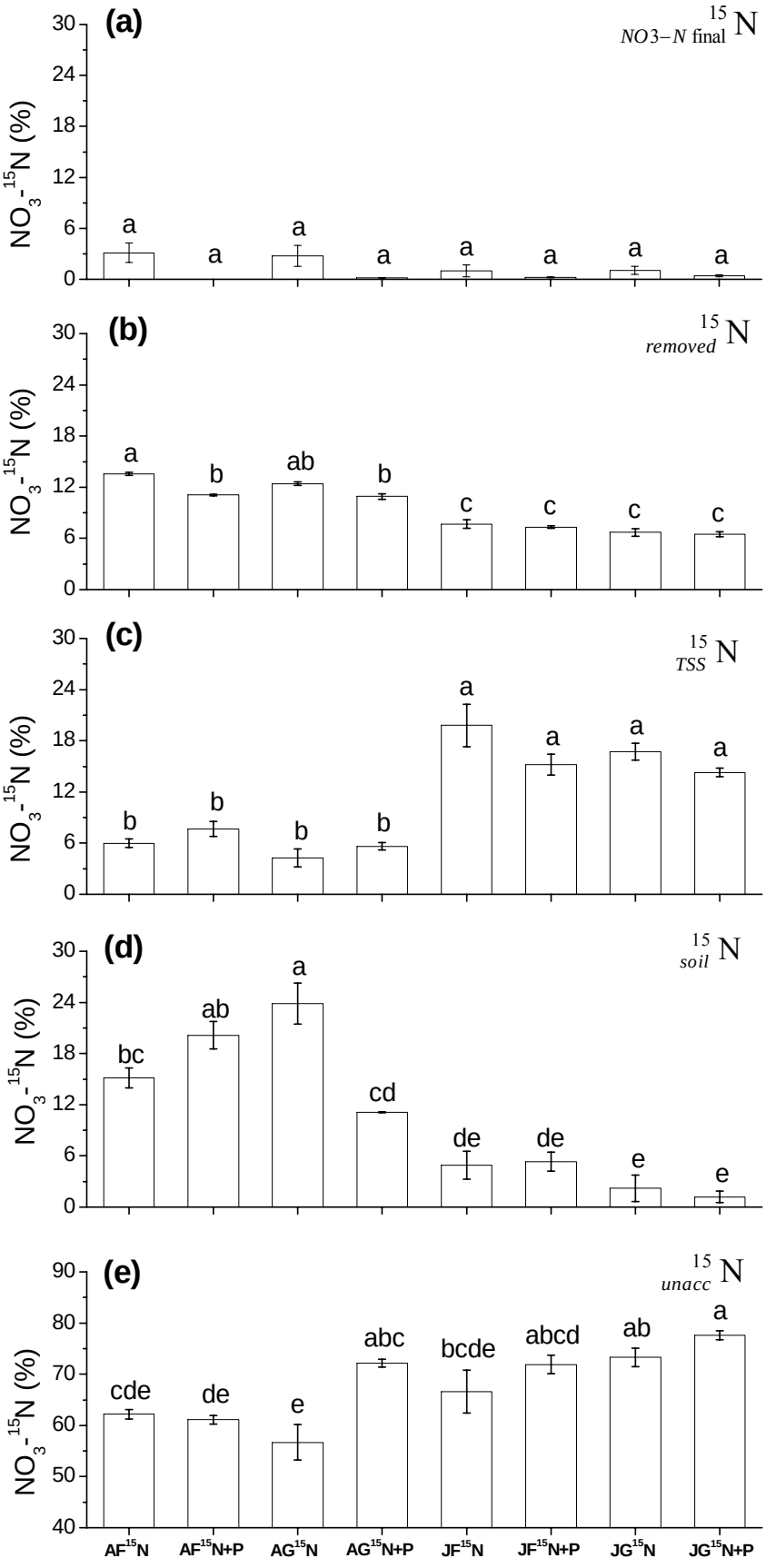
1


a
Forest Soil Cores
April CTR +15N
April 15N+P
July CTR + 15N
July 15N+P
DIP (PO4-P, mg L-1)
b
Grassland Soil Cores
April CTR +15N
April 15N+P
July CTR + 15N
July 15N+P
DIP (PO4-P, mg L-1)
Days

1


a
Forest Soil Cores
April 15N
April 15N +P
July 15N
July 15N +P
April + July CTR
NO3-N (mg L-1)
b
Grassland Soil Cores
April 15N
April 15N +P
July 15N
July 15N +P
April + July CTR
NO3-N (mg L-1)
Days

1


(a)
^{15}N $NO3-N$ final
(b)
^{15}N removed
(c)
^{15}N TSS
(d)
^{15}N soil
(e)
^{15}N unacc
NO_3-^{15}N (%)
AF^{15}N
AF^{15}N+P
AG^{15}N
AG^{15}N+P
JF^{15}N
JF^{15}N+P
JG^{15}N
JG^{15}N+P

1